Dharam P. Abrol

Pollination Biology

Biodiversity Conservation and Agricultural Production

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Foreword

We dwell in the midst of yet another world food shortage that exacerbated by escalating prices the world over. Coupled to the apparent instability of climate cycles in recent years, one-fourth of our growing human population is fast approaching famine. Concomitantly, this situation includes rampant declines in honeybee populations across three continents, for as yet incompletely resolved reasons, and with no remedy or end in sight. These problems have been further aided and abetted by a lack of prophylactic progress in the conservation of biodiversity and increased agricultural production.

The above notwithstanding, there has been no shortage of interest in studies on honeybees in relation to pollination. Indeed, a brief perusal of this subject at the website Google scholar shows that during the last century the publication of research papers in this area has grown exponentially, and in just the last decade, some 15,000 items have appeared. In the event, it is both fair and pertinent to ask: “Is there actually need for yet another work on pollination biology, the conservation of biodiversity, and agricultural production”?

The answer depends on whether we are after the analysis, perhaps in great detail, of a particular aspect of a system; or seek a holistic treatise concerned with complete systems within a social human context. For the former, there are several excellent, scholarly works available. Works of the latter kind are few and far between. The present tome “Pollination biology – Biodiversity conservation and agricultural production” is of the latter kind. This work originates in the Himalayan region where agriculturalists have pioneered practical studies in pollination that combine basic ideas rooted in three facets: biological conservation, rural development and increased agricultural production and the role of pollination in improving food security and livelihoods.

Professor Abrol develops the theme that pollination is basic to agricultural and natural productivity and that this is an ancient co-evolved and intricate process involving animals and plants in mutualisms. The value of pollination to agriculture is of great and inestimable value in the global economy of *Nature*. Indeed, pollination is essential for sexual reproduction in plants and their seed and fruit sets.

These can be increased considerably in areas where there is a dearth of natural pollinators by introducing pollinators, a practice that has yielded excellent results.

The value of bees in pollination is undisputed. Nonetheless, Abrol evaluates systems for maintaining honeybees on crops that are insect- pollinated. Factors that attract honeybees to flowers, floral competition, and methods for increasing numbers of pollen and nectar foragers as well as techniques for attracting honey bees to, and retaining them on, target crops are fully probed. Wild bees provide pollination services that often go unnoticed, yet are critical to the success of some forms of agriculture. The impact that bees have on our food production systems should serve as a reminder to our dependence, in general, on the ecosystems around us.

Against this, on the one hand the use of pesticides for pest control and the role of honeybees for crop pollination on the other have become essential components of modern agriculture and without either global food production would be seriously impaired. Unfortunately, these two practices are not always compatible, as honeybees are susceptible to many commonly used chemicals for the control of insect pests. The major constraint confronting pollinator-plant interactions is the indiscriminate and excessive use of pesticides for controlling insect pests. Moreover, reduction in the population of these beneficial insects due to insecticides incurs significant environmental, ecological and economic costs.

The energetics of these systems is rather interesting. Pollinators are highly selective in their floral visits and choose those flowers which best meet their energetic needs. The energy needs and foraging dynamics of pollinators are dependent upon prevailing weather conditions which regulate the schedule of activities thus influencing the energy budget. Much of Professor Abrol's own research has been on the role of energetics in pollinator-plant interactions and indicates directions for future lines of research for the enhanced understanding of pollination biology. Energetic costs of pollination have been ameliorated by the *Evolution* of plant volatile production in pollination ecology and in pollinator-plant relationships are reviewed here. This interrelationship between the two is governed by biochemical factors such as scent, colour and nutritional value of nectar and pollen.

Pollinators and pollination are crucial in the functioning of almost all terrestrial ecosystems including those dominated by agriculture because they are in the front line of sustainable productivity through plant reproduction. But, any programmes specifically focused on pollination require formal education at all levels as well as informal capacity building amongst farmers, land managers, policy makers and other target groups, including the public as a whole. This is, indeed, an awesome task and we must congratulate Professor Abrol for this uncommon blend of pure and applied science placed in the broader human social context.

Grahamstown, South Africa Randall Hepburn

Preface

Pollen, the small spore, plays an important role in the sexual reproduction of angiosperms as does the sperm in the animals. However, the pollen grains are non-motile requiring some foreign agent for their carry over to the female counter part. Wind, water and gravity are some of the abiotic agents, but through them the pollen carryover is undirected and very large number of pollen has to be produced to ensure successful pollination. Still the effectivity of pollination by these agents is low. On the other hand in a large number of plant species, pollination is effected by the bioagents. This is especially true in plants exhibiting self-incompatibility, protandry or protogyny. Pollination by bees and birds is of special importance. Efficiency of pollination by bioagents is the direct measure of mutualism specialization which is reflected in terms of success of reproduction as evidenced by quality and quantity of produced seeds/fruits. Higher the degree of mutualism, specialization more should be interdependence between the two participating organism – the plants and the pollinators. The extermination of one would adversely affect the survival and/or propagation of the other. In other words, loss of pollinators should mean decline in the reproductive propagation of several cross-pollinated plant species including reduction in crop seed production. Conversely, conservation of several plant species and increase in seed production of cross-pollinated crops could be ensured by the conservation of natural pollinators and vice-versa.

During the past four decades, human population has increased more than two folds exerting a tremendous pressure on the natural resources and the land especially for food, fuel and timber. As a consequence, vast forests have been converted into agricultural land and mountains have become barren due to ruthless cuttings and grazing, thus extensively destroying the food and habitat of several pollinators species. Along with these, use of chemicals, too, have greatly wiped out the population of natural pollinators, thus resulting in failure of reproduction in several cross-pollinated plant species including the agricultural crops. This book on pollination biology addresses two basics questions. How the pollination can be utilized in the (1) conservation of plant species and (2) for crop seed/fruit production. The various aspects related to pollination, plant reproduction, pollinators behaviour, ecology and management and their safety are discussed to serve as guide to evolve future strategies for sustainable agriculture without disturbing the environment and the natural balance.

The land resources are being limited and increased agricultural production is to be obtained through intensive farming i.e. higher cropping intensity, better seed and greater use of fertilizers. New cropping patterns are likely to create new problems, new pests may appear or pests now considered minor may become major. In some crops, any amount of fertilizer, irrigation or pesticide use may not even yield a fraction of yield unless pollinated by bees. Honeybees play an important role in the pollination of large portion of the angiosperms of the world and maintain natural vegetation needed for survival of the ecosystems and the world as whole. The magnitude and direction of all manner of anthropogenic global environmental change have lately come to dominate the conversation at national/international levels and the debate is raging over the validity of various projections of consequences and diverse proposals for remediation. Of the multitude of ways humans could be harming the planet, however, one that has largely been ignored is the "pollinator crisis" – the perceived global decline in the number and viability of animal species that facilitate reproduction of flowering plants, the overwhelming majority of plants in terrestrial communities. In her hugely influential book *Silent Spring* published more than 50 years ago, Rachel Carson recognized the central role of pollinators. They are the proverbial birds and the bees, along with many other insect species and even a handful of mammals that maintain human health and terrestrial biodiversity. Carson painted a bleak picture of a world with "fruitless falls". In the intervening decades, reports have quietly accumulated from virtually every continent of shortages or extinction of pollinators of various descriptions. Ironically, despite its apparent lack of marquee appeal, pollinator decline is one form of global change that actually does have credible potential to alter the shape and structure of the terrestrial world. Over the past decade, the public has begun to take notice and ask whether a pollinator crisis is brewing and, if so, what can be done to avert it.

The book emphasizes conserving and culturing honey bees, non-Apis bees and pollinators other than bees. It also addresses the biology of pollination and managing bees for optimum crop pollination. Individual pollination requirements and recommendations for some of the most important crops are discussed. The book has a unique blend of basic and applied science to understand the pollination biology in a much wider context.

The writing of this book has been possible with the active help and support of a wide spectrum of people has helped in one way or the other. This book is outcome of my personal experiences and the contributions of several workers which have been incorporated. I express my humble and profound thank to all of them whose hard work has enabled me to compile the suitable information in a such a manner that it would be useful to those interested in basic and applied aspects of pollination biology. The illustrations and figures are either original or redrawn from other sources which have been cited individually in the figure legends. All the authors whose work has been used/refereed deserve special appreciation and heartiest acknowledgments.

I am particularly indebted to Professor Dr. Raghavendra Gadagkar, Centre for Ecological Sciences, Indian Institute of Sciences Bangalore for his help, guidance and encouragement. I also thank my university authorities for the excellent working atmosphere and needed encouragement for compiling such a voluminous book.

I am also extremely thankful to Springer who took great pains and keen interest in publication of this book in a very impressive way.

I am highly indebted to Professor Randall Hepburn, Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa who has been very kind to write the foreword of this book. I also thank Dr. Uma Shankar, Debjyoti Isha and Sandeep for their help and support. Last but not the least my sincere thanks are due to my wife Professor Dr. Asha Abrol, son Er. Rajat and daughter Er. Vitasta for their endurance and help during writing of this book.

Jammu Dharam P. Abrol

Contents

Chapter 1
Introduction

Abstract Pollination, the transfer of pollen grains to the stigma of the plant gynoecium is a crucial step in the sexual reproduction of flowering plants. The majority of flowering plants rely on animals for the transfer of pollen. Because flower visitors gain no direct benefit by pollinating flowers, rewards must lure them. The most common way plants attract animals to visit their flowers is by providing food such as nectar, pollen or oils. While searching for these rewards in the flower, pollen from the flower's anthers may stick to the body of the animal. When the animal visits subsequent flowers in search of more rewards, pollen from its body may adhere to the stigma of these flowers and again, new pollen may stick to the body of the animal. Pollination is basic to agricultural and natural productivity and an ancient co-evolved process involving animals and plants in mutualism. The value to agriculture is huge and to global economy of nature inestimable. Nevertheless, pollination is a threatened system from highly managed agriculture to remote wilderness. Pesticides take their toll, insecticides directly killing pollinators and herbicides indirectly by reducing pollinator forage. Habitat destruction has reduced pollination in croplands and natural areas. Honey bee diseases threaten to change the demography of beekeeping and availability of pollination. Encouragement of wild pollinators, domestication of unused potential pollinators, and more environmentally sensitive human exploitation of the world are needed as part of conservation, forestry, agroforestry, sustainable agriculture and development.

1.1 Introduction

Sexual reproduction of many crops and the majority of wild plants is dependent on animal pollination through insects, birds, bats and others, with insects playing the major role. Among the insect pollinators, solitary and social bees provide most pollination in both managed and natural ecosystems. Most of the world's staple foods, including wheat, corn, and rice reproduce without insect pollination. These crops

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account for 65% of global food production, still leaving as much as 35% depending on pollinating animals (Klein et al. 2007). In part due to the massive scale and homogeneity of modern agriculture, the majority of crops requiring pollination are dependent on managed pollinators, and especially on managed honeybees (Aizen et al. 2008).

No other group of insects are of more benefit to humans than bees. More than one-third of the world's crops require pollination to set seeds and fruits, and most meat and dairy industries rely on bees for pollination of clover and Lucerne (Dias et al. 1999). Crops relying on bee pollination include apple, citrus, tomato, melon, strawberry, apricot, peach, cherry, mango, grape, olive, carrot, potato, onion, pumpkin, bean, cucumber, sunflower, various nuts, a range of herbs, cotton, alfalfa and lavender. The annual value of this service is estimated at US$112 billion worldwide (Southwick and Southwick 1992). Even crops that do not require pollination for harvesting, such as those producing fibre or timber, still require pollination to produce further generations, and crops such as cotton that do not require pollination to produce seeds, provide greater yields when pollinators are available (Allen-Wardell et al. 1998). The European honeybee (*Apis mellifera*) dominates crop pollination worldwide, but local native bee species also play their part.

Pollination is an ecosystem service that is key to food security. Pollinators are essential for many fruit and vegetable crops. In agriculture, especially amongst pollen-limited crops, promoting pollination services is a means of increasing productivity without resorting to expensive agricultural inputs of pesticides or herbicides. Indeed, pollination services are most likely underpinning productivity in many crops without farmers even recognising it, so long as habitat and alternative pollinator forage are readily available as they often are in small holder farming systems. By developing larger and larger fields and landscapes for agriculture, we remove the habitat that pollinators may need. Increasing dependence on pesticides for pest control is also highly detrimental to beneficial insects such as pollinators, unless planned and undertaken with extreme care. Pollination is a service *Nature* provides that we have tended to take for granted, and that we often do little to encourage until we start to lose it. As wild ecosystems are increasingly converted to more human dominated uses to meet the compelling demands of food security, it is critical for us to understand what pollination services are most important for food security, and how we can preserve pollinator services in sustainable farming systems.

A crop's pollinator dependence differs between species, including between crops and crop varieties. Some plants must be cross-pollinated, others do not need pollinators but produce better fruit and seed if pollinated, and a number of them are strictly self-pollinated. Further, plants differ in their pollinator-type requirements; some require specific pollinators while others are pollinated by a variety of visitors, and many are wind pollinated. Effective pollinators of the same crop may vary from one site to another. Specific knowledge on pollinator dependence and types is important for agriculture and biodiversity (including agro-biodiversity) conservation. Managed bees are vital to the production of more than 90 crops, including almond, alfalfa and sunflower seed, apple, cherry, melon, and berries. Honey bees (*Apis*) alone pollinate crops that have an added value of over $14 billion. Only a few species of bees can be used for commercial pollination, and their health and improved management are critical to agricultural production. The most versatile commercial pollinator is the honey bee, which also produces its own unique agricultural product, honey.

The presumption of ample honey bees for crop and ecosystem pollination was severely challenged in the past several years by enigmatic declines of honey bee colonies throughout the world (Aizen and Harder 2009; vanEngelsdorp et al. 2007). Due to the link between animal pollinators and global food security, any decline of managed honeybees and the loss of wild pollinators are of increasing concern. Undoubtedly, the global health of honeybees is at risk. Honeybee well being is negatively affected by the intensive use of pesticides and fungicides in agriculture (Barnett et al. 2007; Desneux et al. 2007; Karise 2007) and the chronic exposure to acaricides needed to combat the parasitic mite Varroa destructor. Furthermore, destruction and fragmentation of natural and semi-natural habitats as well as land-use intensification in agricultural landscapes have significant negative effects on honeybees and other pollinators (Kremen et al. 2004, 2007; Rathcke and Jules 1993; Steffan-Dewenter and Westphal 2008; Tscharntke et al. 2005). In addition and perhaps most importantly, honeybees are attacked by parasitic mites (*Varroa destructor, Acarapis woodi, Tropilaelaps spp.*), fungi (*Nosema* spp., *Ascosphaera apis*), bacteria (*Paenibacillus* larvae, *Melissococcus plutonius*), numerous viruses, and scavengers (from beetles and mice to bears) during any life stage. For some of these parasites and pathogens the consequences for individual bees and colonies are known, while for others they remain elusive. Still, it is clear that they all in one way or another reduce the fitness of their honeybee hosts.

There is a growing niche for non-*Apis* bees that specialize in specific crops or can be used in greenhouses. These species are threatened by shrinking habitat and lack of information about their biological requirements, including their own sets of parasites and diseases. A variety of native and non-native species could be better used to enhance pollination efforts if they could be produced effectively in sufficiently large populations and managed for health and availability. For crops to be pollinated more efficiently there is a need to better understand pollination mechanisms, as well as bee and bee-associated pest management.

Pollination, the transfer of pollen grains to the stigma of the plant gynoecium is a crucial step in the sexual reproduction of flowering plants. The majority of flowering plants rely on animals for the transfer of pollen (Nabhan and Buchmann 1997; Renner 1988). Because flower visitors gain no direct benefit by pollinating flowers, rewards must lure them. The most common way plants attract animals to visit their flowers is by providing food such as nectar, pollen or oils. While searching for these rewards in the flower, pollen from the flower's anthers may stick to the body of the animal. When the animal visits subsequent flowers in search of more rewards, pollen from its body may adhere to the stigma of these flowers and again, new pollen may stick to the body of the animal.

Pollination is an essential part of sexual reproduction in seed-producing plants (spermatophytes), allowing for genetic recombination and the formation of a genetically unique seed. This shuffling of genetic material maximizes the ability of at least some of a plant's offspring to survive in a world of unpredictable environmental changes.

Further, the maintenance of genetic variability in a population is necessary for *Evolution* by natural selection to occur, and therefore is the key to the ability of a plant population to adapt to changing environmental pressures.

Some reshuffling of genetic material occurs in meiosis, the process by which gametes are produced. Therefore, even self-pollination, in which pollen grains are transferred from the stamens to the stigma of a single flower (or from one flower to another on the same plant) allows for the maintenance of genetic variation. But genetic variation in the next generation is maximized by cross-pollination, in which pollen from the flower of one plant is transferred to that of another individual plant.

Many plants rely on wind or water for pollination, but must produce large amounts of pollen to ensure the chance interception of pollen by the stigma. For many plants it has proven advantageous to rely on pollination via animals, such as insects, birds, and bats. By relying upon pollination by animals, the plant wastes less pollen compared with pollination by wind or water. On the other hand, the plant may expend additional energy to promote pollination by animals; one example is the production of nectar to reward pollinating animals. In addition, animal pollinators can transfer disease organisms from one plant to another along with pollen.

Flowers differ tremendously in colour, scent, size and shape; and they are visited by an equally diverse morphological and taxonomic array of animals. The most common flower visitors are insects belonging to the orders Hymenoptera, Lepidoptera, Diptera and Coleoptera. But several species of birds, bats, and other mammals also regularly visit and pollinate flowers. A common and longstanding view in pollination biology is that plants should specialize on a small subset of these visitors in order to ensure effective pollination. And indeed, despite the huge morphological and taxonomical diversity of potential interaction partners, flowers show trait combinations that seem to reflect the morphology, behaviour and physiology of certain pollinator types (Faegri and van der Pijl 1979). For example, red coloured, odourless flowers with deeply hidden and dilute nectar seem to be adapted to hummingbirds or perching birds; blue coloured bilaterally symmetric flowers with moderately hidden and relatively concentrated nectar combined with a pleasant odour are thought to be adapted to bees (Baker 1975). These typical trait combinations (termed ‘pollination syndromes’ in the literature) are found across diverse taxonomic groups of plants and seem to be a result of specialization and convergent evolution.

Plants and animals have coevolved over millions of years, since the Cretaceous period. Plant fertilisation depends on the behaviour of many species of animals, from insects to birds to mammals, which transport pollen from stamens to pistils, a key step in the reproduction of most flowering plants. Pollinators provide an essential ecosystem service that results in the out-crossing and sexual reproduction of many and improving livelihoods and by the role they play in conserving biological diversity in agricultural and natural ecosystems. Reduced agricultural yields and deformed fruit often result from insufficient pollination rather than from a deficiency of other agricultural inputs, such as agrochemicals. In natural ecosystems, the visual clues of insufficient pollination are more subtle than in agriculture, but the consequences can be as severe as the local extinction of a plant species, a noticeable decline in fruit and seed eating animals, the loss of vegetation cover and ultimately, if keystone species are involved, the demise of healthy ecosystems and their services.

Natural ecosystems and many agricultural ones depend on pollinator diversity to maintain overall biological diversity. A variety of materials, including dry wood (especially wood with empty beetle burrows), bare ground, vegetation-free embankments, mud, resins, sand (for some bees), carrion (for certain flies), host plants (for bees, moths and beetles) and caves (for certain bats) contribute to the diverse environment needed to maintain pollinator diversity.

Pollinator diversity is immense. There are more than 20,000 pollinating bee species in the world, as well as numerous other insect and vertebrate pollinators. Pollinators differ from many other providers of essential ecosystem services because they are often part of highly specific pollinator–plant relationships. Where there are very specific niche requirements for the plants and their pollinators, loss of the pollinator can have cascading effects across the ecosystem. For example, some bees that pollinate small herbaceous plants depend on holes in dry wood to nest, and when the wood is removed plant fecundity is reduced.

The importance of pollination in agriculture has been recognised for millennia (Kevan and Phillips 2001). Ancient Assyrian temple carvings depict winged deities pollinating female date palms with male flowers to ensure that dates would form on their trees (Buchmann and Nabhan 1996). Old Mayan screen fold books (the Madrid Codex, now housed in a Madrid museum) indicate that the ancient Maya of Mesoamerica kept stingless bees (*Melipona beecheii*), indicating that they knew how to manage and propagate captive colonies in log hives. Pollination was discovered by Koelreuter (1733–1806) and Sprengel (1750–1815) who are regarded as father of pollination ecology. Much of this ancient knowledge was lost until essentially modern times, with the rediscovery of sexuality in tulips by Arthur Dobbs in 1750 and other early floral biologists. The irony, however, is that although the importance, and fragility, of pollination for agriculture and *Nature* conservation has been known for a long time, there appears to have also been a popular belief that flowering plants always somehow seem to get pollinated and bear fruits and seeds and carry on into the next generation. Thus the science of pollination ecology has not advanced adequately, and this makes ample room for new and established researchers to contribute to knowledge about pollinators and the plants they pollinate, whether in natural or agroecosystems. Surprisingly, even the identities of major and minor pollinators for many major crops plants worldwide remain unknown.

Pollination refers to the transfer of pollen from the male parts of the flower to the female parts. This is especially critical in plants where different sexes are found in different plants or flowers. Pollination is a resource that is vital to agricultural productivity. Insect pollinators for example are practically essential in fruit and vegetable crop production. This is especially because pollinators increase or enhance seed set, improve seed and fruit quality, as well as improve genotype progeny. Pollination may be a key to fruit and seed vegetable productivity when all the other conventional inputs of water, fertilizer and pest control are taken into consideration. The pollinators however are currently under threat arising from: agricultural development, habitat fragmentation, agricultural chemicals (pesticides and herbicides), destruction of foraging and nesting sites, spread of pests and diseases. Bee poisonings for example from pesticides result in annual losses of $14.3 million in the USA alone.

Nature is rapidly disappearing all over the planet, and we have reached, on a geological time scale, the last minute where we have a chance to avert a huge biological disaster – the large-scale loss of pollinator services. All this is well known to biologists, ecologists, agronomists and other *Nature* experts from many fields. Most people around the world, however, including decision makers, are poorly informed about the enormous biological disaster we may soon face, owing to a serious shortage of pollinators. Recognition of the importance of pollinators and pollination services will be a vital part of the world's ethical and practical drive to eliminate extreme poverty in India and other countries.

In addition to playing a crucial role in pollination and thereby improving crop yields, honeybees contribute in a balanced way to rural development efforts leading to secure and sustainable livelihoods. It is generally known that bees are needed to pollinate our crops but it is not well known that the economic value of bee pollination is several times more the value of the world-wide production of honey. Besides honeybees, the specific pollinator role played by Non-*Apis* bees, such as bumble bees, solitary bees and tropical stingless bees is of immense significance. A great majority of angiosperm (flowering) plants depend upon animals for their pollination. Of the animals that visit plants and are responsible for the spread of the pollen, a great majority belongs to the insects, for example flies (Diptera), beetles (Coleoptera), butterflies (Lepidoptera), but most important, bees (Hymenoptera: Apoidea). Bees because of their morphological adaptations for the collection of pollen are considered to be the most efficient pollinators.

Certain groups of bees are able to perform specialized pollen collecting behavior, e.g. "buzz-pollination". In a wide range of angiosperm families, pollen can only be released when the stamens are shaken by vibrating bees. This buzz-pollination is performed by bumblebees, carpenter bees and by stingless bees of the genus *Melipona*, but not by honeybees. The production of crops, that need to be pollinated in enclosed environments like greenhouses, and therefore in the absence of natural pollinators, implies a new dimension for the application of bees as pollinators. In view of the available management technology and the actual pollination value, the honeybees are considered to be the most significant tool for seed production. However, other species, like the bumblebee and several solitary bee species are also being used for the pollination of greenhouse crops and ornamentals (Estes et al. 1983).

Despite an increasing recognition of their important role in pollination, the population and diversity of honey bees is declining due to the habitat loss through land use changes, increasing monoculture and negative impacts of pesticides and herbicides. During the last few years, there have been an impending "pollination crisis" in certain parts of the world due to decline of honeybee colonies due to attack by pests and diseases combined with a general increase in the area of bee-pollinated crops. In some countries the demand for pollination is increasing, at the very time that the supply of managed pollinators is decreasing. This pollination crisis is raising further the interest in management, culture and conservation of pollinating bees. Modern intensive agriculture and certain ways for managing our environment may have important consequences for the ecological position and the conservation of bees in this environment. Certain developments are considered to be detrimental for beekeeping. The use of agro-chemicals and of genetically modified crops are much discussed in this respect.

There are several reasons why honey bees are perhaps one of the most studied insects (probably next to *Drosophila* in terms of amount of money spent and number of papers published). Honey bees play a critical role in agriculture. The most important role honey bees play is actually not honey production, but pollination. The value of crops that require pollination by honey bees, in the United States alone, is estimated to be around $24 billion each year and commercial bee pollination was valued around $10 billion annually. There is also a trend to consume more bee-pollinated crops (such as fruits and vegetables), making honey bees more and more important in agriculture.

The honey bees are not domesticated in true sense but one had to understand and adjust his methods to gain maximum from the hard toil of honeybees. To be a successful beekeeper one must learn about honeybees and beekeeping, about the instincts governing the activity of a bee colony at different stages of its development, about the ways to master these instincts and hoe to use them in practical beekeeping.

Contribution of apiculture to Indian agriculture and horticulture is very valuable. The country has over 50 million hectares under crops that are benefited by bee pollination. Among the crops that give increased yields due to pollination services by bees are oilseeds, pulse crops, vegetables and fruits. The significance of this can be appreciated, considering the recurring shortages of edible oils, pulses and other food crops.

Pollination is basic to agricultural and natural productivity and an ancient co evolved process involving animals and plants in mutualism. The value to agriculture is huge and to global economy of *Nature* inestimable. Nevertheless, pollination is a threatened system from highly managed agriculture to remote wilderness. Pesticides take their toll, insecticides directly killing pollinators and herbicides indirectly by reducing pollinator forage. Habitat destruction has reduced pollination in croplands and natural areas. Honey bee diseases threaten to change the demography of beekeeping and availability of pollination. Encouragement of wild pollinators, domestication of unused potential pollinators, and more environmentally sensitive human exploitation of the world are needed as part of conservation, forestry, agroforestry, sustainable agriculture and development.

The splendour, variety and colour of flowers arises from their need for pollination – the transference of pollen grains from the male organs, the stamens to the female stigmatic organs or ovaries in flowers. For 200 million years, insects and flowers have been closely and mutually interrelated in evolution as reciprocal selective factors. They have evolved together to produce some amazingly specialized and ingenious pollination mechanisms. The entomophilous species of plants may be adapted to certain insects, e.g. figs to a wasp, *Blastophaga; Phlox* to a diurnal butterfly, *Hemoris; Yucca* to a tineid moth, *Pronuba*; red clover to bumblebees; *Trollius* to a blade fly, *Chiastochaeta*; etc. In the case of some orchids, e.g. *Ophrys insectifera*, the flowers have very striking resemblances with the females of certain wasp species of *Scolia*. Male wasps visit the flowers not for nectar or pollen, but just due to the visual simulation of flowers resembling their females, thus pollinating them incidentally. This dramatic relationship between plants and their pollinators is one of the most significant events in organic *Evolution*.

The economic value of animal pollination to world agriculture has been estimated to be 200 billion US dollars per year. More than one lakh different animal species play roles in pollinating the 250,000 kinds of wild flowering plants on our planet. In addition to bees, wasps, moths, butterflies, flies and beetles, as many as 1,500 species of birds and mammals serve as pollinators. Hummingbirds are the best known wildlife pollinators in the Americas, but perching birds, flying foxes, fruit bats, snails, slugs, possums, lemurs and even a gecko function as effective pollinators elsewhere in the world.

The population of both wild and managed pollinators is declining at alarming rates owing to alteration in their food and nesting habitats, shrinkage in natural ecosystems, i.e. forests and grassland ecosystems, pesticide poisoning, diseases and pests, over-collecting, smuggling and trading in certain rare and endangered species. Insects (butterflies, moths, bees, wasps, ants, beetles, etc.) numbering about 500 species are an important supplementary source of calories and proteins in many regions of the world. In a recent field study at Cornell University in the U.S.A., it was found that monarch butterfly caterpillars eating Bt corn toxic pollen blown on to milkweed plants near Bt corn fields had suffered significant adverse effects leading to death of nearly 20% of the caterpillars. These chemicals and toxins can eliminate nectar sources for pollination, destroy or adversely affect larval host plants for moths and butterflies, and deplete nesting materials for bees. Gardeners, orchard growers, farmers and urban dwellers can switch to more pollinator-friendly organic methods of cultivation to reduce wildlife exposures to insecticides, herbicides and fungicides.

There are over 1,500 species of butterflies in the Indian subcontinent, but their population is dwindling because of the indiscriminate use of insecticides and chemical weed-killers as well as atmospheric pollution. Many other manmade environmental changes like deforestation, extension of farming and unrestricted urbanization are also threatening some species of butterflies to extinction by destruction or disturbance of their larval as well as adult food plants, feeding grounds and shelters. The Travancore Evening Brown, the Malabar Tree Nymph, Bhutan Glory and Kaiser-I-Hind Butterfly are listed as endangered due to the wanton destruction of habitats in various parts of the subcontinent. Many of the most spectacular and endangered species have various levels of protection under local legislation. However, there is a major trade in the spectacular tropical species for incorporation in ornaments and souvenirs. The international demand for insects is greater than most people realize. Next to bees and moths only, butterflies are most efficient pollinators of flowers to help turn them into food crops, fruits and seeds so essential for the survival of man and animals. Wildlife farming, based on sustainable exploiting wild creatures, can help to save endangered species like butterflies and their habitats.

Over the past decade, farmers in the Himalayan region have been complaining about decline in apple production and quality due to pollination-related problems. The general observation of farmers is that, in the past, there used to be a lot of insects such as wild bees, butterflies and moths during the apple flowering season but now they have all disappeared. The scarcity of natural insect pollinators has, therefore, become a critical factor in inadequate pollination. The solution lies in supplementing populations of crop pollinators such as honeybees, bumblebees, sting less bees, solitary bees etc. Hand pollination of apples is a common practice in Maoxian County of Sichuan, China. Awareness about the value of honeybees as crop pollinators has to be raised at all levels among planners, policy makers, beekeepers or farmers. In western countries, farmers are already using honeybees and solitary bees (species of *Osmia, Megachille, Nomia, Xylocopa* etc.) for pollination of different crops. The focus of beekeeping needs to change from conventional honey production to crop pollination.

1.2 Role and Importance of Pollinators

Over and above its direct economic value to humans, pollination by animals provides essential maintenance of the structure and function of a wide range of natural communities, and it enhances aesthetic, recreational, and cultural aspects of human activity. In view of that economic and ecological importance, there is a need to identify species for which there is evidence of decline, analyzes the putative causes of those declines, and discusses their potential consequences, need of monitoring, conservation and their restoration.

The angiosperms—flowering plants that produce seeds often enclosed within an edible fruit—are among the planet's most successful life forms. Reproductive systems of angiosperms vary greatly among species, but two processes are necessary for sexual reproduction in all angiosperms: pollination—the transfer of pollen from the anthers of a stamen to the stigma of a pistil—and fertilization—the fusion of the sperm nuclei from pollen with the egg nucleus in the ovary to produce an embryo. Some plants self-pollinate, that is, pollen transfer occurs within the same flower or among the flowers on a single plant, usually because the anthers touch the adjacent stigma. The majority of flowering plants, however, depend on the transfer of pollen from other individuals (cross-pollination).

Although some species rely on abiotic forces, including wind and water, for pollen transfer, more than three-fourths of the planet's angiosperms rely on over 200,000 species of animal pollinators to various extents to meet their reproductive needs. Fossil records show that angiosperms underwent a remarkable diversification between 130 million and 90 million years ago.

1.3 Barriers to Self-Fertilization

Flowers can be staminate (bearing only male reproductive organs), pistillate (bearing only female reproductive organs), or perfect (bearing male and female reproductive organs). Individual plants can be monoecious (bearing staminate and pistillate flowers), dioecious (staminate and pistillate flowers borne on separate plants), or even trioecious (staminate, pistillate, and perfect flowers borne on separate plants). Within dioecy, various conditions can be found in different species; *gynodioecy*, for example, is the term applied to the breeding system of species in which individuals bear either female or hermaphrodite flowers (Richards 1997). Almost three-quarters of all plant species produce perfect flowers. Approximately 5% are dioecious, and slightly more than 5% are monoecious (Molnar 2004).

Pollination can occur within the flowers of a single plant, among different flowers of a single plant, and among flowers of different plants. A plant that is self-fertile and self-pollinating is called *autogamous* if pollination and fertilization take place within the same flower. A plant is *geitonogamous* if pollination and fertilization take place between flowers of the same plant, whereas a plant that is cross-pollinated and cross-fertilized is *xenogamous*. It is common for plants to receive mixtures of self and outcross (nonself) pollen grains, especially if the male and female parts are in the same flower (—a perfect or hermaphrodite flower).

Perpetual self-fertilization could be problematic for plants because of the many potential genetic complications associated with inbreeding (Charlesworth and Charlesworth 1987). Accordingly, adaptations that reduce the likelihood of selfing exist in many taxa. Dioecy and monoecy promote outcrossing, and that they achieved ecological dominance 100 million to 70 million years ago (Davies et al. 2004). Chief among the many explanations offered for their spectacular ascendancy is the development of mutualistic associations with animals for the dispersal of pollen (Baker and Hurd 1968; Faegri and van der Pijl 1979; Labandeira et al. 1994; Stebbins 1950, 1974) and seeds (Herrera 1989; Kevan 1984; van der Pijl 1982). Mutualistic associations with animals provide mobility of gametes to otherwise predominantly sessile terrestrial plants, which allows for greater genetic variation in plants as well as access to a wider range of ecological opportunities through seed dispersal. For flowering plants, use of an animal partner to transport pollen increases the area in which potential mates can be found and promotes outcrossing, the merger of gametes from genetically distinct individuals. Increasing genetic variability through recombination associated with outcrossing is key although monoecious plants can receive self-pollen from male flowers on the same plant. Many monoecious species produce male and female flowers at different times, and the probability of selfing is reduced. Similarly, in plants with hermaphrodite flowers, self-pollination within flowers is avoided when the male and female floral parts mature at different times. In some species, the chance of self-pollination is reduced because the male and female parts of the same flowers are separated. In a subset of those species, the male and female parts of the flower move closer together as the flower ages, allowing self-pollination as a “last resort” before the flower is too old to set fruit.

As a further deterrent to selfing, many flowering plant species are self-incompatible—that is, pollen that is deposited on a stigma within the same flower (or another flower on the same plant) is unable to achieve fertilization. Self-incompatibility is controlled in complex and variable ways, and it involves the interplay of incompatibility alleles (of which there may be many) and their effects in the two parent plants (Matton et al. 1994). The effectiveness of self-incompatibility mechanisms ranges from absolute to weak, and the mechanisms for blocking self-fertilization can break down as a result of aging or external factors, especially heat.

Breaking those barriers down ensures sexual reproduction (seed set and fruit set) even when cross-pollination is not possible. It is important to note, however, that despite the ubiquity of outbreeding, many species persist exclusively and successfully with self-pollinating and self-fertile flowers. Moreover, some self-fertile plants that can self-pollinate (including some legumes) are of agricultural importance. They can establish themselves in nonindigenous areas where their natural pollinators are absent. The nature and evolutionary biology of plant-breeding systems are presented in detail by Richards (1997). To allowing organisms to adapt to spatially and temporally variable environments, genetic variability in plant populations could help to facilitate the *Evolution* of resistance to pathogens and herbivores.

After fertilization is complete, the production of fruit ensues. A flower's ovary may contain a single ovule and produce a fruit that bears only a single seed (as in the almond, avocado, coconut, plum, or cherry), or it may contain hundreds of ovules and produce a fruit bearing hundreds of seeds (as in the tomato, kiwi fruit, cucumber, watermelon, or squash). Because each seed results from the union of a sperm cell from a pollen grain and an egg cell, some plants require many hundreds of pollen grains to fertilize all of the available egg cells. If a flower receives an inadequate number of pollen grains, some of the egg cells will not be fertilized and accordingly seeds will not develop. Economic consequences of such incomplete fertilization include production of undersized or misshapen fruit that, for a market crop, has less value. Adequate pollination often requires that individual flowers be visited by many pollinators or that one to several pollinators make multiple trips to the same flower.

Some fruits of economic importance are seedless by design. They are generally the product of selective breeding or genetic manipulation that would not be sustainable in nature (Schery 1972). Seedless bananas, for example, are the products of sterile triploid plants arising either spontaneously or as a result of hybridization of diploid and tetraploid individuals and are propagated vegetatively. Parthenocarpic fruits, such as clementines (seedless tangerines), are those in which fruits develop in the absence of successful fertilization; fertilization could fail because these self-incompatible cultivars are grown in monoculture orchards. Seedless grapes, in contrast, are stenospermocarpic; fertilization takes place, but the resulting fruit is seedless because the immature embryo fails to develop (Schery 1972).

1.4 Pollinators in Natural and Agricultural Ecosystems

Pollinator-plant interactions have been estimated to encompass almost 400,000 species, the precise *Nature* of the relationship between plant and pollinator varies enormously. Although some animals visit flowers for nectar or pollen, not all flower visitors bring about pollination. Effective pollinators often have behavioral and anatomical traits that greatly increase the efficiency and accuracy of pollen delivery

(Barth 1991; Faegri and van der Pijl 1979; Proctor et al. 1996; Lewinsohn et al. 2006). In general, pollination is a mutually beneficial interaction; pollinating animals receive some form of nutritional "reward" for visitation and pollen delivery. Pollen itself can be a reward, serving as the primary food resource for most larval bees and as an important source of protein for some flies, butterflies, birds, and bats (Roulston and Cane 2000). Other plants provide nectar, oils, resins, fragrances, pheromone precursors, and other resources to induce visitation and pollen delivery (Barth 1991; Buchmann 1987; Dafni et al. 2005; Roulston and Cane 2000; Roulston et al. 2000).

Plants and pollinators vary in their degree of interdependence. Some plant species depend primarily on a single species or genus of pollinator, which in turn has restricted sources of pollen or nectar. An example of a closely dependent association is the relationship between plants in the genus *Yucca* (Agavaceae) and their pollinators, the aptly named yucca moths of the genus *Tegeticula* (reviewed in Pellmyr 2003). In this mutualism, estimated to be more than 40 million years old, the adult yucca moth is the primary pollinator of yucca and the developing yucca seeds the main nutritive source for the caterpillar. The female moths have unique structures, called tentacles, which are used to collect and compact comparatively large quantities of pollen (up to 10% of the moth's weight) from yucca flowers. After gathering a pollen mass, the moth flies off and visits another flower, in which she lays eggs. Then, in a distinctive series of stereotyped behaviors, she places part of the pollen load directly on the stigma surface to achieve pollination and subsequent fertilization, thereby guaranteeing a food source for her offspring.

Such specialized relationships, however, are the exception in plant-pollinator interactions. In many cases, if not most, associations are highly opportunistic. For instance, Kandori (2002) over a 2 year period of study found that at least 45 species of insects in 5 orders visited *Geranium thunbergii* flowers in a natural population; of these, 11 species in 3 orders served as principal pollinators. Principal pollinators of a particular species can vary spatially as well as temporally; the alpine sky pilot, *Polemonium viscosum*, is pollinated primarily by bumble bees at high elevations and by flies at low elevations in its native Rocky Mountain range (Galen et al. 1987). Humans have understood the agricultural importance of pollination—that plants require pollen transfer to produce fruits and set seed—for at least 3,500 years. However, the idea that seeds result ultimately from the deposition of pollen grains on stigmatic surfaces was not clearly articulated until the seventeenth century (Camerarius 1694) and even then was slow to gain acceptance. The systematist Carolus Linnaeus, for example, identified the sexual organs of plants as important components of his classification system, to the disapprobation of the eighteenth century's religious establishment.

The idea that animals play a role in cross-pollination, the transfer of pollen from one individual to another, was not clearly articulated until close to a century later (Kölreuter 1761; Sprengel 1793). Kolreuter's painstaking observations in nature including entire days spent watching single plants, gave him a remarkable insight into the use of insects by flowers and flowers by insects. In most cases he described multiple types of insects visiting a given plant species and although this was not explicitly discussed. The impression is that some of the insects were observed visiting several plant species. Kolreuter recognized that such generalized niche relationship set the stage for hybridization between related plant species.

Joseph Gottlieb Kölreuter, a professor of natural history at the University of Karlsruhe, Germany, demonstrated that insect visitation was a prerequisite for seed production in several economically important fruits, vegetables, and ornamental flowers and put his knowledge to practical use by developing technique for artificial fertilization and conducting the first cross-hybridization of two plant species (Mayr 1986; Sinnott 1946).

The great insights and practical achievements of Kölreuter and Sprengel failed for the most part to inspire their contemporaries, but a half-century later their work had a profound influence on the thinking of another biologist—Charles Darwin. The publication of *The Origin of Species by Means of Natural Selection or The Preservation of Favoured Races in the Struggle for Life* (*The Origin of Species*, in short) in 1859 ushered in a new era of experimental pollination biology. In his preface, Darwin described the process of coadaptation, which is what allows living organisms to serve as selective agents in the same manner as abiotic forces and specifically mentioned pollination as an example.

Darwin's extensive writings on plant-pollinator relationships, not only in *The Origin of Species* but also in *The Various Contrivances by which British and Foreign Orchids are Fertilised by Insects and the Good Effects of Intercrossing* in 1862 and other subsequent publications, summarized an extensive literature and described his own meticulous experiments, thereby providing compelling evidence of the significance of pollination in the lives of plants. Demonstration of the *Evolution*ary mechanism to account for the reciprocally adaptive relationship between plants and their pollinators provided the impetus for an explosion of interest in pollination biology (Delpino 1868–1875; Knuth 1906, 1908, 1912; Müller 1869; Müller and Delpino 1869) that laid the foundation for agricultural applications and for contemporary experimental studies.

1.5 Population Management of Pollinators

Recognition of the mechanisms of biotic pollination led to important agricultural innovation, with extensive economic consequences; management of pollinator species allowed for enhanced crop productivity and for commercialization (and export) of numerous crop plants. Of different pollinating insects, *Apis mellifera* L., the western honey bee, is the premier actively managed pollinator worldwide, highly valued for its activity as a pollinator and for its production of wax and honey (Delaplane and Mayer 2000; Free 1993; Kearns et al. 1998; McGregor 1976).

Native to Eurasia, the honey bee has been hunted for its honey and wax for at least 6,000 years (Dobbs 1750; Crane 1983, Crane 1990 and records of semidomestication and hive management date back to ancient Egypt (Crane 1999). *A. mellifera* rapidly became the primary pollinator for modern agriculture, and managed colonies were transported around the world, first arriving in North America with European colonists in the 1600s (Sheppard 1989). Modern apiculture in North America dates to 1862, when L. L. Langstroth, a Philadelphia minister who kept bees as a hobby, exploited the concept of "bee space" to construct movable-frame, top-bar hives that allowed beekeepers to harvest honey, manipulate their colonies, and increase efficiency without harming the bees (Langstroth 1862). Langstroth's invention resulted in the large-scale commercial beekeeping and honey industry that exists today.

Honey bees pollinate more than 100 commercially grown crops (Delaplane and Mayer 2000; Free 1993; Kearns et al. 1998; McGregor 1976). Other species of pollinators for which active management systems have been developed include several species of bumble bees (*Bombus*), mainly for pollination of greenhouse tomatoes (de Ruijter 1997; Hughes 1996; Kevan et al. 1991; Macfarlane et al. 1994; Plowright 1996; van Heemert et al. 1990), and leafcutting bees (*Megachile rotundata*) (Bohart 1972a; Frank 2003), which pollinate most of the alfalfa in parts of the arid Pacific Northwest. To a lesser extent, alkali bees (*Nomia melanderi*) (Bohart 1972a) also are managed for alfalfa pollination (Stephen 2003).

Mason bees, including the Japanese horn-faced bee, *Osmia cornifrons*, are managed to some extent, mainly for pollination of apple orchards in the eastern United States (Batra 1982; Bohart 1972b), although they are used extensively in Japan for pollinating the entire apple crop. Several native *Osmia* species, notably *O. lignaria*, are used to pollinate apples in the northwestern United States (Bosch et al. 2000; Bosch and Kemp 2002) and in eastern Canada (Sheffield 2006) and to pollinate cherries (Bosch and Kemp 1999, 2000, 2001). Methods for cultivating this species are well developed (Griffin 1993; Torchio 2003).

Literature on the culture and management of many alternative pollinators is available (Batra 1994a, b; Bosch and Kemp 2001; Free 1970; Kevan et al. 1990; Shepherd et al. 2003; Torchio 1990, 2003). For some crops, bumble bees, megachilids, and other native bees are more efficient pollinators than are honey bees (Cane 2002; Javorek et al. 2002; Maeta and Kitamura 1981; Tepedino 1997) and *Osmia* species serve as alternative pollinators for almonds (Bosch et al. 2000; Bosch and Kemp 2000; Torchio 2003), red raspberries and blackberries (Cane 2005), pears (Maeta et al. 1993), blueberries (MacKenzie et al. 1997) and sweet clover (Richards 2003).

For delivery of various biological control agents to protect field and greenhouse-grown crops against fungal pathogens and pests (Kevan et al. 2005). Bees are used to deliver *Bacillus subtilis* to blueberry flowers to suppress *Monilinia vaccinicorymbosi*, or mummy berry disease, a devastating fungus (Dedej et al. 2004). They also have been used to deliver *Trichoderma harzianum* 1295-22, a commercially produced agent for control of the pathogenic fungus *Botrytis cinerea* on strawberries (Kovach et al. 2000). There is a continuing effort to investigate the potential of honey bees as biological monitors for environmental contaminants (Bromenshenk et al. 1995) and land mines (Bromenshenk et al. 2003).

In addition to active management, pollinators can also be managed passively—that is, their activities can be manipulated by altering environmental conditions to promote their diversity and population growth or to influence particular behavior (Shepherd et al. 2003; Vaughn et al. 2004). Passive management includes farming to promote the growth of floral resources, providing artificial nest materials and nest sites, and protecting nesting habitat. All of these practices are designed to increase the diversity of the pollinator community and the abundances of particular species (Kevan et al. 1990).

1.6 Value of Pollination

Pollination as a biotic process has both commercial and ecological value. In the context of agriculture, pollination provides a wide range of benefits to a broad diversity of commodities across the world. In some cases, production of the commodity itself results directly from the act of pollination (for example, fruit production). In other cases, although pollination does not result in production of the commodity itself, the process contributes to crop propagation (for example, production of seeds used to grow a root crop such as carrots) or quality (for example, size of tomatoes has been linked to repeated pollination). There are indirect benefits as well, through food-chain relationships. Alfalfa seed, a bee-pollinated crop with an annual value of $109 million (direct effect), is used to produce hay for livestock forage that is valued at $4.6 billion per year (indirect effect) (Morse and Calderone 2000). Although these indirect effects tend to exaggerate the economic value of pollination, they have been used in several widely cited studies. The annual value of honey bee pollination to U.S. agriculture has been variously estimated at $150 million (Rucker et al. 2005), $1.6–5.7 billion (Southwick and Southwick 1992), $9 billion (Robinson et al. 1989a, b), $14.6 billion (Morse and Calderone 2000), and $18.9 billion (Levin 1983). The annual benefit of honey bee pollination in Canada has been estimated at $443 million by Scott-Dupree et al. (1995).

The contributions of *A. mellifera* are not unique because alfalfa leafcutting bees and bumble bees also pollinate crops. An estimated $2 billion to $3 billion value in annual crop pollination can be attributed to the activities of native bees and other insects (Losey and Vaughan 2006; Prescott-Allen and Prescott-Allen 1986; Southwick and Southwick 1992).

Some vertebrates also operate as pollinators of ecologically and economically important plants. Tropical trees of the family Bombacaceae, which includes species used for timber, silk cotton, balsa wood, and other products, rely primarily on bats for pollination (Bawa 1990; Watson and Dallwitz 1992). Many columnar cacti and agaves, which are important sources of alcoholic beverages (tequila, mescal) and other products (sisal fibers), also depend on bats and birds for pollination (Arizaga and Ezcurra 2002; Arizaga et al. 2002; Fleming et al. 2001a, b; Grant and Grant 1979; Rocha et al. 2005; Valiente-Banuet et al. 1996; but see also Slauson 2000, 2001). Globally, pollinators are fundamentally important for the production of roughly 30% of the human diet and most fibers (cotton and flax), edible oils, alcoholic beverages, nutraceuticals, and medicines created from plants (Buchmann and Nabhan 1996; McGregor 1976; Roubik 1995).

Estimating the value of pollinators and pollination in natural ecosystems and predicting the consequences of their losses are considerably more challenging than estimating their economic value in agriculture. Such estimates are complicated by both the number of species involved (globally, more than 400,000) and the relative paucity of information available for most of those species. For example, in their effort to calculate the economic value of ecological services provided by insects, Losey and Vaughan (2006) did not attempt to place a dollar value on the contributions of pollinators to maintenance of natural plant communities, although it is reasonable to assume that a significant proportion of plants in uncultivated terrestrial communities rely upon pollinators. These plants, in turn, contribute to many ecosystem services of value to humans, such as water filtration, carbon sequestration, and flood and erosion control (Daily et al. 1997). An added complication is that insect pollinators may contribute ecosystem services other than pollination in their larval stages. The value of these services is equally difficult to calculate, particularly without a complete understanding of all aspects of pollinators' life histories.

1.7 Pollination Crisis

The concept of a pollinator "crisis"—localized extinctions and possibly a global decline in the number and viability of pollinating species contributing to trophic collapse (Dobson et al. 2006)—began to gain recognition as a critical issue in the early 1990s. Major losses in managed honey bee colonies led to concern in the United States about this critical pollinator (Watanabe 1994). The publication of *The Forgotten Pollinators* (Buchmann and Nabhan 1996), which extended the concern to nonmanaged species and placed the issue within the greater context of biodiversity decline, galvanized the ecological community. Buchmann and Nabhan's book concluded with a call for a U.S. national policy on pollination and pollinators. Subsequent emphasis of pollination as a fundamental "ecosystem service" (Daily et al. 1997) led to an explosion of interest in the international policy arena (Allen-Wardell et al. 1998; Costanza et al. 1997; Eardley et al. 2006).

The science of pollination ecology and floral biology has, however, now been mainstreamed in biodiversity conservation. In the mid-1990s, scientists and agriculturists around the world were concerned that a worldwide decline of pollinator diversity was occurring, and this prompted policymakers at the Fifth Meeting of the Conference of Parties (COP) of the Convention on Biological Diversity (CBD) to establish an International Initiative for the Conservation and Sustainable use of pollinators (also referred to as the International Pollinators Initiative, or IPI) in 2000. Fifth Meeting of the Conference of Parties (COP) considered this to be a cross-cutting initiative within the programme of work on agricultural biodiversity to promote coordinated action worldwide, and so requested the development of a Plan of Action for the IPI. Subsequently, the Executive Secretary of the CBD requested the Food and Agriculture Organization of the United Nations (FAO), in collaboration with key experts, to develop a Plan of Action for the IPI. This Plan of Action, which built on recommendations from the São Paulo Declaration on Pollinators, was adopted at COP 6 (decision VI/5) in 2002. On a global scale, however, conservationists, farmers, foresters, horticulturists, soil conservationists, landscape architects, town planners and other stakeholders need to work with policymakers on the economic and ecological importance of pollinator biodiversity conservation.

This book discusses the interplay between pollinators, agriculture, and the environment. Although honey bees are well recognized as pollinators, managed bumble bees and solitary bees are also critical for the successful pollination of certain crops, while wild bees provide a free service. Bee pollination is important for production of native plants used for restoration of wild lands. Managing bees for pollination is complex and must consider bee natural history, physiology, pathology, and behavior. Furthermore, transporting bees from native ranges to new areas for pollination services can be controversial, and should be done only after assuring that a non-native bee introduction will not disrupt the ecosystem. Even though bees are small, unobtrusive creatures, they play large roles in the ecosystem. The connection between bees and humankind is symbolic of a broader interconnection between humans and the natural world.

The present book contains 23 chapters and is an attempt to provide information on all aspects of pollination biology. This book deals with many different subjects related to pollination that are seldom put side by side. It considers issues such as the assessment of pollinators and pollination services, adaptive management of crop plants and wildlife, capacity building and how pollination can be mainstreamed into policy decisions. The economic and agricultural aspects of pollinators are discussed, as well as their biological role in *Nature*. All these matters are explained at the level of detail that is needed to fully understand the importance of the work on animal pollination. This book presents other valuable data on the feasibility of pollination programmes. The book deals with historical perspective, basic concepts, applied pollination, role of honeybees and wild bees on crop pollination, value of bee pollination, planned honeybee pollination, non-bee pollinators, safety of pollinators, pollination in cages, pollination for hybrid seed production, biochemical basis of pollination, pollination energetic, climate change and pollinators, pollinators as bioindicators, decline in pollinators, the problem of diseases, consequences of introduced honeybees upon native bee communities, genetically modified plants and bees, conservation of pollinators, the role in improving food security and livelihoods, capacity building and awareness for pollinators.

The book has a wider approach not strictly focused on crop production compared to other books on the subject that are strictly oriented towards bees but has a generalist approach to pollination biology, where due space is given to non-bee pollinators such as birds, bats, flies and mammals. Interestingly, the book also highlights relationships between introduced and wild pollinators and consequences of such introductions on communities of wild pollinating insects. The chapters on biochemical basis of plant-pollination interaction, pollination energetics, climate change and pollinators and pollinators as bioindicators of ecosystem functioning provide a base for future insights into pollination biology.

References

Aizen M, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr Biol 19:915–918

Aizen M, Garibaldi L, Cunningham S, Klein A (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. Curr Biol 18:1572–1575

Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S et al (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Cons Biol 12:8–17

Arizaga S, Ezcurra E (2002) Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette. Am J Bot 89:632–641

Arizaga S, Ezcurra E, Peters E, de Arellano FR, Vega E (2002) Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. I. Floral biology and pollination mechanisms. Am J Bot 87:1004–1010

Baker HG (1975) Sugar concentrations in nectars from hummingbird flowers. Biotropica 7:37–41

Baker HG, Hurd PD Jr (1968) Intrafloral ecology. Annu Rev Entomol 13:385–414

Barnett EA, Charlton AJ, Fletcher MR (2007) Incidents of bee poisoning with pesticides in the United Kingdom, 1994–2003. Pest Manag Sci 63:1051–1057

Barth FG (1991) Insects and flowers: the biology of a partnership (trans: Biederman-Thorson MA). Princeton University Press, Princeton, 408 pp

Batra SWT (1982) The hornfaced bee for efficient pollination of small farm orchards. Research for small farms. In: Kerr WH and Knutson LV (eds) Research for small farm, USDA Miscellaneous Publication 1422, pp 116–120

Batra SWT (1994a) *Anthophora plumipes villosula Sm.* (Hymenoptera: Anthophoridae), a manageable Japanese bee that visits blueberries and apples during cool, rainy, spring weather. Proc Entomol Soc Wash 96:98–119

Batra SWT (1994b) Diversify with pollen bees. Am Bee J 134:591–593

Bawa KS (1990) Plant-pollinator interactions in tropical rain forests. Annu Rev Ecol Syst 21:399–422

Bohart GE (1972a) Management of wild bees for the pollination of crops. Annu Rev Entomol 17:287–312

Bohart GE (1972b) Management of habitats for wild bees. In: Proceedings tall timbers conference on ecological animal control by habitat management no. 3, Tallahassee, pp 253–266

Bosch J, Kemp WP (1999) Exceptional cherry production in an orchard pollinated with blue orchard bees. Bee World 80(4):163–173

Bosch J, Kemp WP (2000) Development and emergence of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). Environ Entomol 29:8–13

Bosch J, Kemp WP (2001) How to manage the blue orchard bee as an orchard pollinator. Sustainable agriculture network handbook series book 5. National Agricultural Library, Beltsville, 88pp

Bosch J, Kemp WP (2002) Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. Bull Entomol Res 92(1):3

Bosch J, Kemp WP, Peterson SS (2000) Management of *Osmia lignaria* (Hymenoptera: Megachilidae) populations for almond pollination: methods to advance bee emergence. Environ Entomol 29(5):874–883

Bromenshenk JJ, Smith GC, Smith GC, Watson VJ (1995) Assessing ecological risks in terrestrial systems with honey bees. In: Butterworth FM (ed) Biomonitors and biomarkers as indicators of environmental change. Plenum Press, New York, pp 9–30

Bromenshenk JJ, Henderson CB, Seccomb RA, Rice SD, Etter RT, Bender SFA, Rodacy PJ, Shaw JA, Seldomridge NL, Spangler LH, Wilson JJ (2003) Can honey bees assist in area reduction and landmine detection? J Mine Action 7(3):24–27

Buchmann SL (1987) The ecology of oil flowers and their bees. Annu Rev Ecol Syst 18:343–369

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington, DC

Camerarius RJ (1694) Epistola ad M.B. Valentini de sexu *Planta*rum [Letter on the Sexuality of plants]. In: Ostwald's Klassiker der exakten *Naturwissenschaften*, No. 105, 1899. Verlag von Wilhelm Engelmann, Leipzig

Cane JH (2002) Pollinating bees (Hymenoptera: Apiformes) of U.S. alfalfa compared for rates of pod and seed set. J Econ Entomol 95(1):22–27

Cane JH (2005) Pollination potential of the bee *Osmia aglaia* for cultivated red raspberries and blackberries (Rubus: Rosaceae). HortScience 40(6):1705–1708

Charlesworth D, Charlesworth B (1987) Inbreeding depression and its *Evolution*ary consequences. Annu Rev Ecol Syst 18:237–268

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Crane E (1983) The archaeology of beekeeping. Duckworth, London, 260 pp

Crane E (1990) Bees and beekeeping. Comstock, Ithaca

Crane E (1999) The world history of beekeeping and honey hunting. Routledge, London

Dafni A, Kevan PG, Husband B (eds) (2005) Practical pollination biology. Enviroquest Ltd., Cambridge

Daily GC, Matson PA, Vitousek PM (1997) Ecosystem services supplied by soil. In: Daily G (ed) *Nature*'s services: societal dependence on natural ecosystems. Island Press, Washington, DC, pp 113–132

Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. Proc Natl Acad Sci USA 101(7):1904–1909

de Ruijter A (1997) Commercial bumblebee rearing and its implications. In: Richards KW (ed) Proceedings of the 7th international symposium on pollination. ISHS Acta Horticulturae 437, Belgium, pp 261–269

Dedej S, Delaplane KS, Scherm H (2004) Effectiveness of honey bees in delivering the biocontrol agent *Bacillus sutilis* to blueberry flowers to suppress mummy berry disease. Biol Control 31:422–427

Delaplane KS, Mayer DF (2000) Crop pollination by bees. CAB International, Oxon

Delpino F (1868–1875) Ulteriori osservazione sulla dicogamia nel regno vegetale. Atti della Societa Italiana di Scienze Naturali Milano 1 and 2:265–332

Desneux N, Decourtye A, Delpuech JM (2007) The sublethal effects of pesticides on beneficial arthropods. Annu Rev Entomol 52:81–106

Dias BSF, Raw A, Imperatri-Fonseca VL (1999) International pollinators initiative: the Sao Paulo declaration on pollinators. Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees, Brazilian Ministry of the Environment, Brazil, 79 pp

Dobbs A (1750) Concerning bees and their method of gathering wax and honey. Phil Trans R Soc 46:536–549

Dobson A, David Lodge D, Alder J, Cumming GS, Keymer J, McGlade J, Mooney H, Rusak JA, Sala O, Wolters V, Wall D, Winfree R, Xenopoulos MA (2006) Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology 87(8):1915–1924

Eardley C, Roth D, Clarke J, Buchman S, Gemmill B (eds) (2006) Pollinators and pollination: a resource book for policy and practice. African Pollinator Initiative, Pretoria, 77 pp

Estes J, Bonnie B, Amos J, Sullivan R (1983) Pollination from two perspectives: the agricultural and biological sciences. In: Jones CE, Little RJ (eds) The handbook of experimental pollination biology. van Nostrand Reinhold, New York, pp 173–183

Faegri K, van der Pijl L (1979) The principles of pollination ecology, 3rd edn. Pergamon Press, Oxford

Fleming TH, Sahley CT, Holland JN, Nason JD, Hamrick JL (2001a) Sonoran Desert columnar cacti and the *Evolution* of generalized pollination systems. Ecol Monogr 71:511–530

Fleming TH, Tibbitts T, Petryszyn Y, Dalton V (2001b) Current status of pollinating bats in the southwestern United States. In: O'Shea T, Bogan M (eds) Monitoring bat populations in the United States. U.S. Geological Survey, Fort Collins

Frank G (ed) (2003) Alfalfa seed and leafcutter bee production and marketing manual. brooks. Irrigated Alfalfa Seed Producers Association, Alberta, 160 pp

Free JB (1970) Insect pollination of crops. Academic Press, New York

Free JB (1993) Insect pollination of crops, 2nd edn. Academic Press, San Diego

Galen C, Zimmer KA, Newport ME (1987) Pollination in floral scent morphs of *Polemonium viscosuma* mechanism for disruptive selection on flower size. Evolution 41:599–606

Grant V, Grant KA (1979) The pollination spectrum in the southwestern American cactus flora. Plant Syst Evol 133:29–37

Griffin BL (1993) The orchard mason bee. Knox Cellars Publishing, Bellingham, Washington, DC

Herrera CM (1989) Seed dispersal by animals: a role in angiosperm diversification? Am Nat 133:309–322

Hughes MJ (1996) Commercial rearing of bumble bees. In: Matheson A (ed) Bumble bees for pleasure and profit. International Beekeeper Research Association, Cardiff, pp 40–47

Javorek SK, Mackenzie KE, Vander-Kloet SP (2002) Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). Ann Entomol Soc Am 95(3):345–351

Kandori I (2002) Diverse visitors with various pollinator importance and temporal change in the important pollinators of *Geranium thunbergii* (Geraniaceae). Ecol Res 17(3):283–294

Karise R (2007) Foraging behaviour and physiology of bees: impact of insecticides. Ph.D. thesis, Estonian University of Life Sciences, Tartu, Estonia, pp 1–123

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. Annu Rev Ecol Syst 29:83–112

Kevan PG (1984) Pollination by animals and angiosperm biosystematics. In: Grant WF (ed) Plant biosystematics. Academic, Toronto, pp 271–292

Kevan PG, Phillips TP (2001) The economic impacts of pollinator declines: an approach to assessing the consequences. Conserv Ecol 5(1):8

Kevan PG, Clark EA, Thomas VG (1990) Insect pollinators and sustainable agriculture. Am J Alternative Agr 5:13–22

Kevan PG, Straver WA, Offer M, Laverty TM (1991) Pollination of greenhouse tomatoes by bumblebees in Ontario. P Entomol Soc Ont 122:15–19

Kevan PG, Shipp VL, Kapongo JP, Al-mazra'awi MS (2005) Bee pollinators vector biological control agents against insect pests of horticultural crops. In: Guerra-Sanz M, Roldán Serrano A, Mena Granero A (eds) First short course on pollination of horticulture plants. CIFA, La Mojonera, Spain, pp 77–95

Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Royal Soc B 274:303–313

Knuth P (1906) Handbook of flower pollination. Oxford University Press, Oxford

Knuth P (1908) Handbook of flower pollination, vol 2 (trans: Ainsworth Davis JR). Clarendon Press, Oxford, 705pp

Knuth P (1912) Handbook of flower pollination, vol 2 (trans: Ainsworth Davis JR). Clarendon Press, Oxford

Kölreuter JG (1761) Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Leipzig

Kovach J, Petzoldt R, Harman GE (2000) Use of honeybees and bumble bees to disseminate *Trichoderma harzianum* 1295–22 to strawberries for *Botrytis* control. Biol Control 18:235–242

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G et al (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecol Lett 7:1109–1119

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G et al (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol Lett 10:299–314

Labandeira CC, Dilcher DL, Davis DR, Wagner DL (1994) Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. Proc Natl Acad Sci USA 91:12278–12282

Langstroth LL (1862) The hive and the honey bee. C.M. Saxton, New York

Levin MD (1983) Value of bee pollination to U.S. agriculture. Bull Entomol Soc Am 29:59–51

Lewinsohn TM, Prado PI, Jordano P, Bascompte J, Olesen JM (2006) Structure in plant-animal interaction assemblages. Oikos 113:174–184

Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. Bioscience 56:311–323

Macfarlane RP, Patten KD, Royce LA, Wyatt BKW, Mayer DF (1994) Management potential of sixteen North American bumble bee species. Melanderia 50:1–12

MacKenzie KE, Javorek S, Richards KW (1997) The potential of alfalfa leafcutter bees (*Megachile rotundata* L.) as pollinators of cranberry (*Vaccinium macrocarpon* Aiton). Acta Hortic 437:345–351

Maeta Y, Kitamura T (1981) Pollinating efficiency of *Osmia cornifrons* in relation to the number of bees required for economic fruit production. Honeybee Sci 2(2):65–72

Maeta Y, Goukon K, Tezuka T (1993) Utilization of *Osmia cornifrons* as a pollinator of Japanese pears (Hymenoptera, Megachilidae). Chugoku Kontyu 7:1–12

Matton DP, Nass N, Clarke AE, Newbigin E (1994) Self-incompatibility: how plants avoid illegitimate offspring. Proc Natl Acad Sci USA 91:1992–1997

Mayr E (1986) Joseph Gottlieb Köreuter’s contributions to biology. Osiris 2(2):135–176

McGregor SE (1976) Insect pollination of cultivated crop plants. USDA handbook 496. Department of Agriculture, Agricultural Research Service, Washington, DC, 411pp

Molnar S (2004) Plant reproductive systems. http://www.geocities.com/we_evolve/Plants/breeding_sys.html. Accessed 10 Mar 2006

Morse RA, Calderone NW (2000) The value of honey bees as pollinators of U.S. crops in 2000. Bee Cult 128(3):1–15

Müller H (1869) DeCandolle. Prodromus systematis naturalis regni vegetabilis 16:16

Müller H, Delpino F (1869) Application of the Darwinian theory to flowers and the insects which visit them. Am Nat 5:271–297 (trans Packard RL, 1871)

Nabhan GP, Buchmann SL (1997) Pollination services: biodiversity’s direct link to world food stability. In: Daily GC (ed) Nature’s services: societal dependence on natural ecosystems. Island Press, Washington, DC, pp 133–150

Pellmyr O (2003) Yuccas, yucca moths, and coevolution: a review. Ann Mo Bot Gard 90:35–55

Plowright C (1996) Bumble bee rearing. Melissa 9:10–12

Prescott-Allen C, Prescott-Allen R (1986) The first resource: wild species in the North American economy. Yale University Press, New Haven

Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Timber Press, Portland

Rathcke BJ, Jules ES (1993) Habitat fragmentation and plant-pollinator *interactions: from specialization to generalization*. In Waser N, Ollerton J (eds) The University of Chicago Press, Chicago and London, pp 173–199

Renner SS (1988) Effects of habitat fragmentation on plant-pollinator interactions in the tropics. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. Blackwell Science, Oxford, pp 339–360

Richards AJ (1997) Plant breeding systems, 2nd edn. Garland Science, London

Richards KW (2003) Potential use of the alfalfa leafcutter bee *Megachile rotundata* to pollinate sweet clover. J Apicult Res 42(1/2):21–24

Robinson WS, Nowogrodzki R, Morse RA (1989a) The value of honey bees as pollinators of U.S. crops. Part I of a two-part series. Am Bee J 129:411–423

Robinson WS, Nowogrodzki R, Morse RA (1989b) The value of honey bees as pollinators of U.S. crops. Part II of a two-part series. Am Bee J 129:477–487

Rocha M, Valera A, Eguiarte LE (2005) Reproductive ecology of five sympatric *Agave littaea* (Agavaceae) species in Central Mexico. Am J Bot 92:330–1341

Roubik DW (ed) (1995) Pollination of cultivated plants in the tropics. Food and Agriculture Organization Agricultural Services Bulletin 118, Rome, 196 pp

Roulston TH, Cane JH (2000) Pollen nutritional content and digestibility for animals. Plant Syst Evol 222(1–4):187–209

Roulston TH, Cane JH, Buchmann SL (2000) What governs the protein content of pollen grains: pollinator preferences, pollen-pistil interactions, or phylogeny? Ecol Monogr 70:617–643

Rucker RR, Thurman WN, Burgett M (2005) Internalizing reciprocal benefits: the economics of honeybee pollination markets. North Carolina State University, Department of Agricultural and Resource Economics, Raleigh, NC, Unpublished manuscript http://legacy.ncsu.Âedu:8020/classes/ecg701001/personal/Internalization_of_Reciprocal_Benefits-full_March_2005.pdf. Accessed 6 Mar 2005

Schery RW (1972) Plants for man, 2nd edn. Prentice-Hall, Englewood Cliffs NJ

Scott-Dupree C, Winston M, Hergert G, Jay SC, Nelson D, Gates J, Termeer, B and Otis G (1995) A guide to managing bees for crop pollination. Canadian Association of Professionals Apiculturists. Canadian Department of Agriculture, Aylesford, 41pp

Sheffield CS (2006) Diversity and management of bees for the pollination of apples in the annapolis valley of Nova Scotia. Ph.D. thesis University of Guelph, Guelph, Ontario

Shepherd MD, Buchmann SL, Vaughan M, Black SH (2003) Pollinator conservation handbook: a guide to understanding, protecting, and providing habitat for native pollinator insects. The Xerces Society in association with the bee works. The Xerces Society, Portland, 45 pp

Sheppard WS (1989) A history of the introduction of honey bee races into the United States. Am Bee J 129:617–619

Sinnott EW (1946) Botany principles and problems, 4th edn. McGraw-Hill, New York, p 726

Slauson LA (2000) Pollination biology of two chiropterophilous agaves in Arizona. Am J Bot 87:825–836

Slauson LA (2001) Insights on the pollination biology of *Agave* (Agavaceae). Haseltonia 8:10–23

Southwick EE, Southwick L Jr (1992) Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. J Econ Entomol 85:621–633

Sprengel CK (1793) Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen [The secret of *Nature* in the form and fertilization of flowers discovered]. Friedrich Vieweg der Ältere, Berlin

Stebbins GL (1950) Variation and *evolution* in plants. Columbia University Press, New York

Stebbins GL (1974) Flowering Plants. *evolution* above the species level. Harvard University Press, Cambridge, MA

Steffan-Dewenter I, Westphal C (2008) The interplay of pollinator diversity, pollination services and landscape change. J Appl Ecol 45:737–741

Stephen WP (2003) Solitary bees in North American agriculture: a perspective. In: Strickler KV, Cane JH (eds) For non-native crops, whence pollinators of the future? Thomas Say Publications in Entomology, Entomological Society of America, Lanham, pp 41–66

Tepedino VJ (1997) A comparison of the alfalfa leafcutting bee (*Megachile rotundata*) and the honey bee (*Apis mellifera*) as pollinators for hybrid carrot seed in field cages. In: Richards KW (ed) Proceedings of the 7th International symposium on pollination, Lethbridge, Alberta. International Society for Horticultural Science, Leiden, the Netherlands, pp 457–461

Torchio PF (1990) Diversification of pollination strategies for U.S. crops. Environ Entomol 19(6):1649–1656

Torchio PF (2003) The development of *Osmia lignaria* Say (Hymenoptera: Megachilidae) as a managed pollinator of apple and almond crops: a case history. In: Strickler K, Cane JH (eds) For nonnative crops, whence pollinators of the future? Proceedings, entomological society of America. Thomas Say Publications in Entomology, Lanham, pp 67–84

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol Lett 8:857–874

Valiente-Banuet A, Arizmendi MC, Rojas-Martínez A, Domínguez-Canseco L (1996) Ecological relationships between columnar cacti and nectar feeding bats in Mexico. J Trop Ecol 12:103–119

van der Pijl L (1982) Principles of dispersal in higher plants. Springer, Berlin, p 214

van Heemert C, de Ruijter A, van den Eijnde J, van der Steen J (1990) Year round production of bumble bee colonies for crop pollination. Bee World 71(2):54–56

vanEngelsdorp D, Underwood R, Caron D, Hayes J Jr (2007) An estimate of managed colony losses in the winter of 2006–2007: a report commissioned by the apiary inspectors of America. Am Bee J 147:599–603

Vaughan M, Shepard M, Kremen C, Black SH (2004) Farming for bees: guidelines for providing native bee habitat on farms. The Xerces Society for Invertebrate Conservation, Portland

Watanabe ME (1994) Pollination worries rise as honey bees decline. Science 265:1170

Watson L, Dallwitz MJ (1992) The families of flowering plants: descriptions, illustrations, identification, and information retrieval. http://delta-intkey.com/. Version: 2 June 2006

Chapter 2
Historical Perspective

Abstract This chapter traces the history of pollination. The basic principle of sex differentiation in plants may have been known as early as 1500 B.C. Hebrews learned the value and art of date pollination from Egyptian and Babylonian experts. An Assyrian architectural relief of that period shows two divine creatures, each presumably holding a male date inflorescence over a female inflorescence. The Arabic writer, Kazwini, who died about 682 A.D., as saying that the date is the only tree that is artificially fertilized. Growers of dates today use this method to assure a set of dates in their groves. In 1694, Rudolph Jacob Camerarius stated that there are two different parts of the flower, the stamens and the pistil, and that they must work together to produce ripe seed. Arthur Dobbs (1750) was the first to observe how bees pollinated flowers.

2.1 Development of the Knowledge of Plant Pollination

The mechanisms of pollination and fertilization were guessed from the practical utilization of agriculture and seed production more than 5000 years ago, when Assyrian priests had rituals of dusting pollen from the male date palms on the inflorescences of female trees (Fig. 2.1 a, b). The Greek philosopher, Theophrastus (300 B.C.) has also inferred on the union of the two sexes for the production of seed in plants. However, the idea was not generalized until 1682, when the botanist Nehemias Grew stated that pollen must reach the stigma to insure the development of seeds. In 1694 Rudolph Jacob Camerarius published «De sexu *Planta*rum epistole», in which he stated that based upon his experiments there are two different parts of the flower, the stamens and the pistil and that they must work together to produce ripe seed. After Brown's (1833) detailed descriptions, it would be Amici (1824, 1830), to firstly observe pollen tubes and its passage down the style and into the ovule (Amici 1824, 1830, 1847) (Fig. 2.1a, b). The contact between the tip of the pollen tube and the egg cell remained unanswered until Strasburger proved that the pollen tube does not stay intact, but its apical tip disintegrates upon contact with the embryo sac and

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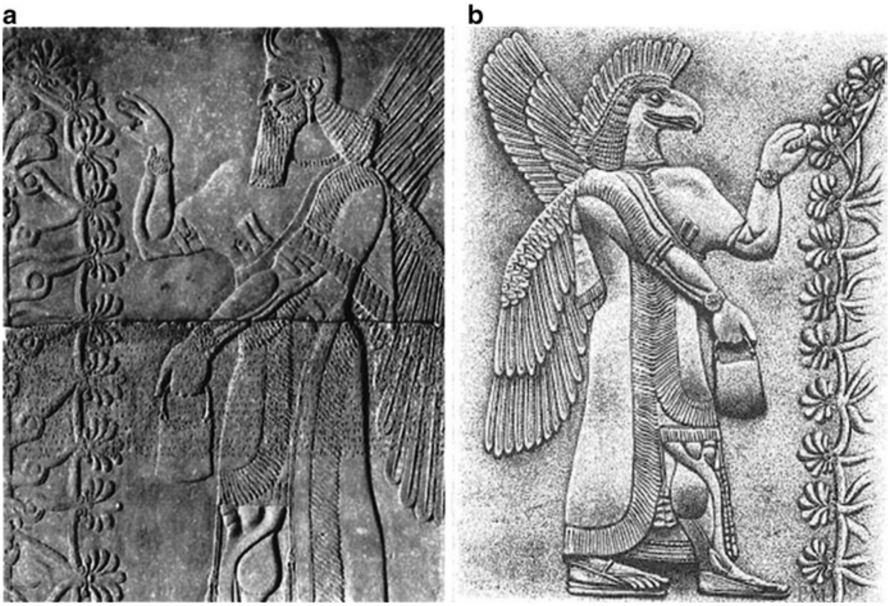

Fig. 2.1 Historical perspective of the discovery of sexual reproduction in plants. (a,b) Ancient representations of the first historical evidence that pollen had to be brushed on the stigma surface as a means to assure seed production. As long as 5000 B.C. Both Assyrian priests (b) and Egyptian gods were pictured on ceremonial fertilization of date palms

that one of its "nuclei fuses with the nucleus of the egg" (Maheshwari 1950; Cresti and Linskens 1999). It was left for Darwin (1862) to prove conclusively the importance of pollination in perpetuation and vigor maintenance of plants. Double fertilization was afterwards simultaneously described by Sergius Nawashin and Leon Guignard in the dawn of the nineteenth century and nowadays is believed to be a ubiquitous phenomenon (Friedman 2001).

The German physician and botanist Rudolf Jakob Camerarius (1665–1721) is credited with the first empirical demonstration that plants reproduce sexually. Camerarius discovered the roles of the different parts of a flower in seed production. While studying certain bisexual (with both male and female reproductive organs) species of flowers, he noted that a stamen (male pollen-producing organ) and a pistil (female ovule-producing organ) were both needed for seed production. The details of fertilization were discovered by scientists several decades after Camerarius's death. Among the many other scientists who followed Camerarius's footsteps in the study of pollination, one of the most eminent was Charles Darwin. In 1862, Darwin published an important book on pollination: *The Various Contrivances by which Orchids Are Fertilized by Insects*. In part, Darwin wrote this book on orchids in support of his theory of *Evolution* proposed in *The Origin of Species*, published in 1859. Darwin demonstrated that many orchid flowers had evolved elaborate structures by natural selection in order to facilitate cross-pollination. He suggested that orchids and their insect pollinators evolved by interacting with one another over many generations, a process referred to as co-evolution (Ames 1946).

Though the idea of occurrence of sex in plants was given by Theophrastus the fourth century B.C. but it was only during the end of the nineteenth century, when plant reproduction and mechanism of pollination were discovered by Muller (1882–1883). He wrote a book fertilization of flowers in German which was translated into English in 1883. Later, Knuth published three volumes on flower pollination in German which were translated into English later in 1906–1908. Aristotle put forward the idea of relationship between bees and flowers, but it was Koelreuter and Dobbs in 1870 who first described the detailed structure and the role of insects in pollination. Sprengel (1793) put forward a theory stating that "every peculiarity of plant anatomy and physiology is related to the peculiarity of structure and behavior of the insects which visit and pollinate flowers" the research work of Darwin 1883 using both hand and insect pollination techniques, helped greatly in understanding the theories of plant perpetuation and vigour maintenance through cross pollination and are being followed even today.

The practical use of honeybees for pollination of cultivated crops and increasing their yield started with the practice of moving honeybee colonies to the crops in bloom. Mr. M.B. Waite was deputed by USDA in 1880 to analyses crop failure in an orchard of 22,000 Bartlett pear trees in Virginia, USA. He found that it was due to the problem of self sterility in the pear plants, and further reported the necessity of cross pollination for a good fruit set. Since pear pollen was too heavy and sticky to be transferred by wind, Waite recommended the use of honeybees for pear pollination by moving them into pear orchards. Similarly, honeybees were utilized for apple pollination in the late nineteenth century. In Australia and the banks of Margabi river in Central Asia, apple fruit trees became sterile as honeybees did not exist there prior to the turn of present century. After the introduction of bees to these regions, apple orchards started bearing fruit. Benton (1896) also suggested 5–6 colonies of *Apis mellifera* per 100 trees for the pollination of self sterile commercial varieties of apple in USA.

The transfer of the male sex cells to the female portion of the flower and the fusion of the cells in the ovule is a critical period in the life of a plant. In the manipulation of pollinating agents, man contributes to the efficiency of this fusion and to the insurance that the plant will be productive of fruit or seeds to his benefit.

The basic principle of sex differentiation in plants may have been known as early as 1500 B.C. Goor (1967) stated that the Hebrews learned the value and art of date pollination from Egyptian and Babylonian experts. An Assyrian architectural relief of that period shows two divine creatures, each presumably holding a male date inflorescence over a female inflorescence (Faegri and van der Pijl 1966). Kerner (1878) stated, "When we consider that from time immemorial, Chinese and Japanese gardeners have produced asters, camellias, chrysanthemums, peonies, pinks, and roses, of which the majority are the results of crossing, we may assume with certainty that the practice of dusting flowers of one species with pollen of another species first came into use in those countries." Werkenthin (1922) quotes the Arabic writer, Kazwini, who died about 682 A.D., as saying that the date is the only tree that is artificially fertilized. Growers of dates today use this method to assure a set of dates in their groves. However, if this indicated recognition of sex in plants, the idea was not carried over to other plants. It was not until 1682 that a botanist, Nehemias Grew, stated that pollen must reach the stigma to insure the development of seeds. Apparently, however, he assumed that the stamens of a flower shed their pollen directly onto the stigma of the same flower (Dowden 1964).

In the 1500s, German botanist Valerius Cordus (1515–1544) used the word pollen, Latin for powder or fine flour, to describe flower dust. In 1592, a Venetian named Prospero Alpini (1553–1616 or 1617) studied Egyptian flora while serving as physician to his government's consul in Cairo and published observations on the fertilization of date palms. He also disproved classical plant correlations. In the 1600s, an Englishman, John Ray (1627–1705), attempted a grand systematic description of all known plants and animals. Out of this came, in 1660, a three-volume work that listed and classified the plants in the area surrounding Cambridge. That effort was significant in that it sought to organize plants along lines of similarity and discussed, for the first time, sexuality among plants. Another Englishman, Nehemiah Grew (1641–1712), wrote in 1682 of the possibility of plant sexuality, suspecting that the parts of the flower played separate roles in plant reproduction. Rudolph Camerarius (1665–1721), a German botanist, conducted extensive research at the Botanic Garden in his home town of Tubingen. In 1694, he noted that the flower anthers, the pollen-bearing parts of the stamen, were the plant's male organs, while the style and stigma were the female organs. He not only confirmed what Ray, Grew, and others had suspected earlier, but also described the pollination process.

English botanist Stephen Hales (1677–1761) applied his interest in both plants and animals to describe the similarities in their circulation systems: that sap is to a tree what blood is to a horse or dog. His experiments led him to recognize plants' ability to absorb water and air and the importance of light in their growth. He summarized his conclusions in his book *Vegetable Staticks* (1727). The German botanist Joseph Gottlieb Koelreuter (1733–1806) published accounts of his research on plant pollen during a 5 year period beginning in 1761. His successful cross-pollination of tobacco plants was his effort to prove the conclusions that Camerarius had reached earlier. Koelreuter also noted the uniformity and sterility of most hybrid plants, and observed the roles of nectar, wind, and insects in the transmittal of plant pollen. He is considered the father of plant hybridization. Another German botanist, Christian Konrad Sprengel (1750–1816), began research in 1787 on the pollination of geraniums, publishing his findings in 1793. He went further than Koelreuter by describing in greater detail flower structures and the role of insects. He discovered that the ability of some flowers to self-pollinate was attributable to the different maturation times of the anther and stigma.

German botanist Wilhelm Hofmeister (1824–1877) studied simple plants such as ferns and mosses in the late 1800 s, discovering that these plants alternated generations, sexually reproducing in one generation while reproducing asexually in the next. He looked at *Plant Cell* division in microscopic detail and observed that plant ovules developed into embryos. He seems to have come close to discovering chromosomes in plant cells and is considered the father of modern botany. Gregor Mendel's discoveries of chromosomes and the laws of heredity in the late 1800s and the practical application of plant cross breeding by Luther Burbank in the early 1900s led to a new era in agriculture. For the first time in the long history of farming, agronomists could directly manipulate the reproduction of their crops. Plant breeding became an important part of mass crop production during the twentieth century. Further discoveries of gene structure – in particular the discovery of DNA (deoxyribonucleic acid) – has opened a new branch of agricultural research called genetic engineering.

Scientists hope that crop quality, quantity, and consistency can be achieved in the laboratory by altering gene structures and through the use of cloning techniques. Although much progress has been made in these areas of research, many individuals and groups voice concerns about the environmental impact and the effect on food safety of these processes. As man becomes more deeply involved with reproductive processes, utmost care must be taken to prevent environmental catastrophes that could affect both man and nature.

In 1750, Arthur Dobbs, communicated to the Royal Society of London that the pollen was the male element which, after falling upon the stigma, was capable of fertilizing the ovary. He further concluded that the pollen must come from its own species (Grant 1949a). Watson (1751) reported that he transported date pollen 20 miles and pollinated a previously fruitless tree. In 1761, Koelreuter who is usually regarded as the discoverer of sexuality in plants concluded that bees are agents in the transfer of pollen from the male to the female elements of the flower (Grant 1949b). He was the first to cross-pollinate and produce a hybrid between two plant species (Sinnott 1946). In 1763, Arena also wrote rather fully on the subject of cross-pollination in plants and noted that it was carried out by insects (Lutz 1918).

Sprengel (1793), however, was the first to really explore sex in plants, the important part played by pollinating insects, and the significance of cross-pollination in plant life. His work stimulated future work on sex in plants and the part played by insects. Thomas Andrew Knight (1799) showed the value of cross-pollination between plants and hybrid vigor: ". . . *Nature* intended that a sexual intercourse should take place between neighboring plants of the same species." He noted that the location of the pollen within the blossom was ". . . generally well adapted to place it on the bodies of insects; and the villous coat of the numerous family of bees, is not less well calculated to carry it." The value of cross-pollination was later supported by Herbert (1837).

Not until 1830, however, was the observation made by Amici on the formation of the pollen tube and its passage down the style and into the ovule. This was soon followed by recognition of the fact that there is sexual fusion between gametes in the ovule (Sinnott 1946). It was left for Darwin (1889) to prove conclusively and to dramatize the importance of pollination in perpetuation and vigor maintenance of the plant species. He studied scores of species, using both hand and insects to pollinate the plants on which he measured the value and significance of cross-pollination. Much of the work on plant pollination since his time is based upon the theories he promulgated. Little has been added to the knowledge of pollination requirements of some plant species since his work was published.

Interestingly, in parallel with the taxonomic work of species description, there was a progressive discovery of insect pollination. In their 1996 book, Proctor, Yeo and Lack describe the work of Camerarius, Bradley, Müller, Logan and others during the first half of the eighteenth century, when botanists discovered that the "*Farina Fecundens*" produced by the stamens and the stigma were necessary to set seeds, and the first cross hand-pollinations were performed. During the second half of the eighteenth century biologists such as Dobbs and Kölreuter discovered that insects, and particularly bees, visited flowers in search of nectar and incidentally were carrying the "*Farina*", and thus were pollinating agents for numerous flowering plant species (Proctor et al. 1996). During this period, Lamarck (1778) discovered the heat produced by spadixs of *Arum italicum*. Sprengel (1793) produced the first systematic study of insect pollination on about 500 plant species and described several pollination mechanisms, in particular flowers which temporarily trap insects (e.g. *Aristolochia*). 60 years later (1857–1876), Darwin studied the plant variation and insect pollination systems (particularly self-pollination avoidance) within the frame of his theory of natural selection. At this time, Hildebrand (1867) wrote the first book on floral biology, followed by Delpino (1868) who proposed a flower classification (two volumes) based on different floral types in relation to pollination. Delpino studied numerous pollination mechanisms, including those of *Arum italicum* and in 1870 of *A. maculatum*. In the same way, Müller (1883) wrote three books on plant–pollinatorinsect relationships, describing many pollination mechanisms, including *Arum maculatum*. In 1883, Arcangeli described the pollinating fauna of *Arum italicum* and in 1886 he studied *Arum pictum*. Knuth (1895–1905) wrote a handbook (3 volumes) on flower pollination in which *Arum italicum*, *A. maculatum*, *A. pictum* and *A. dioscoridis* are cited. The understanding of the insect trap mechanism was elucidated 40 years later thanks to experimental studies of the pollination of *Arum maculatum* and *A. nigrum* (Schmucker 1925; Knoll 1926). These studies showed the role of the appendix, the hairs and the floral chamber in attracting and capturing the insects, and also in seed production. During the last 60 years, only the pollination of *Arum maculatum* has been studied, and this only in England. Nevertheless the genus *Arum* is the most documented among Araceae.

The first contribution of great importance on pollination from the United States was the discovery by Waite (1895) of self-sterility in pears and the need for insect-transfer of pollen between varieties. This initiated a new wave of interest particularly in fruit pollination, although many contributions on the value of pollination had already appeared (Crane 1876; Hutchinson 1886; Muller 1883), and the various apicultural journals were beginning to extoll the virtues of the honey bee as the best pollinating agent. Benton (1896) recommended ". . . 4 or 5 well-populated hives of honey bees for every hundred large apple trees, the hives to be placed in or near the orchard." The renting of colonies for orchard pollination service had its beginnings the first decade of this century (Beuhne 1909; Stricker 1971).

The acute need that developed for legume seed during World War II stimulated the establishment of the USDA Legume Seed Research Laboratory at Logan, Utah. The combined efforts at this laboratory established the value of honey bees in the pollination of alfalfa for seed production (Utah Agr. Expt. Sta. 1950). As a result,

Table 2.1 Chronological sequence of workers who have contributed to pollination studies with dates of their publications

Year	Reference
1761	Koelreuter
1793	Sprengel
1799	Knight
Nineteenth century	
1863	Cheeseman, Darwin,
1871	Delpino, Hildebrand,
1871	Kerner, Knuth,
1875–1893	Loew, Müller,
1883–1885	Thomson, etc.
Twentieth century	
1901–1939	
1927–1948	Daumann, Frisch
1927–1929	Hagerup, Knoll,
1929–1954	Pijl, Porsch, etc.
1940–1979	
1960	Baker, Cruden,
1961–1978	Dodson, Free,
1961	Grant, Leppik,
1962–1979	Levin, Macior,
1964	Meeuse, Vogel, etc.

several hundred thousand colonies of honey bees are currently being used to pollinate this crop alone. The chronological sequence of important workers and their contributions is summarized in Tables 2.1 and 2.2.

The latest stage of development in the management of pollinating insects in production of crops is the large-scale use of wild bees, primarily the gregarious ground-nesting alkali bee (*Nomia melanderi* Cockerell) and the equally gregarious tube-nesting leafcutter bee (*Megachile pacifica* Panzer) (Bohart 1912; Stephen 1959).

Some other sources of information on pollination should be mentioned. Clements and Long (1923) spoke in general terms about pollination of numerous plant species. Hooper (1921), Hutson (1926), Kenoyer (1916), and Wellington et al. (1929) discussed the pollination of several specific crops, and Farrar (1931) became concerned about the strength of colonies of honey bees used for pollination. Other smaller but key papers published in the United States include those by Bohart (1960), Bohart and Todd (1961), Eckert (1959), Hambleton (1944), Todd and McGregor (1960), and Vansell and Griggs (1952). Some broad spectrum publications in other countries include: (Australia) Gale (1897); (England) Butler and Simpson (1953), and Free (1960); (India) Krishnamurthi and Madhava Rao (1963); (Italy) Giordani (1952); (Jamaica) Chapman (1964), and Purseglove (1968); and (Russia) Krishchunas and Gubin (1956), Gubin and Khalifman (1958), and Kasiev (1964).

For up-to-date knowledge and completeness, none of these surpasses the recent excellent publication by Free (1970). He dealt thoroughly with the pollination needs and the management of pollinating insects to supply those needs for each family of plants he considered to be benefited by such pollination.

Table 2.2 Chronological sequence of important contributions by different workers

1500s	German botanist Valerius Cordus (1515–1544)	Used the word pollen, Latin for powder
1592	A Venetian named Prospero Alpini (1553–1616 or 1617)	Observations on the fertilization of date palms
1600s	An Englishman, John Ray (1627–1705)	Systematic description of all known plants and animals.
1660	An Englishman, John Ray (1627–1705)	First time, sexuality among plants
1682	Another Englishman, Nehemiah Grew (1641–1712)	Possibility of plant sexuality, suspecting that the parts of the flower played separate roles in plant reproduction
1694	Rudolph Camerarius (1665–1721), a German botanist	Flower anthers, the pollen-bearing parts of the stamen, were the plant's male organs, while the style and stigma were the female organs but also described the pollination process.
1727	English botanist Stephen Hales (1677–1761)	That sap is to a tree what blood is to a horse or dog. His experiments led him to recognize plants' ability to absorb water and air and the importance of light in their growth. He summarized his conclusions in his book *Vegetable Staticks* (1727).
1761	The German botanist Joseph Gottlieb Koelreuter (1733–1806)	Koelreuter also noted the uniformity and sterility of most hybrid plants, and observed the roles of nectar, wind, and insects in the transmittal of plant pollen. He is considered the father of plant hybridization.
1793	Another German botanist, Christian Konrad Sprengel (1750–1816)	Began research in 1787 on the pollination of geraniums, publishing his findings in 1793. He went further than Koelreuter by describing in greater detail flower structures and the role of insects. He discovered that the ability of some flowers to self-pollinate was attributable to the different maturation times of the anther and stigma.
Late 1800s,	German botanist Wilhelm Hofmeister (1824–1877)	He looked at *Plant Cell* division in microscopic detail and observed that plant ovules developed into embryos. He seems to have come close to discovering chromosomes in plant cells and is considered the father of modern botany
Mid 1800s	The Austrian monk and botanist Johann Gregor Mendel (1822–1884)	Conducted important pollination studies in Brno (now in the Czech Republic) . He studied heredity by performing controlled cross-pollinations of pea plants thereby laying the foundation for the study of heredity and genetics.
Late 1800s	Gregor Mendel's	Discoveries of chromosomes and the laws of heredity in the late 1800s and the practical application of plant cross breeding.

(continued)

Table 2.2 (continued)

1876	Darwin	He discovered that *Angraecum sesquipedale*, an orchid native to Madagascar was pollinated by a Madagascan moth with a one-foot-long tongue. The moth's tongue uncoils to sip the nectar of *A. sesquipedale* as it cross-pollinates the flowers. Darwin continued his studies of pollination in subsequent years. In 1876, he wrote another important book on pollination biology, *The Effects of Cross and Self Fertilization in the Vegetable Kingdom*.
Early 1900s	Luther Burbank in the early 1900s	Led to a new era in agriculture. Plant breeding became an important part of mass crop production during the twentieth century. Further, discoveries of gene structure – in particular the discovery of DNA (deoxyribonucleic acid) – has opened a new branch of agricultural research called genetic engineering.

The science of botany evolved from humankind's desire to know how plants live and reproduce. Their reproduction systems are functionally similar to those of animals. Most plants grown for agriculture have their sexual organs in their flowers. Whether the plants cross-pollinate or self-pollinate, it is essential that fertilization takes place for the production of seeds.

References

Ames O (1946) The evaluation of the orchid flower. Am Orchid Soc Bull 14:355–360

Amici GB (1824) Observations microscopiques sur diverse espèces de plantes. Ann Sci Nat Bot 2(41–70):211–248

Amici GB (1830) Note sur le mode d'action du pollen sur le stigmate. Extrait d'une lettre d'Amici à Mirbel. Ann Sci Nat Bot 21:239–332

Amici GB (1847) Sur la fécondation des Orchidées. Ann Sci Nat Bot 7(8):193–205

Benton F (1896) The honey bee, a manual of instruction in apiculture. US Dept Agr Div Ent Bul 1 N S Rev Ea, 118pp

Beuhne R (1909) Bees and fruit fertilization. Victoria Dept Agr J 7(11):693–696

Bohart GE (1912) Management of wild bees for the pollination of crops. Ann Rev Ent 17:287–312

Bohart GE (1960) Insect pollination of forage crops. Adv Agron 12:72–88

Brown R (1833) Discovery of cells and the development of cell theory. Trans Linn Soc 16:685

Bohart BE, Todd FE (1961) Pollination of seed crops by insectsYearbook of Agriculture, vol. 245. Department of Agriculture, United States

Butler CG, Simpson J (1953) Bees as pollinators of fruit and seed crops. Report Rothamsted Experimental Station England, UK, pp 167–175

Clements EE, Long EL (1923) Experimental pollination: an outline of the ecology of flowers and insects, 336th edn. Carnegie institute of Washington publication, Washington, DC, 274 pp

Crane, JE. (1876). The relation of bees to fruit culture. In 3rd Biennial report of the Vermont State Board of Agriculture, pp 253–270

Cresti M, Linskens HF (1999) The discovery of sexual reproduction in higher plants. Acta Biol Crac Ser Bot 41:19–29

Darwin C (1862) Fertilization of orchids by insects. Murray, London, p 15

Darwin C (1869) Notes on the fertilization of orchids. Annals and magazine of natural history september 1869:1–19.

Delpino F (1868–1875) Ulteriori osservazioni e considerazioni sulla dicogamia nel regno vegetale. Atti Soc Ital Sci Nat 11,12:179–233

Dowden AO (1964) The secret life of flowers. 45 pp. The odyssey press, New York

Eckert JR (1959) The Kangaroo Island Ligurian bees. Gleanings in Bee Culture 86:660–663, 722–725

Faegri K, van der Pijl L (1966) The principles of pollination biology. Pergamon Press, New York

Farrar CL (1931) The evaluation of bees for pollination. Jour Econ Ent 24:622–627

Free JB (1960) The pollination of fruit trees. Bee World 41(141–151):169–186

Free JB (1970) Insect pollination of crops. Academic, London, New York

Friedman WE (2001) Developmental and evolutionary hypotheses for the origin of double fertilization and endosperm. C R Acad Sci III 324:559–567

Gale A (1897) The influence of bees on crops. Agr Gaz NS Wales 8:264–276, 337–339, 423–425, 490–493, 581–584, 620–623, 734–736, 831–833, 908–910

Giordani G (1952) Bees and flower pollination . National Apicultural Institute of Bologna. [in Italian.] Aa-120/54, 59 pp

Goor A (1967) The history of the date through the ages in the holy land. Econ Bot 21:320–340

Grant V (1949a) Arthur dobbs (1750) and the discovery of the pollination of flowers by insects. Bull Torr Bot Club 76(3):217–219

Grant V (1949b) Pollination systems as isolating mechanisms in angiosperms. Evolution 3:82–97

Gubin AF, Khalifman IA (1958) Flowers and bees. Agrobiologiya, Moscow 1–139 USSR, Moscow: Moskovskii rabochii. [in Russian.] Aa-64/59, 194 pp

Hambleton JI (1944) The role of bees in the production of fruit and seed. Jour Econ Ent 37:522–525

Herbert W (1837) Amaryllidaceae with a treatise on crossbred vegetables. In: Muller H (ed) (1883) The fertilization of flowers Macmillan Co., Inc., London, p 371. [Translated and edited by d'arcy thompson.]

Hildebrand F (1867) Diegeschlechter-vertheilungbei den pflanzen. Wilhelm Engelmann, Leipzig, 92pp

Hooper T (ed) (1921) Guide to Bees and Honey: Amazon.Co.UK: Ted Hooper: Books

Hutchinson WZ (1886) The relation of bees to horticulture, benefits and injuries. Mich Hort Soc Proc 16:13–15

Hutson R (1926) The relation of honey bees to fruit pollination in New Jersey. NJ Agr Exp Sta Bull 434:1–32

John Ray (1627–1705) was an English naturalist. His classification of plants in his *Historia Plantarum*, was an important step towards modern taxonomy

Gottlieb Koelreuter J (1733–1806) A German who demonstrated the existence of sexes in plants and produced a plant hybrid by crossing two species of tobacco

Kasiev TI (1964) Problems of nectar production of cotton and the role of honey bees in increasing its yield. 215 pp. Baku, Azerbaidzhan Goz. lzd. [In Russian.]

Kenoyer LA (1916). *Pollination of economic plants.* In Iowa State Apiarist Report 1915:24–30

Kerner A (1878) Flowers and their unbidden guests.(trans: Ogle W), C. Kegan Paul & Co, London, 164 pp

Knight TA (1799) An account of some experiments on the fecundation of vegetables. Roy Soc London Phil Trans pt I 89:195–204

Knoll F (1926) Abh Zool-Bot Ges Wien 12:381–481

Knuth P (1895–1905) Handbuch der blutenbiologie iiii. Engelmann, Leipzig, 2973 pp

Krishnamurthi S, Madhava Rao VN (1963) Certain problems in pollination of fruit crops. So Indian hort 11(1, 2):1–17

Lamarck [J.P.A.M] (1778) *Flore françoise*, ou, Description succincte de toutes les plantes qui croissent naturellement en France :disposée selon une nouvelle méthode d'analyse, & à laquelle on a joint la citation de leurs vertus les moins équivoques en médecine, & de leur utilité dans les arts. Tome premier. pp. 1-4, i-cxix, [1]-132, i-xxix, pls I-XVIII. Paris: De l'Imprimerie Royale

Lutz FE (1918) Fieldbook of insects. G.P. Putnam's sons, New York and London, 509 pp

Maheshwari P (1950) An introduction to the embryology of angiosperms. McGraw-Hill, New York, 453 pp

Muller H (1883) The fertilisation of flowers (trans: D'Arcy W. Thompson). Macmillan, London, 669 pp.

Nehemiah Grew, who, with the Italian botanist Marcello Malpighi, may be considered as co-founder of the science of Plant Anatomy. Grew was drawn to the study of plant structure at the age of twenty-three, and seven years later he produced his earliest work on the subject, *The Anatomy of Vegetables Begun*, which was published by the Royal Society in 1672. In 1682 he published his *magnum opus, The Anatomy of Plants*, prefaced by an Epistle Dedicatory

Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Harper Collins Publishers, London, 479 pp

Rudolf Jakob Camerarius (1665–1721), German botanist and physician (latinization of "Camerer") (1665–1721) German physician and botanist. Professor at Tubingen (from 1688); demonstrated sexuality in plants (reported 1694)

Schmucker T (1925) Beiträge zur biologie und physiologie von Arum maculatum. Flora 118(119):460–475

Sinnott EW (1946) Botany – principles and problems, 4th edn. Mcgraw-hill book co., inc, New York and London, 726pp

Sprengel CK (1793) The secret of *Nature* in the form and fertilization of flowers discovered. 4 sects. [in German]

Stephen WP (1959) Maintaining alkali bee beds for alfalfa seed production. Oreg Agr Expt Sta Bul 568, 23pp

Stricker MH (1971) Pollination pioneer: Richard d. Barclay 1888–1938. Gleanings bee cult 99:358–360

Theophrastus (300 BC) Enquiry into plants and minor works on odors and weather signs. Book 2, p 8, paragraph 3–4, p 155 (trans: sir arthur hort). Harvard University Press, Boston, 475 pp

Todd FE, McGregor SE (1960) The use of honey bees in the production of crops. Ann Rev Ent 5:265–278

Utah Agricultural Experiment Station (1950) Growing alfalfa for seed in utah. Utah Agr Expt Sta Cir 125, 72 pp

Vansell G, Griggs WH (1952) Honey bees as agents of distribution. US.D.A. Yearbook.: 88–107

Waite MB (1895) The pollination of pear flowers. US Dept Agr Div Veg Path Bul 5, 86 pp

Watson W (1751) Some observations upon the sex of flowers. Roy Soc London Phil Trans 47: 169–183

Wellington Ra, Stout AB, Einset O, and others (1929) Pollination of fruit trees. N.Y. (Geneva) Agr Expt Sta Bul 577, 54 pp

Werkenthin FC (1922) The founders of the art of plant breeding. Iowa Acad Sci 29:291–310

Wilhelm Friedrich Benedikt Hofmeister (18 May 1824 – 12 January 1877) was a German biologist and botanist. He "stands as one of the true giants in the history of biology and belongs in the same pantheon as Darwin and Mendel." He discovered the regular alternation of sexual and asexual generation in plants (1862), which is the basis for the explanation of the life cycle in all known plants

Chapter 3
Pollination – Basic Concepts

Abstract Many varieties of commercial crops are self-sterile and require cross-pollination of their flowers in order to produce fruit or seeds. In such crops, productivity can be enhanced by managing cross-pollination through insects such as honeybees and other natural pollinating insects. Pollination is essential for sexual reproduction and the formation of abundant seeds and fruit. It is, therefore, important for enhancing crop productivity. Other methods will not yield the desired results without cross-pollination; many crops will not even produce seeds or fruit.

3.1 Introduction

Flowers are the reproductive parts of a plant, where seeds are formed. For the cycle to begin, a pollen grain, which is often carried on an insect or by the wind, comes in contact with the stigma (or female part) of the same flower species. Fertilization takes place when pollen from the anther (male organ) unites with a female ovule, which forms the seed and fruit. The transfer of pollen from male to female sex organs is called **pollination.** All plants must be pollinated before seed (or fruit) will set. Pollen is transferred from the anthers to the stigma by wind, water, gravity, mammals, birds, humans and insects. If the transfer takes place on the same blossom or on another blossom on the same plant, it is called self-pollination.

Cross pollinated flowers must have transfer of pollen from one flower to the next. Even self-pollinated plants may benefit from cross-pollination with hybrid vigor, or more rapid and complete growth. Male sterility has been found in many crops and plant breeders exploit this characteristic to develop hybrids which are then dependent on cross pollination. Most flowers secrete nectar, a sugary, scented liquid to help attract insects to the flower. This is usually offered deep within the flower near the base where petals originate from around the ovary. In seeking nectar or gathering pollen, the insect accidentally brushes against anthers so that pollen grains are transferred to the stigma. Pollination is not a deliberate behavior but an accidental one performed by the insect as they collect food.

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Pollination is an important step in the reproduction of seed plants: the transfer of pollen grains (male gametes) to the plant carpel, the structure that contains the ovule (female gamete) (Sprengel 1793). The receptive part of the carpel is called a *stigma* in the flowers of angiosperms and a *micropyle* in gymnosperms. The study of pollination brings together many disciplines, such as botany, horticulture, entomology, and ecology. Pollination is important in horticulture because most plant fruits will not develop if the ovules are not fertilized. **Pollination** means the transfer of pollen from the male part of the flower, the anthers, to the receptive female part, the stigma. The story may be summed up as getting the right pollen to the right place at the right time. In some plant species pollination is achieved by pollen grains carried in the wind. Most fruit species require some insect to carry pollen to the flowers. **Fertilisation** occurs when the pollen grains on the stigma germinate and grow down the stem of the stigma (the style). The sperms of the pollen unite with the ovules in the ovary of the flower and subsequently produce seed. Flowers may be fully pollinated but not necessarily fertilised because they have received incompatible pollen. The pollen does not germinate or grow on the stigma or reach and fertilise the ovules. In such a case, unless the species is parthenocarpic, no fruit will result. Not all plants require pollination and fertilisation, as some are able to produce fruit parthenocarpically; that is, the fruit will develop without fertilisation of the flower and production of seed.

3.2 Types of Pollination

Two types of pollination may occur: self- and cross pollination.

3.2.1 Self Pollination

It is the transfer of pollen from anther to the stigma of same flower or to the flowers of the same or other plants of the identical genetic material such as apple flowers.

3.2.2 Auto-Pollination

In some plants pollen is automatically deposited on the stigma when the flower opens and this type of self pollination may be called auto pollination.

3.2.3 Cross-Pollination

It is the transfer of pollen between plants which are not of identical genetic material i.e. pollen gametes are not genetically identical to the ovule gametes e.g. cross variety pollination of apples, cross inbred lines pollination for hybrid seed production. The most important and efficient carrier of pollen from anther to stigma is the honeybee. An understanding of the activities of honeybees is essential if the best return is to be obtained in fruit production.

3.2.4 Self Fruitful

Self fruitful are capable of setting fruit with its own pollen. The pollen in such cases is heavy, sticky and for commercial crop production, it must be moved from flower to flower by bees.

3.2.5 Self Unfruitful or Self in Compatible

Varieties which do not set commercial fruit/seed when self pollinated are called self unfruitful or self incompatible. Most apple varieties are in this category. There is a need to plant other varieties with compatible pollen so that cross variety pollination takes place.

3.2.6 Cross Fruitful Varieties

Varieties which set a commercial crop when properly interplanted for cross pollination. They have compatible pollen.

3.2.7 Cross Unfruitful or Incompatible Varieties

This condition usually refers to a physiological incompatibility. The pollen may not send down a pollen tube to deliver the male gamete to the ovule or the embryo may abort after union of gametes. Some varieties have sterile (non viable) pollen. As a rule physiological incompatibilities exist between varieties with a close genetic relationships. There are varying degrees of incompatibilities which may be altered by different environmental conditions.

3.2.8 Monoecious Plants

Monoecious plants are those plants which staminate (male) flowers and the pistillate (female) flowers are separate but on the same plant e.g. maize, cucumbers etc.

3.2.9 Dioecious Plants

Dioecious plants are those plants which staminate and the pistillate flowers are on different plants e.g. willow, poplars.

3.2.10 Gynoecious Plants

The term gynoecious F_1 hybrids has been applied to certain cultivars of picking cucumbers and they are often referred to as “gynoecious” varieties. The cultivars have predominantly pistillate flowers.

Many of the fruit crops, legumes, vegetables, and oilseed crops depend upon pollinating insects for set of fruit or seeds. Inspite of the best agronomic practices-proper seedbed preparation, fertilization, soil moisture, cultivation, pest control, and harvesting methods-bountiful harvests are not obtained if pollination is neglected.

3.3 Flower Structure

In order to understand the entire pollination process, the knowledge of the flower structure and fruit setting is necessary. The flower has a simple basic pattern, but with seemingly infinite variations. Typically, the flower (Fig. 3.1) is composed of

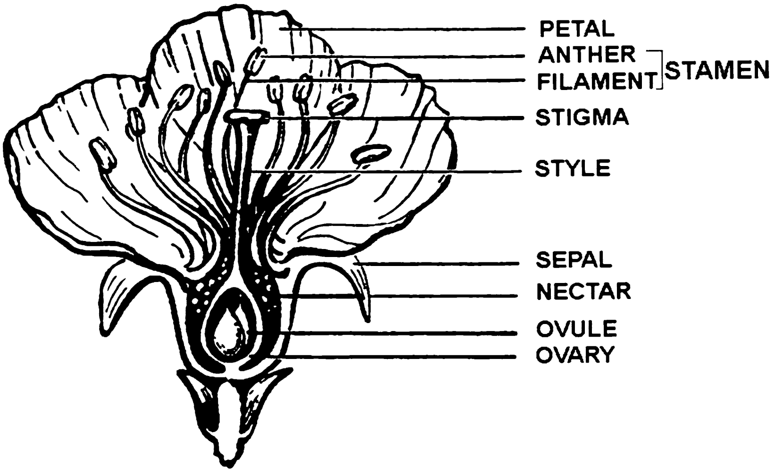

Fig. 3.1 Typical structure of a generalized flower

the *sexual organs*, protected by delicate colorful *petals* that form a tube or crown like *corolla*, and which in turn are supported and partially protected by the usually green, more durable *sepals*, collectively called the *calyx*. The calyx and corolla combined are referred to as the *perianth*. There may be leaf like *bracts* just below the sepals.

The *male* part (or *androecium*) of the sexual organs are the *stamens*, which consist of the hair like *filaments* bearing the pollen-producing anthers on the extremities. At the appropriate time, these anthers *dehisce* or split open and disgorge the male element, the numerous microscopic and usually yellow grains of *pollen*. Evidently, there are four series of floral parts, usually arranged in whorls, each with its own set of functions.

The **sepals** (collectively the **calyx**) is the lowermost whorl (painted green) functions to protect the *entire flower in the bud* as its other parts are developing. As the flower opens the calyx often folds out of the way.

The **petals** (collectively the **corolla**) constitute the second whorl of parts of a flower (painted red). Their primary function is to attract animal pollinators via a visual signal, such as color, pattern, and shape. Neither the calyx nor corollas are involved directly in production of gametes; however, their roles are critical to the success of the reproductive process in flowering plants.

The **stamens** constitute the third whorl of floral parts. Each generally consists of a stalk-like filament tipped by an anther. The anthers (painted yellow) are is the structures in which the pollen grains are produced.

The female part of the flower (the **pistil**) consist of three parts: The **ovary** (painted blue), the chamber that *contains* the **ovules/seeds**; the **style**, the tissue through which the **pollen tube cell** grows to the vicinity of the ovules; and the **stigma**, the receptive tissue that recognizes legitimate pollen and promotes the germination of the pollen grain.

Many crops – apples, citrus, peaches, pears, plum, sunflowers, cabbage, cauliflower, and mustard – produce hermaphrodite (bisexual) flowers that have both male and female sex organs. However, there are crops – various cucurbits – that produce monosexual (either male or female) flowers on the same or different branches of the same plant. There are also crops – kiwi fruit and *lapsi* – that produce male and female flowers on different plants.

The transfer of pollen grains from the anther to the stigma of the same flower or another flower of the same plant or another plant of the same species is called pollination (Fig. 3.2). An agent that helps in the transfer of pollen is a pollinator. Pollination leads to fertilization, i.e., the union of male and female nuclei. After pollen grains attach to the surface of the stigma, they send pollen tubes through the style to the ovary. The male nucleus of each pollen tube then unites with the ovule effecting fertilization. After fertilization, the ovule and associated tissues develop into seeds and fruits. Therefore, pollination is crucial for fertilization and the development of seeds and fruits.

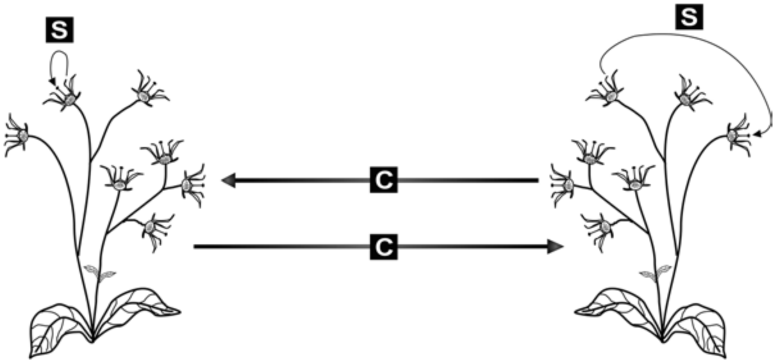

Fig. 3.2 Showing three methods of pollen transfer

3.3.1 *Nectaries and Nectar Secretion*

Flowers frequently have one or more *nectarines*. Nectaries vary in size from microscopic to the 11-in. nectary of the orchid (*Angraecum sesquipedale* Thou.) (Darwin 1877). The nectary is most often located within the flower, usually at the base of the sexual column inside the circle of petals. In cotton, however, there is a nectariferous ring just outside the base of the petals on the inner base of the calyx. Nectaries are also found outside the flower, on the stem or leaves. Nectar secretion within the flower usually starts about the time the flower opens and ceases soon after fertilization. Secretion of nectar on the stems and leaves is not influenced directly by flowering and may continue for several weeks.

The amount of nectar secreted varies from infinitesimal in numerous species to more than an ounce in the orchid *Coryanthes* spp.(Kerner 1878) and in *Protea mellifera* Thunb, which natives in Africa reportedly remove and drink (Langstroth 1913; Holmes 1963); Nichol (1952) reported that the nectar of the *Agave parryi* Engelm. Flower stalk was gathered by Indians in the Southwest and used as a syrup. Numerous bee specialists have calculated the amount of nectar produced in the flowers of various crops (Todd and Mcgregor 1960).

3.3.2 *Stigma Receptivity*

When the stigma is receptive to pollen, it is coated with a colorless, relatively tasteless stigmatic fluid. If viable, compatible pollen comes in contact with this moist stigma, it adheres, germinates, and sends a pollen tube bearing the tube nucleus and the two sperm nuclei down through the style into the ovary and, finally, into one of the ovules. *Fertilization* follows this *pollination* process by the sexual union of one of the two sperm nuclei of the pollen grain and the egg nucleus of the ovule to form the fertilized egg or zygote. Through this process of sexual union, a viable seed is formed that is capable of producing another complete plant.

In general, the sooner pollination can occur after a flower opens the greater the likelihood that fertilization of the ovule and seed development will occur. As time elapses, the pollen may be lost to insect foragers, wind, gravity, or damage by heat, moisture, or drying out. Also, processes may set in that result in the shedding of the fruit.

Pollination also requires consideration of pollenizers. (The terms "pollinator" and "pollenizer" are often confused: a ***pollinator*** is the agent that moves the pollen, whether it be wind, bees, bats, moths, or birds; a ***pollenizer*** is the plant that provides the pollen.) Some plants are **self-fertile** or **self-compatible** and can pollinate themselves. Other plants have chemical or physical barriers to self-pollination and need to be cross-pollinated: with these **self-infertile** plants, not only pollinators must be considered but pollenizers as well. In pollination management, a good pollenizer is a plant that provides compatible, viable and plentiful pollen and blooms at the same time as the plant that is to be pollinated.

3.3.3 Pollination and Pollenizer

Pollination can be **cross-pollination** with a pollinator and an external pollenizer, **self-pollenization** with a pollinator, or **self-pollination** without any pollinator:

Cross-pollination (***syngamy***): pollen is delivered to a flower of a different plant. Plants adapted to outcross or cross-pollinise have taller stamens than carpels to better spread pollen to other flowers.

Self-pollenization (***autogamy***): pollen moves to the female part of the same flower, or to another flower on the same individual plant. This is sometimes referred to as self-pollination, but this is not synonymous with autogamy. Clarity requires that the term "self-pollination" be restricted to those plants that accomplish pollination without an external pollinator (example: the stamens actually grow into contact with the pistil to transfer the pollen). Most peach varieties are autogamous, but not truly self-pollinated, as it is generally an insect pollinator that moves the pollen from anther to stigma. Plants adapted to self-fertilize have similar stamen and carpel length.

Cleistogamy: pollination that occurs before the flower opens is always self-pollination. Some *cleistogamous* flowers never open, in contrast to ***chasmogamous*** flowers that open and are then pollinated. Cleistogamous flowers must of necessity be self-compatible or self-fertile plants. Other plants are self-incompatible. These are end points on a continuum, not absolute points.

Hybridization is effective pollination between flowers of different species of the same genus, or even between flowers of different genera (as in the case of several orchids).

3.4 Pollination and Fertilization

Pollination is usually considered in the combined sense of transfer of pollen and set of fruit or seed. In fact, it is not so, for this purpose two sets of factors are involved: (1) transfer of viable pollen from the anther to a receptive stigma, and (2) sprouting of the pollen grain and growth of the pollen tube down the style into the ovary, and ultimately the union of male nuclei of the pollen grain with female germ cells in the ovule that results in seed development. Pollination is of no value without fertilization. A plant may be spoken of as *self-fertile* or *self-compatible* if it can produce fruit without the need for the transfer of pollen to it from another cultivar. If the plant is not receptive to its own pollen, it is *self-sterile*. Even self-pollinating plants are frequently benefited by *cross-pollination*, the transfer of pollen from one flower to another. They may also benefit from having the pollen more thoroughly transferred and distributed over the stigma at the most receptive period. A plant is *cross-compatible* if it can normally be pollinated with pollen of another cultivar, but it is *cross-incompatible* if it is not receptive to pollen of certain cultivars.

3.5 Pollinating Agents

The process of pollination requires pollinators as agents that carry or move the pollen grains from the anther to the receptive part of the carpel. Faegri and van der Pijl (1979), in their classic book on pollination ecology, defined two major types of pollen dispersal: *Biotic pollination* in which the pollen dispersal agent is an animal (i.e., either an invertebrate or a vertebrate); and *abiotic pollination* where pollen is dispersed by an inanimate physical agent, such as wind or water. The various flower traits that attract different pollinators are known as pollination syndromes. Methods of pollination, with common pollinators or plants, are:

3.5.1 Biotic Pollination

Invertebrates

Beetles: Cantharophily
Flies: Myophily
Hymenopterans
Wasps: Sphecophily
Bees: Melittophily
Ants: Myrmecophily
Lepidopterans
Butterflies: Psychophily
Moths: Phalaenophily

Vertebrates

Birds: Ornithophily
Mammals: Therophily
Marsupials: Metatherophily
Placentals: Eutherophily
Bats: Chiropterophily
Rodents: Sminthophily

3.5.2 Abiotic Pollination

Self-pollination: Autogamy + Cleistogamy
Wind-pollination: Anemophily
Water-pollination: Hyphydrophily.
Gravity pollination

3.5.3 Abiotic Vectors

3.5.3.1 Wind

Wind pollination is the dominant type of abiotic pollination and is especially prevalent in several plant families, including the grasses (Poaceae) and sedges (Cyperaceae). Most gymnosperms (including pines, firs, spruces, etc.) are also wind-pollinated. Abiotic pollination is, with few exceptions, a wasteful process. The plant must release as much pollen as possible, given the low probability that wind or other physical forces can effect transfer of grains of that pollen to a receptive stigma.

To this end, anemophilous plants have morphological adaptations that increase pollen dispersal and capture. Modifications of the flowers include a highly reduced perianth (no need to be showy) and green to dark brown to reddish bracts and perianth. It has been suggested that dark red is important for the temperature conditions of the blossom, especially of the bud. The flowers of anemophilous species are often found above or outside the leaves which may increase their access to wind currents. Some species flower before the leaves are out, which allows maximum wind speed around the flowers.

Flowers of anemophilous species are generally unisexual (either monoecious or dioecious species) and are often temporally or spatially separated from flowers of the opposite sex. This separation not only prevents self-fertilization and increases outcrossing but prevents stigmas from being clogged by self pollen. One common arrangement of anemophilous flowers is for the female flowers to be located higher on the plant than male flowers so that pollen will not just fall down onto stigmas of the same plant.

Because of the high inefficiency of wind pollination, anemophilous species produce huge numbers of pollen grains. Filaments are frequently very long, causing the anthers to extend outside the surrounding perianth. Some species even have "explosive" anthers. The filaments are under strong tension in the bud stage and spring out, throwing pollen into the air, after the flower has opened. Anthers generally do not open unless the weather is favorable, i.e. warm and dry, because pollen is rapidly washed out of the air in rain.

Pollen grains of anemophilous species are usually very small (diameter of 10–20 mm), which increases their buoyancy. Some relatively large conifer pollen grains solve the problem of buoyancy by the addition of one or more air-sacs, which give a larger surface area without appreciably increasing weight. Great quantities of pine pollen have been found hundreds of kilometers away from the nearest forests. The typical rate of fall for wind pollen in calm air is of the magnitude of a few centimeters per second. Also contributing to buoyancy is the tendency of grains of anemophilous species not to adhere to each other but to be smooth and dry. Conversely, in entomophilous species, the pollen grains are usually highly ornamented and/or sticky, increasing the probability of their attaching to insects.

The female portion of anemophilous flowers has evolved to capture and utilize wind-born pollen. In contrast to the large number of pollen grains, the number of ovules per flower is generally rather low in anemophilous species; many species have but one ovule, so each flower only produces one seed. To capture wind-borne pollen, anemophilous flowers usually have greatly enlarged stigmas. For example, feather-like stigmas are often found in grasses and brush-like stigmas are found in cattails (*Typha* spp.), both of which increase the ability of the plant to "capture" pollen.

Several common plants use both anemophily and entomophily. Several species of *Plantago,* a common roadside weed, have inconspicuous, green flowers that produce massive numbers of pollen grains. These plants have been shown to be pollinated by wind in some circumstances, but they are also frequently pollinated by honeybees and flies. Other evidence comes from the loads of pollen-collecting bees; these frequently contain pollen from anemophilous species, sometimes exclusively.

3.5.3.2 Water

Another much rarer form of abiotic pollination is hydrophily, or water pollination, which can occur through a variety of mechanisms. In some flowers, the pollen is released into the water and floats to the water surface. The female flowers emerge onto the surface, receive pollen, and are then withdrawn back under the water. The most famous case is of *Vallisneria* in which the whole male flower is released instead of individual pollen grains; the pollen itself therefore does not touch the water surface. The female flowers create small depressions in the surface tension of the water. These depressions cause nearby floating male flowers to slide down allowing the anthers to contact the stigma of the female flower. In accordance with this effective mode of pollination, the number of pollen grains per male flower is drastically reduced.

3.5.3.3 Gravity

Pollination by gravity also called geophily is found in self pollinated crop plants. In this case pollen falls because of gravity on to receptive stigma of other flowers. However, gravity is highly unreliable and a rare and insignificant pollinating agent.

3.5.4 Biotic Vectors

3.5.4.1 Biotic Pollinating Agents

Biotic pollinating agents (biotic agents) include bees, wasps, butterflies, moths, birds, bats, and flies. Biological pollination is also called zoophily. Animals visit flowers for nectar and/or pollen, and they incidentally transfer pollen grains from one flower to another flower of the same or another plant. Characteristics of crop plants that are pollinated by biotic agents include

1. some kind of relationship between the pollen vector and the flowers,
2. the production of relatively small amounts of pollen,
3. pollen grains that vary in size and external sculpture and are sticky in *Nature*,
4. the production of flowers of attractive colours and odours, and
5. Flowers that have nectaries that produce nectar.

Most plant species have adopted one of two very different kinds of relationships with biotic pollen vectors (Herrera 1996). One option is to be a generalist and try to attract a wide variety of different pollinators. The other is to specialize (and often coevolve) with a single type of pollinator. Species that generalize can occur in a wide variety of habitats and survive conditions under which some of the pollinators cannot persist (Nilsson 1988). On the other hand, they encounter a great deal of "foreign" pollen from other species, which can clog stigmas and prevent pollination e.g. *Dacus carota*. Flowers on these species are often grouped together in large showy, flat or gently rounded inflorescences. On their inflorescences one can usually find a motley crowd of insects – bees, wasps, flies and beetles of many kinds, and even some butterflies, although these are generally considered specialists.

Specialists can adapt to have very specific and highly efficient pollination mechanisms but are restricted to co-occurring with their pollinators. It is these mutualists that draw the most attention in pollination biology with their intricate and sometimes outlandish mechanisms for pollination.

Whether adapted as generalists or specialists, animal-pollinated plants share several characteristics. The pollen is sometimes larger than in anemophilous species, is often sticky and/or highly ornamented with spines and bumps, and sometimes adheres in clumps of several grains. The number of pollen grains, sometimes expressed as a ratio with the number of ovules, is much lower in biotic pollination than in anemophilous species. Stamens are located so as to contact the pollinators, rather than to be exposed to wind. However, much of the floral structure is related to attracting specific types of animals to act as pollinators.

The important biotic pollinating agents include:

Birds

Pollination by birds, called ornithophily, occurs in a few plants in the Hindu Kush-Himalayan region but is very common in some places, e.g., South America and Australia. Some birds – bronzy hermit humming bird, broad-tailed humming bird, male purple sunbird, cape sugar bird, and tawny crowned honey eater – visit flowers of a particular plant species for nectar, and so pollinate them. These pollinating agents visit only those few crop plants that produce plenty of nectar, for example, avocado and pineapple are visited by humming birds.

Mammals

Certain mammals – Queensland blossom bat, short-nosed fruit bat, honey possum, and Namaqua rock mouse – visit flowers of a particular plant species for nectar, and so pollinate them. Mammals are, however, the pollinating agents of only a few plants (Ayensu 1974).

Insects

Insect pollination, also called entomophily, is found in many agricultural and horticultural crops. Different kinds of insects such as bees, flies, beetles, butterflies, moths and wasps are important pollinators of many plants. Crops that require insect pollination to set fruit and seed are called entomophilous. Entomophily occurs in many plants. Agricultural crops, horticultural crops, forage crops, ornamental plants, and other wild plants are all effectively pollinated by insects that visit flowers for nectar and/or pollen. Bees are one of the most effective and reliable pollinators.

3.6 Why Is Cross-Pollination Important?

Pollination is crucial for the production of fruit and seed. There are many plants that cannot produce fruit and seed if pollinated by their own pollen and so require cross-pollination. Such plants include those in which male and female parts are either borne on separate plants or on separate parts/flowers of the same plant. Cross-pollination is also essential in those crops in which male and female parts are borne on the same flower but they are physically excluded from each other (McGregor 1976).

Cross-pollination in normally self-pollinated crops also results in higher yields and better quality fruit and seed.

1. Cross-pollination is important in many partially or fully self-incompatible/self-sterile varieties of agricultural and horticultural crops; for example, commercial varieties of cabbage, cauliflower, broccoli, radish, apple, almond, peach, pear, plum, etc.
2. Cross-pollination is also important for fruit and seed production in plants that produce unisexual flowers; for example, species belonging to the families *Actinidiaceae, Anacardiaceae, Cucurbitaceae*.
3. Cross-pollination enhances the yield and quality of many self-pollinated crops.

3.7 Attractants and Rewards for Biotic Pollinators

Christian Sprengel (1750–1816) was one of the first to realize that bees and other flower visitors do not provide their pollen-carrying services free of charge. The plant must offer a reward in the form of something the pollinators need, either for their own survival or for that of their offspring. To secure the services of pollinators, the plants also must advertise these rewards. Flowers announce their rewards by being conspicuous in color, scent, size, or shape, making it easier for visitors to pick them out from their surroundings. Recognize that animals perceive flowers in many different ways, and certainly in different ways than do humans; what seems like an inconspicuous flower to us may be like a flashing neon sign to an insect or bird.

The most common rewards are nectar and pollen. Pollen may have been the original reward (bribe) by which flowers began attracting insects in the Cretaceous period some 140 million years ago. Because pollen is the male gametophyte, it is obvious that some pollen must be transported and not consumed for fertilization to take place, but flowers always produce much more pollen than is necessary. Pollen is a highly nutritious and well-balanced food material containing protein, sizable amounts of starch, sugars, fat or oil, minerals, antioxidants, and vitamins such as thiamin. It is also rich in free amino acids. There can be no doubt therefore about its value as a food for insects and mammals. Plants that offer pollen as a reward often produce it in huge quantities.

In order to minimize the loss of viable pollen to pollinators, some plants produce, in the same flower, two types of anthers, normal ones, which produce healthy pollen, and others that yield sterile or at least less viable but still very nutritious and probably tasty pollen. Good examples of food stamens can be found in mullein (*Verbascum thapsus*) and partridge pea (*Cassia* spp.). In dayflower (*Commelina sativa*), the feeding anthers do not produce pollen, but offer a milky fluid instead.

Some orchids have hit upon still another way to offer imitation pollen. They produce “food hairs” on the lower lip of the flower, which easily fall apart into individual cells, rich in starch. Orchids cannot offer pollinators some of their pollen for food because, as, all the orchid pollen within a flower comes in neat little packages called pollinia and any attempt to sacrifice a few grains would sacrifice the whole pollinium.

Finally, it should be pointed out that not all the credit for pollen movement should be given to the insect pollinators. Pollen itself has been shown to “jump” from the stamens onto the insect, then from the insect onto a receptive stigma. It is known that electrostatic charges can build up on the body of a foraging honeybee and that these charges may reach a magnitude of several hundred volts. The bee is therefore flying at the center of its own highly charged electrostatic field. Most floral surfaces are well insulated, but the pistil is an exception: indeed a path of very low resistance leads from the stigma to the ground, almost like the earthing track of a lightning conductor. The result is that the bee’s electrostatic field is attracted to the stigma, and with it the pollen.

Nectar is another important reward offered by many plants. Many scientists believe that nectar was already being produced before flowers first appeared on the scene. Primitive ancestral plants appear to have had many nectaries on their leaves, stems, and other non-floral areas. These nectaries may have been important for excreting excess sugars in maturing portions of plants. It is quite conceivable that these nectaries were simply incorporated into the structures we call flowers at the time those structures developed.

Nectar is an ideal substance to offer as a reward (Baker and Baker 1990). It is easily produced by plants, it can be produced quickly as demand requires, and, being a sugar solution, it is readily digested and quickly assimilated as a source of energy. However, nectar has been modified in some species to reward specific pollinators. One critical factor is the amount of nectar, as flowers “want” to reward pollinators without satiating them. If too much nectar is provided, the pollinator has no need to forage further, and pollen will not be transported. On the other hand, flowers of different species, and even within species, are competing with one another for pollinators, and those that provide the most nectar are likely to attract the most pollinators.

Another way in which nectar can vary is in concentration and content. Bird-pollinated flowers usually have a fairly dilute nectar, with a sugar concentration between 20% and 30%. Birds simply cannot suck up a nectar that is too syrupy. On the other hand, horse-chestnut flowers may have a sugar concentration as high as 70%, with the results that bee visitors have to dilute it with their own saliva before they can suck it up (Baker et al. 1998).

The observation that certain nectars, and consequently some honey, can be poisonous has received a great deal of attention. Some of Xenophon’s 10,000 soldiers were incapacitated on their epic homeward trek from Persia after consuming poisonous honey. In all likelihood, the culprit was *Rhododendron ponticum*. Other species are also known to produce poisonous nectar or pollen, although the reasons for doing so are not clear. Of course, nectar that is poisonous to one pollinator (or humans!) may not be poisonous to another. Many other types of rewards are offered in the great diversity of types of flowers. Some flowers produce fatty oils (glycerides) to offer visiting bees instead of a sugary nectar. The bees that pollinate these species have specialized hairs to collect, transport, and temporarily store the somewhat sticky oil. In general, it is only the female bees that collect the oil, and it is they who mix the collected oil with pollen to produce a nutritious and protein-rich "bee-bread" for their larvae.

Other species produce resins and waxes, which can be valuable as nest-building materials, especially in wet-tropical areas. Some flowers may provide heat as a reward (Stanton and Galen 1989). Figures are well known to provide environments for their pollinators in which to raise offspring, and a few orchids offer shelter from adverse conditions.

How do plants let the pollinators know that they offer these rewards? The primary attractants of flowers include color, size and shape, and scent. Plants use pigments contained in vacuoles to generate the huge variety of flower colors that we see around us. These pigments include anthocyanins (blues to reds), betacyanins (red), anthoxanthins (ivory to yellow), chlorophyll (greens), and carotenes (orange to yellow). Virtually the only purpose for floral color is to attract pollinators. Plants combine these pigments, along with special surface textures, to create the many additional colors, as well as shiny and velvety appearances. As we shall see below, these colors are often intended to attract specific pollinators, as pollinators differ greatly in the ability to see color and pattern.

Of course, many flowers produce scents, usually to attract pollinators (they sometimes smell nice to humans as well). These aromas must be manufactured at a cost to the plant. Many classes of pollinators have keen senses of smell. Their preferences vary from pollinator to pollinator, as does their color vision, and the scents given off by flowers reflect these differences. In many orchids, the scent is so specific that one, and only one, species of insect will visit each species of orchid.

Flowers of different species are distinguished more by their smells than by their colors, simply because there are many, many odor categories and relatively few colors. For this reason, odor may be even more important than color in establishing a phenomenon known as flower constancy. Flower constancy can be defined as the "loyalty" a pollinator displays towards the flower of just one plant species. Constancy is a learned behavior pattern and should never be confused with the inborn, specific pollination connection that may exist between a particular insect species and a particular species of flower. The pollinator exhibiting constancy may be perfectly capable of pollinating other flower species, but will stick to its original behavioral pattern even when flowers that have more nectar or pollen to offer are becoming available in the environment.

At first sight, such faithfulness may seem foolish, yet it can be advantageous for both the pollinator and the plant species to which it is loyal. The plant benefits in not having its pollen wasted on flowers of another species, and the pollinator, having the opportunity to concentrate all its efforts on one type of flower, soon learns to handle it with maximum efficiency and speed. Think of it as you might majors in college. Once you have invested time in a major, another may appear to be better for you in terms of income or satisfaction level but it is difficult to switch majors because of the time and knowledge already invested in your current one.

Table 3.1 Pollination syndromes: traits of flowers pollinated by different pollinators

Trait	Bee	Fly	Beetle	Butterfly	Moth	Bird	Bat	Wind
Color	Yellow, blue, purple, or UV (Bees can't see red.)	Dull red to dark brown	Dull white, purple, or brown	Red, blue and purple	Pale, pink, green, or white	Bright red or orange	Dull white or green or purple	Dull or pale green, yellow or brown, may be absent or reduced
Flower scent	Fresh and pleasant	Putrid ("decaying flesh")	Strongly fruity or fetid	Faint, mild, fresh and sweet	Strong and sweet, emitted at night	None, birds cannot smell	Strong and musky, emitted at night	None
Flower shape/ depth	Shallow; have a landing platform or lip; can be tubular:can have nectar guides, snapdragons	Shallow; funnel-like or complex trap like the dutchman's pipe	Large, regular, bowl-like; Magnolias, *Victoria amazonica*	Narrow tube or spur, with a wide landing pad, yarrow	Regular; tubular without a lip, horizontal, yucca flower	Large, container-like; tubes, funnels, cups; strong supports for perch. (Hummingbirds don't use perch.)	Regular, brush or bowl or trumpet-like; closed by day; flower positioned outside foliage	Regular, small, anthers and stigmas exerted
Reward	Nectar and/or pollen	Nothing, the flies are fooled	Edible flower parts	Nectar, ample, deeply hidden	Nectar, abundant, deeply hidden	Nectar, abundant, deeply hidden	Nectar, abundant, somewhat hidden	
Time of floral opening	Day and night	Day and night	Day and night	Day and night	Night	Day and night	Night	Day and night

3.8 Pollination Syndromes

More than 100,000 different animal species – and perhaps as many as 200,000 – play roles in pollinating the 250,000 kinds of flowering plants on this planet. In addition to countless bees, wasps, moths, butterflies, flies, beetles and other invertebrates, as many as 1,500 species of vertebrates such as birds and mammals serve as pollinators, including hummingbirds, perching birds, flying foxes, fruit bats, possums, lemurs and even a lizard (gecko) (Ingram et al. 1996).

Honey bees, birds, bats and insects play a vital role in pollination of most fruits and vegetables. with over 90% of all flowering plants and over three-quarters of the staple crop plants that we use for food rely on animals for pollination. Of the hundred or so crops that make up most of the world's food supply, only 15% are pollinated by domestic bees, while at least 80% are pollinated by wild bees and other wildlife (Prescott-Allen and Prescott-Allen 1990; Free 1993; Ingram et al. 1996; Buchmann and Nabhan 1996; Nabhan and Buchmann 1997).

Often it is possible to guess what pollinates a plant just by looking at the shape, color and scent of a flower. These characteristics that help us predict the pollinator are called pollination syndromes. The following is a list of pollinator types and their respective pollination syndromes (Faegri and van der Pijl 1979) (Table 3.1).

References

Ayensu ES (1974) Plant and bat interactions in West Africa. Ann Missouri Bot Gard 61:702–727

Baker HG, Baker I (1990) The predictive value of nectar chemistry to the recognition of pollinator types. Isr J Bot 39:157–166

Baker HG, Baker I, Hodges SA (1998) Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. Biotropica 30(4):559–586

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island, Washington, DC

Darwin C (1877) The different forms of flower on plants of the same species. Murray, London

Faegri K, van der Pijl L (1979) The principles of pollination ecology, 3rd edn. Pergamon, Oxford

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London

Herrera CM (1996) Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In: Lloyd DG, Barrett SCH (eds) Floral biology. Studies of floral evolution in animal pollinated plants. Chapman & Hall, New York, pp 65–87

Holmes EO (1963) *Protea mellifera*, queen of nectar producing plants. Am Bee J 103:216–217

Ingram M, Nabhan GC, Buchmann SL (1996) Impending pollination crisis threatens biodiversity and agriculture. Tropinet 7:1

Kerner A (1878) Flowers and their unbidden guests. The translation revised, and edited by w. Ogle. Kegan, London. 164 pp

Langstroth LL (1913) The hive and the honey bee. Rev. By C. P. Dadant, Dadant and sons, Hamilton, III, 575 pp

McGregor SE (1976) Pollinating agents and their comparative value. In: Insect pollination of cultivated crop plants, agriculture handbook, vol 496. USDA, Washington, DC, pp 19–23

Nabhan GP, Buchmann SL (1997) Pollination services: biodiversity's direct link to world food stability. In: Daily GC (ed) Nature's services: societal dependence on natural ecosystems. Island, Washington, DC, pp 133–150

Nichol AA (1952) The natural vegetation of Arizona. Ariz Agr Expt Sta Tech Bul 127:188–230

Nilsson LA (1988) The evolution of flowers with deep corolla tubes. Nature 334:147–149

Prescott-Allen R, Prescott-Allen C (1990) How many plants feed the world? Conserv Biol 4:366–374

Sprengel CK (1793) Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen [The secret of *nature* in the form and fertilization of flowers discovered]. Friedrich Vieweg der Ältere, Berlin

Stanton ML, Galen C (1989) Consequences of flower heliotropism for reproduction in an alpine buttercup (*Ranunculus adoneus*). Oecologia 78:477–485

Todd FE, Mcgregor SE (1960) The use of honey bees in the production of crops. Ann Rev Ent 5:265–278

Chapter 4
Applied Pollination: Present Scenario

Abstract Production of cross-pollinated crops can be increased considerably in areas where there is a dearth of natural pollinators by brining pollinators like domesticated bees to the crop when it is in bloom. This practice has yielded excellent results and the techniques is widely used in advanced countries to enhance production, particularly of self-sterile crop varieties; and significant investment is made in research in evolving more efficient techniques as well as pollinators.

4.1 Introduction

Accounts of applied crop pollination in European countries have been well documented (see McGregor 1976; Free 1993; Roubik 1995; Delaplane and Mayer 2000) especially with honeybee *Apis mellifera* L, but similar studies in Asian countries are still fragmentary and inconclusive. The continent Asia carries about three fifth of world population. However, crop production in the Asian countries is still low and not enough to sufficiently feed the people dwelling there. One of the major reasons for low crop production is the ignorance to modern agricultural technology and insufficient facilities for research and development. Asia presents a wide variety of climatic Zones and accordingly several kinds of crops are grown. Many of these are entomophilous requiring essentially the cross-pollination of their flowers for fruit/seed production whereas several others are greatly benefited from insect pollination. Studies on pollinators and importance of bee pollination in crops grown in Asia were started long back, however, the work remained scattered. It is only recently that organized research work on floral biology, melittophily and pollination ecology of several crops was carried out. Pollinators of various crops were identified and their pollination requirements were determined. This chapter briefly reviews the applied pollination research carried out on Asian crops by the local workers. The research on biology of Asiatic pollinators, especially that on solitary bees, has not been included, and work on brief floral biology/fertility status, pollinators, pollinators,

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pollination and pollinator requirements of these crops wherever available has been included. These crops have been divided into seven groups according to their use.

4.2 Pollination of Fruit Crops

Pollination requirements of different fruit crops are summarized in Table 4.1. However, the detailed information on pollinator complex of each fruit crop is as given below:

4.2.1 Almond

Almond (*Prunus amygdalus*) was found to flower at low temperature when honeybee colonies were in weakest condition; hence fruit set remained low. Therefore, need for honeybee pollination was greatly felt (Muttoo 1952). Mann and Singh (1981b) reported that honey bees were the commonest visitors to almond flowers. However, pollination requirements for this crop in Asia are not known. Abrol et al. (1990) observed mosquitoes and musca in low numbers in Jammu and Kashmir whereas Singh (1988) recoded four species of *Eristalis*, one species of *Episyrphus*, *Metasyrphus*, *Scaveva* and *Orthellia* as most important pollinators of almond in Himachal, India.

Abrol (1988b) recoded *Apis cerana*, *Xylocopa valga* and *Lasioglossum spp.* as dominant flower visitors and important pollinator of Almond. He found that flower buds covered with muslin cloth did not set any fruit while 100 uncovered buds set 30 fruits indicating that almond exclusively depend on insect for pollination. The observations made on flowering phenology, insect visitors and environmental conditions showed that a period of 10–12 was the most crucial for almond pollination. He suggested that as almonds flower in March when the weather is unfavourable for foraging insects the induction of late flowering will improve fruit setting.

4.2.2 Apricot

Japanese apricot (*Prunus mume*) flowered in early spring when there were too few wild bees for adequate pollination (Nakanishi 1983). Honeybees visited a male sterile cultivar infrequently and thus yields were low on these trees. UV reflectance was found to decide the honeybee preference. However, pollination requirements of this crop in Asia are not available.

4.2.3 Apple

Fruit set in three varieties of apple (*Malus sylvestris*) viz. Red-golden, Red-delicious and American mother was found to be greatly increased by insect pollination

Table 4.1 Floral biology and pollinate on requirements of important fruit crops

Crop	Extent of cross pollination	Chief pollinators	Bloom period (days)	Stigma receptivity (days)	Pollination requirements
Almond	Cross pollination essential	Honeybees	30	3–4	5–8
Apple	All commercial varieties require cross pollination	Honeybees, bumblebees and *Halictus*	9	2–3	2
Apricot	Cross pollination beneficial	Honeybees	15–20	4–5	2–5
Banana	Pollination not essential	Bats, birds	–	–	–
Black currents	Cross pollination essential	Honeybees	21	5–6	–
Blueberry	Self sterile to cross fertile	Honeybees, bumblebees, solitary bees and flies	21	5–8	3–12
Cherries	Cross pollination essential	Honeybees	7–8	First 2 days after opening of flowers	2–3
Chestnut	Self sterile	Honeybees, rose chaffers, wild bees and wind	–	45	–
Citrus	Vary from self sterile to self fertile	Honeybees	30	6–8	1–2
Craneberry	Cross pollination essential	Honeybees, bumblebees	2–3 weeks	3	1 hive/2.5 ha
Grapes	Self sterile to self fertile	Honeybees and other insects, wind	20–25	3	0.5–1
Guava	Self to cross pollination	Honeybees and other insects	25–45	4	–
Hazelnut	Self sterile	Wind	–	30–90	–
Litchi	Self fruitful cross pollination essential	Honeybees, hoverflies, caliphorids, *Musca sp.* flies.	26–36	3	4
Loquat	Self to cross pollination	Honeybees and other insects	–	–	–
Mango	Self to cross pollination	Honeybees, house flies, ants etc.	–	5	7–8

(continued)

Table 4.1 (continued)

Crop	Extent of cross pollination	Chief pollinators	Bloom period (days)	Stigma receptivity (days)	Pollination requirements
Olive	Self sterile to self fertile	Honeybees and wind	–	–	–
Papaya	Self to cross pollination	Sphinax moth, honeybees, butterflies, hummingbird, sunbird	–	–	–
Peach	Mostly self fertile and few self sterile	Honeybees other hymenopterans, dipterans and wind	20–24	3	2–3
Pears	Partly or entirely self-sterile	Honeybees, flies, beetles	7	4–5	–
Persimmon	Cross pollination not necessary	Honeybees, bumblebees and wind	25–30	3–4	–
Pistachio	Cross pollinated	Wind, honeybees	–	–	–
Plum and prune fruits	Vary from self compatible to self incompatible	Honeybees, wild bees, blowflies, bumblebees	5	Become receptive 2 days before the anther dehiscence	2–3
Pomegranate	Self and cross pollination	Honeybees, beetles, wind	–	–	–
Raspberry	Cross pollination beneficial	Honeybees	3–6 weeks	2–3	1–2
Sapota	Self sterile	Wind, honeybees and other insects	–	–	–
Strawberry	Cross pollination beneficial	Honeybee and wild bees	45–60	3	1–10

Source: Modified after Verma 1990

(Sharma 1961). Honeybees, *Eristalis sp.* and *Syrphus sp.* were the main visitors. Red-delicious had higher fruit set near the bee colony and decreased with distance. Flies were found to outnumber *Apis cerana indica* at all locations on all fruit blossoms at different elevations in Himachal Pradesh (India). Rai and Gupta (1983) also stressed the need of bee pollination in the fruit set of apple. However, exact pollination requirements of the crop in Asia have not yet been studied. On apple bloom besides honeybees frequent insect visitors are species of *Eristalis* at different places on Shimla hills Himachal Pradesh, India (Verma and Chauan 1985). Singh and Mishra (1986) recoded 9 species of insects visiting apple flowers in different areas of Himachal Pradesh. Kanwar 1987 reported a species of wild pollinating fly playing an important role in apple pollination. Verma and Chauhan recorded 44 species of insects pollinating apple flowers in Shimla hills Himachal Pradesh. Abrol (1989a) presented a detailed list of pollinators of different crops under Jammu and Kashmir (India) conditions.

4.2.4 Cherry

Abrol (1989b) reported *Xylocopa valga*, *Colletes eous*, *Lasioglossum sp.*, *Halictus sp.*, *Andrena flavipes Syrphus sp.*, *Apis cerana indica*, and *Apis mellifera* as important pollinators of cherry flowers. Mattu et al. (1994) found predominant presence of *Syrphus*, *Eristalis*, *Fannia*, *Musca* and *Dolichopus* on cherry bloom. Abrol (2005) found that more than 11 species of insects belonging to order Hymenoptera and Diptera frequented cherry flowers. Of all the flower visiting insects, honey bees *Apis mellifera* and *Apis cerana* were the most abundant and comprised more than 55% of the total flower visiting insects. Percentage fruit set was significantly higher at 100 m (28.2%) from the apiary than at 500 m (9.0%). Similarly, number of colonies/ha also significantly influenced the fruit set fruit yield/plant in the cherry orchards.

4.2.5 Carambola

Phoon (1985) studied pollination in carambola (*Averrhoa carambola*). Its flowers were found to be visited by *Apis cerana* and *Trigona thoracica* at Serdang (Malaysia). Introduction of a pollinizer and 4 colonies of *A. cerana* to one orchard increased fruit production by 5–6 times over the last year's production. However, in another orchard increase in the number of colonies from 2 to 4 resulted in a 2-fold increase in the year's production. Nand (1971) reported that sweet and sour varieties of carambola set 52–67% fruit when pollinated by honeybee, *A. mellifera*, flies and other insects, but there was no fruit set when insects were excluded.

4.2.6 Coconut

Coconut (*Cocus nucifera*) has staminate and pistillate flowers. Kidavu and Nambiyar (1925) and Patel (1938) considered both wind and insect pollination as important pollinators of coconut.

4.2.7 Grape

Iyer and Randhawa (1965) found that cross-pollination was not only essential in self-sterile cultivars of grape (*Vitis vinifera*) but that it was also beneficial in self-fertile cultivars. Mann and Tanda (1984) reported that honeybee, *A. dorsata* was the dominant visitor to this plant at Ludhiana (India). Besides, the two species of syrphid flies also visited the blooms of this crop.

4.2.8 Jujube

Singh (1984) reported seven dipterous and 11 hymenopterous species of pollinators of jujube (*Zizyphus jujuba*) at Jodhpur (India). The commonest species were the fly (*Musca domestica*) and honeybee (*Apis cerana*). Honeybees were the efficient pollen carriers, but their activity was restricted to a limited time of day and their visits per flower were lower. Dhaliwal (1975) enlisted the pollinators of ber (*Z. mauritiana*). However, pollination requirements of this plants are not known. Sihag and Abrol (1986) recorded *Apis florea* as an important pollinator of ber flowers under subtropical conditions of Hisar, Haryana, India.

4.2.9 Litchi

Khan (1929)studied the floral biology of litchi (*Litchi chiensis*) and found that these bore male and female flowers on same panicles. Das and Choudhary (1958) reported no set of fruit on bagged panicles. Chaturvedi (1965) reported 43% fertilized flower on open pollinated branches, no fruit set on branches bagged with muslin and 15.5% on branches bagged under mosquito cloth. Pandey and Yadava (1970) studied pollination requirements of litchi. *Apis* spp. and *Trigona* spp. comprised 98–99% of the total visitors. They reported that only 0.03–0.1% of flowers caged to exclude insects set fruits, whereas 0.7–11.2% (100 times as many) flowers exposed to pollination set fruit. Phadke and Naim (1974) found that on branches bagged to exclude insects, fruit set was one quarter of that obtained on open trees. Badiyala and Garg (1990) studied the pollinators and pollination of seven cultivars of litchi. Amongst the various insect pollinators, *A. melliferabees* comprised 95%. In the unbagged inflorescences there was 4.5% more pollination as compared to the bagged ones. Per cent increase in fruit set as a result of bee pollination in various litchi cultivars ranged between 100% and 190.6%, fruits per panicle between 77.47% and fruit weight between 8.17% and 18.19% over the control trees. They recommended the utilization of honeybee, *A. mellifera* for pollination of litchi. Abrol (2006a) reported that litchi flowers attracted insects belonging to 6 orders, 12 families, 22 genera and 29 species. Of all these insects, honeybees *Apis dorsata*, *A. mellifera*, *A cerana* and *A. florea* were the dominant flower visitors and comprised more than 65% of the total flower visiting insects. The other important insects frequenting litchi flowers were *Musca* sp. and *Syrphus* sp; the latter group of insects mostly collected nectar and were not considered as the reliable pollinators.

4.2.10 Loquat

Pollination requirements of loquat (*Eriobotrya japonica*) were studied by Khan at Peshawar (Pakistan). Fruit production was compared for panicles which were (i) pollinated by honeybees, (ii) pollinated by other bees in an orchard without honeybees, and (iii) self-pollinated (bagged to exclude insects). Fruit set was 83%, 46% in i, ii and iii, respectively. The number of ripe fruits were 59, 28 and 2, and weights of fruits/panicle 708, 252 and 21 g, respectively. It was recommended that honeybees colonies should be introduced to loquat to loquat orchards for pollination. Abrol (1988a) found that *Apis cerana indica*, *Bombus asiaticus* and *Bombus albopleuralis* as important pollinators of loquat (*Eriobotrya* flowers).

4.2.11 Mango

Naik and Rao (1943) studied the floral biology of Mango (*Mangifera indica*) and did not find any parthinocarpic fruit set in 100,000 flowers studied. Mukherjee observed that when flowers opened, they secreted considerable quantity of nectar which attracted large number of insects. Singh et al. (1962) reported that crossed flowers set fruits whereas selfed ones did not, indicating a degree of self-sterility. Singh (1969) observed that flowers of mango had none of the characteristics of wind pollinated flower, and he considered mango to be an insect pollinated plant. Singh (1961) reported that 65% of the perfect flowers were never pollinated – a strong indication that wind was not an effective pollinating agent. In larger plantings, particularly of monoclonal cultivars, lack of adequate fruit set was frequently complained (Singh 1969). Some selfings and some wind pollination in mango was observed by Wagle (1929), but insects (bees, ants and flies) were found to play an important role in fruit set.

4.2.12 Muskmelon

Annand (1926) reported that thrips might be the pollinators of muskmelon (*Cucumis melo*). Srivastava (1991) studied 23 species of cucurbitaceae at Rewa (India). Several insect species were visitors to these plants. They described flowers as bee flower, butterfly flower, or fly flower depending upon the predominant pollinators. Sakamori et al. (1977) reported that there was no difference between bee pollination and artificial pollination on fruit size or quality, but pollination using bees required only one third as much human labour. Nandpuri and Brar (1966) made studies on the floral biology of muskmelon. Grewal and Sidhu (1978) collected a few *A. melliferabut* most abundant was *Nomioides* spp. Grewal and Sidhu (1980) reported that insects visits were required for more fruit set in muskmelon and 5 visits in the morning to a flower were more effective.

4.2.13 Papaya

Cheema and Dani (1929) reported that flowers of papaya (*Carica papaya*) bagged to exclude pollen could set fruit, but it was seedless; both size and quality reduced.

4.2.14 Passion Fruit

Hand pollination of yellow passion fruit (*Passoflora* spp.) was found to increase the fruit set by 21% over open pollination (Sriram and Raman 1961).

4.2.15 Kiwifruit (Actinidia deliciosa)

Abrol (2000) reported honeybees *Apis cerana indica*, *Apis mellifera*, *Xylocopa valga*, *Colletes eous*, *Andrena flavipes*, *Halictus sp.*, *Lasioglossum sp.*, *Bombus asiaticus*, *Megachile sp.*, *Syrphus sp.*, and *Musca sp.*, as important pollinators of Kiwi fruit (*Actinidia deliciosa*).

4.2.16 Peach

Most cultivars of peach (*Prunus persica*) were reported as self fertile and a few as self fertile (Kamato et al. 1967). Randhawa et al. (1963) studied the floral biology of peach. the flowers opened after 0600 h, most of them were open by

10,000 h and remained open during night. The stigma was receptive for 3 days. Bhalla et al. (1983b) reported that peach was visited by honeybee, *A.c. indica*, *Andrena reticulata*, *Ceratina hieroglyphica*, *Bombus sp.*, *Syrphid flies*, *Wasps (Vespa sp.)* and some beetles. Khan (1930) concluded that cross-pollination was necessary to obtain good yields and that bees were chief agents for cross-pollination. The set was higher in unbagged than bagged flowers (Sharma 1961; Mann and Singh 1981a).

Rana et al. (1994) reported that dipterans constituted 11.8% of the insect visitors of plum, Kumar et al. (1989) observed as many as 17 species of bees on peach and apricot. Abrol et al. (2005) observed that peach and plum flowers attracted insects belonging to 4 orders, 14 families, 22 genera and 27 species. Of all these insects, honey bees *Apis dorsata*, *A. mellifera*, *A. cerana* and *A. florea* were the dominant flower visitors and comprised more than 73.79% and 93.91% of the total flower visiting insects in peach and plum flowers, respectively. The other important insects frequenting peach and plum flowers were *Xylocopa* sp., *Andrena* sp., *Megachile* sp., *Musca* sp. and *Syrphus* sp. Kumar et al. (1989) recorded xylocopa as the only bee species on plum bloom. Abrol and Bhat (1990) recorded *Xylocopa valga* as important pollinator of peach, plum and pear flowers.

4.2.17 Pear

Rai and Gupta (1983) reported the role of honeybees in pear (*Pyrus* spp.) pollination. Japanese pear (*P. serotina*) was not very attractive to honeybees as it produced little nectar (Noda 1987). Honeybee colonies were recommended to be placed in the middle of the orchard when 30% flowers were open on a sunny warm day to avoid competition with crops like milk vetch and rape. Initial good activity of bees, which decreased gradually, gave a good fruit set.

4.2.18 Persimmon

Persimon (*Diospyros kaki*) gave a commercial set without pollinating insects but the set was higher on unbagged branches (Sharma 1961). Fukae et al. (1987) reported that honeybee (*A. mellifera*) visited two cultivars of persimmon in two orchards. For satisfactory fruit production, a flower required at least 20 honeybee visits. Results on fruit production were better on trees open to honeybee pollination for 7 days or those trees whose flowers were artificially pollinated; but 1–2 days pollination by honeybees was unsatisfactory. It was calculated that one colony was sufficient for 4 ha of the crop. The use of hive inserts was found to be very effective. Hand pollination was effective when weather conditions were poor.

4.2.19 Strawberry

In South Korea, hoverflies (Syrphidae) and solitary bees, especially andrenidae, were common visitors to strawberry (*Fragaria* sp.) flowers (Woo et al. 1986). In India, honeybees and other insects visited the flowers (Singh 1979). Honeybees are utilized for fruit production of strawberries in the plastic green houses in South Korea and Japan (Katayama 1987; Sakai and Matsuka 1988; Ahn et al. 1989). As a result, the numbers of deformed fruits were lower and crop yields were higher than the green houses when honeybees were not used. Singh (1979) reported honeybees and some other insects as the most important flower visitors of strawberry. Several investigators reported that among the various insects (honeybees, flies, beetles, thrips, butterflies) visiting strawberries honeybees accounted for about 63% (Pion et al. 1980; Woo et al. 1986). Abrol (1989c) found *Apis cerana* as an important pollinator of strawberries and comprised more than 80% flower visitors. The other pollinators included *Lasioglossum* species, *Xylocopa* spp. ants and flies. Abrol and Kumar (2009) found that the insect pollinators belonging to 4 orders, 7 families and 19 species frequented strawberry flowers. Of all these insects, honey bees viz. *Apis cerana*, *A. mellifera*, *A. florea*, *A. dorsata* were the dominant flower visitors. Their abundance was in the order: *A. melliferra>A. cerana>A. florea>A. dorsata*. The other insect visitors included soil nesting solitary bees such as *Andrena leana*, *A. ilerda*, butterflies, houseflies, syrphid flies and some beetles. The percentage of fruit set was much higher in open pollinated plants than control. There was 11.20% malformed fruit in open pollinated plots as compared to 17.44% in controlled one.

4.2.20 Watermelon

Ohbayashi (1976) studied pollination requirements of watermelon (*Citrullus lanatus*). Honeybees were predominant visitors to watermelon fields, with few halictid bees and hover flies. It was estimated that one colony of honeybees per ha was required for pollination.

4.3 Pollination of Vegetable Crops

4.3.1 Cucumber

In Kuala Lumpur (Malaysia), Balsam pear/bitter cucumber (*Momordica charantia*) was found to be pollinated by small bees (Sands 1928). In India, Shrivastava (1991) reported that flowers were pollinated by the beetle *Epilachna panctata* and pyralid moth. At Hisar (India), *Xylocopa fenestrate* visited this plant for nectar and pollen (Sihag 1990), and was found to be the most efficient pollinator (Sihag 1993).

4.3.2 Carrot

Sihag (1985b) reviewed the floral biology of carrot (*Daucus carota*). Protandry is most prevalent in carrots. Therefore, these require cross pollination. Nand (1971) stated that honeybees, flies and other insects were the chief pollinating agents of the completely cross pollinated carrot crops. Sihag (1986) studied the pollinators and pollination in carrot in Hisar (India). The dominant flower visitors were two bee sp. viz. *Andrena leaena* and *Apis florea*, and some dipterns viz. *Eristalis* sp., *Sarcophaga* sp., and *Musca* sp., whereas non-dominant visitors included some lepidopterans. Number of seeds/plant in open plots increased by 5 times, weight of seeds/plant by 4.4 times weight of seeds/ha by 4 times over the bagged plots. However weight of 1,000 seeds was greater in caged plots and per cent germination in two treatments was alike. Kumar and Rao (1991) reported that *Halictus splendidulus*, *H. vachalii*, *Allodape* sp. and *Nominoides* sp. were the most common visitors to carrot at Solan, Himachal Pradesh, India. *H. splendidulus* was found to be the most efficient pollinator. Sharma and Sharma (1968) and Alam et al. (1987b) also reported the effect of bee pollination on seed yield of carrot in India and Bangladesh. Sihag (1986) stressed the need of managed pollination in carrot.

In earlier studies also, dipteran flies and hymenopterous insects has been recorded visiting carrot flowers (Abrol 1997). Goyal et al. (1989) at Solan, Himachal Pradesh, India recorded 71 species of insects belonging to 31 families and 8 orders frequenting carrot flowers. The present findings also corroborate the studies of Kumar et al. (1989) who reported bees as the most frequent visitor of carrot blossoms. Abrol (2006b) found that the dwarf honeybee *Apis florea* L. was the most abundant flower visitors and comprised more than 94% of the total flower visiting insects.

4.3.3 Cole Crops

Sihag (1985a) reviewed the floral biology, melottophily and pollination ecology of cruciferous crops. Cole crops (*Brassica oleracea*) are generally self-sterile or self-incompatible (Kakizaki 1922; Sihag 1985a). Sharma et al. (1974) reported that 34 species of insects visited cauliflower bloom at solan (Himachal Pradesh, India). Kakkar (1980) reported that population of *A.c. indica* on this crop at Solan was highest following by *Eristalis* spp., *Halictus* Sp., *Lassioglossum* sp. and other insects. Adlakha and Dhaliwal (1979) stated that *A.c. indica* was a better pollinator of cauliflower than *A. mellifera*. Verma and Joshi (1983) concluded that *A.c. indica* was the superior pollinator of this crop than other insects. Pod setting, number of seeds per pod and seed weight were increased by bee pollination. Tewari and Singh (1983) also observed higher pod set in this crop near the hives of *A.c. indica* which was correlated with the abundance of bees. At Hisar, Sihag (1986) studied the pollinators and pollination requirements of cauliflower (*B.o.* var. *botrytis*). *Andrena leaena*, *Apis florea* and *Apis dorsata* were the dominant visitors to this crop; and *Melissodes* sp., *Xylocopa fenestrata*, *Pithitis smaragdula*, *Polistes* sp., some dipterns and lepidopterans visited in small numbers. Foraging behaviour revealed that only honeybees and solitary bees acted as pollinators (Sihag 1986, 1988). Bee pollination (open plots) resulted increase in mean pod (siliqua) length (2.5 times), pods/plant (75 times), number of seeds per pod (4.4 times), weight of seeds per ha (250 times) over the caged plots. Therefore utilization of honeybees for pollination of this crop was recommended. Alam et al.(1987a) studied pollination in cauliflower at Gazipur (Bangladesh). Honeybee (*Apis cerana*) visited the flowers. Open plots had 11.5 seeds per siliqua compared with nine seeds per siliqua in caged plots. Percentage of filled seeds was 169.70 and 54.20 for the two treatments.

4.3.4 Eggplants

Kakizaki (1931) reported that in most of his crosses of egg plant (*Solanum melongena*) the first harvest time was earlier and production exceeded the best by 17%. Capinpin and Alviar (1949) also reported that hybrids fruited earlier than the parents.

4.3.5 Okra

Purewal and Randhawa (1947) reported that okra (*Hibiscus esculentus*) was self-fertile. However, 4–18% cross-pollination also occurred. Chaudhary et al. (1973) reported *A.c. indica* and *Halictus* sp. as the chief pollinators of okra. Weight and length of capsules of okra and seed number were found to be significantly higher in open pollinated than in bagged flowers (Mishra and Gupta 1987).

4.3.6 Onion

Sihag (1985c) reviewed the floral biology and fertility status of onion (*Allium cepa*). Due to the presence of protandry, bee pollination in this crop seemed essential. Jadhav (1981) reported that on Patna-Red variety of onion, more than 70% of the insect pollinators were honeybees. Kumar et al. (1985) and Singh and Dharamwal (1970) also reported high increase in yield of insects pollinated plants. Rao and Lazar (1980) found that *A.c. indica*, *A. florea* and *Trigona iridipennis* constituted 6.83, 42.76 and 44.56 more fruits than the bagged ones. Bee pollinated umbels had 9.8% seed set with an average of 4.2 seeds whereas bagged umbels had 9.8% and 1.9 seeds. Mode of pollination even influenced the quality. The weight of 1,000 seeds and seed germination from open pollinated and bagged umbels were 0.6 g, 0.3 g, and 90 and 7.5%, respectively. Of the several pollinating insects visiting onion flowers under temperate conditions of Kashmir *Megascolia flavifrons* was an important pollinator of onion flowers (Abrol 2009). Abrol (2010a, b) found *Apis florea* as a predominant pollinator of onion flowers.

4.3.7 Pumpkin

Because the flowers of pumpkin (*Cucurbita pepo*) are unisexual, the mechanical transfer of pollen is essential for fruit set. Atwal (1970) recorded that pollinating insects visited the flower from 0700 to 1030 h and ceased when the flowers began to close. Bhambure (1958b) studied the importance of honeybees in pollination of cucurbits. Honeybees and bumblebees were reported to be the chief pollinators of pumpkin at Ludhiana (Punjab, India) (Brar and Nandpuri 1969). Grewal and Sidhu (1979) compared the fruit set and fruit shape in plants of *C. pepo* caged to exclude bees, caged with 20–30 *Pithitis smaragdula* females and uncaged plants. Bee pollination lessened the misshapen (deformed) fruits and increased the fruit set compared with open pollinated and caged plants without bees. Five bee visits to a flower were considered to be essential for the normal fruit set. Hayase (1954) stated that the seed number and fruit weight was increased in proportion to the amount of pollen deposited on the stigma.

4.3.8 Radish and Turnip

Radish (*Raphanus sativus*) and turnip (*Brassica rapa*) were found to be self-incompatible (Sihag 1985a). Therefore, external agents were required for pollination. *Andrena leaena*, *A. dorsata* and *A. florea* were the dominant visitors to these crops; *Mellissodes sp.*, *Xylocopa fenestrate*, *Pithis smaragdula*, *Polistes* sp., some dipterns and lepidopterns visited in small numbers. Only the honeybees and solitary bees collected pollen and acted as pollinators. In open pollinated plots where pollinating insects were present in two crops, mean pod length increased by 2.5–3 times, pods/plan by 17–27 times, number of seeds per pod by 4–5 times, weight of seeds/plant by 60–150 times and seed yield/ha by 60–120 times over the caged plots (where insects were excluded). In these crops, utilization of managed pollination for higher seed yield was recommended (Sihag 1986).

4.3.9 Vegetable Sponge and Ribbed Gourd

Vegetables sponge (*Luffa cylindrical*) was monoecious, having male and female flowers on the same plant (Singh 1958). *Xylocopa fenestrate* visited the crop for pollen and nectar and acted as a candidate pollinator of these crop plants (Sihag 1993). In the ribbed gourd (*L. acutangula*) sphingid moth was also reported to the pollinator (Shrivastava 1991).

4.3.10 White Flower Gourd

White flower gourd/bottle gourd (*Lagenaria ciceraria*) had unisexual flowers. *X. fenestrata* visited the crop for pollen and nectar (Sihag 1990) and acted as pollinator (Sihag 1993). Shah and Patel (1966) obtained a higher per cent age of fruit set with hand pollination than was obtained in the open, indicating an insufficiency of pollinating agents in the area. Bug (*Crytopeltis tenuis*) was reported to be the pollinator of this crop at Rewa, India (Shrivastava 1991).

4.4 Oilseed Crops

4.4.1 Cruciferous Oilseeds

Sihag (1985a) reviewed the floral biology, melittophily and fertility status of cruciferous oilseed crops. Insect pollination was found to increase the seed yield in almost all the crops. Kapil et al. (1971) reported that *A. florea*, *A. dorsata* and *Andrena ilerda* were the most important pollinators of rapeseed and mustard in the plains of Punjab and Haryana (India). Other species included *Megachile*, *Nomia*, *Nomioides*, *Colletes*, *Ceratina*, *Anthiphora* and *Xylocopa spp.* Kapil and Kumar (1975) also reported the foraging behaviour of *A. dorsata* on *Brassica juncea* and found that most nectar collectors resulted in pollination. On mustard, Naim and Phadke (1976) reported that *A. cerana* had high degree of fidelity but *A. dorsata* was not present. Rahman (1940) studied the pollinators of *Brassica napus* in India. He concluded that the dwarf honeybee (*Apis florea*), the wild bees (*Andrena ilerda* and *Halictus* sp.) and the fly (*Eristalis tanax*) were the most important pollinators. Latif et al. (1960) showed the rapeseed production in fields with bees was more than double than that in the fields where bees (*A. cerana*) were absent. Mohammad (1935) stated that in toria (*Brassica campestris* var. toria) and brown-seeded sarson (*B. campestris* var. brown sarson) 12% and 20% of bagged flowers set, whereas 91% of the yellow sarson (*B. campestris* var. yellow sarson) in bags set. He also stated that plants from cross-pollinated seeds were more productive. Howard and Khan et al. (1916) indicated that *B. juncea* was self-fertile but abetted by wind. Akhtar (1932) indicated that *B. nigra* was largely self-sterile. Sihag (1986) studied the pollination requirements of 6 cruciferous oilseed crops viz., *B. campestris* var. toria, *B. napus*, *Eruca sativa*, *B. carinata*, *B. hirta* and *B. juncea* former three species were self-incompatible whereas latter three were self-incompatible. *Apis florea*, *A. dorsata, A. melifera*. *Andrena ilerda* and *Andrena leaena* were the dominant visitors whereas some solitary bees, wasps, dipterans and lepidopterans were the non-dominant visitors. Only the honeybees and solitary bees collected pollen and acted as pollinators of these crops. Experiments on crop yields carried out in open and caged plots (or bagged branched) revealed that in self-incompatible crops mean pod (Sililqua) length, number of seeds per pod, weight of seeds per plant and weight of seeds per ha were significantly greater in open plots. Self-compatible crops were also found to be benefited by the insects visits. Singh (1958), Deodikar and Suryanarayana (1972) Bisht et al. (1980) and Bhalla et al. (1983a) also reported the role of honeybees and insect pollinators in the seed production of some of these crops. Ohsawa and Namai (1987) used artificially reared drone flies (*Eristalis cerealis*) as pollinators in isolation cages of *B. campestris* cv. *Nazawana* and *B. juncea* cv. *Kikarashina*. In cages without flies, pod set was 19% in *B. campestris* and the number of seeds per flower was very low. *B. juncea* had a pod set of 91% and 11.9 seeds/flower. By increasing the number of flies, there was a significant correlated increase in seed set. In both cultivars, a seed set of nearly 100% was achieved with a pollinator level of 6 flies/plant.

4.4.2 Flax

Henry and Chin (1928) reported that honeybees, a small bee and thrips were visitors to flax (*Linum usitatissimum*) in India, and thrips were the important agents in cross-pollination. However, no pollination requirements of this crop are available from Asia.

4.4.3 Niger

In niger (*Guizotia abyssinica*), cross-pollination was common as Howard et al. (1919)found that the stigma lobes rarely curled back sufficiently to touch their own style; indicating that the plants were self-sterile. This explains why isolated plants set no seeds. Although the flowers are hermaphrodite, they are not self-pollinating. Bhambure (1958a) confined plants in two cages (1.2 × 1.2 m) and tagged 40 flower heads in each cage. In one of these, bees (*A. cerana*) were released. In the cage with bees, 40 seeds per head developed. In the one without bees, only 15 seeds per head were obtained. Chavan (1961) also obtained similar data. Honeybees (*Apis cerana* and *A. dorsata*) were the efficient pollinators of niger at Pune (India) (Rao and Suryanarayana 1990). Average number of filled grains/head was 20 times higher, number of unfilled grains was 22 times higher in open pollinated plots over the caged one. Average seed yield was 3 times higher in plots caged with *A. cerana* bees and 4 times higher in open pollinated plots over the control indicating the need for managed pollination.

4.4.4 Oil-Palm

Hardon and Turner (1967) considered that the flowers of oil palm (*Elacis guineensis*) in Malaya were wind pollinated. However, large amount of pollen was produced which was distributed at least 55 ft from the original source. No other information on this tree is available from Asia.

4.4.5 Peanut

On peanut (*Arachis hypogea*), *A. cerana* generally ignored the flowers (Divan and Salvi 1965). But Heide (1923) stated that the flowers were visited actively and persistently by *A. cerana* from 0700 to 2100 h. Shibuya et al. (1955) associated one seededness with insufficient pollen on the stigma. Srinivasalu and Chandrasekaran (1958) reported that in peanut varied differences existed for cross-pollination in relation to the protrusion of stigma out of the keel.

4.4.6 Sesame

Srivastava and Singh (1968) obtained yield increases of 43.66% over the best parents when they crossed cv. Meghna with local cultivars, and 38% when they crossed Cv. Meghna with wild plants of sesame (*Sesamum indicum*). This indicated that hybrids might be produced that would out yield current cultivars. They strongly indicated that insect pollination would be beneficial in the production of hybrid seed in sesame. *A.c. indica* was the most frequent visitors to sesame (Rao et al. 1981) and the bees were particularly active in the morning foraging for nectar and pollen. Seed yield was maximal in plants visited by *A. dorsata*.

4.4.7 Sunflower

Sihag and Kaur (1994) reviewed the floral biology and pollination ecology of sunflower (*Hilianthus annuus*). Majority of research on sunflower pollination indicate that honeybees are the primary pollinating agents and that colonies should be provided to the field for higher seed yield (Barbier and Abid 1966; Sihag and Kaur 1994). Panchabhavi and Devaiah (1977) listed the pollinators of sunflower. Khalifman (1959) stated that heavy honeybee visits to sunflower not only increased seed set but also limited the damage by the sunflower moth (*Homoeosoma nebulella*), a delayed effect called hysteresis. Honeybees and other wild bees were the insect visitors to sunflower (Vaish et al. 1978; Swaminathan and Bhardwaj 1982). Visits of *A.c. indica* and other insect pollinators was high during forenoon (Deodikar et al. 1976;

Panchabhavi and Devaiah 1977; Vaish et al. 1978); and were positively correlated with RH and temperature (Deshmukh 1977; Vaish et al. 1978; Swaminathan and Bhardwaj 1982). *A.c. indica* and *Xylocopa* spp. were reported to be the most important pollinators of sunflower (Shrivastava and Shrivastava 1986). Crops like moongbean, sesame and niger when grown in the vicinity reduced the visits of pollinators to sunflower to negligible. Several studies made in India clearly reveal the role of honeybees in the seed production of sunflower, and in their absence seed yield was low (Sihag and Kaur 1994). Dhoble and Shinde (1982) reported that seed set in sunflower covered with nylon net was markedly lower than that of an open pollinated crops. Much higher seed yield and weights from plots with *A. cerana* colonies than from plots without bees were reported by Deodikar et al. (1976) and Thakar (1974). Panchabhavi et al. (1976) and Channabasavanna (1979) recorded 27% increase in seed set in the field where bee colonies were moved. Shrivastava and Shrivastava (1986) reported that in pollinated plants there were 658 grains was full. Bhattacharya et al. (1982) indicated that the honeybees were the chief-pollinators of sunflower, and excluding honeybees by bagging of floral heads resulted in the reduction in seed yield, seed weight, seed viability and oil contents. Wakhle et al. (1978) also reported increase in oil contents by bee pollination in sunflower. Abrol (1996) recorded *Bombus haemorrhoidalis*, *Apis cerana*, *Xylocopa aestuans*, *Halictus sp.*, *Syrphus sp.*, *Formica sp.*, butterflies and moths as important pollinators of sunflower.

4.5 Pollination of Forage Crops

4.5.1 *Alfalfa*

Alfalfa (*Madicago sativa*) needed specialist pollinators for pollination (Sihag 1988, 1992), because flowers of this crop required tripping by suitable pollinators. Some solitary megachild bees were identified as specialist pollinators of this crop. *A. florea, Nomioides spp. Pithitis smaragdula, Megachile flavipes* and *M. nana* were the common insect pollinators of this crop at Hisar (Kapil et al. 1974; Kapil and Jain 1980) whereas *M. flavipes* and *Ceratina binghami* were the efficient pollinators of alfalfa at Ludhiana (Goyal and Atwal 1975). But, these bees deserted the crop bloom in favour of *Parkinsonia aculeata* which also bloomed at the same time (Sihag 1982). Moriya et al. (1956) showed that the higher percentage of pods developed from flowers that were pollinated the same day after they opened. 7,744 and 13,488 bees per acre gave 3.64 and 20.3 kg per acre yield compared with 0.3 kg per acre for plants caged to exclude insects (Kapil et al. 1970).

4.5.2 *Berseem*

Berseem (*Trifolium alexandrinum*) is a self-compatible forage crop, but tripping is essential for seed set (Chowdhury et al. 1966), wind however, was unimportant.

But, insect pollination was absolutely necessary for profitable seed production (Latif 1956; Narayanan et al. 1961). The bee species which visited Berseem flowers at Ludhiana (Punjab, India) included *A. florea*, *A. mellifera*, *A. dorsata*, *M. flavipes* and *Pithitis smaragdula* (Dhaliwal and Atwal 1976). Narayanan et al. (1961) obtained from 19.58 to 70.54 seeds per head of open pollinated Berseem plants, but only 0.27–0.64 per head where insects were excluded by 16-mesh wire gauge cages. He reported that honeybees were the primary pollinators of Berseem, as they collected both nectar and pollen. Shelar and Suryanarayana (1983) recommended 12.25 colonies per ha of *A. cerana* for the pollination of Berseem.

4.5.3 Vetch

Vetch (*Vicia sp.*) required insects for pollination. Fertilization of *V. villosa* was considered impossible when the plant was isolated from insects (Svetsugo and Kobayashi 1952). The value of honeybee pollination in seed setting of cicer milk vetch (*Astragalus cicer*) was studied at the Gifu (Japan) Agricultural experimentation station (Anonymous 1954). Seed production in cages where bees were excluded was only about 70 lb/acre; in cages with honeybees it was almost double, 130 lb/acre and in open plots, 980 lb/acre. The difference was due to the difference in level pollination.

4.6 Pollination of Fibre Crops

4.6.1 Cotton

In cotton (*Gossypium* spp.) usually only half of the flowers were reported to produce mature bolls (Sen and Afzal 1937). Afzal and Khan (1950) reported 2% natural crossing with 7 or 8 visits per flower by the insects daily. In India, principally *A. dorsata*, *A. florea*, *Anthophora confuse* and *Elis thoracica* were the visitors (Khan and Afzal 1950). Afzal and Trought (1934) also included that mote formation might be due to defective pollination. The stigma is normally receptive to the pollen the time the flower opens or before, but receptively was found to drop sharply after about noon (Janki et al. 1968). Mahadevan and Chandy (1959), using cultivars M.U.T. and 'M.C.U.-2' in India obtained 23–34% and 40–53% respectively more cotton in open plots than in plots caged to exclude bees. Sidhu and Singh (1962) also in India, compared production in cages with *A.c. indica* and *A. florea*, and in cages without pollinators. They obtained an increase of 17.45–18.98% in favour of the pollinating insects. The increase was attributed to more and larger bolls. Similar results were also reported on Asiatic cotton by Tanda and Goyal (1978, 1979a, c) and Tanda (1983, 1984). Foraging behaviour of *A. mellifera* and *A.c. indica* on desi (Asiatic) cotton was compared by Tanda and Goyal (1979b). They confirmed that wind pollination was not involved in G. arboretum pollination (Tanda and Goyal 1979d).

4.6.2 Kenaf

Kenaf (*Hibiscus cannabinus*), a fibre crop, has been classified as across-pollinated crop. In a hand pollinated experiment, Dubey and Singh (1968) observed that more than 50% setting took place between 5 and 9 a.m., however, it began at 23, 00 h and extended up to next 14, 00 h. Pollinators and pollination requirements of this crop are not known.

4.6.3 Sunhemp

Abrol and Kapil (1988) enlisted the pollinators of sunhemp (*Crotolaria juncea*). Sihag (1990) observed that *Xylocopa fenestrata* gathered nectar and pollen from sunhemp. This crop was not pollinated by *A.c. indica*, as they collected pollen by boring through the lateral portion of the keel (Jitendra Mohan 1973). But *Xylocopa fenestroides* when caged on the flowering plants gave 65% seed set against 26% in the open field. Grewal and Singh (1979) listed the insect visitors to this crop. *Megachiie Lanata*, *M. fasciculata* and *X. fenestrate* were the most important pollinators.

4.7 Pollinators of Pulses Crops

4.7.1 Pigeon Pea

A high degree of cross-pollination ranging from 5 to 40% was observed in pigeon pea (*Cajanus cajan*) by Matta and Dave (1931). Williams (1977) reported that *Apis dorsata*, *Chalicodoma* sp. and some others were the dominant visitors to pigeon pea at Hyderabad (India). At Ludhiana (India), 5 species of bees visited pigeon pea viz. *A. mellifera*, *A. dorsata*, *Xylocopa sp. Megachile lanata* and *Ceratina binghami*. *A. florea* was not found to visit pigeon pea at all (Brar et al. 1992). Experiment carried on seed yield revealed that in caged plots with *A. mellifera*, caged plots without bees and open plots, number of pods/plant ranged from 280 to 326, 284.2 to 317.2 and 934.0 to 1128.4, respectively whereas respective figures for seed yield (g)/plot (2×2 m^2) were 47.94 – 50.04, 48.84 – 50.68 and 195.39 – 203.9. *A. mellifera* alone did not contribute to the seed yield, role of other bee species was also there.

4.8 Pollination of Spices, Condiments and Beverages etc.

4.8.1 *Cacao*

Gnanaratnam (1954) studied pollination in cacao (*Theobroma cacao*). Flowers of cacao which were bagged to exclude insects were invariably shed indicating that flowers are not self-pollinating. Some plants were found to be self-incompatible, some were male sterile or sterile. Therefore, many of the flowers were doomed to be shed. The pollen of cacao was found to be sticky and was released in petal pouches where wind was unlikely to disturb it. Midges were found to be the pollinators. Two species viz. *Forcipomyia quasiingrami* and *Lasiohela nana* were important (Barroga 1964). Fruit set in flowers of cacao in Malaysia was 5.2%. Flowers caged to exclude insects set no fruit. *Forcipomyia* carried pollen on the body needed to effect pollination (Ibrahim 1987).

4.8.2 *Cardamom*

On cardamom (*Elettaria cardamomum*) honeybees constituted 98% of the flower visitors and even one bee visit was sufficient to pollinate the flower (Siddappaji and Channabasavanna 1980). Cardamom panicles exposed from the layer of leaf mulch to open pollination by bees improved fruit set by about 14 times (Pattanshetti and Prasad 1974). The flowers pollinated by bees gave 66% fruit set, but only 1% in control flowers (Pattanshetti and Prasad 1973). Chandran et al. (1980) noticed an increase of 37.2 and 27.9% fruit set in plants having access to bee visits compared with plants having no insect visits. Madhusoodan and Dandin (1981) also reported that plots supplied with bee hives gave 35–45% higher yield than control plots.

4.8.3 *Chicory*

In chicory (*Chichorium intybus*) fertilization within and between heads occurred as a result of insect pollination (Dinakaran and Sundaraj 1960). No further information is available from Asia on this crop.

4.8.4 *Fennel, Coriander and Cumin*

In fennel (*Foeniculum vulgare*), Narayanan et al. (1960) found that *Apis florea* constituted 81% of the visitors to fennel in India, and they recommended that cultivars more attractive to bees be developed. They also recommended keeping of colonies around or in fennel fields. Shelar and Suryanarayana (1981) made some preliminary studies on the pollination of coriander. Sihag (1985b) reviewed the floral biology, melittophily and pollination ecology of umbeliferous crops. Flowers of fennel (*Foeniculum vulgare*), coriander (*Coriandrum sativum*) and cumin (*Cuminum cyminum*) were protandrous and needed foreign pollen vector for pollination. Sagar (1981) demonstrated the role of insects in cross pollination of fennel. Sihag (1986) studied the pollinators and pollination of these crops. *Andrena leaena*, *Apis florea*, *Apis dorsata* and some dipterns were the dominant visitors to these crops, whereas some solitary bees, wasps and lepidopterans were non-dominant visitors. Only honeybees and solitary bees collected pollen from these crops and acted as pollinators. The experiment on yield parameters revealed significant increases in open pollinated plots over the caged plots. Increases in number of seeds/plant from 2 to 5.5 were from 2.5 to 6 times, in weight of seeds/plant from 2 to 5.5 times, and weight of seeds/ha from 2 to 5 times in plots receiving insect visit (open) over those which did not receive any insect visit (caged). Abrol (1985) found *Apis florea* as most dominant pollinator of fennel, *Foeniculum vulgare*. The other insect visitors included some bees, wasps and ants. Sihag (1986) recommended utilization of managed pollination for getting higher seed yield in these crops.

4.8.5 Tea

Tea (*Camellia sinensis*) is virtually self – sterile and almost entirely cross- pollinated crop (Wu 1967). Self pollen grain tube was found to grow much slowly in the style than foreign pollen tube (Simura and Oosone 1956).

References

Abrol DP (1985) Analysis of biophysical interactions in causing forgaging behaviour of some bees- a study in bioenergetics. PhD thesis, Haryana Agricultural University, Hisar, 286pp

Abrol DP (1988a) Ecology and behaviour of three bee species pollinating loquat (*Eriobotrya japonica* Lindley). Proc Indian Nat Sci Acad 54 B:161–163

Abrol DP (1988b) Insect pollination studies in Almond (*Prunus amygdalus* L.). Curr Sci 57(7):397–398

Abrol DP (1989a) Studies on abundance, diversity, behaviour and importance of native pollinators for crop production. Korean J Apic 4(2):25–40

Abrol DP (1989b) Insect pollinators of cherry (*Prunus avium* L.). J Anim Morphol Physiol 36(2):243–245

Abrol DP (1989c) Studies on ecology and behaviour of insect pollinators frequenting strawberry blossoms and their impact on yield and fruit quality. Trop Ecol 30(1):96–100

Abrol DP (1996) Sunflower pollination: abundance and diversity of pollinating insects and their effect on seed yield. Indian Bee J 58(2):60–63

Abrol DP (1997) Bees and beekeeping in India. Kalyani Publishers, Ludhiana, 450pp

Abrol DP (2000) Insect pollinators of kiwifruit (*Actinidia deliciosa*). Indian Bee J 62(3–4): 55–57

Abrol DP (2005) Foraging ecology of insect pollinators visiting cherry flowers and their impact on fruit production. Korean J Apic 20(2):159–168

Abrol DP (2006a) Diversity of pollinating insects visiting litchi flowers (*Litchi chinensis Sonn.*) and path analysis of environmental factors influencing foraging behaviour of four honeybee species. J Apic Res Bee World 45(4):180–187

Abrol DP (2006b) Factors influencing flight activity of *Apis florea* F, an important pollinator of *Daucus carota* L. J Apic Res Bee World 45(2):2–6

Abrol DP (2009) Bees and Beekeeping in India. 2nd Edition Kalyani Publishers Ludhiana, India, 719 p

Abrol DP (2010a) *Megascolia flavifrons* – an unusual pollinator of onion flowers. Adv Pollen Spore Res 28:51–56

Abrol DP (2010b) Foraging behaviour of *Apis florea* F., an important pollinator of *Allium cepa* L. J Apic Res Bee World 49(4):318–325

Abrol DP, Kapil RP (1988) Pollination studies in Crotolaria Juncea L. Sci Cult 54(7):243–244

Abrol DP, Kumar A (2009) Foraging activity of *Apis* species on strawberry blossoms as influenced by pesticides. Pak Entomol 31(1):57–65

Abrol DP, Bhat AA (1990) Studies on `Thai sac brood virus' affecting indigenous honeybee Apis cerana indica Fab. colonies – prospects and future strategies - I.Journal of Animal Morphology and Physiology 37(1/2):101–108

Abrol DP, Bhat AA, Khan AR (1990) Factors affecting pollination activity of honeybees and fruit set in almond. In: Veeresh GK, Kumar ARV, Shivashankar T (eds) Social insects: an Indian perspective. ISUSI-Indian, Bangalore, pp 50–53

Abrol DP, Sharma D, Monobrullah M (2005) Abundance and diversity of pollinating insects visiting peach and plum flowers and their impact on fruit production. SKUAST J Res 4(1): 38–45

Adlakha RL, Dhaliwal HS (1979) Insect pollination of seed cauliflower (*Brassica oleracea var. botrytis*) with particular reference to the role of honeybees. Indian Bee J 41(1/2):13–16

Afzal M, Khan H (1950) Natural crossing in cotton in western Punjab. Agron J 42:14–19, 89–93, 202–205, 236–238

Afzal M, Trought T (1934) Motes in cotton. I. Punjab-American cotton. Indian J Agric Sci 4:554–575

Ahn SB, Kim IS, Choi WS, Choi KM (1989) Survey on the use of honeybee pollination of strawberries grown in plastic greenhouse. Korean J Apic 4(1):1–8 (Korean)

Akhtar AR (1932) Studies in Indian *Brassicas*. I. Sterility and selective pollen tube growth. Indian J Agric Sci 2:280–292

Alam MZ, Quadir MA, Ali M (1987a) Pollinating behaviour of honeybee, *Apis indica* F. and its influence on seed production of cauliflower. Bangladesh Hortic 15(1):25–30

Alam MZ, Quadir MA, Ali M (1987b) Effect of bee pollination on seed production of carrot, *Daucus carota* L. Bangladesh J Bot 16(2):199–201

Annand PN (1926) Thysanoptera and the pollination of flowers. Am Nat 60:177–182

Anonymous (1954) Honeybees and the seed production of Chinese milk vetch. Gifu Agr Expt Sta Bull, 11pp (in Japanese)

Atwal AS (1970) Biology, ecology and utilization of insects other than Honeybees in the pollination of crops. Final Research Report (1965–1970) PL-480 Project, Punjab Agriculture University, Ludhiana, 115pp

Badiyala SD, Garg R (1990) Studies on the pollination and fruit production by *Apis mellifera* l. in seven cultivars of Litchi (*Litchi Chinensis* Sonn.). Indian Bee J 52(1–4):28–30

Barbier EC, Abid M (1966) Pollination and seed formation in sunflower. Al Awamia 21:63–83

Barroga SF (1964) Progress report on the study of insects, particularly midges associated with pollination of *Theobroma Cacao*, April 1963. Philipp J Plant Ind 29(3/4):123–133

Bhalla OP, Verma AK, Dhaliwal HS (1983a) Foraging activity of insect pollinators visiting stone fruits. J Entomol Res 7:91–94

Bhalla OP, Verma AK, Dhaliwal HS (1983b) Foraging activity of insect pollinators visiting stone fruits. J Entomol Res 7(2):91–99

Bhambure CS (1958a) Effect of honeybee activity on niger (*Guizotia abyssinica* Cass) seed production. Indian Bee J 20:189–191

Bhambure CS (1958b) Further studies on the importance of honeybees in pollination of cucurbitaceae. Indian Bee J 20(10):148–149

Bhattacharya P, Samuli RC, Ghos MR, Dasgupta SK, Roy A (1982) Sunflower seed yield as influenced by pollination and insect pests. In: Proceedings of the 10th international sunflower conference, Sulfers Paradise, pp 132–234

Bisht DS, Naim M, Mehrotra KN (1980) Studies on the role of honeybee in rapeseed production. In: Proceedings of the 2nd international conference on apiculture tropical climate, New Delhi, pp 491–496

Brar JS, Nandpuri KS (1969) Study on floral biology of *Cucurbita pepo* Linn. J Res Ludhiana (Supplement) 6(3):186–792

Brar HS, Jhaji HS, Gatoria GS (1992) Abundance and activity of the bee visitors of pigeon pea (*Cajanus cajan* (L.) Millsp.) and role of *Apis mellifera* L. in its pollination. Indian Bee J 54(1–4):76–80

Capinpin JM, Alviar MA (1949) Hetrosis in eggplant. Philipp Agric 33:126–141

Chandran K, Rajan P, Joseph D, Suryanarayana MC (1980) Studies on the role of honeybees in the pollination of cardamom. In: Proceedings of the 2nd international conference on apiculture tropical climate, New Delhi, pp 497–504

Channabasavanna GP (1979) Role of insect pollinators in sunflower production. Curr Res 8(1):1–3

Chaturvedi RB (1965) Preliminary studies in the sex distribution, pollination and fruit development in litchi (*Litchi chinensis* Sonn.). Allahabad Farmer 39(2):49–51

Chaudhary B, Choomsai MLA, Menon MGA (1973) Insect pollination in some vegetable crops. Haryana J Hortic Sci 2(1/2):56–62

Chavan VM (1961) Niger and safflower. Indian Central Oilseed Company, Hyderabad, 150pp

Cheema GS, Dani PG (1929) Seedlessness in papayas. Agric J India 26(3):206–207

Chowdhury JB, Mehta RK, Joshi AB (1966) Pollination in berseem. Indian J Genet Plant Breed 26:118–120

Das CS, Choudhary R (1958) Floral biology of Litchi (*Litchi chinensis* Sonn.). South Indian Hortic 6(1):17–22

Delaplane KS, Mayer DF (2000) Crop pollination by bees. CABI Publication, Cambridge

Deodikar GB, Suryanarayana MC (1972) Crop yields and bee pollination. Indian Bee J 34:53–64

Deodikar GB, Seethalakshmi VS, Suryanaryana MC (1976) Flower biology of sunflower with special reference to honeybees. J Palynol 12(1/2):115–125

Deshmukh SD (1977) Effects of bee visits and climate on sunflower pollination. Sci Cult 43(12):543–545

Dhaliwal JS (1975) Insect pollination in ber (*Ziziphus mauritiana* Lamk.). Curr Sci 44(14):527

Dhaliwal JS, Atwal AS (1976) Note on the effect of air temperature, relative humidity and wind velocity on bees visiting berseem at Ludhiana. Indian J Agric Sci 46(1):50–51

Dhoble YS, Shinde YM (1982) Role of insect pollinators for effective seed setting in sunflower. J Maharastra Agric Univ 7(1):103

Dinakaran M, Sundaraj DD (1960) Preliminary studies on chicory (*Chicorium intybus* L.) with special reference to floral biology. S Indian Hortic 8(1/2):23–27

Divan VV, Salvi SR (1965) Some interesting behavioual features of *Apis dorsata* Fab. Indian Bee J 27(1):52

Dubey RS, Singh SP (1968) Note on stigma receptivity in kenaf. Indian J Agric Sci 38(1): 195–197

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, New York, p 684

Fukae Y, Hamachi F, Tsujikava Y (1987) A detailed analysis of the effect of honeybee introductions on the pollination of persimmons. Honeybee Sci 8(4):167–171

Gnanaratnam JK (1954) Pollination mechanism of cacao flower. Trop Agric (Ceylon) 110:98–104

Goyal NP, Atwal AS (1975) Studies on the relation of the population of insect pollinators with seed production in lucerne (Medicago sativa), Indian J Ecol 2:58–61. Keywords: bee botany, India.

Goyal NP, Singh M, Kandoria JL (1989) Role of insect pollination on seed production in carrot, *Daucus carota* L. Indian Bee J 51(3):89–93

Grewal GS, Sidhu AS (1978) Insect pollinators of some cucurbits in Punjab. Indian J Agric Sci 48(2):79–83

Grewal GS, Sidhu AS (1979) Note on the role of bees in the pollination of *Cucurbita pepo*. Indian J Agric Sci 49(5):386–388

Grewal GS, Sidhu AS (1980) Studies on insect pollination in *Cucumis melo* Linn. In: Proceedings of the 2nd international conference on apiculture tropical climate, New Delhi, pp 527–544

Grewal GS, Singh G (1979) Notes on insect pollinators of sunhemp in Punjab. Indian J Agric Sci 49(10):822–824

Hardon JJ, Turner PD (1967) Observations on natural pollination in commercial plantings of oil palm (*Elacis guineensis*) in Malaya. Exp Agric 3(2):105–116

Hayase H (1954) Cucurbita-crosses. Iv. The development of squash fruit as affected by placement of pollen on stigma. Hokkaido Nat Agric Stn Res B 64:22–25 (In Japanese)

Heide FFR (1923) Biological observations of Arachis hypogea L. (Dutch East Indies). Alg Proefsta V Landb Meded 14:1–19

Henry AW, Chin Tu (1928) Natural crossing in flax. Am Soc Agron J 20:1183–1192

Howard A, Howard GLC, Rahman KA (1919) Studies in the pollination of Indian crop. Indian Dept Agric Mem Bot Serv 7:214–272

Ibrahim AG (1987) Effects of insects pollinators on fruit set of cocoa flowers. In: Proceedings of the 10th international cocoa research conference, Santo Domingo, Dominican Republic, pp 303–306, 17–23 May 1987

Iyer CPA, Randhawa GS (1965) Hybridization studies in grapes: investigations on the direct influence of pollen on some fruit and seed characters. Indian J Hortic 22(2):107–121

Jadhav LD (1981) Role of insects in the pollination of onion (Allium cepa) in the Maharastra state, India. Indian Bee J 43(3):61–63

Janki RP, Singh R, Prakash R, Haque MF (1968) Floral biology of cotton (Gossypium spp.). Indian J Agric Sci 38(3):528–535

Jitendra Mohan KV (1973) Some observations on the bee pollination in sunhemp (*Crotolaria juncea*) and their importance in breeding work. Jute Bull 35:214–216

Kakizaki Y (1922) Self-sterility in Chinese cabbage. J Hered 13:374–376

Kakizaki Y (1931) Hybrid vigor in egg-plant and its practical utilization. Genetics 16:1–25

Kakkar KL (1980) Prospects of bees as pollinating agents of cauliflower. In: Proceedings of the 2nd international conference on apiculture tropical climate, New Delhi, pp 545–556

Kamato K, Yoshida M, Kurihara A, Makino Y (1967) Studies on pollen sterility of peach Hiratsuka Hort. Res Stn Bull Ser A 6:91–104 (In Japanese)

Kanwar SM (1987) Fruit bud formation, pollination and fruit set. In: Apples production technology and economic. Tata McGraw Hill Publishing Company, New York, pp 151–181

Kapil RP, Jain KL (1980) Biology and utilization of insect pollinators for crop production. Final Tech Report, Department of Zoology, Haryana Agricultural University, Hisar, 81pp

Kapil RP, Kumar S (1975) Foraging activity of *Apis dorsata* Fab. on Brassica juncea Hook and Thomas. J Bombay Nat Hist Soc 71(2):327–331

Kapil RP, Grewal GS, Kumar S, Atwal AS (1970) Role of *Ceratina binghami* CKII in seed setting of setting of *Medicago sativa* L. Indian J Entomol 32:335–341

Kapil RP, Grewal GS, Kumar S, Atwal AS (1971) Insect pollinators of rape seed and mustard. Indian J Entomol 33(1):61–66

Kapil RP, Grewal GS, Kumar S, Atwal AS (1974) Insect pollinators of alfalfa, *Medicago sativa* L. Indian J Entomol 36(3):214–220

Katayama E (1987) Utilization of honeybees as pollinators for strawberries in plastic greenhouse in Tochigi Prefecture. Honeybee Sci 8(4):147–150

Khalifman IA (1959) Heterosis in plants as the after-effects of pollination by bees (Hysteresis). Bee World 40:303–313

Khan KSAH (1929) Pollination and fruit formation in Litchi. Agric J India 24:183–187

Khan KSAR (1930) Some observations on the pollination of peaches (Prunus persica Benth. and Hook.) Agr Jour India 25(6):492–494

Khan H, Afzal M (1950) Vicinism in cotton. Indian Cotton Grow Rev 4(4):227–239

Khan BM, Shahid M, Choudhary MI (1916) Effect of honeybee pollination on fruit – setting and yield of loquat. Pak J For 36(2):73–77

Kidavu MG, Nambiyar EK (1925) Pollination in coconut. Madras Dept Agric Yearbook 1925:43–49

Kumar J, Rao KVK (1991) Pollinating efficiency of some bees visitors to the carrot (*Daucus carota* L.) crop in mid hills of Himachal Pradesh (India). Indian Bee J 53(1–4):34–38

Kumar J, Mishra RC, Gupta JK (1985) The effect of mode of pollination on *Allium species* with observations on insects as pollinators. J Apic Res 24(1):62–66

Kumar J, Rao KVK, Gupta PR, Dogra GS (1989) Temporal distribution of bees (Hymenoptera: Apoidea) on spring flowering crops in mid hills of Himachal Pradesh, India. Indian Bee J 51(2):55–58

Latif A (1956) Role of *Apis indica* F. in the pollination of Egyptian clover (Trifolium alexandrinum Linn.). Pak J Sci Res 8(1):48–50

Latif A, Qayyum A, Abbas M (1960) The role of Apis indica in the pollination of (oil seeds) “Toria” and “Sarson” (Brassica campestris var. Toria and Dichotoma). Bee World 41: 283–286

Madhusoodanan KJ, Dandin SB (1981) Flower biology of cardamom (Elettaria cardamomum L.) in relation to the foraging behaviour of honeybees (Apis spp.). Indian Bee J 43(4):104–108

Mahadevan V, Chandy KC (1959) Preliminary studies on the increase in cotton yield due to honeybee pollination. Madras Agric J 47:23–26

Mann GS, Singh G (1981a) A note on activity and abundance of flower visiting insects of peach (*Prunus persica* L.) at Ludhiana (Punjab). Prog Hortic 13(3/4):25–27

Mann GS, Singh G (1981b) Activity and abundance of flower visiting insects of almond (*Prunus amygdalus* Matsch) at Ludhiana (Punjab). J Bombay Nat Hist Soc 78(3):617–618

Mann GS, Tanda AS (1984) Activity and abundance of insects visiting grape flowers in Punjab (India). In: Proceedings of the 3rd international conference on apiculture tropical climate, Nairobi, p 139

Matta DN, Dave BE (1931) Studies in *Cajanus indicus*. Indian Dept Agric Mem Bot 19:1–25

Mattu VK, Chaudhary DK, Kumar L (1994) Foraging ecology of *Apis cerana* F. and *Apis mellifera* L. in pollinating stone fruit. Pest Manag Econ Zool 2(1):35–39

McGregor SE (1976) Insect pollination of cultivated crop plants. Agricultural Research Service, United States Department of Agriculture, Handbook, Washington, p 496

Mishra RC, Gupta JK (1987) Effect of modes of pollination on fruit characteristics of okra, *Abelmoschus esculentus* (L,) moench. Proc Indian Nat Sci Acad 53 B(2):157–160

Mohammad A (1935) Pollination studies in toria (*Brassica napus* var. Dicchotoma prain), and sarson (*B. campestris* L. var. Sarson Prain). Indian J Agric Sci 5:125–154

Moriya N, Ikeda J, Hoshino M (1956) Studies on the seed production of alfalfa. 2. Effect of rainfall on seed production. 3. Effect on nitrogen applied before and after the bud formation stage on flowering, pod and seed-setting. Proc Crop Sd Soc Jpn 25(2):111–112 (In Japanese)

Muttoo RN (1952) Uttar Pradesh Government beekeeping station, Jeolikot, District Nainital, Uttar Pradesh - A summary of 14 years work (1938–1952), Indian Bee J 14:40–51

Naik KC, Rao MM (1943) Studies on the blossom biology and pollination in mangoes (*Mangifera indica* L.). Indian J Hortic 1(2):107–119

Naim M, Phadke KG (1976) Bee flora and seasonal activity of *Apis cerana* indica at Pusa (Bihar). Indian Bee J 38(1–4):13–19

Nakanishi T (1983) Preferences of honeybee foraging on male fertile and male-sterile flowers of Japanese apricote (Prunus nume). Honeybee Sci 4(1):1–8

Nand D (1971) Pollination, fruit set and development in carambola (Averrhoa carambola Linn). Indian J Hortic 28:278–284

Nandpuri KS, Brar JS (1966) Studies on floral biology in muskmelon (Cucumis melo L.). J Res Ludhiana 3(4):395–399

Narayanan ES, Sharma PL, Phadke KG (1960) Studies on requirements of various crops for insect pollinators. I. Insect pollinators of saunf (Foeniculum vulgare) with particular reference to the honeybees at Pusa (Bihar). Indian Bee J 22(1/3):7–11

Narayanan ES, Sharma PL, Phadke KG (1961) Studies on requirements of various crops for insect pollinators II. Insect pollinators of berseem-Egyptian clover (Trifolium alaxandrinum) (L.) with particular reference to honeybees and their role in seed setting. Indian Bee J 23(4/6):23–30

Noda M (1987) Utilization of honeybees for the pollination of plum and pear, unattractive to honeybees, in Tokushima Prefecture. Honeybee Sci 8(4):159–162

Ohbayashi N (1976) Protection and utilization of pollinators in watermelon: efficiency of honeybees in watermelon fields. Bull Kamagawa Hortic Exp Stn 23:49–53

Ohsawa R, Namai H (1987) The effect of insect pollinators on pollination and seed setting in *Brassica campestris* cultivar Nozawana and *Brassica juncea* cultivar Kikarashina. Japanese Journal of Breeding 37:453–463

Panchabhavi KS, Devaiah MA (1977) A note on the activities of insect pollinators on sunflower during winter and summer seasons at Bangalore. Curr Sci 6:88–89

Panchabhavi KS, Devaiah MA, Channabasavanna GP (1976) The effect of keeping *Apis cerana indica* F colonies on the seed set of sunflowers, Helianthus annuus Linn. Mysore S Sci 10(4):631–636

Pandey RS, Yadava RPS (1970) Pollination of litchi (Litchi chinensis) by insects with special reference to honeybees. J Apic Res 9(2):103–105

Patel JS (1938) The coconut: a monograph. Madras Government Press, Madras, 262 pp

Pattanshetti HV, Prasad ABN (1973) Bees help pollination of cardamom flowers. Curr Res 2(8):56–57

Pattanshetti HV, Prasad ABN (1974) Exposing the cardamom panicles from a layer of leaf mulch to open pollination by bees and thereby improving the fruit set. Curr Sci 3(8):90

Phadke KG, Naim M (1974) Observations on the honeybees visitation to the litchi (*Nephelium Iitchi*) blossoms at Pusa (Bihar, India). Indian Bee J 36(1–4):9–12

Phoon AGG (1985) Pollination and fruit production of carambola, Averrhoa carambola, in Malaysia. In: Proceedings of the 3rd international conference on apiculture tropical climate, Nairobi, pp 12–133

Pion S, de Oliveira D, Paradis RO (1980) Agents pollinasateurs et productivite du fraisier ‘Redcoat’, *Fragaria* x *ananassa* Duch. Phytoprotection 61:72–78

Purewal SS, Randhawa GE (1947) Studies on *Hibiscus csculentus* (Lady finger) (Okra) I. Chromosome and pollen studies. Indian J Agric Sci 17:129–136

Rahman KA (1940) Insect pollinators of toria (*Brassica napus* Linn. var. Dichotoma Prain) and sarson (*B. campestris* Linn. var. Sarson Prain) at Lyallpur. Indian J Agric Sci 10(3):422–477

Rai KK, Gupta BP (1983) Role of honeybees and other insects as pollinators in apple and pear. Indian Bee J 45(2/3):56–57

Rana RS, Verma LR, Mattu VK (1994) Foraging activity and abundance of insect pollinators on plum bloom. In: Pollination biology-environmental factors and pollination. Rajendra Scientific Publishers, Hisar, pp 20–31

Randhawa GS, Yadav IS, Nath N (1963) Studies on flowering, pollination and fruit development in peach grown under subtropical conditions. Indian J Agric Sci 33(2):129–138

Rao GM, Lazar M (1980) Studies on the behaviour and pollination on onion (Allium cepa L.). In: Proceedings of the 2nd international conference on apiculture tropical climate, New Delhi, pp 580–589

Rao GM, Suryanarayana MC (1990) Studies on the foraging behaviour of honeybees and its effect on the seed yield in Niger. Indian Bee J 52(1–4):31–33

Rao GM, Lazer M, Suryanarayana MC (1981) Foraging behaviour of honeybees in sesame (*Sesamum indicum* L.). Indian Bee J 43(4):97–100

Roubik DW (1995) Pollination of cultivated plants in the tropics. FAO Agricultural Service Bulletin 118, FAO, Rome

Sagar P (1981) Role of insects in cross pollination of fennel crop at Ludhiana. S Res Ludhiana 18(4):388–392

Sakai T, Matsuka M (1988) Honeybee pollination in Japan, with special reference to strawberry production. Honeybee Sci 9(3):97–101

Sakamori M, Yabe K, Osuka M (1977) Growing muskmelon with honeybee pollinators. Res Bull Aichi-ken Agric Res Centre 9:15–21

Sands WN (1928) The bitter-cucumber or peria. Malaya Agric 16(2):32

Sen KRD, Afzal H (1937) Variation in the characters of cotton in relation to the position of boils on the plant. Indian J Agric Sci 7(1):35–47

Shah RC, Patel RM (1966) Studies on pollination in cucurbitaceae. Indian J Genet Plant Breed 26(1):94–97

Sharma PL (1961) The honeybee (Apis indica) population among insects visiting temperate-zone fruit flowers and their role in setting fruit. Bee World 42:6–7

Sharma PL, Sharma BR (1968) Role of insects in the pollination of *Daucus carota* (carrots) and Beta vulgaris (Sugarbeet). Indian J Hortic 25(3/4):216

Sharma PL, Dhaliwal HS, Kakar KL (1974) Insect visitors and pollinators of cauliflower (*Brassica oleracea var. botrytis*) seed crop bloom. Himachal J Agric Res 2(2):74–78

Shelar DG, Suryanarayana MC (1981) Preliminary studies on pollination of coriander (*Coriandrum sativum* L.). Indian Bee J 43(4):110–111

Shelar DG, Suryanarayana MC (1983) Effect of pollination by honeybee (*Apis cerana indica* Fabricious) on the yield of lucerne. Indian J Agric Sci 53(3):190–191

Shibuya T, Sato H, Suzuki M (1955) Morphological and physiological studies on subterranean fluctuation of legume-crops. Proc Crop Sci Soc Jpn 24:16–19, In Japanese, English Summary

Shrivastava U (1991) Insect pollination in some cucurbits. In: Proceedings of the 6th international symposium, Palm, pp 445–451

Shrivastava OS, Shrivastava GP (1986) Nocturnal pollination in sunflower, *Helianthus annuus* L. In: Kapil RP (ed) Pollination biology: an analysis. Inter-India Publications, New Delhi, pp 59–65

Siddappaji C, Channabasavanna GP (1980) Role of honeybees in the pollination of cardamom (*Elettaria cardamomum* (L) Meton). In: Proceedings of the 2nd international conference on apiculture tropical climate, New Delhi, pp 640–648

Sidhu AS, Singh S (1962) Role of honeybees in cotton production. Indian Cotton Grow Rev 16(1):18–23

Sihag RC (1982) Effect of competition with Parkinsonia aculeata L. on pollination and seed production in Medicago sativa L. Indian Bee J 44(4):89–90

Sihag RC (1985a) Floral biology, melittophily and pollination ecology of onion crop. In: Varghese TM (ed) Recent advances in pollen research. Allied Publishers, New Delhi, pp 277–284

Sihag RC (1985b) Floral biology, melittophily and pollination ecology of cultivated cruciferous crops. In: Varghese TM (ed) Recent advances in pollen research. Allied Publishers, New Delhi, pp 241–268

Sihag RC (1985c) Floral biology, melittophily and pollination ecology of cultivated umbelliferous crops. In: Varghese TM (ed) Recent advances in pollen research. Allied Publishers, New Delhi, pp 269–276

Sihag RC (1986) Insect pollination increases seed production in cruciferous and umbelliferous crops. J Apic Res 25(2):121–126

Sihag RC (1988) Characterization of the pollinators of cultivated cruciferous and leguminous crops of sub-tropical Hisar, India. Bee World 69(4):153–158

Sihag RC (1990) Behaviour and ecology of the sub-tropical carpenter bee, *Xylocopa fenestrata* F. 2. Host plant association. Indian Bee J 52(1–4):38–40

Sihag RC (1992) Utilization of waste stems of sarkandas and castor as nesting tunnels for culturing/keeping wild bee pollinators of some crops. Bioresour Technol 42:159–162

Sihag RC (1993) Behaviour and ecology of the subtropical carpenter bee, *Xylocopa fenestrata* F. 6. Crop hosts, foraging dynamics and pollination potential. J Apic Res 32(2):94–101

Sihag RC, Abrol DP (1986) Correlation and path coefficient analysis of environmental factors influencing flight activity of *Apis florea* F. J Apic Res 25:202–208

Sihag RC, Kaur G (1994) Floral biology, melittophily and pollination ecology of sunflower. In: Sihag RC (ed) Pollination biology: pollination plant reproduction and crop seed production. Rajendra Scientific Publishers, Hisar, pp 69–82

Simura T, Oosone K (1956) Studies on the fertilization of the tea plant. Tkushugaku Zasshi – Jpn Jap J Breed 6:11–14 (In Japanese)

Singh DP (1958) Rape and mustard. Indian Central Oilseed Committee, Gandhi Bhawan

Singh SN (1961) Studies on the morphology and viability of the pollen grains of mango. Hort Adv 5:121–144

Singh LB (1969) Mango. In: Ferwerda FP, Wit F, Veenman FH, Zonen NV (eds) Outlines of perennial crop breeding in the tropics. Veenen and Zonen, Wageningen, pp 309–327

Singh Y (1979) Pollination activity on strawberry at Jeolikot, District, Nainital, India. Indian Bee J 41(1/2):17–19

Singh MP (1984) Studies on the activity of some insect pollinators on jujube (*Zizyphus mauritiana* Lamk.). Entomon 9(3):177–180

Singh S (1988) Insect pollination studies on Almond. Ph.D. thesis, Dr. Y.S. Parmar University of Horticulture and Forestry, Solan, Himachal Pradesh

Singh JP, Dharamwal SS (1970) The role of honeybees in seed setting of onion at Pantnagar, Distt. Nainital, Uttar Pradesh, India. Indian Bee J 32(1/2):23–26

Singh R, Mishra RC (1986) Flower visiting flies of fruits in Himachal Pradesh. Proc Indian Nat Sci Acad 52B(4):451–453

Singh RN, Majumdar PK, Sharma DK (1962) Self-incompatibility in mango (*Mangifera indica* L. var. Dashehari). Curr Sci 31(5):209

Srinivasalu N, Chandrasekaran NR (1958) A note on natural crossing in groundnut, Arachis hypogea Lian. Sci Cult 23:650 (Calcutta)

Sriram TA, Raman KR (1961) Some aspects of flowering and fruiting in yellow passion fruit and Granadilla. S Indian Hart 9(1–4):30–37

Srivastava DP, Singh SN (1968) Heterosis in sesame. Indian Bot Soc J 47(1/2):79–88

Svetsugo I, Kobayashi S (1952) Studies on Vicia villosa Roth, with special reference to the fertilization and seed production. Proc Crop Sci 21(1/2):150–151 (In Japanese)

Swaminathan R, Bhardwaj SC (1982) Bee pollinators of sunflower and their foraging behaviour. Indian Bee J 44(2):32–34

Tanda AS (1983) Assessing the role of honeybee in a field of Asiatic cotton (*Gossypium arboreum* L.). Am Bee J 123(8):593–594

Tanda AS (1984) Bee pollination increases yield of two interplanted varieties of Asiatic cotton (Gossypium arboreum L,). Am Bee J 122(7):539–540

Tanda AS, Goyal NP (1978) Effect of bee pollination on ball retention in Gossypium arboreum Linn. Seeds Farms 4(8):45–46

Tanda AS, Goyal NP (1979a) Pollen dispersal by insects in desi cotton (Gossypium arboreum Linn,). Seeds Farms 5:56–59

Tanda AS, Goyal NP (1979b) Some observations on the behavior of *Apis mellifera* Linn. and *Apis cerana* indica Fab. workers in a field of desi cotton (*Gossypium arboreum* Linn.). Am Beef 119(2):106

Tanda AS, Goyal NP (1979c) Insect pollination in Asiatic cotton (*Gossypium arboreum*). J Apic Res 18(1):64–72

Tanda AS, Goyal NP (1979d) Preliminary observations on the effect of intervarietal bee pollination of desi cotton (*Gossypium arboreum* Linn.). Indian J Entomol 41(3):281–282

Tewari GN, Singh K (1983) Studies on insect pollinators in relation to seed production in cauliflower (Brassica oleracea var. botrytis L.). Indian Bee J 45(1 and 2):54–55

Thakar CV (1974) Experiments on pollination of sunflower. Indian Bee J 36(1–4):36–38

Vaish OP, Agrawal SC, Joshi MJ (1978) Frequency of insect visitors for pollen foraging on sunflower in relation to daily temperature and humidity. In: Proceedings of the 8th international sunflower conference, Minneapolis, pp 148–l57

Verma LR (1990) Beekeeping in integrated mountain development: economic and scientific perspective. Oxford and IBH Publishing Co, New Delhi

Verma LR, Chauan P (1985) Distribution, abundance and diversity of insect pollinators in apple orchards of Shimla hills. Indian J Ecol 12:286–292

Verma SK, Joshi NK (1983) Studies on the role of honeybee in the pollination of cauliflower (Brassica oleracea var. botrytis). Indian Bee J 45(2/3):52–53

Wagle PV (1929) A preliminary study of pollination of the Alphonso mango. Agric J India 24(14):259–263

Wakhle DM, Nair KS, Phadke RP (1978) Effect of bee pollination on the oil and protein content in the seeds of sunflower (*Helianthus annuus* L.). Indian Bee J 40(1):1–2

Williams IH (1977) Behaviour of insects foraging on pigeon pea (*Cajanus cajan* (L.) Millsp.) in India. Trap Agric Trinidad 54(4):353–356

Woo KS, Choo HY, Choi KR (1986) Studies on the ecology and utilization of pollinating insects. Korean JApic 1(1):54–61

Wu CT (1967) Studies on the percentage of fruit-setting of self-and cross- pollination and its relation to some economic characters of the Ft hybrids in tea plant. J Agric Assoc China 59:24–39 (In Chinese)

Chapter 5
Honeybee and Crop Pollination

Abstract Honeybees are the most important pollinators of agricultural and horticultural crops. Most fruit, small seed and many vegetable crops require pollination for the production of economic yields. The value of the honeybee as a pollinator is far greater than its value as a honey producer. Not all crops need pollination. Some can produce fruit without fertilization of the flower. Some flowers are self pollinated, which means that pollen is transferred from the anther to the stigma of the same flower or flowers on the same plant variety. Although this transfer can be achieved by wind or rain, insect pollinators are the most effective. Of all the insects, hive bees are the most practical for crop pollination can be reared in sufficient numbers and placed in orchards wherever and whenever required for effective pollination. It has been found that the use of hive bees results in a manifold increase in yields and an improvement in the quality of produce.

5.1 Introduction

The value of bees as pollinator was first discovered by Koelreuter (1761), while Knight first noted the relation between plants and hybrid vigour. Darwin's concept of natural selection opened the way for a fuller understanding of the correlationship of bees and flowering plants with resultant appreciation of factors affecting mutual adaptation, speciation and distribution.

Honeybees (*Apis* spp.) are the, most important pollinators of agricultural and horticultural crops. Honeybees have attributes that makes them valuable for crop pollination. These can be marshaled in adequate numbers at desired places. Their body parts are modified to effect pollination. Their body size and proboscis length suits them to forage many varied types of flowers. Their wide host range enables them to pollinate many types of crops. They work for longer durations and are also less effected by adverse climatic conditions as compared to other insect pollinators. Their foraging behaviour patterns are highly favourable to qualify them as most efficient pollinators of crops. In addition to pollination services, colonies can be

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managed to produce honey, bee wax, propolis, royal jelly etc. which are all saleable products.

The honeybee is well adapted for pollination. Each colony contains thousands of individuals which are available to forage for the food (pollen and nectar) that's required to rear their replacements. Like other bees, their sense of smell, eyes, mouthparts, and numerous branched body hairs are ideally suited for finding food sources, sipping nectar, and collecting and distributing pollen. Honeybees visit a wide variety of flower types. In a single day, one bee makes 12 or more trips from the hive, visiting several thousand flowers. On each trip, it confines its visit to one plant species, collecting one kind of pollen. It has a complex communication system that enables the colony to find and collect food with maximum efficiency. These characteristics make honeybees most valuable agent for cross-pollinating crops.

They are relatively abundant and manageable. Bees from a colony will visit a large number of plants over a large area, collecting pollen and nectar, with individual bees visiting one species of flowers in the same location until the supply of nectar or pollen is exhausted. This loyalty or constancy is not found in some other social bees, which visit different plant species during the same trip in the fields. This indiscriminate behavior reduces the effectiveness of the bee species as a pollinator because the pollens are mixed.

5.2 Honeybee's Adaptations as Pollinators

Honeybees have evolved numerous adaptations which make them the most efficient pollinators. Some of the more important ones are:

1. Social unit: Because the entire colony overwinters, large numbers of bees are ready to forage in early spring, as compared to other bees such as the bumble bee, where only the queen overwinters.
2. Forked body hairs: These hairs enable the bee to pick up pollen and move it around better than insects with simple, unforked hairs, or insects without any body hairs. Branched hairs are capable of carrying up to five million pollen grains.
3. They have specialized mouth parts, honey sac, honey combs for storing nectar and pollen a efficient distribution over available territory.
4. Corbiculae – the pollen basket: they have intricate pollen baskets. Pollen baskets are structures on the hind legs of worker honeybees which allow these bees to carry pollen back to the colony.
5. Antennae cleaner: This is a structure on the front legs, which enables the bee to clean the antennae.
6. Communication from bee to bee: By dancing, and other specialized systems of communication, scout bees can transmit information about a crop to other bees, thus greatly improving pollination activity.
7. Colonies of bees can be moved to crops needing pollination. Each colony contains large populations of foragers to work crops within a narrow pollinating

window. Bees will usually work only one type of flower on each trip, (flower fidelity) not mixing pollen types and because of these reasons the honeybees are desirable pollinating agents for cultivated crops.

The flowering plants and honeybees co-evolved long before the appearance mankind on the earth. It is a known fact that only where pollinators lived could plant evolves a mechanism of reproduction that involved pollination. A majority of 2,50,000 flowering plants on the earth has amazingly complex relationships with the bees and to other less important pollinators.

5.3 Benefits of Honeybee Pollination

As a result of cross pollination by bees, somatic reproductive and adaptive heterosis or hybrid effects occur in plant progeny. Such hybrid effects bring the following qualitative and quantitative changes in the economic and biological aspects of the plants. It stimulates germination of pollen on stigma of flower, increase viability of seed embryo and plant, more nutritive and aromatic fruits are formed, increases vegetative mass and stimulates faster growth of plants, increases numbers and size of seed and yield of crops, increases fruit set and reduces fruit drop, increases nectar production in the nectaries of flowers, enhances resistances to diseases and pests and increases oil content of oilseed crops.

Not all crops need pollination. Some can produce fruit without fertilization of the flower. Some flowers are self pollinated, which means that pollen is transferred from the anther to the stigma of the same flower or flowers on the same plant variety. Although this transfer can be achieved by wind or rain, insect pollinators are the most effective. Other flowers are cross pollinated. In these cases, the pollen is transferred from the anther of a flower on one plant variety to the stigma of a flower on a different plant variety. Plants requiring cross pollination usually cannot produce fruit from their own pollen. Again, the most important and efficient carrier of pollen from the anther to the stigma for such plants is the honeybee.

Wind probably is the most important pollinating agent, insofar as it benefits our existence. Most of the forest trees, practically all the grasses and grains, with the exception of some that are completely self-pollinated, and many weeds are wind-pollinated. The flowers of most wind-pollinated plants are either male or female. The male flowers produce an abundance of pollen to be carried by the wind. The female flowers usually have large stigmatic areas to receive the pollen. Corn is a good example of a wind-pollinated crop.

Birds of several different species feed upon nectar, pollen, or insects in some flowers and serve as pollinators. None is of significance in pollinating our cultivated crops. Their visits are confined largely to deep-throated, usually showy wild flowers.

Insects of many species visit flowers and pollinate them. These include bees, wasps, moths, butterflies, beetles, thrips, and midges. Bees are the most efficient and the only dependable pollinators, because they visit flowers methodically to collect nectar and pollen and do not destroy the flower or the plant in the process. Various species of bees, including the managed wild bees are highly efficient. An estimated 80% of our insect pollination is done by bees.

5.4 Honeybees and Pollination

Modern agriculture has come to depend greatly upon honeybees to fulfill its pollination needs. This insect has several valuable qualifications for this role. The colonies easily can be concentrated when and where needed to satisfy pollination requirements, and by using techniques developed for honey production their numbers can be increased in a relatively short time. The honeybee is adapted to many climates and can successfully revert to its original wild state in most parts of the world, quickly becoming part of the natural reservoir of pollinators. Pollinators qualifications for efficient pollination are as given below:

5.4.1 Constancy

The insect should show flower fidelity that is it must restrict itself to the blossom of the plants of one species at a time so that pollen grains left by it during its visits on the stigmas of the flowers may fertilize the ovules. Insects which flit from flowers to of one plant species to those of another will cause little fertilization. However, too much specialization may limit the usefulness of the insect.

5.4.2 Thoroughness

The visitors should work their way into the flowers so that they come into touch with the essential organs namely, anthers of stamens and stigmas of carpels. Otherwise, they will not be able to transfer pollen from one flower to the other. If they take both nectar and pollen for food, they will be more effective as compared to those who visit the blossoms for nectar only. The contact of the latter class of insects with pollen grains is accidental and no sure results can be expected.

5.4.3 Working Hours

Those visitors which start their work early in the day and continue late in the evening naturally put in more work quantitatively. Further, those visitors which work for comparatively long periods during inclement weather such as cloudy and cold days will be beneficial to those crops which put forth blossoms under such conditions.

5.4.4 *Total Population*

It would be highly desirable to have big population of pollinating insects at the blossoming time of crop so that a maximum yield of the crop is obtained and the number of insects available at the time does not act as limiting factor. If the pollinators and their placement are under the control of man, it would be an added advantage.

Though certain species of insects have adapted to pollination of certain crops on a commercial scale, namely *Blastophaga* spp. to figs or flesh flies-*Phorima* and *Lucila* to onions in breeding cages, most insects general pollinators.

Over 25,000 species of bees are found in the world. These include honeybees, bumble bees, stingless bees and solitary bees. Bees are the most effective pollinators of crops and natural flora and are reported to pollinate over 70% of the world's cultivated crops. It has also been reported that about 15% of the 100 principal crops are pollinated by domestic bees (i.e. manageable species e.g. hive-kept species of honeybees, bumble bees, alfalfa bees, etc.), while at least 80% are pollinated by the wild bees (Kenmore and Krell 1998). These non-honeybee pollinators are estimated to provide the pollination services worth US$ 4.1 billion per year to the US agriculture (Prescott-Allen and Prescott-Allen 1990).

5.5 Honeybees as the Most Efficient and Manageable Pollinators

As explained, many varieties of crops are partially or completely self-incompatible and cannot produce fruit or seed without cross-pollination of their flowers. Moreover, it is not only self-incompatible varieties that benefit from cross-pollination, but self-fertile varieties also produce better quality fruit and seeds if they are cross pollinated (Free 1993). While other agronomic inputs, such as the use of manure, fertilizers, pesticides and irrigation are important, without cross-pollination desired crop yield and quality of harvest cannot be achieved.

Honeybees are the most widely known of all the bees because they provide honey, beeswax and other products and beekeeping is a prevailing tradition among mountain farming communities. They are the most efficient pollinators of cultivated crops because their body parts are especially modified to pick up pollen grains, they have body hair, have potential for long working hours, show flower constancy, and adaptability to different climates (Free 1964, 1966; McGregor 1976). Research has shown that pollination by honeybees increases fruit set, enhances fruit quality and reduces fruit drop in apple (Dulta and Verma 1987). Among different species of honeybees, the hive-kept species (*Apis cerana* and *Apis mellifera*) are of special value because they can be managed for pollination and moved to fields/orchards where and when necessary for pollination. Pollination using honeybees is the most cost-effective method for pollinating apple and other fruit crops. Use of beekeeping is, therefore, the most promising method of cash crop pollination in the Himalayan region.

In fact, the main significance of honeybees and beekeeping is pollination, whereas hive products are of secondary value. It has been estimated that the benefit of using honeybees for enhancing crop yields through cross-pollination is much higher than their role as producers of honey and beeswax. Various estimates have been made to prove the economic value of honeybees in agriculture in developed countries. Recent estimates by Morse and Calderone (2000) show that the value of honeybee pollination to crop production in the US is US$ 14.6 billion. Similar estimates have been made for other countries. For example the value of honeybee pollination has been estimated at Can $ 1.2 billion in Canadian agriculture (Winston and Scott 1984), US$ 3 billion in EEC (Williams 1992), and US$ 2.3 billion in New Zealand (Matheson and Schrader 1987). Codoret (1992) estimated that the direct contribution of honeybee pollination to increase farm production in 20 Mediterranean countries was US$ 5.2 billion per year – 3.2 billion in developing countries and two billion in other countries. Similarly, Chen (1993) estimated the value of honeybees to four major crops in China, including cotton, rapeseed, sunflower and tea, at US$ 0.7 billion.

Honeybees are reported to play a vital role in enhancing the productivity levels of different crops such as fruit and nuts, vegetables, pulses, oilseeds and forage crops. A number of studies have been done to show the impact of honeybee pollination on different cash crops. However, the role of honeybees is not very well understood in the countries of the Himalayan region. Most of the research work has been done in developed countries of the world where honeybees are being used for the pollination of various crops. However, the limited research carried out in the countries of the Himalayan region has proved that bee pollination increases the yield and quality of various crops. Bee pollination increased yield and fruit quality in apple (Dulta and Verma 1987), peach, plum, citrus, kiwi (Abrol 1991; Gupta et al. 2000) and strawberry (Partap 2000; Partap et al. 2000). Bee pollination did not only increase the fruit set but also reduced fruit drop in apple, peach, plum and citrus (Dulta and Verma 1987; Partap 2000; Partap et al. 2000). Reports have also indicated an increase in fruit juice and sugar content in citrus fruits (Partap 2000). In strawberry, bee pollination reportedly reduces the percentage of misshapen fruits (Partap 2000).

Studies have shown that honeybee pollination enhanced seed production and quality of seed in various vegetable crops such as cabbage, cauliflower, radish, broad leaf mustard and lettuce (Abrol 1991; Partap and Verma 1992; 1994; Verma and Partap 1993; 1994). These results confirm the usefulness of bee pollination and its role in increasing crop productivity and improving the quality of fruits and seeds (Tables 5.1–5.4)

Scientific evidence confirms that bee pollination also improves the yield and quality of other vegetable crops such as asparagus, carrots, onion, turnips and several

Table 5.1 Expected increase in crop yield due to bee pollination

Crop	Pollination requirements	Expected percent increase in yield due to cross-pollination	No. of bee colonies needed per ha
Almond	Highly cross pollinated	20	5–8
Apple	Highly cross pollinated	20	2–3
Citrus	Often cross pollinated	20	2–3
Coconut	Pollen transfer is essential	5	2–3
Grape	Often cross pollinated	20	2–3
Guava	Cross pollinated	10	2–3
Mango	Bee visit is helpful	3	2–3
Papaya	Pollen transfer is essential	10	2–3
Mustard rape	Mostly cross pollinated	20	3–5
Sesamum	Often cross pollinated	20	2–3
Sunflower	Cross pollinated	20	2–4
Cotton	Often cross pollinated	10	2–6

Table 5.2 Percentage increase in yield of some crops due to bee pollination

Crop	Increase (%)	Crop	Increase (%)
Fruit crops		*Fodders and legumes*	
Apple	18.00–69.50	Alfalfa	23.00–19,733
Almond	50.00–75.00	Berseem	193.00–6,800
Apricot	5.00–10.0	Clovers	40.00–33,150
Cherries	56.00–1,000	Vetches	39.00–20,000
Citrus	7.00–223.00	Birds foot	3.00–1,000
Grapes	23.00–54.00	*Miscellaneous crops*	
Guava	12.00–30.00	Buck wheat	63.00–100.00
Litchi	453.00–10,246	Coffee	17.00–39.00
Plums	536–1,655	Cotton	2.00–50.00
Vegetable crops		Field beans	7.00–90.00
Cole crops	100.00–300.00	*Oil seed crops*	
Radish	22.00–100.00	Mustard	13.00–222.00
Carrot	9.00–135.00	Safflower	4.00–114.00
Turnip	100.00–125.00	Sunflower	21.00–3,400
Cucumber and squashes	21.00–6,700	Sesame	24.00–40.00
Onion	353.00–9,878	Niger	17.00–45.00
Cabbage	100–300.00	Linseed	2.0–49.00

other crops (Deodikar and Suryanarayana 1972; 1977; Woyke 1981). Recent experiments carried out in different parts of the northeast Himalayan region show that honeybee pollination does not only increase fruit set in rapeseed and sunflower but also increases the oil contents in these oilseed crops (Singh et al. 2000).

The quality of pollination is determined by the number of colonies per unit area, strength of bee colonies, placement of colonies in the field, time of placement of bee colonies, and the weather conditions. Experiences from pilot experiments have

Table 5.3 Summary of pollination management of different crops

Crop	Blooming period of the crop	Number of *A. mellifera* colonies/ha	Number of *A. cerana* colonies/ha	Time of placement of colonies
Fruit crops				
Almond	Mid-February to mid-March	5–8	10–12	5–10% bloom
Apple	April (7–10) days	5–8	10–12	5% bloom
Apricot	Mid-February (2–3 weeks)	2–3	4–6	5–10% bloom
Avocado	April–May	5–8	10–12	10–15% bloom
Cherry	February (7–10) days	2–3	4–6	5% bloom
Citrus	March–April	2–3	4–5	5–10% bloom
Kiwifruit	March–April	8–9	16–20	5–10% bloom
Litchi	March–April	2–3	4–6	5–10% bloom
Mango	February	2–3	4–6	5–10% bloom
Peach	February–March (3–4 weeks)	1–2	2–3	5–10% bloom
Persimmon	March–April (2 weeks)	2–3	4–6	5–10% bloom
Plum	February (1–2 weeks)	2–3	4–6	5% bloom
Strawberry	February–April (2 months)	>15	25	5–10% bloom
Vegetable crops				
Cabbage	February–March	5	8–10	10–15% bloom
Carrot	March–April	5–8	10–12	10–15% bloom
Cauliflower	March–April	5	8–10	10–15% bloom
Cucumber	June–September	1 for monoecious 8 for dioecious	2–3 for monoecious 12–16 for dioecious	10–15% bloom
Cucurbits (pumpkin, squash gourd)	June–September	5–8	10–12	10–15% bloom
Okra	June–September	1–2	2–3	10–15% bloom
Onion	April	5–8	10–12	5–10% bloom
Radish	March–April	2–3	4–6	10–15% bloom
Turnip	February–March	2–3	4–6	5–10% bloom
Oilseed crops				
Mustard and rape	December–January February–March	3–5	5–8	10–15% bloom
Niger	August–September	3–5	6–8	5–10% bloom
Safflower	March–April	5	4–6	5–10% bloom
Sunflower	June	5	8–10	5–10% bloom
Spice crops				
Cardamom	March–April	2–3	4–6	10–15% bloom
Chilli	July–September	2–3	4–6	10–15% bloom
Coriander	February–April	2–3	4–6	10–15% bloom

Source: Partap 1999

Table 5.4 Yields in cages without bees in percent of yields in cages with honeybees

Crops	Percentage increase	Crops	Percentage increase
Fruits		Legumes	
Malus domestica	6–29	*Trifolium pretense*	1–34
Ribes nigrum	40–29	*Trifolium repens*	9–19
		Trifolium hybridum	0–8
Oil plants		*Trifolium incarnatum*	3–14
		Medicago sativa	0–68
Brassica napus	50–72	*Melilotus alba*	0–6
Brassica napus	35–51	*Onobrychus viciifolia*	0–14
Brassica rapa	78–89	*Vicia villosa*	3–37
Brassica rapa	39–69	*Vicia faba*	83
Sinapis alba	51–75	*Coriandrum sativum*	63
Helianthus annuus	70–86	*Fagopyrum esculentum*	14–53
Papaver somniferum	49–91	*Phacelia tanacetifolia*	12–62

shown that the best results are achieved by placing strong bee colonies, having large amount of unsealed brood, free of diseases, at the time of 5–10% flowering in the crop (Free 1993; Verma and Partap 1993).

5.6 Pollination Behavior of Honeybees

Honeybees are cold-blooded animals. They depend upon the surrounding temperature for their activity outside the colony. For pollination purposes, bee flights should be expected within the temperature range of 55–100 F. Below 55 few bees fly outside the hive, and when they do it is only for cleansing or orientation flights. As temperature increases, more bees search for water to cool the colony. Strong winds slow bee flight activity and stop it completely when it exceeds 25 mph. Hot winds will also reduce nectar secretion, thereby reducing flower attractiveness. Hot, dry conditions also reduce the favorable climate for pollen germination.

Applying pesticides to crops near other plants that are attractive to bees should be done carefully. For example, mow dandelion in orchards before bloom to eliminate competition for bee visits and reduce the risk of pesticide injury.

5.7 Factors Affecting Bee Populations

The number of colonies of honeybees and the number of bees in each hive can be influenced by bee diseases, pesticide sprays, poor nectar flows, and seasonal changes. A single, wide-scale pesticide application for control of a harmful pest can weaken or destroy many colonies. Drought or prolonged periods of rain, cool temperatures, and early frosts, all limit nectar production by plants. In these cases, the beekeeper may need to feed his bees.

5.8 Manipulate Bees for Crop Pollination

A. One mistake often made by a fruit, vegetable, or seed producer regarding bee pollination is to assume that "the neighbor's bees" will provide sufficient pollination of his crop. There are several reasons why a producer who does this can be disappointed at harvest time with low yields:

Although honeybees from a single hive will fly 2–3 miles from the colony, the radius of greatest efficiency and greatest pollination is only 200–300 yards from the colony. The reason for this is mathematical, because the farther away from a colony a bee flies, the greater the number of acres it can potentially visit. There are many flowers competing for the bee's attention; some may be more attractive or "profitable" to work than the crop needing pollination. Bees will not fly a great distance to forage on an unattractive crop.

B. By moving bees directly into a field, a grower can increase the flight activity in that area. However, there are several considerations he should make, and procedures he should follow:

Colony arrangement: Bees are most efficient when closest to the colony; therefore, to achieve the most efficient distribution of foragers, the colonies should be distributed at 300–500 yard intervals. Inexperienced foragers work closer to the hive, then disperse with age and experience. Some crops or specific varieties of some crops are unattractive to bees. In such cases, a solution is to flood the area with bees. Sugar sprays and attractants have failed to increase pollination. Provide water for bees to minimize wasted effort by foragers.

5.9 Protecting Bees from Pesticides

Until better methods of covering or otherwise protecting bees during insecticide sprays are developed for use under the humid conditions in Ohio, the only safe way to protect honeybee colonies is to remove them from the area of the spray. This is difficult, or impossible in some situations, particularly if a large number of acres are to be sprayed (as for mosquito control or gypsy moth), or if many hives are involved. USDA suggests that beekeepers cover hives with burlap during insecticide sprays and keep the burlap wet. This method has been only moderately successful in Ohio, perhaps because bees are too hot and humid under the burlap. Confining bees to the hive by screening the entrance and the top after removal of the inner cover might prevent overheating and minimize losses, as long as there is no direct hit by the insecticide on the open colony.

5.10 Minimum Colony Strength

Each hive, enclosing the colony or swarm of bees, is a family unit and consists of a laying queen, a few drones, and several thousand worker bees. Because the worker bees pollinate crops, it is important to understand how their populations change throughout the spring and summer. In early spring, a colony may have 10,000–20,000 workers, but by summer the colony should have reached a population of 40,000–60,000 workers. During these months the lower portion of the hive, called the brood chamber, is filled with eggs, larvae, and pupae called brood, which are reared in the cells of the comb. Generally, the larger the brood area, the greater the demand for nectar and pollen, thus the greater foraging activity by the bees. This in turn results in more pollination. Colonies used in pollination rental must have brood, and the amount of brood is a strong indication of the effectiveness of the colony for pollination.

5.11 Value of Bee Pollination to Agriculture

Unfortunately, the pollination mechanisms of some crops are poorly understood, particularly in some modern hybrids and new varieties. A few crops have been investigated and the pollination requirements are well known. Some scientists have estimated that the dollar value of bee pollination is worth more than one billion dollars per year in the United States, when determined in value of crops involved. The contribution of bee pollination to the production of agricultural crops is considerable. Without this contribution, modern agriculture would be seriously affected.

5.12 Unmeasured Pollination Benefits

There are areas where it is almost impossible to place a dollar value on bee pollination. One is the contribution that pollination of plants makes to wildlife food production. Another is the natural beauty resulting from pollination of wildflowers. Many shrubs and countless annual plants reproduce by bee pollinated berries and seed, which provide food for birds and other animals. Ornithologists may suggest that humans “feed the birds in the winter,” but the birds also depend upon naturally grown seed and fruit resulting from bee pollination. The beekeeper with a small scale operation is very valuable in providing honeybees for this unmeasured contribution to pollination, because there are many smalltime, hobbyist beekeepers spread throughout the state who increase food production for wildlife. Thus, it is difficult to place a dollar value on the enjoyment created by birds, wildflowers, and wild animals for the *Nature* enthusiast.

5.13 Honeybees as Pollinators

Domesticated species: There are two most important hive species. European honeybee, *Apis mellifera* L. is a native of old world except tropical Asia and introduced to most parts of the new world. It has a foraging range of 3 km. The Indian hive bee, *A. cerana indica* F., a native of tropical Asia is prevalent in a wide region with a flight range of 1.5 km. It is even a better pollinator than *A. mellifera* because of their longer foraging period and many other characters (Sihag and Mishra 1995).

Wild species: Two other species, *A. dorsata* (rock/giant bee) and *A. florea* (little bee) are also native of tropical Asia and efficient pollinators. But these cannot be managed for long time, as they do not live in artificial hives. Their foraging range is 2.5–4.0 and 1 km, respectively. Small amounts of pollen are collected by honeybees in tomato and they require buzz pollination. So bumblebees can do the better job than honeybees. However in closed conditions 2 colonies are required in an 800–1,000 m^2 greenhouse (Houbaert and Jacobs 1992).

5.14 Management of Honeybees for Pollination

Due to their morphological characters, social behaviour and management practices followed by our farmers, honeybees have become the most important and mostly the only pollinators of the crops. The uncertainty of populations and the difficulty in maintaining and using solitary bees, bumblebees and other pollinators' places all the onus of planned pollination on honeybees alone (VanEngelsdorp and Meixner 2010). The following points are most important to consider a colony for pollen foraging and getting desired pollination outputs.

5.14.1 Foraging Strength of Colonies

In order to get maximum honey and pollination benefits from a colony, it must be full-sized and populous not a growing one – as the brood/bee ratio diminishes in it, so a greater proportion of bees is available for foraging. Matheson (1986, 1991) suggested that a colony used for pollination should contain at least seven frames with 60% brood (at least 25% in egg or larval stage) in the brood chamber, a young prolific queen, at least 12 frames covered with bees, sufficient empty combs for expansion and enough honey and pollen stores to sustain it. Separate colony strength standards were also recommended for field colony and orchard colony by Roubik (1995).

5.14.2 Pollination Requirement and Concentration of Colonies

The number of colonies/ha recommended also varies with crop. It also depends on local conditions including the number of honeybees and other pollinators already

Table 5.5 Pollination requirement of different crops as given below

Sr.	Crops	Pollination requirement number of colonies/ha
1	Apple	2–3
	Almond	5–8
	Citrus	2–3
	Sunflower	2–4
	Turnip	2–5
	Coconut	2–3
	Cauliflower	3–5
	Mango	2–3
	Watermelon	1–5
	Mustard	3–5
	Pumpkin	1–2
	Sesame	2–3
	Guava	2–3
	Onion	2–8
	Lucerne	3–6
	Cotton	2–6
	Papaya	2–3
	Grape	2–3
	Sprouting Brussels	5
	Musk melon	1–5
	White clover	0.2–1.0
	Kiwi fruit	8
	Berseem	3–4
	Buckwheat	3
	Carrot	6
	Cherry	2–5
	Citrus	2–5
	Cucumbers	6–20
	Hairy vetch	3.5–7.5
	Pears	4–6

present, the size of the crop and the presence of competing crops of the same and different species like weed species. It has also been observed that placement of colonies influences the distribution of bees on the crop. Crops differ in their profitability of saturation pollination. Blueberries show a direct correlation between the amount of pollination, the number of seeds, the rate of growth and the size and the yield of the fruit. Placement of honeybee colonies in or near the crop can be an important factor for different crops. Information of foraging areas of individual bees is useful to indicate best varietals interplanting arrangement in fruit orchards, row arrangement and cross-hybridization by bees and isolation distances required to prevent varietals contamination of bee pollinated seed crops. In general, 3–5 colonies/hectare placed equidistant from each other within the crop are recommended (Table 5.5).

It is generally recommended to have around 2.5 colonies/hectare but it will depend on many factors like concentration of flowers, their attractiveness, competing insects and crops, species, place, percentage of flowers open at a time, etc. and the number of colonies required may be increased or decreased accordingly.

5.14.3 Foraging Efficiency of Colonies and Their Distance from the Crop

Honeybees are capable of foraging at an enough honey and pollen stores to sustain it. Considerable distance from their hives but their efficiency is indirectly proportional to the distance covered. Generally foraging range is 2.5 km for *Apis mellifera*, 1.5 km for *A. cerana*, 3 km for *A. dorsata* and 1 km for *A. florea*. *Apis mellifera* have been observed to forage up to 11.3 km but foragers were concentrated within 0.6 km of their hives. (Plate 1a) The yields of the crops are more when the colonies are kept up to a distance of 0.5 km and decrease to almost half at a distance of 1.0 km and these impacts are even greater in poor season. The number of foraging bees on a crop diminishes with increase in the distance from the hive (Free 1993). In general, placing the hive within 0.5 km radius increases the crop pollination. Recruitment of nest mates to the nearby sites is also greater as this information is more easily communicated. Colonies placed near crops collect more pollen and nectar, spend less time collecting load of pollen and nectar, the number of flights increases for both types with proximity to the floral source.

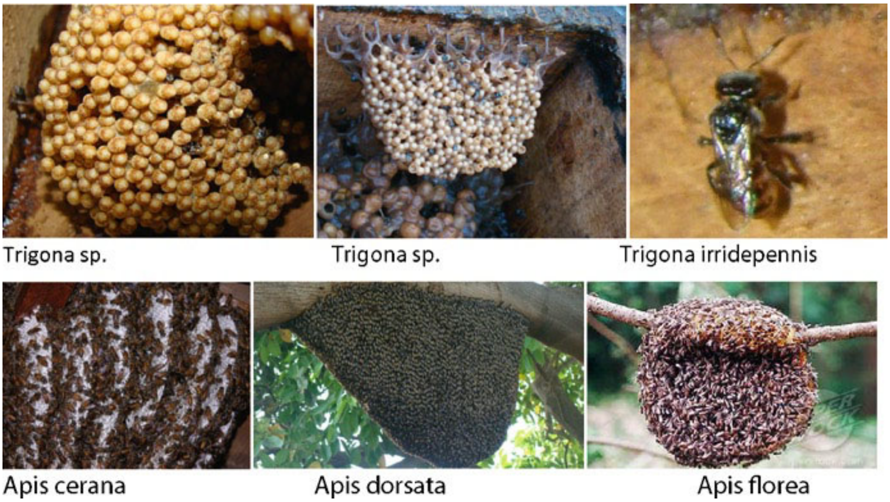
Trigona sp.
Trigona sp.
Trigona irridepennis
Apis cerana
Apis dorsata
Apis florea

Plate 1a Nest of various honeybee species and *Trigona* sp.

5.14.4 Moving Colonies to Crops

It is advisable to take as short migrations as possible because of the risks involved in long distance migration which result in killing of brood and low foraging efficiency. The settling and arrangement of colonies after migration is very important. Formal arrangement with identical lives should be avoided as it may result in drifting of foragers especially during their first flight which may result in weakening of some colonies and strengthening of others, lowering the mean foraging potential, honey production and pollination efficiency. The colonies should be arranged irregularly in different directions and spacing. They should be put near landmarks and windbreaks and different colored boards may be placed above the entrance.

5.14.5 Time of Moving Colonies on Crops

The origin of food stores of a colony plays important role in determining the species as they did before moving them. But the predominance of one species at the new site results in changing their foraging behavior. Therefore, colonies should be moved to the crop needing pollination only when it is sufficiently flowering. The colonies should be moved to a target crop when bloom is between 5% and 10%, influence the number of foragers that are turnaround on it. Care must be taken to avoid the blooming of too many flowers as an important part of the crop may fail to be pollinated. It is practical to move a few colonies to the crop at the beginning of flowering and the rest when more flowers have bloomed (Sale 1983).

5.14.6 Replacement or Rotation

Colonies should be replaced or rotated with fresh ones when they begins to forage outside target crop. Colonies involved in these/findings should be at least 2.4 km apart or the bees may return to their former sites. This system is particularly useful, where the target crop e.g. Pear is relatively unattractive top bees.

5.14.7 Temporary Placement

The flowers of crop generally present their pollen/nectar at a certain times of the day Thus confining the bees to their hive until the target crop is presenting its pollen/nectar appear to maintain bees, at least temporarily, on a crop.

5.14.8 Removing Floral Competition

Weeds or other non target crops should be eliminated or mowed when in flower, to avoid competition for foraging bees.

5.14.9 Pollen Dispensers

Pollen dispensers (pollen inserts) apply pollen to bees leaving Hives so that they can cross pollinate when few pollinizers varieties are available. This may increase pollination efficiency of bees without necessarily maintaining more of them in a target crop. Dispensers may stimulate foraging activity and that may induce bees to forage for the type of pollen in the dispenser.

5.14.10 Disposable Pollination Units (DPU's)

DPU's are small comb less colonies housed in inexpensive containers that are trucked or parachuted into target crops that are inaccessible, and then destroyed or left to die when flowering is over.

5.14.11 Arrangement of Colonies

Arrangement of colonies in crop is very important to ensure uniform distribution of foraging bees which will depend on the plant species, amount of nectar and pollen available/unit area, weather conditions and physical features of the area like topographic gradients, wind direction, shelter, etc. Placing colonies in the middle of the crop increases foraging area (Free 1993). Ideally colonies should be distributed singly over the crop which is always not feasible and practical. So, colonies should be kept in small groups of 4–5 at distances of about 200 in throughout the crop to provide sufficient overlap of foraging area between different groups. The colonies should face the direction of sun in the winter and should be sheltered during summer and rainy season. Windbreaks (natural and artificial) greatly benefit during chilly and windy conditions (Kumar et al. 1998).

5.15 Evaluating Honeybee Colonies for Pollination

Honeybees are accurately described as indispensable pollinators. The reasons for the success of honeybees as pollinators are seen in certain aspects of their biology. Honeybees forage for nectar and pollen from many thousands of plant species, so they efficiently pollinate a wide variety of crops we all consider important. The second reason is that, while foragers from one hive may visit many species of plants in a given day, individual foragers display flower fidelity or constancy. When a forager begins collecting nectar or pollen from the flowers of one species of plant, she will continue to visit flowers of only that species for at least one foraging trip and more often for several days, or until the resource is no longer producing nectar or pollen. This is obviously important to the plant she visits as it requires pollen from a flower of the same species for pollination.

The third reason honeybees are so successful in commercial agriculture is that colonies are mobile. Hives are easily moved to locations where native pollinators may not occur in sufficient numbers to adequately pollinate a crop. The most important question regarding pollination for the commercial purposes include: How many colonies are necessary to insure maximum pollination of a given crops. This is a difficult question to answer because absolute pollination requirements are not established for most agriculturally important plant species.

Furthermore, bloom periods, bloom density, bloom attractiveness, blossom structure, competing bloom, and weather play major roles in determining how well honeybees will forage on and ultimately pollinate a given crop. Finally, the quality of individual colonies needs consideration in determining how many to use. We designed this publication primarily to assist growers and beekeepers in evaluating the quality of colonies used in commercial pollination.

5.15.1 Colony Size and Efficiency

The older worker bees in a colony serve as foragers. As a colony grows in worker population, the proportion of bees old enough for foraging increases. As a general rule, smaller colonies send out a smaller percentage of bees as foragers. On the other hand, larger colonies send out not only more bees but also a higher proportion of the population as foragers. The greater value of larger colonies for pollination can be illustrated by the amount of honey produced by colonies of different populations. The ability of a direct result of the number of bees foraging and the amount of forage available. It is the foragers that pollinate the flowers they visit.

One colony of 30,000 bees produces 1½ times as much honey as the sum of two colonies with 15,000 bees each.

One colony of 45,000 bees produces 1½ times as much honey as three colonies with 15,000 bees each.

One colony of 60,000 bees produces 1½ times as much honey as four colonies with 15,000 bees each.

5.15.2 Management of the Colonies

The natural growth of the colonies can be increased with a variety of techniques. Colonies provided with supplemental food such as sugar syrup and/or pollen supplement early in the season will be stimulated to grow more rapidly.

5.15.3 Amount of Comb

A standard unit, used by most beekeepers, is the Langstroth deep-hive body When used with ten frames, it provides 2,700 in.^{2} of comb. Therefore, a pollination colony requires more than one standard deep-hive body, or its equivalent. A commonly used unit is two standard deeps or one deep (2,700 in.^{2}) with an additional semi-deep-hive body (2,000 in.^{2}).

5.15.4 Amount of Brood

A healthy honeybee colony during the foraging season will possess eggs, larvae, and pupae. Brood indirectly influences the pollinating efficiency of a colony. Larvae require food, especially pollen. Many studies have shown a direct correlation between the amount of brood in a colony and the amount of pollen returned to the hive by the foragers.

5.15.5 Number of Bees

Since the older bees in a colony do the pollination, the regulations take into account the relative number of bees a colony should have. How many bees are on a well covered standard comb? Studies have shown that one standard comb, when completely covered, accommodates about 2,400 adult bees. Therefore, the total number of adults in a minimum standard colony would be approximately six frames fully covered or 14,400 and 24,000 adults on ten frames.

5.15.6 Food Requirement

A colony of honeybees requires nectar and pollen for normal growth. The food requirement of a hive is met in two ways, by the daily activities of foraging bees and from food stored in the combs. The egg-laying capacity of a queen 3 or more years old is usually not enough to maintain a colony at proper strength for pollination or honey production.

5.16 Challenges in Managed Crop Pollination

Honeybees by far are the most important agents of cross-pollination. Apart from direct benefits derived from honeybees in the form of honey and beeswax, indirect benefits realized by way of increased yields of certain farm crops and forest

Table 5.6 Crops dependent on bees for pollination

Category of crops/fruits	Name of the crop
Vegetables	Pumpkin, cucumber, bottle gourd ridgegourd, carrot, radish, cabbage, knolkhol, cauliflower, onion, soyabean
Oilseeds	Sarson, toria, sunflower, niger, sesame, safflower, linseed
Pulses	Tur, urad, mung, beans, guar, pea, cowpea
Forage legumes	Lucerne, berseem, clovers
Fruit crops	Oranges, pears, apples, peach, plum, almond, cherry, persimon, strawberry, guava, pomegranate, Jamun, fig, craneberry, grapes, lemon, raspberry, blackberry
Other crops	Buckwheat, cotton, coffee, tobacco, sweet clover
Plants of forest importance	Toon, shisham, soapnut, wild raspberry, stain, Wild cherry, shain, Euretia sp., Robina sp., Trifolium sp., Eupatorium sp. Azadirachta sp, maple chestnut, eucalyptus, willow, linden, catalpa and magnolia etc.

products due to their pollination services are immense. Compared to the value of honey and beeswax, monetary returns in the form of increased yields may be 20 times or even more. In case of highly cross-pollinated crops like almond, clovers, some varieties of apple, melons, any amount of fertilizer or cultural practices may not even give a fraction of yield unless pollinated by insects. There are some crops which exclusively depend upon bees for production of seeds/fruits (Table 5.6).

The fact that the bee pollination enhances crop yields has been established (Free 1993; Abrol 1993; Deodikar and Suryanarayana 1977). Evidently, bee/insect should be encouraged for increased and sustainable agriculture production. In India, the total cultivated area is about 160 million hectares and at least one third (if not half) of the areas is under entomophilous crops which require insect pollination. At a very modest rate of 3 colonies per hectare we need 160 million colonies of honeybees but against this requirement we have just less than one million bees colonies at present. This would be possible only if the apiculture as a whole gets boost and number of colonies are multiplied and managed. Besides, it is very necessary to survey different agroclimatic zones to determine the distribution and abundance of pollinating insects so that pollinators specific to different zones are multiplied and managed. Regions with less abundance should be supplemented with apiaries.

Honeybee colonies are active throughout the year. They can be profitably used both for honey production and pollination and can be aced in crops/orchards wherever and whenever required. Honeybees also are trained to pollinate specific crops. The extracts of flowers the crop to be pollinated is fed to the bees in sugar syrup. The bees get conditioned to the aroma of the crop, visit the flowers thereby effecting pollination. For pollination purposes, strong colonies of honeybees be maintained to coincide with the flowering of the crop.

5.17 Management During Pollination

The individual crops may vary in their requirement of bee colonies for pollination. The number of bees required depends on the number of flowers available in a given area for pollination and therefore, on the species of the crop, planting method, age of the crop, stage and duration of flowering etc. The number of bees available for foraging depends on the ecotype of the bees, management of the colony, competing flower species number of wild pollinators and weather conditions. Generally 3–9 bee colonies of good strength are needed for 1 ha of crop. A large number of colonies help pollination, but may be unsuitable for either honey production or colony multiplication. Keeping this in view, optimum number of colonies per hectare have to be placed in the fields after migration. It is advisable to keep colonies near the plants to be pollinated. Colonies may be unloaded from the truck and distributed evenly all over the field. In northern regions, during winter, colonies can be kept in the open sunshine with entrance facing south-east. In more tropical regions shady cool places are necessary.

Efficiency in pollination depends largely on the management of colonies. The basic need for management of colonies for pollination is to keep the colonies in peak foraging activity, which is possible when there is peak brood rearing activity (Plate 1b). Some of the management practices which help in this are (i) provision of clean, new combs to provide adequate space for constant brood rearing, (ii) preventive methods against diseases or pests which divert the attention of colonies (iii) provision of a young newly mated vigorous queen etc. Dilute simulative feeding (one part of sugar to two or three parts of water by measure) proves beneficial in making bees collect pollen. Thick syrup should, however, be avoided.

In order that colonies fix up their visits to the crop to be pollinated, it is advisable to migrate colonies to the field when the crop starts flowering. It is often very important to synchronize flower opening and bee activities. Colonies freshly migrated to a crop are more likely to visit the crop than those remaining there for a long time. Shifting of a few colonies at a time to the field, 2–3 times during the flowering of the crop, may help in thorough pollination. Visits to the crop by foragers can often be enhanced by feeding colonies with sugar syrup in which a few fresh flowers and pollen of the crop are soaked for some time. Such feeding is best given in the nights or early in the morning before bees go out.

It may not be uncommon when the crop to be pollinated is ignored by the bees, which may find other plants in the same place more attractive. When such a contingency arises, bringing new colonies to the field and conditioning them to the crop as above may be helpful. The earlier colonies can be shifted to a place at least 2–3 km away from the field for a few days and can be brought back with the above arrangements for conditioning them to the crop. A knowledge of the bee foraging behaviour and ecology of the crop helps in soling such problems.

Apis dorsata on Brassica juncea A. cerana on B. juncea A. mellifera on B. juncea

Bombus hemorrhoidalis on cauliflower Xylocopa fenestrata on B.juncea Apis ceran on onion flowers

Trigona sp. on onion flowers Apis florea on carrot Apis florea on cucurbits

Apis dorsata on cucurbits Xylocopa fenestrataon cucurbits Apis florea on strawberry

l)

Bombus hemorrhoidalis on Citrus Bombus tunicatus on brinjal Bombus hemorrhoidali on citrus

Plate 1b Foraging activity of various insect pollinators on different crops

Bombus tunicatus on thistle B.trifaciatus on nerium B. simillimus on Impatiens gladulifera

Megachile sp. on Cassia absus Xylocopa fenestrata on C. absus Apis cerana on citrus

Plate 1b (continued)

The farmer's role in pollination of crop by bees can also be over-emphasized. Planned cropping pattern to avoid unnecessary competition between crops in attracting bees, removal of weeds, proper manuring, irrigation and other cultural practices for healthy growth of the crop, using less toxic insecticides or sparing use of insecticides and similar toxic chemicals, arc some of the responsibilities of the farmers for effecting efficient pollination.

Beekeeping is as much an art as a technique – It needs good deal of practical experience of some years. The busy farmer may not be able to achieve efficiency in a short time in good beekeeping. The forage gap periods and hot summers of plains may make it difficult for him to maintain bee colonies in adverse periods. He may initially prefer, therefore, to hire bee colonies for pollination when crops are in full bloom just as he hires sheep for manuring. Bee colonies are hired for pollination in western countries, especially in the United States. As 20–40% increase in many crop yields by bee pollination is possible, it may not be unfair on the part of the farmer to spare a portion of the increased yield to the beekeeper as his fees for pollination service.

During this periodic migration of colonies by a beekeeper the farmer himself can learn beekeeping technique and should try to have, gradually, a few of his own bee colonies rather than depend upon beekeepers in adjacent hills, wherever this is feasible. By this way a farmer can become self-reliant. He will have the satisfaction of getting some quantity of *Nature*'s precious sweet honey, from his own farm and at the same time will add to his crop-yield both in quality and quantity.

It is clear from above that beekeeping in addition to being a cottage industry to produce honey and beeswax, provide job opportunities, creasing economic returns of the small land holders, is an effective Id increasing farm productivity, maintaining environmental quality and staining balanced agriculture.

5.18 Management of Bee Pollination of Crops

Following groups of bees can be managed for pollination of crops:

1. Honeybees: Two species honeybees are effectively managed and utilized for pollination purpose. These are: *Apis mellifera* L. and *A. cerana* F. Honeybee species can effectively be utilized for pollination of crops because
    (a) Honeybees are dependent on flowers for pollen and nectar as their food (Free 1993).
    (b) The bees possess some morphological adaptations favourable for pollen carry over and transfer (Free 1993).
    (c) The honeybees can be kept in the hives and are very easy to be managed (Singh 1960; Dadant and Sons 1992).
    (d) Due to their polylectic *Nature*, honeybees visit large number of plants (Sihag 1990a, b), therefore, they can pollinate a wide variety of crops (McGregor 1976; Free 1993; Sihag 1995a).
    (e) Their abundance on the crop can easily be manipulated (Jay 1986).
    (f) Honeybees have better communication system *for* food searching and gathering. When a honeybee forager begins foraging on a plant species, continues to do so until the resource gets exhausted. This behaviour of individual foragers has been termed as floral fidelity or constancy (Wells and Wells 1983; Waser 1986). This is very important *for* the plant species they visit for the effectivity of pollination.
    (g) Behaviour of honeybees can be manipulated by modifying the reward system of the plant/or nectar and pollen storage in the hive (Free 1965a, b, c, 1967; Baker 1971; AI- Tikrity et al. 1972) or colony's unsealed brood (Free 1967; Cale 1968).
    (h) Colonies of honeybees can be moved to a place of short pollinators supply (Jay 1986; Mardan 1995).

Due to their habits of making nest in the cavities and having multiple OS, these bees can be domesticated in the wooden hives. For effective nation of a crop, following points are taken into account.

1. Time of placement of honeybee colonies
   When 5–10% of the flowering has initiated, honeybee colonies are placed on the crop.
2. Site of placement of honeybee colonies
   The colonies are placed near the target crops so that they can actively move and bring about cross pollination and less energy is utilized in travelling:
3. Method of placement of honeybee colonies
   Colonies are placed either in groups or are scattered, and further, either around the target crop or scattered in between as per the convenience of the beekeeper.

References

Abrol DP (1991) Conservation of pollinators for promotion of agricultural production in India. J Anim Morphol Physiol 38(1–2):123–139

Abrol DP (1993) Ecology and utilization of insect pollinators frequenting pear flowers and their impact on fruit production. Korean J Apic 8(1):18–21

Al-Tikrity WS, Benton AW, Hillman RC, Clarke WW Jr (1972) The relationship between the amount of unsealed brood in honeybee colonies; and their pollen collection. J Apic Res 11:9–12

Baker RJ (1971) The influence of food inside the hive on pollen collective by a honeybee colony. J Apic Res 10:23–26

Cale GH (1968) Pollen gathering relationship to honey collection and egg laying in honeybees. Am Bee J 108:8–9

Chen Y (1993) Honeybee diseases and their prevention and control. In: Chen Y, Li Z, Qiu Z, Qiao Y, Yan H, Jin Z, Wang S, Wang Y, Qiu J, Huang W (eds) Apiculture in China, Agric. Pub. House, Beijing, China, pp 52–59

Codoret JP (1992) Doorway doses help defeat honeybee's 'Vampire enemy. Ceres FAO Rev 24:8–9

Dadant and Sons (1992) In: Dadant CP (ed) The hive and the honeybee. Dadant and sons, Hamilton

Deodikar GB, Suryanarayana MC (1972) Crop yields and bee pollination. Indian Bee J 34:53–64

Deodikar GB, Suryanarayana MC (1977) Pollination in the service of increasing farm production in India. Adv Pollen-Spore Res 2:60–82

Dulta PC, Verma LR (1987) Role of insect pollinators on yield and quality of apple fruit. Indian J Hort 44:274–279

Free JB (1964) Comparison of the importance of insect and wind pollination of apple trees. Nature Lond 201:726–727

Free JB (1965a) The effect on pollen collecting of feeding honeybee colonies with sugar syrup. J Agric Sci Camb 64:467–468

Free JB (1965b) The behaviour of honeybee foragers when their colonies are fed with sugar syrup. J Apic Res 4:85–88

Free JB (1965c) The ability of bumblebees and honeybees to pollinate red clover. J Appl Ecol 2:289–294

Free JB (1966) The pollinating efficiency of honeybee visits to apple flowers. J Hon Sci 41:91–94

Free JB (1967) Factors determining the collection of pollen by honeybee foragers. Anim Behav 15:134–144

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London, 684pp

Gupta JK, Rana BS, Sharma HK (2000) Pollination of kiwifruit in Himachal Pradesh. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Uma Partap (eds) Asian bees and beekeeping: progress of research and development. Proceedings of the fourth international conference, 23–28 Mar 1998, Kathmandu. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, 274pp

Houbaert D, Jacobs FJ (1992) Accelerated fruit setting of tomatoes by insect pollination. In: Bees for pollination. Proceedings of an EC workshop, Brussels, 2–3 Mar 1992, pp 207–218

Jay SC (1986) Spatial management of honeybees on crops. Ann Rev Ent 31:49–65

Kenmore P, Krell R (1998) Global perspectives on pollination in agriculture and agroecosystem management. In: International workshop on the conservation and sustainable use of pollinators in agriculture, with emphasis on bees, Sao Paulo, 7–9 Oct 1998

Koelreuter JG (1761) vorlaufige nachricht von einigen das geschlecht der pflanzen betreffenden versuchen und beobachten. Engelmann, Leipzig, 50pp

Kumar J, Mishra RC, Thakur SS (1998) Use of honeybees for increasing agricultural yields. In: Mishra RC, Rajesh G (eds) Perspectives in Indian apiculture. Agro Botanica, Bikaner, pp 187–211

Mardan M (1995) Varied pollinators for sub-tropical Asian crops. In: Roubik DW (ed) Pollination of cultivated plants in the tropics. FAO (UN), Rome, pp 142–148

Matheson AG (1986) Colony standards for Kiwifruit pollination. N Z Beekeep 189:20–22

Matheson AG (1991) Managing honeybee pollination of Kiwifruit (Actinidia deliciosa) in New Zealand – a review. Acta Hort 288:213–219

Matheson AG, Schrader M (1987) The value of honeybees to New Zealand's primary production. Ministry of Agriculture and Fisherie, Nelson

McGregor SE (1976) Insect pollination of cultivated crop plants. Agriculture hand book No 496, Agriculture Research Service, United States. Department of Agriculture, Washington, DC, 411pp

Morse RA, Calderone NW (2000) The value of honeybees as pollinators of U.S. crops in 2000. Bee Cult 128(3):2–15

Partap U (1999) Pollination management of mountain crops through beekeeping. Trainers' resource book. ICIMOD, Kathmandu, Nepal.

Partap U (2000) Foraging behaviour of *Apis cerana* on citrus (*Citrus sinensis* var. Red Junar) and its impact on fruit production. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Uma Partap (eds) Asian bees and beekeeping: progress of research and development. Proceedings of the fourth AAA international conference, Kathmandu, 23–28 Mar 1998. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, 274pp

Partap U, Verma LR (1992) Floral biology and foraging behaviour of *Apis cerana* on lettuce crop and its impact on seed production. Progress Hortic 24:42–47

Partap U, Verma LR (1994) Pollination of radish by *Apis cerana*. J Apic Res 33:237–241

Partap U, Shukla AN, Verma LR (2000) Impact of *Apis cerana* pollination on fruit quality and yield in peach and plum in the Kathmandu valley of Nepal. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Uma Partap (eds) Asian bees and beekeeping: progress of research and development. Proceedings of the fourth AAA international conference, Kathmandu, 23–28 Mar 1998. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, 274pp

Prescott-Allen R, Prescott-Allen C (1990) How many plants feed the world? Conserv Biol 4:366–374

Roubik DW (1995) Pollination of cultivated plants in the tropics. FAO Agricultural Services Bulletin No. 118. FAO, Rome, 196pp

Sale PR (1983) Kiwifruit culture. Wellington, New Zealand: Government Printing Office.

Sihag RC (1990a) Behaviour and ecology of the sub-tropical carpenter bee, *Xylocopa fenestrata* F.1. Adaptive response to high temperatures Indian Bee J 52(1–4), 36–37

Sihag RC (1990b) Behaviour and ecology of the sub-tropical carpenter bee. *Xylocopa fenestrata* F.2 Host plant association Indian Bee J 52(1–4), 38–40

Sihag RC, Mishra RC (1995) Crop pollination and *Apis cerana*. In: Kevan PG (ed) The Asiatic Hive Bee: Apiculture, Biology and Role in Sustainable Development in Tropical and Subtropical Asia, Enviroquest Ltd., Cambridge, Ontario, (Canada) pp 135–142

Singh LB (1960) The mango. Leonard Hill, London

Singh B, Gatoria GS, Singh L (2000) Effect of priming the queen cell cups on mass queen rearing in *Apis mellifera* Linn. Colonies. Indian Bee J 63(3):68–71

vanEngelsdorp D, Meixner MD (2010) A historical review of managed honeybee populations in Europe and the United States and the factors that may affect them. J Invertebr Pathol 103:S80–S95

Verma LR, Partap U (1993) The Asian hive bee, Apis cerana, as a pollinator in vegetable seed production. ICIMOD, Kathmandu, p 52

Verma LR, Partap U (1994) Foraging behaviour of *Apis cerana* on cabbage and cauliflower and its impact on seed production. J Apic Res 33:231–236

Waser NM (1986) Flower constancy: definition cause and measurement. Am Nat 127(5): 593–903

Wells H, Wells PH (1983) Honey bee foraging ecology: optimal diet, minimal uncertainty or individual constancy? J Animal Eco 52:829–836

Williams GC (1992) Natural selection. Oxford University Press, Oxford
Winston ML, Scott SC (1984) The value of bee pollination to Canadian apiculture. Can Beekeep 11:134–135
Woyke HW (1981) Some aspects of the role of the honeybee in onion seed production in Poland. Acta Hort 111:91–98

Chapter 6
Wild Bees and Crop Pollination

Abstract Bees represent a great diversity. According to Michener (The bees of the world. The John Hopkins University Press, Baltimore/London, 913 pp, 2000) more than 16,325 species of bees have been recognized, belonging to 425 genera, reorganized under 7 families. Though much has been known still much more needs to be investigated. In India much has been explored on various aspects on honey bees (Apis) such as their domestication, management and crop pollination, however, this is not true for non-Apis bees which also play an important role in the pollination of various crops and flowerings plants growing in the wild which maintain the stability of ecosystems. Use of wild bees assumes greater significance as the number of honeybee colonies is drastically reducing due to numerous reasons like monoculture cropping pattern, destruction of natural habitat, attack of diseases and pesticides misuse for protection of crops.

6.1 Management of Wild Bees for Pollination

Insect pollination of agricultural crops is a critical ecosystem service. Fruit, vegetable or seed production from 87 of the 115 leading global food crops depends upon animal pollination (Klein et al. 2007). The value of insect pollination for worldwide agricultural production is estimated at 153 billion, which represents 9.5% of the value of the world agricultural production used for human food in 2005 (Gallai et al. 2009). The area cultivated with pollinator-dependent crops has increased disproportionately over the last decades, suggesting that the need for pollination services will greatly increase in the near future. The Apis mellifera has occupied dominating position in commercial pollination around world because this is highly social bee. But of the other hand wild bees are also valuable pollinators. We have always under evaluated their contribution perhaps because of our limited insight into their behaviour mechanism for nesting. The other reason may be that we are more reliable on the easily manageable honey bees which provide by-products also. But today the modern beekeeping suffers from a magnitude of problems, including parasitic mites,

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honey bee diseases, unability of honey bees to work at low temperature and adverse climatic conditions. These difficulties threatens the honey bees general utility as an agricultural pollinator (Torchio 1990). This contributes to the concern to beekeepers, growers of insect-pollinated crops, and policy-makers over recent widespread declines in honey bee populations (Colony Collapse Disorder).

For agricultural as a whole the diversification of pollination assemblages for crops is clearly important. Wild and domesticated non-Apis bees effectively complement honey bee pollination in many crops. Examples of management of non-Apis species for agricultural pollination include the use of bumble bees, primarily for the pollination of greenhouse tomatoes, the solitary bees Nomia and Osmia for the pollination of orchard crops, Megachile for alfalfa pollination, and social stingless bees to pollinate coffee and other crops. The value of the alfalfa leaf cutting bee M. rotunda (F.) as a better pollinator than honey bees for alfalfa has been clearly demonstrated by Richard (1987). He concluded that the real impact of introduction of Megachile bees stating that alfalfa seed yield increased from 50 to 350 kg/ha and with more careful handling it can be raised upto 1,000 kg/ha.

There are about 19,000 described species of bees in the world (Linsley 1958) and, with the exception of one species, Apis mellifera L., the domestic honey bee, all of them are grouped under the general term “wild bees.” These include:

Short-tongued bees:	
Family	Important genera
Andrenidaea	Andrena, Panurginus, Perdita, Pseudopanurginus
Colletidae	Colletes, Hylaeus
Halictidae	Agapostemon, Dufournea, Halictus, Nomia
Melittidae	Hesperapis, Melitta
Long-tongued bees:	
Anthophoridae	Anthophora, Melissodes, Nomada, Xylocopa
Apidae	Apis, Bombus, Euglossa, Melipona, Trigona
Megachilidae	Anthidium, Lithurgus, Megachile, Osmia

The term “wild bee” is used commonly for all bees except honey bees in the genus Apis. Bees generally are distinguished from other flying hymenopterous insects by their characteristic plumose body hairs. Bees are of many sizes, shapes, and colors. Some of the smallest bees, Perdita, are less than 3 mm; whereas the largest leafcutter bee is over 80 mm. Almost the entire range of colors is found among the brightly marked bees, including many beautiful metallic species. One can easily observe many species of bees actively visiting flowers for nectar and pollen or engaged in the processes of constructing nests. According to an estimate there are at least 30,000 species of bees in the world. This number of species is more than all the fish, bird, and reptile species combined (Bohart 1972).

Most bee species construct either single or complex nests underground. Some make earthen, leaf, or resin nests on rocks and plants. Other bees make or utilize crevices in rocks or plant stems, insect borings, and plant galls for their nesting sites. Most bees live a solitary existence-each female after mating locates and builds her nest without the aid of other bees, and usually at a distance from her sister bees. However, some bees are quite gregarious and nest close to one another, sometimes in dense populations of up to a million nests in a few acres of soil. Some bees prefer to nest at the same site year after year, but others relocate their nests each season. A small percentage of our wild bees are social or semisocial; that is, there is a division of labor among the bees occupying a single nest (Michener 2000).

6.2 Value of Wild Bees as Pollinators

One cannot easily determine the figure on the value of wild pollinators, simply because total impact on the environment is not known. Studies on the impact of each pollinator species on fruit or seed production of our major crops is almost nonexistent. The reproduction of wild flowering plants is often taken for granted to aid in maintaining soil moisture and fertility, and to provide food not only for wild life but for our domestic livestock as well. How many billions of dollars are these benefits worth? It is easy to document the value of crop species visited by bees, but here again the importance of wild bees as crop pollinators has been neglected. It has long been the general consensus that honey bees adequately pollinate crops and there is little need for wild bees. Unfortunately, it is not true since adequate research on the economic benefits of wild pollinators has not been done. Interestingly, the research completed on the few wild pollinator species has revealed relatively higher returns compared with its investment costs.

The dependence on one species for crop pollination sometimes creates problems. It seems wise to make greater efforts to study, conserve, and try to manage as many species of wild bees as possible. There are several crops that are under pollinated by the honey bees, either because the bees are not physically adapted to pollinate them or the crops are not attractive to honey bees. Some of our most important crops, valued at billions of dollars, are in this category. These crops are alfalfa, soybeans, cotton, vegetable seed, and sunflowers, each of which is adapted to specific types of pollinators. Recent research on the utilization of several species of wild bees as crop pollinators is just beginning to indicate some of their economic benefits, e.g. the alfalfa leafcutter bee. The alkali bee was the first wild bee to be utilized as a crop pollinator in the United States beginning in the early 1950s. Since that time, the alfalfa leafcutter bee and the blue orchard bee have been domesticated as crop pollinators.

6.3 Diversity of Wild Bees

Friese (1923) estimated that out of 20,000 species of bees (Superfamily; Apoidea), only four species of honeybees (now nine) and 300 species of stingless bees (Family: Meliponinae) live in the permanent perennial colonies. The majority of the bees are solitary where a female constructs a nest consisting of one or more brood cells stocked with nectar or pollen that provide food for the larvae that will emerge from

Table 6.1 Families, subfamilies, principal tribes, and the distribution of bees (superfamily Apoidea) (Based on Michener 1974a, b)

S. No.	Family	Subfamily	Distribution
1	Colletidae		Worldwide
2	Oxaeidae		New world
3	Halictidae	Dufoureinae	Holarctic; African and Oriental regions; Chile
		Nominae	Old world tropics; South temperate regions; Holarctic
		t. Augochlorini	South and central America, some in Canada
		t. Halictini	Worldwide but less abundant in subtropics
4	Andrenidae	Andreninae	Chiefly Holarctic some in Africa and S. America
		Panurginae	Africa, Eurasia, New World
5	Mellitidae	Ctenoplectrinae	Paleotropics
		Macropidnae	Holarctic
		Melittinae	Holarctic, Africa
		Dasypodinae	Holarctic, Africa
6	Fidelidae		S. Africa and Chile
7	Megachilidae	Lithurginae	Worldwide (tropical and warm regions)
		Megachilinae	
		t. megachilini	All continents
		t. anthidini	All continents
8	Anthophoridae	Nomadinae	Worldwide
		Anthophorinae	
		t. Exomalopsini	Neotropics
		t. Ancylini	Mediterranean and eastward into Asia
		t. Tetrapedini	Neotropics
		t. Melitomini	Western hemisphere
		T. Canephorulini	S. America
		t. Eucerinodini	S. America
		t. Eucerini	All continents(except Australia)
		t. Anthophorini	Worldwide
		t. Centridini	Americas (tropical and warm parts)
9	Apidae	Bombinae	
		t. Euglossini	Neotropics
		t. Bombini	Holarctic
		Apinae	
		t. Meliponini	Tropics worldwide
		t. Apini	Eurasia and Africa (introduced to all parts of the world)

the eggs she deposits just before the sealing of the cell. In general, two thirds of the bee fauna is comprised of the solitary bees (Michener 1965; Linsley 1958; Bingham 1897; Batra 1977). Michener (2000) apprehended 16,325 species of bees, grouped under 425 genera (Table 6.1). The taxa found in whole of the world were reorganized under seven families. Still much needs to be known from different regions of the world about the existence of different species of solitary bees, more particularly, from the Oriental region.

6.4 Why Wild Bees Management

The expensive need for insect pollination in modern agriculture has made bees a vital factor in crop production. To most people, the word bee suggests only the common honeybee, perhaps also bumblebees; but the bees are in fact a super family of the order Hymenoptera, containing an estimated 20,000 species. They are in fact a group of flower-visiting wasps termed as bees that has abandoned the wasp habit of provisioning nests with insect or spider prey and instead feeds its larvae with pollen and nectar, collected from flowers or with glandular secretions ultimately derived from the same sources. They are a large and diversified group, considered to be consisted of nine families (Michener 1974a, b). Except in certain Colletidae which carry pollen with nectar in the crop, the structures used for carrying pollen consist of scopal hairs having various locations and arrangements. One such group is the Masaridae, a family of wasps closely related to the Vespidae and in the superfamily Vespoidea. The other group of wasps which abandoned predation as a source of larval food was from an entirely different source than the masarids, namely the wasps of the superfamily Sphecoidea. From this group arose the bees. Bees, entirely dependent on flowers for food, could not have arisen before the appearance of the angiosperm plants.

How early bees arose from the sphecoid wasps is unknown; it might have been as late as the middle Cretaceous since angiosperms also became the dominant vegetation in middle Cretaceous times. Primitive angiosperms had relatively shallow flowers, such as can be used as pollen and nectar sources by short-tongued insects, including many beetles, wasps, and the short-tongued bees. The first five families, listed as Colletidae. Halictidae. Oxaedae, Andrenidae and Mellitidae are characterized by usually short mouthparts and are often grouped as the short-tongued bees. The other four families-Fidelidae, Megachilidae, Anthophoridae and Apidae are classified as long tongued families, all are equipped with elongated glossae, maxillary galeae and basal segments of the labial palpi forming the sucking apparatus for taking advantage of nectar sources with deep tubular flowers. Flowers with deep corolla tubes probably arose in co-Evolution with their principal pollinators. The legume crops and their pollinators such as alfalfa-megachilid constitute an important example. There is close relationship between bumble bee species and their major plant hosts accordingly to their length. The worldwide distribution of these bees and their remarkable ability for proliferation are the results of their higher degree of adaptability (Stephen et al. 1969; Michener 1974a, b).

In many colonies there are interrelations among individuals, such that behavior of one influences the behaviour or development of another. All these interrelations are termed social interactions. Feeding of a larva by a bee is an example of a social interaction. As indicated previously, colonies of bees range from those that seem almost insignificant-two or three bees in a burrow in the ground or in a hollow stem- to the large colonies of the honeybees. The kinds and amount of division of labour and communication among bees in colonies very greatly. Species are often called solitary, communal, social, and so forth. Such terms are generally applied to the most complex type of organization attained during life cycle of the species. In the majority of species of bees each female makes her own nest, or sometimes several of them, without regard to the locations of other nests of the same species. Such bees mass-provision the cells by placing enough pollen and nectar in each to provide for the entire growth of a larva. After oviposition, the mother seals the cell and goes on to construct and provision another. Ordinarily she dies before her progeny mature and emerge from their cells; therefore there is no contact between generations. Probably the majority of species of Solitary bees have only a single generation per year, the adults emerging and flying about during a relatively brief season, sometimes only 2 or 3 weeks. Such species pass the rest of the year in the nest. The feeding stage of the larva is ordinarily brief, often only a few days, and most of the year is passed in the pupal stage or as young adults either still in their natal cells or in special hibernating or aestivating places. Some solitary bees, however, regularly have two generations per year, for example one in spring and another in the autumn, while others go through a succession of overlapping generations so that, except in the spring, all stages can be found at anytime during the warmer months of the year.

Nest aggregations occur most commonly among bees that burrow in the soil. Aggregations of such burrows may vary from a few to ten nests scattered that one wonders if they constitute an aggregation at all, to small, dense clusters of nests like those of Lasioglossum versatum in Kansas. Some bees that make burrows in stumps or logs instead of soil also form aggregations. For example, one may find numerous nests of carpenter bees (Xylocopa) in a single post or building. Bees mostly megachilids that construct exposed cells of mud and other materials brought to the site sometimes also form aggregations of nests: for example Chalicodoma muraria sometimes covers large portions of walls in southern Europe and North Africa with masses of its cells. Communal quasisocial and semi-social groups are so similar superficially that the convenient collective term parasocial has been proposed for them. Parasocial colonies are simply any colony in which the adult bees consist of a single generation, unlike the eusocial forms in which two generations of adults are ordinarily present. A communal colony consists of a group of females of the same generation using a single nest each making, provisioning, and ovipositing in her own cells. In the enormous genus Alldrella, most species are solitary, some nesting in aggregations. However, Alldrella bucephala and A. ferox live in colonies that are probably communal. These are small colonies with two to several females, usually of about the same age and of the same generation, cooperatively construct and provision cells. More than one bee working on a given cell. As in communal groups, each female has enlarged ovaries and is mated, indicating that each is an egg layer. Some species of Nomia are possibly quasisocial, although knowledge of their colonies is inadequate (Batra 1966a). The best known of such species is N. capitata from India. These are small groups which show cooperative activity and division of labor among adult females as in eusocial groups. Polygynous young colonies of other halictines (Vleugel 1961) are often temporarily semisocial in that division of labor develops among gynes, one becoming the egg layer or queen, the others auxiliaries or, in effect, workers. These are family groups each consisting of one adult female and a number of immature offsprings which are protected and fed by the adults. The mother leaves or dies before or at about the time that the young reach maturity. There is no division of labour among adults, as is found in semisocial and eusocial groups. Young colonies of Bombus, before workers are produced, are subsocial; the queen progressively feeds the growing larvae in a more or less subdivided common cell. However, the true social Hymenoptera, for which the word eusocial was coined by Batra (1966b), live in colonies which are family groups consisting of individuals of two generations, mothers and daughters. Usually in bees a eusocial colony contains only one queen and the bulk of the females are workers (daughters). Division of labor, with some individuals functioning as egg layers or queens and other as workers. That is, with more or less recognizable castes occurs in both the semi social and eusocial colonies but not in the other types of colonies.

Colonies are long-lived and sustained through periods of adversity by food for adult as well as larval consumption, stored in the nests but in brood cells. Integration within colonies is complex and involves a variety of behaviour patterns, pheromones and physiological adaptations that would have no obvious function in solitary forms. Aggressive behaviour among individual of the same colony is rarely evident, nor is the egg eating that is often associated with such behaviour. Communication concerning food sources and at swarming time, concerning nest sites is well developed in many of these bees. Larvae are fed at least in large part on glandular secretions of workers. Populations of colonies are commonly in the thousands (upto over 60,000 for Apis, 180,000 for some species of Trigona), although some species often have colonies of only 1 or 200. Only Bombus and the highly eusocial bees store food in quantity outside of brood cells for use of adults and for transfer to larvae or brood cells as needed. In most groups of social insects interactions between adults and young (i.e., brood-eggs, larvae, pupae) are universal and important parts of the social organization. Exchange of food between larvae and adults is well known in ants and vespid wasps, and it has often been supposed that Iarval activity or secretions are of great importance in maintaining the social group. In most kinds of bees, however, there are no contacts between adults and young ones because the cells in which the youngs are reared are closed before the eggs hatch, each cell being mass provisioned with enough food to provide for the entire growth of the larva. Progressive feeding, which of course involves adult-larva contact from time to time during the growth of the larvae occurs among bees only in Apis, Bombus and most allodapines. Even the highly eusocial meliponines have mass-provisioned cells which, together with the cocoons spun by the mature larvae, completely enclose the immature stages for the whole developmental period.

The number of species of solitary bees is greatest in the warmer, more arid sections of the world, particularly in the semidesert areas as typified by those of western North America, North America, South Africa, Australia, northwestern Argentina, and South-central Eurasia. An abundant and diverse solitary bee fauna is common adjacent to mountainous areas where moderate rainfall conditions exist. The rich bee fauna found in mountains adjacent to arid or semiarid areas is only partially explained by the stratification into altidudinal zones. The varied soil type and exposures, rock niches, beetle holes in wood, and pithy-stemmed plants offer many diverse nesting niches. The world-wide distribution of bees and the remarkable proliferation of species attests to their high degree of adaptability. Numerous definitions have been proposed to distinguish between social and solitary bees, but recent information has shown that hard and fast distinctions cannot always be nude.

The biology of behaviour of the solitary bees has attracted the attention of an increasing number of research workers during the past 15 years: those exploring the value of solitary bees for pollination purposes (Bohart 1972; Stephen 1969) and those attempting to evaluate the significance of biological patterns as a supplementary tool for the determination of phylogenetic relationships among bees (Michener 1974a, b). In the Northwest about half of the Megachile rotundata larvae of the first generation pupate and emerge as adults in the late summer. In some seasons a small percentage of the progeny of the second generation emerge as a third generation, although they usually have little time for nesting before being killed by cold temperatures). Some Megachile and Hylaeus and some Anthophora have more than one complete generation and overwinter as prepupae. Some single-generation species overwinter as adults in their netal cells. For example, Osmia/ignaria usually emerges as an adult in April and dies for about 3 weeks, The type of life cycle described above is apparently an adaptation for early spring emergence, although some species exhibiting it (for example, Osmia tera) do not until late spring. It is interesting to note that another species with relatively late emergence. Osmia californica, usually has some individuals overwintering as prepupae. Other bees overwintering as unemerged adults include most Osmia and Andreno and some Antbophora, Megachile, and Emphoropsis. Bumblebees undergo a life history similar to that of halictines. The overwintered female is sole egg layer for several generations, which overlap broadly because egg laying is continuous. The overwintering female (queens) which are distinctly larger than the earlier generations of workers, are usually produced after the worker: brood ratio is favourable for intensive feeding of queen brood. The Xylocopinae overwinter as emerged adults, as do halictines and many apids. However, both sexes of Xylocopines overwinter in a dormant condition and mate in the spring (some mating is reported to take place also in the fall). The females usually overwinter in the natal nest with males from other nests often joining them.

In many megachilids, males appear more numerous but the exact ratio v: Exact causes leading to the variance are not well understood. In Megachile rotumdata, the ratio of males to females in large samples taken from different nesting popula has been seen to vary from I:I to 10:1. The difference in ratios is directly correlated with the diameter of the tunnel in which they are nesting. Emergence of males in advance of females is evident in the alkali bee and in Megachile rotundata, as in most other species of bees that have been studied. This phenomenon, referred to as protandry, is a general rule among solitary bees and is interpreted a Evolutionary adaptation, assuring the presence of males for mating with emerging females.

The availability of suitable substrates for nesting is one of the most common factors limiting the population and distribution of bee species. The principal type nesting microenvironments include soil, wood, small and large cavities and even fully exposed surfaces. Species nesting in soil may select horizontal to gently sloping surfaces or vertical banks. The vertical surface may be bare or overhung with vegetation, or rarely with a grassy cover, and its exposure may provide maximum minimum shade. Vertical banks are usually dry, but they may be moist in shaded gullies or dram ditches. The soil surface may be wet or dry, but appreciable moist is usually available where and when the cells are constructed. At least one observation has been made of Anthophora species tunneling in moderately hard sand-stol Ceratina, some Megachile. Some Xylocopa and several genera of small sphecid wasps burrow in the soft pithy plant stems of plants such s raspberry, black-berry and sunflower in constructing nesting tunnels. A wide variety of nesting material is utilized by megachilids. Their nests may be found in mail shells (Old World Osmia), pockets or cracks in rocks (many osmiines), attached to twigs or rock surfaces (some Dianthidirim), or in narrow crevices ill almost any material (Megachile rotundata). Tendency of bees to renest in close proximity to their parent's nest is one of the main causes of gregariousness, and that selection of a peculiar soil condition has a minor effect. Most burrowing bees construct laterals from the main burrow with one or more cells arising from each lateral. Exceptions occur among species that construct a main burrow with one or more cells attached to the end, along the sides, or arranged within the main burrow in linear series. After the cells are provisioned and capped, the nest, or a portion of it, is plugged. Some species only plug the area immediately exterior of each cell, others completely backfill the laterals, and still other plug the entrance when the nest is completed. Most species that arrange their cells in line series construct complete cells, i.e. provide walls as well as top and bottom for each cell (most Megachile. Anthidium). In Megachile, the rounded base of each cell inserted into the concave apex of the cell below, resulting in a nearly intact, weakly differentiated column of cells.

The number of cells per nest ranges from one to several thousand. Most solitary soil burrowing species make only one nest, which contains as many cells as foraging conditions and the reproductive potential of the bees allow. Nest of Nomia melanderi, may contain from 5 to 24 cells, depending upon the availability of forage and the quality of the substrate in which they are nesting. Some species of Osmia normally select small pockets in rocks that accommodate only one cell, but the same species may place several cells in somewhat larger holes. Megachile rotundata will accept tunnels which accommodate only a single cell but more commonly uses long tubular cavities in which it places as many as 20 cells. The reproductive potential of this species is even higher (upto 40 eggs), but there seems to be an upper limit to the number of cells it places in a single tube, independent of its length.

The world wide distribution of these bees and their remarkable ability for proliferation are the result of their higher degree of adaptability. Floral fidelity is the major attribute of these species making them sure of maintaining species characteristic within plant species. Based upon degree of association in between bees and the plant species i.e. the number of plant types visited for pollen collection, the bees are termed monolactic (visiting one species) oligolactic (visiting few related genera) or polylactic (visiting many types of plants). The solitary bee species arc mostly oligolactic. Differences in seasonal adaptability, the pattern of origin vis-a-vis individual bee specialization basically determine bees abundance for pollen collection on a particular plant. The principle factor which determines the effectiveness of such pollinators for a particular crop or plant species depends upon the bee abundance, bee flight period, bee flight hours per day and the number of flowers visited per day. The factors which contribute to bee survival in Nature and their propagation depends upon the availability of natural or man made nesting devices of preferred dimensions, abundance of natural parasitic, or predators, incidence of disease or pesticide poisoning, and the natural brood mortality during active or the dormant season. Most important is the synchronization of the bee flight period with the major blooming period of the crop. This is achieved through appropriate provisions of nesting devices and regulating development of adults so that there is synchrony in adults formation with crop blooming. Following are the characteristic features of such bee management programmes for crop pollination.

(i) Provision of appropriate nesting devices of brood cell formation.
(ii) Collection and safe storage of brood nest of cells at low temp.
(iii) Checking/controlled emergence of parasites or removal diseased cells.
(iv) Incubation of cells at appropriate temperature to regulate formation.

6.5 Diversity of Bees in India

Unlike other commonly known insects, excluding honey bees that belong to genus Apis, bees have least attracted the attention of Indian taxonomists and biodiversity workers. No doubt various aspects on honey bees (Apis) such as their domestication, management and crop pollination have been considerably explored in India. However, this is not true for non-Apis bees. Most of them forage on wild flowerings located in the forests, buffer zones or more often that grow as weeds all along the cultivated crops. The wild flowerings infact constitute the primary resource for nectar and pollen for most of bees. Non-Apis solitary bees also visit cultivated crops in good populations but, as an alternate to wild flowerings.

In North India, Batra (1977) recorded 89 species of solitary bees out of the 97 species studied. The occurrence of major bee genera in India shows that bees belonging to family Megachilidae and Anthophoridae are most commonly distributed in India. Since India is a vast subcontinent with marked topographical and climatic differences, the climatic and floristic conditions vary from tropical and subtropical to subtemperate and temperate conditions. This is the reason that bee fauna from one region differs from the other. Most bees are distributed from valleys through plains to seashores. The Indian species of Bombus is generally restricted to higher elevations especially in the Himalayan ranges. Bingham (1897) recorded 24 species of Bumble bees from higher elevations of Kashmir; Himachal through Sikkim and Assam. Mani (1962) reported four species of bumble bees at elevations of over 4,000 m at Himalaya. Williams (1991) has recorded 28 species of bumble bees from Kashmir including areas under illegal control of Pakistan. Xylocopa species and Pithitis smaragdula in the north western states of India remained confined to 914 m (Kapil and Dhaliwal 1968a, b) and 391 m (Kapil and Kumar 1969) above the mean sea level. The other species are generally abundant in warmer, semi-arid areas, yet distributed in temperate and mountain hill ranges also. The number of species reported in each genera holds the following numerical order: Halictus 52, Nomia 25, Bombus 28, Xylocopa 19, Megachile 44, and others are still less (Bingham 1897; Batra 1977).

Table 6.2 summarizes the occurrence of various bee fauna in different parts of India. Around 92% of known species were recorded from northern (Jammu and Kashmir, Punjab, Uttaranchal, U. P., Himachal Pradesh, Haryana) or western part (Rajasthan, except extreme north and eastern green parts and Gujarat) and remaining 8% were described from rest of the Indian regions. In other words, maximum investigations on biosystematics and floral relationships of bees have been made from the northern territories and a huge area of southern peninsula is left to be explored. The calculation concerning diversity of bees has revealed that a total of 633 species grouped under 60 genera are found in our country. Certainly, this is not a satisfying number for a huge area with enough of climatological variations, such as India besides, synonymies for many species is still pending to be worked out. Author feels that present publication will provide an overview of the bee fauna and will be used as a foundation study by the Melittologists of the nation to fill the gaps in future. The recentmost biosystematic arrangement presented here will be further useful to the biodiversity, ecological and pollination-workers of the country.

A detailed historical account, regarding discovery of different genera and species of non-Apis bees from south Asian countries up to Indonesia has earlier been published by Gupta and co-workers during 2003.

The country has been subdivided under certain specific area based upon homogeneousness of ecological factors facilitating the presentation. The regions specified are:

Extreme northern region: It includes high altitude of Himalayas ranging between 6 and 7,000 ft and more in Jammu and Kashmir, Himachal Pradesh and Uttaranchal.

Northern region: This indicates the medium and low altitudes area and, plains of Tarai at and south of Himalayan range i.e. including southern J and K, Punjab, Haryana, eastern Rajasthan adjacent to U. P, U. P. and plains of Bihar.

Western region: Almost whole of Rajasthan (excluding eastern hilly-green region) and Gujarat.

Western Ghats: Western hilly Maharashtra, Goa, western Karnataka and, otherwise specified Lakshadweep and Minicoy Islands.

Table 6.2 Diversity of bees in India (Gupta 2003)

S. no.	Family	Subfamily	Tribe	Genus	No. of species	Broad distribution in India
1	Colletidae Lepeletier	Colletinae Lepeletier	–	1. Colletes Latreille, 1802	005	Northern region
		Hylaeinae Viereck	–	2. Hylaeus Fabricius, 1793	014	13 in Northern region and 2 in Southern region
2	Andrenidae Latreille	Andreninae Latreille	–	1. Andrena Fabricius, 1775	034	Widely distributed in northern region
3	Halictidae Thomson	Rophitinae Schenck	–	1. Systropha Illiger, 1806	002	Punjab and northern Rajasthan
		Nomiinae Robertson	–	2. Nomia Latreille, 1804	067	Widely distributed throughout India
			–	3. Pseudapis Kirby, 1900	002	Northern region
			–	4. Steganomus Ritsema 1873	003	Northern and western Ghat regions
		Nomioidinae Börner	–	5. Ceylalictus Strand, 1913	003	Discontinuous: extreme northern, coastal western and south–central region
			–	6. Nomioides Schenck, 1867	003	Deserts of north-western region
		Halictinae Thomson	Halictini	7. Halictus Latreille, 1804	055	47 in hilly region of north extending upto north east and 8 in west, central and western ghats
				8. Homalictus Cockerell, 1919	006	North and north eastern region
				9. Sphecodes Latreille, 1804	017	11 in north and north eastern region and 6 in south Rajasthan and Gujarat
				10. Thrinchosto-ma Saussure, 1890	002	Northeastern region
4	Melittidae Schenck	Melittinae Schenk	Melittini	1. Melitta Kirby, 1802	001	North and north eastern region
5	Megachilidae Latreille	Fideliinae Cockerell	Pararhophitini	1. Pararhophites Friese, 1898	002	1 in northwestern region and 1 in Gujarat
		Megachilinae Latreille	Lithurgini	2. Lithurgus Berthold, 1827	014	Discontinuous distribution: northern, western coastal, extreme southern and northeastern region

Osmiini	3. Chelostoma Latreille 1809	001	Sikkim and allied hilly territories of north east, continue upto Myanmar
	4. Heriades Spinola, 1808	022	17 in Himachal Pradesh, Uttaranchal and north-eastern hills and 5 in southern Rajasthan and Gujarat
	5. Hoplitis Klug, 1807	010	8 in Northwestern region and 2 in western coastal region
	6. Noteriades, Cockerell, 1931	004	Himachal Pradesh
	7. Osmia Panzer, 1806	005	4 in Himachal Pradesh, Uttaranchal and 1 in eastern coast of southern region
	8. Protosmia Ducke, 1900	001	Northern (medium hilly) region
	9. Pseudoheriades Peters, 1970	005	Northwestern region (and eastern buffer zone of Thar)
	10. Wainia Tkalců, 1980	002	So far recorded from Lonavala [Maharashtra only]
Anthidiini	11. Acedanthi-dium Michener and Griswold, 2000	001	Northern (Himachal Pradesh and Uttaranchal only)
	12. Anthidiellum Cockerell, 1904	001	Northeastern region
	13. Anthidium Fabricius, 1804	004	Northern and northwestern hilly and xeric regions
	14. Dianthidium Cockerell, 1900	004	Northwestern xeric region
	15. Eoanthidium (Popov, 1950)	002	Northwestern xeric region
	16. Euaspis Gerstaecker, 1857	002	1 in northeastern region and 1 widely distributed in almost whole of India except, extreme southern region

(continued)

Table 6.2 (continued)

S. no.	Family	Subfamily	Tribe	Genus	No. of species	Broad distribution in India
				17. Icteranthidi-um Michener, 1948	002	Northwestern xeric area
				18. Indanthidium Michener and Griswold, 1994	001	So far recorded from Pune
				19. Pachyanthi-dium Friese, 1905	003	Discuntinuous: Kangra, Bengal, Kerala, Bombay and Panchmarhi
				20. Trachusa Panzer, 1804	004	Discontinuous: northwestern region, Central region, Bombay
				21. Trachusoides Michener and Griswold, 1994	001	So far recorded from Appangala (Karnataka)
			Dioxyini	22. Aglaoapis Cameron, 1901	001	So far recorded from Bombay
			Megachilini	23. Coelioxys Latreille, 1809	032	Widely distributed all over country
				24. Megachile Latreille, 1802	105	Widely distributed all over country
6	Apidae Latreille	Xylocopinae Latreille	Xylocopini	1. Xylocopa Latreille, 1802	036	Widely distributed all over country
			Allodapini	2. Braunsapis Michener, 1969	006	Discontinuous: northern, parts of western and extreme southern region
			Ceratinini	3. Ceratina Latreille, 1802	014	Almost throughout India
		Nomadinae Latreille	Nomadini	4. Nomada Scopoli, 1770	013	Mostly confined to northern regions
			Epeolini	5. Epeolus Latreille, 1802	003	2 in north and northeastern region and 1 in Central region
			Ammobatini	6. Parammobato-des Popov, 1931	001	Distinct territory not known [label indicates only India, perhaps extreme northern India]
				7. Pasites Jurine, 1807	001	Southern region
		Apinae Latreille	Ancylini	8. Tarsalia Morawitz, 1895	001	Western Ghats

		Eucerini	9. Eucera Scopoli, 1770	003	Northwestern region
			10. Tetralonia Spinola, 1839	015	13 in Northern region and 2 in Central region
			11. Tetraloniella Ashmead, 1899	002	1 in extremity of northeastern region and 1 in central region
		Anthophorini	12. Amegilla Friese, 1897	021	Widely distributed all over country
			13. Anthophora Latreille, 1803	010	Widely distributed all over country
			14. Elaphropoda Lieftinck, 1966	004	Mountains of extreme northeast region
			15. Habropoda Smith, 1854	014	Confined to northern to northeastern region
		Melectini	16. Melecta Latreille, 1802	002	Extreme northern region
			17. Tetralonioi-della Strand, 1914	003	Southern slopes of Himalaya through northeastern region upto Indonesia
			18. Thyreus Panzer, 1806	006	Widely distributed all over country
		Bombini	19. Bombus Latreille, 1802	026	Exclusively along the high and medium range of mountains in Himalaya
		Meliponini	20. Lisotrigona Moure, 1961	001	Central region
			21. Trigona Jurine, 1807	003	Arid zone in western region and Northeastern upto Indonesia
		Apini	22. Apis Linnaeus, 1758	005	2 Widely distributed, 1 introduced and 1 confined to very high altitudes in Himalaya
006	012		060	633	

Table contains the taxonomic categories found and known from India

Central region: Whole of M. P., most of the Maharashtra, Chhattisgarh, Andhra Pradesh, excluding coastal area.

Northeastern region: Includes hills of eastern Himalayan range, all the seven states of the northeast and Districts like Darjeeling and Siliguri in W. Bengal.

Eastern region: Excluding hilly north, West Bengal, hilly South Bihar, Orissa and extreme coastal area of Andhra Pradesh.

South-central: The region include Karnataka, and northern parts of Tamilnadu.

Extreme southern region: Specified for Pondicherry, coastal Tamilnadu and Kerala and, otherwise not specified Andaman and Nicobar Islands.

6.5.1 Family Stenotritidae Cockerell

The smallest family of bees that consists of only 2 genera namely, Ctenocolletes Cockerell with 10 species and, Stenotritus Smith with 11 species. Both are exclusively found in Australia and, so far no species has been recorded from anywhere else in the world.

6.5.2 Family Colletidae Lepeletier

This is a medium size family subdivided into five subfamilies namely, Colletinae Lepeletier, Diphaglossinae Vachal, Xeromelissinae Cockerell, Hylaeinae Viereck and Euryglossinae Michener. Among them, subfamily Colletinae and Hylaeinae are the lone representatives of this family, known by one genus each, in India. The moderately populated genus Colletes, represented by five species, is restricted to northern region so as other identically populated genus Hylaeus with 15 species. It was interesting to note that three species of Colletes are more or less confined to middle range height (around 5,000–6,000') in southern slopes of greater Himalaya in Uttaranchal and Sikkim. All of them are quite limited in their distribution. On the contrary, species found in plains and those reaching upto Rajasthan in south, are comparatively widely distributed. The area of species distribution may be apprehended as J and K, Punjab, Haryana, Himachal Pradesh, Uttaranchal, eastern Rajasthan and one species record exists from Sikkim and Pune.

Probably, majority of species of this genus are also distributed in intermediate area namely, union territory of Delhi, northern U.P. as well as the green northern Rajasthan. Practically there exists no ecological barrier between the noted territory and the probable area of distribution. These areas require intensive surveys. Species of Colletes have been collected digging deep burrows on sloppy surfaces of hard grounds in Sikkim. Grewal et al. (1970a) described the life history of C. nursei from Punjab. This author has also collected many females in Punjab while busy excavating burrows in sandy, bare and dry crop fields. Batra (1977) made many ecological observations on nesting sites of Colletes. Batra (1968a, b) and Gupta and Yadav (2001) noted down different floral species visited by some species of this genus.

Genus Hylaeus in major contains those species which were earlier grouped under genus Prosopis. The name Hylaeus has priority thus accepted. Prosopis however, still is a subgenus of reorganized Hylaeus (Michener 2000: p. 182). It is a world wide genus having representatives on all continents. Most of the species collected from oriental region are yet to be assigned a subgeneric category. Species of our destined area have been collected from Kashmir, Punjab, Rajasthan, northern part of W. Bengal and Sikkim. Two out of 15 species known from our country were collected from southern extremities probably reaching upto Sri Lanka (Wijesekara 2001). An intensive survey to the nation waits so that exact picture of its distribution would be marked on the map of our country. Species of this genus are known to visit some cultivated crops in Punjab (Batra 1968a, b).

6.5.3 *Family Andrenidae Latreille*

It is a large family of bees subdivided under four subfamilies namely, Alocandreninae Michener, Andreninae Latreille, Panurginae Leach and Oxaeinae Ashmead. However, in our country this family is represented by subfamily Andreninae only having the single representative genus Andrena. Species of this genus can be marked all over northern India, more particularly plains of Punjab, Haryana, Himachal Pradesh, Rajasthan, Uttaranchal, U. P., Bihar and W. Bengal. Two species were collected one each from western coast of Maharashtra, the central Maharashtra and Assam. 34 species are known so far after judging synonymies. Major bulk of them show affinities for their western allies found in Pakistan, Afghanistan and, upto Turkey. On the contrary, eastern species are fairly distributed upto Myanmar and Malaysia. Precisely, most of species seem to have adapted for their specific eco-geographical environments in India but many more have their affiliates towards both neighbouring territories. An intensive survey of the remaining part of the country would yield several new species and their floral data, unknown so far.

Rahman (1940) briefly described a nest of Andrena ilerda, collected near a toria field. This is not yet known that species of Andrena excavate the tunnels themselves or they occupy pre-existing subterranean burrows. However, the highly branched, 50–60 cm. deep burrows have at least one cell at the end. Wain (1968) also recorded nests of A. bellidoides in the hills of western ghats. They were constructed gregariously. Grewal et al. (1970b) published the nesting behaviour of Andrena leaena.

The personal observations made by this author during all these years concluded that species of this genus bear a good affection for the flowerings of cruciferous crops. The oil seed producing region all along the Shivalik and Aravali range harbours comparatively good population of many species. Mohammad (1935), Rahman (1940), Batra (1968a, b), Atwal (1970), Bhalla et al. (1983), Kumar et al. (1988), Kumar et al.

(1994), and Gupta and Yadav (2001) have listed many species of Andrena collected on different cruciferous crops in the mentioned area. Abrol (1986b, 1988a, 1989) detailed the behavioural aspect of some Andrena species from J and K.

6.5.4 Family Halictidae Thomson

This is a considerably large family having many semisocial bee species, commonly known as sweat bees. It is further subdivided into four subfamilies namely, Rophitinae Schenk, Nomiinae Robertson, Nomioidinae Börner and, Halictinae Thomson. The group is represented by 160 species in our country. Subfamily Rophitinae and Nomioidinae consist of a limited number of species with a restricted distribution whereas, subfamily Nomiinae and Halictinae are widely distributed.

The single representative of Rophitinae, genus Systropha was reported with two species limited to western Punjab and northern Rajasthan. Batra and Michener (1966) described one of them alongwith its subsoil formed nest and the larva. Identically, two representatives of Nomiinae, genus Pseudapis and Steganomus are confined to certain pocket area of the country. The third representative, genus Nomia with 67 species, is widely distributed all over India. Subfamily Nomioidinae is known by genus Ceylalictus and Nomioides both with three species each. Among them first one exhibits discontinuous distribution and the second is found in the arid region of north-west.

Subfamily Halictinae is further subdivided into tribe Augochlorini and Halictini. Among them Halictini has representation in our country and, of fairly wide occurrence. Two species of genus Thrinchostoma are known exclusively from the north-eastern region of the country. In major its species were recorded from the eastern countries next to India. Genus Homalictus, found in similar territory, is comparatively widespread, reaching upto the north at the southern slopes of Himalayan all along the range from north to northeast. Genus Sphecodes is also represented in the area inhabited by Homalictus but in addition to its 11 species, 6 are found in the southern hilly zone of Rajasthan and at the tail end of Aravali hills in Gujarat. The species found in western zone have affinities with their western allies. Genus Halictus, represented with 55 species, is largely confined to the northern territories and at low level hills of central and western parts of the country. The aspect of taxonomy of the family needs intensive investigations for most of the area of our country besides, the bionomics and biology.

Works pertaining to the nesting biology of a few species of Lasioglossum, Nomioides, Nomia and Halictus appeared so far, were published during 1960s to 1980s. Among them significant contributions regarding social behaviour and nests of nomiine bees, specially observations made for several species of Lasioglossum and Halictus, were published by Batra (1964a, b, 1965, 1966a, b, c, 1968a, b, 1970, 1971, 1995a, 1997a, b, etc.), Kukuk (1980), and Batra and Bohart (1970). Same aspect was described for many other halictid bees of Indo-Malaysia regions by Sakagami, Ebmer and Tadauchi (1996), and Sakagami and Ebmer (1987). Most of the halictids nest gregariously in the moist subterranean soil (resembling Colletes). However, their burrows were comparatively shallower culminating into 5–6 collateral branches. Each of which further bear around 1–3 or even 9 cells at the end. Precisely, a nest is a cooperative effort of as many as 20–25 females, suggesting their gregarious or semisocial behaviour. Nest tunnels were lined by mandibular secretions that provided evidence that they were self-excavated by females (Rahman 1940; Sakagami and Michener 1962, 1963; Sakagami and Wain 1966).

A comparative account of the properties of nest-building secretions of Nomia, Anthophora, Hylaeus and other bees was presented by Batra (1972). Batra (1978b) further presented aggression, territoriality, mating and nest aggregation of some solitary bees that belong to Halictidae, Megachilidae, Colletidae and the earlier known family Anthophoridae.

Kumar et al. (1994) compared the pollination efficiency of bees by making comparison in the rate of visits made on toria in Himachal Pradesh. They identified Halictus catullus and Halictus splendidulus alongwith some other bees, on this crop. The regional studies made with regard to identification of species of various genera pollinating some selected crops, were published by Batra (1968a, b) and Gupta and Yadav (2001).

6.5.5 Family Melittidae Schenck

This fifth family of bees is of rare occurrence in India. Michener (2000) further classified it into three Subfamilies, Dasypodainae Börner, Meganomiinae Michener and Melittinae Schenck. Among them Melittinae, including tribe Melittini, with single Genus Melitta, known with single species [M. harrietae (Bingham 1897)] reaches India. It is found in a very scanty population in the extreme north and north eastern hilly regions at the middle range altitude in Himalaya (Gupta 2003). It has many allies in the hilly and arid countries, west and east to India. The family has numerous representatives in Africa and countries in the middle east. Probably, high range of Himalaya imposed a restrictive entry of erstwhile Palaearctic species into our country. Comments on nesting of a species of Ctenoplectra were recorded by Bingham (1897) from Tenasserim. This genus is now placed in tribe Ctenoplectrini, under subfamily Apinae of Apidae.

So far nothing is known about the nesting behaviour and pollination aspects etc. about Melitta in India. Malyshev (1923) described them for some species known from Russian region.

6.5.6 Family Megachilidae Latreille

Until now it exists as the largest family of bees with regard to number of taxa known from India. Gupta (1993) consolidated 161 species of bees included in this family found in six states in northwest. It detailed taxonomy alongwith their flower records.

Still work pertaining to synonymy for several taxa of the country, is pending besides, the multi-seasonal expeditions of the southern peninsular region. As a whole, 24 genera with 229 species are included in this family from India.

The taxonomic categories of this family have undergone a fair amount of shuffling by virtue of cladistic analysis made by Roig-Alsina and Michener (1993). This resulted into recognition of two subfamilies namely, Fideliinae and Megachilinae (Michener 2000).

Subfamily Fideliinae is represented by a single tribe Pararhophitini in India, including genus Pararhophites with two species. The small bees of this genus love xeric conditions and were largely known in the western area beyond Indian limits. Its two species were collected from area adjacent to Baluchistan [Ferozpur, at the western border of Punjab, reaching upto Rajasthan] and second was found in Junagarh in Gujarat [yet to be named]. These bees were collected while pollinating flowers of Convolvulus at both vicinities. The nests of one species were found in good aggregation made in subterraneous burrows in Baluchistan (McGinley and Rozen 1987).

Subfamily Megachilinae includes five tribes and all have good representation in our country. The first, Lithurgini represented by genus Lithurgus Berthold (14 species), has discontinuous distribution. Species like L. atratus and L. dentipes have been of great concern with regard to their pollination of Cotton (Malvaceae) and, earlier many have commented upon their nests build in hollow sticks (Horne 1870, 1872; Malyshev 1930; Lieftinck 1939).

Second tribe Osmiini includes numerous genera but most of them are known from the colder regions in the north and arid northwest. Genus Chelostoma, represented by a single species is an exception. It was initially recorded from Sikkim and is found upto Myanmar. On the contrary, Genus Heriades (22 species) is widespread in Himachal Pradesh, adjacent Punjab and extends southward all along Aravali hills upto Gujarat, in a scattered pattern. These small black bees have great affection for Compositae flowers (Gupta and Yadav 2001). Hoplitis (ten species) also has more or less similar distribution pattern however, its two species were recorded at northern territory of the western coast. Noteriades (four species) and Protosmia (one species) are restricted to Himalayan range. Former is found at medium altitudes in Himachal Pradesh and the later is exclusively confined to high mountains in the extreme north.

After making taxonomic revisions, genus Osmia is reduced to five species found in India. Most of them are restricted to Himachal Pradesh and Uttaranchal at medium range mountains. Its one species was exclusively recorded from Karaikal located at south-eastern coast. Genus Pseudoheriades is quite widely distributed in Rajasthan and coastal Gujarat. The nests and immatures of one of its species were described from ‘Moonj straws’ (Gupta and Sharma 1995: misident. as of Heriades). Recently many more bees were collected from western Rajasthan and Gujarat by this author [yet to be named]. More particularly they were collected while busy pollinating Coconut at Somnath, Veeraval and Diu in Gujarat. Genus Wainia was exceptionally recorded from Lonavla in Maharashtra with two species.

Tribe Anthidiini has fair representatives in our country but mostly with a discontinuous distribution. Genus Acedanthidium, Anthidiellum, Eoanthidium, Icteranthidium, Indanthidium, Trachusoides are known with merely one or two species. Euaspis (=Parevaspis), the cleptoparasite, is almost cosmopolitan throughout the country. Its one species Euaspis abdominalis is found in the northeastern states extending upto Myanmar and Malaysia. The second, Euaspis carbonaria is found almost everywhere except the extreme southern region of the country. Both species are well known cleptoparasites of Megachile. Species of Pachyanthidium, Trachusa and Dianthidium are found in different pocket areas at different parts of the nation. However, most of the species are of prominent occurrence in arid zones of the northwest. A thorough expedition would yield many more species of this tribe.

Tribe Dioxyini, represented by a good number of taxa in the countries beyond the western limits of India, is known by a single genus Aglaoapis here. Its single species, Aglaoapis brevipennis was collected from Bombay around a century ago and until now not found anywhere else.

Tribe Megachilini, now consist of only two genera namely, Megachile that include the leaf cutting and mason bees and, its well known cleptoparasitic genus Coelioxys. Both are found almost everywhere all over the country (Gupta 2003). Species of genus Megachile (exceeding 130 in number), have attracted many authors with regard to their nesting and pollination aspects.

The comments on nests of various leaf cutting bees were initially published by Horne (1868, 1870, 1872), Maxwell-Lefroy and Howlett (1909), Bingham (1897, 1898a, b, 1908), and Dutt (1912). Until then, the interesting act of cutting leaf pieces with its mandibles, followed by their transportation to the nesting site by a female megachiline bee attracted enough attention all over the world. They use leaf cuttings, petals, mud, soil, pebbles and plant resins etc. for the construction of their nest chambers in self excavated or existing horizontal burrows in muddy walls or in subterranean soil. The nesting biology for a few Indian species was described by Pagden (1934), Malyshev (1930), Piel (1930), and Wain (1968). Later Kapil et al. (1970a, b), Kapil et al. (1975), Chaudhary and Jain (1978), Gupta and Sharma (1995), and Gupta et al. (2003) included nesting behaviour, immatures and correlated aspects in their studies.

The family includes several good pollinators of Leguminosae, Compositae, Solanaceae and, several fruit crops etc. Rahman (1940) could identify very few species of Megachilini on Sarson and Toria. Batra (1968a, b) identified several megachilids pollinating many cultivated and wild crops in Ludhiana. Mishra et al. (1976) and Batra (1976a, 1979a) presented some more works related to pollination of some cultivated crops from Himachal Pradesh and Punjab, respectively. Abrol (1986a, 1988b, c) noted Megachile nana and Megachile flavipes (sic) on alfalfa and recorded their eco-pollination behavioural relationships. Kumar et al. (1993) recorded around 9% of bees belonging to Megachile and 28% belonging to Ceratina, on Cichorium intybus in Himachal Pradesh. Gupta (1993) presented the complete flower record of megachilid bees collected from six states in the northwest. Gupta and Yadav (2001) recorded a good number of megachilids from four cultivated crops in eastern Rajasthan and adjacent U. P.

The personal observations made by this author during his studies with bees for more than previous two decades concluded some of the good and effective megachilid species. They can be listed as: Megachile bicolor, M. lanata, M. cephalotes, M. gathela, M. albifrons and M. creusa for almost whole of the northern half of the country.

6.5.7 *Family Apidae Latreille*

Based upon the cladistic analysis of Roig-Alsina and Michener (1993), the reorganized Apidae consists of subfamilies Xylocopinae, Nomadinae and Apinae (Michener 2000). Table 6.1 lists the three named subfamilies, their 12 tribes and corresponding 22 genera found in India. So far 192 species have been grouped under different generic categories. Still works related to synonymies of several species is pending and many of them would face taxonomic shuffling or would be synonymized. Species of Xylocopa (36 species and subspecies) [just concluded taxonomic revision, and is being published separately in this volume of the book. Author], Ceratina (14 species), Amegilla (21 species), Anthophora (10 species) and, Thyreus (6 cleptoparasitic species), are widely distributed.

On the contrary, Braunsapis (6 species, having discontinuous distribution), Nomada (13 species, mostly confined to northern region, upto the area of western arid Rajasthan), Tetralonia (15 species, out of them only two were recorded from M.P. and adjacent Maharashtra and rest are confined to north India), Habropoda (14 species, all restricted to Himalayan range) and, Bombus (restricted around or above the altitude of 3,000 ft in Himalaya), are region specific.

A few genera namely, Epeolus (three species), Parammobatodes (one species with doubtful occurrence in India), Pasites (one species), Eucera (three species found in northwest), Tetraloniella (two uncommon species), Elphropoda (four species) and Melecta (with two species in extreme north, in Himalaya), Tetralonioidella (three species all found throughout the Himalayan range upto east), Lisotrigona (one species known from Madhya Pradesh) and, Tarsalia (one species from Poona) come under the category of lesser known genera in the country. The social stingless bees belonging to genus Trigona (three species on record) were originally collected from all over the Himalayan range however, during past two decades, many more have been collected from several additional territories, by this author. They were Agra, Allahabad, Jamalpur (Bihar), Jabalpur and, Pachmarhi [M.P.] and, recently during the summers of 2003, more specimens of this genus were collected at Dwarka and Somnath, i.e. at the costal Gujarat and, more as a surprise during September 2003, many more specimens of this genus have been collected on the flowers of Techtona stans (Bignonaceae) in Jodhpur.

Genus Apis, the honey bee, has five representative species in our country. Among them Apis mellifera the Italian honey bee, was introduced in India during sixties in the previous century. It ultimately 'merged' with Apis indica and now 'becomes' a cosmopolitan species by virtue of its adoption in artificial domestication programme by ICAR stations all over India. Engel (2002) has recently published the information concerning honey bees of India. Apis dorsata (with three subspecies *A. d. dorsata,* *A. d. laboriosa and A. d. bighami*), *Apis cerana, Apis florea* and *Apis andreniformis* are the other species. *Apis andreniformis* and *Apis dorsata binghami* are known with limited distribution records. The first of these was recorded from Khasia hills and second was collected from Sikkim and Meghalaya. Apis dorsata laboriosa, the giant Himalayan honey bee is confined to the high altitudes in northern region. Roubik et al. (1985) noted distribution and nesting of A. d. laboriosa. Batra (1996) described its biology and declared it as a good pollinator of apple at high altitudes in Garhwal (Uttaranchal). Qayyum and Ahmad (1967) described the biology of A dorsata. Thakar and Topani (1961, 1962) detailed the nesting behaviour of *A. dorsata* and *A. florea*. Sharma and Thakur (1999) put forward the morphometric characterization of A. dorsata and, Sharma et al. (2000) detailed the diurnal activity of *A. cerana* and *A. mellifera* on different flora.

Since early times the carpenter bees that belong to genus Xylocopa have been of great interest to mankind therefore, enough observations on nestings and immatures were made on various species of this genus. Horne (1872), Perkins (1899), Maxwell-Lefroy and Howlett (1909), Dover (1924), Dutt (1912), Kannan (1925), Iwata (1964), Ma (1938, 1954), and Beeson (1938) published comments on their nests and nesting behaviour. Sakagami and Yoshikawa (1961), Kapil and Dhaliwal (1968a, b, 1969), and Bhaskar and Gopinath (1975) further recorded their biology from woods, trees, logs and bamboos in northern India.

Green (1899) recorded interesting sleeping habits of Crocisa ramose. Malyshev (1925, 1936) described the nesting habits of several Anthophora and other solitary bee species. Schwarz (1939), detailed social species of Trigona found in Indo-Malayan region. Sakagami (1960, 1966) noted Ethobiological aspect of several Allodape and other genera of Apidae. Lieftinck (1955, 1957, 1962, 1964, 1972, 1974) made remarks on ethobiology of many species that belong to former Anthophoridae such as Crocisa, Xylocopa, Thyreus, Melecta, and Habropoda etc. Iwata (1964) referred the egg of Xylocopa as the largest among all insects.

Kapil and Kumar (1969), Batra (1972, 1977, 1980), Pagden (1957), Batra, Sakagami and Maeta (1993), Reyes and Sakagami (1990), Reyes and Michener (1990), Batra and Norden (1996), and Williams (1991, 1994, 1998) are the few references, dealt with nesting behaviour and immatures of some Indian species of Ceratina, Anthophora, Amegilla, Braunsapis, Bombus and Trigona.

Identically, thousands of references regarding pollination are available for this family of bees, from all over the world. However, when referring to Indian works, some of the important ones may be listed as follows:

Howard et al. (1920) first of all referred a number of pollinators, including honey bees, for several Indian crops. Work of Mohammad (1935) concerning pollinators of toria and sarson has been referred above. Similarly, role of Apis indica was studied by Latif et al. (1960) on toria and sarson. Several notes on the pollinators of leguminous crops including alfalfa were put forward by Batra (1977, 1991, 1994b, c, 1995a). Sandhu et al. (1976) used Ceratina (Pithitis) smaragdula in India on alfalfa. Rai and Gupta (1983) published a useful note on the role of honey bees on the pollination of apple and pear. Abrol (1989, 1990, 1992) described the ecology and behaviour of pollinators of strawberry and apple, including honey bees in major. Sharma and Gupta

(1993) listed the flowering plants visited by Apis mellifera and Apis cerana. They concluded a total of 119 species of flowering plants in Solan (H.P.) among them 72 were visited regularly. Out of these 41 species provided both nectar and pollen, 22 nectar only and 9 species of plants were visited exclusively for pollen. Goyal and Gupta (1994) presented a detailed account of beekeeping with Apis mellifera in India. Batra (1995b) wrote on the use of solitary bees for blueberry pollination. Recently, Sharma and Gupta (2001) published the impact of bee pollination on sustainable production in apple orchards. Kumar and Singh (2001) recorded a preference for competing flora with sunflower for honey bees. Kumar et al. (2002) made observations on different modes of honeybee pollination and its effect upon the oil content in seeds of sunflower.

6.6 Alkali Bees

The alkali bee (Nomia melanderi Cockerell) has been known for many years to be a highly efficient and effective pollinator of alfalfa, particularly in the area north and west of Utah. It is a highly gregarious solitary bee that nests in large numbers in saline soils with a silt loam or fine sandy loam texture. Alkali bees are nearly as large as honey bees. They are black, with iridescent copper-green stripes across the abdomen. The male bee has much larger antennae than the female. Being gregarious, alkali bees may construct 100,000 or more nests in an area 40 by 50 ft. Nesting sites with an estimated 200,000 nests have been reported (Bohart 1952). The nest are 10 mm (0.4 in.) vertical tunnel, may extend 10 in. below the surface but is usually only 3–5 in. deep. There may be 15–20 cells usually arranged in a single comb-shaped cluster. Each cell is an oval cavity, slightly larger than the main tunnel, about one-half inch long, lined first with soil and then with a waterproof transparent liquid applied with the bee’s glossa. Each cell is provisioned with a 1.5–2 mm oval pollen ball, made up of 8–10 bee loads of pollen mixed with nectar. The soil removed from the tunnel is dumped at the tunnel entrance to form a conical mound 2–3 in. across. The adult bees emerge from late June to late July, depending upon the location and season. The males appear a few days ahead of the females. Before emergence, each bee is confined to its natal cell for 3 days as an egg, 8 days as a growing larva, 10 months as a full grown dormant larva, 2 weeks as a pupa, and several days as a hardening, maturing adult. During the approximate 1 month of her active adult life, the female constructs, provisions, and lays an egg in each of 15–20 cells. There is usually only one generation a year but sometimes three generations appear from May to September.

6.7 Leafcutter Bees

There are many species of leafcutter bees that visit blooming alfalfa, As its name implies, this highly gregarious solitary bee lines its nests with circular sections cut from alfalfa leaves, although it will cut sections from petals of large ornamental flowers. The nests are in hollow tubes or tiny holes above ground. The charcoal-gray adult bee is only slightly larger than a housefly. The female bee emerges from May to July (depending upon location), mates, and immediately searches out a nesting hole. She prefers a tube or tunnel into which she can barely fit (five 30-s of an inch) but will accept a somewhat larger one if necessary. When one is found, she begins the construction of a cell in it. She builds the first cell at the base of the tube, using freshly cut oblong pieces of leaves. This cell is then filled about half full with a mixture of pollen and nectar. An egg is placed on the food, and the cell is capped with circular pieces of leaf. Another cell is immediately started directly above the first one, and the process is repeated until the tube is nearly filled with cells. After the final cell is sealed with a large number of circular leaf pieces, another tube is begun if pollen and nectar continue to be available. A female may live 2 months and lay 30 or 40 eggs during her lifetime. About two out of three adults that emerge from the cells will be males. Leafcutter bees are advantageous for alfalfa pollination because they usually forage within fields where they nest, making them less susceptible to being killed by pesticides applied to adjacent fields, collect pollen from and trip the alfalfa flower readily at the rate of 8–10 florets per minute; are predictable in incubation of adult stages; gregarious and nest in manmade objects; select older leaves for nesting and are not destructive of shrubs and trees and have sturdy leaf cells and cocoons and thus are suited to mechanized management operations.

6.7.1 Nesting Materials and Shelters

Many kinds of nesting media have appeared during the last two decades of leafcutter bee management, and there are many claims of success (Tables 6.3 and 6.4). Substantial population increases have been obtained in several types of nesting media, but the most commonly used materials are boxes of soda straws, drilled boards (with or without removable backs), grooved boards, plastic wafers, and rolled-cardboard units. There are advantages and disadvantages to each type used. These characteristics are shown in Table 6.1, although grower choice-unproved data from bee production-appears to determine which media are used.

Field shelters have changed from the initial small A-frame capable of holding a few boards to the large, self-contained, incubation-emergence type mounted on a trailer and capable of holding.

Some additional recommendations for shelters are:

1. Use the conspicuous, larger sizes to attract and keep bees at the shelters;
2. Ventilate each shelter to prevent an accumulation of heat at the top or through the sides;
3. Place chicken wire or grills across the open end of the shelter to provide protection from birds;
4. Remove debris from emerging bees, nest cleaning, and leaf drop from the floor to prevent an increase in scavenger beetles or moths;
5. Mount shelters on a trailer with wide tires so movement does not jar the bees.

Table 6.3 Nesting behavior, nest acceptance and temperature tolerance of subtropical Megachild and Xylocopinae bees (Source: Sihag 1991, 1992)

			Nest tunnel accepted		Temperature for activity
Bee species	Crops pollinated	Nesting behavior	Diameter (mm)	Length (cm)	0°C
Megachile haryanensis (M.nana)	Alfalfa	Leaf cutter bee	4.5–5.5	10–12	26–43
Chalicodoma rubripes (M.flavipes)	Alfalfa	Masson bee	5.5–6.5	10–12	28–43
C.lanata (M.lanata)	Pigeon pea	Masson bee	6.5–7.5	10–12	26–38
Chalicodoma cephalotes (M.cephalotes)	Pigeon pea	Masson bee Utilizes resin/animal faecal material for partitioning and closing the cells/tunnels	5.5–6.5	10–12	27–41
Xylocopa fenestrata	Cucurbits	Carpenter bee	10–12	23–30	25–48
Xylocopa pubescens	Cucurbits	Carpenter bee	10–12	23–30	25–48
X.valga	Almonds, apples	Carpenter bee	10–12	23–30	5–30
X.aestuans	Cucurbits	Carpenter bee	10–12	23–30	10–47

Table 6.4 Relative desirability of various nesting materials for rearing of Megachild bees

Characteristics	Drilled boards	Plastic blocks with holes	Drilled boards, removable backs	Grooved wood	Grooved polystrene	Paper straws	Plastic straws	Corrugated paper
Low cost	++	–	+	+–	+–	+++	++	+++
Availability	++	–	++	–	++	+	++	+
Strength (sturdiness)	+++	++	++	++	+–	–	+	–
Light weight	–	+	–	–	++	++	++	++
Compactness	+	+	+	+	+	++	++	++
Insulating property	++	++	++	+	++	+	+	+
Ventilation qualities	+	–	+	++	–	+	–	+
Separability from cells	–	+	++	++	++	–	–	–
Cleanability for reuse	–	+	++	++	++	–	–	–
Inspectability of contents	–	+	++	++	++	+	+	–
Resistance to chaicids	++	+	++	–[a]	+–	–	+	–
Attractiveness to bees	++	+–	+	++	+–	++	+–	+–
Safety from most birds	++	+	++	++	+	+–	+–	(?)
Saftey from most mammals	++	–	++	++	+–	–	+	(?)
Ease of storing[b]	+	+	++	++	++	+	+	+

+++ excellent, ++ good, + fair, – poor, +– mixed reports

[a] Assuming some warping of boards and poor fit of backing

[b] Principal factor is storage seperately from cells; secondary factors are compactness. Assumption made that holes are well occupied

6.8 Carpenter Bees

Gupta (2003) has reported 45 species and subspecies of carpenter bees under the genus Xylocopa Latreille 1802 in the Indian region. Genus Xylocopa Latreille is the single genus included within tribe Xylocopini, in subfamily Xylocopinae of the recently redefined family Apidae. Earlier it was included under family Anthophoridae, now merged into Apidae (Michener 2000). Carpenter bees are almost worldwide in distribution.

Some of the principal characters helpful in recognizing species of Xylocopa are: their large size; loss of stigma, the very long prestigma and marginal cell (Danforth 1989), and the strongly papillate distal parts of the wings. Other distinctive features are: quite long first flagellar segment, longer than the combined length of second and third; short but distinct proboscis with heavily sclerotized components, the postpalpal part of the galea expanded like a blade and presumably used to cut into the corollas of tubular flowers to rob the nectar. All carpenter bees have three submarginal cells in their forewings but the first and second are sometimes partly or wholly fused owing to the disappearance of the posterior part or the whole of the first submarginal crossvein. An unusual feature of most male Xylocopini, not known in any other bees, is a large gland opening on the metanotal-propodeal line. Its product seem to play a role in courtship, and its presence results in unusual sexual differences in the form and structure of the posterior part of the thorax, which becomes elongated when the gland is large (Minckley 1994). Unlike other tribes of Xylocopinae, Allodapini and Ceratini, bees of the genus Xylocopa have no arolia, though a densely hairy plata often projects somewhat between the claws. Often one can recognize a Xylocopa by their typical lyriate flying pattern.

Michener (2000) synonymized Lestis Lepeletier and Serville 1828 and Proxylocopa Hedicke 1938 with Xylocopa following the cladistic analysis of Minckley (1998). Both are presently reduced to the rank of subgenera of Xylocopa. Subgenus Lestis is known from Australia with only two species. Subgenus Proxylocopa includes the only ground-nesting carpenter bees. Its 16 species are distributed in desert areas of some parts of Europe, Israel towards east up to western China (including parts of Quetta and Kashmir). Eardley (1983) illustrated the presence of the mesosomal gland in males of both subgenera, denoting their affinities within Xylocopa. Identification keys, separately made for the subgenera found in the Western Hemisphere and for the Eastern Hemisphere, were presented in Michener (2000).

6.8.1 Future Prospects of Carpenter Bees

Carpenter bees possess several advantages as potential crop pollinators compared to other non-Apis bees. Many solitary bees have a short activity season and/or are specialist foragers, and therefore do not provide a broad alternative to honey bee pollination. Carpenter bees, on the other hand, have long activity seasons and feed on a wide range of plant species. In addition, they are capable of buzz-pollination. This makes them potentially more versatile as agricultural pollinators. Hibernation occurs in the adult stage, and females start foraging whenever temperatures reach high enough values. This means that it is relatively easy to manipulate the onset of foraging in greenhouses. Another important advantage is that the genus has a worldwide distribution. This implies that local species of Xylocopa can potentially be used over wide areas, reducing the need to import exotic pollinators. The possibility to lure these bees into suitable artificial nesting material allows provisioning of nesting material that can be easily used in agricultural settings and moved to places where pollination services are needed.

In spite of higher per-capita pollination efficiency in some crops, carpenter bees are clearly inferior to honey bees in terms of pollinator work force, as they do not form large nests. Therefore they are expected to contribute most to crop pollination when honey bees are ineffective. For example, the high termoregulatory ability of carpenter bees enables them to forage at higher ambient temperatures than honey bees. This makes them attractive candidates as pollinators in hot areas and in hot microclimates, such as in glass houses. The crepuscular and nocturnal activity of some species may also allow them to pollinate night-flowering crops, which are not visited by honey bees.

Several problems remain in the management of carpenter bees for crop pollination, which call for further research. Most important is the need to develop an efficient captive breeding program for carpenter bees, which would include controlled selection of genotypes, mating, and nest founding. Such protocols have already been developed for other non-Apis pollinators, such as Osmia lignaria and Osmia cornuta. They include guidelines for nest construction and placement, overwintering and transportation of the bees. A complementary challenge is to enhance reproduction of wild Xylocopa populations, through provisioning of nesting material to their natural habitat. The availability of nesting resources was shown to correlate with the community structure of wild bees. Moreover, experimental enhancement of nest site availability has led to dramatic increases in wild populations of Osmia rufa. These findings suggest that Xylocopa populations, and the pollination services they provide, may also benefit from nest site enhancement in agro-ecosystems. Additional information about the pathogens and parasites of the genus is needed as well. A combination of ecological, physiological, and molecular genetic studies is likely to provide these essential data (Fig. 6.1).

6.9 Other Bees

6.9.1 Stingless Bees

6.9.1.1 Meliponiculture

Members of the Apidae subfamily Meliponinae or “stingless bees” are social insects. Some species have clusters of as many as 80,000 individuals; other species, less than 100. The two important genera are Melipona and Trigona. They are of economic

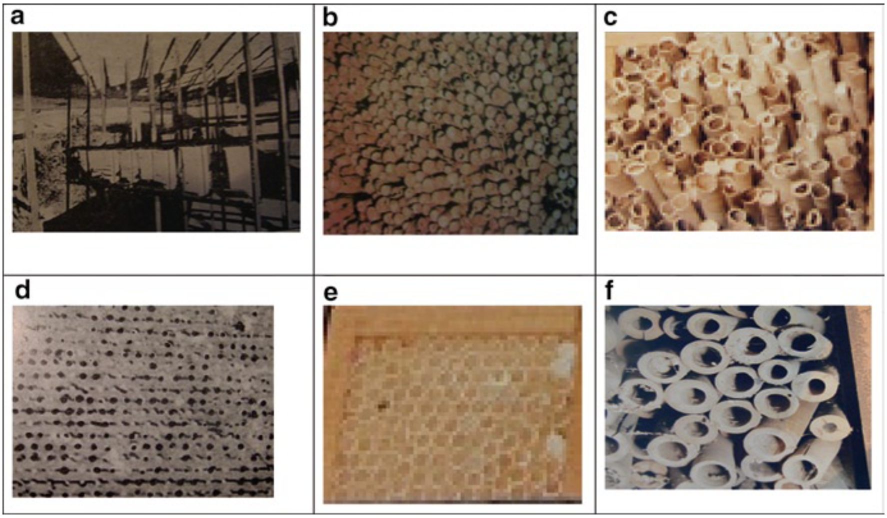

Fig. 6.1 Management of solitary bees. (**a**) Field hut for nesting solitary bees (**b**) Pithy stems for Pithitis species (**c**) Castor stems for nesting of Xylocopa and Megachile species (**d**) Soda water straws in wooden blocks for Megachile bees (**e**) Soda water straws for Megachile bees (**f**) Bamboo stems for nesting of Xylocopa

significance in Mexico as well as Central and South America. Trigona spp. also occurs in Africa, Southern Asia, and Australia. They have widespread distribution over the tropical and subtropical areas of the world. They are valuable pollinators of many crops, and have been reared for the production of honey and "wax".

The females possess weak or vestigial stingers but are unable to inflict pain with them, hence the term "stingless bees." Some species have mandibles sufficiently strong to inflict a mild bite or to pull hairs, or they may crawl into the ears or nostrils of the intruders. Others emit a caustic liquid from the mouth that, in contact with the skin, causes intense irritation. Most species, however, are not bothersome to man, and he may safely manipulate them with ease, even to having his face within inches of a Trigona nest containing many thousands of individuals.

Stingless bees were kept by man centuries before the arrival of Columbus or the common honey bee (Bennett 1964). Some species produce an acceptably delectable honey, as much as half a gallon per colony per year. Others produce less desirable, thin (35% moisture versus half that amount in our domestic honeys), strongly acid honeys. One species (Trigona (Lestrimellita) limao Smith) produces a honey used to induce vomiting (Bennett 1965). The most common species used in meliponiculture is Melipona beechii Bennett.

When the wax is secreted from the glands on the abdomen of stingless bees it is similar in appearance to that of Apis mellifera, but it is then mixed with propolis and the product, called cerumen or Campeche wax, is more or less black. Cerumen is used for waterproofing on farms and in villages, in ink and lithography, and in other restricted ways.

Originally, the colonies were kept in gourds, tree trunks, or similar cavities, but an improved hive has been developed that permits easy manipulation an transportation of these bees. This hive is about a cubic foot in volume – sufficient for the 3,000–5,000 bees.

Life histories and habits. The size of stingless bees varies from 2 to 14.5 mm. Trigona duckei Friese is the smallest species of stingless bee known; Melipona interrupta Latrielle is the largest. M. beechii is slightly smaller than Apis mellifera. The colors of the different species vary from black to brown, red, orange, yellow, and white.

The nest entrance is frequently reduced to permit only a single bee to enter at a time. The nest may be covered by a membranous wax and propolis network, which envelops and protects the nest and brood. There may be a single or multiple layer of brood – the individual cells vertical in some species, horizontal in others – or the cells may be in a cluster like grapes. Some species use the brood cells only once, then they are destroyed and reconstructed. The honey and pollen are not stored in the brood comb but in irregular cells outside of the broodnest.

The queens of Trigona are reared in queen cells, similar to those of Apis mellifera. Melipona queens develop in cells that externally seem to be no different from those that produce drones and workers, usually one queen to 3–6 workers. The workers of Melipona fill the cell with food before the egg is deposited. Each colony has a single sovereign queen but tolerates numerous virgins. A 4,000 worker bee population of M. beechii may have 50 virgin queens living harmoniously with the mother queen. Mating occurs in the air.

Honey bees are the main source of pollinators for many crops. Like honey bees stingless bees also play a significant role in pollinating crops and non crop species in natural habitats. Stingless bees are small to medium sized bees with vestigial stings. These bees are sometimes called dammer bees, as they collect dammer, a kind of resin for construction of their nest along with wax produced from their body. They also live in permanent colonies and multiply through a process of swarming. They cannot sting because these bees have no venom apparatus. They show a level of social organisation comparable to that of honey bees. They chase away the intruders by biting. They survive well under tropical and subtropical conditions. Melipona and Trigona are the most important genera of stingless bees. They occur in the tropics of South America, South Africa and South East Asia. Melipona consists of 50 species and is confined to the neotropics. It has more complex communication system and some larger species are capable of buzz pollination.

6.9.2 Stingless Bees Are Better Pollinators Why?

Stingless bees may be better pollinators of some crops than honeybees.
Stingless bees thrive much better in tropical areas.
It can be more environmental friendly to use a native species to do a job than to rely on an introduced species.
The commercial use of native species can help to protect them.

They can be effectively used in green house pollination because of their limited foraging distance and the owner gets the maximum benefit.

6.9.3 Floral Preference

Stingless bees are generalist flower visitors. They visit a broad range of plant species. They are adaptable, and learn to exploit the resources offered by introduced plants. They prefer small flowers, dense inflorescence, flowers with corolla tube shorter than their tongues, flowers with long corolla tubes that are wide enough for the bees to enter, flowers on trees and white or yellow flowers. Stingless bees are opportunistic foragers. They show a higher preference for macadamia with 100% of the bees from hives in orchards visiting the macadamia flowers. Stingless bees respond well to heavy flowering of macadamia. When flowering is heavy, the stingless bee colonies become much busier as the workers take advantage of the temporary abundance of pollen. Stingless bees are common in orchards, which has surrounding natural eucalyptus vegetation. Natural vegetation provides nest sites and other food for the bees. The more natural vegetation around the orchard, the greater the bee population.

In tomatoes and egg plant the pollen is held inside tube-shaped anthers in the flower. To pollinate these flowers a large bee must grip the flower and vibrate it vigorously to release the pollen. This is called buzz pollination. In tropical America, there are larger species of stingless bees of the genus Melipona which are capable of buzz pollination.

6.9.4 What Makes a Stingless Bee a Good Pollinator?

6.9.4.1 Polylecty

The workers from a colony can visit many different types of plants. This behaviour, called polylecty, enables a colony to potentially pollinate many types of plants. In addition, they can also quickly adapt to new plants that they have not known before.

6.9.4.2 Floral Constancy

Each individual worker on a trip usually visits only one plant species. This behaviour, called floral constancy, makes these bees efficient pollinators because each bee only carries pollen between the flowers of one plant species.

6.9.4.3 Domestication

Stingless bee colonies can be domesticated. They can be hived, inspected, propagated, fed, re-queened, controlled for natural enemies, opened for extraction of honey and otherwise managed. The potential of stingless bees for crop pollination is enhanced by the ability to transfer colonies into artificial hive. These hives can be propagated so that growers do not need to relay on natural populations. Hive can also be transported wherever needed for pollination or for colonies strengthening.

6.9.4.4 Perennial Nature

Stingless bee colonies live for a long time. They do not have to be restarted.

6.9.4.5 Adaptability

Stingless bee colonies are active over a wide range of climatic conditions and if the climatic conditions become unsuitable, the colonies can be moved to better area.

6.9.4.6 Hoarding Food

Large food reserves are stored in stingless bee nests so the bees can survive for long periods when food is scarce. The workers will also collect more nectar and pollen than their current need. This can result in huge numbers of bees visiting a particularly good food source, resulting in intensive visitation of preferred flowers.

6.9.4.7 Shorter Foraging Distance

Stingless bees have short flight range. Hence, their importance is increased in using them for green house pollination.

6.9.4.8 Forager Recruitment

Scout bees in a colony find new flowers for the colony to use. Middle aged foragers function as scout bees. They return to the hive and communicate the location of the flowers to other worker bees. These workers can then quickly reach the flowers and forage upon them. If the flowers continue to be productive, even more workers will be brought in. This behaviour, called forager recruitment, allows large numbers of worker bees to quickly find a good food source.

6.9.4.9 Communication Mechanisms

Different communication strategies are used by the scout bees for sharing the information about the discovery of a floral patch to the nest mates. The returning forager

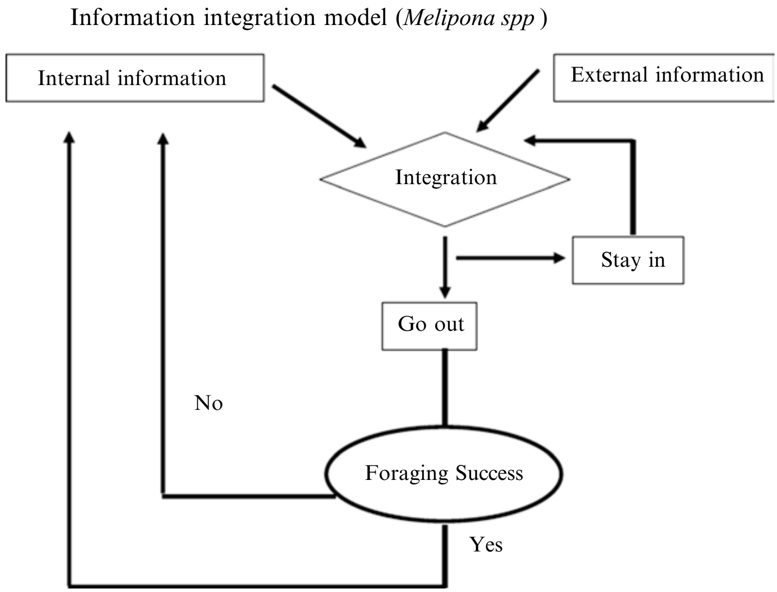

Fig. 6.2 Information integration model on Melipona species

may produce a weak sound while passing the nectar to the hive bee (Trigona silvistri) In T. testaceicornis the incoming foragers alert their nest associates by their, sound and run which make the nearby bees to repeat their sounds and the whole colony buzzes and the responsive bees leave out for foraging due to mass sound production. In T. jatty returning foragers alert their inmates by strong sounds, zig zag running and frequently striking other bees. Foragers of T. postica mark an odour trail between the food source and the colony with their mandibular gland secretions.

Stingless bee foragers have to make foraging decisions based on information that may come from two different sources: information learned and memorized through their own experience (internal information) and information communicated by nest mates or directly obtained from their environment. The information integration model of Melipona is given above (Fig. 6.2):

6.9.5 Crop Pollination

Stingless bees are important pollinators of crops in tropical and subtropical parts of the world (Table 6.5). There are many crops for which stingless bee pollination has not been thoroughly investigated (Heard 1999). Neglect probably reflects the lack of knowledge rather than lack of importance.

Table 6.5 Crops pollinated by stingless bees

S. no.	Crop group	Crop
1	Fruits	Peach, Plum, Pear, Guava, Citrus, Litchi, Strawberry, Jack fruit, Bread fruit
2	Vegetables	Cucumber, Water melon, Squash, Bittergourd, Sweet pepper, Egg plant, Onion
3	Pulses	Pigeon Pea
4	Oil seeds	Sun flower, Castor, Niger
5	Spices	Cardamom, Coriander
6	Trees	Indian jujube, Subabul, Soap nut, Kapok, Tamarind, Sago palm, Rubber, Eucalyptus Some of the crops, like papaya, passion fruit, banana, custard apple, oil palm, cocoa, cashew, black pepper which stingless bees visit, are pollinated by quite different means.

More than 1,000 plant species are cultivated in the tropics for food, beverages, fibre, spices, and medicines. The pollinators of most of these crops are not known. However stingless bees are known to visit some of these crops. No crop is known to be dependent on stingless bees exclusively for cross pollination. But the yields of many crops benefit greatly from their pollination services. The crops for which stingless bee pollination can be valuable in India are mango, coconut and chow chow.

6.9.5.1 Mango

Stingless bees are the most common insects visiting mango flowers in studies in Australia and Brazil. In Australia, Trigona bees were also shown to be the most efficient pollinators of mango as they left many pollen grains on the stigma after a visit. This efficiency is due to the large amount of pollen carried on the bees' bodies and the close contact they made with the stigma. Furthermore, Trigona bees flew more frequently from the tree to tree and thus were probably the most effective crosspollinators.

Honey bees are not strongly attracted to mango flowers and are only occasionally observed. Files are the most common visitors to mango flowers in many parts of the tropics and are probably also efficient pollinators. Thus, stingless bees and flies are the most important pollinators of mango (Anderson et al. 1982).

6.9.5.2 Strawberry

Imported stingless bees have been evaluated in Japan for pollination of strawberries in glasshouses. Japan has no native stingless bees but they have imported colonies of stingless bees from Indonesia and Brazil. One study found that the stingless bees foraged much more effectively in the confined space of glasshouses than honey bees did. This study also found that, to produce high quality strawberries, 11 honey bee visits or 30 stingless bee visits were required per flower. However, another study showed that only four stingless bee visits produced well-formed fruits (Kakutani et al. 1993). The following is the list of crops grown in India visited and occasionally or partially pollinated by stingless bees.

6.9.5.3 Coconut

Honey bees and stingless bees are effective pollinators of coconut flowers throughout the tropics. Stingless bees are found to be very active on dwarf coconut palm. Coconut flowers grow in a cluster which include both male and female flowers. Studies overseas and in India showed that stingless bees visit both male and female flowers. Most bees visiting female flowers in search of nectar carried loads of coconut pollen from previously visited male flowers. Many of these then visited male flowers on the same inflorescence before leaving. This behaviour causes efficient movement of pollen grains to where they are needed. Yields are also higher when hives of honey bees are kept in coconut Plantations. Thus, there is evidence that both honey bees and stingless bees help to pollinate the coconut crop (Batra 1995a, b, c).

6.9.6 Pollination of Non-crop Species

Stingless bees are efficient pollinators of non-crop species in natural habitats. They play a vital role in sustaining the forest flora, epiphytic orchids and rare aquatic plants. In some cases stingless bees may do harm for some crops by removing nectar or pollen without pollinating the flowers. This makes the flowers less attractive to the other insects or birds which are the effective pollinators of that crop. In some extreme cases stingless bees may cause more serious harm. For example, stingless bees have been reported to damage the flowers of the canola crop and drive away the effective pollinators of passion fruit.

6.9.7 Advantages of Stingless Bees over Honey Bees

Stingless bees are generally harmless to humans and domesticated animals. So they can be safely kept close to a house and be handled by people who are allergic to honey bee stings.

Small size of stingless bees allows them to have access to many kind of flowers, whose opening are too narrow to permit penetration by other bees. Hence, they co-exist peacefully with commercial bees. They collect and utilize considerable nectar and pollen throughout most of the year, therefore, numerous flowers must be visited and pollinated.

They can be manipulated in hives like honey bees. The hives are small, easily handled, and relatively inexpensive.

The foraging range of stingless bees is shorter than commercial bees. Hence they can be very well utilized for pollination.

Stingless bees are able to forage effectively in glasshouses. Honey bees usually do not forage well in confined spaces. However, if condensation develops inside the glasshouse panels they get trapped.

Stingless bee colonies are not able to swarm away as honey bees because the mature stingless bee queen is unable to fly. Stingless bees can, however, set up a new nest when the old one is full, but part of the colony always remains in the original location.

Stingless bees are resistant to the diseases and parasites of honey bees. They are not affected by the virus diseases of honey bees or mites. However, stingless bees have their own natural enemies but these are not shared with honey bees and are not very serious.

The byproducts of honey and cerumen are usable.

6.9.8 Disadvantages of Stingless Bees

Stingless bees cannot tolerate cold weather; therefore, they are limited to the tropical and subtropical regions. The byproducts are produced only in small quantities, and they are less desirable than those of the honey bee.

In conclusions stingless bees possess many characteristics that enhance their importance as crop pollinators both as wild populations and managed pollinators. Their character such as perenniality, polylecty, floral constancy, recruitment and harmlessness make them better pollinators. Challenges to their wide spread use include the lack of availability of large number of colonies and the dearth of knowledge about meliponiculture. Improved domestication practices would increase colony availability for planned pollination there by reducing reliance on natural populations. Stingless bees provide substantial economic benefits by their crop pollination service which are to be quantified in many crops. Stingless bee pollination has not been properly studied for many crops there is still much to be learnt and there are many management problems with stingless bees still to be solved. Stingless bees display greater diet breadth and range of foraging behaviour than honey bees which make them the potential pollinators of future best suited to the needs of particular crops and habitat (Roubik 1995a, b).

6.10 Bumblebees

Bumblebees, along with other bees, are instrumental in pollinating many plants, shrubs and trees for the production of fruits, nuts and seeds that feed wildlife and allow regeneration of our forests and grasslands. Bumblebees are excellent pollinators.

Their tongues are longer than honeybees and so are much better at pollinating deep-throated flowers; tomato and bell pepper plants, for example, are more successfully pollinated by bumblebees. Pollination of tomatoes can reach near 100% if pollinated by bumblebees. Bumblebee nests are used world wide in such greenhouse environments. The bumblebee colonies spend their lives in greenhouses, building hives in boxes equipped with a small opening for entrance and exit. Bumblebees are the most efficient pollinators of plant species of great economic importance. They can work well in confinement and especially in small enclosures. They have extensively been used for pollination in cages for several crops like Brassica oleracea, B. napus, Cichorium endivia, Raphanus sativa, Lycopersicon esulentum etc. They have been reported to increase seed yield from 110 to 210 kg/ha in red clover at differing bumblebee densities. They can work at extremely low temperatures (−3.6°C) at which no other insect pollinator can fly, exploit flowers with deep corollas and have higher foraging rate. Bumble bees have been reared/domesticated for pollination purposes in several countries of the world like France, Japan, Korea, Germany, Canada, Sweden, Brazil, U.K., U.S.A. and many other countries. However, no such attempt has been made from temperate areas of India to explore their potential for planned crop pollination. Their species composition, distribution pattern and factors affecting population dynamics and rearing under artificial conditions remain unexplored from India.

For one out of every three bites you take, thank a bee, butterfly, bat, bird, or other pollinator. Animals provide pollination services for over three-quarters of the staple crop plants that feed humankind, and for 90% of all flowering plants in the world. We are facing an “impending pollination crisis,” in which both wild and managed pollinators are disappearing at alarming rates due to habitat loss, pesticide poisoning, diseases and pests. Pollinator declines may destabilize food production and ecosystem functions globally. Bumblebees are increasingly used in glasshouse cultivation, where a honeybee hive would be too large, e.g., cabbage pollination in Holland (Free and Butler 1959), kiwi fruits and tomatoes. So bumblebees are of great economic importance, and with the increase of glasshouse cultivation, and the spread of the mite, Varroa jacobsoni, causing a decline in honeybee populations, their importance can only increase.

6.10.1 The Distribution and Diversity of Bumblebee in the World

The distribution of bumble bee fauna is still poorly understood and much needs to be known. The documented information is rather fragmentary and far from complete. The Indian species of bumbus has generally been restricted to higher elevations especially Himalayan ranges. Bingham (1897) listed 24 species of bumblebees from higher elevations of Kashmir, Himachal through Sikkim and Assam. Mani 1962 listed four species of bumble bees at elevations over 4,000 m at Himalayas. Williams (1991) recorded 28 species of bumblebees from Kashmir Himalayas. Abrol (1998) has recorded Bombus haemorrhoidalis from intermediate areas of Jammu range. There are about 25 British species according to Prys-Jones (19 species of Bombus and 6 species of cuckoo bumblebees). More than 300 species of bumble bees have been identified from north temperate zones extending through Europe, Asia and North America. The bumble bee fauna has extensively studied in several countries of the world which include France, Japan, Germany, Korea, Italy, U.K, Canada, Sweden, U.S.A, Newzealand, China and Finland. More than 25 species have been recorded from U.K (Prys-Jones and Corbet 1987). Chang–Whan and Ito (1987) identified 212 species of bumble bees and 5 species of parasitic bumble bees (Psithyrus) from Korean peninsula. Bumble bee fauna of central Italy has been reported to consist of nine species of bumble bees and three species of Psithyrus (Intoppa and De Pace 1983). In a similar study, Ito (1985) recorded 15 species of bumble bees and one species of Psithyrus from North Korea. Teras (1985) reported the occurrence of 12 species of bumble bees in southern Finland. In these countries much work has been done on their management and utilization for crop pollination (Hobbs et al. 1962; Free 1963). Roseler (1977) devised methods for rearing bumble bees in green houses and developed many suitable domiciles. Griffin, et al. (1990) developed techniques for commercial rearing of Bombus terristris (L.); B. ruderatus (Fabr.) and B. subterraneus to match their emergence with flowering phenology of the crop. Several investigators have designed nest boxes of wood or polystyrene for rearing of bumble bees (Van Heemert et al. 1990; Eijnde et al. 1991; Ptacek 1991). However, the success rate varied from species to species.

6.10.2 Effectiveness of Bumble Bees and Honey Bees as Pollinator

The main agricultural crop that bumblebees pollinate is the greenhouse tomato (*Lycopersicon esculentum*). Worldwide, this involves about 95% of all bumblebee sales and comprises a total of over 40,000 ha of greenhouse culture. The growing season of tomato plants in greenhouse cultures typically lasts between 7 and 11 months, depending upon the climatic conditions of the area. Up to 50 bumblebee colonies are used per hectare during the growing season. The value of these bumblebee pollinated tomato crops is estimated to be 12,000 million per year. Other crops that bumblebees pollinate (both indoor and outdoor) are listed in Table 6.6. The colony density needed in tomato and in other crops depends upon factors like flower density and attractiveness (Griffiths and Robberts 1996). A cherry tomato crop, for instance, requires at least twice as many colonies per hectare than a beef tomato crop, because it contains so many flowers.

As mentioned before, bumblebees release pollen from tomato flowers by means of sonication. To do this, they grasp the anther cone with their mandibles, which leaves brown bite marks on the flowers. This behavior can damage the receptacle if the ratio bees/flowers is too high: the bees may visit individual flowers over and

Table 6.6 Crops commercially pollinated by bumblebees (Source: Velthuis and van Doorn 2006)

Crop	Latin name	References
Tomato	*Lycopersicon esculentum*	van Ravestijn and Nederpel (1988)
Pepper (sweet, hot)	*Capsicum annuum*	Shipp et al. (1994), Porporato et al. (1995), Abak et al. (1997), Meisels and Chiasson (1997), Dag and Kamer (2001), Kwon and Saeed (2003), and Ercan and Onus (2003)
Eggplant	*Solanum melongena*	Abak et al. (1995)
Melon	*Cucumis melo*	Fisher and Pomeroy (1989)
Watermelon	*Citrullus lanatus*	van Ravestijn and Kraemer (1991) and Stanghellini et al. (1997, 1998a, b, 2002)
Cucumber	*Cucumis sativa*	Stanghellini et al. (1997, 1998b, 2002)
Courgette (zucchini)	*Cucurbita pepo*	
Strawberry	*Fragaria x ananassa*	Paydas et al. (2000a, b)
Raspberry	*Rubus idaeus*	Willmer et al. (1994)
Blackberry	*Rubus fruticosus*	
Currant (red, black)	*Ribes sativum, R. nigrum*	
Cranberry	*Vaccinium macrocarpon*	MacFarlane et al. (1994b) and MacKenzie (1994)
Blueberry	*Vaccinium corymbosum*	Whidden (1996) and Stubbs and Drummond (2001)
(Highbush, lowbush, rabbiteye)	*V. angustifolium, V. ashei*	Sampson and Spiers (2002) and Javorek et al. (2002)
Apple	*Malus domestica*	Goodell and Thomson (1997) and Thomson and Goodell (2001)
Pear	*Pyrus communis*	
Cherry	*Prunus cerasus, P. avium*	
Kiwifruit	*Actinidia deliciosa*	Pomeroy and Fisher (2002)
Peach	*Prunus persica*	
Apricot	*Prunus armeniaca*	
Plum	*Prunus domestica*	Calzoni and Speranza (1996)

over again, desperately trying to release pollen, and their bites can damage the tissue which causes malformations of the fruits. This phenomenon is called over-pollination and may occur not only in tomatoes (e.g., Jackson 1993), but also in sweet peppers (see, e.g., van Ravestijn and de Bruijn 1991) and strawberries (see, e.g., Lieten (1993)). When this phenomenon is observed, the grower must either close the hives temporarily or remove some of them. Tomato varieties with relatively small flowers, like cherry tomatoes, are more vulnerable to over pollination than other varieties.

Honey bees can also pollinate most of the crops mentioned in Table 6.6 but they are often less efficient than bumblebees (see, e.g., Free and Butler 1959; Holm 1966a; Alford 1975; Prys-Jones and Corbet 1991; Goulson 2003a; Pouvreau 2004). Which pollinator is economically preferable depends on the local costs and on the climatic conditions. Bumblebees are to be preferred when the temperature and/or the light intensity are low, both in the greenhouse and in the open field. Honeybees usually do not forage at an air temperature less than 16°C, whereas bumblebee workers are still active at temperatures down to 10°C (Heinrich 1979). Bumblebees stop foraging when the temperature rises above 32°C (Kwon and Saeed 2003, for *B. terrestris*): they are able to fly at air temperatures up to 35°C, but instead stay at the nest to ventilate the brood (Heinrich 1979; Vogt 1986). Honeybees usually treat flowers more tenderly than bumblebees and thus have a lower risk of causing over-pollination. They are known, however, to cause damage to the incipient fruits of strawberry plants (e.g., Lieten 1993).

Sometimes it is preferable to use a number of individual bees instead of an entire colony. Minderhoud (1950), Sneep (1952), and Kraai (1958), for example, used just queens and males for the production of hybrid *Brassica* seeds. Similarly, small packages containing only a number of bumblebee males (with trade names like Machopol and Masculino) are used today for seed production in onions (*Allium cepa*), cabbages (*Brassica* spp.), and leeks (*Allium ampeloprasum*). These bees can be used only in completely enclosed environments since they would otherwise leave the place by lack of bondage to a colony. The price of bumblebee colonies differs from one country to the next, depending upon the species that is reared, the volume of the market, transport costs, etc.

Honey bees were found to visit on blackcurrant (Ribes nigrum), raspberry (Rubus ideaus) and strawberry (Fragria ananassa), but bumble bee queens were found only on black currant. Bumble bees spent less time on each flower and visited more flowers per bush than honey bees. Honey bees were numerous on raspberry than bumble bees, but bumble bee collected proportionally more pollen. Only few bumble bee found to visit strawberry (Free 1968). However Poulsen (1973) observed more number of bumble bees visiting field beans, working more rapidly as compared to honey bees. Honey bee workers and bumble bee queens were found to remove and deposit different amount of pollen in apple, because of different foraging behavior. Apple stamens restricted access to the nectaries by short tongued Apis particularly on Delicious group, because bees collected nectar side ways without contact with stigma. In contrast, Bombus queen approached the flowers from above, landing directly on the anthers and stigmas, (McGregor 1976). Bumble bees have long been suggested as useful alternative to honey bees in pollination under greenhouse conditions where they do not appear to become easily disoriented as honey bees (Free 1970a, b). Fisher and Pomeroy (1989) studied the pollination of greenhouse muskmelon, Cucumis melo by bumble bees in New Zealand. They observed that bumble bees foraged on melon flowers from dawn until dusk. Flowers pollinated by bumble bees attained 90% fruit with exportable weight. Ravestijn and Kraemer (1991) compared the pollinating efficiency of honey bees and bumble bees on melon and found that fruit numbers and weight/m^2 area were slightly greater with bumble bees pollination than with honey bees. Most pears are self unfruitful and need insect vector for cross pollination. Mayer et al. (1986) found that in the Pacific Northwest, Bartlett and all other pear varieties require cross pollination. Pear blooms before over wintered queens of most bumble bee species have begun to rear their workers. Therefore, few bumble bee foragers were observed on pear flowers. The number of honey bees foraging pear bloom at the same time was higher than the bumble bees. Free (1993) suggested that more bumble bees will forage at low temperature at which honey bees activity is limited for pear pollination. In Mediterranean coastal regions malformed fruits production of strawberries was prevented by bee-pollination method (Ahn et al. 1989), but unfortunately honey bees do not work on cold days when temperature was lower than 12°C. Pinzauti (1991) suggested that grower should introduce bumble bees to their greenhouses especially in winter months to get early, high yield, large and regular shaped strawberries. Paydas et al. (2000a, b) reported both honey bees and bumble bees to be effective in early production of strawberries. In this respect bumble bees were generally more efficient in pollination in cold weather conditions. The effectiveness of honey bee and bumble bee pollination on fruit set and abortion of cucumber and watermelon was studied by Stanghellini et al. (1997). They revealed that cucumber flowers visited by Bombus impatiens had lower per cent fruit abortion than Apis mellifera, when compared at equal bee numbers. Stanghellini et al. (2002) used the commercial bumble bee colonies as back up pollinators for honey bees to produce cucumber and watermelon in large quantities. Several pollinators have been tested on Capsicum annuum under greenhouse conditions. B. impatiens was found to be well established for sweet pepper pollination (Shipp et al. 1994; Meisels and Chiasson 1997). Arnon and Kammer (2001) compared the effectiveness of bumble bees and honey bees on sweet pepper pollination under greenhouse conditions in Europe and Israel. They found that the average yield in honey bee plot (22.6 kg) was similar to the bumble bee plot (23.4 kg). In Mediterranean countries, greenhouses are not regularly heated and pollen production and its quality are declined by low temperature and it brings the fruit set problems in egg plant. Abak et al. (1997) studied the effect of bumble bee and vibrations on the yield and fruit characteristics of egg plants in unheated greenhouses. Yield increased by 25% using bumble bee pollination during 3 years of experimentation. Bumble bee pollinated fruits also increased by 14% in weight and 7% in length as compared to vibration pollination. Bumble bees were found to be efficient pollinators of flowers in the unheated greenhouses during the winter and spring months in the Mediterranean coastal region. Dasgan et al. (2004) investigated the effectiveness of bumble bees as an alternative pollinator for melon plants in Turkey. Fruit weight, fruit height, fruit diameter and number of seeds per fruit of bumble bee pollinated plants were significantly higher than honey bee pollinated. The yields obtained were found similar (6 kg/m^2) by both these pollinators, while the average fruit weight (1,166 and 991 g), height (15.42 and 12.63 cm) and number of seeds (628 and 579 seeds/fruit) were higher in bumble bee pollinated plants than honey bees. Zaitoun et al. (2006) compared the effect of honey bees and bumble bees on the length and sugar content in strawberry. The plants pollinated by bumble bees had fruits with higher fruit length (4.2 cm), diameter (4.1 cm) and volume (269.3 cm^3) and per cent sugar content (7.8%), than the honey bees pollinated (fruit length 3.9 cm, diameter 3.7 cm, volume 227.9 cm^3 and per cent sugar content 7.6%).

6.10.3 Bumble Bee Foraging Activity

The foraging activity of B. dahlbomii and B. terrestris was studied in native and non-native vegetation in Chile by Ruz and Herrera (2001). They observed B. dahlbomii in January, with very active colonies whereas the B. terrestris was found first time in wild during April-May. B. terrestris was observed to forage faster than B. dahlbomii and other native bees. Therefore, in long term it may cause impact over slower forager species while exploiting the same resource. Free (1955) studied the foraging behaviour of four species of bumble bees living in artificial nest boxes in England. He found that the foraging population showed slight peak at 10–11 a.m. and a tendency to collect pollen load increased during the day. About 15% of the foragers spent the night away from the nest. He also worked on the division of labour in artificial boxes and found that half of the workers had no specific duties, but two-thirds were either foragers or house bees. The amount of pollen collected was related to the amount of brood in the nest. Paarmann (1977) compared the activity of honey bees and bumble bees on morella cherry. Honey bees were found to be more active around noon but bumble bees in the evening hours, however, during cold days honey bees did not fly out whereas bumble bees were more active in the afternoons. Willmer et al. (1994) studied the behaviour and activity patterns of Apis mellifera and of five species of Bombus on raspberry in Scotland. They found that Bombus spp. favoured young flowers strongly, early in morning when pollen was more abundant while A. mellifera visited unselectively. Bombus spp. carried more pollen on their bodies than A. mellifera and deposited more pollen on raspberry stigmas. Bumble bees also foraged substantially for longer periods of the day in poorer weather. Asada and Ono (1996) classified foraging behavior of bumble bee in four categories viz. buzzing on flower and hanging on anther, grooming pollen grains adhering to leg hairs, while hanging on anther, flight from flower to flower and flight towards the cage and resting. Abak and Guler (1994) reported that pollen amount and fertility of greenhouse egg plant were generally lower in winter, but if the effective pollinators like bumble bees were used, cultivars are able to set the fruit. Bumble bees were found to forage from 7:00 to 14:00 h in January, 6:00 to 18:00 h in February and March on sunny days. Bumble bee pollinated flowers gave higher fruit yield (25%) as compared to vibration pollination. Fruit size also increased 14% in weight and 7% in length and number of seeds per fruit was higher in bumble bee pollinated fruits than from vibration pollination.

6.10.4 Foraging Activity on Different Crops Grown in Polyhouse

Fisher and Pomeroy (1989) recorded the bumble bee activity in greenhouse condition on melon plant in England. They observed that bees were entering and leaving the each hive during 5 min period at 2 h intervals from 0600 to 1800 h in December. The numbers of male and hermaphrodite flowers visited by bees were also recorded. Ravestijin and Sande (1991) used bumble bee, Bombus terrestris for pollination of glasshouse tomato in Naaldwizk. Flowering started on an average on 1st February ± 7 days and bumble bee colonies were placed in the glasshouse on 31st January. He found that the one active bumble bee worker may pollinate at least 500 plants/day i.e. 250 m^2 area of glasshouse. Therefore, use of 10–15 colonies/hac. were seemed more than sufficient to ensure effective pollination. Hive traffic and greenhouse foraging of Bombus impatiens was recorded on sweet peppers (Capsicum annuum L.) in Canada (Meisels and Chiasson 1997). B. impatiens flight activity was measured every third day from 29 June to 13 July at 2 h intervals from 0700 to 1500 h. Hive traffic was found higher during the first 3 days from 29 June to 13 July and greenhouse foraging was greatest during the first 4 days from 29 June to 13 July. Abak et al. (1997) observed the bumble bee, (Bombus terrestris) activity on egg plants grown in unheated greenhouse in Turkey. They found that bumble bees start foraging from 0700 to 1400 h in January, 0600–1800 h in February and March. However, the peak activity was observed between 0900 and 1100 h and then decreased gradually. The flight activity stopped between 1300 and 1400 h and started again in afternoon between 1500 and 1800 h.

6.10.5 Life Cycle

Bumblebee colonies have a yearly cycle. Queens that have mated in late summer hibernate, usually in the soil, and emerge in spring. The queens found the new colony themselves, they search for a suitable nest site, deserted small rodent nests are popular sites, then they build a wax honey pot and fill it with regurgitated nectar (honey). This store will enable them to survive a day or two of bad weather without foraging. The queens also build up a store of pollen, some of this they eat, and the rest they form into a ball mixing it with nectar. The pollen stimulates the ovaries to produce eggs, which the queen lays in batches of 4–16 on the ball of pollen. The ball of pollen with the eggs is placed within reach of the honey pot, this enables the queen to brood the eggs and drink honey at the same time. After this stage the various species differ slightly in the way the larvae are fed. The larvae pupate and emerge as adults; the queen usually lays another batch of eggs while the first batch is still in the larval stage.

When new workers first emerge their hair is silvery in colour, within an hour or two it changes to the colours seen in foraging bees. The workers can start to forage after only 2 or 3 days, this means that the queen can spend more time egg laying. The average worker's life lasts about 4 weeks, and in that short time she might develop foraging preferences. Not all adults leave the nest to forage, some of the smallest workers may stay in the nest and perform "household" duties; these small workers may also have weak or deformed wings, but may live longer than the foragers and have less worn coats and wings, as they rarely fly.

The size a colony reaches depends on the species concerned and the food supply, some can have as few as 30 bees, and Bombus terrestris can reach as many as 400. Males are usually produced once the stores reach a sufficient quantity, or if the queen dies or loses her influence. When the adult males emerge they spend a few days in the nest, but do no work, then they leave the nest for good and forage for themselves. They can often be seen sheltering under the heads of flowers when it rains or when it gets dark. Not all workers return to the nest every night, some spend the night outside, sheltering under flowers as the males do. New queens emerge about a week or so after the males. They mate, drink lots of nectar to build up their fat body, which will enable them to survive the winter hibernation, then find a suitable place to hibernate.

There are some very important differences between the bumblebee life cycle and the honeybee life cycle. There is no mouth-to-mouth exchange of food between adult bumblebees, nor do adults groom each other or the queen. As yet no “queen substance” has been found; in honeybee hives workers licking the queen and each other pass the queen substance throughout the hive, and this pheromonal control enables the queen to maintain dominance. Bumblebee queens appear to maintain dominance purely by aggressive behaviour. They are usually bigger than the workers and the queen opens her mandibles and head-butts the most dominant worker from time to time. This is usually sufficient until unfertilized eggs are laid, or a worker’s ovaries develop.

6.10.6 Foraging and Constancy

Bumblebee larvae eat most of the pollen brought back to the nest, adult bees eat very little. Until the end of the final instar the larvae have a blind gut, faeces are voided all at once during the spinning of the cocoon and final instar. The highest growth rate occurs during the last instar so most pollen will be consumed during this time. The exine (outer wall) of the pollen grain is made of a tough carotenoid polymer which is highly resistant to decay and so can be identified in the larval faeces.

Brian (1951) analysed the larval faeces of three nests, one each of Bombus pascuorum, B. lucorum and B. hortorum. The nests were located quite close to each other, so the bees would have probably been foraging from the same area. She found considerable differences in the kinds of pollen eaten by the larvae of the different species. In a later study (1957) she found that bumblebees prefer to forage from flowers with corollas a little shorter than their tongue length. She thought that this might increase foraging speed, and also it seemed that they did not like pushing their heads into the flowers.

Inouye (1980) found that, in general, shorter-tongued bees foraged faster on short-corolla flowers than long-tongued bees, although he found it difficult to measure the foraging times of long-tongued bees on shorter corolla flowers because of “their apparent reluctance to feed on short corolla flowers”. With captive bees feeding from artificial flowers in the laboratory it was found that the probing time increased gradually with depth of flower, providing the flower was shallower than the bee’s tongue, but beyond that depth probing time increased much more rapidly, as the bees stretched their tongues but failed to reach the nectar (Harder 1983a, b).

Free (1970a) measured constancy by analysis of pollen loads of bees returning to the nest, he found that 63% of B. pascuorum and 34% of B. lucorum loads contained a mixture of pollen from different flower species, however many of these "mixed" loads contained 98% or more pollen from one plant species.

The analysis of pollen indicates some of the plants the bee visits, but it does not necessarily show all the plants visited by bees, as not all bees collect pollen on foraging trips. Some bees specialize in pollen collection, some in nectar, some in both, but all will change according to the needs of the colony. Pollen load analysis does not show the foraging patterns of nectar gathering bees.

Heinrich (1976) in the U.S.A. studied bumblebees foraging in an old field. He confirmed the species preferences of earlier studies, but also found that each individual preferred a small subset of the overall species group. He named the main foraging flower the "major" and the secondary flower(s) the "minor(s)".

The foraging environment of the bumblebees is constantly changing. Individual flowers and groups of flowers of the same and different species come into bloom and die at different times with different life-spans. Nectar changes throughout the day in volume and concentration (Prys-Jones and Corbet 1987) and throughout the life of the flower (Real and Rathke 1991; Willmer et al. 1994); soil conditions and daily temperature and humidity changes also affect the quantity of nectar available. Worker and queen bees aim to gather more food than they themselves will consume, in order to build up a store of surplus food. Males do not aim to build up a store; they forage only for themselves, so their foraging patterns might be expected to be different. In this constantly changing environment individual bees may get a different perception of which flower species is most rewarding. The best strategy for an individual bee is to forage from whatever species of flower it perceives to be the most rewarding, and change to another species when the original species is less rewarding and the new species is abundant enough to provide sufficient nectar.

An optimal forager would visit all flowers with rewards above a certain level, in its foraging area, to minimize energy costs and maximize energy gains (Real 1983), but individual bumblebees regularly ignore apparently rewarding flowers. It has been shown that flower complexity can cause learning problems in bees (Heinrich 1976) and that bumblebees are often constant to a guild of species with the same morphology (Manning 1956), or colour (Darwin 1891). Real (1983), in Costa Rica, found a slightly greater bumblebee constancy in a guild of species differing only slightly in morphology, than in a guild differing only in colour. As the number of different types of flower increases the constancy to one or a few types increases (Waser 1986). Laverty (1993) found that constancy was higher for the more morphologically complex species than for the simpler species however, even with the simpler species, bumblebees switched to a new species that had a similar corolla length and handling method, more frequently than would be expected if the switch was random.

Tests done in captivity have shown that bumblebees can recognise rewarding flower "types" by their colour, odour, or shape of flower, and that they will accept flowers that are slightly different from the typical type (Dukas and Waser 1994). No communication system for recruiting workers to rewarding flowers has been discovered in bumblebees (Brian 1957; Free and Butler 1959; Heinrich 1979; Laverty 1980), there appears to be no bumblebee equivalent of the honeybee waggle dance; however one bumblebee foraging in a group of flowers appears to attract others (Brian 1957).

6.10.7 Efficiency

On many crops, bumblebees (Bombus species) are 2–4 times more effective pollinators per bee than honeybees (Apis mellifera) and solitary bees such as the alfalfa leafcutter (Megachile rotundata). This is due to a 50–200% faster flower working rate and an average of 50 or more % longer hours worked each day. The importance of the working day remains underappreciated, and it is virtually unquantified worldwide. The greatest differential in average working days between bumblebees and honeybees occurs in wetter and cooler regions or seasons during crop flowering. For a few crops, bumblebees can be 10–20 times more effective pollinators per bee than nectar collecting honey bees. This is either because bumblebees either contact the stigma more consistently on cranberries, blueberries, red clover, some vetches or their larger bodies contact much more of the stigma e.g. curcurbits (pumpkins, squashes, melons, cucumbers), cotton, kiwfruit, cranberries, feijoa. As well they may carry about twice as much pollen on their body hairs for transfer to stigmas.

6.10.8 Pollinator Effectiveness

Two pollen collecting honey bees = one bumble bee based on working rate and a 30% longer working day for bumble bees. On a favorable, 10 h day one bumble bee would visit 6,000 flowers and on an average 4–5 h day 2,500–3,000 flowers will be visited. Pollen collecting honey bees are 10 times more effective in pollen transfer than nectar collecting honey bees. This is based on working method (contact with the stigma) and pollen on parts of the body that contact the stigma.

Three factors make the delivery rate of honey bee inferior to bumble bee colonies:

Honey bees have 2–3 times the average foraging range of bumble bees except in adverse weather.

Honey bees communicate within the hive about the quality of the sources of food, while each bumble bee determines from what flowers are yielding resources best from experience and sampling. Thus honey bees have the ability to shift to masses of better yielding flowers more rapidly than bumble bees.

Honey bees forage freely from a wider range of flowers than the short tongued bumble bees. Hence competing pollen sources are more important for honey bees than bumble bees. Put another way the main bumble bee species visiting cranberry flowers have a better preference for cranberry flowers.

6.10.9 *Colony Characters and Development*

At their peak each colonies of commercially reared species can have 200–400 bees including the non stinging males. Maximum foraging averages 2–3 bees entering or leaving per minute. During summer a honeybee colony has 20–50,000 bees and the better colonies have 100–150 bees foraging from them per minute.

6.10.10 *What Are Cuckoo Bumblebees?*

A cuckoo bumblebee, like the bird it is named after, lays its eggs in another bumblebee's nest and leaves the workers of that nest to rear the young. Of course the eggs she lays are either queens or males, and the cuckoo queens emerge in late spring or early summer, much later than ordinary bumblebee queens. The cuckoo differs physically from ordinary queen bumblebee in that she has no pollen basket on her rear legs, does not exude wax from between her abdominal segments, is slightly less hairy than ordinary bumblebees, and all species have shortest tongues. Cuckoos have a much harder body than normal bumblebees, and because no wax is exuded there are no weak points between the abdominal segments, so if there is a fight between a cuckoo and another worker or queen it is almost impossible for the queen or worker to force her sting into the cuckoo body. Apart from that cuckoo bumblebees usually have the same pattern of hair colour as the bumblebees' nests they lay in.

6.10.11 *Domestication of Bumble Bees*

Macfarlane et al. (1990), have also reared the spring collected queens kept in two screen cages and fed with 50% sugar solution and ground corbicular pollen by maintaining at 18–250°C temperature. Most of the workers have reported the successful domestication of queens collected during spring. Plowright and Jay (1966) have reared the hibernated queens in plastic cages at 300°C temperature and 60% relative humidity. Frison (1927) found a greater incidence of colony formation in boxes containing a single queen than housing pair of queens, close to the present observations where the queens were kept singly inside the boxes. Similarly, Ptacek (1985) has reared the bumble bee in wooden boxes and fed with 60% honey solution and pollen dough made of corbicular pollen. Ono et al. (1994) reared Bombus hypocrita and B. ignitus in laboratory from post hibernating queens. Queens were kept in wooden boxes consisting of brood chamber and feeding chamber and were supplied with sucrose solution (50%) and fresh pollen pellets.

Mah et al. (2001) who found the average developmental time in B. ardens ardens, B. hypocrita sapporoensis and B. ignitus from egg to adult being 28, 27 and 28 days, respectively. Similar study was conducted by González et al. (2004), who reported 29.6 days to be the average developmental time in B. atratus. Yeninar and Kaftanoglu (1997) reported three successive phases in colony development that is colony initiation, switch point and competition. They found that during colony initiation queen makes egg cups, lays diploid eggs and start producing worker bee. With the first worker emergence, worker assists the queen in feeding. Switch point occurred on an average 18.9 ± 1.3 days after the first worker bee emerged and competition point occurred at an average of 31.8 ± 10 days after the emergence of first worker bee. Similarly, in the present study queen started to make egg cups, laid diploid eggs and start producing workers after 23 ± 2 days of wax secretion.

Several workers have given various nest box designs for rearing the colonies in captivity. Macfarlane et al. (1983) found that box can be made from any type of material (plywood, concrete, polysterene, plastic), but should be constructed to allow for the escape of water vapours as excessive humidity makes colonies susceptible to mould. Rosler (1985) used different methods of rearing Bombus sp. to induce the colony in captivity. In series I queens were kept in container consisting wax paper carton, but none of the eggs laid survived for more than few days. In series II queens were installed in a wooden container consisting of two boxes with glass roof and corrugated floor. Queens built their egg cells directly on the cardboard floor of the outer box. During the development of first brood, some queens neglected larvae because of wax envelope surrounding them. The design of series III was similar to series II, but divided into two unequal parts. The larger chamber contained feeding tube and was lined with corrugated cardboard and had a glass roof and smaller chamber was lined with upholsters cotton. This design was more suited for rearing the queens in captivity. On the other hand, queens which had constructed their first egg cells upon the pollen lump rarely built more cells upon the floor. In the present study two chambered wooden box used for rearing were found similar to Rosler and Jay (1966), but with out lined corrugated floor and more number of queens were found to construct their egg cells upon the pollen lump than the floor of the box.

6.10.11.1 Providing Nest Sites

Bumble bees are opportunistic. They don't often excavate. Instead, they utilize deserted rodent nests and burrows, cavities in compost heaps, under boards, between railroad ties, in woodpiles, in vacant birdhouses, wall voids, etc. Bumblebees like to nest in warm, sheltered sites, different species have differing nest preferences, however, the easiest ones to provide for are the ground and surface nesters.

Encourage the nesting of bumble bees by building and placing artificial nesting boxes.

Don't remove small pile of twigs and leaves which may provide a home to a colony.

An upturned flowerpot or a roof slate with some nesting material could provide a nest site. The very best nesting material is the contents of a mouse or other small mammal's nest, but clipped pieces of dried grass or dry moss will do. It is important that there are no ant nests close by as they will rob the bumblebee nest in the early days.

An old teapot buried in the ground with the spout providing an entry tunnel makes a good secure nest site if it can be kept free from damp.

It is reported that bumblebees prefer to nest in north facing sites in places having hotter summers and south facing in colder climates.

6.10.11.2 Hibernation Sites

Generally these are not south facing as they would warm up too quickly in the spring causing the queen to emerge before there was sufficient flowers in bloom supplying nectar and pollen. So hibernation sites tend to be in cooler places. Under tree roots and at the base of walls and hedges seem to be the most popular places. The main thing is dryness, so damp areas are out.

6.10.12 Bumblebee for Pollination of Crop

6.10.12.1 Pollinator Role of Bumblebees

Populations of short and medium tongued species of bumblebees (notably B. impatiens, B. affinis, B. terricola, B. vagans, and B. perplexus) provide backup pollination that adds an element of reliability to pollination of other crops which include lotus, Dutch, alsike clovers, sunflower, buckwheat, Phacelia, chicory, pip and stone fruits and berries. Long tongued bumblebee species (B. fervidus, B. pennsylvanicus and the rarer B. borealis, and B. auricomus) on the other hand prefer other flowers to cranberries. They are affective pollinators of red clover, many vetches, faba or tick and runner beans, blueberries, cherries, and curcurbits. Bumble bees tolerate a wider range of insecticides than honeybees and solitary bees (alkali bees Nomia melanderi); alfalfa leafcutter bees; and perhaps mason bees (Osmia spp.). Osmia lignaria (American) and O. cornutu (Japanese) in USA are of potential value for fruit pollination. Proper pollination is essential for optimal fruit set and production. In the past, growers relied on honeybees, manual pollination or plant growth regulators, depending on the crop being grown. All these methods have drawbacks:

In general, honeybees don't work well in greenhouses or tunnels. They are generally less effective or inadequate during periods of low temperatures (under 15°C) and cloudy weather. Bumblebees do things differently: unlike honeybees, they do not have a permanent colony. In autumn, a bumblebee colony dies out and only the young, mated queens hibernate each separately in the soil. In spring, a queen starts a new colony. She lays a first batch of eggs, from which larvae emerge after 4–5 days.

In the beginning, the queen has to do all the foraging by herself. The larvae are fed with a mixture of nectar and pollen gathered from flowers. When the first adult workers have appeared, the queen no longer leaves the nest. The workers begin to forage and to take care of the brood. After the production of 150–400 workers, young queens and drones (males) are born. From this time on, the activity of the colony decreases; the old queen stops laying eggs and eventually dies. With a young, mated queen, a new cycle can start.

Bumblebees require pollen as a protein source for the build-up of the colony. They also need nectar as a carbohydrate (sugar) source. Since the flowers of certain plants (e.g. tomatoes) do not produce any nectar, the colony needs to be provided with a sugar solution.

6.10.13 Communication

A returning honeybee forager performs a figure-of-eight dance on the combs which tells her workmates the whereabouts of a good source of food. Although no method of recruiting workmates to good food sources has been found in bumblebees yet, recent work has shown that a returning forager does perform a dance over the combs which excites her workmates making them leave the nest. The method of communication is believed to be a pheromone (a chemical substance secreted by one animal which influences the behaviour of other animals), however it seems only to encourage other workers to go out to forage; there does not seem to be any other information conveyed by the pheromone.

6.10.14 Profit and Loss

Bumblebees need energy to fly, so when they leave on a foraging trip they carry nectar in their stomach to fuel them. The amount of nectar needed is roughly about 10% by volume of the amount collected in one foraging trip. A bumblebee making about ten average foraging trips would expect to provide the nest with about 3 ml of honey a day. However practically all the pollen collected in the pollen basket is stored for larval consumption.

6.10.15 Scent Marking Visited Flowers

Foraging bumblebees tend to avoid flowers already visited by other bumblebees of the same species, though they often visit the same patch of flowers, or even the same spike, as in foxglove. This is because bumblebees can scent mark the flowers they have visited and these scent markings can also be recognized by other species of bumblebee.

6.10.16 Distances Flown

Bumblebees are what are called “central place foragers” the central place being the nest. They fly out to the source of nectar/pollen then fly back. Bombus pratorum tends to forage fairly close to the nest, while others, Bombus terrestris, lucorum and lapidarius, will often ignore or desert apparently “good” foraging sites to travel great distances to other sites. The distance a bumblebee is willing to travel to gather food obviously has great implications when considering sites for the planting of genetically modified plants with non-sterile pollen. It is believed that bumblebees could travel as far as 8 km to forage.

6.10.17 Foraging Preferences

Bumblebees have to learn how to get the nectar from flowers. In some flowers such as the daisy like Compositae this is fairly easy, and involves repeated probing for small rewards while standing on the platform-like flower. Other flowers are more of a challenge, for example monkshood (Aconitum napellus) is a very complicated flower, and the bumblebee must learn just how to get inside to reach the comparatively large reward. So because the bumblebee must spend time learning how to get at the nectar in the various shapes and colours of flower available, they tend to specialize on one or two types or species of flower at a time. In fact many of them will visit only one species of flower as long as there are sufficient of them to provide enough nectar. It is this behaviour, called “constancy” that makes the bumblebee an invaluable pollinator of crops, as pollen deposited on the stigma (female part leading to ovary) of a different species is just wasted pollen and will not fertilise the flower, so will not lead to fruit or seed production.

6.10.18 Nest Searching by Queens

Generally we will find bumblebees on flowers, in the nest, and travelling between the two. However in spring we can find bumblebees in odd places, these are the queens and they are searching for a suitable place to nest, or just somewhere to have a rest or spend the night. She will investigate dark corners, mouse holes, garages and sheds. There have even been cases where a queen has gone into a pocket. She will hover and fly low over the ground oblivious to everything, and is quite easy to follow at this time.

6.10.19 Natural Enemies

Bumble bees have a number of natural enemies. The most destructive parasite is a species of flesh fly maggot. Other pests of bumble bees are lesser house fly maggots, certain sap beetles, scavenger and predator mites, the dried fruit moth caterpillar, and many others depending on geographical area. Mammals such as shrews, mice, and skunks can also be very destructive to bumble bee colonies. Human beings are probably the most destructive entity to bumble bees inasmuch as they often spray insecticides to blooming plants. Keep in mind that bumble bees are just as sensitive, if not more so, to garden chemicals as are honeybees. The rule of thumb for the gardener is – Never spray insecticides to blooming plants. Paying attention to this rule will ensure that you maintain bumble bees as efficient native pollinators in your garden.

6.10.20 Advantages of the Use of Bumblebees

Bumblebees are good pollinators of the crops for the following reasons

Why Bumblebees and not honeybees?

The bumblebee is capable of vibrating the flower using the unique “buzz pollination” mechanism. The tomato flower needs vibration for proper pollination and fruit set under greenhouse conditions. The bumblebee does this in an optimal way far superior to other methods. The bumblebee is less affected by extreme weather conditions than the honeybee.

Bumble bees are cool weather operators. Unlike honey bees, bumblebees are active at low temperatures (5°C), in windy conditions and under cloudy skies. Their bodies have an interesting adaptation that assists them in being flight functional in cool temperatures when other insects cannot fly. Their thorax is almost always totally or partially black and often “bald”. The black color absorbs heat quickly and warms up the flight muscles allowing them to fly after only being exposed to sunlight for a short time.

The bumblebee is better adapted to perform under confined greenhouse conditions. Bumblebees are not only excellent pollinators in open air, but are especially valuable in greenhouses and plastic tunnels . The bumblebee is less inclined to look for alternative sources of pollen and nectar outside the greenhouse. Therefore, it will stay in the greenhouse even if the latter is opened for ventilation purposes.

Many species have longer tongues than honeybees, so they can pollinate flowers with long, narrow corollas. They are very hairy and their hairs are branched and so are perfect for picking up and transferring pollen. Bumblebees can completely replace manual pollination and use of hormones, resulting in less labour costs. Higher fruit production and quality: In crops, such as tomatoes, peppers and blueberries, bumblebee pollination results in higher yield as well as larger and higher quality fruits.

6.10.21 Applications

6.10.21.1 Tomatoes

Bumblebees can totally replace the use of manual vibrators and hormone application, provided the plants produce viable pollen. Bumblebees grasp the tomato flower and vibrate their thorax to shake the pollen loose. This leaves a small brown mark on the anther cone, making it possible to monitor their work.

A colony can pollinate 1,000–3,000 m^2 of crop for 6–8 weeks. The number of colonies required depends upon the type of glasshouse or tunnel, the season, the variety, the number of plants per square metre and the competition from wild flowers.

6.10.21.2 Sweet Peppers

Sweet peppers pollinated by bumblebees will contain more seeds, resulting in a better shape and a thicker pericap. One colony is sufficient for the pollination of 3,000–5,000m^2 during 6 to 8 weeks.

6.10.21.3 Strawberry

The big bumblebees are able to transport large quantities of pollen. The bumblebees land on the flower base (receptacle) of the strawberry flower and pollinate all the pistils in doing so. The flower base will develop into a beautiful, smooth fruit. Thanks to the activity of the bumblebees, less deformed fruits are produced. Bumblebees also work at low temperatures and under cloudy skies.

6.10.21.4 Soft Fruit: (Cranberries, Raspberries, Blueberries, Black and Red Currant, etc.)

Bumblebees assure an excellent fruit set, especially during periods when honeybees are not active: in winter and in spring, and during cold and cloudy weather. Fruit quality is improved and commercial yields increase substantially by using bumblebees for pollination.

6.10.21.5 Top Fruit

Bumblebees are less dependant on the weather during inflorescence. They are also impervious to the Varroa mite.

6.10.21.6 Seed Production

Convinced of the many advantages, seed producing companies use the Biobest bumblebees in order to achieve high seed production (alfalfa, red clover, sunflowers, etc.).

6.10.21.7 Zucchini and Melons

Bumblebees are very effective for pollination of zucchini and melons. The bumblebees will visit male flowers (for pollen) as well as female flowers (for nectar).

6.10.21.8 Other Crops

Because of their physiology, bumblebees are impeccable pollinators and can be introduced in lots of cultures.

6.10.22 Key Benefits

Delivered to farm at will
Larger Fruit
Less labor with no fruit damage as in mechanical vibrator

The bumblebee is an ideal pollinator for protected crops and an important backup for outdoor crops during marginal seasons. Greenhouse tomato is the major crop, but other crops such as greenhouse sweet pepper, strawberry, eggplant, melon and courgette, and outdoor fruit crops like cherry, plum and blueberry also respond well.

Sophisticated mass production of bumblebees enables pollination services to thousands of hectares of greenhouse tomatoes in Israel. Bumblebee hives are exported, in increasing quantities, to Europe, Japan, South Korea and Russia.

The bumblebee is capable of vibrating the flower using the unique “buzz pollination” mechanism. The tomato flower needs vibration for proper pollination and fruit set under greenhouse conditions. The bumblebee does this in an optimal way far superior to other methods.

The bumblebee is less affected by extreme weather conditions than the honeybee.

The bumblebee is better adapted to perform under confined greenhouse conditions. The bumblebee is less inclined to look for alternative sources of pollen and nectar outside the greenhouse. Therefore, it will stay in the greenhouse even if the latter is opened for ventilation purposes.

6.11 Role of Non Apis Bees in Crop Pollination

Following are the under mentioned few crops in which the will bees have been successfully domesticated and managed for pollination (Tables 6.7 and 6.8).

Table 6.7 Important non-Apis bee pollinators of some agricultural crops in India

Crop/plant	Family	Bee species	References
Alfalfa (Medicago sativa)	Leguminosae	Megachile bicolor, M. disjunta, M. flaviceps, M.femorata, M. lanata, Nomia oxybeloides, N. divisus, N. pusilla, Pithitis smaragdula and Xylocopa fenestrata	Kapil et al. (1974), Abrol (1986a)
		Megachile nana M. flaviceps M.femorata M.cephalotes	Kapil et al. (1975)
		Braunsapis spp.	Kapil and Jain (1980)
		M. lanata M.cephalotes M. cephalotes Pithitis smaragdula	Abrol (1985)
		M. flaviceps M. nana	Abrol (1986b)
Berseem (Trifolium alexandrium)		M. flaviceps M. nana	Abrol (1986b)
White clover (T.repens)		Bombus asiaticus B.albopleuralis	Abrol (1987)
Red clover (T.repens)		Bombus asiaticus B.albopleuralis	Abrol (1987)
Pigeon pea (Cajanus cajan)		Megachile lanata M.bicolor M.flavipes M.cephalotes M.femorata	Chaudhary and Jain (1978)
		Megachile lanata Xylocopa fenestrata X. pubescens M.bicolor M.cephalotes	Abrol (1985)
Sunhemp (Crotolaria juncea)		X. pubescens X. fenestrate	Kapil and Dhaliwal (1968a, b)
		Megachile lanata M. fasciculata X. fenestrate	Grewal and Sidhu (1978)
		Megachile lanata	Abrol and Kapil (1986)
		M. bicolor	Abrol (1987a)
Pea (Pisum sativum)	Compositae	X. fenestrata X. pubescens Megachile lanata	Kapil et al. (1975)
		Braunsapis spp.	Kapil and Jain (1980)
		X. fenestrata X. pubescens M.cephalotes M.flavipes	Abrol (1985)
		B.albopleuralis Bombus asiaticu Lasioglossum spp.	Abrol (1987)
Sweet potato (Ipomoea batatas)	Convolvulaceae	X. fenestrata B.albopleurali Bombus asiaticus	Abrol (1987)

(continued)

Table 6.7 (continued)

Crop/plant	Family	Bee species	References
Egg plant (Solanum melongena)		B. asiaticus	Abrol (1987)
		X. fenestrata Ameigilla delicata A.subcosrulea Nomia caliphora Pithitis spp.	Batra (1967)
Onion (Allium cepa)	Liliaceae	Nomioides spp.	Kapil et al. (1975)
		Lasioglossum spp. Nomioides spp. X. fenestrate	Abrol (1987)
Field mustard (Brassica campestris)	Cruciferae	Nomioides Megachilids Andrenids Halictids	Kapil et al. (1971)
		Andrena ilerda A.leaena	Abrol (1986c)
Rape (Brassica napus)		Andrena ilerda	Mohammad (1938)
		Halictids	Rahman (1940)
Raya (Brassica juncea)		Andrena ilerda	Kapil et al. (1971)
		A.leaena Andrena ilerda	Abrol (1985), Abrol (1986b)
Taramira (Eruca sativa)		A.leaena Andrena ilerda Colletes Halictus spp.	Kapil et al. (1971)
Cabbage and cauliflower (B. oleracea)		Andrena ilerda Lassioglossum spp. Pithitis smaragdula	Batra (1967)
Raddish (Raphanus sativus)		Anthophora spp. Nomia spp. Lassioglossum spp. Colletes spp.	Batra (1967)
Pumpkin and squashes (Cucurbita spp.)	Cucurbitaceae	X. fenestrata X. pubescens Halictus spp. Nomioides spp.	Atwal (1970)
Smooth loofah (Luffa aegyptica)		X. fenestrata X. pubescens P. smaragdula	Kapil et al. (1970)
Cucumbers (Cucumis melo)		Nomia spp. P. smaragdula Nomioides variegata Halictids	Kapil et al. (1970)
		Lasioglossum spp.	Abrol and Bhat (1987)
Cotton (Gossypium spp.)	Malvaceae	Lithurgens attratus	Batra (1977)
Corriander (Corraindrum sativum)	Umbelliferae	Nomioides spp. Halictidae X. fenestrate	Abrol (1985)
Saunf (Foeniculum vulagre)		Halictis spp. X. fenestrate	Abrol (1985)
Carrot (Dacus carota)		Lasioglossum spp. Sphecoides Hyleaus Nomioides Braunsapis Pithitis smaragdula	Batra (1967)
Jowain (Traechyspermum ammi)		Andrena spp. Nomioides Halictus spp. Lasioglossum spp.	Batra (1967)
Orange and lemon Citrus spp.	Rutaceae	Lasioglossum spp. X. fenestrata	Batra (1977)

(continued)

Table 6.7 (continued)

Crop/plant	Family	Bee species	References
Guava (Psidium guajava)	Myrtaceae	X. pubescens X. fenestrata Megachile lanata	Batra (1977)
Mango (Mangifera indica)	Anacardiaceae	Xylocopa spp. Megachile spp. Nomia spp. Lasioglossum spp.	Batra (1967)
Pomegranate (Punica granatum)	Punicaceae	Nomioides Lasioglossum Halictus spp.	Batra (1967)
Apples (Pyrus malus)	Rosaceae	Colletes nursei Lasioglossum spp. Cattulum Osmia cornifrons	
		Andrena spp. Bombus haemorrhoidalis Halictus vacchalli Osmia spp. Pithitis spp. X.fenestrata Nomia spp.	Batra (1984)
Almond (P.amygdalus)		Lasioglossum spp. Xylocopa valga	Abrol (1987)
Cherry (P.avium)		Xylocopa valga Nomia spp.	Abrol (1987)
Pear (P.cumminis)		Xylocopa valga Nomia spp.	Abrol (1987)

Table 6.8 Non-*Apis* pollinators of crops in India (Batra 1977)

Crop	Pollinators
Brassica toria var. dichotoma and B. campestris var.Sarson (Toria)	Andrena ilerda, Halictus sp. Andrena leaena, Andrena sp., Colletes spp., Anthophora sp.
Brassica juncea (Raya)	Andrena ilerda, Andrena leaena
Eruca sativa (Taramira)	Anthophora vedetta, Colletes nursei, Andrena ilerda
Brassica oleracea (cabbage and cauliflower)	Lasioglossum spp., Andrena ilerda, Pithitis smargdula
Raphanus sativus (Raddish)	Nomioides variegata., N.divia, Colletes nursei, Andrena leaena, Tetralonia pruinosa
Medicago sativa (Alfalfa)	Pithitis smargdula, Megachile flavipes, Andrena levilabris
Trifolium alexandrium (Berseem)	Pithitis smargdula, Lasioglossum cattulum
Crotolaria juncea (Sunnhemp)	Xylocopa amethystine, Megachile anthracina, M. lanata, M. fasciculate
Indigofera spp. (Indigo)	Nomia capitata (capitata)
Gossypium spp. (Cotton)	Anthophora confusa, Andrena ilerda
Luffa spp. (Ghiyatori)	Xylocopa spp., Tetralonia ovata, Megachile coelioxyoides, Nomia eburneigera, N.curvipes, Lasioglossum cattulum, Lasioglossum albescens
Momordica charantia (Butter gourd)	Nomioides spp., Pithitis smargdula
Solanum melongena (Egg plant)	Xylocopa fenestrata., Amegilla delicata, Nomia callichlora, N. oxybeloides, Lassioglossum cattulum
Psidium guajava (Guava)	Xylocopa fenestrata, Megachile lanata
Citrus sinensis (orange)	Lassioglossum cattulum
Malus sylvestris (Apple)	Colletes nursei, Lassioglossum cattulum

6.11.1 Pollination in Alfalfa

Alfalfa (Medicogo sativa) is a perennial herbaceous protein rich legume. It is one of the most important fodder crop throughout the world. It is a cross plant and its flowers being typically papilionaceous has staminal column held inside keel. Tripping i.e. release of staminal column is considered to be a prerequisite, of cross pollination (Free 1993). Most investigators have concluded that long tongued bees are not very important in alfalfa seed production particularly in dry or arid conditions because of the fact that the honey bee collect nectar from alfalfa flowers from the side of the keel, thus avoid the mechanical shock of the staminal column. Most of the workers has emphasized importance of certain non-Apis species in the pollination of its flowers. Among a variety of wild bees associated with alfalfa flowers, the investigations based in U.S.A. and Alberta (Canada) showed that leaf cutter bee (Megachila rotundata) and a alkali bee (Nomia mellandari could be exploited and propagated as alfalfa pollinator (Bohart 1972)).

A variety of non-Apis bees have been reported to be associated with some other crops in this region (Kapil and Jain 1980). They reported megachilid species associated with alfalfa under local conditions. The studies (Sihag 1990) have suggested the inclusion of some of these bees M. flavipas, M. femorata, M. lanata and M. cephalates under the genus Chalcodoma. The major period of their activity for alfalfa pollination in the April-May months. Their broods however undergo dormancy as mature larvae first in the months of June-July and then in winters. Until mid March, there are many overlapping generations in the months of September to November. High day temperature and dry condition favour their foraging activity, brood formation viz-a-viz alfalfa pollination. One important non-Apis alfalfa pollinators are Mellita leporilla. Atlthoph quadrifasciata and few other species of Alldrella and Megachile.

The leaf cutter bee earlier called as Megachile pacifica, is a fast nest gregarious bee and it nest in any such tunnel available in wood above the ground. It has been found to accept the man made artificial nesting devices including tunneled wooden block, corrugated boards or the plastic tubes of appropriate tunnel size i diameter. Its native region is South-West Asia and it spread to eastern USA around 1930. Today, it is successfully managed for alfalfa pollination in many states of USA and southern parts of Canada as well as many of the European countries. It is to, termed as million dollars bee as it involve the inputs and outputs of millions of dollars in making various mechanical devices and nesting materials and management techniques for alfalfa seed production (Plate 2).

The alkali bee is another fast nesting gregarious bee. It however nest in big alkaline soil. Once established favourable site may produce as many as 2 lakh cells per acre. The best sites are bare or slightly vegetated tender silty loamy soils. Main advantage in its management is that its nests can't be easily removed, stored or transported. There have been many refinements in developing artificial nesting sites. The most important step has been to keep the site puffy a little moist by providing plastic films several feet below the surface. Heated calli are sometimes employed

Plate 2 Nesting materials for management of wild bees

to enhance pupation and emergence of adults to coincide with alfalfa blooming. In addition to rains moulded soil, rats, skunks, birds and variety of other parasites are its natural enemies. A temperature of 30°C is most appropriate for rapid pupation of the diapausing larvae.

Pithitus smaragdula, a green metallic bee is another important alfalfa pollinator. It is a small carpenter bee and it makes nesting tunnels in cut pithy stems such as common reeds (Erianthus munja).

6.11.2 Other Crops

The wild bees are associated with many other crops also. The crops like clovers (Ladino clover, red clover, Egyptian clover, white clover and sweet clover), soybea pigeon-pea sunhemp, broad bean, mustard, rape, coffee, papaya, cotton, sunflower safflower and apples are few other important crops which could be benefited for cross pollination. A variety of humble bees belonging to the genus Bombus utilized for pollination of clovers. The bumble bees are semisocial bees as these initiate nesting as an individual female, but later establish a large size colony. Osmia coerulescens, a leaf cutter bee has also be reported to increase seed yields in red clover in USA Osmia corniifrons has been successfully managed for apple pollination in northern and central Japan. It nest in bamboo and hollow reed. The stingless bees commonly termed as ‘melipona’ bees are another important non-Apis group of true social bees which resembles to Apis species as these form large colonies and yield sufficient honey for human consumption. The indigenous people of tropical America and Africa have for centuries managed various species of stingless bees for honey. Continuously changing climatic conditions and over exploitations of forests and barren lands for agriculture have been the major hurdles in natural propagation of wild bees. In north India alone there has been about 73% decline in their natural population during 1976–1978 (Jain 1993). Looking upon their utility and importance and their implications in preserving flora, there is a need to protect and conserve these bees for pollination.

Inspite of being represented in large numbers, non-Apis bee pollinators have-received little attention. The probable reason seems their unpredictable seasonal availability, lack of knowledge about their biology and host plant relationship. It was only in the mid sixties that scientific interests were generated to study and understand their life processes in India (Atwal 1970). Failure of honeybees in the pollination of alfalfa which requires tripping (Kapil et al. 1977; Kapil and Jain 1979, 1980) dwindling of bee colonies due to acute floral dearth in heavy monsoon during June to September and similar effects during severe winter in Himalayan ranges from November to February and prevalent bee diseases has created the necessity for exploration of alternate yet suitable non-Apis bee pollinators to augment crop yields in India. In addition to alfalfa, clovers and fruits like apple, pear, peach, almond and several other crops such as sunflower, hybrid tomato, cotton, onion, carrot and cucurbits (Kapil and Dhaliwal 1968a, b) can be future potential crops requiring the services of the non-Apis pollinators.

6.12 Non-Apis Bees and Future Prospects

Honey bees (Genus Apis Linnaeus) have often been credited with pollination services that are actually performed by other bee species. Hundreds of entomophilous crops are now known that are very poorly pollinated by honey bees. The act in major is shared by non-Apis or the so called wild bees (Parker et al. 1987). There are few estimates available for the value of non-Apis pollination. Estimations declared the value of wild bee industry was well over US $ 1 million per year in terms of expenditures and benefits in USA alone (Bohart 1970, 1972). The benefits increased up to a range of US $18–40 million in 1981 and, the total involvement of money over crossed US$ 81 billion (Levin 1983).

Recent technological advances in agronomic practices have focused primarily on improving yield, increasing the number of crops grown and increasing the area of harvestable crops. These advancements have been applied indiscriminately to the majority of crops and, in a very short duration, they have transformed farms into intensive monoculture systems. The positive results of these practices are impressive. The quality and quantity of food has increased, food costs have decreased, numerous fresh fruits and vegetables of high quality are available for much longer period, the quality and types of prepared food products have greatly improved and, the large labour force once required has been reduced, at the same time crop area have increased. On the other hand, the technical advances and intensive farming practices have evolved numerous negative impacts on crop pollination and non-Apis populations (Richards 1993).

A number of conservation studies have concluded that clearing land of trees and increased cultivation have inadvertently eliminated many of the nesting sites previously used by non-Apis pollinators (Renner 1996; Cane 2001). Frequent applications of broad-spectrum weedicides and pesticides have been responsible for the rapid decline of pollinator numbers within agricultural areas (Batra 1995c). Changing irrigation practices have had long-term negative effects on soil nesting pollinators. Overgrazing of rangeland and the use of herbicides have indirectly reduced the presence of pollinators by decreasing diversity of pollen-nectar resources and, by eliminating required plant resources that are utilized by various wild-non-Apis bees in nest construction (Batra 1979b, c). One of the consequences of an increased food supply for the world has been inadvertently depopulating both numbers and species of native pollinators within agricultural environment (Roubik 2001). This situation must be addressed if our agricultural ecosystem has to be sustained.

Second interesting aspect of pollination with honey bee for several crops lies in the fact that after one or two morning forages honey bees are least interested in pollen collection. It prefers collection of nectar only and pollens are attached to the scopal bristles accidentally (Sharma and Gupta 1993). In such events, honey bee enters and after drinking nectar moves out of the corolla tube so swiftly that a flower hardly receives any help in tripping. In the field, less than 1% of the self-tripped flowers produce seed and most of the non-tripped flowers fail to do so. Studies available with regard to many leguminous crops have reported several non-Apis bees as intentional trippers and they continue to do so for many full days (Zaleski 1956). They deposit pollens in their nest chamber adjacent to their egg that hatch later as larva and feeds upon it. The process usually requires at least 3–15 days as per nest size of the species. Apparently, several wild-solitary bees are known for their effective pollination values abroad. Otherwise also, majority of non-Apis females are supported with dense brush of pollen collecting scopa and in larger area of the body so that maximum amount of pollen load may be collected in each trip to the field (Torchio 1987).

The benefits we derive from native pollinators are believed to be increasing as the honey bee industry experiences continued difficulties from mites and diseases. Furthermore the crops that are better pollinated by bees other than honey bees, are being grown more intensively. To protect the native bee pollinators, two alternatives have been suggested, one is the preservation and management of habitats and another is artificial domestication and management of bee species (Stephen and Every 1970; Williams et al. 1991). Bohart (1970, 1972) quoted that honey bees are not entirely satisfactory in their use for the maximum output, in enclosures. On the contrary, non-Apis species when invited to artificial nesting devices, have been found much more effective pollinators. Apparently, a newer aspect has evolved which deals with "artificial domestication and management of wild bees for crop pollination (ADMP)".

In North America 3,500 species of wild-solitary bees have been recorded, commonly referred as "Pollen Bees" (Batra 1994a). Alfalfa leafcutter bee (Megachile rotundata), blue orchard bee (Osmia lignaria propinqua), fuzzy foot bees (Anthophora pilipes) and, mustached bees (Anthophora abrupta) are some of the wild-bee cross pollinators which are successfully used in the artificial domestication and management programme, to enhance the crop pollination (Batra 1982, 1991, 1993, 1994b). Robinson et al. (1989) detailed several parameters applicable for the pollinators. In brief, such programmes intends to sustain a good population of pollinators close to the crops by providing them artificial nesting devices and, the normal principle usually understood was ‘higher the number of pollinators higher will be seed yield’. Kapil et al. (1970a, b) recorded some of the insect pollinators and noted their comparative abundance. However, after certain threshold limit population increase of the pollinator does not put any further positive impact upon the seed yield (Strickler 1997). Instead, a consistency in increase in floral resource has to be maintained to sustain higher population of pollinator on the crop (Strickler 1999; Strickler and Freitas 1999), otherwise fear concerning escape of bee species would persist.

A few other successful programmes exist that has enhanced the number of native pollinators for fruit crops such as, using horn faced bees Osmia cornifrons in Japan and use of Osmia cornuta in Europe (Maeta 1978; Torchio and Asensio 1985; Maccagnani et al. 2003) and its introduction and establishment in USA (Batra 1978a). Identically, many species of Megachile, Heriades and Osmia are found in sufficient numbers and need intensive investigations in this direction because they are quite efficient visitors of several cultivated crops in northern India (p.o. author).

Certainly, ADMP has emerged as a new entomological industry (Bohart 1970). In India, the studies relevant to pollination of some more crops and the efficiency of several bee species were recently commenced by Kumar et al. (1994), Sharma and Gupta (2001), and Kapila et al. (2002). Some of these workers have made significant contribution by using the criteria such as amount of carried pollen loads, number of visits made on flowers etc. for different bee species. Megachiline bees have the maximum area for the collection of pollen grains (beneath their abdomens) hence usually top the list with regard to carried pollen loads.

Author hereby suggest that several correlated aspects should be undertaken in future such as, bee foraging studies coinciding with rotation of crops; population studies correlating different bee species on different crops; pollinator efficiency studies; effects of insecticides on various pollinator bee species; study of immatures, their developmental periodicities and, its variation under controlled environment, so that supply of broods as seeds may be implemented in practice, alongwith blooming of different crops; brood transfer techniques; studies relating parasites-predators and pests of adults and broods and, their mortality rate; impact of ecological factors on adults and broods; crop yield studies; development of nesting devices for different bee species so as to retain maximum population of bees on crops etc. These will ultimately help initiate artificial domestication and management programme in the country for many useful bee species to obtain better seed yields.

References

Abak K, Guler HY (1994) Pollen fertility and the vegetative growth of various eggplant genotypes under low temperature greenhouse conditions. Acta Hortic 36(6):85

Abak K, Dasgan HY, Ikiz O, Uygun N, Sayalan M, Kaftanoglu O, Yeninar H (1997) Pollen production and quality of pepper grown in unheated greenhouses during winter and the effects of bumblebees (*Bombus terrestris*) pollination on fruit yield and quality. Acta Hortic 437:303–307

Abrol DP (1985) Analysis of biophysical interactions in causing foraging behaviour of some bees – a study in bioenergetics. Ph.D. thesis, Haryana Agricultural University, Hisar, 286 p

Abrol D (1986a) Time and energy budgets of alfalfa pollinating bees Megachile nana and Megachile flavipes Spinola (Hymenoptera, Megachilidae). Proc Indian Acad Sci Anim Sci 95(5):579–586

Abrol D (1986b) Wing beat frequencies of Andrena ilerda and Andrena leaena (Hymenoptera, Andrenidae). Ann Biol Ludhiana 2(1):98–99

Abrol DP (1986c) Ecophysiological adaptations between pollinating bees and their flowers. Environ Ecol 4:161–162

Abrol DP (1987a) Analysis of environmental factors affecting foraging behaviour of *Megachile bicolor* F. on Crotalaria juncea L. Bangladesh J Agric Res 12:5–14

Abrol DP (1987b) Influence of thermal and energetic constraints on the pollination activity of *Xylocopa pubescens* Spinola. Environ Ecol 5:90–93

Abrol D (1988a) Ecology and behaviour of three bee species pollinating loquat (Eriobotrya japonica Lindley). Proc Indian Natl Sci Acad B Biol Sci 54(2/3):161–164

Abrol D (1988b) Effect of climatic factors on pollination activity of alfalfa-pollinating subtropical bee Megachile nana Bingham and Megachile flavipes Spinola (Hymenoptera: Megachilidae). Acta Oecol Gen 9(4):371–378

Abrol D (1988c) Foraging range of subtropical bees, Megachile flavipes, Megachile nana (Hymenoptera: Megachilidae) and Apis florea (Hymenoptera: Apidae). J Indian Inst Sci 68(1/2):43–48

Abrol D (1989) Studies on ecology and behaviour of insect pollinators frequenting strawberry blossoms and their impact on yield and fruit quality. Trop Ecol 30:96–100

Abrol D (1990) Energetics of nectar production in some apple cultivars as a predictor of floral choice by honeybees. Trop Ecol 31:116–122

Abrol D (1992) Energetics of nectar production in some strawberry cultivars as a predictor of floral choice by honey bees. J Biosci Bangalore 17(1):41–44

Abrol DP (1998) Mites associated with bumble bee, *Bombus haemorrhoidalis* Smith (Hymenoptera: Apidae: Bombini). Indian Bee J 60(3):153–154

Abrol DP, Kapil RP (1986) Factors affecting pollination activity of *Megachile lanata* Lepel. Proceedings of the Indian Academy of Science. Anim Sci 95:757–769

Ahn SB, Kim IS, Cho WS, Choi KM (1989) Survey on the use of honeybee pollination of strawberries grown in plastic green house. Korean J Apic 4(1):1–8

Alford DV (1975) Bumblebees. Davis-Poynter, London

Anderson DL, Sedgley M, Short JRT, Allwood AJ (1982) Insect pollination of mango in Northern Australia. Aust J Agric Res 33:541–548

Arnon D, Kamer Y (2001) Comparison between the effectiveness of honeybee (*Apis mellifera*) and bumblebee (*Bombus terrestris*) as pollinators of greenhouse sweet pepper (*Capsicum annuum*). Am Bee J 141:447–448

Asada S, Ono M (1996) Crop pollination by Japanese bumblebees, *Bombus* spp. (Hymenoptera: Apidae): tomato foraging behaviour and pollination efficiency. Appl Entomol Zool 31:581–586

Atwal AS (ed) (1970) Insect pollinators of crops. Punjab Agricultural University Press, Ludhiana, 116 p

Batra SWT (1964a) Behavior of the social bee, Lasioglossum zephyrum, within the nest (Hymenoptera: Halictidae). Insectes Sociaux 11: 159–185. In: Proceedings of north central branch of the entomological society of America, Indianapolis, 19:74–75

Batra SWT (1964b) Organisms associated with Lasioglossum zephyrum (Hymenoptera: Halictidae). J Kans Entomol Soc 38:367–389

Batra SWT (1965) Behavior and ecology of the sweat bees (Halictidae) of India, Year book American Philosophical Society for 1965, pp 299–300

Batra SWT (1966a) Social behaviour and nests of some nomiine bees in India. Insectes Sociaux 13(3):145–153

Batra SWT (1966b) Nests and social behaviour of halictine bees of India. Indian J Entomol 28:375–393

Batra SWT (1966c) The life cycle and behavior of the primitively social bee, Lasioglossum zephyrum (Halictidae). Dissertation Abstracts 25(10), (Abstract)

Batra SWT (1968a) Crop pollination and the flower relationships of the wild bees of Ludhiana, India (Hymenoptera, Apoidea). J Kans Entomol Soc 40:167–177

Batra SWT (1968b) Behavior of some social and solitary halictine bees within their nests: a comparative study (Hymenoptera: Halictidae). J Kans Entomol Soc 41:120–133

Batra SWT (1970) Behavior of the alkali bee, Nomia melanderi, within the nest. Ann Entomol Soc Am 63(2):400–406

Batra SWT (1971) Nesting habits of Halictine bees (Halictidae: Hymenoptera). In: Atwal AS (ed) Insect pollinators of crops. Punjab Agricultural University Ludhiana, Punjab, pp 103–108

Batra SWT (1972) Some properties of the nest-building secretions of Nomia, Anthophora, Hylaeus and other bees. J Kans Entomol Soc 45:208–219

Batra SWT (1976a) Comparative efficiency of alfalfa pollination by Nomia melanderi, Megachile rotundata, Anthidium florentinum and Pithitis smaragdula (Hymenoptera: Apoidea). J Kans Entomol Soc 49(1):18–22

Batra SWT (1977) Bees of India (Apoidea), their behaviour, management and a key to the genera. Orient Insects 11(3/4):289–324

Batra SWT (1978a) Establishment of Osmia cornifrons in the United States. Coop Plant Pest Rep 3:166

Batra SWT (1978b) Aggression, territoriality, mating and nest aggregation of some solitary bees (Halictidae, Megachilidae, Colletidae, Anthophoridae). J Kans Entomol Soc 51(4):547–559

Batra S W T (1979a) Osmia cornifrons and Pithitis smaragdula, two Asian bees introduced in the eatern United States for pollination. In: Proceedings of the IVth international symposium on pollination, Maryland. Agriculture experiment station special miscellaneous publication, 1:307–312

Batra SWT (1979b) Insects associated with weeds of the northeastern United States: Quickweeds, Galinsoga celiata and G. parviflora (Compositae). Environ Entomol 8:1078–1082

Batra SWT (1979c) Insects associated with weeds in the northeastern United States. II. Cinquefoils, Potentilla norgegica and P. recta (Rosaceae). J New York Entomol Soc 87:216–222

Batra SWT (1980) Nests of the solitary bee, Anthophora antiope in Punjab, India. J Kans Entomol Soc 53:112–114

Batra SWT (1982) Hornfaced bees for efficient pollination of small farm orchards, pp 116–120. In: Kerr H, Knutson L (eds) Research for small farms. USDA Miscellaneous Publications No. 1422, 301 p

Batra SWT (1984) Solitary bees. Sci Am 259:120–127

Batra SWT (1991) Bees and pollination in south Asia. Ann Entomol 9(2):7–9

Batra SWT (1993) India's buzzy biodiversity of bees. Curr Sci 65(3):277–280

Batra SWT (1994a) Diversify with pollen bees. Am Bee J 134(9):591–593

Batra SWT (1994b) Shaggy fuzzyfoot bees. Pomona 27(3):57–59

Batra SWT (1994c) Anthophora pilipes villosula Sm (Hymenoptera: Anthophoridae), a manageable Japanese bee that visits blueberries and apples during cool, rainy, spring weather. Proc Entomol Soc Wash 96:98–119

Batra SWT (1995a) The evolution of "eusocial" and the originof "pollen bees". Md Nat 39(1–2):1–4

Batra SWT (1995b) Solitary bees for blueberry pollination. In: Proceedings of the 7th southeastern blueberry conference, Savannah, 1995, pp 69–72

Batra SWT (1995c) Bees and pollination in our changing environment. Apidologie 26:361–370

Batra SWT (1996) Biology of Apis laboriosa Smith, a pollinator of apples at high altitude in the Great Himalaya Range of Garhwal, India (Hymenoptera: Apidae). J Kans Entomol Soc 69:177–181

Batra SWT (1997a) Fruit pollinating bees of the Garhwal Himalaya, U. P., India. Acta Hortic 437:325–328

Batra SWT (1997b) Biology of Lasioglossum (Evylaeus) matieanense (Bluthgen) [Hymenoptera: Halictidae], the predominant pollinating bee in orchards at high altitude in the Great Himalaya of Garhwal, U. P., India. Proc Entomol Soc Wash 99:162–170

Batra SWT, Bohart GE (1970) Brood care in halictid bees. Science 168:875 [also in Science 170:651–652]

Batra SWT, Michener CD (1966) The nest and description of a new bee, Systropha punjabensis from India. J Kans Entomol Soc 39:650–658

Batra SWT, Norden BB (1996) Fatty food for their brood: how Anthophora bees make and provision their cells. Mem Entomol Soc Wash 17:36–44

Batra SWT, Sakagami SF, Maeta Y (1993) Behaviour of the Indian allodapine bee Braunsapis kaliago, a social parasite in nests of B. mixta. J Kans Entomol Soc 66(3):345–360

Beeson CFC (1938) Carpenter bees. Indian For 64:135–137

Bennett CF Jr (1964) Stingless beekeeping in western Mexico. Geogr Rev 51(1):85–92

Bennett CF Jr (1965) Beekeeping with stingless bees in Western Panama. Bee World 46:23–24

Bhalla OP, Verma AK, Dhaliwal HS (1983) Insect visitors of mustard bloom (Brassica campestris var. sarson), their number and foraging behaviour under mid-hill conditions. J Entomol Res 7(1):15–17

Bhaskar V, Gopinath K (1975) Nocturnal pollination in Antirrhinum majus by Xylocopa rufescens. J Bombay Nat Hist Soc 72(2):602–604

Bingham CT (1897) The fauna of British India, including Ceylon and Burma. In: Hymenoptera, vol I, Wasps and bees, Taylor & Francis, London, xxix + 579 pp, 4 pls (Reprinted (1975), To-day and Tomorrow's, New Delhi)

Bingham CT (1898a) On some species of Indian Hymenoptera. J Bombay Nat Hist Soc 12:115–130

Bingham CT (1898b) Note on Eumenes conica Fabr. and Megachile disjuncta Fabr. and their parasites, Chrysis fuscipennis Brulle and Parevaspis abdominalis Sm. J Bombay Nat Hist Soc 12:585–588

Bingham CT (1908) Notes on the aculeate Hymenoptera. Rec Indian Mus 2:347–368 [Apidae: P. 360–368]

Bohart EG (1952) Pollination on native insects. USDA Year Book Agric 2302:107–121

Bohart GE (1970) Commercial production and management of wild bees-A new entomological industry. Bull Entomol Soc Am 16(1):8–9

Bohart GE (1972) Management of wild bees for the pollination of crops. Ann Rev Entomol 17:287–312

Brian AD (1951) The pollen collected by bumblebees. J Anim Ecol 20:191–194

Brian AD (1957) Differences in the flowers visited by four species of bumblebees and their causes. J Anim Ecol 26:69–96

Calzoni GL, Speranza A (1996) Pear and plum pollination: honey bees, bumble bees or both? Acta Hortic 423:83–90

Cane JH (2001) Habitat fragmentation and native bees: a premature verdict? Conserv Ecol 5(1):3, http://www.consecol.org/vol5/iss1/art3

Chang-Whan K, Ito M (1987) On the bumble bee from the Korean Peninsula (Hymenoptera: Bombidae). Entomol Res Bull 13:1–42

Chaudhary JR, Jain KL (1978) Nesting and foraging behaviour of a mason bee, Megachile lanata (Megachilidae: Hymenoptera). Indian J Entomol 40(4):405–411

Dag A, Kamer YM (2001) Comparison between the effectiveness of honeybee (*Apis mellifera*) and bumblebee (*Bombus terrestris*) as pollinators of greenhouse sweet pepper (*Capsicum annuum*). Am Bee J 141:447–448

Danforth BN (1989) The evolution of hymenopteran wings: the importance of size. J Zool Proc Zool Soc Lond 218(2):247–276

Darwin C (1891). The effects of cross and self fertilisation in the vegetable kingdom, 3rd edn. John Murray, London

Dasgan HY, Özdogan AO, Kaftanoglu O, Abak K (2004) Effectiveness of bumblebee pollination in anti-frost heated tomato greenhouses in the Mediterranean Basin. Turk J Agric For 28:73–82

Dover C (1924) Some observations on the bionomics of Xylocopa aestuans Linnaeus (Apidae). Trans Entomol Soc Lond 73:144–149

Dukas R, Waser NM (1994) Categorization of food types enhances foraging performance of bumblebees. Anim Behav 48:1001–1006

Dutt GR (1912) Life histories of Indian insects (Hymenoptera). Mem Dep Agric India Entomol Ser 4:183–267

Eardley CD (1983) A taxonomic revision of the genus Xylocopa Latreille (Hymenop., Anthophoridae) in Southern Africa, vol 58. Entomological Memoir, Department of Agriculture, Pretoria, pp 1–67

Eijnde J, van den de Ruijter A, Steen van den J (1991) Method for rearing *Bumbus* terrestris continuously and the reproduction of bumble bees colonies for pollination purposes. Acta Hortic 288:154–158

Engel MS (2002) The honey bees of India, Hymenoptera: Apidae. J Bombay Nat Hist Soc 99(1):3–7

Ercan N, Onus AN (2003) The effects of bumblebees (*Bombus terrestris* L.) on fruit quality and yield of pepper (*Capsicum annuum* L.) grown in an unheated greenhouse, Isr. J Plant Sci 51:275–283

Fisher RM, Pomeroy N (1989) Pollination of greenhouse muskmelons by bumble bees (Hymenoptera, Apidae). J Econ Entomol 82:1061–1066

Free JB (1955) The collection of food by bumble bees. Insects Soc 2:303–311

Free JB (1963) The flower constancy of honeybees. J Anim Ecol 32:119–131

Free JB (1968) The foraging behaviour of honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.) on blackcurrant (*Ribes nigrum*), raspberry (*Rubus idaeus*) and strawberry (*Fragaria x Ananassa*) flowers. J Appl Ecol 5:157–168

Free JB (1970a) The flower constancy of bumblebees. J Anim Ecol 39:395–402

Free JB (1970b) Insect pollination of crops. Academic, London/New York

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London/San Diego

Free JB, Butler CG (1959) Bumblebees. The MacMillan Co., New York

Friese H (1923) Die europaischen Bienen (Apidae). Walter de Gruyter & Co., Berlin, 456 pp

Frison TH (1927) The fertilization and hibernation of queen bumblebees under controlled conditions (Bremidae: Hym.). J Econ Entomol 20:522–526

Gallai N, Salles JM, Settele J, Vaissiere BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68:810–821

González JM, Terán JB, Matthews RW (2004) Review of the biology of *Melittobia acasta* (Walker) (Hymenoptera: Eulophidae) and additions on development and sex ratio of the species. Caribb J Sci 40(1):52–61

Goodell K, Thomson JD (1997) Comparisons of pollen removal and deposition by honey bees and bumblebees visiting apple. Acta Hortic 437:103–107

Goulson D (2003a) Effects of introduced bees on native ecosystems. Annu Rev Ecol Evol Syst 34:1–26

Goyal NP, Gupta JK (1994) Development of beekeeping with Apis mellifera L. in India: present status and future scope. Indian Bee J 56(3/4):127–131

Green EE (1899) Sleeping habits of a bee, Crocisa ramose. Ent M Mag 35:214

Grewal JS, Sidhu AS (1978) Insect pollinators of some cucurbits in Punjab. Indian J Agric Sci 48:79–83

Grewal GS, AS Atwal, Kumar S, Kapil RP (1970b) Nesting behaviour of Andrena leaena Cam. 22 Int Beekeeping Congr 1969:422–424

Grewal GS, Atwal AS, Kumar S, Kapil RP (1970b) Some observations on the nest architecture of Colletes nursei (Cam.). Indian J Entomol 32:184–186

Griffin RP, Macfarlane RP (1990) Bumble bee rearing in New Zealand. In: 11th international congress IUSSI 1990, Bangalore

Griffiths D, Robberts EJ (1996) Bumble bees as pollinators of glasshouse crops. In: Matheson A (ed) Bumble bees for pleasure and profit. IBRA, Cardiff, pp 33–39

Gupta RK (1993) Taxonomic studies on the Megachilidae of north-western India. Reprinted 1999. Scientific Publishers, India. v+294 p., 1032 figs

Gupta RK (2003) An annotated catalogue of the bee species of the Indian region. URL: http://geocities.com/beesind2. [93 genera including 1284 species]

Gupta RK, Sharma SL (1995) Description of the nest and immature stages of Heriades tolawasensis Sharma and Gupta (Hymenoptera, Megachilidae, Osmini). Entomon 20(1):35–39

Gupta RK, Yadav S (2001) Apoidean species composition on Crotalaria juncea L., Cajanus cajan (L.), Helianthus annus L., and Brassica compestris L. var sarson Prain in eastern Rajasthan, India (Hymenoptera). Opuscula zoologica fluminensia 198:1–10

Gupta RK, Naval RK, Charan SK (2003) Nesting biology of the solitary bee, Megachile (Pseudomegachile) creusa Bingham (Hymenoptera, Megachilidae). Mellifera 3(5):11–18 (Turkish) and 43–50(English)

Harder LD (1983a) Flower handling efficiency of bumble bees: morphological aspects of probing time. Oecologia Berlin 57:274–280

Harder LD (1983b) Functional differences of the proboscides of short and long-tongued bees (Hymenoptera, Apoidea). Can J Zool 61:1580–1586

Heard TA (1999) The role of stingless bees in crop pollination. Annu Rev Entomol 44:183–206

Hedicke H (1938) †ber einige Apiden vom Hindu-kush. Deutsche Entomologische Zeitschrift 1938:186–196

Heinrich B (1976) The foraging specializations of individual bumblebees. Ecol Monogr 46:105–128

Heinrich B (1979) Majoring and minoring by foraging bumblebees *Bombus vagans*. Ecology 60:245–255

Hobbs GA, Nummi WO, Virostek JF (1962) Managing colonies of bumble bees for pollination purposes. Can Entomol 94(11):1121–1132

Holm SN (1966a) The utilization and management of bumble bees for red clover and alfalfa seed production. Annu Rev Entomol 11:155–182

Horne C (1868) Notes on the habits of some Indian hymenopterous insects. Proc Entomol Soc Lond 1868:xlix

Horne C (1870) Notes on the habits of some hymenopterous insects from the North-west Provinces of India. With an appendix, containing descriptions of some new species of Apidae and Vespidae collected by Mr. Horne: by Frederick Smith, of the British Museum. [Illustrated by plates from drawings by the author of the notes]. Trans Zool Soc Lond 7:161–196

Horne C (1872) Notes on the habits of some hymenopterous insects from the northwest provinces of India. Trans Zool Soc Lond 7:161–196

Howard A, Howard LC, Khan AR (1920) Studies in the pollination of Indian crops. Mem Dep Agric India Bot Ser 10(5):195–220

Inouye DW (1980) The effect of proboscis and corolla tube lengths on pattern and rates of flower visitation by bumblebees. Oecologia Berlin 45:197–201

Intoppa F, De Pace F (1983) Bumble bees of central Italy and their pollination activity. First contribution. Estratto da Redia 66:389–399

Ito M (1985) Additional notes on the bumble bee fauna of North Korea (Hymenoptera: Apidae). Folia Entomol Hung 66(1):5–22

Iwata K (1964) Egg giantism in subsocial Hymenoptera with ethological discussions on tropical bamboo carpenter bees. Nat Life southeast Asia 3:399–431

Jackson A (1993) Natural route to pollination. Grower 42(4):25–26

Jain KL (1993) Anthesis and nectar secretion pattern in alfalfa (*Medicago sativa* L.). Indian Bee J 55:37–41

Javorek SK, MacKenzie KE, Vander Kloet SP (2002) Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). Ann Entomol Soc Am 95:345–351

Kakutani T, Inoue T, Tezuka T, Maeta Y (1993) Pollination of strawberry by the stingless bee, *Trigona minangkabau*, and the honey bee, *Apis mellifera*: an experimental study of fertilization efficiency. Res Popul Ecol 35:95–111

Kannan K (1925) Xylocopa and Hyperechia in India. Proc Entomol Soc Lond 1925:12–13

Kapil RP (1970) Role of honeybees in agriculture. Indian Bee J 32:53–57

Kapil RP, Dhaliwal JS (1968a) Defense of nest by the female of Xylocopa fenestrata Fab. (Xylocopinae, Hymenoptera). Insectes Sociaux 15(4):419–422

Kapil RP, Dhaliwal JS (1968b) Biology of Xylocopa species. I. Seasonal activity, nesting behaviour and life cycle. J Res Punjab Agric Univ 5(3):406–419

Kapil RP, Dhaliwal JS (1969) Biology of Xylocopa species. II. Field activities, flight range and trials on transportation of nests. J Res Punjab Agric Univ 6(1):262–271

Kapil RP, Kumar S (1969) Biology of Ceratina Binghami Cockerell (Ceratinini: Hymenoptera). J Res Punjab Agric Univ 6(2):359–371

Kapil RP, Jain KL (1979) Management of megachild bees for the pollination of alfalfa. In: Proceedings pollination ecology and applied palynology, Department of Zoology, Haryana Agricultural University, Hisar, 1979, pp 21–30

Kapil RP, Jain KL (1980) Biology and utilization of insect pollinators for crop production. Final Technical report PL-480 Project, Haryana Agricultural University, Hisar, p 120

Kapil RP, Grewal GS, Atwal AS (1970a) Biology and nesting behaviour of Megachile lanata Fabricius. In: 22nd international beekeeping congress, Munich, 1969:449–458

Kapil RP, Grewal GS, Kumar S, Atwal AS (1970b) Insect pollinators and their comparative abundance. In: Atwal AS (ed) Insect pollinators of crops. Final report of the PL-480 Project No. A7-Ent-19. At P. A. U. Ludhiana

Kapil RP, Grewal GS, Kumar S, Atwal AS (1971) Insect pollinators of rape seed and mustard. Indian J Entomol 33(1):61–66

Kapil RP, Grewal GS, Kumar S, Atwal AS (1974) Insect pollinators of alfalfa, *Medicago sativa* L. Indian J Entomol 36(3):214–220

Kapil RP, Chaudhary JP, Jain KL (1975) Biology and utilization of insect pollinators for crop production. SEC annual report, Department Zoology Haryana Agricultural University, Hissar 50 p

Kapil RP, Jain KL, Chaudhary JP (1977) Adaptive behaviour of megachild bees to alfalfa. In: XXVI international congress apiculture, Australia, 1977, pp 403–413

Kapila RK, Singh B, Sharma JK, Lata S, Thakur SP (2002) Effect of insect pollinators on seed yield and its quality in radish (Raphanus sativus L.). Seed Res 30(1):142–145

Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA et al (2007) Importance of pollinators in changing landscapes for world crops. Proc R Soc Lon B Biol Sci 274:303–313

Kraai A (1958) Bijen en hommels bij het veredelingswerk, Meded. Dir Tuinb 21:291–297

Kukuk PF (1980) Diurnal activity of a primitively social bee, Lassioglossum zephyrum within the nest. J Kans Entomol Soc 53(1):149–156

Kumar M, Singh R (2001) Preference for competing flora with sunflower for foraging of honeybees. J Appl Biol 11(1/2):70–71

Kumar J, Rao VK, Gupta JK (1988) Pollination efficiency of bees visiting cauliflower crops. In: Proceedings of the 4th international apiculture in tropical climates, Cairo, p 17

Kumar J, Mishra RC, Gupta JK (1993) Foraging activity and abundance of insect visitors to chicory (Cichorium intybus L.) in mid-hills of Himachal Pradesh, India. Indian Bee J 55(3/4):31–36

Kumar J, Rao KVK, Gupta JK (1994) Pollination efficiency of bees visiting blossoms of Brassica campestris L. var. toria in mid-hills of Himachal Pradesh, India. Indian Bee J 56(3/4):202–206

Kumar M, Chand H, Singh R, Ali MS (2002) Effect of different modes of honeybee pollination on oil content in seeds of sunflower (Helianthus annus L.). J Entomol Res 26(3):219–221

Kwon YJ, Saeed S (2003) Effect of temperature on the foraging activity of *Bombus terrestris* L. (Hymenoptera: Apidae) on greenhouse hot pepper (*Capsicum annuum* L.). Appl Entomol Zool 38:275–280

Latif A, Qayyum HA, Ul-Haq M (1960) Role of Apis indica in the pollination of toria and sarson. Bee World 4(11–12):283–286

Latreille PA (1802) Histoire Naturelle des fourmis, et recueil de mémoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes. Crapelet, Paris, xvi + 445 pp

Laverty TM (1980) Bumble bee foraging: floral complexity and learning. Can J Zool 58: 1324–1335

Laverty TM (1993) Costs to foraging bumblebees of switching plant species. Can J Zool 72:43–47

Lepeletier de Saint-Fargeau ALM, Serville A (1828) [Articles in] In: M Diderot, PA Latreille et al (eds) Encyclopédie Méthodique, Histoire Naturelle, Insectes, Paris, 10:345–832

Levin MD (1983) Value of bee pollination in US agriculture. Bull Entomol Soc Am 29:50–51

Lieftinck MA (1939) Uit het leven van Lithurgus atratus, een Indisch houtbijtje. De Tropische Naturae 28:193–201

Lieftinck MA (1955) The carpenter-bees (Xylocopa Latr.) of the Lesser Sunda Islands and Tanimbar (Hymenoptera, Apoidea). Verhandlungen der Naturforschenden Gesellschaft in Basel 66:5–32

Lieftinck MA (1957) Revision of the carpenter-bees (Xylocopa Latr., subgenus Maiella Michener) of the Papuan region (Hymenoptera, Apoidea). Nova Guinea (NS) 8:325–376

Lieftinck MA (1962) Revision of the Indo-Australian species of the genus Thyreus Panzer (=Crocisa Jurine) (Hym., Apoidea, Anthophoridae) Part 3. Oriental and Australian species, vol 53. Zoologische Verhandelingen, Leiden, 1–212, plates 1–3

Lieftinck MA (1964) The identity of Apis aestuans Linnaeus (Hymenoptera, Apoidea) and related Old World carpenter bees (Xylocopa Latr.). Tidjschrift voor Entomologie 107:137–158

Lieftinck MA (1972) Further studies on old world melectine bees, with stray notes on their distribution and host relationships. Tijdschrift voor Entomologie 115(7):253–324, 2 plates

Lieftinck MA (1974) A review of the central and east Asiatic Habropoda F. Smith, with Habrophorula, a new genus from China. Tijdschrift voor Entomologie 117(5):157–224

Lieten F (1993) Misvormde vruchten door overbevlieging. Groenten en Fruit/Vollegrondsgroenten 14(9 April):11

Linsley EG (1958) The ecology of solitary bees. Hilgardia 27:543–599

Ma Tsing-chao (1938) The Indian species of the genus Xylocopa Latr. (Hymenoptera). Rec Indian Mus 40:265–329

Maccagnani B, Ladurner E, Santi F, Burgio G (2003) Osmia cornuta (Hymenoptera, Megachilidae) as a pollinator of pear (Pyrus communis): fruit- and seed-set. Apidologie 34(3):207–216

MacFarlane RP, Griffin RP, Read PEC (1983) Bumble bee management options to improve 'grasslands pawera' red clover seed yields. Proc N Z Grassl Assoc 44:47–53

MacFarlane J, Lipa J, Liu HJ (1990) Year around production of bumble bee colonies for crop pollination. Bee World 71:54–56

MacFarlane RP, Roderick P, Griffin RP (1994a) Detection of *Melittobia acasta* (Eulophidae) in bumble bee (*Bombus*, Apidae) colonies. Melanderia 50:28–33

Macfarlane RP, Patten KD, Royce LA, Watt BKW, Mayer DF (1994b) Management potential of sixteen North American Bumble bee species. Melanderia 50:1–12

MacKenzie KE (1994) The foraging behaviour of honey bees (*Apis mellifera* L) and bumble bees (*Bombus* spp.) on cranberry (*Vaccinium macrocarpon* Ait). Apidologie 25:375–383

Maeta Y (1978) Comparative studies on the biology of the bees of the genus Osmia of Japan, with special reference to their managements for pollination of crops. Bull Tohoku Nat Agric Exp Stat no 57:1–221 + errata 1–7 [In Japanese, English summary]

Mah YI, Lee MY, Bilinski M (2001) Some characteristics of Korean indigenous bumble bee species (Hymenoptera; *Bombus* spp.) under laboratory conditions. Acta Hortic 561:287–291

Malyshev SI (1923) The nesting habits of Melitta leporina Pz. Izvestiya Leningradskovo nauchnovo Instituta imeni P. F. Leshaft [Bulletin de l'Institut Leshaft] 6:1–7 [In Russian, English summary]

Malyshev SI (1925) The nesting habits of Anthophora Latr Trav Soc Nat Leningrad, Se Zool Physiol 55:137–183

Malyshev SI (1930) Nistgewohnheiten der Steinbienen Lithurgus Latr. Zeitschrift für Morphologie und Ökologie der Tiere 19:116–134

Malyshev SI (1936) The nesting habits of solitary bees. A comparative study. Eos, Madrid 11:201–309, pls III–XV

Mani MS (1962) Introduction to high altitude entomology. Methuen and Co., London, 305

Manning A (1956) Some aspects of the foraging behaviour of bumblebees. Behaviour 9:164–201

Maxwell-Lefroy H, Howlett FM (1909) Indian insect life. The Thacker, Spink and Co., Calcutta/Simla, 786 p

Mayer DF, Johansen CA, Burgett M (1986) Bee pollination of tree fruits. Publication, Pacific Northwest Cooperative Extension, No PNW 0282

McGinley RJ, Rozen JG Jr (1987) Nesting biology, immature stages and phylogenetic placement of the Palaearctic bee Pararhophites (Hymenoptera: Apoidea). Am Mus Novit 2903:1–21

McGregor SE (1976) Insect pollination of cultivated crop plants, vol 496, Agricultural handbook. U.S. Government Printing Office, Washington, DC

Meisels S, Chiasson H (1997) Effectiveness of *Bombus impatiens* Cr. as pollinators of greenhouse sweet peppers (*Capsicum annuum* L.). Acta Hortic 437:425–429

Michener CD (1965) A classification of the bees of the Australian and South Pacific Regions. Bull Am Mus Nat Hist 130:1–362

Michener CD (1974a) The social behavior of the bees: a comparative study. Belknap, Cambridge, MA

Michener CD (1974b) The social behavior of the bees. Harvard University Press, Cambridge, MA, 404 pp

Michener CD (2000) The bees of the world. The John Hopkins University Press, Baltimore/London, 913 pp

Minckley RL (1994) Comparative morphology of the mesosomal 'gland' in male large carpenter bees. Biol J Linn Soc Lond 53:291–308

Minckley RL (1998) A cladistic analysis and classification of the subgenera and genera of the large carpenter bees, Tribe Xylocopini (Hymenoptera: Apidae). Scientific Papers, Natural History Museum, University of Kansas No. 9:1–47

Minderhoud A (1950) Het gebruik van bijen en hommels voor bestuiving in afgesloten ruimten. Meded Dir Tuinb 17:32–39

Mishra RC, Dogra GS, Gupta PR (1976) Some observations on insect pollinators of apple. Indian Bee J 38(1–4):20–22

Mohammad A (1935) Pollination studies in toria (Brassica napus L. var. dichotoma Prain) and sarson (Brassica campestris L. var. sarson Prain). Indian J Agric Sci 5:125–154

Ono M, Mitsuhata M, Sasaki M (1994) Use of introduced *Bombus terrestris* worker helpers for rapid development of Japanese native B. hypocrite colonies (Hymenoptera:Apidae) Appl Entomol Zool 29:413–419

Pagden HT (1934) Biological notes on some Malayan aculeate Hymenoptera III. J Fed Malay States Mus 17(3):487–492

Pagden HT (1957) Notes on communal flight activities of stingless bees. Malay Nat J 12:15–19

Parker FD, Batra SWT, Tepedino VJ (1987) New pollinators for our crops. Agric Zool Rev 2:279–304

Paydas S, Eti S, Kaftanoglu O, Yasa E, Derin K (2000a) Effects of pollination of strawberries grown in plastic greenhouses by honeybees and bumblebees on the yield and quality of the fruits. Acta Hortic 513:443–451

Paydas S, Eti S, Sevinc S, Yasa E, Derin K, Kaska N, Kaftanoglu O (2000b) Effects of different pollinators to the yield and quality of strawberries. Acta Hortic 522:209–215

Perkins RCL (1899) On a special acarid chamber formed win the basal abdominal segment of the genus Koptorthosoma (Xylocopinae). Ent Mon Mag 35:37–39

Piel O (1930) Nidification de Megachile monticola Smith, chez Xylocopa rufipes Sm., pictifrons Sm. Notes d'Entomologie Chinoise, Musée Heude, fasc 5:108, 2 pls

Pinzauti M (1991) Possibilità di allevamento controllato di *Osmia rufa* L. e *Osmia cornuta* Latr. (Hymenoptera: Megachilidae) per l'impollinazione dei frutteti 1: nota preliminare. In: Proceedings of the XVI national Italian congress on entomology, Martina Franca, pp 537–544

Plowright RC, Jay SC (1966) Rearing bumble bee colonies in captivity. J Apic Res 5:155–165

Pomeroy N, Fisher RM (2002) Pollination of kiwifruit (*Actinidia deliciosa*) by bumble bees (*Bombus terrestris*): effects of bee density and patterns of flower visitation. N Z Entomol 25:41–49

Porporato MM, Pinna A, Marletto MF (1995) Pollination of sweet pepper in greenhouse by *Bombus terrestris* (L.) and *Apis mellifera* L. Apic Mod 86:99–112

Poulsen MH (1973) The frequency and foraging behaviour of honeybees and bumblebees on field beans in Denmark. J Apic Res 12:75–80

Pouvreau A (2004) Les insectes pollinisateurs, OPIE, Office pour les insectes et leur environnement. Delachaux et Niestlé, Paris, 189 p

Prys-Jones OE, Corbet SA (1987) Bumble bees. Cambridge University Press, Cambridge, MA

Prys-Jones O, Corbet SA (1991) Bumble bees. Cambridge University Press, New York, 86 p

Ptacek V (1985) Testing three methods of rearing bumble bees. Sbornik Vedeckych Praci Vyzkumny A Slechtitelsky Ustav Picninarsky v Troubsko u Brna 9:59–67

Ptacek V (1991) Trials to rear bumble bees. Acta Hortic 288:144–148

Qayyum HA, Ahmad N (1967) Biology of Apis dorsata. Pak J Sci 19(3):109–113

Rahman KA (1940) Insect pollinators of toria (Brassica napus Linn. var. dichtoma Prain), and sarson (Brassica campestris Linn.var. sarson Prain) at Lyallpur. Indian J Agric Sci 10:422–447

Rai KM, Gupta BP (1983) Role of honey bees and other insects as pollinators in apple and pear. Indian Bee J 45(2/3):56–57

Real L (ed) (1983) Pollination biology. Academic, New York

Real LA, Rathke BJ (1991) Individual variation in nectar production and its effect on fitness in Kalrnin latifolia. Ecology 72:149–155

Renner SS (1996) Effects of habitat fragmentation on plant pollinator interactions in the tropics. In: Newbery DM, Prins HT, Brown ND (eds) Dynamics of tropical communities. Blackwell Scientific, Cambridge, UK, pp 339–361

Reyes SG, Michener CD (1990) Observations on a parasitic allodapine bee and its hosts in Java and Malaysia. Trop Zool 3:139–149

Reyes SG, Sakagami SF (1990) A new socially parasitic Braunsapis from India with notes on the synonymy of Braunsapis mixta (Hymenoptera: Xylocopinae: Allodapini). J Kans Entomol Soc 63(3):458–461

Richards KW (1987) Alfalfa leafcutter bee management in Canada. Bee World 68(168):178

Richards KW (1993) Non-Apis bees as crop pollinators. Revue Suisse de Zoologie 100(4):807–822

Robinson WS, Nowogrodski R, Morse RA (1989) Pollination parameters. Glean Bee Cult 117:148–152

Roig-Alsina A, Michener CD (1993) Studies of the phylogeny and classification of long-tongued bees. University of Kansas Science Bulletin 55:124–162

Roseler PF (1977) Rearing bumble bee colonies. In: Proceedings of the VIIIth international congress IUSSI, Wageningen

Roseler PF (1985) A technique for year-round rearing of *Bombus terrestris* (Apidae, Bombini) colonies in captivity. Apidologie 16:165–170

Roubik DW (1995a) Stingless bee colonies for pollination. In: Roubik DW (ed) Pollination of cultivated plants in the tropics, vol 118, FAO agricultural service bulletin. FAO, Rome, pp 150–154

Roubik DW (1995b) Pollination of cultivated plants in the tropics. FAO Agric Ser Bull 118: 1–196

Roubik DW (2001) Ups and downs in pollinator populations: when is there a decline? Conserv Ecol 5(1):2 [Online] URL: http://www.consecol.org/Vol5/iss1/art2

Roubik DW, Sakagami SF, Kudo I (1985) A note on distribution and nesting of the Himalayan honeybee Apis laboriosa Smith. J Kans Entomol Soc 58(4):746–749

Ruz L, Herrera R (2001) Preliminary observations on foraging activities of *Bombus dahlbomii* and *Bombus terrestris* (Hym.: Apidae) on native and non-native vegetation in Chile. Acta Hortic 561:165–169

Sakagami SF (1960) Ethobiological peculiarities of the primitive social bees, Allodape Lepeltier and allied genera. Insectes Sociaux 7:231–249

Sakagami SF (1966) Comparative ethology of Apidae. Soc Syst Zool circ 35:1–6 [In Japanese]

Sakagami SF, Ebmer PAW (1987) Taxonomic notes on oriental halictine bees of the genus Halictus (subgenus Seladonia). Linzer Biologische Beiträge 19:301–357

Sakagami SF, Michener CD (1962) The nest architecture of the sweatbees (Halictinae): a comparative study of behavior. University of Kansas Press, Lawrence, viii + 135 p

Sakagami SF, Michener CD (1963) Nest architecture in halictine bees. Symposia Genetica et Biologica Italica 12:266–274

Sakagami SF, Wain FL (1966) Halictus latisignatus Cameron: a polymorphic Indian halictine bee with caste differentiation. J Bombay Nat Hist Soc 63:57–73

Sakagami SF, Yoshikawa K (1961) Bees of Xylocopinae and Apinae collected by the Osaka City University Expedition to Southeast Asia 1957–58, with some biological notes. Nat Life Southeast Asia 1:409–444

Sakagami SF, Ebmer PAW, Tadauchi O (1996) The halictine bees of Sri Lanka and the vicinity, III. Sudila (Hymenoptera, Halictidae) Part I. Esakia 36:143–189

Sampson BJ, Spiers JM (2002) Evaluating bumblebees as pollinators of 'misty' southern highbush blueberry growing inside plastic tunnels. Acta Hortic 574:53–61

Sandhu AS, Sidhu BS, Mehdiratta PD (1976) Note on the use of Pithitis smaragdula (Fab.) as a pollinator for the breeding of lucerne. Indian J Agric Sci 46(7):347–349

Schwarz HF (1939) The Indo-Malayan species of Trigona. Bull Am Mus Nat Hist 76:83–141

Sharma HK, Gupta JK (1993) Diversity and density of bee flora of Solan region of Himachal Pradesh (India). Indian Bee J 55(1/2):9–20

Sharma HK, Gupta JK (2001) Impact of bee pollination on sustainable production in apple orchards. Pest Manag Econ Zool 9(1):45–48

Sharma V, Thakur ML (1999) Morphometric characterization of giant honey bee Apis dorsata Fab. (Hymenoptera: Apidae) from Doon Valley. Ann For 7(1):125–135

Sharma HK, Gupta JK, Rana BS (2000) Diurnal activity of Apis cerana F. and A. mellifera L. on different flora during spring and honey flow period. Pest Manage Econ Zool 8(2):151–154

Shipp JL, Whitfield GH, Papadopoulos AP (1994) Effectiveness of the bumble bee, *Bombus impatiens* Cr. (Hymenoptera: Apidae), as pollinator of greenhouse sweet pepper. Sci Hortic 57:29–39

Sihag RC (1990) Behaviour and ecology of the sub-tropical carpenter bee. *Xylocopa fenestrata* F.2 Host plant association. Indian Bee J 52(1–4):38–40

Sihag RC (1991) Methods of domiciling and bee keeping with alfalfa pollinating sub-tropical megachilid bees. Korean J Apic 6(2):81–88

Sihag RC (1992) Utilization of waste stems of sarkandas and castor as nesting tunnels for culturing/keeping wild bee pollinators of some crops. Bioresour Technol 42:159–162

Sneep J (1952) Selection and breeding of some Brassica plants. In: Proceedings of the 13th international horticultural congress, pp 422–426

Stanghellini MS, Ambrose JT, Schultheis JR (1997) The effects of honey bee and bumble bee pollination on fruit set and abortion of cucumber and watermelon. Am Bee J 137:386–391

Stanghellini MS, Ambrose JT, Schultheis JR (1998a) Seed production in watermelon: a comparison between two commercially available pollinators. Hortic Sci 33:28–30

Stanghellini MS, Ambrose JT, Schultheis JR (1998b) Using commercial bumble bee colonies as backup pollinators for honey bees to produce cucumbers and watermelon. Hortic Tech 8:590–594

Stanghellini MS, Ambrose JT, Schultheis JR (2002) Diurnal activity, floral visitation and pollen deposition by honey bees and bumble bees on field-grown cucumber and watermelon. J Apic Res 40:27–34

Stephen WP, Every RW (1970) Nesting media for the propagation of leaf cutter bee. Oregon State University, Corvallis [Cooperative Extension with US Department of Agriculture] Fact Sheets No. 175:1–2

Stephen WP, Bohart GE, Torchio PF (1969) Biology and external morphology of bees. Agricultural Expriment Station. Oregon State University, Corvallis, 140 p

Strickler K (1997) Seed and bee yields as a function of forager populations: Alfalfa pollination as a model system. J Kansas Entomol Soc 69(4):Suppl (1996):201–215

Strickler K (1999) Impact of flower standing crop and pollinator movement on alfalfa seed yield. Environ Entomol 28(6):1067–1076

Strickler K, Freitas S (1999) Interactions between floral resources and bees in commercial alfalfa seed fields. Environ Entomol 28:178–187

Stubbs CS, Drummond FA (2001) *Bombus impatiens* (Hymenoptera: Apidae): an alternative to *Apis mellifera* (Hymenoptera: Apidae) for lowbush blueberry pollination. J Econ Entomol 94:609–616

Teras I (1985) Food plants and flower visits of bumble bees (Bombus: Hymenoptera: Apidae) in Southern Finland. Acta Zoologica Fennica 179:1–120

Thakar CV, Topani KV (1961) Nesting behaviour of Indian honeybees I. Differentiation of worker, queen and drone cells in the combs of Apis dorsata Fab. Bee World 42:61–62

Thakar CV, Topani KV (1962) Nesting behaviour of Indian honeybees II. Nesting habits and cell differentiation in Apis florea Fab. Indian Bee J 24:27–31

Thomson JD, Goodell K (2001) Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. J Appl Ecol 38:1032–1044

Torchio PF (1987) Use of non-honey bee species as pollinators of crops. Proc Entomol Soc Ont 118:111–124

Torchio PF (1990) *Osmia rubifloris*, a nature developed as a commercially managed pollinator of blueberry (Hymenoptera: Megachilidae). J Kans Entomol Soc 63:427–436

Torchio PF, Asensio E (1985) The introduction of the European bee, Osmia cornuta Latr. into the US as a potential pollinator of orchard crops and a comparison of its manageability with *Osmia lignaria propingua* Cresson. J Kans Entomol Soc 58(1):42–52

Van Heemert C, de Ruijter A, Van EJ, Vander Steen J (1990) Year round production of bumble bee colonies for crop pollination. Bee World 71:54–56

van Ravestijn W, de Bruijn J (1991) Belang bestuiving door insekt blijft onduidelijk. Groenten en Fruit 51:18–19 (13 December)

van Ravestijn W, Kraemer C (1991) Hommel doet het goed op mini watermeloen. Groenten en Fruit 46:18–19 (15 November)

van Ravestijn W, Nederpel L (1988) Trostrillers in België aan de kant: hommels doen het werk. Groenten en Fruit 6:38–41 (12 Februari)

van Ravestijin W, Sande J (1991) Use of bumblebees for the pollination of glasshouse tomatoes. Acta Hortic 288:342–345

Velthuis HHW, van Doorn A (2006) A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. Apidologie 37:421–451\

Vleugel DA (1961) Ueber die Zahl der Individuen in der Nestern der halbsozialen Biene Halictus calceatus Scop. und Verwandten in der ersten Generation. In: 11th international congress entomology, 1:586–588

Vogt FD (1986) Thermoregulation in bumblebee colonies. I. Thermoregulatory versus brood-maintenance behaviors during acute changes in ambient temperature. Physiol Zool 59:5 5–59

von Paarmann W (1977) Untersuchungen zur Bedeutung van Hummeln (Bombus spp.) fur die Bestaubung bluhender Obstbaume. Zeitschrift fur angewandte Entomologie 84:164–178

Wain FL (1968) Notes on the biology of a new bee, Andrena bellidoides LaBerge (Hymenoptera: Apoidea) from western India. Entomologist (London) May:101–104

Waser NM (1986) Flower constancy, definition, cause and measurement. Am Nat 127:593–603

Whidden TL (1996) The fidelity of commercially reared colonies of *Bombus impatiens* Cresson (Hymenoptera: Apidae) to lowbush blueberry in Southern New Brunswick. Can Entomol 128:957–958

Wijesekara A (2001) An annotated list of bees (Hymenoptera: Apoidea: Apiformis) of Sri Lanka. Tijdschrift voor Entomologie 144:145–158

Williams PH (1991) The bumble bees of the Kashmir, Himalaya (Hymenoptera: Apidae, Bombini). Bull Br Mus Nat Hist Entomol 60:1–204

Williams PH (1994) Phylogenetic relationships among bumble bees (Bombus Latr.): a reappraisal of morphological evidence. Syst Entomol 19:327–344

Williams PH (1998) An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). Bull Nat Hist Mus [Lond] (Entomol) 67:79–152

Williams IH, Simpkins JR, Martin AP (1991) Effect of insect pollination on seed production in linseed (Linum usitatissimum). J Agric Sci 117(1):75–79

Willmer PG, Bataw AAM, Hughes JP (1994) The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecol Entomol 19:271–284

Yeninar H, Kaftanoglu O (1997) Colony development of Anatolian bumblebees (*Bombus terrestris*) under laboratory conditions. Acta Hortic 437:277–282

Zaitoun SA, Mazary S, Schindler M, Wittmann D (2006) Diversity of bees (Hymenoptera, Apiformes) in extensive orchards in the highlands of Jordan. Arxius de Miscel·lània Zoològica 4(2006):42–48

Zaleski A (1956) Lucerne investigation. II. Pollination and seed setting in Lucerne strains. J Agric Sci 48:236–244

Chapter 7
Value of Bee Pollination

Abstract This chapter summarizes how agricultural production and bees are inter-dependent. Honey bees are the most commonly used agricultural pollinators in the world, but are threatened by an increasing number of hive pests. In addition, not all crops are well pollinated by honey bees (e.g., tomatoes, alfalfa seed, and crops grown in greenhouses and under row covers). Fortunately, the world holds a huge diversity of bee species, although only a few of these are managed specifically as crop pollinators. Wild bees provide pollination services that often go unnoticed, yet are critical to the success of some forms of agriculture. The impact that bees have on our food production systems should serve as a reminder to our dependence, in general, on the ecosystems around us.

7.1 Introduction

Pollination as a biotic process has both commercial and ecological value. Wind-pollinated crops and tuber species represent the major source of energy in the human diet (FAO 2005), but insect-pollinated crops are critical for the supply of vegetable proteins (soybean, oil palm, rape seed, beans, peas), dietary fibres (vegetables), vitamin A and C (fruits and vegetables) and to provide for a balanced and varied diet. There is a still another category for example 'alfalfa, clovers lespedeza' which make a part of the diet of domestic animals as green fodder or hay and ultimately recycled to contribute indirectly to our diet as milk and its products, beef, pork, poultry and lamb.

The vital role honeybees play in enhancing the productivity levels of different crops such as fruits and nuts, vegetables and pulses, oil and forage crops has often been underestimated especially in developing countries all over the world. The economic returns of increased crop production through cross-pollination by honeybees are difficult to quantify yet these far outweigh direct values of honeybees as producers of honey and other hive products. In the context of agriculture, pollination provides a wide range of benefits to a broad diversity of commodities across the world. In some

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cases, production of the commodity itself results directly from the act of pollination (for example, fruit production). Throughout the world over, three thousand plant species are directly used as food either as seed-beans, peas and soyabeans; as fruits – apples, pears, almonds, cherries, tomatoes, egg plant and score of others as seeds and fruits – flax, coconuts, cotton, oil palm, olives, pea nuts, mustard and sunflower serve as source for edible oils.

7.2 Indirect Impacts of Pollination

In other cases, although pollination does not result in production of the commodity itself, the process contributes to crop propagation (for example, production of seeds used to grow a root crop such as carrots) or quality (for example, size of tomatoes has been linked to repeated pollination). There are indirect benefits as well, through food-chain relationships. Alfalfa seed, a bee-pollinated crop with an annual value of $109 million (direct effect), is used to produce hay for livestock forage that is valued at $4.6 billion per year (indirect effect) (Morse and Calderone 2000). Although these indirect effects tend to exaggerate the economic value of pollination, they have been used in several widely cited studies (Tables 7.1 and 7.2). Productivity can simply not include what is obtained as a food through plants and animals; it involves a system which needs be energized from time to time, either naturally or by man's efforts. Constant enrichment of soil nutritionally by some leguminous crops through nitrogen fixation is an example of a basic structure in productivity. Obviously pollination makes a critical junction not less important than other coaxial junctions and perhaps without which even the basic system may break down. On this functional analogy, it has been estimated that about one third of our total diet is dependent directly or indirectly upon crops, primarily pollinated by insects. Their role in maintaining ecological relationships has further been established in situations where absence of insect pollination has resulted in drastic reduction of many soil holding and soil enriching plants. Evidently, need for insect pollination has made the bees a vital component in crop production technologies and sustainable development of agriculture.

The annual value of honey bee pollination to U.S. agriculture has been variously estimated at $150 million (Rucker et al. 2005), $1.6–5.7 billion (Southwick and Southwick 1992), $9 billion (Robinson et al. 1989a, b), $14.6 billion (Morse and Calderone 2000), and $18.9 billion (Levin 1983). The annual benefit of honey bee pollination in Canada has been estimated at $443 million by Scott-Dupree and colleagues (1995). Values reported by Morse and Calderone (2000) and by Levin (1983) include indirect benefits of the honey bee pollination required for seed production in alfalfa hay, asparagus, broccoli, carrot, cauliflower, celery, onion, and sugar beet. Levin (1983) included 10% of the value of cattle and dairy production that he attributed to alfalfa hay whose seed requires bee pollination. Attributing the full market value of such indirect effects to pollination exaggerates the economic value of pollination services, because indirect products like alfalfa hay or cattle require many production inputs besides alfalfa seed. Even the alfalfa seed made possible by pollination requires that farmers provide other costly production inputs.

Table 7.1 Value of U.S. agricultural production attributable to honey bee pollination: comparison of studies

Study	Reference year	Total value ($ billion)	Direct crop value ($ billion)	Indirect crop value[a] ($ billion)	Animal value ($ billion)	Notes
Levin (1983)	1980	19.0	5.9	6.0	7.2	Author attributes 10% of cattle value to bees via alfalfa hay
Robinson et al. (1989a, b)	1985	9.7	6.1	3.6	0	
Southwick and Southwick (1992)[b]	1986	5.7	5.7	0	0	Value based on price elasticity of supply change
Morse and Calderone (2000)	1996–1998	14.6	7.8	6.7	0	
	2004	0.15	0.15	0	0	Value is pollination fees paid

[a] Crops that receive indirect benefits include alfalfa hay, asparagus, broccoli, carrot, cauliflower, celery, onion, and sugar beet

[b] Estimate for no replacement of bees; no price effects

Table 7.2 Estimated value of the honey bee to U.S. crop production, by major crop category, 2000 estimates

Crop category (ranked by share of honey bee pollinator value)	Dependence on insect pollination (%)	Proportion of pollinators that are honey bees (%)	Value attributed to honey bees ($ millions)
Alfalfa, hay and seed	100	60	4,654.2
Apples	100	90	1,352.3
Almonds	100	100	959.2
Citrus	20–80	10–90	834.1
Cotton (lint and seed)	20	80	857.7
Soybeans	10	50	824.5
Onions	100	90	661.7
Broccoli	100	90	435.4
Carrots	100	90	420.7
Sunflower	100	90	409.9
Cantaloupe/honeydew	80	90	350.9
Other fruits and nutsc	10–90	10–90	1,633.4
Other vegetables/melonsd	70–100	10–90	1,099.2
Other field cropse	10–100	20–90	70.4
Other field cropse	10–100	20–90	70.4
Total	–	–	$14,563.6

Source: Morse and Calderone (2000). The value of honey bees as pollinators of U.S. crops in 2000, March 2000, Cornell University, at http://www.masterbeekeeper.org/pdf/pollination.pdf

These and other limitations of estimating economic values are discussed. Given the estimates currently available, consistent comparisons can be made across those economic values based on the direct effects of pollinators.

7.3 Pollinating Agents

The different pollinating insects play important role in enhancing agricultural productivity (Fleming et al. 2009). Besides, honeybees, alfalfa leaf cutting bees and bumble bees also pollinate crops (Table 7.3). An estimated \$2–3 billion value in annual crop pollination can be attributed to the activities of native bees and other insects (Losey and Vaughan 2006; Prescott-Allen and Prescott-Allen 1990; Southwick and Southwick 1992).

Some vertebrates also operate as pollinators of ecologically and economically important plants. Tropical trees of the family Bombacaceae, which includes species used for timber, silk cotton, balsa wood, and other products, rely primarily on bats

Table 7.3 Species list of known pollinators for global crops that are grown for direct human consumption

Pollinator group	Species
Honey bees	*Apis cerana* Fabr., *A. dorsata* Fabr., *A. florea* Fabr. and *A. mellifera* L.
Stingless bees	*Melipona favosa* Fabr., *M. subnitida* Ducke, *M. quadrifasciata* Lepeletier, *Nanotrigona perilampoides* Cresson, *N. testaceicornis* Lepeletier, *Trigona cupira* Sm., *T. iridipennis* Smith, *T. (Lepidotrigona) terminata* Smith, *T. (Tetragonoula) minangkabau* Sakagami, *T. toracica* Smith and *Scaptotrigona depilis* Moure
Bumble bees	*Bombus affinis* Cresson, *B. californicus* F. Smith, *B. hortorum* L., *B. hypnorum* L., *B. impatiens* Cresson, *B. lapidarius* L., *B. (Thoracobombus) pascuorum* Scop., *B. sonorus* L., *B. terrestris* L. and *B. vosnesenskii* Radoszkowski
Solitary bees	*Amegilla chlorocyanea* Cockerell, *A. (Zonamegilla) holmesi* Rayment, *Andrena ilerda* Cam., *Anthophora pilipes* Fabr., *Centris tarsata* Smith, *Creightonella frontalis* Fabr., *Habropoda laboriosa* Fabr., *Halictus tripartitus* Cockerell, *Megachile* (Delomegachile) *addenda* Cresson, *M. rotundata* Fabr., *Osmia aglaia* Sandhouse, *O. cornifrons* Radoszkowski, *O. cornuta* Latreille, *O. lignaria lignaria* Say, *O. lignaria propinqua* Cresson, *O. ribifloris* Cockerell, *Peponapis limitaris* Cockerell, *P. pruinosa* Say, *Pithitis smaragdula* Fabr., *Xylocopa* (Zonohirsuta) *dejeanii* Lepeletier, *Xylocopa frontalis* Oliver and *Xylocopa suspecta* Moure
Wasps	*Blastophaga psenes* L
Hover flies and other flies	*Eristalis cerealis* Fabr., *E. tenax* L. and *Trichometallea pollinosa* Townsend
Thrips	*Thrips hawaiiensis* Morgan and *Haplothrips (Haplothrips) tenuipennis* Bagnall
Birds	*Turdus merula* L. and *Acridotheres tristis* L.

for pollination (Bawa 1990; Watson and Dallwitz 1992). Many columnar cacti and agaves, which are important sources of alcoholic beverages (tequila, mescal) and other products (sisal fibers), also depend on bats and birds for pollination (Arizaga and Ezcurra 2002; Arizaga et al. 2002; Fleming et al. 2001; Grant and Grant 1979; Rocha et al. 2005; Valiente-Banuet et al. 1996; but see also Slauson 2000, 2001). Globally, pollinators are fundamentally important for the production of roughly 30% of the human diet and most fibers (cotton and flax), edible oils, alcoholic beverages, nutraceuticals, and medicines created from plants (Buchmann and Nabhan 1996; McGregor 1976; Roubik 1995).

Estimating the value of pollinators and pollination in natural ecosystems and predicting the consequences of their losses are considerably more challenging than estimating their economic value in agriculture (Sutton and van den Belt 1997; Costanza et al. 2004). Such estimates are complicated by both the number of species involved (globally, more than 400,000) and the relative paucity of information available for most of those species. For example, in their effort to calculate the economic value of ecological services provided by insects, Losey and Vaughan (2006) did not attempt to place a dollar value on the contributions of pollinators to maintenance of natural plant communities, although it is reasonable to assume that a significant proportion of plants in uncultivated terrestrial communities rely upon pollinators. These plants, in turn, contribute to many ecosystem services of value to humans, such as water filtration, carbon sequestration, and flood and erosion control (Daily et al. 1997). An added complication is that insect pollinators may contribute ecosystem services other than pollination in their larval stages. The value of these services is equally difficult to calculate, particularly without a complete understanding of all aspects of pollinators' life histories.

Dobson et al. (2006), however, developed a system for assessing the susceptibility of different ecosystem services to species loss. According to this system, which takes into consideration trophic level interactions, redundancies, and competition, ecosystem services are classified into Types A through E, with Type A services at one extreme identified as those in which species losses are mostly compensated for by co-occurring species and Type E services identified as "the most brittle services; for these services, small changes in species biodiversity result in large changes in the provisioning of ecosystem services." In Type C, an intermediate response, a linear decline in ecosystem service is expected with each species loss. In this system, pollination is considered a Type C or E service for most ecosystems, with species losses having significant impacts on trophic stability.

7.4 Economics of Plant Pollination

Worldwide, more than 3,000 plant species have been used as food, only 300 of which are now widely grown, and only 12 of which furnish nearly 90% of the world's food. These 12 include the grains: rice, wheat, maize (corn), sorghums, millets, rye, and barley, and potatoes, sweet potatoes, cassavas or maniocs, bananas, and coconuts (Thurston 1969). The grains are wind-pollinated or self-pollinated, coconuts are partially wind-pollinated and partially insect pollinated, and the others are propagated asexually or develop parthenocarpically. However, more than two-thirds of the world's population is in Southeast Asia where the staple diet is rice. Superficially, it appears that insect-pollination has little effect on the world's food supply – possibly no more than 1%.

The animal products we consume contribute about an equal amount to our diet. These include beef, pork, poultry, lamb, and dairy products – derived one way or another from insect-pollinated legumes such as alfalfa, clover, lespedeza, and trefoil. More than half of the world's diet of fats and oils comes from oilseeds – coconuts, cotton, oil palm, olives, peanuts, rape, soybeans, and sunflower (Guidry 1964). Many of these plants are dependent upon or benefited by insect pollination. When these sources, the animal and plant products, are considered, it appears that perhaps one-third of our total diet is dependent, directly or indirectly, upon insect-pollinated plants.

Another value of pollination lies in its effect on quality and efficiency of crop production. Inadequate pollination can result not only in reduced yields but also in delayed yield and a high percentage of culls or inferior fruits (Gates 1917). With ample pollination, the grower may also be able to set his blooms before frost can damage them, set his crop before insects attack, and harvest ahead of inclement weather. Earliness of set is an often overlooked but important phase in the crop economy. The value of pollination on the succeeding generation of crops is also frequently overlooked. The value of hybrid seed is not reflected until the subsequent generation. Vigor of sprouting and emerging from the soil is often a vital factor in the plant's early survival. Other responses to hybrid vigor include earliness of development, plant health, and greater production of fruit or seed.

7.5 Signs of Inadequate Pollination

There are numerous ways a grower, with little or no intimate knowledge of the life and habits of pollinating insects, can measure the effectiveness of the pollination of his crop by observing the compact clusters of fruits or seeds, and uniform set. For example, adequate pollination is indicated by two or more muskmelons near the crown or base of the vine, or a majority of the apples developing from the king, or primary flower, at the tip of the cluster or well formed with heavier berries. In a watermelon field, adequate pollination would be indicated by a high percentage of melons in the number 1 class, that is, symmetrical, completely developed throughout, and of satisfactory weight.

7.6 Ecological Relationships

The value of insect pollination, is not only limited to the cultivated crops but the absence of pollinating insects would be having drastic effect in uncultivated areas, where most soil-holding and soil-enriching plants would die out (Bohart 1952).

Baker and Hurd (1968) also recognized this important ecological relationship, for they stated that “insect pollination is still extremely important among the fortes of the grasslands, in the shrub and herb layer of the temperate forest and in the desert. It remains undiminished in the tropics.”

Abelson (1971) stated that development of extraordinarily productive farm crops with monoculture and the use of limited strains of plants makes the food supply vulnerable to plant enemies. The slightest weakening may give the enemy the advantage. The spectacular increases in yield, and a virtual genetic wipe-out, is likely to aggravate the problems. These narrow genetic bases and loss of gene pools are invitations to disaster. Cross-pollination can be one means of preventing such a disaster. This vulnerability to disaster was enlarged upon by Horsfall et al. (1972), who cited such examples as the chestnut blight at the turn of the century, the Bengal famine of India in 1943, and the Irish famine of the 1840s.

The somewhat related warning by Tinker (1971) that one plant species in 10,000 or 20,000 species faces extinction is indicative of the growing problem of a continual adequate food supply of the pollinators. In recent years there has been an increasing accumulation of data to indicate that seed yields of insect-pollinated crops may often be lower than they need be, not because of climate, soil, or cultural factors, but simply because of decline in the population of pollinating insects due to destruction of their nesting places or their accidental killing by insecticides used for harmful insects.

The aesthetic value of pollination to ornamentals, wild flowers, and forest and range plants in terms of beauty of the landscape is recognized for specific plants (Alcorn et al. 1962; Grant and Grant 1965; McGregor et al. 1962; Meeuse 1961) and in general but it cannot be measured. Nor can we measure the related ecological value in terms of seeds, fruits, and nuts produced, which are used as food for various forms of wildlife, but this value, too, is doubtless considerable.

7.7 Commercial Pollination Potentials

Insect pollination is not only a critical ecosystem function but also an essential input in the production of a host of agricultural crops grown world-wide. Of the approximately 300 commercial crops (Richards 1993) about 84% are insect pollinated (Williams 1996). Insects are responsible for 80–85% of all pollinated commercial hectares (Williams 1996), with fruits, vegetables, oilseeds, legumes and fodder (Richards 2001), representing approximately one-third of global food production (Richards 2001; Buchmann and Nabhan 1996; Allen-Wardell et al. 1998; Klein et al. 2007), mostly pollinated by *Apis mellifera* L. (honeybees) (Free 1993). However, the bulk of the world’s staple foods are wind-pollinated, self-pollinated or propagated vegetatively, and there is a bias where values ascribed to insect pollination come from high-value per unit crops (i.e. fruits, nuts, hybrid seed, and intermediate goods for the livestock and dairy industries) (Richards 1993, 2001; Ghazoul 2005). These authors therefore argue that global food security will not be threatened if insect pollinators decline or disappear, although this ignores the diverse diet that human beings rely on (Klein et al. 2007).

Modern commercial crop production is increasingly dependent on managed pollinators (e.g. the introduction of honeybee colonies into orchards or fields to improve crop production), and less on wild insects living on the periphery of crop fields (Richards 2001). The honeybee is regarded as the most important commercial pollinator, and although other bee species are also used for commercial pollination [alkali bees (*Nomia*); mason bees (*Osmia*); leafcutter bees (*Megachile*); bumble bees (*Bombus*)], at least 90% is performed by honeybees (Richards 1993; Williams 1996). Honeybees are excellent generalist pollinators, with commercial pollination being the most important derived value of commercial beekeeping worldwide (Richards 2001; Morse and Calderone 2000).

The "value" of managed honeybee pollination has been used to justify honey price support schemes (Robinson et al. 1989a, b; Richards 1993; Cook et al. 2007); invasive weeds as necessary bee forage (Gill 1985; Allsopp and Cherry 2004); and for the preservation of indigenous vegetation (Turpie et al. 2003). In turn the "value" of the wild pollination services forms part of a case for the conservation of natural biodiversity. The "global pollinator crisis" has become a *cause celebre* for those concerned with the environmental consequences of modern agriculture (Buchmann and Nabhan 1996; Klein et al. 2007; Tilman et al. 2002; Kremen et al. 2007). This resulted in the International Pollinator Initiative being approved as a Convention on Biological Diversity programme. The basic premises of the initiative are that: firstly, global food security is threatened by the decline in managed honeybees and by the loss of wild pollinators; and secondly, that sustainable agriculture requires the development of alternative non-*Apis* pollinators, improvement in habitat management for wild pollinators, and improved agricultural management practices in general (Tilman et al. 2002). Concerns about the global health of pollinators, and their link to food security, have been accentuated by the threat posed to honeybees by parasitic mites (*Varroa destructor* and *Acarapis woodii*) and by the as yet unexplained Colony Collapse Disorder (CCD) (Oldroyd 2007) which have seen massive honeybee losses in the USA and elsewhere.

An intense debate has developed around the respective contributions of wild and managed pollination service components, and the impact if one or the other were to be lost. Recently, Ghazoul (2005) questioned the existence of a global pollinator decline, arguing that human food security is not vitally dependent on animal (mostly insect) pollination. This view was challenged by Steffan-Dewenter et al. (2005), who cited several examples where food security has been linked to insect pollination. This debate raises the issue of whether the value of pollination as an ecosystem service can justify biodiversity conservation (Allen-Wardell et al. 1998; Ghazoul 2005) and whether crop pollination by managed pollinators, mostly honeybees, can be described as an ecosystem service (Allen-Wardell et al. 1998; Klein et al. 2007), and consequently, the legitimacy of advocating the preservation of wild pollinators on the basis of the derived value from managed pollinators (Buchmann and Nabhan 1996). Evidently, managed pollination may be regarded as a commercial input to agricultural crop production (Deciduous Fruit Producers Trust (DFPT) (2005), and not an ecosystem service (Cook et al. 2007). Although crop production is regarded by some as an ecosystem service itself (e.g. Hassan et al. 2005), this can only be true for subsistence agriculture where there are no managed inputs (i.e. fertilizers, pesticides etc.). Determining the value of crop pollination ecosystem services requires distinction between the value derived from the use of managed pollinators, and value derived from wild pollinators.

Generally, a balanced perspective on the importance of both wild and managed pollination services is lacking. For example, a recent study states that wild bees will be able to replace the pollination services provided by the domesticated honeybee, amidst the catastrophic effects of CCD (Oldroyd 2007) in the USA (Winfree et al. 2007). However, although this may be true for feral honeybees in the area (also contributing to wild pollination services), no mention is made of the importance of managed honeybee pollination services in the same area. It is thus misleading to suggest wild pollination services could replace managed services based on the findings of this study.

Irrespective of this ecological debate, monetary valuation dominates natural resource conservation management decision- and policy-making. It is therefore necessary to present the importance of wild (and managed) pollinator services in monetary terms, because human decision-making is driven by financial considerations (Costanza et al. 1997; Gill 1991; Curtis 2004). Unfortunately, the free market as a value estimator does a poor job in quantifying the monetary value of ecosystem services (Randall 1983; Goodstein 2008). Relative inclusiveness of market prices for ecosystem services derived benefits, are not an accurate reflection of the total value due to the difference between private and public perceived value (de Lange and Kleynhans 2007). Finding a sensible alternative is therefore required for informed private and public decision-making. If the original service provided by wild pollinators is undervalued, it is likely that the cost to substitute this service with managed pollinators, will also be undervalued.

The value of wild and/or managed pollinators in commercial crop production has been estimated in many countries using different methods (Table 7.3). Recently, the annual value of maintaining feral honeybee pollination ecosystem services in Australia by preventing the introduction of varroa mites, was calculated as between AUS$16.4–38.8 million (US$12.6–30.7 million) (Cook et al. 2007).

Current methods either under-estimate (Burgett et al. 2004) or over-estimate the service value (by equating the value of pollination services to the proportion of total production value dependent on insect pollination) (Morse and Calderone 2000; Losey and Vaughan 2006) (Table 7.1). To distinguish between the managed and wild components, we calculate the value of managed pollination as the proportion of pollination attributed to managed pollinators multiplied by the insect dependent production value. In turn, the value of wild pollination is calculated as the difference between the (total) insect dependent production- and managed pollination values (Losey and Vaughan 2006). Recently, the use of general insect dependence factors and the proportional allocation to managed pollinators have been criticised as being neither based on published data sources nor being regionally specific (Cook et al. 2007). This calls for a global review of the importance of insect pollination to crop production, based on experimental evidence. For example the value calculated by Cook et al. (2007) to estimate what it would cost to substitute all feral honeybee colonies in Australia with managed ones, still assigns pollination value based on the dependence and proportion managed pollination given by Morse and Calderone (2000) for the USA, based on data from McGregor (1976).

In addition, the proportional total production value approach is flawed in several respects. Firstly, it exaggerates the economic value of pollination services because it discounts the other inputs required in the production of the commodity. A successful fruit or seed crop depends on many factors, e.g. labour and irrigation, in addition to adequate pollination Bos et al. (2007). Secondly, it depends on markets having an infinite elasticity of demand and is economically unrealistic (Gill 1991). That is, that increasing or decreasing production levels would have no impact on price, or on pollinator value. And finally, the proportional total production approach ignores that insect pollination is substitutable with alternatives.

A more accurate value of insect pollination services will improve conservation management decision-making capabilities, and consideration of pollination alternatives will assist crop producers. Growers might need to substitute insect pollination with alternatives for a number of reasons. These include beekeeper unwillingness to introduce their bees for pollination because of agrichemical poisoning or insufficient payment (Ya et al. 2003), the likelihood of spreading horticultural disease or bee pests (Cook et al. 2007; Oldroyd 2007), insufficient service delivery by managed bees (Free 1993), or disappearance of wild insect pollinators (Richards 1993; Klein et al. 2007; Kremen et al. 2007; Oldroyd 2007).

While a number of previous studies have concerned themselves with pollination markets (Cook et al. 2007; Burgett et al. 2004; Johnson 1973) only Olmstead and Wooten (1987) and Southwick and Southwick (1992) estimated the value of insect pollination by alternative means. These studies did not, however, pursue the *Nature* and costs of replacements to insect pollination, and no other such studies have attempted to calculate the plausibility and cost of substituting insect in the pollination of crops. We take a different approach to valuation by estimating industry-wide replacement costs for wild and managed insect pollination services. We adopt an approach where the value of wild and managed insect pollination services are equivalent to the amount of income lost if these components were to be replaced by alternative (non-insect) means of pollination. Consequently the replacement cost is proposed as an estimate of the relative value of these services.

Value estimates are first in biogeographical order and then chronology. The ‘proportion’ of agricultural produce refers to the portion of crop value that can be attributed to managed bees for pollination (as opposed the remaining portion that is attributable to wild insect pollination).

7.8 Impact of Pollinators on World Crops

The total value of crops used for human food is 1.68 trillion euros and 10 of the 20 most important crops worldwide from an economic standpoint depend to some extent on insect pollinators (nine of them are directly dependent on insects for their production). Based on the crops that amount to 99% of the total world crop value, 54% of this value rest upon crops that depend on insect pollinators. Among these, vegetables, oilseed crops and fruits are the most important crops that are dependent of pollinators (Table 7.4).

Table 7.4 Biogeographic-specific estimated value of managed bee pollination for commercial crops

Country	Value	Method (as described by authors)	Reference
USA	US$ 40.0 billion	Proportion of fruit, nuts, vegetable seed, oilseed, fodder and value derived from fodder due to managed bee pollination.	Martin (1975)
USA	US$ 18.9 billion	Proportion of fruit, nuts, vegetable seed, oilseed, fodder and value derived from fodder due to managed bee pollination.	Levin (1984)
USA	US$ 4.6 billion	Proportion of fruit, nuts, vegetable seed, fodder seed and oilseed due to insect pollination.	O'Grady (1987)
USA	US$ 0.18–3.0 billion	Proportion of some fruit, nuts, vegetable seed, fodder seed and oilseed due to insect pollination, incorporating yield fluctuations.	Olmstead and Wooten (1987)
USA	US$ 9.3 billion	Proportion of fruit, nuts, vegetable seed, fodder seed and oilseed due to managed bee pollination.	Robinson et al. (1989a, b)
USA	US$ 1.6–5.7 billion	Values based on decreasing commodity costs resulting from improved yield due to commercial pollination.	Southwick and Southwick (1992)
USA	US$ 14.6 billion	Proportion of fruit, nuts, vegetable seed, fodder seed and oilseed due to managed bee pollination.	Morse and Calderone (2000)
Canada	US$ 0.66 billion (Can$ 782 million)	Proportion of fruit, nuts, vegetable seed, fodder seed and oilseed due to managed bee pollination.	Winston and Scott (1984)
Russia	US$ 0.08 billion (2.2 billion roubles)	Additional yield in all insect pollinated crops resulting from managed bee pollination	Soldatov (1976)
EU	US$ 6.4 billion (5 billion ecus)	Proportion of fruit, nuts, vegetable seed, fodder seed and oilseed due to insect pollination.	Borneck and Merle (1989)
UK	US$ 0.38 billion (£202 million)	Proportion of fruit, nuts, vegetable seed, fodder seed and oilseed due to managed bee pollination.	Carreck and Williams (1998)
Australia	US$ 0.5–0.9 billion (AUS$ 0.6–1.2 billion)	Values based on decreasing commodity costs resulting from improved yield due to commercial pollination.	Gill (1991)
New Zealand	US$ 1.54 billion (NZ$ 2.25 billion)	Total market value of all insect pollinated crops	Matheson and Schrader (1987)
South Africa	US$ 0.61 billion (ZAR 4.1 billion)	Proportion of fruit, nuts, vegetable seed, fodder seed and oilseed due to managed bee pollination.	Allsopp (2004)

The value of bee pollination in Western Europe is estimated to be 30–50 times the value of honey and wax harvests in this region. In Africa, bee pollination is sometimes estimated to be 100 times the value of the honey harvest, depending on the type of crop. In a country like Denmark, about 3,000 tonnes of honey is harvested every year. It has a value of 60 million DKK or about €7.6 million. However, the value of oilseeds, fruits and berries created by the pollination work of bees is estimated to be between 1,600 and 3,000 million DKK, equivalent to €200 and €400 million.

Some types of crops have flowers that may only be pollinated during a short period. If such a crop is not pollinated during that time, the flowers will fall and no seeds, berries or fruit will develop. There have to be sufficient numbers of bees in the pollinated crop. This is especially important in crops where the single flower may only be pollinated in a restricted time or in crops where the nectar pollination, or bee visits only take place during days where the temperature is at a certain level. In such a crop, the pollination in some years has to take place within 3 or 4 days. This can be the case in growing white clover seed. The flowers only produce some special smelling products attracting the bees to the flowers when the ground temperature is above 15°C. When the temperature is lower, only a few bees are interested in visiting the clover flowers. It means that the whole pollination work in some years has to be done in a very few days, where thousands of worker bees are needed to do the job. If the farmer does not provide fields with honeybees or other bees for pollination, the whole harvest can fail. In years with plenty of hot days during the blooming season, bumblebees, solitary bees and the few honeybees will have time to do the pollination and the farmer can get a good harvest, even without bringing in pollinating bees. The risk for the farmer is the unpredictability of the weather in temperate areas where white clover is grown for seed production. The white clover flower has evolved so that the bees can reach and collect the nectar. A honeybee can therefore visit 18–20 flowers in 1 min.

To measure the need for honeybee pollination, crop areas in Russia with white clover were covered during blooming, so that no bees could enter. In the covered square only 1 gm of seed was harvested, but in the uncovered area of the same size 331 g of seeds could be harvested. Lack of bees for pollination can mean a loss for the farmer of maybe 75% of the crop. It is recommended to white clover growers that they provide their fields with two to three colonies per hectare to secure the best pollination. A single coffee flower is only open for 3–4 days when blooming. If a bee or another insect does not pollinate the flower during these days, it will wither, and no coffee bean will be produced. Clever coffee farmers take care that there are plenty of honeybees or stingless bees for pollination in the farm.

Insect pollination and pollinator protection are not included in most of the training books for agronomists, extension officers and farmers. Many farmers all over the world do not recognize the need for bee pollination and consequently many bees are killed by careless use of pesticides. Even many beekeepers and honey hunters do not know about pollination and cannot inform the farmers about the need for protection of bees.

In Europe, Australia, New Zealand and North America, fruit and berry growers, and white clover growers pay beekeepers to bring bees for pollination in the blooming season. They know this will give a far better chance for a good harvest. Some farmers believe that the beekeeper will get a big honey harvest when moving bees to fields for pollination, and therefore they do not want to pay for the work. However, this is not necessarily the case. The beekeepers often lose many bees when moving hives for pollination purposes, and they often do not get a worthwhile honey harvest from pollination work. It is therefore necessary for beekeepers to be paid for the service. In Denmark, there are rules for payment for pollination concerning the size of the bee colony being rented. It is recommended that there should be at least four combs with unsealed brood, to ensure that bees have to collect a lot of pollen for feeding the brood. It is sometimes found that the farmer or owner of a *Plantation* wants the beekeeper to pay to place the beekeepers' hives in the farm. If neither beekeepers nor farmers are aware of the pollination value of the bees, this situation will never change. The farmer receives a smaller harvest and the beekeeper does not gain access to a good site for the bees. The pollinatory value of bees, even in the same crop, can vary from one place to another. This is because there are many variables: the temperature, the water table, the other pollinator insects in the environment, and other available forge for bees, etc. For example, opinions differ on the value of bees in coconut pollination: one example from India mentions a double harvest of coconut because of bee pollination Bee pollination gives better quality and quantity of harvest.

Bee pollination not only results in a higher number of fruits, berries or seeds, it may also give a better quality of produce, and the efficient pollination of flowers may also serve to protect the crops against pests. The better weight due to sufficient pollination arises from the development of all seeds in a fruit.

An apple, for example, will only develop all the seeds inside if it has been pollinated by several bees and fully fertilized. It is possible for an apple flower to develop about ten seeds. If all the seeds do not develop, the fruit itself does not develop where the seeds are not developing. This results in poorly shaped apple of low weight. The same can be the case with strawberries, where a fully developed strawberry needs about 21 visits of bees: at least this is the case for the old varieties of strawberries; some new ones are not so dependent on bees. A single strawberry can have 400–500 seeds (or actually small nuts) sitting on the surface of one berry. The higher number of seeds developing fully – the bigger and more even shaped the berry will be.

Research with bilberries showed the following interesting result: in bilberries grown close to an apiary, fertilization and berry production occurred in 89.1% of the flowers. In an area without bees, fertilization and berry production was only 47.5%. The average weight of a berry was 0.578 g for the bilberries close to bees, and 0.348 g without bees. Harvest of berries from 100 flowers was 51.1 g with bees in the neighbourhood, and only 16.8 g where the bees were not present.

The bee pollination in *Brassica* oilseed production creates a higher content of oil in the seed. Sufficient bees will also take care that all the plants in the field are pollinated in the same period, so the seeds ripen at the same time. This allows harvest of a uniform crop, with less green and unripe seeds among the ripe ones. That will give the farmer a higher price.

A sufficient number of bees for pollination can also protect the crop against serious pest attacks. A single *Brassica* flower is waiting for pollination and fertilization

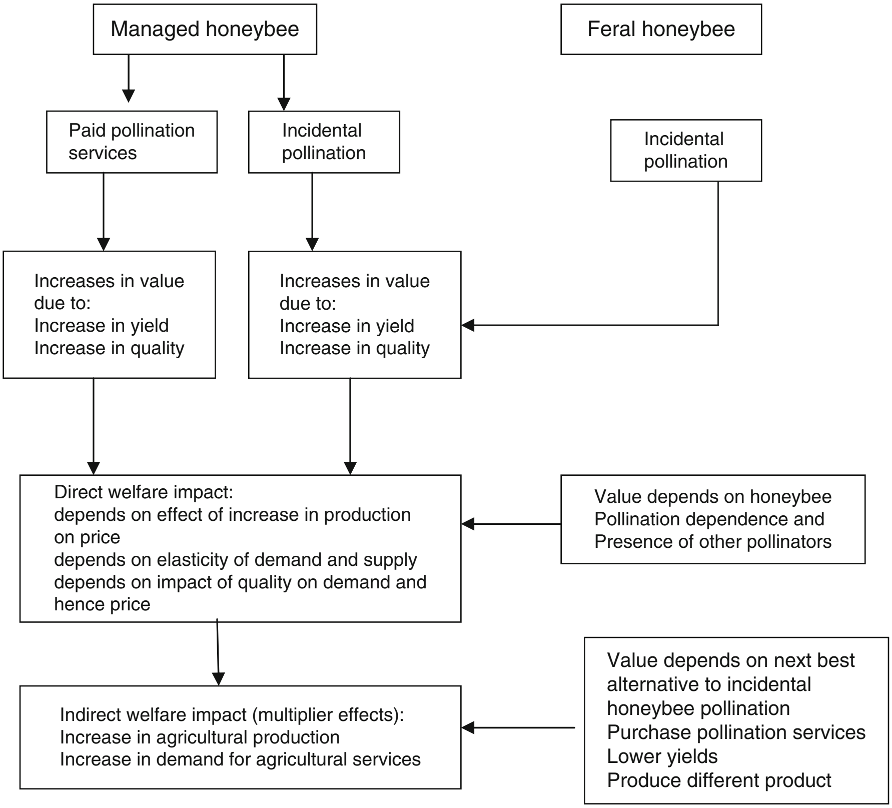

Fig. 7.1 Identifies the sources of economic benefit arising from honeybee pollination services. Both direct and indirect benefits from managed and feral honeybee pollination provide a comprehensive estimate of the value of pollination services (Source: Gordon and Davis 2003)

before it closes and falls off. If bee pollination is needed, yet there are not enough bees present, pollination can take many days. In that time the flower is attacked by different pests eating the pollen, sucking the sap, laying eggs in the flower, or spoiling it in other ways. If there are sufficient bees in the field, the flowers will only have to be open for a short time, and the different pests will not have so much time for their destruction. In that way, adequate numbers of bees ensure rapid and efficient pollination and protect crops against pests (Fig. 7.1).

7.9 Use of Other Bees for Pollination

Solitary bees play a great role in the pollination of wild plants. They also pollinate many cultivated plants. The sizes of natural populations of solitary bees fluctuate greatly from year to year and from place to place, and this makes them difficult to rely on for the pollination of crops. A few species are utilised by farmers for the pollination of special crops. The availability of suitable nesting places seems to be a regulating factor for many solitary bees and a simple way to increase the bee population is by creating artificial and better nest places. In many countries where industrial farming is dominant, the natural population of solitary bees has declined as their natural habitat was destroyed. Nevertheless, some farmers and beekeepers try to use these bees for agriculture.

The most commonly used solitary bees are Alfalfa leaf cutter bees *Megachile rotundata*, *Osmia* species of bees including *Osmia cornifrons* and others, and Alkali bees *Nomia melanderi*. The bees are solitary, which means that the female bee alone takes care of the next generation. However, these species are all gregarious, meaning that they like to nest close to each other, and that seems to stimulate their activities. Bumblebees *Bombus* spp. are social bees like the honeybees, and are used for specialized pollination work.

The use of all these bees is for pollination only: no honey can be harvested from them. The use and study of solitary bees first started and became an industry in Japan after the Second World War. The problem was that many farmers were lacking bees for pollination because the honeybees had been killed from heavy use of pesticides. Some solitary bees are especially well adapted for pollinating fruit trees. The *Osmia* bees for example, develop so that they emerge just at the blooming time of the trees, and they live as flying adults for just a few weeks. The possibility to spray trees just before and after blooming was one of the ideas behind the great interest in using these bees. The use of solitary bees for pollination is not a new invention. Farmers in Egypt have long used bundles of dry straw, or rolled straw mats as artificial nests for leaf cutter bees. 'Bringing the "mat-bees" to the fields' was when bundles with larvae and pupae inside were taken from old cultivations where bees are present, to new irrigated areas in the desert to ensure sufficient pollination of new crops of tomatoes, alfalfa and others.

Leafcutter bees *Megachile rotundata* are only half the size of a European *Apis mellifera* honeybee. They are black with white stripes. The males have green eyes when they are young. They occur naturally in the countries around the Mediterranean Sea, and have now been spread to other continents. Leafcutter bees nest in straw or other organic horizontal tunnels with a diameter of about 6 mm and about 10–12 cm long. When the bees come out of the straw cell after about 21 days of development (dependent on the temperature), they mate and the females start building new leaf cells inside the straw. The cells are like small hollow cigars made of pieces leaf, and two thirds filled with pollen and honey. When an egg is placed in the cell, it is sealed with other leaf pieces and a new one is built outside the first. There can be 10–13 cells in a row before a new straw is used. When a tunnel is finished and filled with cells, the bee closes the entrance hole with up to 100 round pieces of leaf. This protects against parasitizing wasp and other insects that want to attack the larvae. The eggs in the first two to three cells develop to females, the rest into males. The males develop some days faster than the females, and in that way the tunnel is clear when the female bees are ready to emerge. They prefer to nest in tunnels where the entrance is a little lower than the other end. The females can fly around for about 9 weeks, and then they die. The male bees are only flying for about 2 weeks.

Nests can be made artificially from poles with drilled holes 6 mm in diameter, but when working with bigger populations it is necessary to use a nest type where the tunnels can be opened to remove the cells for storing and artificial hatching next year. The farmer can arrange the hatching time, and most of the small parasite wasps can be removed before they are spread to the new breeding place in the field. Leafcutter bees do not need any water throughout their life and they are therefore excellent pollinators in arid areas. The cells with larvae inside can be kept in cool rooms with a temperature of 3–5°C until they are needed for pollination. Then they are placed in a hot room at 30°C with high air moisture, and they will hatch in 17–26 days. These bees are used extensively in Russia, Canada, USA and New Zealand – especially for pollination of alfalfa (lucerne). Canada exports US$1 million worth of leaf cutter bees every year.

Mason or osmia bees are indigenous bees of Europe: the most commonly seen in spring is *Osmia rufa*. The female is reddish brown and at 10–13 mm long is a little smaller than the European honeybee. The widespread *Osmia lignaria* is indigenous to North America and has the same size but is darker in colour. The males are more slender than the females in both species. Like leafcutter bees, the females collect pollen in the hairs underneath their bodies.

The life cycles are similar to that of the leafcutter bees, but mason bees make their cells from mud, resin, dung, leaves and petals. They can be attracted to nest in bundles of tubes like bamboo sticks. The preferred diameter of the tunnels is 7–8 mm. *Osmia rufa* works at lower temperatures than *Megachile* spp. and can be used for very early pollination in greenhouses. The *Osmia* cells are kept in refrigerators at the same temperature as the leafcutter bees. They overwinter in their last pupae stage and can be taken directly from the refrigerator to the greenhouse where they will start to emerge the next day. The *Osmia* bees are highly effective pollinators of fruit trees, and are used for almond tree pollination in California. Much development work still needs to be done with these bees. Alkali bees are black with yellow bands on the abdomen and a light yellow layer of hair over the whole body. They are of same size as the European *Apis mellifera* honeybee, although more slender. Alkali bees are present in many of the north western states of the USA. Their importance as pollinators of alfalfa was first detected around 1940, and from the 1950s, many seed growers started to build nest places for alkali bees. They are used together with leafcutter bees for pollination of lucerne. The alkali bee has been introduced to France and New Zealand where they are used for pollination. The alkali bee makes nests in the ground: they can make their tunnels very close-up to 540 nests in one square meter. The males emerge from the end of June up to the middle of July, with the females emerging 1 week later. The females and males mate, and the same day the females start digging a nest tunnel. During the night, the tunnel is finished and the next day the first cell is made and supplied with pollen. The following day the first egg is laid and a new cell constructed. The bee will continue building up to 15–20 cells before she dies. The bees overwinter as prepupae and the development continues when the earth becomes warm again the following spring. The alkali bees require a special soil type for nesting: fine salty sand and clay with a moisture content of 25%. Artificial nesting areas can be made by digging a 1 m deep hole – one to 20 acres in size. The bottom is covered with a layer of plastic and on top of that is placed a 15 cm layer of fine gravel or sand. On top of that is another layer of about 85 cm with a mixture of fine sand and clay. The top layer is mixed with 2–5 kg of salt per square meter, to draw the moisture from the bottom layer. The bottom layer is supplied with water to a certain height. A simpler system has been developed with plastic drain tubes supplying the nesting ground with water. Salt is just sprayed on the surface of the ground. Bees can be transferred from one nest place to a new one by transplanting blocks with over wintering pupae. One acre with one million alkali bee nests can pollinate 200 acres of alfalfa.

Small bumblebee colonies are most often used in greenhouses. As with the solitary bees there are no problems with stinging, and people working in the greenhouses prefer bumblebees to fly around instead of honeybees. Cardboard nest boxes with bumblebees can be bought every spring for greenhouse pollination. A box with a colony consists of one queen and about 20 workers in the beginning. The price for the farmer is about €130 (2003), bought from the Netherlands. It has been a significant business in Southern Europe to catch bumble queens during spring for export to the Netherlands or other European countries, but this activity has damaged local populations of wild bumblebees in many places.

Honeybees are responsible for the production of a diverse range of valuable commodities. such as honey, beeswax, propolis and royal jelly. However, the contribution of the honeybee industry extends beyond the value of honey and other apiary products. In undertaking their daily routine of foraging for nectar and pollen, honeybees come into contact with numerous flowering plants, and in so doing effect fertilisation of those plants through the transfer of pollen. While numerous vectors – such as other insects, birds, animals and wind can carry out pollination, honeybees are the most significant pollinators of some crops due to the efficiency of their foraging activities (Gibbs and Muirhead 1998). Indeed, 65% of horticultural and agricultural crops require honeybees for pollination (Gibbs and Muirhead 1998). The value of pollination services carried out by honeybees is likely to substantially exceed the value of honey and other apiary products.

7.10 The Value of Honeybee Pollination Services

A credible estimate of the value of honeybee pollination services is important information for the honeybee industry. Honeybee pollination is essential for some crops, enhances fruit set in others and can play a major role in improving fruit quality.

honeybee pollination services at between has been valued at

$600 million and $1.2 billion	Gill's (1989)
$1.2 billion	Gibbs and Muirhead (1998)
$3.1 billion	Gibbs and Muirhead (1998)
US$14.6 billion	Morse and Calderone (2000)

7.10.1 Unmeasured Pollination Benefits

There are areas where it is almost impossible to place a dollar value on bee pollination. One is the contribution that pollination of plants makes to wildlife food production. Another is the natural beauty resulting from pollination of wildflowers. Many shrubs and countless annual plants reproduce by bee pollinated berries and seed, which provide food for birds and other animals. Ornithologists may suggest that humans "feed the birds in the winter," but the birds also depend upon naturally grown seed and fruit resulting from bee pollination. The beekeeper with a small scale operation is very valuable in providing honeybees for this unmeasured contribution to pollination, because there are many smalltime, hobbyist beekeepers spread throughout the state who increase food production for wildlife. Thus, it is difficult to place a dollar value on the enjoyment created by birds, wildflowers, and wild animals for the *Nature* enthusiast.

Pollination is an ecosystem service that is key to food security. Pollinators are essential for many fruit and vegetable crops. In agriculture, especially amongst pollen-limited crops, promoting pollination services is a means of increasing productivity without resorting to expensive agricultural inputs of pesticides or herbicides. Indeed, pollination services are most likely underpinning productivity in many crops without farmers even recognising it, so long as habitat and alternative pollinator forage are readily available as they often are in smallholder farming systems.

By developing larger and larger fields and landscapes for agriculture, we remove the habitat that pollinators may need. Increasing dependence on pesticides for pest control is also highly detrimental to beneficial insects such as pollinators, unless planned and undertaken with extreme care. Pollination is a service *Nature* provides that we have tended to take for granted, and that we often do little to encourage until we start to lose it. As wild ecosystems are increasingly converted to more human dominated uses to meet the compelling demands of food security, it is critical for us to understand what pollination services are most important for food security, and how we can preserve pollinator services in sustainable farming systems.

A crop's pollinator dependence differs between species, including between crops and crop varieties. Some plants must be cross-pollinated, others do not need pollinators but produce better fruit and seed if pollinated, and a number are strictly self-pollinated. Further, plants differ in their pollinator-type requirements; some require specific pollinators while others are pollinated by a variety of visitors, and many are wind pollinated. Effective pollinators of the same crop may vary from one site to another. Specific knowledge on pollinator dependence and types is important for agriculture and biodiversity (including agro-biodiversity) conservation (Tables 7.5 and 7.6).

Similarly in Netherlands, Hein (2009) found that insect pollination is essential for global agriculture and human food security (Table 7.1). Some fruits and vegetables require insect-mediated pollination for the production of the fruit or vegetable itself, such as almonds, apples, apricots, blueberries, cantaloupes, citrus, cucumbers, kiwi, peach, plum, squash, sunflower and watermelon. For other fruits or vegetables, insect pollination is not a strict requirement for fruit bearing, but it substantially increases yields (e.g. tomatoes, coffee)? (Klein et al. 2007). In addition, a large number of fruits and vegetables require insect pollinators for seed

Table 7.5 Estimation of the value of honey bee pollination in Canada – 1998

Crop	Dependence on insects	Honey bee portion	Dependence on honey bees (%)	Production value ($'000)	Honey bee contribution ($'000)
Tree fruit					
Apples	1.00	0.85	85	161,533	137,303
Apricots	0.70	0.80	56	1,031	577
Sour cherries	0.70	0.90	63	256	161
Sweet cherries	1.00	0.90	90	7,709	6,938
Nectarines	0.35	0.80	28	4,557	1,276
Peaches	0.35	0.80	28	27,165	7,606
Pears	1.00	0.90	90	13,551	12,196
Prunes and plums	0.80	0.90	72	3,875	2,790
Berries					
Grape	0.10	0.10	15	8,555	586
Kiwis	0.90	0.90	81	328	266
Blueberries	1.00	0.90	90	56,626	50,963
Raspberries	0.90	0.80	72	21,313	15,345
Strawberries	0.30	0.80	24	51,156	12,277
Cranberries	1.00	0.90	90	28,395	25,556
Cucurbits					
Cucumbers	1.00	0.90	90	10,468	9,421
Melons	1.00	0.80	80	560	448
Pumpkin	1.00	0.60	60	5,947	3,568
Squash and zucchinis	1.00	0.60	60	4,145	2,487
Oilseeds					
Canola/rapeseed	0.20	0.90	18	2,512,354	452,224
Sunflower	0.20	0.80	16	19,699	3,152
Mustard	0.20	0.80	16	1,519	243
Soybeans	0.10	0.50	56	52,000	32,600
Forage legume seeds					
Alfalfa seed	1.00	0.10	10	9,500	950
Clover seed	1.00	0.70	70	1,229	860
Pulses and other crops					
Fababeans	0.50	0.80	40	1,920	768
Buckwheat	0.80	0.80	64	1,534	982
Total				5,813,850	781,543

Sources: Statistics Canada 22-003 Feb 2000, Provincial Ministries of Agriculture, Bureau de la Statistique de Quebec, Provincial Apiculturists

production (Kremen et al. 2001). Sustaining global agriculture depends on pollination by managed bee populations, as well as on wild insects including wild bee populations, as discussed below. The main insect group involved in managed pollination are the bees, and in particular the honey bee (genus *Apis*). Despite of the important production of honey worldwide the role of honey bees as a pollinator

Table 7.6 List of major insect-dependent crops

Crop	Latin name	Main pollinator	Insect dependency (%)
Apple	*Malus domestica*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), Digger bees (*Andrena spp.*), Bumble bees (*Bombus spp.*), Mason bees (*Osmia spp.*)	80–100
Coconut	*Cocos nucifera*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), Ants	10–40
Coffee	*Coffea Arabica*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*)	20–40
Grape	*Vitis vinifera*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*)	0–10
Orange	*Citrus spp.*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), Rock bee (*Apis dorsata*), Golden wasp (*Vespa magnifica*), Oriental wasp (*Vespa orientalis*), Red pumpkin beetle (*Aulacophora foveicollis*), Housefly (*Musca domestica*)	10–30
Mango	*Mangifera indica*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*)	80–100
Melon	*Cucumis melo*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), *Halictidae lassioglossum*	80–100
Cucumber andgherkins	*Cucumis sativus*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), Lady beetle (*Coccinella spp.*), Red pumpkin beetle (*Aulacophora foveicollis*)	50–90
Oil palm fruit	*Elaeis guineensis*	Various	0–10
Onion + shallots (seed production)	*Allium cepa*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), Syrphid fly (*Milesia semiluctifer*), Halictid bees, Drone flies	90–100
Peanuts	*Arachis Hypogeal*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*)	10
Squash and pumpkin	*Cucurbita spp.*	Squash bee (*Peponapis pruinosa*), *Halictus tripartitus*	90–100
Soybean	*Glycine max*, *G. soja*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*)	10–40
Seed cotton	*Gossypium spp.*	Various	20–30
Sunflower	*Helianthus Annuus*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), Bumble bees Long-horned bees	50–100
Rapeseed	*Brassica napus oleifera*	European honeybee (*Apis mellifera*), Asiatic honeybee (*Apis cerana*), Lady beetle (*Coccinella spp.*), Bumble bee (*Bombus spp.*), Syrphid fly (*Milesia semiluctifer*), Carpenter ant (*Xylocopa spp.*)	50–100

(continued)

Table 7.6 (continued)

Crop	Latin name	Main pollinator	Insect dependency (%)
Tomato	*Lycopersicon esculentum*	Halictid bees (*Halictidae spp.*) (field) Bumble bees (*Bombus spp.*) (greenhouse and field), Honey bees (*Apis mellifera* and other spp.)	10–50
Water melon	*Citrullus lanatus*	Yellow face bumble bee (*Bombus vosnesenskii*), California bumble bee (*Bombus californicus*), Squash bee (*Peponapis pruinosa*), Sweat bees (*Halictus spp.*), Long-horned bees (*Melissodes spp.*)	70–100

Sources: Gordon and Davis 2003; Roubik 2002; Freitas 2005; Klein et al. 2007

remains the most important economic contribution, outweighing the importance of all the other hive products together. Honey bees can be easily kept, and are capable of pollinating a wide spectrum of plants. It has been estimated that, worldwide, close to 100 crops are pollinated by honey bees (McGregor 1976). Other bees that are widely used for pollination in agriculture are bumblebees (*Bombus spp.*), leafcutter bees (*Megachile spp.*, in particular *M. rotundata*) and mason bees (*Osmia spp.*, in particular *O. lignaria.*). Bumble bees are used, for instance, for tomatoes, eggplants, peppers, melons, raspberries and blackberries.

There are several studies that analyze the value of pollination services at the national scale, in particular for the US, several European countries, Australia and New Zealand (Table 7.7). For these countries, there is relatively much information on the impact of pollination on crop productivity per crop (the first step of the production factor method). Comparing different studies, there appears to be some remaining uncertainty in the impact of pollination on crop production, depending on the crop and the crop variety (e.g. McGregor 1976; Free 1993; Buchmann and Nabhan 1996; Morse and Calderone 2000; Klein et al. 2007).

There have been several attempts to analyze the value of the pollination service at the global scale. Costanza et al. (1997) provide a value estimate of $117 billion per year for all pollination ecosystem services, whereas Richards (1993) finds that the value of pollination in global agriculture alone amounts to $200 billion per year. Gallai et al. (2009) estimate the economic value of the pollination services worldwide to be 153 billion euro (considering impacts on agriculture only). However, these value estimates focus on establishing the relation between pollination and crop production, and have assumed constant prices for crops. This is not a realistic approach in case a global decline in the pollination service is assessed, as such a decline would lead to major price increase of insect-pollinated crops (see sections above). Note that this is recognised in Gallai et al. (2009), who discuss the importance of price elasticity and show an approach for calculating global consumers (but not producers) surpluses related to crop pollination – however without applying this approach to determine a more reliable estimate of the global value of the pollination service.

Table 7.7 Comparison of the value estimates of the reviewed case studies

Country	Total value agricultural pollination in US$ billion/1	Value of insect pollination in US$ billion	Value of pollination service compared to value of agriculture	Source
Canada	25	1.2	0.05	Winston and Scott (1984)
USA	219	Between 6 and 14	0.05	Southwick and Southwick (1992); Morse and Calderone (2000)
EU-15	188	5.0	0.02	Borneck and Merle (1989)
France	53	0.5	0.01	Borneck and Bricout (1984)
United kingdom	18	0.3	0.02	Carreck and Williams (1998)
Australia	16	1.1	0.07	Gill (1991); Gordon and Davis (2003)
New Zealand	5	1	0.16	Gibbs and Muirhead (1998)
World	868			

Source: World Bank (2003)

Bees are important both ecologically and economically for the ecosystem service role they play as pollinators. Insects are the most important animal pollinator groups, with approximately 70% of angiosperm plants being insect pollinated (Free 1993; Schoonhoven et al. 1998). Among the pollinating insects, bees are one of the most important and specialised groups (Danforth et al. 2006). There are over 19,500 valid species of bee on the planet described thus far (Ascher et al. 2008), though there are likely to be many more species that are to be described (Michener 2000). Morphologically bees are adapted to collect, manipulate, transport and store pollen very effectively and efficiently (Thorp 2000; Danforth et al. 2006). Bees species exhibit both generalist and specialist foraging behaviour, thus making them very important economically and ecologically (Waser and Ollerton 2006). Economically, animal pollination services have been valued at $65–75 billion globally (Pimentel et al. 1997) and honeybee pollination alone in the United States was evaluated at $14.6 billion in 2000 (Morse and Calderone 2000). Bees are often considered keystone species in ecosystems, thus bee loss or decline can result in reduced fruit and seed-set in plants and can lead to disruption of plant-pollinator networks leading to possible extinction cascades (Steffan-Dewenter and Tscharntke 1999; Waser and Ollerton 2006). There has been widespread concern over the status of bees worldwide in recent decades (Allen-Wardell et al. 1998; Kearns et al. 1998) with a number of publications documenting large scale declines (e.g. Corbet et al. 1991; Buchmann and Nabhan 1996; Kremen and Ricketts 2000; Biesmeijer et al. 2006).

There are a number of existing policy platforms that impact on the conservation of the world's bee fauna. These frameworks operate at a number of political and geographical hierarchical levels, from global to regional and national initiatives. All these policies must ultimately impact at the national and local level, which is where most actions are brought into practice.

7.11 Economic Value of Insect Pollination

Worldwide Estimated At U.S. $217 Billion. This figure amounted to 9.5% of the total value of the world agricultural food production. The study also determined that pollinator disappearance would translate into a consumer surplus loss estimated between €190 and €310 billion. The results of this study on the economic valuation of the vulnerability of world agriculture confronted with pollinator decline are published in the journal Ecological Economics. According to the study, the decline of pollinators would have main effects on three main crop categories (following FAO terminology); fruits and vegetable were especially affected with a loss estimated at €50 billion each, followed by edible oilseed crops with €39 billion. The total economic value of pollination worldwide amounted to €153 billion in 2005, which represented 9.5% of the value of the world agricultural production used for human food that year. The scientists also found that the average value of crops that depend on insect pollinators for their production was on average much higher than that of the crops not pollinated by insects, such as cereals or sugar cane (€760 and €150 per metric ton, respectively). The vulnerability ratio was defined as the ratio of the economic value of insect pollination divided by the total crop production value. This ratio varied considerably among crop categories with a maximum of 39% for stimulants (coffee and cocoa are insect-pollinated), 31% for nuts and 23% for fruits. There was a positive correlation between the value of a crop category per production unit and its ratio of vulnerability; the higher the dependence on insect pollinators, the higher the price per metric ton.

In the USA the value of crops pollinated by honeybees is placed at US$ 24 billion and the value of commercial bee pollination at US$ 10 billion. In Philippine the value of commercial bee pollination is about PhP 500 billion. Honey production in the USA is valued only at US$ 285 million. Countries like Canada, Germany, Italy, Japan, France, Great Britain, Australia, New Zealand, China, Argentina, Mexico, India, the Netherlands, Korea, Vietnam, to name a few, have developed the beekeeping industry, and in so doing their crop production has increased tremendously so that they have enough for their own consumption and for export. Take, for instance, Vietnam, which has two million hives of native and imported bees, this country boasts of the most productive crops in Southeast Asia. In Israel the beekeepers therein were able to commercialize the culture of bumblebees for crop pollination, particularly for greenhouses. They export these bees throughout the world. The fact is, there is no country on this planet that has productive crops without a developed beekeeping industry.

7.12 Monetary Losses in Crop Yields Due to Decline of Pollinators

Pollinator populations are under severe pressure worldwide because of man-made intensification in land use, including the use of pesticides and fertilizers. The majority of wild and crop plants are fully or partially dependent on pollinators for their reproduction. Loss of pollinators has already caused measurable declines in the populations of many wild plants in Europe. Brading et al. (2009) estimated that the annual cost to the Egyptian economy of losing its pollinators would be approximately LE 13.5 billion ($2.4 billion), 3.3% of the 2003 GDP. The results (Table 7.1) are dominated (46%) by the impact of pollinator loss on alfalfa, predicted to cause annual losses of more than LE 6 billion (more than US $ 1 billion). It is true that even if seed production were reduced, this might not affect the production of the fodder itself. However, in the long term, there would be a substantial impact. For valuable crops, such as melons, pollinator loss would also have a huge economic impact, an annual loss of almost LE 1.9 billion (US $ 333 million). Overall, according to these calculations, almost LE 13.5 billion (US $ 2.4 billion) would be lost every year. Since Egypt's GDP in 2003 was LE 411 billion (UNESCO 2007), this represents about 3.3% of GDP. They suggested that Egypt needs to implement strategies to prevent and reverse declines in pollinator populations. Changing farming techniques (i.e. reducing intensification, conserving pollinator-friendly areas), and enforcing restrictions on pesticide use would go a long way to achieving this (Table 7.8).

7.13 Economic Valuation of Bee Pollination Services

The demand for agricultural produce of good quality, low cost and predictable supply has led in the past century to massive transformations of rural environments as a result of the process of agricultural modernisation and the pursuit of increased food production. Modernisation has been characterized by externally developed packages of technologies that rely on externally produced inputs such as the use of high yielding varieties of crops and animal breeds, fertilizers, pesticides and machinery (Pretty 1995). A range of environmental and health impacts have also been associated with such practices. These include, *inter alia*, land use changes, habitat destruction, deforestation, soil erosion, water and air pollution and the loss of biodiversity (UNEP 2004).

One particular aspect of the impact of modern agriculture on the environment has been the reduction in insect pollination. Such services have an estimated annual global value of US$ 65–70 billion (Pimentel et al. 1997) and are growing given the demand by an increasing human population for food crops dependent on pollination. Modern agricultural systems therefore face a trade-off between the benefits of increasing production and the environmental costs associated with this increased production. Under such circumstances, environmental economic analysis can assist in ensuring that such trade-offs are made in such a way that social welfare is maximised.

Table 7.8 Monetary losses based on the average yield reduction that would be the consequence of loss of pollinators in Egypt for the crop production of 2004

Commodity	Latin name	Pollination effect	Pollination loss %	Value (m LE)	loss (m LE)	Notes
Field crops						
Clover, alfalfa	*Trifolium* spp., *Medicago sativa*	Seeds	65	9429.0	6128.9	Estimated % loss: dependent on seeds in long term
Cotton	*Gossypium* spp.	Parts eaten	25	3131.3	782.8	
Fodder (not alfalfa)	Various	Seeds	25	313.9	78.5	Estimated % loss
Lufa	*Luffa aegyptiaca*	Seeds	65	109.8	71.4	Probably 95% but some selfing occurs
Sunflower	*Helianthus annuus*	Parts eaten	25 1	96.5	24.1	
Linseed, flax, straw	*Linum usitatissimum*	Seeds	5	111.9	5.6	
Safflower seed	*Carthamus tinctoria*	Parts eaten	5	46.0	2.3	
Kenaf	*Hibiscus cannabinus*	Parts eaten	65	2.7	1.8	Probably needs pollinators
Egyptian lupin	*Lupinus albus*	Seeds	5	11.4	0.6	Mainly selfing
Sugar beet	*Beta vulgaris vulgaris*	Seeds	0	357.6	0	
Barley	*Hordeum* spp.	Independent	0	228.2	0	
Rice	*Oryza* spp.	Independent	0	6678.6	0	
Sugar cane	*Saccharum officinarum*	Independent	0	2191.1	0	
Sorghum	*Sorghum* spp.	Independent	0	1001.8	0	
Wheat	*Triticum* spp.	Independent	0	8903.9	0	
Maize/corn/ sweetcorn	*Zea mays*	Independent	0	7361.4	0	
Fruit crops						
Melon	*Cucumis melo*	Parts eaten	95	1031.8	980.2	
Mango	*Mangifera indica*	Parts eaten	65	1323.3	860.1	
Apple	*Malus 'domestica'*	Parts eaten	65	930.7	605.0	
Cantaloupe	*Cucumis melo*	Parts eaten	95	547.7	520.3	
Peach	*Prunus persica*	Parts eaten	65	623.3	405.2	
Watermelon	*Citrullus lanatus*	Parts eaten	95	399.5	379.5	
Apricot	*Prunus armeniaca*	Parts eaten	65	169.0	109.8	

(continued)

Table 7.8 (continued)

Commodity	Latin name	Pollination effect	Pollination loss %	Value (m LE)	loss (m LE)	Notes
Orange	*Citrus* spp.	Parts eaten	5	2166.6	108.3	
Banana	*Musa* spp.	Breeding potential	5	1345.4	67.3	Estimated % loss
Fig	*Ficus carica*	Parts eaten	25	258.4	64.6	
Pear	*Pyrus communis*	Parts eaten	65	91.3	59.4	
Guava	*Psidium guajava*	Parts eaten	25	235.9	59.0	
Strawberry	*Fragaria* spp.	Parts eaten	25	134.6	33.6	
Tangerine, mandarine	*Citrus* spp.	Parts eaten	5	595.1	29.8	
Plum	*Prunus x domestica*	Parts eaten	65	47.3	30.7	
Lemon, lime	*Citrus* spp.	Parts eaten	5	296.5	14.8	
Prickly pears (Cactus)	*Opuntia*	Parts eaten	25	48.9	12.2	
Custard apple	*Annona* spp.	Parts eaten	95	10.8	10.3	
Pomegranate	*Punica granatum*	Parts eaten	25	39.5	9.9	
Medlar (Loquat)	*Eriobotrya japonica*	Parts eaten	65	2.1	1.4	
Sour orange	*Citrus* spp.	Parts eaten	5	19.2	1.0	
Kaki persimmon	*Diospyros kaki*	Parts eaten	5	14.4	0.7	
Grapefruit, pomelo	*Citrus* spp.	Parts eaten	5	1.9	0.1	
Olive	*Olea europaea*	Independent	0	698.2	0	
Date	*Phoenix dactylifera*	Independent	0	1255.1	0	
Grape	*Vitis vinifera*	Independent	0	1912.5	0	
Herb crops						
Rosemary	*Rosemarinus officinalis*	Breeding potential	65	155.4	101.0	Estimated % loss
Marjoram	*Origanum majoranae*	Breeding potential	65	58.6	38.1	Estimated % loss
Karkadeh	*Hibiscus sabdariffa*	Parts eaten	65	51.4	33.4	Probably needs pollinators
Coriander	*Coriandrum sativum*	Parts eaten	65	48.9	31.8	
Basil	*Ocimum basilicum*	Breeding potential	65	38.9	25.3	Estimated % loss

Wormwood	*Artemisia* spp.	Seeds	65	37.1	24.1	Estimated % loss
Fenugreek	*Trigonella foenumgraecum*	Parts eaten	65	35.1	22.8	Estimated % loss
Parsley	*Petroselinum crispum*	Breeding potential	65	27.9	18.2	Estimated % loss
Cumin	*Cuminum cyminum*	Parts eaten	65	24.6	16.0	
Sage	*Salvia* spp.	Seeds	65	22.9	14.9	Estimated % loss
Oregano	*Origanum vulgare*	Breeding potential	65	22.9	14.9	Estimated % loss
Mint	*Mentha* spp.	Breeding potential % loss	65	20.5	13.3	Estimated % loss
Fennel	*Foeniculum vulgare*	Seeds	65	12.4	8.0	
Anise	*Pimpinella anisum*	Seeds	65	9.8	6.4	
Dill	*Anethum graveolens*	Seeds	25	24.1	6.0	Estimated % loss
Caraway	*Carum carvi*	Parts eaten	25	17.5	4.4	
Henna	*Lawsonia inermis*	Parts eaten	65	2.8	1.8	Estimated % loss
Other aromatics	Various	Seeds	25	1.5	0.4	Estimated % loss
Coriander, green	*Coriandrum sativum*	Seeds	65	0.4	0.3	
Nut crops						
Almond	*Prunus dulcis*	Parts eaten	65 8	201.2	130.8	
Sesame seed	*Sesamum orientale*	Parts eaten	25	157.4	39.4	
Peanut, groundnut	*Arachis hypogaea*	Parts eaten	5	437.6	21.9	
Pecan nut	*Carya illinoinensis*	Independent	0	3.8	0	
Vegetable crops						
Squash, courgette, Pumpkin	*Cucurbita* spp.	Parts eaten	95	367.4	349.0	
Cucumber	*Cucumis sativus*	Parts eaten	65	348.7	226.6	
Tomato	*Lycopersicon esculentum*	Parts eaten	5	3797.0	189.8	
Beans, broad, dry	*Vicia faba*	Parts eaten	25	757.9	189.5	
Aubergine (eggplant)	*Solanum melongena*	Parts eaten	25	398.4	99.6	
Potato	*Solanum tuberosum*	Breeding potential	5	1503.9	75.2	Estimated % loss

(continued)

Table 7.8 (continued)

Commodity	Latin name	Pollination effect	Pollination loss %	Value (m LE)	loss (m LE)	Notes
Beans, broad, Green	*Vicia faba*	Parts eaten	25	172.9	43.2	
Molokhayia	*Corchorus olitorius*	Seeds	95	43.6	41.4	Grown from seed, and pollination required
Okra	*Abelmoschus esculentus*	Parts eaten	25	140.4	35.1	
Onion	*Allium cepa*	Seeds	5	580.7	29.0	Estimated % loss
Soybean	*Glycine max*	Parts eaten	25	87.1	21.8	
Carrot	*Daucus carota*	*Seeds*	65	28.7	18.7	
Snake cucumber	*Cucumis melo*	Parts eaten	65	27.3	17.7	
Sweet peppers	*Capsicum annuum*	Parts eaten	5	248.2	12.4	
Artichoke	*Cynara scolymus*	Breeding potential	25	35.7	8.9	Estimated % loss
Cabbage	*Brassica oleracea capitata*	Seeds	5	174.3	8.7	Estimated % loss
Beans, kidney dry	*Phaseolus* spp.	Parts eaten	5	19.8	1.0	
Garlic	*Allium sativum*	Breeding potential	5	139.4	7.0	Estimated % loss
Beans, green	*Phaseolus* spp.	Parts eaten	5	137.0	6.8	
Sweet potato	*Ipomoea batatas*	Breeding potential	5	88.2	4.4	Estimated % loss
Taro	*Colocasia esculenta*	Breeding potential	5	72.2	3.6	Vegetatively reproduced, but pollination by flies
Radish	*Raphanus sativus*	Parts eaten	65	4.9	3.2	Annual, and mainly crosspollinated by insects
Turnip	*Brassica rapa rapifera*	Seeds	65	4.8	3.2	
Rocket	*Eruca vesicaria sativa*	Seeds	25	11.9	3.0	Estimated % loss
Beans, kidney, green	*Phaseolus* spp.	Parts eaten	5	49.8	2.5	
Broccoli, cauliflower	*Brassica oleracea botrytis*	Seeds	5	43.2	2.2	Estimated % loss
Capsicum (chilli pepper)	*Capsicum annuum*	Parts eaten	5	28.2	1.4	

Onion seed	*Allium cepa*	Seeds	5	23.1	1.2	Estimated % loss
Beans, Kidney, dry	*Phaseolus* spp.	Parts eaten	5	19.8	1.0	
Egyptian leek	*Allium ampeloprasum* var. *kurrat*	Seeds	5	9.1	0.5	Estimated % loss
Celery	*Apium graveolens*	Seeds	5	2.3	0.1	Estimated % los
Purslane (Rigla)	*Portulaca oleracea sativa*	Seeds	25	0.3	0.1	Estimated % loss
Leek	*Allium ampeloprasum* var. *porrum*	Seeds	5	0.4	0.02	Estimated % loss
Beetroot	*Beta vulgaris vulgaris*	Independent	0	0.8	0	
Chard	*Beta vulgaris vulgaris*	Independent	0	6.8	0	
Chick pea	*Cicer arietinum*	Independent	0	29.5	0	
Lettuce	*Lactuca sativa*	Independent	0	42.8	0	
Lentil	*Lens* spp.	Independent	0	8.8	0	
Pea	*Pisum sativum*	Independent	0	184.7	0	
Spinach	*Spinachia oleracea*	Independent	0	15.6	0	
Total potential losses						13446.1

There are approximately 5.7 LE to each $US. Pollination losses are taken from Klein et al. (2007); crop values from Economic Affairs Sector (2006)

7.14 Environmental Economics and Its Application to Pollination Services

Economics is about the efficient allocation of scarce resources which have diverse alternative uses. By applying economics to environmental considerations, we can expect to gain some insights into the desirability of incurring environmental costs and benefits given the overall objective of increasing social welfare. From a social welfare perspective, when calculating costs and benefits it is important to take any externalities into account. Externalities are the external costs of market exchange that exist when an activity by one agent causes an uncompensated gain or loss of welfare to another agent (Pearce and Turner 1990). An example of a negative externality is nitrate run-off from a farm affecting nearby residential water supplies. When analysing the financial benefit/cost of an activity, these externalities are usually ignored, leading to decisions that are not in the interest of society as a whole. A number of methods for overcoming such private/public divergences exist and may include regulations or taxes that aim to internalise such externalities. In the example given above, the farmer could be legally obliged to keep run-off below a certain concentration or be taxed per unit emission. In either case s/he would now be obliged to take the run-off into consideration in the farm-production process. Unfortunately, existing national accounting methods in most countries do not provide adequate incentives to do so as they tend to count only (farm) outputs but do not subtract any value for the associated decline in environmental quality (i.e. natural capital).

Approximately 30% of 1,500 crop plant species worldwide depend on pollination by bees and other insects (Buchmann 1996). Pollination services can therefore be understood as a positive externality since, with the exception of commercial pollination services, farmers do not pay for this service which results in increased production. By contrast, the destruction of pollination services by modern farming practices can be understood as a negative externality. Not only does the wider farming community have to find an alternative means of pollination, but the significant worldwide decline in both honey bees and native bees currently being experienced (Dias et al. 1999), also affects the pollination of wild species and has other ecosystem impacts which reduce society's overall welfare (given that a change in environmental quality can be considered to constitute a change in human welfare). Hence, in order to understand the economic importance of pollination services, it is necessary to consider this wide range of benefits which they provide and in order to do so an understanding of how such values can be calculated and the limitations/difficulties faced is required.

7.15 Methods for the Valuation of Pollination Services

A variety of pollination services valuation methods exist and have been applied across a range of crops and countries. The methods used have, *inter alia*, considered (Carreck and Williams 1999): the market value of all (Matheson and Schrader 1987) or some (O'Grady 1987) of the insect pollinated crops grown; others only the proportion attributable to honey bees (Borneck and Merle 1989). Some have included the value of crops grown from seed derived beepollinated plants (Martin 1975), the legume crops and livestock products dependent on them, or even those legumes that fix nitrogen and thereby reduce nitrate fertiliser requirements (Levin 1983, 1984). A relatively more sophisticated consumer surplus approach (i.e. one that measures changes in gains to consumers resulting from pollination induced price changes and thereby accounting for the effect of the existence of potential substitute crops) was also developed by Southwick and Southwick (1989, 1992).

7.16 Constrains to Valuation of Pollination Services

Unfortunately, there is insufficient information to allow such estimates to be made with great accuracy. In particular, more precise information is required, *inter alia*, on (i) the pollination needs of species and varieties of crops; (ii) the effectiveness of particular pollinators; (iii) the value of locally marketed crops which are usually ignored in national accounts; and (iv) a much clearer understanding of the farm-level costs and benefits of different crop and pollination systems (Dias et al. 1999). Considering the urgent need to address the issue of worldwide decline of pollinator diversity, the Conference of the Parties (COP) to the Convention on Biological Diversity (CBD) established an International Initiative for the Conservation and Sustainable Use of Pollinators in 2000 (decision V/5, section II) and requested the development of a plan of action. This action plan explicitly recognises the importance of an improved understanding of the economics of pollination and, in particular, calls for comprehensive analyses in selected production systems of the costs and benefits of alternative management practices and technologies on pollinator conservation and effectiveness, and the valuation of the goods and services provided by pollinator diversity including the pollination requirements and best pollinators of each crop species and the impact of pollinator presence/absence on fruit and seed yield. (CBD/SBSTTA-7 2001)

7.17 Results of Existing Pollination Services Valuation Studies

Nevertheless, despite these existing constraints to valuation, identifying the economic value of pollination services, even in terms of rough orders of magnitude, is important as supporting conservation by determining economic value is an effective approach for protecting ecosystem services. Those studies that have been carried out to date consequently provide useful ballpark estimates of the value of pollination services in a number of countries. These are summarized in Table 7.1. With few exceptions, these studies concentrate on the value of honey bees to agriculture using the following formula:

$$V \times P \times D$$

where
V = annual value of the crop
D = dependency of the crop on insect pollinators
P = proportion of (-effective-) insect pollinators that are honey bees.

Given the scarcity of information available, only the main agricultural crops for which national statistics are available are usually considered in calculating V and P is widely assumed to be 80%. The dependency variable D is calculated in a number of ways, varying from rough estimates of high (D = 0.9), medium (D = 0.5) or low (D = 0.1) or that of farmers opinions to more scientific estimates based on actual research.

The selected studies presented in Table 7.1 reveal that:

Most of the calculations are based on the pollination service contribution of honey bees, as it is argued that bees are responsible for the pollination of some 73% of the world's crops (Roubik 1995) and that the most widely used species in crop pollination is the honey bee. Despite the rough *Nature* of the estimates, it is clear from the magnitude of the results that the value of pollination services is significant. Furthermore, they are frequently many times that the value of bee products such as honey/wax, even though only the latter tend to be properly considered in national accounts. The value of commercial pollination services is also small compared to that provided by *Nature*, suggesting that the market for pollination services has to date only been able to capture a small fraction of the total value of pollination services.

Commercial pollination services have revealed that the benefit/cost ratio of renting pollination services can be very high for the farmer. The overall value of pollination services has grown significantly over the past decade, as a growing human population increases the demand for crops which happen to be dependent on pollination. Commercial pollination services are also likely to benefit in the future, as modern farming systems become more dependent on such services as natural pollinators decline. In addition to crops, seed production, livestock/pasture production and soil fertility can also be significantly influenced by pollination. Aesthetic/existence values for pollinators and the agroecosystems that they maintain through wild species pollination is also likely to be substantial (perhaps even larger than the values for agricultural crops) but have not been calculated to date.

The more sophisticated measures of pollination service value (e.g. the consumer surplus approach) recognise that a loss of bee pollinators may result in alternative crops being produced/consumed, thereby reducing the actual costs of such a loss. The actual cost would therefore depend on: (i) the extent to which crops are dependent on bees; (ii) the profitability of the current crop compared to the next best (non-pollinator dependent) crop; and (iii) the impact on market prices. There is therefore a need to consider both long-term costs and those that are only incurred during the transition period. It is also interesting to consider the incidence of costs. In countries such as Australia, costs would fall almost equally on consumers and producers.

7.18 Conclusions and Ways Forward

Identifying the economic value of pollination services is important as supporting conservation by determining economic value is an effective approach for protecting ecosystem services. In particular, taking the value of such pollination services into account can:

1. provide farmers with a better understanding of the relative costs and benefits of undertaking certain agricultural practices (e.g. agrochemical use, planting of monocultures, habitat conservation);

   However, a range of information constraints need to be overcome before existing pollination service valuation approaches can provide more precise estimates of these values of the type that will be better able to orient the decision-making process. In particular, this will require further research and capacity building with regard to the realisation of activities related to determining the pollination needs of different species and varieties of crops, the effectiveness of particular pollinators and an indepth understanding of the farm-level costs and benefits of different crop and pollination systems.
2. support the identification of conservation priorities and the design of cost-efficient bee diversity conservation programmes. The above economic valuation of pollination services together with an improved understanding of pollinator diversity and conservation costs could be used to design a cost-effective diversity maximizing conservation programme based on the Weitzman (1993) approach. Weitzman's original approach for combining information on the genetic distances between species of wild animal with their extinction probabilities and conservation costs was recently adapted by Simianer et al. (2003) to livestock breeds. Applying such a decision-support tool to pollinator species would allow a given conservation budget to be allocated in such a way as to maximize the diversity of pollinators conserved.
3. support the design of policy instruments and mechanisms that promote the sustainable use of bee pollinators. If the essential pollination services provided by bees are to be maintained, the recent decline in pollinator populations must be reversed. For national agricultural policies that aim to promote sustainable farming and meet consumer demand to be achieved, there must be greater appreciation of the role of pollinators in agriculture and conservation. This also requires the development of policies to halt the erosion of resources, particularly nest sites and food plants that bees require for their survival (Carreck and Williams 1998).

In this context, the development and dissemination of techniques and guidelines to promote agricultural practices that permit the conservation and sustainable use of pollinators need to be developed. Such guidelines should, *inter alia* (Dias et al. 1999): promote pollination as an integral component of sustainable agricultural systems and cropping practices. promote the maintenance and management of natural areas for pollinators in different farming systems and interfaces between ecosystems, such as forest crop margins, protected areas, etc. promote the restoration of pollinators and pollinator habitats following degradation an natural calamities. Nevertheless, while improved awareness among the principal actors (farmers, extensionists, researchers, policy-makers, etc.) influencing pollinator conservation and sustainable use may lead to improved practices, there is also a need to deal with the underlying economic incentives that currently lead to the loss of pollinators. Much clearer incentives for sustainable agriculture need to be provided (not only because of pollinator loss) by ensuring that modern agricultural practices internalise their environmental costs as much as possible. Land use restrictions and obligations to maintain natural habitats within agroecosystems need to be better enforced and the subsidies provided to intensive farming systems need to be reduced (e.g. agrochemical and fuel subsidies, cheap loans for farm machinery purchase, etc.). By contrast, farmers could be subsidised for adopting environmentally-friendly practices that generate positive externalities (e.g. habitat and wildlife conservation, watershed management, reforestation, bee-keeping).

This is also likely to require a significant change in the way national accounts are compiled, so that they properly consider changes in environmental quality and reflect these in indicators of national welfare (unlike the present measure of gross domestic product). The development of niche markets for sustainably produced farm products can also assist this process.

References

Abelson PH (1971) Opportunities in plant science. Science 172:3989

Alcorn SM, Mcgregor SE, Olin G (1962) Pollination requirements of the organ-pipe cactus. Cactus and succulent J 34:134–138

Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S et al (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Cons Biol 12:8–17

Allsopp MH (2004) Cape honeybee (*Apis mellifera capensis* Eschscholtz) and varroa mite (*Varroa destructor* Anderson and Trueman) threats to honeybees and beekeeping in Africa. Int J Tropi Insect Sci 24:87–94

Allsopp MH, Cherry M (2004) An assessment of the impact on the bee and agricultural industries in the Western Cape of the clearing of certain *Eucalyptus* species using questionnaire survey data. Pretoria (South Africa), National Government of the Republic of South Africa, Department of Water Affairs, Internal Final Report

Arizaga S, Ezcurra E (2002) Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette. Am J Bot 89:632–641

Arizaga S, Ezcurra E, Peters E, de Arellano FR, Vega E (2002) Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. I. Floral biology and pollination mechanisms. Am J Bot 87:1004–1010

Ascher J, Eardley C, Griswold T, Melo G, Polaszek A, Ruggiero M, Williams P, Walker K, Warrit N (2008) World Bee Checklist Project – update 2008–2009, manuscript (version 10 Sept 2008), [online] Integrated taxonomic information system. http://www.itis.gov/beechecklist.html. Accessed 13 Feb 2009

Baker HG, Hurd PD Jr (1968) Intrafloral ecology. Annu Rev Entomol 13:385–414

Bawa KS (1990) Plant-pollinator interactions in tropical rain forests. Annu Rev Ecol Systematics 21:399–422

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemûller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354

Bohart EG (1952) Pollination on native insects. USDA Year Book of Agriculture; 2302. United States Department of Agriculture, Washington, DC, pp 107–121

Borneck R, Bricout JP (1984) Evaluation de l'incidence économique de l'entomofaune pollinisatrice en agriculture. Bull Technique Apicole 11:117–124

Borneck R, Merle B (1989) Essai d'une evaluation de l'incidence economique de l'abeille pollinisatrice dans l'agriculture européenne. Apiacta 24:33–38

Bos MM, Veddeler D, Bogdanski AK, Klein A-M, Tscharntke T et al (2007) Caveats to quantifying ecosystem services: fruit abortion blurs benefits from crop pollination. Ecol Appl 17:1841–1849

Brading P, El-Gabbas A, Zalat S, Gilbert F (2009) Biodiversity economics: the value of pollination services to Egypt. Egypt J Biol 11:46–51

Buchmann S (1996) Competition between honey bees and native bees in the Sonoran desert and global bee conservation issues. In: Matheson A et al (eds) The conservation of bees. Academic, New York, pp 125–142

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington, DC/ Chicago, p 126

Burgett M, Rucker RR, Thurman WN (2004) Economics and honey bee pollination markets. Am Bee J 144:269–271

Carreck NL, Williams IH (1998) The economic value of bees in the UK. Bee World 79(3):115–123

Carreck NL, Williams IH (1999) The economic value of bees in the UK. Bee Farmers Association Bulletin 317:21–28

CBD/SBSTTA-7 (2001) Convention on biological diversity Seventh meeting held at Montreal, Canada between 12-16 November 2001 organised by Subsidiary Body on Scientific, Technical and Technological Advice, pp 152

Cook DC, Thomas MB, Cunningham SA, Anderson DL, De Barro PJ (2007) Predicting the economic impact of an invasive species on an ecosystem service. Ecol Appl 17:1832–1840

Corbet SA, Williams IH, Osborne JL (1991) Bees and the pollination of crops and wild flowers in the European Community. Bee World 72:47–59

Costanza R, D'Arge R, De Groot R, Farber S, Grasso M et al (1997) The value of the world's ecosystem service and natural capital. Nature 387:253–260

Costanza R, d'Arge R, de Groot RS, Farber S, Grasso M, Hannon B, Limburg K, Naeem RV, O'Neill J, Paruelo RG, Raskin P, Curtis IA (2004) Valuing ecosystem goods and services: a new approach using a surrogate market and the combination of a multiple criteria analysis and a Delphi panel to assign weights to the attributes. Ecol Econ 50:163–194

Curtis IA (2004) Valuing ecosystem goods and services: a new approach using a surrogate market and the combination of a multiple criteria analysis and a Delphi panel to assign weights to the attributes. Ecol Econ 50:163–194

Daily GC, Matson PA, Vitousek PM (1997) Ecosystem services supplied by soil. In: Daily G (ed) Nature's services: societal dependence on natural ecosystems. Island Press, Washington, DC, pp 113–132

Danforth BN, Sipes S, Fang J, Brady SG (2006) The history of early bee diversification based on five genes plus morphology. Proc Natl Acad Sci USA 103:15118–15123

de Lange WJ, Kleynhans TE (2007) Towards more inclusive long term bulk water resource management. Agrekon 46:371–397

Deciduous Fruit Producers Trust (DFPT) (2005) Key deciduous fruit statistics, 2005. Optimal Agricultural Business Systems, Paarl

Dias B, Raw A, Imperatriz-Fonseca V (1999) International pollinators initiative: the São Paulo declaration on pollinators. Report on the recommendations of the workshop on the conservation and sustainable us of pollinators in agriculture with emphasis on bees. Ministry of Environment, Brazil

Dobson AP, Lodge DM, Alder J, Cumming G, Keymer JE, Mooney HA, Rusak JA, Sala OE, Wall DH, Winfree R, Wolters V, Xenopoulos MA (2006) Habitat loss, trophic collapse and the decline of ecosystem services. Ecology 87:1915–1924

Economic Affairs Sector (2006) Study for estimating national agricultural income 2003/2004. Ministry of Agriculture and Land Reclamation, Economic Affairs Sector, Dokki, Giza, Arab Republic of Egypt

FAO (Food and Agriculture Organization of the United Nations) (2005) FAOSTAT Online. Available at: http://apps.fao.org. Accessed Jan 2005

Fleming TH, Sahley CT, Holland JN, Nason JD, Hamrick JL (2001) Sonoran Desert columnar cacti and the evolution of generalized pollination systems. Ecol Monogr 71:511–530

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London

Freitas BM (2005) Pollination in Brazil, a stock-taking. FAO Consultancy Report, FAO, Rome, 57

Gallai N, Salles J, Settele J, Vaissière BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68:810–821

Gates BN (1917) Honey bees in relation to horticulture. Mass Hort Soc Trans 1:71–88

Ghazoul J (2005) Buzziness as usual? Questioning the global pollination crisis. Trends Ecol Evol 20:367–373

Gibbs D, Muirhead I (1998) The economic value and environmental impact of the Australian bee keeping industry. Report, Australian Bee Keeping Industry, pp 1–47

Gill RA (1985) Biological control of *Echium* species. Industries Assistance Commission, Report No. 371. Australian Government Printer, Canberra

Gill RA (1989) An economic evaluation of alternative management practices and enterprise structures in the Australian beekeeping industry. University of New England, Armidale

Gill RA (1991) The value of honeybee pollination to society. Apiacta 26:97–105

Goodstein ES (2008) Economics and the environment. Wiley, Hoboken

Gordon J, Davis L (2003) Valuing honeybee pollination: a report for the Rural Industries Research and Development Corporation. RIRDC Publication No 03/077 RIRDC Project No CIE-15A:1-42

Grant V, Grant KA (1965) Flower pollination in the phlox family. Columbia University Press, New York/London, 180pp

Grant V, Grant KA (1979) The pollination spectrum in the southwestern American cactus flora. Plant Systemat Evol 133:29–37

Guidry NP (1964) Graphic summary of world agriculture. U.S. Department of Agriculture Miscellaneous Publication 705, 64pp

Hassan R, Scholes R, Ash N (eds) (2005) Ecosystems and human well-being: current state and trends, volume 1. Findings of the conditions and trends working group of the millennium ecosystem assessment. Island Press, Washington, DC

Hein L (2009) The economic value of the pollination service, a review across scales. Open Ecol J 2:74–82

Horticulture crop statistics (1998) The Technical Report for Ontario Horticultural Crops. Ministry of Agriculture, Food & Rural Affairs

Horsfall JG, Brandon GE, Brown WL (1972) Genetic vulnerability of major crops. National Academic Science, Washington, DC, 307pp

Johnson DB (1973) Meade, bees and externalities. J Law Econ 16:35–52

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant pollinator interactions. Annu Rev Ecol Syst 29:83–112

Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA et al (2007) Importance of pollinators in changing landscapes for world crops. Proc R Soc Lon B Biol Sci 274:303–313

Kremen C, Ricketts T (2000) Global perspectives on pollination disruptions. Conserv Biol 14:1226–1228

Kremen C, Adelman SW, Bugg B, Thorp R (2001) Conserving and restoring pollination services in organic farms of Yolo and Solano Counties, Northern California, Wildlife Conservation Society, Department of Biological Sciences, Stanford University, Stanford

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G et al (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol Lett 10:299–314

Levin M (1983) Value of bee pollination to US agriculture. Bull Entomol Soc Am 29:50–51

Levin MD (1984) Value of bee pollination to United States Agriculture. Am Bee J 124:184–186

Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. Bioscience 56:311–323

Martin EC (1975) The use of bees for crop pollination. In: Dadant Sons (ed) The hive and the honeybee. Dadant & Sons Incorporated, Hamilton, pp 579–614

Matheson A, Schrader M (1987) The value of bees to New Zealand's primary production. Ministry of Agriculture and Fisheries, Nelson, p 5

McGregor SE (1976) Insect pollination of cultivated crops. USDA agriculture handbook No. 496, US Government Printing Office: Washington, DC

Mcgregor SE, Alcorn SM, Olin G (1962) Pollination and pollinating agents of the saguaro. Ecology 43:259–267

Meeuse BJD (1961) The story of pollination. Ronald Press, New York, 1961. x + 243 pp. Illus. $7.50

Michener CD (2000) The bees of the world. John Hopkins University Press, Baltimore

Morse RA, Calderone NW (2000) The value of honey bees as pollinators of U.S. crops in 2000. Bee Cult 128:1–15

O'Grady JH (1987) Market failure in the provision of honey bee pollination: a heuristic investigation [dissertation]. University of Vermont, Vermont

Oldroyd BP (2007) What's killing American honey bees? PLoS Biol 5(6):e168. doi:10.1371/journal.pbio.0050168

Olmstead AL, Wooten D (1987) Bee pollination and productivity growth: the case of alfalfa. Am J Agri Econ 69:56–63

Pearce D, Turner K (1990) Economics of natural resources and the environment. Johns Hopkins University Press, Baltimore

Pimentel D, Wilson C, McCullum C, Huang R, Dwen P, Flack J, Tran Q, Saltman T, Cliff B (1997) Economics and environmental benefits of biodiversity. Bioscience 47:747–757

Prescott-Allen R, Prescott-Allen C (1990) How many plants feed the world? Conserv Biol 4:366–374

Pretty J (1995) Regenerating agriculture: policies and practice for sustainability and selfreliance. Earthscan, London

Randall A (1983) The problem of market failure. Nat Res J 23:131–148

Richards KW (1993) Non-Apis bees as crop pollinators. Rev Suisse Zool 100:807–822

Richards AJ (2001) Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? Annals Bot 88:165–172

Robinson WS, Nowogrodzki R, Morse RA (1989a) The value of honey bees as pollinators of U.S. crops. Am. Bee J 129:411–423

Robinson WS, Nowogrodzki R, Morse RA (1989b) The value of honey bees as pollinators of the United States crops. Am Bee J 129:477–487

Rocha M, Valera A, Eguiarte LE (2005) Reproductive ecology of five sympatric *Agave littaea* (Agavaceae) species in Central Mexico. Am J Bot 92:330–1341

Roubik DW (1995) Pollination of cultivated plants in the tropic. Food and Agriculture Organization, Rome. FAO Agricultural Services Bulletin 118:1–196

Roubik DW (2002) The value of bees to the coffee harvest. Nature 417:708

Rucker RR, Thurman WN, Burgett M (2005) Internalizing reciprocal benefits: the economics of honeybee pollination markets. North Carolina State University, Department of Agricultural and Resource Economics, Raleigh, Mar 6, 2005. Unpublished manuscript. Available at: http://legacy.ncsu.Âedu:8020/classes/ecg701001/personal/Internalization_of_Reciproca_Benefits-full_March_2005.pdf

Schoonhoven LM, Jermy T, van Loon JJA (1998) Insect-plant biology: from physiology to evolution. Chapman & Hall, London

Scott-Dupree C, Winston M, Hergert G, Jay SC, Nelson D, Gates J, Termeer B, Otis G (1995) A guide managing bees for crop pollination. Canadian Association of Professionals Apiculturists. Canadian Department of Agriculture, 41p

Simianer H, Marti S, Gibson J, Hanotte O, Rege JEO (2003) An approach to the optimal allocation of conservation funds to minimize loss of genetic diversity between livestock breeds. Ecol Econ 45:377–392

Slauson LA (2000) Pollination biology of two chiropterophilous agaves in Arizona. Am J Bot 87:825–836

Slauson LA (2001) Insights on the pollination biology of *Agave* (Agavaceae). Haseltonia 8:10–23

Soldatov VI (1976) Economic effectiveness of bees as pollinators of agricultural crops. In: Kozin RB (ed) Pollination of entomophilous agricultural crops by bees. Amerind Publishing Co, New Delhi, pp 125–134

Southwick L, Southwick E (1989) A comment on. Value of honey bees as pollinators of U.S. crops. Am Bee J 12:805–807

Southwick EE, Southwick L (1992) Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. J Econ Entomol 85:621–633

Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. Oecologia 121:432–440

Steffan-Dewenter I, Potts SG, Packer L (2005) Pollinator diversity and crop pollination services are at risk. Trends Ecol Evol 20:651–652

Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Thorp RW (2000) The collection of pollen by bees. Plant Syst Evol 222:211–233

Thurston HD (1969) Tropical agriculture – a key to the world food crisis. Bioscience 19:29–34

Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. Nature 418:671–677

Tinker J (1971) One flower in 10 faces extinction. New Sci Sci J 50(751):408–413

Turpie JK, Heydenrych BJ, Lamberth SJ (2003) Economic value of terrestrial and marine biodiversity in the Cape Floristic region: implications for defining effective and socially optimal strategies. Biol Cons 112:233–251

UNEP (2004) Biodiversity. In: Global environmental outlook 4 – environment for development. Progress Press Ltd., Malta, pp 157–192

United Nations Scientific and Cultural Organisation (2007) Biodiversity. Walter Erdelen Françoise Rivière and Ana Luiza Machado Pinheiro compiled, pp 34

Valiente-Banuet A, Arizmendi MC, Rojas-Martínez A, Domínguez-Canseco L (1996) Ecological relationships between columnar cacti and nectar feeding bats in Mexico. J Trop Ecol 12: 103–119

Waser NM, Ollerton J (eds) (2006) Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago

Watson L, Dallwitz MJ (1992) The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: 2 June 2006. http://delta-intkey.com/

Weitzman M (1993) What to preserve? An application of diversity theory to crane conservation. Q. J. Econ. 108(1):157–183

Williams IH (1996) Aspects of bee diversity and crop pollination in the European Union. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) The conservation of bees. Academic, New York, pp 63–80

Winfree R, Williams NM, Dushoff J, Kremen C (2007) Native bees provide insurance against ongoing honey bee losses. Ecol Lett 10:1105–1113

Winston ML, Scott CC (1984) The value of bee pollination to Canadian agriculture. Can Beekeeper 11:134

World Bank (2003) World development indicators. World Bank, Washington, DC

Ya T, Jia-sui X, Keming C (2003) Hand pollination of pears and its implications for biodiversity conservation and environmental protection – a case study from Hanyuan county, Sichuan Province, China. College of the Environment, Sichuan University, Sichuan, China. Available: http://www.fao.org/Ag/AGP/AGPS/C-CAB/Castudies/pdf/6-005.pdf. Accessed 3 Jan 2007

Chapter 8
Planned Honeybee Pollination for Crop Production

Abstract The purpose of this chapter is to examine and evaluate systems for maintaining honey bees on crops that are insect pollinated. Factors that attract honey bees to flowers, floral competition, and methods for increasing numbers of pollen and nectar foragers and techniques for attracting honey bees to, and retaining them on, target crops.

8.1 Introduction

Many commercially important legume, fruit, vegetable, and nut crops require cross-pollination to set seed. Such plants utilize the services of various agents, among them insects, to transfer pollen from anthers to stigmas. The "reward" that insect pollinators receive for this service is food, particularly nectar and pollen. This reward is often "advertised" through floral markers (or cues) such as color, odor, and form. Despite such markers and rewards, the food crop that requires pollination (i.e. target crop) is often less attractive, or rewarding, than other plants flowering in the same area. For this reason, insect pollinators frequently desert the target crop when pollination is urgently required, and there is a consequent loss in yield.

The purpose of this chapter is to examine and evaluate systems for maintaining honey bees on crops that are insect pollinated. Honey bees are one of the major insect pollinators but pose special management problems because they forage on a wide range of host plants. They continuously monitor, sample, and pool information about the most rewarding food sources available and have a highly developed system, of recruiting nest mates to these sites. Thus under certain conditions, maintaining honey bees on target crops is extremely difficult.

This chapter deals with honey bees primarily at the colony level. Factors that attract honey bees to flowers, floral competition, and methods for increasing numbers of pollen and nectar foragers are discussed first. This is followed by a review of techniques for attracting honey bees to, and retaining them on, target crops. Information about honey bees relevant to this discussion has been reviewed under

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the following subject areas: social, foraging, and recruitment behavior (Eickwort and Ginsberg 1980; Gould 1976; Hassell and Southwood 1978; Michener 1974; Ribbands 1953; Von Frisch 1967; Wells and Wells 1984; Wilson 1971), foraging energetics (Heinrich 1981; Pyke et al.1977; Waddington and Holden 1979), plant pollinator interactions (Baker and Hurd 1968; Faegri and van der Pijl 1971; Kevan and Baker 1983; Proctor and Yeo 1973; Real 1983), and pollination (Crane and Walker 1984; Free 1970a, b; McGregor 1976; Richards 1978). For convenience in this review the term “maintenance ”is used to include the attraction of honey bees to the target crop and their retention on that crop and the word “bee” refers to honey bee.

8.2 Management of Honey Bees for Pollination

The bees, especially honey bees, are the major pollinators of cultivated crops. Most fruit, small seed and many vegetable crops require pollination for the production of economic yields. The value of the honeybee as a pollinator is far greater than its value as a honey producer. Not all crops need pollination. Some can produce fruit without fertilization of the flower. Some flowers are self pollinated, which means that pollen is transferred from the anther to the stigma of the same flower or flowers on the same plant variety. Although this transfer can be achieved by wind or rain, insect pollinators are the most effective.

Other flowers are cross pollinated. In these cases, the pollen is transferred from the anther of a flower on one plant variety to the stigma of a flower on a different plant variety. Plants requiring cross pollination usually cannot produce fruit from their own pollen. Again, the most important and efficient carrier of pollen from the anther to the stigma for such plants is the honeybee.

The flowering plants and honeybees co-evolved long before the appearance mankind on the earth. It is a known fact that only where pollinators lived could plant evolves a mechanism of reproduction that involved pollination. A majority of 2,50,000 flowering plants on the earth has amazingly complex relationships with the bees and to other less important pollinators. Detailed reviews on crop pollination by bees has been done by several workers including Bohart (1972), Abrol (1991, 1997, 2008, 2009, 2010a, b, 2011), Sihag and Mishra (1995); Roubik (1995) and Kumar et al. (1998). Bees have evolved the following characters, which make them the most efficient pollinators: branched hairs capable of carrying up to five million pollen grains., intricate pollen baskets., specialized mouth parts., honey sac., bees wax., honey combs for storing nectar and pollen., specialized communication behavior., efficient distribution over available territory. Bees, as we see became the ideal and mostly the only pollinators. Bees are not guests but thoroughly adopted symbionts, because they feed and rear their young ones on the products gathered from the flowers and in turn bees provide cross pollination for plants. There are more than 20,000 bee species in the world, about 400 being social or eusocial 400 are parasitic and remainders are solitary.

8.3 Honey Bees as Pollinators

8.3.1 Domesticated Species

There are two most important hive species. European honey bee, *Apis mellifera* L. is a native of old world except tropical Asia and introduced to most parts of the new world. It has a foraging range of 3 km. The Indian hive bee, *A. cerana indica* F., a native of tropical Asia is prevalent in a wide region with a flight range of 1.5 km. It is even a better pollinator than *A. mellifera* because of their longer foraging period and many other characters Sihag and Mishra (1995).

8.3.2 Wild Species

Two other species, *A. dorsata* (rock/giant bee) and *A. florea* (little bee) are also native of tropical Asia and efficient pollinators. But these cannot be managed for long time, as they do not live in artificial hives. Their foraging range is 2.5–4.0 and 1 km, respectively.

8.3.3 Non-Apis Bees

Some other wild non-Apis bees are recorded from different countries on different crops serving as important pollinators (Crane and Walker 1983) (Table 8.1).

Small amounts of pollen are collected by honey bees in tomato and they require buzz pollination. So bumblebees can do the better job than honey bees. However in closed conditions two colonies are required in an 800–1,000 m^2 greenhouse (Houbaert and Jacobs 1992).

Table 8.1 Important non-*Apis* wild bee pollinators

Sr.No.	Family	Important genera	Number of species
1	Megachilidae	*Anthidium, Litburgus, Megachile* (leaf cutler bees), *Osmia*	20
2	Anthophoridae	*Anthophora, Mellisodes, Nomada, Xylocopa*	13
3	Apidae	*Bombus, Euglossa, Melipona, Trigona*	6
4	Halictidae	*Aagapostemon, Dufournea, Halicutxis, Nomia* (alkali bees)	5
5	Andrenidae	*Anderna, Panurginus, Pseudopanurginus, Perdita*	4
6	Melittidae	*Hesparapis, Melitta*	2
7	Colletidae	*Colletes, Hylaeus*	2

8.3.4 Stingless Bees

Stingless bee of the genus *Trigona* and *Melipona* (more than 50 species) with a wide foraging range on cultivated, fruits and other crops are important pollinators. In *Nature* they are found in burrows, holes, cracks and crevices in the soil, trees and other dwellings. They have been successfully managed in small wooden boxes and used efficiently in crops like litchi. They resemble honeybees in behavior. They are especially effective in crops on small flowers.

8.4 Management of Honey Bees for Pollination

Due to their morphological characters, social behaviour and management practices followed by our farmers, honeybees have become the most important and mostly the only pollinators of the crops. The uncertainty of populations and the difficulty in maintaining and using solitary bees, bumblebees and other pollinators' places all the onus of planned pollination on honeybees alone. The following points are most important to consider a colony for pollen foraging and getting desired pollination outputs.

8.4.1 Foraging Strength of Colonies

Honeybee colonies used for pollination must be strong and healthy and managed to ensure that the maximum number of bees visit the crop to be pollinated. In order to get maximum honey and pollination benefits from a colony, it must be full-sized and populous not a growing one- as the brood/bee ratio diminishes in it, so a greater proportion of bees is available for foraging. An effective pollination hive should have at least 30,000 bees, of which 12,000 would usually be foragers. Matheson (1986, 1991) suggested that a colony used for pollination should contain at least seven frames with 60% brood (at least 25% in egg or larval stage) in the brood chamber, headed by a young prolific vigorous queen with a high egg laying capacity (free of bee diseases), at least 12 frames covered with bees, sufficient empty combs for expansion and enough honey and pollen stores to sustain it. Separate colony strength standards were also recommended for field colony and orchard colony by Roubik (1995).

8.4.2 Pollination Requirement and Concentration of Colonies

The number of colonies needed per hectare of crop will depend on local conditions including the number of honeybees and other pollinators already present, the size of the crop and the presence of competing crops of the same and different species like

Table 8.2 Pollination requirements of crops

Sr.No.	Crops	Pollination requirement (number of colonies/ha)
1	Apple	2–3
2	Almond	5–8
3	Citrus	2–3
4	Coconut	2–3
5	Grape	2–3
6	Guava	2–3
7	Mango	2–3
8	Papaya	2–3
9	Turnip	2–5
10	Cauliflower	5
11	Lucerne	3–6
12	Onion	2–8
13	Water melon	1–5
14	Musk melon	1–5
15	Mustard	3–5
16	Pumpkin	1–2
17	Sesame	2–3
18	Brussels sprout	5
19	Sunflower	2–4
20	Cotton	2–6
21	Broccoli	5

weed species. In Southwestern Haryana, the population of natural pollinators especially the solitary bees is so high that it suffices to great extent the pollination requirement of mustard crop. There is a difference in the number of colonies that could be profitably maintained for honey and the numbers necessary for pollination in a crop. Chaudhary (1998) has summarized the pollination requirement of different crops as given below(Table 8.2).

It is generally recommended to have around 2.5 colonies/ha but it will depend on many factors like concentration of flowers, their attractiveness, competing insects and crops, species, place, percentage of flowers open at a time, etc. and the number of colonies required may be increased or decreased accordingly.

8.4.3 Foraging Efficiency of Colonies and Their Distance from the Crop

Honeybees are capable of foraging at an enough honey and pollen stores to sustain it. Considerable distance from their hives but their efficiency is indirectly proportional to the distance covered. Generally foraging range is 2.5 km for *Apis mellifera*, 1.5 km for *A. cerana*, 3 km for *A. dorsata* and 1 km for *A. florea*. *Apis mellifera* have been observed to forage up to 11.3 km but foragers were concentrated within 0.6 km of their hives. The yields of the crops are more when the colonies are kept up to a distance of 0.5 km and decrease to almost half at a distance of 1.0 km and these impacts are even greater in poor season. The number of foraging bees on a crop diminishes with increase in the distance from the hive (Free 1993).

8.4.4 Moving Colonies to Crops

It is advisable to take as short migrations as possible because of the risks involved in long distance migration which result in killing of brood and low foraging efficiency. The settling and arrangement of colonies after migration is very important. Formal arrangement with identical lives should be avoided as it may result in drifting of foragers especially during their first flight which may result in weakening of some colonies and strengthening of others, lowering the mean foraging potential, honey production and pollination efficiency. The colonies should be arranged irregularly in different directions and spacing. They should be put near landmarks and windbreaks and different colored boards may be placed above the entrance.

8.4.5 Time of Moving Colonies on Crops

The origin of food stores of a colony plays important role in determining the species as they did before moving them. But the predominance of one species at the new site results in changing their foraging behavior. Therefore, colonies should be moved to the crop needing pollination only when it is sufficiently flowering. Hives should not be placed in a crop until at least 5–10% of the crop is in flower. If placed too early, the bees may find an alternative nectar source and not return to the target crop.

Care must be taken to avoid the blooming of too many flowers as an important part of the crop may fail to be pollinated. It is practical to move a few colonies to the crop at the beginning of flowering and the rest when more flowers have bloomed (Sale 1983).

8.4.6 Arrangement of Colonies

Arrangement of colonies in crop is very important to ensure uniform distribution of foraging bees which will depend on the plant species, amount of nectar and pollen available/unit area, weather conditions and physical features of the area like topographic gradients, wind direction, shelter, etc. Placing colonies in the middle of the crop increases foraging area (Free 1993). Ideally colonies should be distributed singly over the crop which is always not feasible and practical. In large crops, it is preferable to place hives in small groups, in and around the crop, rather than in one large group. This ensures a better coverage of the crop. So, colonies should be kept in small groups of 4–5 at distances of about 200 in throughout the crop to provide sufficient overlap of foraging area between different groups. The colonies should face the direction of sun in the winter and should be sheltered during summer and rainy season. Windbreaks (natural and artificial) greatly benefit during chilly and windy conditions (Kumar et al. 1998). Hives should not have a solid barrier, such as a hedge, building or wall, between them and the target crop. They need to be placed on a site which is accessible to the beekeeper at all times, for servicing. Hives should also be sheltered from prevailing winds if possible. Bees generally prefer to work up a hill and along rows. Placement of hives should depend on whether the bees are required to work along rows or across rows.

Alternative nectar sources to the crop to be pollinated should be identified and, if possible, destroyed. If this is not possible, the hives should be sited on the side of the target crop furthest from the undesirable nectar source.

If the target crop is to be irrigated, hives should be placed in a position where they will not be sprayed by the irrigator. It would be better still if the crop were irrigated in the evening when the bees were not flying, as bees do not like working in wet conditions.

8.4.7 Effect of Weather

Weather is the key to maximum use of the pollinating force. Bees rarely fly when the temperature is below 55°F or the wind is more than 15–20 miles per hour. The stronger the colony, the lower the temperature at which the bees may initiate flight. Strong colonies do little pollinating below 55°F and weak ones do little below 60°F. Cool cloudy weather and threatening storms greatly reduce bee flights. The poor weather, bees foraging at more distant locations will remain in the hive and only those that have been foraging nearby will be active. Therefore, over an extended period of inclement weather, colonies may require greater distribution to get adequate coverage.

Bad weather also presents hazards to the plant. Spring frosts can kill fruit bloom, and temperatures of 40–50°F retard pollen germination and tube growth. Fertilization failure may result. If the weather is hot and dry or windy, stigmas may dry out so that deposited pollen does not germinate. Pollen release may be hindered by prolonged rains.

8.4.8 Directing Bees to Crops

Attempts to ‘direct’ the bees to the crops to be pollinated either by feeding them sugar syrup containing the scent of the crop or flowers immersed in the syrup or by spraying the crop with sugar syrup have met with a limited success. Recently the use of “Bee attractants” (Bee-Q and Bee-here) or attractive odors present in the pollen on high value crops met with varied success. Their application though increased forager population but they may be diverted from the flowers and spend much time in searching the plant leaves and sterns for pollen but of no avail (Patil et al. 2000).

8.4.9 Increasing the Attractiveness of Crops

The more appropriate approach for improved pollination is to increase attractiveness of the crop itself to the bees, by developing plant strains with more accessible nectar or pollen, or developing strains producing more nectar. Unfortunately, this factor is not a priority with the breeders and the recent hybrids (of berseem and sunflower) produce very low amount of nectar, further reducing their attractiveness to the bees (Kumar et al. 1998). Onion can be honeybee-pollinated, mainly for seed production, though bees will fly over flowering onion crops to other crops in flower. Onion nectar contains about ten times more potassium than most other plants (3,600–13,000 ppm). Potassium can make the nectar unattractive (that is, repellent) to honeybees in high concentrations. Honeybees forage entirely for nectar, but become heavily dusted with pollen in the process (Kumar and Gupta 1993; Prasad et al. 2000).

8.4.10 Increasing the Proportion of Pollen Gatherers

Increasing the proportion of pollen gatherers, which are more efficient pollinators than the nectar gatherers in a colony, is always beneficial. To increase the proportion of pollen gatherers Goodwin et al. (1991) have suggested several ways. The foragers may be stimulated to gather more pollen by manipulating colony by placing brood frames opposite to the hive entrance or by removing pollen stores from the colonies or by using pollen traps. Another method is by feeding sugar syrup to colonies which will increase its pollination efficiency by greatly increasing the number and proportion of pollen-gatherers.

8.4.11 Using Man-Made Devices to Increase Pollination

Devices like “pollen dispensers” or “pollen inserts” have been used in high valued crops like fruit trees. They are placed at the hive entrance containing hand collected pollen of required compatible cultivar. The out-going bees are forced to carry this pollen. In sunflower the male sterile plants caged with a honeybee colony and a dispenser with pollen had similar percentage of flower set, seed yield and seed oil to the male fertile plants. Newer and more effective dispensers have been developed now using bee collected pollen (Sasaki 1985). The simple “pollen enhancer” having row of soft nylon bristles at the entrance developed by Free et al. (1991) too are effective for the pollination of self in compatible tree fruits and hybrid seed production.

8.4.12 *Use of Synthetic Pheromones*

Use of synthetic queen pheromones to stimulate foraging (especially pollen collection) and Nasanov pheromone whose two components (citral and geraniol) have been reported to increase honeybee foraging in onion (Woyke 1981) and yield of apple (Ohe and Praagh 1983) hold a good promise. Use of synthetic alarm pheromones, a few minutes before insecticide application may help in repelling them from the crop thereby reducing bee loss, and some other pheromones need further refinement.

8.4.13 *Floral Attractants and Floral Competition*

Honey bees locate flowers by sight and odor. They respond to visual nectar guides (Free 1970a, b) and to color of petals in the ultraviolet, blue-green, and yellow spectral range (Kevan and Baker 1983; Prokopy and Owens 1983). Plant height and size of flowers, inflorescences, and floral masses, coupled with the broken outline and movement flowers, also provide markers or cues for bees (Faegri and van der Pijl 1971; Proctor and Yeo 1973; Prokopy and Owens 1983; Free et al. 1984). After visually locating flowers and approaching them, bees respond to floral odors that include olfactory nectar guides (Zaurolov 1981), as well as to pollen odors (Hopkins et al. 1969).

Bees are attracted to flowers that are available in large numbers, that have readily accessible pollen and/or nectar, and that are rewarding in terms of energy (Heinrich 1981; Kevan and Baker 1983; Pyke et al. 1977; Waddington and Holden 1979). The quantity of nectar and the concentration and type of constituent sugars in floral nectars determine their attractiveness to bees (Heinrich 1981; Kevan and Baker 1983; Zaurolov 1981), but little is known about what attracts bees to particular pollens (Hopkins et al. 1969). Although pollen and nectar are presented at different times of day different plant species (Free 1970a, b) and in different sites, bees are able to locate and collect these foods because they have a well-developed time sense and excellent orientation and navigational abilities (von Frisch 1967). The proportion of pollen to nectar that is collected is largely determined by the current "needs" of the colony (Lindauer 1952; Ribbands 1952). Bees often desert commercially important target crops for other more attractive pollen- and nectar-yielding species within flight range (Bohart 1957; Free 1970a, b; McGregor 1976). Additionally, there are numerous examples of intervarietal (intraspecific) and interspecific competition among plants for the attention of bees (Brittain 1933; Free 1970a, b).

8.4.14 *Increasing the Numbers of Pollen and Nectar Collectors*

Pollen collectors are usually more valuable pollinators than nectar collectors (Free 1970a, b), so attempts have been made to increase their numbers and maintain them on commercial crops. Their value as pollinators relates primarily to their fidelity to floral species and to their method of foraging in relation to floral structures

(Free 1970a, b; Ribbands 1953). These largely determine the amount of pollen that adheres to the bee's body and the likelihood of its deposition on other flowers of the same species. Pollen is utilized by adult bees and for producing food for larvae (Dietz 1978); colonies require about 20–30 kg of pollen per season for these purposes (Dietz 1978; Spencer-Booth 1960).

Foragers from colonies with brood are stimulated to collect pollen (Al-Tikrity et al. 1972a, b; Barker 1971; Free 1967). The proportion of bees collecting pollen is directly correlated with the level of egg laying by the queen (Cale 1968) and the amount of brood present (Filmer 1932; Free 1967). Thus, providing colonies with extra frames of brood increases pollen collection (Free 1965a, b, 1967; Rakhmankulov 1957) but may not be feasible because of the labor costs and extra colonies required to provide the brood (Free 1970a, b). The odor of brood, contact with bees that are "tending" brood, and/or direct contact with brood (particularly larvae) increases pollen collection (AI-Tikrity et al. 1972a, b; Free 1979a, b; Rakhmankulov 1957), as does the presence of a queen and either worker larvae or larval extracts (Jaycox 1970a, b). However, increased pollen collection is not wholly dependent on the presence or absence of a queen (Louveaux 1958) or synthetic queen pheromones (Velthuis 1970).

Pollen shortages, regardless of how they are created, affect pollen collecting by the bees of a colony. Pollen collection is increased when combs of pollen are removed from colonies (Rakhmankulov 1957) and when pollen traps, attached to hive entrances, remove pollen loads from returning bees (Moriya 1966; Stephen 1958; van Laere and Martens 1971). Although removing pollen loads from foragers decreases their tendency to collect pollen (Free 1970a, b), other bees in the colony may respond to the pollen shortages. Providing pollen or pollen supplements to colonies to encourage brood rearing results in decreased pollen collection by the bees of a colony (Barker 1971; Free 1967; Moeller 1972). Colonies fed sucrose water solutions ("sugar syrup") or honey during spring or summer collect more pollen (Barker 1971; Free 1965a, b), and this is particularly useful for pollinating crops that flower the spring.

Besides their value as honey producers, nectar-collecting .bees are also important pollinators of such crops as alfalfa, sunflower, plum, pear, peach, apricot, and sweet cherry (Bohart 1957; Free 1970a, b; Martin and McGregor 1973; McGregor 1976). Although the factors that influence bees to collect pollen are fairly well understood, few data are available about what influences bees to collect nectar. The absence of a queen in a colony has been shown to result in enhanced nectar collection (Kashkovovskii 1957), reduced collection (Genrikh 1958), or to have no effect (Lfffler 1961). Bees from colonies that are rearing a new queen collect less nectar (Ribbands 1952), whereas pheromones of the queen, synthetic queen pheromones, or extracts of worker larvae stimulate nectar collection (Jaycox 1970a, b).

8.4.15 Attractants and Sprays

Scented sucrose solutions Sugar syrups, in combination with floral scents, are used to induce bees to visit crops. Success in "directing" bees to crops, using containers of sugar syrup covered with flowers of the target crop (Gluslakov 1958; von

Frisch 1967), prompted the feeding of sugar syrups in which flowers of the target crop had been soaked. Scout bees from fed colonies search for the target crop and communication formation about it to potential foragers (Free 1958; von Frisch 1967). Bees can be directed to a variety of field and orchard crops using this technique (Gluslakov 1958; von Frisch 1967). In some Studies increased yields resulted (Bretschko and Bullmann 1966; Pritsch 1959; Skrebtsova 1957), but in others there was no increase in yield and no increase in pollen foragers or amounts of pollen collected (Free 1958, 1970a, b).

Feeding scented sugar syrups outside the hive is more effective in directing bees to crops as measured by numbers of bees performing "recruitment dances" (von Frisch 1967) and increases in numbers of bees visiting target crops (von Rhein 1957). Scented sugar syrups fed to bees next to colored boards attract bees to certain crops (Lopatina and Nikitina 1960). Also, various landmarks id bees in locating scented syrups that attract bees as they are moved to target crops (Cumakov and Fejf 1959). Distilling essential oils from blossoms and feeding these in sugar syrup to colonies, or feeding sugar syrup with perfumes, increases numbers of foragers at a site (Johnson and Wenner 1970) and increases pollen collection and crop yields (Hohmann 1970; Kurennoi and Barabash 1966).

Directing bees to target crops is not possible if the crops have little or no pollen or nectar available, nor can bees be directed to new crops if they are less rewarding than the ones currently being foraged (Gluslakov 1958; von Frisch 1967). Despite differing opinions, directing bees to crops seems feasible particularly if the odor of the target crop is incorporated into the colony's food stores (Free 1969).

8.4.15.1 Carbohydrate Sprays

Spraying sugar syrup on crops increases numbers of bees on them (Free 1965a, b; von Frisch 1967). However, most bees collect the syrup rather than pollen or nectar from the flowers themselves (Free 1965a, b; Stephen 1958). Bees are also attracted to crops sprayed with honey solutions (MacVicar et al. 1952) or sugar solutions with fennel aniseed oil added (Cumakov 1955) but not to crops sprayed with molasses solutions (Stephen 1958). Only rarely are increases in yield reported when sugar sprays are used on crops (van Zyl and Strydom 1968).

8.4.15.2 Food Supplement Sprays

Beeline® is a wettable powder food supplement that has been tested as a bee attractant to enhance crop pollination (Brakefield 1980). Beeline®, mixed with water or sucrose solutions, is no more attractive to bees than water or sucrose solutions alone (Margalith et al. 1984). Although cucumber yields may slightly higher when sprayed with Beeline® (Margalith et al. 1984), other treated crops show increase in bee visits or yields (Belletti and Zani 1981; Burgett and Fisher 1979; Margalith et al. 1984).

8.4.15.3 Pollen Attractants

Foragers from individual colonies show preferences for certain pollens in the field (Free 1959; Jay 1974, 1986; Nye and Mackensen 1965; Olsen et al. 1979; Wawryn 1973) and for certain pollens offered in containers as choice experiments (Boch 1982; Campana and Moeller 1977; Doull 1966, 1974). Although pollens differ in their nutritional value (Louveaux 1959; Maurizio 1950), bees do not collect them on this basis (Dietz 1978; Doull 1966) nor on the basis of age, moisture content, or color (Doull 1966).Pollen odors attract bees (Levin and Bohart 1955, 1957), and pollen is more attractive than other foods containing protein (Spencer-Booth 1960; Wahl 1963, 1966). The first pollen attractants identified were phytosterols (Hiigel 1962; Louveaux 1959), some of which were extracted in hexane and di-ethyl ether (Taber 1963). Adding pollen extracts to artificial protein diets makes them attractive to bees (Doull 1974; Hohmann 1970; Robinson and Nation 1968). A chemical food marker in pollens has been identified as *octadeca-trans-2, cis-9, cis-* 12-trienoic acid (Hopkins et al. 1969). It is possible that placing this material on crops would assist in maintaining bees on them.

8.4.15.4 Pheromones and the Chemicals

This long been suggested that odors from glands (e.g. the Nasonov gland located on the dorsal side of the abdomen) of worker bees might attract bees to crops (Sladen 1901). When the Nasonov gland is exposed and its odor dispersed, disoriented bees can locate their hive entrance (Ribbands and Speirs 1953; Sladen 1901) and swarms are attracted to temporary landing or new nesting sites (Morse and Boch 1971).

When foraging worker bees feed on sugar syrup in dishes, they expose their Nasonov gland and this attracts other bees (Sladen 1901; von Frisch 1967). The gland is also exposed when bees collect water (Free 1968a, b; Free and Williams 1970, 1973,1974). Components of the Nasonov gland secretion consist of seven terpenoids (Free and Nuttall 1968). Of these, the three most important for attracting bees appear to be geranic acid, geraniol, and (E)-citral, any one which stimulates foragers to release their own Nasonov pheromones, thus making a site even more attractive to bees (Free and Nuttall 1968). Some attempts to attract bees to crops by spraying them with Nasonov gland components have been unsuccessful (Free 1979a, b) while others, using citral and geraniol in sucrose solutions, show promise (Waller 1970). Citral and geraniol also mask repellent odors, attract bees to crops, and increase crop yields (van Praagh and Von der Ohe 1983).

Other bee pheromones (Blum and Brand 1972) and chemical attractants may be useful inducing bees to pollinate crops. For example, without exposing their Nasonov gland at foraging sites, bees deposit a substance that attracts foraging bees and induces them to land (Free and Williams 1970). Bees prefer to visit feeding dishes that have been previously visited by bees, possibly because a chemical from tarsi (i.e. “footprint pheromone”)s deposited at the site (Butler et al. 1969;

Chauvin 1960). Anethole(1-methoxy-4(1-propenyl)benzene), which is not known as bee pheromone, also attracts bees to crops (Ladd and Tew 1983; van Praagh and Von der Ohe 1983). It is important that the usefulness of bee pheromones maintain bees on crops be examined more fully, especially since controlled release systems for applying pheromones to plants are now well developed (Kydonieus and Beroza 1982).

8.4.16 Sprays

Both beekeepers and farmers should be aware of the damage that the indiscriminate use or misuse of sprays can do to bees. Special thought should be given to whether, when and how, sprays should be used. All spraying should be carefully managed to minimize injury to the bees and hives placed so as to minimize any spray drift into entrances. farmers requiring pollination services should enquire from their neighbours whether they intend to conduct a spray program that could have an adverse effect on the pollinating bees.

8.4.16.1 Repellents

Bee repellents are usually used to reduce mortality from insecticide applications (Anderson and Atkins 1968; Johansen 1977) but might be applied to highly attractive non target crops to induce bees to forage on less attractive target crops (Woodrow et al. 1965). Some repellents that appear to useful in laboratory trials are not practical under field conditions (Anderson and Atkins 1968). Despite this, many chemicals repel bees and are promising (Anderson and Atkins 1968; Atkins 1981; Atkins et al. 1975; Woodrow et al. 1965). Repellents such as carbolic acid, acetic acid, propionic anhydride, or benzaldehyde are used to remove bees from honey boxes but are too volatile for field use (Atkins et al. 1975).

Other methods of repelling bees have been reported. Bees are repelled from a crop by feeding them with a 50% solution of calcium chloride in which the flowers of the crop have been sowed (Chesnokova 1958). Mandibular gland pheromones' repel foraging bees (Simpson 1966) as do alarm pheromones (Ferguson and Free 1979). Unrewarding food sources are "marked" with a substance that repels scouts and foraging bees (Free and Williams 1983; Nunez 1967).

Hanging short vertical strips of aluminum around plots deters bees from foraging near them (Wolfenbarger and Moore 1968), but using polished aluminum sheets for reflecting ultraviolet light from the sun within target crops attracts bees (Braines and lstomina-Tsvetkova 1956; Istomina-Tsvetkova and Skrebtsov 1964). It may be feasible to use bee repellents only on small acreages of highly attractive crops that remove bees from valuable commercial crops. Screening trials should include materials that are relatively long-lasting, inexpensive to produce and apply, and do not damage bees or crops.

8.4.17 Selection and Breeding of Honey Bees

Selection and breeding of bees has advanced through the development of instrumental insemination techniques for queen bees along with a better understanding of bee genetics (Cale and Rothenbuhler 1978; Collins et al. 1984; Goncalves and Stort 1978; Kerr 1974; Roberts 1974). There is evidence that flight speed and range, aggressiveness, and resistance to some diseases are genetically controlled (Cale and Rothenbuhler 1978; Goncalves and Stort 1978). Simple laboratory systems are now available to evaluate a queen's genetic potential (Milne 1981).

Bees that have a reduced, or limited, flight range might be used on crops requiring pollination (Gary and Witherell 1977). Observations of foraging behavior and communication "dances "of a diminutive-winged mutant indicate *that* it forages closer to its hive than normally-winged bees (Witherell and Laidlaw 1977). It may be possible to select for strains bees with normal wings that tend to forage close to their hives (Gary and Witherell 1977). Some genetic stocks, already studied, appear to have reduced foraging ranges but these may relate to the bees' preferences for certain crops (Gary and Witherell 1977; Witherell and Laidlaw 1977). Some attempts have been made to modify physical and behavioral characters of bees relative to specific crops. Although pollen-collecting bees are valuable pollinators of red clover (Bohart 1957; Holm and Poulsen 1975), nectar-collectors also pollinate but may not attracted to this crop if their tongues are too short to reach the nectar at the base of the long corolla tubes (Bohart 1957; Free 1970a, b; McGregor 1976). The selection of strains of bees with longer tongues has resulted in more seed being set (Alpatov 1984; Gubin 1947; Smaragdova 1956). The attractiveness of red clover is sometimes enhanced because it produces sufficient nectar (through plant selection and cultural practices) so that the bees can reach it with their tongues (Hawkins 1969). Alfalfa flowers must undergo a complicated process called "tripping" in order to set seed (Bohart 1957). Experienced nectar-collecting bees enter the flowers from the side and do not trip, or get struck by, the sexual apparatus.

Because bees must trip the alfalfa floral apparatus to collect pollen, they usually collect it from other plant species (Bohart 1957). Selection for strains of bees that trip alfalfa has shown only limited success (Kerberg and Lesins 1949; Petersen 1954). Colonies of bees located in the same site show floral preferences that may depend on chance discovery and subsequent utilization of crops (Ribbands 1952; Schwan and Martinovs 1954) or that may be inherited (Nye and Mackensen 1965). Pollen load analyses, and observations marked bees, show that bees from individual colonies have preferences for various pollen-yielding crops (Howell et al. 1972; Mackensen and Tucker 1973; Sheppard et al. 1979; Shimanuki et al. 1967). Genetic lines of bees have been selected for high and low preferences for alfalfa pollen (Gary et al. 1978; Mackenscn and Nye 1966; Nye and Mackensen 1965). Some of these lines also show preferences for alsike clover (Nye 1971) or white clover (Mackensen and Tucker 1973) when alfalfa is not available. Bees also show preferences for certain alfalfa clones (Kauffeld and Sorensen 1980). These studies suggest that the selection of bees that prefer certain nectars, particularly where nectar collectors are known to be important pollinators of crops, should also be undertaken (Free 1970a, b). Selection and use of Italian honeybees with long-tongue (6.8 mm) has been greatly reported for the pollination of red clover. Mackensen and Nye (1969), Nye and Mackensen (1970) and Hellmisch et al. (1985) have demonstrated the possibility of selecting honeybee colonies with high (2–15 times) or low levels of pollen collection for crops like alfalfa.

8.4.18 Management of Honey Bee Colonies

8.4.18.1 Moving Colonies: Timings

The time when colonies are moved to a target crop relative to stage of bloom influences the number of foragers that are retained on it. It is suggested that if colonies are sited near a crop requiring pollination before it has sufficient bloom, foraging bees may visit other flowers and becomes o "attached" (or "fixed") to them that they do not forage on the target crop when it does bloom (Karmo 1958; Ribbands 1952). The importance of shifting colonies to target crops at the correct time–too soon and the bees may forage elsewhere; too late and a portion of the crop may not be pollinated–has been verified in many field, orchard, and berry crops (Free et al. 1960; Howell et al. 1972; Moeller 1973; Shimanuki et al. 1967). Alfalfa and red clover crops bloom for a relatively long period, so moving colonies to these crops when they just begin to flower seems important (Free et al. 1960; Vesely 1966); but it may also necessary to move in more colonies at intervals to keep pace with floral numbers (Free 1970a, b; Todd and Vansell 1952). Crop yield data are required relative to the timing colonies on crops because the bee counts on crops and the pollen trap analyses used in most studies are only indirect measures of pollination efficiency (Moeller 1973).

8.4.18.2 Moving Colonies ~ Distance from Crops

Bees fly long distances to collect pollen and nectar, but they usually collect these floral rewards close ~o their hive when available (Braun et al. 1953; Free 1970a, b; Free and Williams 1974; Gary and Witherell 1977; Ribbands 1951). Recruitment of nest mates nearby sites is also greater because this information is more readily communicated (Boch 1956). Thus, locating colonies close to target crops appears to important in maintaining bees on those crops.

Various colony and plant data show the value of placing colonies near target crops. Colonies placed near crops collect more pollen (Free and Williams 1974; Svendsen 1964) and gain more weight through nectar collection (Eckert 1933; Ribbands 1952; Sturtevant and Farrar 1935). Foragers spend less time collecting a load of pollen than a load of nectar; the number of flights increases for both load types with proximity to the floral source (Free 1970a, b). Counts of bees per unit area of target crop, and amount of pollen collected, decrease as the distance from hive increases (Alpatov 1984; Braun et al. 1953; Gary 1978; MacVicar et al. 1952; Peterson et al. 1960). Yields of target crops are also higher when colonies are close to them (Alpatov 1984; Bohart 1957; Braun et al. 1953; Farkas 1981; Free 1962; Hammer 1961; MacVicar et al. 1952; Peterson et al. 1960).

8.4.18.3 Moving Colonies ~ Number and Placement

Although recommendations are available about the number of colonies required to pollinate given areas of crops (Free 1970a, b; McGregor 1976), opinions differ about where to site colonies so that maximum numbers of bees are maintained on the crop. When colonies are placed within a single species crop that provides copious pollen or nectar, the bees radiate outwards from their colonies as they forage (Free and Smith 1961; Karmo and Vickery 1954; Lee 1961; Weaver 1957).

However, some bees tend to forage relatively close to the colony (Gary et al. 1972; Levin 1959, 1960; Ribbands 1951) while others ignore rewarding local floral sources for more distant ones (Gary et al. 1972). Little is known about the percentage of bees that forage at different distances from their colonies (Gary 1978). During inclement weather, bees forage less and tend to forage close to their colonies (Free and Williams 1974; Jay and Jay 1984; Singh 1950). Thus, more colonies are required to pollinate a crop. Although this sometimes results in “over pollination” of a crop, the risk is probably worth taking when weather conditions are unfavorable (Brittain 1933; Free 1970a, b).

It has been recommended that up to 20 colonies per group should be placed in or near crops (Brittain 1933; Philp and Vansell 1932). Where colonies must be placed outside the crop, they should be arranged so that the bees fly into the prevailing wind; thus while en route to the crop they pick up its odor (Free 1970a, b). To maintain an even distribution of bees on a target crop, groups, each of 3–5 colonies, are placed equidistant from each other within the crop, that distance being determined by the number of colonies per hectare/acre that is recommended for the crop (Free and Williams 1974; Hutson 1925; Jay and Jay 1984; Martin and McGregor 1973; Overley and O’Neill 1946). This number of colonies can be handled easily with mechanized loaders and pallets. Shifting colonies singly throughout a crop probably improves the distribution of bees even more but may be feasible only for small acreages of highly priced crops.

8.4.18.4 Moving Colonies

Replacement or rotation Because most bees expand their foraging range gradually after being released from their colonies at a new site, their colonies should be replaced or rotated with fresh ones when they begin to forage outside the target crop (Al-Tikrity et al. 1972a, b; Free 1979a, b; Istomina-Tsvetkova and Skrebtsov 1964; Karmo and Vickery 1954). Colonies involved these exchanges should be at least 2.4 km apart or the bees may return to their former sites (Karmo 1958; Karmo and Vickery 1954). This system appears to be particularly useful where target crops, like pears, are relatively unattractive to bees (Free and Smith 1961). After colony relocation, bees tend to visit floral species they visited prior to the move if they are available (Free 1959). Also, the total amount of pollen collected at the new site is relative to that collected at the original one (Free 1959). When colonies are relocated on a crop similar to the one they were visiting prior to the move, foraging activity is increased (Levin and Bohart 1957). This is most obvious where colonies are moved from sites with abundant bloom to sites where little bloom is available (Levin and Bohart 1957). In some studies, increased pollination and seed set resulted from moving groups of colonies onto crops in succession (Todd and Vansell 1952), but in others there were increases in seed set (Palmer-Jones and Forster 1972). Although the system of periodically replacing colonies to maintain bees on crops seems feasible, it requires constant monitoring of foraging activities of bees to determine when moves should occur. Also, disorientation of relocated bees may result in losses of bees and reductions in food stores and pollination; and there are costs for equipment and labor to accomplish the moves.

8.4.18.5 Moving Colonies ~ Temporary Confinement

The flowers of crops generally present their pollen (or nectar) at certain times of day. For example, dandelion flowers mostly present their pollen in the morning while most apple pollen is presented in the afternoon (Free 1968a, b, 1970a, b). When colonies are moved to apple orchard and the bees confined to their hives until the afternoon, more pollen collectors forage on apple than on dandelion flowers (Free and Nuttall 1968; Free et al. 1984).Thus, confining the bees to their hives until the target crop is presenting its pollen (or nectar) appears to maintain bees, at least temporarily, on a crop. It has been suggested that confining bees to their hives, at least until midday, may lower the threshold of forage acceptability and, upon release, the bees forage on and accept the nearest crop even if it is relatively unattractive (Free 1970a, b). This hypothesis requires testing. Also, further experiments are required to verify that after temporary confinement bees are retained on selected target crops and to determine the effect on the crop of loss of foraging effort through such confinement (Free 1970a, b). The experiments should include commercial crops that present pollen in the morning (e.g. strawberry, sour cherry, black currant) and in the afternoon (e.g. pear, peach, field beans); other crops that are highly attractive to bees should be within flight range. Such trials should also include assessments of the damage confinement causes to colonies.

8.4.19 Other Methods

8.4.19.1 Removing Floral Competition

Competitive bloom is sometimes unavailable or is removed and thus bees are maintained on target crops. It has been suggested that some cover crops grown beneath fruit trees should be eliminated, or mowed when in flower, to avoid competition for foraging bees (Brittain 1933; Karmo and Vickery 1954). Pollen trap analyses and bee counts show that dandelion, white clover, and mustard attract bees from orchard crops (Free 1968a, b; Jay and Jay 1984; Palmer Jones and Clinch 1974; Stephen 1958). Whether competition from such cover crops should be avoided while orchards are in flower urgently requires investigation, particularly in terms of crop yields. It may be that cover crops retain the nectar-collecting bees in an orchard and these then switch to pollen collecting on target crops. However, while bees forage on cover crops they may be poisoned by residual insecticides that are applied to orchards.

In some cases it is clear that reducing competitive bloom is entirely beneficial (Zivov and Skvorkov 1951). For example, alfalfa seed yields are often high in dry areas where few other plants compete for bee visits (McMahon 1954; Vansell and Todd 1946). After adjacent blooming mustard crops are cut, pollen foraging on alfalfa by bees, and seed set, are increased (Linsley and McSwain 1947). However, bees will fly over 1.5 km for pollen when sweet clover crops are cut near alfalfa fields (Bohart 1957). Cutting alternative areas of an alfalfa field different times during the season (i.e. “staggered cuttings”) provides continuous but reduced amounts of bloom and may increase seed yields (Drake 1949).

8.4.19.2 Pollen Dispensers

Pollen dispensers (or hive inserts) apply pollen to bees leaving a hive so they can cross-pollinate crops when few pollinizer varieties are available. Thus, dispensers may increase pollination efficiency of bees without necessarily maintaining more of them on the target crop (Townsend et al. 1958). It has been suggested that dispensers may stimulate foraging activity and that they may induce bees to forage for the type of pollen in the dispenser (Karmo and Vickery 1954; Lotter 1960), but this requires verification. Reviews of dispenser types, methods of use, relative efficiencies, and their effects on bee behavior are available (Legge 1976). Although dispensers are used in various orchard crops, their value in increasing yields is questionable (Free 1970a, b; Griggs and Iwakiri 1960; Legge 1976; Soost 1965). However, cage trials, behavioral studies, and scanning electron microscopic examination of pollen in dispensers, on bees, on stigmas, and on floral surfaces (De Grandi-Hoffman et al. 1984) may show that pollen dispensers are more valuable as pollination aids, and for maintaining bees on crops, than appears to be the case at present.

8.4.19.3 Disposable Pollination Units (DPU’s)

Disposable pollination units are small comb less colonies housed in inexpensive containers that are trucked or parachuted into target crops that are inaccessible, and then destroyed or left to die when flowering is over (Cantwell et al. 1972; Free 1979a, b). Originally, DPU’s consisted of wooden packages covered with wire screen and wrapped in tar paper (Hutson 1925), but recent tests using cardboard or Styrofoam show promise (Erickson et al. 1974).

8.4.19.4 Studies of Foraging Behavior of DPU

Colonies reveal several common ends. DPU's with laying queens collect more pollen and nectar than queenless units and show greater foraging activity (Kauffeld et al. 1970). Total numbers of bee flights per unit time are directly related to the size of the adult population of the DPU (Kauffeld et al. 1970). Bees from overwintered colonies exhibit greater flight activity, collect more pollen, and fly at lower ambient temperatures than do bees that fly from DPU's that were originally established with 1.4–2.7 kg of adult bees (Erickson et al. 1975; Thorp et al. 1973). About 1.5–2 times as many bees from DPU's are required to match the foraging activity of bees from overwintered colonies (Erickson et al. 1975).

Little pollen, but much nectar, is collected by the bees of DPU's (Erickson et al. 1974, 1975; Thorp et al. 1973). Therefore it may be important to use DPU's in crops that are pollinated mostly by nectar-collecting bees (Erickson et al. 1975). Alternately, the use of egg-laying virgin queens (Kauffeld et al. 1970), synthetic brood or queen pheromones(Free 1967; Jaycox 1970a, b), brood (Jordan 1961), treated comb (Rinderer and Baxter 1978) may stimulate pollen foraging from DPU's. Further trials are required to determine ideal populations of DPU's for pollinating valuable but inaccessible crops (e.g. cranberry, blueberry) that bloom briefly that require emergency pollination because of inclement weather. Studies are also required to ascertain how long foragers from DPU's are maintained on target crops as well as their impact on crop yield.

8.4.20 Pollen Compatibility and Pollinating Fruit Crops

Many fruit crops are pollen self-compatible – peach, some plums, some cherry, pear. Others are completely, or partially, self-incompatible. Examples of these are apple, almond and sweet cherry. Then there are some varieties of sweet cherry, or polyploid apple, that are also cross- incompatible. The problem of self-incompatibility and the optimal fruit-set level becomes intertwined in determining the optimal concentration of pollinating bees. For example, in pollinating peaches a self-compatible crop, the number of honey bee colonies required is generally less than a self-incompatible crop (e.g., apple, almonds).

8.4.21 Orchard Planting Patterns

In pollinating self-incompatible crops the orchardist must consider the pollinizer variety, the timing of pollen dehiscence and the mix of pollen within the orchard. Orchard planting patterns have been developed to take into consideration both the bees foraging patterns and also to maximize the yield of the main variety. Self-incompatible varieties may have pollinizer rows alternating with the main variety, or alternating with two or more rows of the main variety.

8.4.22 How Are Hive Bees Used for Pollination Management?

Some crops (e.g., almond, avocado, citrus, litchi, some vegetable crops) produce good amounts of nectar and pollen and blossom for a long period. There are other crops that produce good amounts of nectar and pollen but blossom for only a short period. There are still other crops, e.g., kiwi fruit, that require cross-pollination but bloom for a short period and produce little or no nectar, but good pollen. These crops can be grouped into the following categories.

1. Crops secreting a good amount of nectar and pollen and having a long blooming period.
2. Crops secreting a good amount of nectar and pollen and having a short blooming period.
3. Crops secreting little nectar but good pollen and having a short blooming period.
4. The use of honeybees for pollination management of crops grown in the Hindu Kush-Himalayan region is described in the following sections. A summary can be found in Table 8.3.

8.5 Managing Pollination of Crops Secreting a Good Amount of Nectar and Pollen and Having a Long Blooming Period

Some fruit crops and almost all vegetable and vegetable-seed crops, oilseed crops, and spices cultivated in mountain and hilly areas of the Hindu Kush-Himalayan region fall into this category. Crops secreting good quantities of both nectar and pollen and having a long blooming period include

1. fruit crops such as almonds, avocados, citrus, litchi, and peaches;
2. vegetable crops such as cabbage, carrot, cauliflower, cucumber, pumpkin, squash, various gourds, okra, radish, and turnip; and
3. oilseed crops such as Indian mustard, mustard and rape, niger, safflower, and sunflower.

8.5.1 Fruit Crops

8.5.1.1 Almond (*Prunus amygdalus; Prunus dulcis)*

Almond blooms from mid-February to mid-March for over a month and produces large quantities of nectar and pollen. The flower has five sepals, five petals, 10–30 stamens, and one carpel with two ovules. After fertilization, one or both of the ovules develop into seeds. Almost all varieties are self-incompatible and depend on

Table 8.3 Summary of pollination management of different crops

Crop	Blooming period of the crop	Number of *A. mellifera* colonies/ha	Number of *A. cerana* colonies/ha	Time of colony placement
Fruit crops				
Almond	Mid-February to mid-March	5–8	10–12	5–10% bloom
Apple	April (7–10 days)	5–8	10–12	5% bloom
Apricot	Mid-February (2–3 weeks)	2–3	4–6	5–10% bloom
Avocado	April–May	5–8	10–12	10–15% bloom
Cherry	February (7–10 days)	2–3	4–6	5% bloom
Citrus	March–April	2–3	4–5	5–10% bloom
Kiwifruit	March–April	8–9	16–20	5–10% bloom
Litchi	March–April	2–3	4–6	5–10% bloom
Mango	February	2–3	4–6	5–10% bloom
Peach	February–March (3–4 weeks)	1–2	2–3	5–10% bloom
Pear	February–March (7–10 days)	5	8–9	5% bloom
Persimmon	March–April (2 weeks)	2–3	4–6	5–10% bloom
Plum	February (1–2 weeks)	2–3	4–6	5% bloom
Strawberry	February–April (2 months)	As many as 15	25	5–10% bloom
Vegetable crops				
Cabbage	February–March	5	8–10	10–15% bloom
Carrot	March–April	5–8	10–12	10–15% bloom
Cauliflower	March–April	5	8–10	10–15% bloom
Cucumber	June–September	1 for monoecious plants	2–3 for monoecious	10–15% bloom
		8 for gynoecious plants	12–16 for gynoecious	
Cucurbits				
(Pumpkin, squash, gourd)	June–September	5–8	10–12	10–15% bloom
Okra	June–September	1–2	2–3	10–15% bloom
Onion	April	5–8	10–12	5–10% bloom
Radish	March–April	2–3	4–6	10–15% bloom
Turnip	February–March	2–3	4–6	5–10% bloom
Oilseed crops				
Mustard and	December–January	3–5	5–8	10–15% bloom
Rape	February–March			
Niger	August–September	3–5	6–8	5–10% bloom
Safflower	March–April	5	4–6	5–10% bloom
Sunflower	June	5	8–10	5–10% bloom
Spice crops				
Cardamom	March–April	2–3[a]	4–6	10–15% bloom
Chilli	July–September	2–3[a]	4–6	10–15% bloom
Coriander	February–April	2–3[a]	4–6	10–15% bloom

[a] No specific recommendation

cross-pollination with other compatible varieties. Since fruit size is not a consideration, all flowers should develop into fruits, i.e., 100% fruit set is required for a commercial crop. An orchard should be planted with two rows of the main variety and one row of the polliniser variety.

The flowers are highly attractive to honeybees. Since it blooms during early spring, hive bees are the best pollinators. For effective pollination, place 5–8 strong colonies of *Apis mellifera* or 10–12 colonies of *Apis cerana* per hectare at the time of 5–10% flowering. Colonies should be distributed evenly throughout the orchard and not in groups.

8.5.1.2 Apple (*Malus domestica)*

The apple blooms during April for a short period of 7–10 days depending on the altitude and weather. The flowers are fragrant and borne in groups of six. Each flower consists of five sepals, five pinkish-white petals, and 20–25 stamens surrounding the carpel having a single ovary, a style, and five stigmas. The ovary is divided into five chambers, each having 1–4 ovules. Although fertilization of every ovule in the ovary is not necessary for fruit development, for a larger perfect fruit, a larger number of ovules should be fertilized. Inadequate pollination results in a low number of seeds, which may result in lop-sided or asymmetrical fruits. Moreover, fruits with few seeds are more likely to drop. Almost all commercial varieties are self-incompatible and require pollen from compatible polliniser varieties. Moreover, the pollen is sticky and so wind pollination is not effective. Pollination largely depends on insects, especially honeybees. The flower produces plenty of nectar and pollen, which helps to increase the strength of honeybee colonies. Strong colonies also collect surplus honey from its flow.

Since the blooming period is very short and 50% of the flowering occurs within 3–4 days, farmers must move bee colonies to the orchard as soon as trees start blooming. Also, because the shape and size of the fruit depends on the number of ovules fertilized, there should be plenty of bees in the orchard. Farmers must place 5–8 colonies of *Apis mellifera* or 10–12 colonies of *Apis cerana* evenly per hectare. To prevent bees foraging on other flowers in the vicinity, remove all weeds and wild plants.

8.5.1.3 Apricot (*Prunus armeniaca*)

The apricot blooms in February-March for 2–3 weeks, depending on the weather. The flower is usually white and occurs either singly or doubly. It has five sepals, five petals, and about 30 stamens surrounding a carpel having a single ovary containing two ovules, one style, and one stigma. It produces plenty of nectar and pollen. Some varieties are self-compatible and some are completely self-incompatible and require pollen from a compatible polliniser. Cross-pollination is essential for self-incompatible varieties and is beneficial to self-compatible varieties. Honeybees are its primary pollinator. For effective pollination, place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare at 5–10% flowering.

8.5.1.4 Cherry (*Prunus avium*)

The cherry blooms during February for 7–10 days. The flower is pinkish-white and produces plenty of nectar and pollen. It has five sepals, five petals, 20–25 stamens, and one pistil consisting of an ovary having one or two ovules, a style, and a stigma. While cross-pollination is essential for self-incompatible varieties, it is also beneficial to self-compatible varieties. Honeybees are the primary pollinators. Pollination is simple. Since its blooming period is short and 50% of the flowering occurs within 3–4 days, place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare as soon as flowering starts.

8.5.1.5 Mango (*Mangifera indica*)

The mango blooms during February and produces 60-cm long panicles; each panicle from contains 200–6,000 red, pink or almost white male and bisexual flowers. Male flowers are more numerous and the percentage of bisexual flowers varies from 1 to 35 depending on the variety. A flower has 4–5 ovate, lanceolate petals inserted in the base of an almost hemispherical disc. The disc of the bisexual flower is surmounted by a greenish-yellow ovary with a slender lateral style. The ovary has one chamber containing one ovule. There are five stamens; one single fertile stamen arises from the disc on the side of the ovary, and sometimes there are two and rarely three fertile stamens. The other stamens are sterile. The male flower is similar but has no ovary and style. The stamens are surrounded by five nectaries. The stigma is receptive at least 1 h before the anther releases pollen, thereby offering an opportunity for cross-pollination. Varieties vary from self-compatible to self-incompatible.

Flowers are visited by pollinating insects. Honeybees collect pollen, nectar from flowers, and juice from damaged fruits. They increase yield and quality of fruit in self-fertile varieties and are essential for fruit set in self-sterile varieties. For high yield and better quality fruit, place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare.

8.5.1.6 Pear (*Pyrus communis*)

The pear blooms during February-March for about 7–12 days. The flowers are white and produced in clusters of 7–8. The flower has five sepals, five petals, 20–25 stamens, and one pistil consisting of an ovary, a style, and a stigma. The stigma is receptive before its anthers release pollen. Some varieties are self-incompatible and some are self-compatible. Cross-pollination is essential for self-incompatible varieties and beneficial to self-compatible varieties.

Flowers produce plenty of nectar and pollen. Honeybees visit mainly for its highly attractive pollen. Pears produce a large number of flowers and, for a satisfactory crop, only 5% are required to set fruit. Commercial varieties are self-incompatible and the blooming period is short with 50% of the flowering occurring within 3–4 days. Therefore, for sufficient pollination, place 5–6 colonies of *Apis mellifera* or 8–9 colonies of *Apis cerana* evenly per hectare as soon as flowering starts.

8.5.1.7 Persimmon (*Diospyros kaki*)

Persimmon blooms during March-April for 1–2 weeks depending on the weather. It produces creamish-yellow flowers. Different varieties of persimmon produce five types of flower: pistillate, pistillate and sporadically monoecious, monoecious, monoecious and sporadically staminate or pistillate, and staminate. The flower has outfolded, prominent, green sepals extending beyond the corolla. The staminate flower has 16–24 stamens and the pistillate one has eight staminods. The blossom hangs downwards and the stigma is sometimes exposed beyond the petals, thus offering an opportunity for wind pollination. However, wind plays a minor role. Some varieties have a high degree of parthenocarpy and develop fruit to maturity without pollination whereas other varieties drop their fruit prematurely or entirely fail to set fruit without pollination. Such varieties produce seedy fruits if pollinated but set a few seedless fruits without pollination.

Flowers produce both nectar and pollen. Honeybees and bumble bees are the dependable pollinators agents. Although there are no recommendations about the number and time of placement of bee colonies, 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* per hectare should be sufficient for adequate pollination.

8.5.1.8 Plum (*Prunus domestica*)

The plum blooms during February for 1–2 weeks depending on the weather. It produces white flowers in clusters of 2–3. The flower consists of five sepals, five petals, 25–30 stamens and a single pistil that has an ovary with a single ovule, a style and a stigma. Varieties vary from completely self-compatible to completely self-incompatible. However, the major varieties are self-incompatible. Flowers produce a good amount of nectar and pollen and are visited by many species of insects. Honeybees are the primary pollinators. The blooming period is short and 50% of the flowering occurs within 3–4 days. Therefore, place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare as soon as flowering starts.

Managing pollination of crops secreting little or no nectar but good pollen and having a long blooming period. Only one crop – kiwi fruit – cultivated in the mountain and hilly areas of the region–falls into this category.

8.5.1.9 Kiwi Fruit *Chinese gooseberry* (*Actinidia deliciosa*)

The Kiwi fruit is native to China and is now cultivated in mountain areas of other countries of the Hindu Kush–Himalayan region, especially India. The plants are dioecious: male and female flowers are produced on separate vines. Male and female vines bloom for 2–4 weeks and 2–6 weeks respectively. The pendulous flowers are 3–5 cm in diameter, and have 5–6 creamy-white petals. They occur singly or in groups of three, and at times have a characteristic scent. The female flower has a many-celled ovary containing up to 1,400 ovules, up to 40 stigmas, and several stamens that produce sterile pollen. The male flower has a vestigial ovary and numerous functional stamens producing fertile pollen. The female flower remains receptive for 7–10 days. Anthers of the male flower release pollen early in the morning of the day it opens. Flowers produce plenty of pollen but little or no nectar. Since male and female flowers are produced on separate vines, mechanical transfer of pollen is necessary. More than 700 ovules in each flower need to be fertilized to produce a commercial crop. There is a positive correlation between the number of seeds and the fruit size. Moreover, because female plants produce only a few flowers, more than 90% fruit set is required for a good commercial crop. Although wind is sufficient to set the fruit, to achieve commercial quantity and quality of fruit, additional pollination by insects, especially honeybees, is necessary. Therefore, place 8–9 colonies of *Apis mellifera* or 16–20 colonies of *Apis cerana* evenly per hectare. Feed the colonies with 60% sugar syrup every evening since flowers do not produce nectar. Sugar feeding also increases pollen collection by bees. Colonies should have large amounts of unsealed brood because this also increases pollen collection.

8.5.1.10 Avocado (*Persea americana*)

Avocado blooms during April-May and may have a flowering period of about 6 months depending on the weather. A fully grown tree may produce about a million flowers in one blooming season. The flower has six sepals in two whorls, one carpel with a single one-chambered ovary, a short style and simple large stigma, and nine stamens inserted in three whorls; each whorl has three stamens. The anthers release pollen through a small hinged flap.

The flower opens in two stages. It opens first for a few hours during which the stigma is receptive but anthers do not release pollen. The flower then closes and opens again on the next day. This time anthers release pollen but the stigma is shrivelled and no longer receptive. After anthers release pollen, the flower closes and never opens again. Thus, flowers are structurally bisexual and functionally unisexual. Cross-pollination is essential for fruit set. In some varieties, the first stage occurs in the morning of the first day and the second stage in the afternoon of the second day. These varieties are called Type A. In other varieties, the first stage occurs in the afternoon of the first day and the second stage in the morning of the second day. These varieties are called Type B. Therefore, both varieties are planted in the same orchard so that pollen is always available when stigmas are receptive.

Flowers produce plenty of nectar and pollen and are visited by insects and birds (such as humming birds in America). Honeybees are the most important pollinator. In order to have maximum fruit set, place 5–8 colonies of *Apis mellifera* or 10–12 colonies of *Apis cerana* evenly per hectare at the time of 10–15% blooming.

8.5.1.11 Citrus (*Citrus spp.*)

Many species of *Citrus* – including grapefruit, lemon, orange, sweet orange, and lime – bloom during March-April and produce plenty of nectar and pollen. A citrus flower usually has five sepals, 4–5 petals, ten stamens united to form two groups of three and one group of four stamens, and one pistil with one ovary having 8–10 chambers with many ovules in each chamber, a small style, and a capitate stigma.

Citrus flowers are usually self-compatible and do not depend on insects for pollination but benefit from cross-pollination by honeybees. For pollination, place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare.

8.5.1.12 Litchis (*Litchi chinensis*)

Litchi blooms during late March or early April for 3–4 weeks, depending on the weather, and produces small, greenish-yellow flowers in terminal clusters. There are three types of flower. The male flower has 5–8 stamens with functional anthers arising from a fleshy disc, but no style. The imperfect hermaphrodite flower has functional anthers, but the style is small and the stigma lobes never separate. The pollen from this type of flower is more viable than that from the male flower. The other type of hermaphrodite flower has a style that grows to full size and the stigma opens to 2–3 lobes, but the anthers do not release pollen. Some varieties produce only male flowers and do not set fruit in some years.

Litchi is self-fruitful but flowers need to be cross-pollinated. Flowers secrete plenty of nectar and are visited by a number of insects. Honeybees are the most important pollinators. To obtain a higher yield and better quality fruit, place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare.

8.5.1.13 Peach (*Prunus persica*)

Peach blooms during February to March, depending on the variety, for 3–4 weeks. The flowers are bright pink or reddish- pink and produce large quantities of nectar and pollen. Usually a flower consists of five small sepals, five oval, bright pink petals, and 15–30 stamens surrounding a single erect pistil having a single ovary containing two ovules, a style, and a stigma. Only one ovule normally develops into seed, leading to an asymmetrical fruit. Many varieties produce pollen at the time the stigma is receptive.

The flowers are highly attractive to honeybees and other insects. The fact that only one ovule must be fertilized for fruit set simplifies pollination. Many varieties are self-fertile and a few are self-sterile. A satisfactory crop from either self-sterile or self-fertile varieties can be obtained when plenty of honeybees and other pollinating insects are present. Since pollination is simple and flowers are attractive to bees, only 1–2 colonies of *Apis mellifera* or 2–3 colonies of *Apis cerana* per hectare of orchard are sufficient.

8.5.1.14 Strawberry (*Fragaria ananassa*)

Strawberry blooms in February-April or November-January depending on the variety. Two to three white flowers are produced on each plant every day. The flower consists of five sepals, five petals, many stamens, and many pistils -each with one carpel on a fleshy conical receptacle. The strawberry is an aggregated fruit; each carpel forms a true fruit called an achene. Achenes containing a fertilized ovule release a hormone that stimulates the growth of the receptacle. If an achene does not contain a fertilized ovule, the receptacle in its area does not grow. When groups of such achenes occur together, the fruit is deformed. These deformed fruits have low market value. Most modern varieties are self-fertile and have bisexual flowers.

Flowers produce good amounts of nectar and pollen and are visited by honeybees. In order to produce a commercial crop, there should be a large number of pollinating insects. It requires as many as 60 visits by a bee (or other insect pollinator) per flower to produce a well-formed, heavy fruit. Therefore, place 15 colonies of *Apis mellifera* or 25 colonies of *Apis cerana* evenly per hectare of field.

8.5.2 Vegetable Crops and Vegetable-Seed Crops

8.5.2.1 Carrot (*Daucus carota*)

Carrot blooms during March-April and produces small white flowers in terminal or primary and secondary umbels. Secondary umbels are classified as second-, third-, fourth-order umbels. First- and fourth-order umbels are important in seed production. The flower is usually hermaphrodite, but there is a tendency to produce male flowers. A flower has five functional stamens and an ovary with two locules containing one ovule each. There are two styles, each terminated by a stigma. Carrot blooms for over a month, and flowers produce good quantities of nectar and pollen which are collected by different insects.

Only two pollen grains are required to fertilize two ovules, and the stigma is receptive to pollen from flowers of the same or another plant for a week or more. However, only about 15% of plants set seed from their own pollen. Honeybees are the most reliable pollinators and increase yield by 9–135% depending on crop variety. For effective pollination, place 5–8 colonies of *Apis mellifera* and 10–12 colonies of *Apis cerana* in 1 ha at a time of 10–15% flowering. Carrots should not be grown in the vicinity of crops that are more attractive to honeybees.

8.5.2.2 Cole Crops (*Brassica oleracea*)

Cole crops include cabbage (*Brassica oleracea capitata*), cauliflower (*Brassica oleracea botrytis*), broccoli (*Brassica oleracea cymosa*), kohlrabi (*Brassica oleracea gongylodes*), Brussels sprouts (*Brassica oleracea gemmifera*), etc. They bloom during March-April for over a month. Flowers open early in the morning and remain open for 2–3 days. Flowers are yellow and have four sepals, four petals, six stamens (two short and four long), and a long ovary containing 10–30 ovules depending on the variety. The style is short and is terminated by a capitate stigma.

Flowers produce good amounts of nectar and pollen. They are generally self-sterile and require cross-pollination to set fruit. Honeybees are the primary pollinators and enhance crop yield. To obtain high yield and good quality seed, place five colonies of *Apis mellifera* or 8–10 colonies of *Apis cerana* evenly per hectare.

8.5.2.3 Cucumber (*Cucumis sativus*)

Cucumber blooms from June to September. Many varieties are monoecious and some are gynoecious. Monoecious varieties produce male and female flowers on the same vine, and gynoecious varieties produce mainly female flowers. Pollen for gynoecious varieties is provided by monoecious plants cultivated alongside them. Generally 10% of the monoecious variety is cultivated with a gynoecious variety. Male flowers appear about 10 days before female flowers and are more numerous. In general the ratio between male and female flowers is 10:1. The male flower has three anthers, two of which have two anthers each (united) and the third has only one. The female flower has an inferior ovary with three locules, each containing many ovules, a short broad style, and three stigma lobes. The stigma is receptive throughout the day but most receptive in early morning. Since anthers and stigma are present separately on male and female flowers, the mechanical transfer of pollen is essential for fruit set.

Cucumbers bloom for a long period and produce good amounts of nectar and pollen. They are visited by various insects. Since the ovary contains a large number of ovules, a large number of pollen grains – and pollinators – are required for effective pollination and good quality fruit. For satisfactory fruit set, a cucumber flower requires 8–10 bee visits, however fruit weight and number of seeds per fruit are improved when bees make up to 50 visits. Honeybees are the most reliable pollinators because they can be managed in large numbers. The amount of pollen that needs to be transferred depends on the ratio between male and female flowers. Since the male:female ratio is higher in monoecious varieties, one colony of *Apis mellifera* or two colonies of *Apis cerana* are required for their pollination. Gynoecious varieties have more female flowers, so eight colonies of *Apis mellifera* or 12–16 colonies of Apis cerana should be distributed per hectare of field.

8.5.2.4 Pumpkin and Squash (*Cucurbita spp.*)

Pumpkin (*Cucurbita pepo*), squash (*Cucurbita moschata*), and other cucurbits bloom for a long period from June to September. Plants are monoecious and produce creamy-yellow to deep orange-yellow male or female flowers on the same vine. In general, male and female flowers occur in the ratio 10:1. Each male flower has three stamens with united filaments and anthers. The female flower has a thick style and two-lobed stigma. It has an easily recognised underdeveloped fruit (ovary) having three chambers, each containing many ovules. The corolla consists of five united petals. Since anthers are present in one flower and stigma on another, mechanical transfer of pollen is essential to fruit set.

Male flowers produce good amounts of pollen, and both male and female flowers produce a large quantity of nectar. Flowers are visited by insects – including honeybees. Pollination is most effective in the early morning because flowers open early and the stigma is most receptive at this time. Honeybees are the primary pollinators and increase production by 3–4 times. Fruit set, seed set, and fruit weight increase with an increase in the number of pollen grains deposited on the stigma. For higher yield and better quality fruit, place eight colonies of *Apis mellifera* and 12–16 colonies of *Apis cerana* evenly per hectare at 10–15% flowering.

8.5.2.5 Okra (*Abelmoschus esculentus*)

Okra blooms for about 3–4 months from June to September. It produces large, solitary, light yellow flowers with a maroon spot at the base of the petal in the leaf axils. The flower has five sepals, five petals, many stamens having filaments united to form a tube around the style and monothecus (one-celled) anthers, and a pistil having a five-chambered ovary with many ovules in each chamber, a style, and five stigmas. Nectar is produced by both floral and extrafloral nectaries.

Flowers are generally self-pollinated, but cross-pollination increases fruit and seed set. Honeybees are the most important pollinators. For effective pollination, place 1–2 colonies of *Apis mellifera* and 2–3 colonies of *Apis cerana* evenly per hectare at 10–15% flowering.

8.5.2.6 Onion (*Allium cepa*)

Onion blooms during April for 3–4 weeks and produces ash-grey flowers in simple oval umbels. Each umbel consists of 40–200 flowers. The flower consists of six petals in two whorls of three petals each, six stamens also in two whorls of three stamens each, and a pistil with a three-celled ovary with two ovules in each cell, a style, and a small stigma. Anthers release pollen within 24–36 h of the flower opening and before the stigma is receptive, therefore self-pollination within the flower is not possible.

Flowers produce a good amount of nectar and pollen. Cross-pollination is carried out by insects – including honeybees. Commercial production of onion seed depends on honeybees as the primary pollinators. For effective pollination, place 5–8 colonies of *Apis mellifera* or 10–12 colonies of *Apis cerana* evenly per hectare at 10–15% flowering. Onion flowers have a typical smell of sulphur and are comparatively less attractive to honeybees; this may cause bees to neglect the crop if other more attractive crop/weeds are blooming in the vicinity.

8.5.2.7 Radish (*Raphanus sativus*)

Radish blooms during March-April for over a month. The white or purplish-pink flowers open in the morning and remain open for 2–3 days. The stigma is receptive for only a few hours. The flower consists of four sepals, four petals, six stamens (four long and two short), and a pistil consisting of an ovary containing 6–12 ovules, a style, and a stigma. Many commercial varieties are self-incompatible, therefore require cross-pollination.

The flower produces a good amount of nectar and pollen. Honeybees are the most effective pollinators. Honeybee pollination increases fruit set, seed set, number of seeds per pod, and seed weight. Seed yield is greatly influenced by the number of honeybees visiting flowers. In order to have higher yields and better-quality seed, place 2–3 colonies of *Apis mellifera* and 4–6 colonies of *Apis cerana* evenly per hectare at 10–15% flowering.

8.5.2.8 Turnip (*Brassica rapa*)

Turnip blooms from March-April for over a month. It produces dark yellow flowers that open in the morning for 2–3 days. The structure of the flower is similar to that of other *Brassica* species. Honeybees are the most important pollinators and increase fruit set, seed set, number of seeds per pod, and seed weight. For higher yields and better quality seed, place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare at 10–15% flowering.

8.5.3 Oilseed Crops

8.5.3.1 Rape and Mustard (*Brassica spp.*)

Many species of *Brassica*, such as rape (*Brassica napus*), sarson (*Brassica campestris* var. sarson), toria (*Brassica campestris* var. toria), Indian mustard or broad-leaved mustard or trowse mustard or rai (*Brassica juncea*), white mustard (*Brassica alba*), and black mustard (*Brassica nigra*) are cultivated widely as oilseed crops throughout the Hindu Kush-Himalayan region. Most of these crops bloom during February-March for over a month. The flowers are bright yellow and are produced in long terminal racemes. They are similar to other cruciferous crops, e.g., cole crops, radishes, and turnips. Some crops, such as winter rape, bloom during December-January. The flower consists of four sepals, four petals, six stamens (four long and two short), and a pistil having a single two-chambered ovary with 6–12 ovules, a style, and a capitate stigma. These crops are usually self-pollinated, but some degree of cross-pollination occurs in *Brassica campestris*.

The flower produces a good amount of nectar and pollen and is highly attractive to honeybees and other natural insect pollinators. Cross-pollination by honeybees increases yield and quality and oil content of seed. Since crops are mainly self-pollinated and flowers are attractive to bees, place 3–5 colonies of *Apis mellifera* or 5–8 colonies of *Apis cerana* evenly per hectare.

8.5.3.2 Niger (*Guizotia abyssinica*)

Niger blooms from September-October for over a month and produces deep yellow flowering heads. A flowering head consists of two types of florets: ray florets and disc florets. Ray florets are a conspicuous yellow and consist of an inferior ovary without stamens or pistils. Disc florets are hermaphrodite (bisexual) and consist of five united petals, five stamens with united anthers, and a pistil having a one-chambered ovary with one ovule, a style, and a bifid stigma. Disc florets produce plenty of nectar and pollen.

Pollination is accomplished by insects, particularly honeybees. Honeybee pollination increases both yield and quality of seed. To produce high yields with a high oil content, place 3–5 colonies of *Apis mellifera* or 6–8 colonies of *Apis cerana* evenly per hectare.

8.5.3.3 Safflower (*Carthamus tinctorius*)

Safflower blooms from March-April and produces 15–150 orange-yellow flowering heads terminating the main axis and branches. The flowering head that terminates the main axis blooms first, then flowering proceeds downwards with those flower heads on the lowest branches opening last. A flower head consists of from 20 to 100 yellow and orange florets surrounded by bracts. Each floret consists of five petals united to form a long corolla tube. The stamens consist of five filaments and five anthers. Anthers are united around the style. The pistil consists of a single one-chambered ovary having one ovule. In many self-fertile varieties, anthers release pollen early in the day, and soon afterwards the style elongates and the stigma appears above the top of the anther tube covered with pollen grains. Thus self-pollination occurs. In self-sterile varieties, the style elongates and passes through the anther tube before anthers release pollen. In such varieties, self-pollination does not occur and cross-pollination is carried out by insects.

Florets produce plenty of nectar and pollen, and the crop is a major source of honey in areas where it is cultivated on a large scale. Honeybees are the most important pollinators. Honeybee pollination not only helps seed production in self-sterile varieties, but also enhances yield and quality of self-fertile varieties. For effective pollination, place five colonies of *Apis mellifera* and 4–6 colonies of *Apis cerana* evenly per hectare at 10–15% flowering.

8.5.3.4 Sunflower (*Helianthus annuus*)

Sunflower blooms during June for 3–4 weeks. The primary stalk has a primary head and one to many secondary heads. However, most commercial varieties are almost all single-headed plants. The corolla is made of five united petals. The main head consists of from 1,000 to 4,000 individual florets and the secondary head has 300–1,500 florets depending on the variety and the size of the head. The flowering head is composed of two types of florets: outer conspicuous yellow ray florets and inner less conspicuous disc florets. Ray florets are sterile and have inferior ovaries without stamens or pistils. Disc florets constitute most of the head. They are hermaphrodite, and anthers mature and release pollen before stigmas are receptive. Disc florets open from the periphery inward, 2–4 circles each day.

Florets produce plenty of nectar and pollen and are visited by insect pollinators. Honeybees are the most important pollinators, and increase yield and quality of seed. A floret sets seed if pollinated early: its ability to produce seed decreases with the length of time it has been open. Therefore, honeybee colonies should be moved to the field at 5–10% flowering. The recommended number of *Apis mellifera* colonies is five and of *Apis cerana* colonies is 8–10, evenly distributed, per hectare.

8.5.4 Spices

8.5.4.1 Large Cardamom (*Amomum subulatum*)

The large cardamom blooms during March-April for about 3–4 weeks and produces pinkish-white flowers on long pedicels in 20 or more lateral racemes of 2–5 flowers each. The flowers subsequently open from the base to the top of the panicle. A cardamom flower consists of a pale green, slender calyx tube from which pinkish or white narrow lobes of corolla (the inside of the corolla is white and the outside pinkish-white) and a large white obovate labellum or staminodium with violet nectaries emerge. The flower has a single functional stamen with a short filament and a large anther. The stigma is in close contact with the distal end of the anther. The pistil consists of a single, inferior, tri-locular ovary with several ovules. The flowers open in the morning and wither by evening. The anthers release pollen when the xflower opens and the stigma is receptive till late morning, thus providing an opportunity for self-pollination.

Flowers produce both nectar and pollen and are visited by insects. Honeybees are the main pollinators. Pollen collectors pass over anthers and stigma, and thus ensure pollination; whereas nectar collectors can reach the nectar without touching anthers and stigma (i.e., without pollinating the flower). Honeybees enhance both fruit and seed set. There is no specific recommendation on the number of colonies to use: 2–3 colonies of *Apis mellifera* and 4–6 colonies of *Apis cerana* per hectare would be sufficient for pollination.

8.5.4.2 Chillies (*Capsicum annum*)

Chillies bloom for a long period from July to September and produce white flowers in extra axillary cymes. A chilli flower has five sepals, five petals, five stamens, and a pistil with a single two-chambered (bilocular) ovary having many ovules in each locule, a style, and a bifid stigma. The flowers produce 1.1–2.6 mg of nectar per flower of 67–69% sugar concentration, depending on the variety. Chillies are generally self-compatible and produce fruits and seeds by self- pollination, but some varieties are self-incompatible. The self-incompatible varieties require cross-pollination by insects.

Honeybees are the most important pollinators. Honeybee pollination increases both the number of fruits per plant and the number of seeds per fruit. There is no specific recommendation on the number of bee colonies to use. Place 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* evenly per hectare at 10–15% blooming.

8.5.4.3 Coriander (*Coriandrum sativum*)

Coriander blooms during February-March for about 3–4 weeks and produces small pinkish-white flowers in compound umbels. A coriander flower has five sepals, five unequal petals, five stamens and a pistil having a single inferior, bilocular ovary with one ovule in each locule, two styles and two stigmas. The flowers produce a good amount of nectar and pollen and are visited by insects. Lack of pollinators generally decreases the seed yield. Honeybees are the primary pollinators. Bee pollination can increase yield by 187%. There is no specific recommendation on the number of bee colonies to use: 2–3 colonies of *Apis mellifera* or 4–6 colonies of *Apis cerana* per hectare should be sufficient for pollination. Managing pollination of crops secreting a good amount of nectar and pollen but having a short blooming period, Some fruit crops; apple, apricot, cherry, pear, persimmon, and plum; fall into this category.

8.6 Conclusions and Future Research

Our vast knowledge of the physical, behavioral, and physiological (especially sensory) characters of honey bees has allowed us to manipulate and exploit them for pollinating our crops. Colonies can be managed to produce maximum populations when required, and information about the best number, timing, and arrangement of colonies on crops is available. Progress towards increasing numbers of pollen or nectar collectors by altering brood composition or food stores of colonies, or by directing bees to target crops through scent training or application of attractants, has been made. Despite this, retention of honey bees on target crops can only be assured if the bees are spatially isolated from competing bloom or are confined on crops that are grown within cages or greenhouses. With some crops it may be necessary to use other more host specific insects (e.g. leafcutter bees on alfalfa) as pollinators.

The selection and breeding of honey bees for physical characters suited to certain crops, for reduced flight ranges, or for preferences for specific pollens or nectars, appears promising. However, these programs are long term and costly not only to produce the genetic lines but also to maintain them; these costs must be carefully balanced against the value of the crop yields obtained. Since elimination of competitive bloom for target crops is rarely feasible, selection and breeding programs should also be continued and/or initiated for certain important crops. Flowers of these crops should be modified to make them highly attractive in terms of visual and olfactory cues, quantity and quality of pollen and nectar rewards, and by elimination of any floral barriers. Cultural practices must also be considered as they enhance nectar, and possibly pollen, production in plants. Perhaps major competitive crops, near target crops, could be made less attractive through selection and breeding programs as well. These programs should concentrate first on crops that have potential as major food resources for humans.

It appears that the ultimate solution for maintaining honey bees on a specific crop may involve a combination of plant and bee breeding programs as well as systems that affect the bee's behavior. Certainly the use of pheromonal and pollen attractants on crops deserves further study. Throughout such studies, it is important to recognize that attracting bees to, and retaining them on, crops is only part of the overall problem. The assumption that when bees are foraging on a crop they are also pollinating it efficiently is not necessarily valid. Therefore, information about the behavior of bees on flowers and how this affects pollination efficiency and crop yields is essential; unfortunately, few studies to date include such information.

The problem of attracting honey bees to target crops, or of preventing their exodus from them, has long challenged the ingenuity of apiculturists and researchers. Because the problems of world food production, relative to the growth of human populations, are increasing daily, the author believes that answers to the problem discussed in this review are urgently required. The solution would further enhance the value of the readily available and easily managed honey bee but, more importantly, it would increase food production.

References

Abrol DP (1991) Conservation of pollinators for promotion of agricultural production in India. J Anim Morphol Physiol 38(1x2):123–139

Abrol DP (1997) Pollination energetics. In: Sihag RC (ed) Pollination biology series, vol I. Rajendra Scientific Publishers, Hisar, pp 75–97

Abrol DP (2008) Plant insect interaction in crucifers. In: Dr Gupta SK (ed) Biology and breeding of crucifers. CRC Press/Taylor and Francis, Boca Raton, pp 129–149

Abrol DP (2009) Bees and beekeeping in India, 2nd edn. Kalyani Publishers, Ludhiana, 719 p

Abrol DP (2010a) Beekeeping–a comprehensive guide on bees and beekeeping. Scientific Publishers, Jodhpur, 896 p

Abrol DP (2010b) Foraging behaviour of *Apis florea* F., an important pollinator of *Allium cepa* L. J Apic Res Bee World 49(4):318–325

Abrol DP (2011) Foraging. In: Hepburn HR, Radloff SE (eds) Honeybees of Asia. Springer, Berlin, pp 257–292

AI-Tikrity WS, Benton AW, Hillman RC, Clarke WW Jr (1972a) The relationship between the amount of unsealed brood in honeybee colonies and their pollen collection. J Apic Res 11:9–12

AI-Tikrity WS, Benton AW, Risuis ML, Clarke WW Jr (1972b) The effect of length of stay of a honeybee colony in a crown vetch field on its foraging behaviour. J Apic Res 11:51–57

Alpatov VV (1984) Bee races and red clover pollination. Bee World 29:61–63

Anderson LD, Atkins EL (1968) Pesticide usage in relation to beekeepers. Annu Rev Entomol 13: 213–238

Atkins EL (1981) Repellents reduce insecticidal kills of honeybees. In: Proceedings of 28th international congress of apiculture, Bucharest 1:305–310

Atkins EL, MacDonald RL, Greywood-Hale EA (1975) Repellent additives to reduce pesticide hazards to honeybees: field tests. Environ Entomol 4:207–210

Baker HG, Hurd PD (1968) Intrafloral ecology. Annu Rev Entomol 13:385–414

Barker RJ (1971) The influence of food inside the hive on pollen collection by a honeybee colony. J Apic Res 10:23–26

Belletti A, Zani A (1981) A bee attractant for carrots grown for seed. Sementi Elette 27:23–27

Blum MS, Brand JM (1972) Social insect pheromones: their chemistry and function. Am Zool 12:553–576

Boch R (1956) The dances of bees for nearby and distant sources. Z Vergl Physiol 38:136–137

Boch R (1982) Relative attractiveness of different pollens to honeybees when foraging in a flight room and when fed in the hive. J Apic Res 21:104–106

Bohart GE (1957) Pollination of alfalfa and red clover. Annu Rev Entomol 2:355–380

Bohart GE (1972) Management of wild bees for the pollination of crops. Annu Rev Entomol 31:49–65

Braines LN, lstomina-Tsvetkova KP (1956) The use of reflectors of ultraviolet radiation from the sun for attracting bees to required areas of crops. Pchelovodstvo 34:23–26 (In Russian)

Brakefield JJ (1980) Report of beeline® trials in top and soft fruit crops. Rep. Murphy Chemical Ltd, Weathampsted

Braun E, MacVicar RM, Gibson DA, Pankiw P, Guppy J (1953) Studies in red clover seed production. Can J Agric Sci 33:437–447

Bretschko J, Bullmann O (1966) Bee visits to blackcurrant. Bienenwelt 8:73–86 (In German)

Brittain WH (1933) Apple pollination studies in the Annapolis Valley, N.S., Canada 1928–1932. Bull Dep Agric Can New Ser 162:1–198

Burgett M, Fisher G (1979) An evaluation of Beeline® as a pollinator attractant on red clover. Am Bee J 119:356–357

Butler CG, Fletcher DJC, Watter D (1969) Nest entrance marking with pheromones by the honeybee *Apis mellifera* L. and by a wasp. Vespula vulgaris L. Anim Behav 17:142–147

Cale GH (1968) Pollen gathering relationship to honey collection and egglaying in honey bees. Am Bee J 108:8–9

Cale GH, Rothenbuhler W (1978) Genetics and breeding of the honey bee. In: Dadant (ed) The hive and the honey bee. Dadant and Sons, Hamilton, pp 157–184

Campana BJ, Moeller FE (1977) Honey bees: preference for and nutritive value of pollen from five plant sources. J Econ Entomol 70:39–41

Cantwell GE, Shimanuki H, Retzer J (1972) Airdropping disposable packages of honey bees. Am Bee J 112:328–329

Chaudhary OP (1998) Role of pollinators in seed production and its quality. In: Seed quality assurance. CCS Haryana Agricultural University, Hisar, pp 86–109

Chauvin R (1960) Active substances relating to behaviour inside the hive. Ann Abeille 31: 185–197

Chesnokova EG (1958) Can bees differentiate between close varieties of agricultural plants? Pchelovodstvo 35:19–22 (In Russian)

Collins AM, Rinderer TE, Harbo JR, Brown MA (1984) Heritabilities and correlations for several characters in the honey bee. J Hered 75:135–140

Crane E, Walker P (1983) The impact of pest management on bees and pollination. Tropical Development and Research Institute, London, 232 pp

Crane E, Walker P (1984) Pollination directory for world crops. International Bee Research Association, London, 184 pp

Cumakov V (1955) Aromatic oils for inducing hive bees to pollinate Trifolium pratense. Za Soc Zemed 5:747–754

Cumakov V, Fejf V (1959) The use of colour in directing honeybees to red clover. Za Soc Zeroed 32:715–726

De Grandi-Hoffman G, Hoopingarner R, Barker K (1984) Pollen transfer in apple orchards: tree to tree or bee to bee? Bee World 65:126–133

Dietz A (1978) Nutrition of the adult honey bee. In: Dadant (ed) The hive and the honey bee. Dadant and Sons, Hamilton, pp 125–156

Doull KM (1966) The relative attractiveness to pollen-collecting honeybees of some different pollens. J Apic Res 5:9–14

Doull K (1974) Effects of attractants and phagostimulants in pollen and pollen supplement on the feeding behaviour of honeybees in the hive. J Apic Res 13:47–54

Drake CJ (1949) Influence of insects on alfalfa seed production in Iowa. J Econ Entornol 41:742–750

Eckert JE (1933) The flight range of the honeybee. J Agric Res 47:257–285

Eickwort GC, Ginsberg HS (1980) Foraging and mating behavior in Apoidea. Annu Rev Entomol 25:421–446

Erickson EH, Detroy BF, Whitefoot LO (1974) Comparative evaluation of containers used as honey bee hives for disposable pollination units. J Econ Entomol 67:197–200

Erickson EH, Thorp RW, Briggs DL (1975) Comparisons of foraging patterns among honey bees in disposable pollination units and in overwintered colonies. Environ Entomol 4:527–530

Faegri K, van der Pijl L (1971) The principles of pollination ecology. Pergamon, Oxford, 291 pp

Farkas J (1981) Honeybee pollination in sour cherry plantations. Kertgazdastig 13:15–29 (In Hungarian)

Ferguson AW, Free JB (1979) Production of a forage-marking pheromone by the honeybee. J Apic Res 18:128–135

Filmer RS (1932) Brood area and colony size as factors in activity of pollination units. J Econ Entomol 25:336–343

Free JB (1958) Attempts to condition bees to visit selected crops. Bee World 39:221–230

Free JB (1959) The effect of moving colonies of honeybees to new sites on their subsequent foraging behaviour. J Agric Sci (Camb) 53:1–9

Free JB (1962) The effect of distance from pollinizer varieties on the fruit set on trees in plum and apple orchards. J Hortic Sci 37:262–271

Free JB (1965a) Attempts to increase pollination by spraying crops with sugar syrup. J Apic Res 4:61–64

Free JB (1965b) The effect on pollen collection of feeding honeybee colonies with sugar syrup. J Agric Sci 64:167–168

Free JB (1967) Factors determining the collection of pollen by honeybee foragers. Anim Behav 15:134–144

Free JB (1968a) Dandelion as a competitor to fruit trees for bee visits. J Appl Ecol 5:169–178

Free JB (1968b) The conditions under which foraging honeybees expose their Nasonov gland. J Apic Res 7:139–145

Free JB (1969) Influence of the odour of a honey bee colony's food stores on the behaviour of its foragers. Nature 222:778

Free JB (1970a) Insect pollination of crops. Academic, London, 544 pp

Free JB (1970b) The effect of flower shape and nectar guides on the behavior of foraging honeybees. Behaviour 7:269–285

Free JB (1979a) Managing honeybee colonies to enhance the pollen-gathering stimulus from brood pheromones. Appl Anim Ethol 5:173–178

Free JB (1979) Progress toward the use of pheromones stimulate pollination by honey bees. In: Proceedings of 4th international symposium on pollination, 1978, College Park 1:7–22

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London, 684 pp

Free JB, Nuttall PM (1968) Effect of the time of day at which honeybee colonies are first allowed flight in a new location on their choice of flower species. Nature 218:982

Free JB, Smith MV (1961) The foraging behaviour of honeybees from colonies moved into a pear orchard in full flower. Bee Worm 42:11–12

Free JB, Williams IH (1970) Preliminary investigations on the occupation of artificial nests by *Osmia rufa* L. J Appl Ecol 7:559–566

Free JB, Williams IH (1973) Genetic determination of honeybee (*Apis mellifera* L.) forage preferences. Ann Appl Biol 73:137–141

Free JB, Williams IH (1974) Influence of the location of honeybee colonies on their choice of pollen sources. J Appl Ecol 11:925–935

Free JB, Williams IH (1983) Scent marking of flowers by honeybees. J Apic Res 22:86–90

Free JB, Free NW, Jay SC (1960) The effect on foraging behavior of moving honey bee colonies to crops before or after flowering has begun. J Econ Entomol 53:564–566

Free JB, Pickett JA, Ferguson AW, Simpkins JR, Williams C (1984) Honey bee Nasonov pheromone lure. Bee Worm 65:175–181

Free JB, Paxton RJ, Waghwchoure ES (1991) Increased the amount of foreign pollen carried by honeybee foragers. J Apic Res 30:132–136

Gary NE (1978) Activities and behavior of honey bees. In: Dadant (ed) The hive and the honey bee. Dadant and Sons, Hamilton, pp 157–184, 185–264

Gary NE, Witherell PC (1977) Distribution of foraging bees of three honey bee stocks located near onion and sunflower fields. Environ Entomol 6:785–788

Gary NE, Witherell PC, Marston J (1972) Foraging range and distribution of honey bees used for carrot and onion pollination. Environ Entomol 1:71–78

Gary NE, Witherell PC, Lorenzen K (1978) A comparison of the foraging activities of common Italian and "Hy- Queen" honey bees. Environ Entomol 7:220–232

Genrikh VG (1958) Influence of the queen on flight and hive activity of bees. Pchelovodstvo 34:8–12 (In Russian)

Gluslakov NM (1958) Problems of beekeeping in the U.S.S.R. in relation to pollination. Bee Worm 39:81–92

Goncalves LS, Stort AC (1978) Honey bee improvement through behavioral genetics. Annu Rev Entomol 31:197–213

Goodwin RH, Houten A, Perry JH (1991) Feeding sugar syrup to honeybee colonies to improve Kiwifruit pollen collection: a review. Acta Hortic 288:265–269

Gould JL (1976) The dance-language controversy. Q Rev Biol 51:211–244

Griggs WH, Iwakiri BT (1960) Orchard tests of beehive pollen dispensers for cross-pollination of almonds, sweet cherries, and apples. Proc Am Soc Hortic Sci 75:114–128

Gubin AF (1947) Honey bees and the pollination of red clover. Sel'sk Khoz Moskva 1:1–277 (In Russian)

Hammer O (1961) Effect of distance on honey production. Nord Bitidskr 13:20–23 (In Danish)

Hassell MP, Southwood TRE (1978) Foraging strategies of insects. Annu Rev Ecol Syst 9:75–98

Hawkins RP (1969) Length of tongue in a honey bee in relation to the pollination of red clover. J Agric Sci 73:489–493

Heinrich B (1981) The energetics of pollination. Ann Mo Bot Gard 68:370–378

Hellmisch RL, Kulincevic JM, Rothenbough WC (1985) Selection for high and low pollen hoarding honeybees. J Hered 76:155–158

Hiigel MF (1962) Studies of several pollen constituents. Ann Abeille 5:97–133 (In French)

Hohmann H (1970) Effect of pollen extracts and scented oils on thc foraging and recruiting activities of the honeybees. Apidologie 1:157–158 (In German)

Holm SN, Poulsen MH (1975) Breeding honeybees for pollen collection from certain crops. In: Proceedings of 3rd international symposium on pollination, Prague 1:229–238

Hopkins CY, Jevans AW, Boch R (1969) Occurrence of octadeca *-trans-2, cis-9, cis-12*-trienoic acid in pollen attractive to the honey bee. Can J Biochem 47:433–436

Houbaert D, Jacobs FJ (1992) Accelerated fruit setting of tomatoes by insect pollination. In: Bees for pollination. Proceedings of an EC workshop, Brussels, Belgium, 2–3 March 1992, pp 207–218

Howell GS, Kilby MW, Nelson JW (1972) Influence of timing of hive introduction on production of highbush blueberries. HortScience 7:129–131

Hutson R (1925) The honey bee as an agent in the pollination of pears, apples and cranberries. J Econ Entomol 18:387–391

Istomina-Tsvetkova KP, Skrebtsov MC (1964) A new method of stimulating the activities of bees. Pchelovodstvo 2:205–222 (In Russian)

Jay SC (1974) Nectar and pollen collection by honeybees from coconut flowers. Bee World 55:105–111

Jay S (1986) Spatial management of bees on crops honey. Annu Rev Entomol 31:49–65

Jay D, Jay SC (1984) Observations of honeybees on Chinese gooseberries (“Kiwifruit”) in New Zealand. Bee World 65:155–166

Jaycox ER (1970a) Honey bee foraging behavior: responses to queens, larvae, and extracts of larvae. Ann Entomol Soc Am 63:1689–1694

Jaycox ER (1970b) Honey bee queen pheromones and worker foraging behavior. Ann Entomol Soc Am 63:222–228

Johansen CA (1977) Pesticides and pollinators. Annu Rev Entomol 22:177–192

Johnson DL, Wenner DL (1970) Recruitment efficiency in honeybees: studies on the role of olfaction. J Apic Res 9:13–18

Jordan R (1961) Bees in hives without brood collect pollen. Bienenvater 82:305–306 (In German)

Karmo EA (1958) Honey bees as an aid in orchard and blueberry pollination in Nova Scotia. In: 10th international congress of entomology, 1956, Montreal, 4:955–959

Karmo EA, Vickery VR (1954) The place of honeybees in orchard pollination. Mimeo Circ NS Dep Agric 67:1–7

Kashkovovskii VG (1957) Influence of the removal of the queen on the productivity of bee colonies. Pchelovodstvo 34:36–38 (In Russian)

Kauffeld NM, Sorensen EL (1980) Foraging behavior of honey bees on two-clone alfalfa combinations differing in bee attractiveness. J Econ Entomol 73:434–435

Kauffeld NM, Levin MD, Roberts WC, Moeller FE (1970) Disposable pollination units, a revived concept of crop pollination. Am Bee J 110:88–89

Kerberg K, Lesins K (1949) Insects pollinating alfalfa in Central Sweden. Lantbruksh6gsk Annlr 16:630–643 (In Swedish)

Kerr WE (1974) Advances in cytology and genetics of bees. Annu Rev Entomol 19:253–268

Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annu Rev Entomol 28:407–453

Kumar J, Gupta JK (1993) Nectar sugar production and honey bee foraging activity in three species of onion (Allium species). Apidologie 24(4):391–396

Kumar J, Mishra RC, Thakur SS (1998) Use of honeybees for increasing agricultural yields. In: Mishra RC, Garg R (eds) Perspectives in Indian apiculture. Agro Botanica, Bikaner, pp 187–211

Kurennoi NM, Barabash IP (1966) The efficacy of methods of pollination and of increasing the grape crop. Sadovod Vinograd Vinodel Mold 10:30–33 (In Russian)

Kydonieus AF, Beroza M (eds) (1982) Insect suppression with controlled release pheromone systems, vol I. CRC Press, Boca Raton, 274 pp

Ladd TL, Tew JE (1983) Attraction of honey bees (Hymenoptera:Apidae) traps baited with lures for Japanese beetles (Coleoptera:Scarabaeidae). J Econ Entomol 76:769–770

Lee WR (1961) The nonrandom distribution of foraging honey bees between apiaries. J Econ Entomol 54:928–933

Legge AP (1976) Hive inserts and pollen dispensers for tree fruits. Bee World 57:159–167

Levin MD (1959) Distribution patterns of young and experienced honey bees foraging in alfalfa. J Econ Entomol 52:969–971

Levin MD (1960) Do foraging bees retain their orientation to a certain distance from their hive, after the hive is moved? Bee World 41:281–282

Levin MD, Bohart GE (1955) Selection of pollens by honey bees. Am Bee J 95:392–393, 402

Levin MD, Bohart GE (1957) The effect of prior location on alfalfa foraging by honey bees. J Econ Entomol 50:629–632

Lfffler A (1961) Does hive disturbance and loss of the queen reduce the foraging activity of bees? Z Bienenforsch 5:131–144 (In German)

Lindauer M (1952) Division of labour in the honeybee colony. Z Vgl Physiol 34:299–345 (In German)

Linsley EG, McSwain JW (1947) Factors influencing the effectiveness of insect pollinators of alfalfa in California. J Econ Entomol 40:349–357

Lotter J (1960) Recent developments in the pollination techniques of deciduous fruit trees. Deciduous Fruit Grow 10:182–190, 212–24, 304–311

Lopatina NG, Nikitina IA (1960) Training bees with the help of visual orienters. Pchelovodstvo 37:39–41 (In Russian)

Louveaux J (1958) Investigations on the collection of pollen by bees. Ann Abeille 1:113–188, 197–221 (In French)

Louveaux J (1959) Investigations on the collection of pollen by bees. Ann Abeille 2:13–111 (In French)

Mackenscn O, Nye WP (1966) Selecting and breeding of honeybees for collecting alfalfa pollen. J Apic Res 5:79–86

Mackensen O, Nye WP (1969) Selective breeding of honeybees for alfalfa pollen collection: sixth generation and out crosses. J Apic Res 8:9–12

Mackensen O, Tucker SC (1973) Preference for some other pollens shown by lines of honeybees selected for high and low alfalfa pollen collection. J Apic Res 12:187–190

MacVicar RM, Braun DR, Jamieson CA (1952) Studies in red clover seed production. Sci Agric 32:67–80

Margalith R, Lensky Y, Rabinowitch HD (1984) An evaluation of Beeline® as a honeybee attractant to cucumbers and its effect on hybrid seed production. J Apic Res 23:50–54

Martin EC, McGregor SE (1973) Changing trends in insect pollination of commercial crops. Annu Rev Entomol 18:207–226

Matheson AG (1986) Colony standards for Kiwifruit pollination. NZ Beekeeper 189:20–22

Matheson AG (1991) Managing honeybee pollination of Kiwifruit (Actinidia deliciosa) in New Zealand – a review. Acta Hortic 288:213–219

Maurizio A (1950) Investigations on the influence of pollen diet and nursing on the longevity and physiological condition of bees. Beih Schweiz Bienen-Ztg 73:58–64 (In German)

McGregor SE (1976) Insect pollination of cultivated crops. USDA Agricultural Research Service, Washington, DC, 411 pp

McMahon HA (1954) Pollination of alfalfa by honeybees. Can Bee J 62:4–6

Michener CD (1974) The social behavior of the bees: a comparative study. Harvard University Press, Cambridge, 404 pp

Milne CP (1981) Laboratory measurement of honey production in the honeybee. 5. Relationship between weekly colony weight gains, and responses on tests of hoarding behaviour, longevity or length of life and pupal weight of the worker. J Apic Res 20:31–33

Moeller FE (1972) Honey bee collection of corn pollen reduced by feeding pollen in the hive. Am Bee J 112:210–212

Moeller FE (1973) Timing of placement of colonies of honey bees for pollination of cranberries. J Econ Entomol 66:370–372

Moriya K (1966) Effects of pollen traps on pollen collection. Jpn J Ecol 16:105–109 (In Japanese)

Morse RA, Boch R (1971) Pheromone concert in swarming honeybees (Hymenoptera:Apidae). Annu Entmol Soc Am 64:1414–1417

Nunez JA (1967) Foragers mark exhausted food sources with scent. Naturwissenschafien 54: 322–323 (In German)

Nye WP (1971) Pollen collection from alsike clover by high and low alfalfa pollen collecting lines and by a commercial line of honeybees. J Apic Res 10:115–118

Nye WP, Machensen O (1970) Selective breeding of honeybees for alfalfa pollen collection: with tests in high and low alfalfa pollen collection regions. J Apic Res 9:61–64

Nye WP, Mackensen O (1965) Preliminary report on selection and breeding of honeybees for alfalfa pollen collection. J Apic Res 4:43–48

Olsen LG, Hooplngarner R, Martin EC (1979) Pollen preferences of honeybees sited on four cultivated crops. J Apic Res 18:196–200

Overley FL, O'Neill WJ (1946) Experiments with the use of bees for pollination of fruit trees. Proc Wash State Hortic Assoc 42:203–214

Palmer Jones T, Clinch PG (1974) Observations on the pollination of Chinese gooseberries variety "Flayward". NZ J Exp Agric 2:455–458

Palmer-Jones T, Forster IW (1972) Measures to increase the pollination of lucerne (*Medicago sativa* Linn.). NZ J Agric Res 15:186–193

Patil BS, Viraktamath S, Lingappa S, Giraddi RS, Parameshwarappa K, Bhat ARS (2000) Effect of Bee-Q and Bee- here on pollination and yield of sesamum. Insect Environ 5(4):151

Petersen HL (1954) Pollination and seed setting in Lucerne. K Vet Landbohoejsk Arsskr 1:138–169 (In Swedish)

Peterson AG, Furgala B, Holdaway FG (1960) Pollination of red clover in Minnesota. J Econ Entomol 53:546–550

Philp GL, Vansell GH (1932) Pollination of deciduous fruits by bees. Calif Agr Ext Serv Cir 62:1–8

Prasad R, Chand H, Singh R (2000) Effect of honeybee, *A. mellifera* pollination on the yield and germination of onion, *Allium cepa* seeds. Shashpa 7(1):53–55

Pritsch G (1959) Investigations of scent training of bees to red clover for increased seed production. Arch Gefliigelz Kleintierk 8:214–239 (In German)

Proctor M, Yeo P (1973) The pollination of flowers. Collins, London, p 418

Prokopy RJ, Owens ED (1983) Visual detection of plants by herbivorous insects. Annu Rev Entomol 28:337–364

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Q Rev Biol 52:137–153

Rakhmankulov FK (1957) How to increase the efficiency of the pollination of red clover by bees. Pchelovodstvo 2:20 (In Russian)

Real E (ed) (1983) Pollination biology. Academic, London, 338 pp

Ribbands CR (1951) The flight range of the honey bee. J Anim Ecol 20:220–226

Ribbands CR (1952) The relation between the foraging range of honeybees and their honey production. Bee Worm 33:2–6

Ribbands CR (1953) The behaviour and social life of honeybees. Bee Research Association, London, p 352

Ribbands CR, Speirs N (1953) The adaptability of the homecoming honey bee. Br J Anim Behav 1:59–66

Richards AJ (ed) (1978) The pollination of flowers by insects. Academic, London, 213 pp

Rinderer TE, Baxter JR (1978) Effect of empty comb in hoarding behavior and honey production of the honey bee. J Econ Entomol 71:757–759

Roberts CW (1974) A standard stock of honeybees. J Apic Res 13:113–120

Robinson FA, Nation JL (1968) Substances that attract caged honeybee colonies to consume pollen supplements and substitutes. J Agric Res 7:83–88

Roubik DW (1995) Pollination of cultivated plants in the tropics. FAO agricultural services bulletin No. 118, FAO, Rome, 196 p

Sale PR (1983) Kiwifruit culture. Government Printing Office, Wellington

Sasaki M (1985) Utilization of pollen loads for artificial pollination of fruit trees. In: The 30th international apicultural congress of Apimondia, Nagoya, Japan, pp 390–393

Schwan B, Martinovs A (1954) Studies of pollen collection by honeybees in Sweden. Medd Husdjursf6rsOk 57:1–35 (In Swedish)

Sheppard WS, Jaycox ER, Parise SG (1979) Selection and management of honey bees for pollination of soybeans. In: Proceedings of 4th international Symposium on Pollination, 1978, College Park 1:123–130

Shimanuki H, Lehnert T, Stricker M (1967) Differential collection of cranberry pollen by honey bees. J Econ Entomol 60:1031–1033

Sihag RC, Mishra RC (1995) Crop pollination and Apis cerena. In: Kevan PG (ed) The Asiatic hive bee. Enviroquest, Ltd, Ontario, pp 135–141

Simpson J (1966) Repellency of the mandibular gland scent of worker honey bees. Nature 209:531–532

Singh S (1950) Behavior studies of honeybees in gathering nectar and pollen. NY Agric Exp Stn Ithaca Mern 288:1–57

Skrebtsova ND (1957) Pollination of buckwheat flowers by bees. Pchelovodstvo 34:48–50 (In Russian)

Sladen FWL (1901) A scent organ in the bee. Br Bee J 29:142, 143, 151–153

Smaragdova NP (1956) Selective ability of bees in pollinating plants. Uch Zap Mosk Gos Univ 183:97–102 (In Russian)

Soost RK (1965) The use of pollen dispensers in citrus. Calif Citrogr 50:247–249

Spencer-Booth Y (1960) Feeding pollen, pollen substitutes and pollen supplements to honeybees. Bee Worm 41:253–263

Stephen WP (1958) Pear pollination studies in Oregon. Tech Bull Oreg Agric Exp Sin 43:1–43

Sturtevant AP, Farrar CL (1935) Further observations on the flight range of the honeybee in relation to honey production. J Econ Entomol 28:585–589

Svendsen O (1964) The pollen harvest of colonies during red clover bloom. Nord Bitidskr 15/16:22–27, In Danish

Taber S (1963) Why bees collect pollen. In: 19th international apicultural Congress, Prague, 19:114

Thorp RW, Erickson EH, Moeller FE, Levin MD, Stanger W, Briggs DL (1973) Flight activity and uniformity comparisons between honey bees in disposable pollination units (DPU's) and overwintered colonies. Environ Entomol 2:525–529

Todd FE, Vansell GH (1952) The role of pollinating insects in legume-seed production. In: Proceedings of 6th international grassland congress, Pennsylvania State University 1:835–840

Townsend GF, Riddell RT, Smith MV (1958) The use of pollen inserts for tree fruit pollination. Can J Plant Sci 38:39–44

van Laere O, Martens N (1971) Influence of artificial reduction of protein on the foraging activity of the bee colony. Apidologie 2:197–204 (In French)

van Praagh JP, Von der Ohe W (1983) The role of scents in pollination by the honeybee. Acta Hortic 139:65–67 (In German)

van Zyl HJ, Strydom DK (1968) The problem of poor fruit set of Packham's Triumph pear trees. Deciduous Fruit Grow 18:121–123

Vansell GH, Todd FE (1946) Alfalfa tripping by insects. J Am Soc Agron 38:470–488

Velthuis HHW (1970) Queen substances from the abdomen of the honey bee queen. Z Vergl Physiol 70:210–222

Vesely V (1966) Pollination services and the results of research on honeybee pollination in Czechoslovakia. Bee Worm 47:135–137 von der Ohe W, van Praagh JP (1983) Versuche zur Duftlenkung in Obstanlagen. Nordwestdeustsche Imkerzeitung 35:100

von Frisch K (1967) The dance language and orientation of bees. Harvard University Press, Cambridge, 566 pp

von Rhein W (1957) The influence of odours in the guidance of bees to increase seed production in red clover (*Trifolium pratense* L.). Z Acker Pflanzenbau 103:273–314 (In German)

Waddington KD, Holden L (1979) Optimal foraging: on flower selection by bees. Am Nat 114: 179–196

Wahl O (1963) Comparative investigations on the nutritive value of pollen, yeast, soya bean flour and powdered milk for the honeybee. Z Bienenforsch 6:209–280 (In German)

Wahl O (1966) Can bees perceive the nutritious value of crops? Z Bienenforsch 8:229–235 (In German)

Waller GD (1970) Attracting honeybees to alfalfa with citral, geraniol, and anise. J Apic Res 9:9–12

Wawryn T (1973) Utilization of honeybees for increasing seed production of red clover. Rocz Nauk Roln Ser A 98:21–42 (In Polish)

Weaver N (1957) The foraging behavior of honey bees on hairy vetch. II. The foraging area and foraging speed. Insectes Soc 4:43–57

Wells PH, Wells H (1984) Can honey bees change foraging patterns? Ecol Entomol 9:467–473

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge, 548 pp

Witherell PC, Laidlaw HH (1977) Behavior of the honey bee (*Apis mellifera* L.) mutant, diminutive-wing. Hilgardia 45:1–30

Wolfenbarger DO, Moore WD (1968) Insect abundances on tomatoes and squash mulched with aluminum and plastic sheetings. J Econ Entornol 61:34–36

Woodrow AW, Green N, Tucker H, Schonhorst MH, Hamilton KC (1965) Evaluation of chemicals as honey bee attractants and repellents. J Econ Entomol 58:1094–1102

Woyke HW (1981) Some aspects of the role of the honeybee in onion seed production in Poland. Acta Hortic 111:91–98

Zaurolov OA (1981) Floral specialization in honeybees. Zh Obshch Biol 42:844–845 (In Russian)

Zivov V, Skvorkov S (1951) Methods of improving pollination of clovers by honeybees. Sel Semenovod Moscow 18:63–64

Chapter 9
Non Bee Pollinators-Plant Interaction

Abstract Global inventories of biodiversity indicate that more than 100,000 different animal species – and perhaps as many as 200,000 – play roles in pollinating the 250,000 kinds of wild flowering plants on this planet. Only 15% of these crops are serviced by domestic honey bees, while at least 80% are pollinated by wild bees and other wildlife. In addition to countless bees, number of non bee pollinators such as wasps, moths, butterflies, flies, beetles and other invertebrates, perhaps 1,500 species of vertebrates such as birds, bats and non-flying mammals (several species of monkey, marsupials, primates, rodents, lemur, tree squirrels) have long been reported to visit flowers and serve as effective pollinators. Birds represent a group of animals that have evolved in parallel with flowering plants along lines of pollination syndromes. Hummingbirds are the best-known wildlife pollinators, but perching birds, flying foxes, fruit bats, possums, lemurs and even a gecko function as effective pollinators. Mammals are not generally known for their pollinating activities, but one group stands out as an exception - the nectar feeding bats. There are also examples of marsupial mammals serving as pollinators, as shown by the "honey possum" of Australia, and there have even been reports of pollination being effected by rodent species. Globally, over 100 species of birds and mammals in 60 genera of vertebrate pollinators are already listed as endangered and untold numbers of invertebrates are at risk as well. Much more research is still required to understand the importance of these animals in pollination.

9.1 Introduction

The process of co-evolution between flowering plants and pollinators has been proceeding for 225 million years (Leppik 1960; Anonymous 2003b). It has been established from fossil record that insects were potentially effective pollinators when first flower appeared. More than 100,000 different animal species – and perhaps as many as 200,000 – play roles in pollinating the 250,000 kinds of flowering

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Table 9.1 Pollinator classes for world's wild flowering plants angiosperms

Pollination categories	Estimated pollinator taxa
Wind abiotic	20,000
Water	150
All insects	289,166
Bees	40,000
Hymenoptera bees and wasps	43,295
Butterflies/moths	19,310
Flies	14,126
Beetles	211,935
Thrips	500
All vertebrates	1,221
Birds	923
Bats	165
Ammals other than bats	133

N = 240,000

plants on this planet. Out of which 70% of plants rely on insect pollinators and 30% of our food comes from insect pollinated plants (Anonymous 2003a). About 80% of all plant pollination is biotic. Of the 20% of abiotically pollinated species, 98% is by wind and 2% by water. Flowers have evolved to effect pollination. Different flowers are adapted to suit a particular pollinator. There are just a limited number of pollination mechanisms that have evolved because there are just a limited number of ways pollen can be successfully transferred from one flower to another. The estimated pollinator classes for world's wild flowering plants is given in Table 9.1.

9.2 Biotic Vectors

Biotic pollination is carried out by animals which act as the pollination agent or the pollen vector. The common pollinating animals include bees, wasps, butterflies, moths, birds, bats, and flies. Most plant species have adopted one of two very different kinds of relationships with biotic pollen vectors. One option is to be a generalist and try to attract a wide variety of different pollinators. The other is to specialize (and often coevolve) with a single type of pollinator. Species that generalize can occur in a wide variety of habitats and survive conditions under which some of the pollinators cannot persist. On the other hand, they encounter a great deal of "foreign" pollen from other species, which can clog stigmas and prevent pollination e.g. *Dacus carota*. Flowers on these species are often grouped together in large showy, flat or gently rounded inflorescences. On their inflorescences one can usually find a motley crowd of insects – bees, wasps, flies and beetles of many kinds, and even some butterflies, although these are generally considered specialists. Specialists can adapt to have very specific and highly efficient pollination mechanisms but are restricted to co-occurring with their pollinators. It is these mutualists that draw the

Table 9.2 Summary of flower types based on pollination mechanisms

Pollinator class	Colour	Scent	Nectar tube	Toughness
Insects	Yes	Yes	Yes	Not tough
Bees	Blue, yellow	Sweet smell	Nose size or Long body width	Not tough
Flies	White cream	Musty or off smell	Open cups	Not tough
Butterflies	Bright colours	No – may stink	Long narrow	Not tough no landing platform
Moths	White to show at night	Strong sweet	Long narrow	Not tough no landing platform
Birds	Red or green or yellow	No	Long wider	Tough, leathery plenty of nectar
Wind	No	No	No	Not tough big anthers, plenty of pollen. Stigmas feathery To catch the pollen

most attention in pollination biology with their intricate and sometimes outlandish mechanisms for pollination.

Whether adapted as generalists or specialists, animal-pollinated plants share several characteristics. The pollen is sometimes larger than in anemophilous species, is often sticky and/or highly ornamented with spines and bumps, and sometimes adheres in clumps of several grains. The number of pollen grains, sometimes expressed as a ratio with the number of ovules, is much lower in biotic pollination than in anemophilous species. Stamens are located so as to contact the pollinators, rather than to be exposed to wind. However, much of the floral structure is related to attracting specific types of animals to act as pollinators (Tables 9.2 and 9.3).

In addition to countless bees, wasps, moths, butterflies, flies, beetles and other invertebrates, as many as 1,500 species of vertebrates such as birds and mammals serve as pollinators, including hummingbirds, perching birds, flying foxes, fruit bats, possums, lemurs and even a lizard (gecko) (Ingram et al. 1996). Honey bees, birds, bats and insects play a vital role in pollination of most fruits and vegetables. With over 90% of all flowering plants and over three-quarters of the staple crop plants that we use for food rely on animals for pollination. of the hundred or so crops that make up most of the world's food supply, only 15% are pollinated by domestic bees, while at least 80% are pollinated by wild bees and other wildlife (Prescott-Allen and Prescott-Allen 1990; Ingram et al. 1996a; Nabhan and Buchmann 1997).

Besides bees which are major pollinators in diverse ecosystems, crops and landscapes, there are other group of animals which play a dominant in sustain ecosystem biodiversity and food security which include.

Table 9.3 Pollination syndromes in relation to insects (Faegri and van der Pijl 1979)

Syndrome	Floral morphology	Colour	Odour	Primary attractants	Sexual organ	Remarks
Beetles Canterophily	Actinomorphic, no special shape, large shallow, often bowl shaped blossoms	Dull nectar guides absent	Strong fruity	Mostly pollen, sometimes nectar; open easily accessible	Exposed	
Flies myophily	Actinomorphic, regular, simple, no depth effect	Light or dull, whitish nectar guides frequently absent	Imperceptible	Nectar; open easily obtainable	exposed	
Bees melitophily	Zygomorphic with great depth effect, mechanically strong adequate landing facility	Light yellow or blue nectar guides present	Weak, fresh	Nectar hidden deep but less deep than moth flowers, abundant pollen open (pollen source from bees often from simple flowers)	Concealed	Syndrome of honeybees, bumblebees and larger (tropical) solitary bees. Most solitary bees in temperate Europe are primitive and comparable to e.g. beetles
Wasps vespidae	Not described	Dull brown	Not described	Nectar accessible	Exposed	Not considered as a real syndrome
Butterflies psychophily	Actinomorphic erect radial good landing facilities	Dull brown vivid, including red simple nectar guides	Weak	Nectar in ample quantities, hidden in tubes or spurs	Exposed	
Moths phalaenophily	Actinomorphic or zygomorphic, horizontal	White or faint nectar guides absent	Strong nocturnal	Nectar in large quantities deeply hidden in tubes or spurs	Exposed or concealed	Nocturnal anthesis

9.2.1 Coleoptera

The coleopterans, with over 300,000 species, constitute the largest animal order in the world. Coleoptera are considered to be the most primitive pollinators have gnawing mouthparts and seemingly primitive instincts, which generally preclude their effective participation in the pollination process. Beetles are unable to land precisely on blossoms and hence most anthophilous species are restricted in their visits to the simplest flowers, chiefly of the "dish and bowl" type (Leppik's (1956) amorphic and haplomorphic blossom classes) characteristics of aminoid or fermenting fruit scent (e.g. *Magnolia*)., in which pollen, nutritive tissues, or very exposed and easily accessible nectar is offered as the nutrient reward.

In such flowers, the beetles imbibe floral secretions (including nectar if present), eat pollen, and chew on floral parts or special food bodies. Many flowers, often specialized and not exhibiting the syndrome of cantharophily are visited and some beetles seem restricted to floral diets as adults. Flower visiting coleopterans have structural adaptations which include forward projection of the mouth parts by up tilting of the head and associated prolongation of the prothorax and the neck. Maxillary setae may also be elongated. These modifications allow the beetles to reach deeper nectarines and extract nectar more readily e.g. Cerambycidae. In tropical American *Nemognatha* the maxillae are elongated to exceed the body length and may reach deep into such long tubular flowers as those of *Ipomoea*.

The importance of odour as a beetle attractant has recently been demonstrated in the Araceous species *Typhonium brownii* (Monteith 1973). Several authors (e.g., Grant and Grant (1965), Faegri and van der Pijl (1966)) have suggested that beetle pollination may be secondary in some cases, i.e., "represented in taxa, the ancestors of which were pollinated by more highly developed insects" (Faegri and van der Pijl 1966).

9.2.2 Diptera

The dipterans with suctorial and lapping mouth parts are also considered to be primitive pollinators. In most families of Nematocera, the proboscis is short, but variable in form and flowers visited by these flies are have readily accessible and exposed nectar in tubes that are short (e.g. *Achillea*, *Senecio,Polygonum,*various crucifers). However, specialized pollination mechanisms exist between Nemaocera and some highly evolved plants e.g. mosquitoes and *Habenaria* orchids. Whether Nematocera represent an in term stage in the pollination mechanisms is still unresolved. The Brachycera contain a wider variety of flower visitors. They visit deeper tubed flowers. Among the Cyclorrhappa, the Aschiza include the most important anthophilous diptera, the Syrphidae.tse flies feed on nectar and pollen of a wide variety of flowers worldwide. The members of small family Conopidae (Acalypterae) stand out as anthophiles. They have long proboscides, upto 6 mm in *Sicus* and 4 mm in *Conops.*

9.2.3 Flies as Flowers

Flies must eat, and their names often suggest their diverse sources of food: fungus gnats (Mycetophilidae), fruit flies (Drosophilidae and Tephritidae), flower flies (Syrphidae), blow flies (Calliphoridae), dung flies (Scathophagidae), horse flies (Tabanidae), flesh flies (Sarcophagidae), and so on. One of the most important food sources is from flowers, especially with respect to the adult energetic requirements for flight in dispersing, finding mates, mating, and searching out sites for oviposition (Hocking 1953; Larson et al. 2001). Flowers offer an open banquet, well advertised by their colours, sizes, shapes, and scents (Kevan and Baker 1983; Proctor et al. 1996). Aside from the menu of sugar-rich nectar and protein-rich pollen, flowers sometimes give other rewards such as protection, places to find mates, and oviposition sites (Kevan and Baker 1983; Kevan 2001).

Nectar, the main staple for fuelling flies' activities, is more nutritious than sugar water. It contains various sugars in various ratios, small amounts of amino acids, sometimes oils, vitamins, minerals, phenolics, and other compounds, some of which reflect the *Nature* of the flowers' pollinators (Baker and Baker 1990). Flowers used, and sometimes pollinated by, short-tongued flies sometimes present nectar with sugars so highly concentrated that the flies must spit onto the crystals to dissolve them for ingestion. Long-tongued flies, such as tangled-veined flies (Nemestrinidae) and some horse flies (Tabanidae) of South Africa (Goldblatt and Manning 2000), have no other source of sugar for energy than dilute protected nectar provided by flowers with deep tubes. A wide variety of flies feed upon pollen, notoriously the flower flies (Syrphidae). It is presumably, the source of protein for general nutrition and maturation, of the ovaries and testes (Kevan and Baker 1983). Some, other flies appear to have switched from feeding on blood to feeding on pollen, as in some biting midges, (Ceratopogonidae) that bite pollen to remove the, nutritious protoplast from within (Downes 1958). Some flowers entice flies to visit them, but may not offer, any reward except shelter. The aroids (Araceae) and, *Aristolochia* species are infamous for temporarily trapping, insects (mostly flies and beetles) (Proctor et al. 1996). They, retain the insects for about a day in the young, inflorescences that have receptive stigmata, but allow them, to escape as the stigmata age and the anthers split open, and dust the captives with pollen. Cross-pollination is thus, effected. Some flowers, such as *Stapelia* species,(Asclepiadaceae) of South Africa and the floral giants of, the genus *Rafflesia* (Rafflesiaceae) of South East Asia, dupe saprophagous flies into visiting the flowers and laying, eggs. In most instances, the maggots starve and die. The, scents of these flowers are of carrion, dung, or animal, musk, and the colours tend to be dull and also attract by mimicking oviposition sites (Proctor et al. 1996).

Although there are huge numbers of records of flies as flower visitors, proof of their importance as pollinators is often wanting. To be a pollinator, a fly must carry pollen in such a way that it is transferred from the anthers to the stigmata. This may be simply accomplished within the same flower or on the same plant. Self-pollination may be achieved, but if the plant is self-incompatible, it is of no consequence.

Fertilization must occur if pollination is to be considered successful from the plant's perspective (Free 1993; Roubik 1995). From the fly's perspective, a visit to a flower is a success if a reward is obtained, regardless of whether or not pollination or fertilization results. The process of fertilization in flowering plants (Angiospermae) sets them aside from other plants, and based on fossil and molecular evidence, it is suspected that this system of fertilization (aka pollination) arose more than 135 million years ago (Sun et al. 1998; Sanderson and Doyle 2001). It is also suspected that insects have been involved since the very beginning. Pollination by insects (entomophily),and particularly Diptera (myiophily),can be considered to be basic to angiosperm *Evolution* (Labandeira 1998; Grimaldi 1999).

The long-horned flies (suborder Nematocera) mostly have short suctorial and lappingmouthparts that restrict them to feeding on exposed nectar at open flowers, such as roses, euphorbs, saxifrages, and carrots (Larson et al. 2001). Some may be more important as pollinators than usually considered. In particular, there are orchids (e.g. *Platanthera* (*Habenaria*) spp.) that are pollinated by mosquitoes (Kevan et al. 1993). Cacoa (*Theobroma cacao*), from which chocolate is made, is pollinated by several kinds of midges (Ceratopogonidae and Cecidomyiidae) (Free 1993; Roubik 1995). Moth flies (Psychodidae) are temporarily trapped in and pollinate Lords and Ladies (*Arum maculatum*) in Europe and North America (Proctor et al. 1996). It is a common myth that black flies (Simuliidae) pollinate blueberry flowers (Hunter et al. 2000). Among the short-horned flies (suborder Brachycera), there are many records of flower visiting (Larson et al. 2001). The bee flies (Bombyliidae), with their long outstretched proboscides, are often seen sucking the nectar from flowers and form one of the most recognizable and diverse families at flowers (Plate 3a). It is interesting that the relationship of the flower-loving flies (Apioceridae) and flowers has been rarely documented, even for the somewhat misnamed and endangered Delhi Sands Flower-Loving Fly (*Rhaphiomidas terminatusabdominalis*) that actually belongs in the family of Mydasflies (Mydidae). Some small-headed flies (Acroceridae),

Plate 3a Flower flies (Syrphidae) are the best known of the flower feeding flies. They feed on both nectar and pollen. The figure shows feeding on onion and wild rose flowers, respectively

with special hairs, seem especially adapted to carrying and feeding on pollen. The Brachycera contains some of the most highly adapted flower-visiting and pollinating flies as exemplified by the South African tangle-veined flies (Nemestrinidae) and some horse flies (Tabanidae),which have extremely long tubular mouthparts that may exceed the remaining body length (Goldblatt and Manning 2000). A number of dance flies (Empididae) are implicated as significant pollinators because of their long, mouthparts, and some genera, such as *Anthalia, Anthepiscopus*, and *Iteaphila,* are known to be obligate, pollen feeders (Grimaldi 1999). The flower flies (Syrphidae) are perhaps the Diptera most well known as flower feeders. They feed on nectar and on pollen. Sometimes pollen feeding by female flower flies has been correlated with their ovarian maturation (Schneider 1969). The scuttle flies (Phoridae) are probably under-appreciated as flower visitors and as possible pollinators, and most records come from the tropics (Larson et al. 2001).

Flower feeding is recorded in about two dozen families among the house flies and their relatives (the Schizophora) (Larson et al. 2001). However, for most, the records are sparse and mostly descriptive. Among the small fruit flies (Drosophilidae) are species that feed on nectar that supports a microflora of yeasts (Lachance et al. 2001). Some of these species are important in crop pollination, such as for mangoes, and for horticultural seed production in enclosures (Free 1993). The blow flies (Calliphoridae) are well known as visitors to dung- and carrion mimicking blooms. They often effect pollination, but their egg-laying activities serve no reproductive purpose for the flies (Proctor et al. 1996). The maggots die on the vegetable substrate, except in some exceptional cases in *Aristolochia* flowers. Many species of root maggot flies (Anthomyiidae: etymologically from the Greek for flower-fly) and tachinid flies (Tachinidae) feed on nectar of open bowl-shaped flowers. The special relations of seed parasitic Anthomyidae and *Trollius europaeus* (Ranunculaceae) involves mutualistic pollination relationships (Pellmyr 1992). Among the flesh flies (Sarcophagidae) *Blaesoxipha fletcheri* may be an important pollinator of pitcher plants (*Sarracenia* spp.). Some Diptera, such as the Common Tiger Fly, *Coenosia tigrina* (Muscidae), and the Arctic Dung Fly, *Scathophaga apicalis* (Scathophagidae), hunt prey at flowers (Larson et al. 2001).

Pollination by flies seems to be particularly important in Arctic and alpine areas (Kevan 1972; Levesque and Burger 1982; Primack 1983; Pont 1993), South Africa (Vogel 1954; Goldblatt and Manning 2000), and New Zealand (Primack 1978). In the Arctic, for example, several species of Diptera fly between the flowers of adjacent plants and feed on nectar in such a way as to transfer pollen of the Arctic Aven, *Dryas integrifolia*. They assume two stances: (1) perched on the central styles and stigmata while dipping between the styles and stamens so that their dorsal surfaces collect pollen from the anthers, (2) perched on the anthers and dipping for nectar so that their dorsal surfaces rub the stigmata (Kevan 1972). Even though there are many records of flies visiting flowers, there are many taxa that seem to avoid flowers. The robber flies (Asilidae), most stiletto flies (Therevidae) and long-legged flies (Dolichopodidae) serve as examples. That said, there is much to be learned about the importance of flower visiting to flies, and about the importance of that habit to plants and pollination.

Although there are many records of large and conspicuous flies as flower visitors, there are few that demonstrate their importance as pollinators. In the blossoms that entrap and detain flies, the pollination relationship (sapromyiophily) is clear (Proctor et al. 1996), but in most more colourful and showy flowers, pollination is less well documented. Another relatively unstudied area of myiophily involves small flies, such as Phoridae, Sciaridae, Mycetophilidae, Piophilidae, and so on (Larson et al. 2001). As Carol Kearns (2001) so ably discusses, new discoveries about flower relations and Diptera are waiting to be found within the broad aspects of biogeography, systematics, behaviour, and physiology of this diverse and multi-faceted order.

9.2.4 Pollination by Butterflies (Psychophily)

Butterflies are sun lovers that like to perch while feeding. They have long and slender probosces, can perceive a wide spectrum of colors, and have an excellent sense of smell. With few exceptions, they are nectar feeders. From these characteristics, one can easily deduce the characteristics of typical butterfly-pollinated flowers. They are open in the daytime, produce a goodly amount of nectar, possess a long, thin corolla tube (often with a "spur" or out-pocketing which contains the nectar), and are generally vividly colored (often red), although sometimes white. They also provide their butterfly visitors with a platform to land and walk on. The flat-topped inflorescences of verbena, lantana, red valerian, milkweeds, and various composites provide excellent examples of butterfly-pollinated species. The spike inflorescence of purple loosestrife and some violets represent yet another type of butterfly-pollinated flower.

9.2.5 Pollination by Moths (Phalaenophily)

Hawkmoths, also known as sphinx moths because of the peculiar position their caterpillars adopt when disturbed, are the nocturnal counterparts of hummingbirds. Like hummingbirds, hawkmoths normally feed on the wing, and, because they are usually quite large, fly at high speeds. In some ways, they operate rather like warm blooded animals, having higher energy requirements than most insects and thus high nectar needs. Some moths can consume a good teaspoon of nectar at a single sitting. Hawkmoths are highly specialized flower visitors, equipped with a long, thin, and very flexible proboscis, which is kept coiled up when the animal is not feeding but which can be stretched out to take nectar. The tongue is usually extended just as the moth reaches its floral target.

Not surprisingly, flowers that cater to hawkmoths open in the evening and are extremely fragrant. They are snow-white or light-colored, offer no landing platform and may have fringed petals – possibly for guidance. Many have both visual and olfactory nectar guides. The corolla tube is long and narrow, a feature that discriminates against other, short-tongued, visitors, and nectar is abundant. Typical hawkmoth flowers are evening primrose (*Oenothera biennis*), some tobacco flowers (Nicotiana spp.), and most honeysuckle (*Lonicera*) species.

9.2.6 Pollination by Thrips

Pollenivory is quite common (Kirk 1997) in thrips and many species of Thysanoptera are known to utilize pollen, consequently, their potential to effect pollination is possible. However, thrips have generally been considered only a minor or secondary contributor to pollination of some plants as they lack a number of characters that are deemed essential to be an “efficient pollinator” (Kirk 1997) such as no specific organs or structures that carry pollen and they carry only a small number of pollen grains per individual; and they are assumed to be poor fliers with little directed flight, and rarely leave their flowers. But these traits are not always true for thrips, nor are these traits always limitations. Thrips do have some directed flight, and some species do move between flowers very often. Members of both *Frankliniella* and *Thrips* genera are considered important pollinators of some crops. Finally, even though individual thrips only carry a few grains, sometimes up to hundreds of grains (Kirk 1997), they can move between plants and flowers in high numbers. Even Darwin (1876, 1877) observed the movement of thrips carrying pollen between convolvulus flowers interfering with his pollination experiments. Until recently, though, there have been no definitive studies showing that thrips are essential for pollination of any plant species. As more attention is being paid to thrips activities and behaviors, more discoveries are being made that speak to their potential as pollinators.

Thien et al. (2000) reviewed the characteristics of the pollination biology of 29 basal angiosperm families, including all the basal dicots (e.g., Magnoliaceae, Lauraceae, Monimiaceae, Annonaceae, and Nymphaeaceae) and one basal monocot (Araceae). One common feature of these basal families is that most of their species are insect pollinated, with wind pollination a rarity. The dominant pollinators in these 29 basal angiosperm families are members of Coleoptera and Diptera, these two orders being involved in pollination of species in 17 and 14 families, respectively. Hymenoptera (mostly bees) and thrips are secondary pollinators, found in 7 and 9 of these families, respectively. One implication of these results is that Coleoptera and Diptera, being associated commonly with basal angiosperms, as well as pollinators of some gymnosperms, are possibly the more primitive pollinators and have shifted to and became more specialized on higher angiosperms. Other pollinators, such as moths, butterflies, birds, and bats, likely evolved later. However, Thien et al. (2000) caution that thrips importance in pollination is often overlooked.

9.2.6.1 Pollination Syndrome

Although the utility of the term “pollination syndrome” (i.e., plants, sometimes unrelated, with similar floral traits and similar types of pollinator) has been questioned (Johnson and Steiner 2000), it may serve as a good starting point for analyzing particular associations of pollinators with their floral hosts. Flowers that tend to be associated with 'thripophily' (Kirk 1997) are medium sized, with white to yellow color, they are sweetly scented with or without nectar, their structure is compact, globose, or urceolate, with pollen chamber or shelter, and their pollen grains are small and dry.

Some of these traits do fit the floral morphologies of some recently reported subtropical plants, where thrips play a role in pollination. (1) Webber and Gottsberger (1995) found thrips visitors carrying pollen between flowers on two species of Amazonian Annonaceae, *Bocageopsis multiflora* and *Oxandra euneura.* Flowers are small and white (<4 mm across) with a tiny pollen chamber formed by overlapping petals and stamens. Other members of this family have medium to large sized flowers and are pollinated by beetles. The sweet odors were stronger during the day. (2) Two species of *Macaranga* (Family Euphorbiaceae) trees are likely pollinated by thrips: *M. velutiniflora*, a newly described species in Borneo (Davies 1999), and *M. hullettii*, a common species in southeast Asia (Moog et al. 2002). A phlaeothripid species of the genus *Neoheegeria* has been found on both male and female flowers of *M. hullettii* carrying pollen. The trees are dioecious, and both male and female inflorescences are tiny and hidden. The staminate flowers are about 1 mm long, and multiples of these flowers are enclosed by a greenish bracteole. Female flowers are slightly larger but subglobose. A vanilla-like odor is emitted from flowers of *M. hullettii.* (3) *Thrips setipennis* were the only insects found on both male and female flowers, and are the likely pollinators, of *Wilkiea huegeliana* (Monimiaceae), a rainforest tree in Queensland, Australia (Williams et al. 2000). Individual flowers are tiny (<4.5 mm), white and have only a tiny ostiole by which these insects enter the flower.

In these studies, thrips use tiny and sometimes hidden flowers rather than medium to large flowers, but globose and urn-like shapes and small openings are common. Because thrips have been widely overlooked, pre-conceived notions about thripophily should not be taken as complete, and the focus should be placed on searching for thrips on plant species where pollinators are not known, regardless of their floral traits.

Discovery of Thrips Pollination of Cycads

One unusual thrips pollination system has been discovered on cycads in Australia that should bring much more focus on thrips as pollinators. Cycads (Cycadales) are dioecious plants of Paleozoic origin, and are considered the basal clade among extant gymnosperms (Bowe et al. 2000; Chaw et al. 2000). Cycads were most diverse during the Mesozoic Era - Jurassic period (144–213 MYA), when the first flowering plants were evolving (Friis et al. 1987; Thomas and Spicer 1987). During most of the twentieth century, cycads were thought to be wind-pollinated like other gymnosperms. The first study to show that cycads were insect pollinated was by Norstog et al. (1986). They observed pollen laden weevils, *Rhopalotria mollis* (Sharp), moving from male cones to female cones of *Zamia furfuracea*, and they demonstrated that seed set significantly declined when beetles were excluded from female cones. Strong mutualisms between specialist beetles in the weevil super family (Coleoptera, Curculionoidea) (Oberprieler 1995a, b), and their cycad hosts are now known across most cycad-bearing continents.

The cycad genus *Macrozamia* (Zamiaceae) is found only in Australia, and there are approximately 40 extant species. Most of these species are found near the east coast, with three species being found in the southwestern coastal area near Perth. However, one species, *M. macdonnellii*, is found in the central desert interior, in scattered isolated populations throughout the Macdonnell and Hart Ranges, at least 1,400 km in all directions from all other *Macrozamia* species. Numerous insect species have been found on male and female cones of *Macrozamia* (Forster et al. 1994), but only beetles, primarily *Tranes* spp. (Coleoptera, Curculionidae), and wind were thought to be pollen vectors, even though thrips in the genus *Cycadothrips* (Terebrantia: Aeolothripidae) had been observed by the thousands in male cones of several species. *Cycadothrips chadwicki* Mound was reported on male cones of *M. communis* (Mound 1991; Chadwick 1993) and *C. emmaliami* Mound and Marullo was found on both male and female cones of *M. riedlei* in southwestern Australia (Mound et al. 1998). During October through December 1999, a study was undertaken to examine the potential for *C. chadwicki* to pollinate *Macrozamia communis*, a cycad found on the southeastern coast of New South Wales, using exclusion experiments as well as determining pollen loads and behavioral observations (Terry 2001).

In this study, thrips were observed moving between cones, including from male to female cones, during the day time only. Average pollen loads of thrips were determined by counting the pollen grains around thrips bodies caught on sticky traps as they were leaving male cones or arriving on female cones. Those leaving male cones had slightly higher loads than those arriving at female cones (Table 9.4). Thrips visited and carried pollen to female cones. Seed set was high in cycad cones where weevils were excluded and was not significantly different from open controls (62% versus 59.9%, controls versus beetle exclusion, respectively). Further, excluding wind from vectoring pollen did not significantly reduce seed set (62% versus 57.7%, control versus wind exclusion, respectively). Total pollen grains delivered to each female ovule was estimated to be over 1,000 grains, more than sufficient to achieve fertilization.

While this study was underway, a new species, *Cycadothrips albrechti* Mound and Terry, was discovered on male cones of *Macrozamia macdonnellii*, the desert cycad of central Australia. Mound and Terry (2001) examined the interaction between this thrips species and its cycad host, to determine the potential for the thrips to pollinate *M. macdonnellii*. A brief summary of the results of the observations on this desert cycad and a discussion of the significance of other cycad studies follows.

Cycadothrips albrechti was the only potential pollinator species found on cones in a survey of several different *M. macdonnellii* populations. As many as 50,000 thrips per male cone were estimated on some male cones during pollen dehiscence, based on subsamples of individual sporophylls from male cones. Thrips mated and oviposited on male cones, and both adults and larvae fed on pollen inside sporangia. During pollen dehiscence, male cones emitted a very strong and pungent odor that

Table 9.4 Pollen grains carried by thrips on two plant species *M. communis* and *M. macdonnellii*

Pollen grains per thrips or ovule	*M. communis*	*M. macdonnellii*
Leaving male plant	41.9 (6.3)	20.5 (3.8)
Arriving at female plant	20.5 (2.8)	15.1 (3.2)
Ovule 1	1,218	5,700

humans could detect at least 10 m away from cones. Thrips moved out of *M. macdonnellii* male cones daily *en masse* in the late afternoon. Female *M. macdonnellii* cones were receptive (had tiny gaps between sporophylls, emitted odor similar to male cone, attracted thrips) for perhaps only 1 day. Over 5,000 thrips were caught on one sticky trap collar (2 cm wide and 45 cm diameter) around a receptive female cone in a single afternoon. Pollen loads per thrips leaving male cones averaged around 20 grains per thrips, and averaged slightly over 15 grains on thrips arriving at female cones (Table 9.4). Pollen loads and estimates of total thrips visitation at the female cone indicated a pollen delivery of >5,700 grains per ovule in a single afternoon. Thus *C. albrechti* appears to be the sole pollinator of this species.

Implications of Thrips Pollination of Cycads

Surveys of insects on *Macrozamia* cones (see review by Terry 2001) suggest that at least four *Macrozamia* species are pollinated by only *Cycadothrips* spp.; eight species are pollinated only by *Tranes* spp. weevils (Coleoptera: Cuculionidae); and three species have both insects. More than 20 other *Macrozamia* species have not been surveyed for cone visitors. On other continents, only beetles are associated with cycads, although researchers have not specifically looked for thrips and may have overlooked them. If a thrips/cycad association is found only on Australian *Macrozamia*, then thrips association with cycads may be recent. *Macrozamia* genus is at least late Cretaceous in origin (Pole and Douglas 1999) based on fossil records, but fossils of thrips on cycads are lacking. However, biogeographical information can be used in lieu of fossil evidence to establish a possible age of thrips associated with *Macrozamia.*

The cycad genus *Macrozamia* is found on both east and west coasts of Australia as well as in a small area within the central desert region. These cycads probably had a continent wide distribution during a previous geological period, and species now survive only in a few areas as relicts. *Cycadothrips* is the only pollinator found in all three regions, and this thrips is not found on other plants. Marine incursions and subsequent drying in the southern part of Australia during the Eocene 50 MYA may have isolated the eastern and western species of the southern *Macrozamia* populations and their pollinators (Ladd and Connell 1993), but even earlier vicariance events are possible. The massive marine intrusion during the Cretaceous ~114–119 MYA (Cranston and Naumann 1991; Beynon et al. 1992) fragmented the continent into eastern, central, and western islands. These islands match the current *Macrozamia* and *Cycadothrips* distributions and endemism. Thus, one possibility is that thrips mutualism with *Macrozamia* existed before these events. Because this argument is circumstantial, however, further corroborating evidence is needed to give more validity to this time frame.

It is possible that thrips were involved in early cycad pollination systems before weevil involvement. Cycads are at least Permian in origin and the earliest *Macrozamia* fossil is dated at 65 MYA. This is from New Zealand, which separated from Australia around 85 MYA. The earliest fossil of the weevil superfamily, Curculionoidea, is from the Late Jurassic, represented by Nemonychidae, and the modern families (Brentidae and Curculionidae) in the early Cretaceous, although the modern weevil genera such as *Tranes* spp. that are associated with cycad pollination did not evolve until the Cenozoic Era, in the Paleocene or Eocene (Oberprieler 1995b). Evidence suggests that weevil pollinators of modern cycads are derived from angiosperm dwelling ancestors that developed in reproductive organs or bored in wood, rather than from the older gymnosperm feeding weevil lineage, Nemonychidae, which has never been found on either fossil or extant cycads (Oberprieler 1995a, b). It is now believed that each cycad bearing continent has had an independent *Evolution* of its weevil pollinators. If this is true, then other pollinators of cycads presumably existed before these weevils evolved.

The insect order Thysanoptera is Paleozoic in origin (Kukalova-Peck 1991; Labendeira and Seposki 1993); thus ancestors in the basal groups of Thysanoptera predate angiosperms and some of the modern genera of cycads. Finally, the genus *Cycadothrips* has been placed in its own sub-family, Cycadothripinae within one of the basal thysanopteran families, Aeolothripidae.

Although the exact relationships among these basal families and of the Cycadothripinae among its sister taxa are unresolved, this genus is among the basal clades of Thysanoptera (Marullo and Mound 1995), suggesting that ancestors of this clade were likely around during the *Evolution* of some gymnosperms and before angiosperms. Based on this information, thrips may be among the oldest pollinators of plants.

9.2.6.2 The Role of Thrips in Pollination

The efficiency of thrips –flower association for pollination depends upon the dynamics of pollen transfer through thrips. Thus availability of pollen and nector as reward, pollen stigma interaction, pollen wall architecture, mechanism of pollen attachment to thrips are the critical factors in thrips-flower interaction. Synchronization of anthesis and nectar availability with the development of the pollinator as well as behavioural aspects of thrips, plays an essential role. Generally thrips are considered as pure pollinators because unlike bees and butterflies they carry pollen grains of only one plant species. Active involvement of thrips in pollination is well documented by anand and blies on cocao, Odland and Porter on *Capsicum annum*, Hagerup and Carlson on onion, Syed on oil palm, Appanah and Chen on Dipterocarpus and Kirk on *Echium Plantagineum*. Indian work on thrips pollination biology was initiated at the entomology research Institute, Madras and are documented in the contributions of Ananthakrishnan and coworkers, Velayudhan and Annadurai and Gopinathan and Varatharajan on a few species of Asteraceae, Solanaceae and Fabaceae.

Asterceae

Synchronization of flowering periodicity with the developmental phase of the pollinating thrips appears to be controlled by the population build-up of thrips, eventually leading to dispersal. This is established in our studies on thrips pollination of Tridax procumbens, Wedelia chinensis, Synedrella nodiflora, Vernonia cinerea, Ageratum conyzoides and Cosmos bipinnatus (all Asteraceae). Our studies have also established the relation between the host succession, population building of thrips and possible implications for their associated *Evolution*.

For instance, the succession patterns of the host plants Wedelia, Synedrella, Vernonia, Ageratum and their flowering periodicities enable Microcephalothrips abdominalis to maintain their population through out the year. The continued availability of hosts with the ample intra-floral resources facilities thrips to build their population.

The adaptive *Nature* of the pollinator to the flower appears impressive in *M. abdominalis* which has a 9–12 day life cycle. Oviposition in this species coincides with the emergence of the petals of the disc florets of *Wedelia chinensis* in its late bud stage, so that the larval emergence, anthesis and nectar production in the flowers are all synchronized. The disc florets of Asteraceae are protandrous and when their stigmas emerge through the staminal columns they carry pollen grains also on their lower surfaces. The nectary is located at the base of the style with minute stomata- like apparatuses, which are distributed diversely in different species, with the guard-cells containing plenty of starch grains. Nectar secretions coincides with pollen maturation, maximal secretion occurring when the stigmas are receptive, providing an opportunity for fertilization by the foraging insects with mature pollens on their bodies. Pollen loads were heavy with *Frankliniella schultzei* carrying 129–180 grains. Pollen loads of different species range from 25 to 200 in the adults and the larvae, the adults having an increased load due to greater surface area such as wing fringes, abdominal setae, as well as the antenna.

Incidentally, a limitation of the food reward in the flowers encourages the foragers to visit other plants. Species living in the heterogamous capitula spend lesser energy for their migration due to corymbose arrangements of the heads. Thus, as visualized by Heinrich and Raven, a balance exists between the nectar/pollen availability and the incidental calorific reward of a flower on the one hand, and the energy expenditure by the pollinator on the other. Experiments to measure the role of *Thrips Hawaiiensis* in the pollination of *C. bipinatus* revealed that 50–60% seed-setting is contributed by thrips only, about 70–90% seed setting rare was obtained under natural conditions where the pollination was effected through a combined effort of thrips, bees and butterflies.

Solanaceae

Flowers of *Solanum melongena* harbour both *F.schultzei* trybom and *Ceratothripoides cameromni* Priesner with the former being more abundant and frequent. The solanum type of flower is very conducive for the development of thrips, since the adults can penetrate the flowers during the bud stage itself and the larvae can emerge even prior to the opening of the flower. Flowers of *S. melongena* are all oligandrous with most of their anthers enlarged with excess of pollen and moderate quantity of nectar. The larvae hatching from eggs placed near the nectarines confine themselves to their respective flowers till they become adult and show active movements, more often towards the stigma. The cloud of pollen, resulting from poricidal dehiscence of the anthers gets scattered all over the flower and also on to the various parts of body of thrips. The larvae of *F. schultzei* are more efficient pollen carriers than the adults. The peak receptive period of the stigma coincides with the exudation of a sticky fluid which helped adherence of the pollen. Hence, self-pollination occurs due to the random movement of thrips. The continuous build-up of population of thrips in a flower leads to inter-specific and intra-specific competition resulting in the dispersal of thrips; this enhances the chances of cross-pollination as in Asteracea. The synchronized events occurring in the life cycle of the pollinator and the development of the flower is a vital factor in thrips pollination of *S. melongena* . Studies on the pollination potential of the thrips species in other solanaceous plants like *S. torvum,S. xanthocarpum, S.trilobatum, S. nigrum and Capsicum frutescens* indicates that the larvae of *F. schultzei* have a higher pollen- carrying potential than the adults in all the stages of floral development. Maximum pollen attachment on the bodies of larvae is on the lateral sides of the abdomen and the last abdominal segment, while in the adults of *F. schultzei* the maximum number is along the fringes of the thoracic wings. In some species, pollination by thrips alone accounts for 93% of the flowers pollinated. In solanaceous flowers, smaller number of *Haplothrips gowdeyii* with in the flowers of *Dolichos lablab* .The flowering phenology of Dolichos and the life cycle of thrips synchronize with each other: anthesis occurs between the fifth and the ninth day of the flower development; nectar secretion commences and the stigma become receptive from the 7th to the 12th day; duration of the life cycle of the pollinator is 12–18 days. Initial infestation of the flower by *M. distalis* occurs between the 3rd and 5th day of the bud, with the adults feeding on the fleshy regions of the standard and keel petals. They oviposit essentially along the basal region of the keel petals. After an incubation period of 4–5 days, larvae emerge coinciding with the maximal secretion of the nectar. Following flower shedding, older larvae move towards soil for pupation and adults emerge after 3 days to reinfest a new inflorescence. *D.lablab* blooms during Oct–June; the peak of flowering season is between December and early March, and coincides with population build-up of thrips. This increase in population seems to be due to dispersal of thrips among crop such as *Cajanus indica,Sesbania aegyptiaca,* and *Vigna catjang* which incidentally harbour the same species of thrips and also flower during the same period. Weeds like*T.procumbens* (Asteraceae), *Rullia tuberosa* (Acanthaceae), *Ipomaea* spp. (Convolvulaceae) serve as perennial reservoirs for thrips, especially for *F. schultzei.* Emasculated buds in the second and third row from the tip of the

Plate 3b Nectar feeding bird collecting nectar from *Bauhinia variegata*

inflorescence set to pods when thrips were released. This confirmed interfloral movements of larvae and adults of thrips and suggested their possible role in cross-fertilization.

Fabaceous flowers are generally considered self-fertile. But when thrips get associated with them, both the plants and thrips are benefited mutually: the thrips obtain the food reward, and the plants benefit by pollen grains. In spite of their small size, thrips help in realizing 50–70% viable seeds indicating their pollination potential.

In thrips-pollinated *Lantana camara* flowers, the presence of thrips is only within yellow flowers and are totally absent from orange and scarlet flowers the colour changes from orange to shades of red, scarlet and mauve tend guide the yellow flower thrips. Pollination also triggers the biogenesis of anthocyanins that mark the carotenoids and flavonoids in the petals of lantana. Sabah oil palm pollination by T. hawaiiensis provides an interesting instance. The populations of this species were higher in the male inflorescence than in female flowers and each male inflorescence harboured a maximum of 1,000 individuals per spikelet. The very high density on male inflorescences appears to be an adaptive factor for effective population.

9.2.7 Pollination by Birds (Orinthophily)

Birds that feed on nectar are highly specialized and feed on little else (Plate 3b). Thus, they depend on flowers with large amounts of nectar available on a year-round basis (Tables 9.5–9.7). Plants in temperate areas cannot bloom year round and must therefore rely on migratory bird species which feed elsewhere during the winter. In the tropics, bird pollination of flowers is at least as important as insect pollination. At least 2,000 species of birds feed on nectar, flower-inhabiting spiders, and insects, or (rarely) pollen. Even some fruit-eaters among tropical birds will occasionally

Table 9.5 Approximate daily requirements of nectar feeding birds and daily nectar production of some Australian plants, in full flower (Ford et al. 1979)

Birds	Nectar requirements 10–50 Kcal/day
Eucalyptus cosmophylla	100 kcal/plant/day
Callistemon macropunctatus	20
Small *Eucalyptus*	20
Banksia	1–20
Xanthorrhoea	2.5
Grevillea	2–6
Astroloma	2
Adenanthos	1.5
Amyema	1–2
Correa	1
Epacris	0.1–0.5

consume nectar. In New Zealand, which has no native bees pollination by birds is the rule rather than the exception.

Many of these birds are highly specialized to feed on nectar. Their bills are long and narrow, and their tongues are tube-shaped or have brush-like tips. They include hummingbirds, sunbirds, honeyeaters, honey creepers, and brush-tongued parrots. One can often determine their food-plants by looking at the pollen attached to their bills and feathers. This method can work even with museum skins and even in some cases with species that are now extinct.

Most of these birds also have very high metabolic rates, so their caloric intake per gram body weight must be high. Although few people who watch hummingbirds flit from flower to flower are aware of it, these birds are constantly on the verge of starvation. To meet their energy needs they must visit thousands of nectar-rich flowers every day. Night provides severe problems: some hummingbirds have solved this problem by essentially going into hibernation every night. Their temperature drops, and their rate of metabolism may go down to about one-fifteenth of the peak daytime value, so they save a great deal of energy.

Birds have excellent color vision and appear to favor red. In contrast, their sense of smell is very poor. These traits are reflected in the flowers they feed on. Bird-pollinated flowers have no odor. The amount of nectar produced can be quite large, up to a cupful a day in some cases. The colors of bird-pollinated flowers vary enormously. Many are red, but others are yellow or blue or almost any other color. Red flowers may be common simply because bees cannot see them well, so little nectar is lost to ineffective pollinators. To provide food during all active hours, bird pollinated flowers are generally open all day. Flower size and shape can vary, but corollas are often tubular (and are larger in diameter than butterfly flowers) and are sturdily constructed as a protection against the probing bills of their visitors. The ovules are usually below the perianth (that is, they have "inferior ovaries"), out of harm's way. Usually, stamens are quite numerous and often stick out of the flower, in which case they are brightly colored and quite strong.

Table 9.6 Characteristics of a typical bird-pollinated flower, and those of the main Australian genera pollinated by birds (Source: Ford et al. 1979)

Genus	Colour[a]	Flower/inflorescence shape	Smell	Nectar[b] (cal/fl. or inflor.)	Anther/ nectary distance (mm)	Source
"Typical syndrome"	Red	Tubular, bell, cgullet/ brush	NONE	Plentiful	Distant	Faegri and van der Pijl (1966)
Callistemon	Red, green	Open/brush	None	5–20/fl.	20	Paton and Ford (1977)
Calothamnus	yellow, red	Semi-tubular/brush	None	10/fl.	25	
Eucalyptus	White, red, yellow	Open/brush	None	1–65/fl.	5–15	Paton and Ford (1977)
Darwinia	Red, yellow	Small tube/bell	None	9	5–15	Keighery (1975a, b, c)
Adenanthos	Red, pink, orange, yellow	Gullet	None	2–5/fl.	20	Paton and Ford (1977)
Grevillea	Red, yellow, orange, green, pink, black	Gullet	None	5–10/fl.	25–30	Paton and Ford (1977)
Banksia	Yellow, orange, red, cream, greenish, brown	Gullet/brush	Strong musky	100–2,000.	20–50	Paton and Ford (1977)
Dryandra	Yellow	Gullet	Heavy nauseous	50–100.	20–30	Robinson (1947)
Amyema	Red, green, orange, grey	Open/brush	None	2–10/fl.	20–30	Paton and Ford (1977)
Correa	Green, red, white	Tube	Slight fruity	5–20/fl.	20–30	Paton and Ford (1977)
Brachyloma	Pink	Small tube	None	5/fl.	3–5	Paton and Ford (1977)
Epacris	Red, white, pink	Tube	None	0.5–2/fl.	10–20	Paton and Ford (1977)
Astroloma	Red, white	Tube	None	7–12/fl.	15–20	Paton and Ford (1977)
Eremophila	Red, yellow	Gullet	None	50/fl.	30–50	Paton and Ford (1977)
Xanthorrhoea	White	Open/brush	Musky	20/fl.	10–20	Paton and Ford (1977)
Anigozanthos	Red, yellow, green	Gullet	None	50/fl.	30–80	Mees (1967)

[a] Commonest colour first, bird-pollinated species only

[b] Daily production, nectar production varies greatly between species, individual plants, and days. CA gullet-shaped flower has a zygomorphic tube, usually with one or more slits

Table 9.7 The main flower visiting families of birds (After Proctor and Yeo 1973)

Bird family	Distribution
Coerebidae (Honeycreepers)	Tropical America
Dicaeidae (Flowerpeckers)	Asia, Australasia
Drepanididae (Hawaiian honeycreepers)	Hawaiian Islands
Meliphagidae (Sugar-birds)	South Africa
(Honey-eaters)	Australasia
Nectariniidae (Sunbirds)	South-west Africa, Asia, Philippines, Australasia
Psittacidae: subfamily Loriinae (Brush-tongued parakeets)	Australasia
Trochilidae (Hummingbirds)	North and South America
Zosteropidae (White-eyes)	Africa, Asia, Australasia

The visiting bird is normally touched on the head or breast as it feeds. However, in some flowers the stamens are "explosive" and cover the bird with pollen. Hummingbirds, which are only found in the Americas, feed on the wing and so hummingbird flowers hang down or are downward-facing and lack a landing platform. In Asia and Africa, however, many of the flower-birds do not hover and, accordingly, the plants offer them a landing-platform or perch.

Ford et al. (1979) recorded over 100 species of birds visiting the flowers of some 250 species of plants in Australia. Honeyeaters and lorikeets were the most persistent flower feeders and some species depended almost entirely on nectar as a source of energy. Silvereyes, parrots, wood swallows, pardalotes, thornbills, and a few other species of passerines occasionally visit flowers. The genera most frequently visited are *Eucalyptus, Callistemon, Banksia, Grevillea, Adenanthos, Dryandra, Epacris, Astroloma, Amyema, Correa, Xanthorrhoea, Anigozanthos,* and *Eremophila.* Some flowers, e.g., those *of Eucalyptus,* are very generalised in structure and are visited and pollinated by insects as well as birds. Other plants have shown a range of adaptations to attract birds to their flowers or deter insects. Birds require significant rewards so that flowers must produce copious nectar. Flowers are often clumped into inflorescences (e.g., *Banksia*) or individual flowers become large and tubular or gullet-shaped (*Eremophila*). Flowers visited by birds are often red, though yellow (*Adenanthos*) and green (e.g., *Amyema, Correa*) are common. Hairs in tubular flowers, and lack of attractive smell may deter insects without affecting birds (e.g., *Astroloma*). In Australia the relationships between birds and plants are not as specific as those shown for hummingbirds and some of their flowers in tropical America. Most species of birds visit a wide range of plants, and most plants are visited by a wide range of birds. Pollen is usually placed on the forehead, face, and chin feathers of the bird or on its beak. Birds have been proved to be effective pollinators of many plants in temperate Australia. Birds may be more reliable pollinators than insects when the climate and flowering season are unpredictable, or during winter when many of the specifically birdpollinated plants flower. Birds may also increase the chance of outcrossing as they fly further between plants than insects. Therefore, massive nectar production is unlikely to place a strain on plants, unless water is scarce. Finally, it is possible that birds may provide a service in addition to pollination, they may protect the plant from herbivorous insects.

Godley (1979) and Lloyd (1985) found that there are over 30 plant species whose flowers are visited by birds (Godley 1979). Only about half of the plants concerned are clearly adapted to bird pollination (Lloyd 1985), notably *Fuchsia, Sophora* and *Phormium,* which have large tube-like flowers and are commonly visited by nectar-feeding birds such as bellbird (*Anthornis melanura*) and tui (*Prosthemadera novaezelandiae*). Birds which visit (and potentially pollinate) the flowers of forest plants in New Zealand are the bellbird, tui, stitchbird (*Notiomystis cincta*), kaka (*Nestor meridionalis*), red-crowned parakeet (*Cyanoramphus novaezelandiae*), yellow-crowned parakeet (*C. auriceps*), saddleback (*Philesturnus carunculatus*) and silvereye (*Zosterops lateralis*) (Godley 1979). This is a relatively small suite of flower-visiting birds (Ford et al. 1979). Throughout most of the mainland forests of New Zealand, the only birds which commonly visit flowers are bellbird, tui and silvereye, because stitchbird and saddleback are extinct on the main islands and kaka and parakeets occur only in large tracts of forest. Despite this, is it unlikely that any New Zealand plant is threatened by a lack of specialised bird pollinators. Few, if any, plants are exclusively pollinated by birds and there is no evidence of tight co*Evolution* between particular bird species and particular flowers. For example, the flowers of *Sophora* (a tree which is commonly regarded as being pollinated by honeyeaters) are visited by at least four bird species, as well as bees, butterflies and moths. As further evidence of non-specialisation, the species S. *microphylla* occurs not only in New Zealand, but also Chile, where it is visited by hummingbirds and large bumble bees (Godley 1979). Godley (1979) considered that, although a diversity of flower types is visited by birds in New Zealand, most are visited 'incidentally' and the advantage to the plant is unclear, since birds may foster self-pollination more than anything else, especially in plants with monomorphic flowers. He stressed that more attention should be given to the end result of pollination, i.e., the percentage of ovules which produce seeds. Until such research is carried out, the importance of birds as pollinators in New Zealand forests remains uncertain.

Knox et al. (1985) reported that characteristics of the flowering trees of *Acacia terminalis* may be interpreted as adaptations for bird pollination. Each leaf bears a single red nectary up to 12 mm long on its petiole. Nectaries show greatest secretory activity at flowering (max. 15 μl/nectary/day), and nectar was found only in the early morning. The nectar contains a mean of 16% sugars (max. >50%) and is hexose rich with 18 amino acids, especially glutamine and phenylalanine. Analyses of foraging dynamics and pollen loads from feathers of passerine birds further support this interpretation.

Clout and Hay (1989) reported that Bird-pollinated flowers are known to secrete relatively dilute nectars (with concentrations averaging 20–25% w/w). Many southern African plants that are pollinated by passerine birds produce nectars with little or no sucrose. Moreover, these hexose nectars are extremely dilute (10–15%). This suggests a link between sugar composition and nectar concentration. Nectar originates from sucrose-rich phloem sap, and the proportion of monosaccharides depends on the presence and activity of invertase in the nectary. Hydrolysis of sucrose increases nectar osmolality and the resulting water influx can potentially convert a 30% sucrose nectar into a 20% hexose nectar, with a 1.56 times increase in volume. Hydrolysis may also increase the gradient for sucrose transport and thus the rate of sugar secretion. When sucrose content and refractometer data were compared, some significant correlations were seen, but the occurrence of sucrose-rich or hexose-rich nectars can also be explained on phylogenetic grounds (e.g. *Erythrina* and *Protea*). Hexose nectars may be abundant enough to drip from open flowers, but evaporation leads to much variability in nectar concentration and increases the choices available to pollinators.

Raju (2005) reported that *Woodfordia floribunda* has ornithophilous flowers suited for pollination by passerine birds. The flowering phase, when the shrub is leafless, and the red nectariferous flowers attract various passerine bird species. The visiting birds probe the flowers legitimately to collect nectar and in so doing, their beaks and foreheads strike against the sex organs effecting pollination. Furthermore, the birds move frequently between different shrubs in search of more nectar and in the process cross-pollination is promoted. Hand-pollination tests indicate that this plant species sets fruit through self and cross-pollination and the same is confirmed by very high natural fruit set rate. Bees and butterflies also visit the flowers for pollen and/or nectar but their role in pollination is almost negligible. The fruit is a capsule, with numerous tiny, light seeds, and is enclosed by a persistent membranous calyx. As the calyx is red, it attracts passerine birds during the fruiting phase. Some passerine birds involved in pollination during the flowering phase are also attracted to the growing fruits and feed on the seeds when the latter are mature and ready for dehiscence. In this way, such birds act as seed dispersers. Therefore, *W. floribunda* is adapted both for pollination and for seed dispersal by passerine birds.

9.2.8 Fly and Beetle Pollination (Myophily and Cantharophily)

Faegri and van der Pijl (1966) have suggested that a greater diversity of pollination methods is found among flies than among any other insect group and, since numerous dipteran taxa frequently visit flowers to ingest nectar (or rarely pollen), the order is important in pollination ecology. Both flies and beetles present a wide variety of pollinators and pollinator syndromes, making it difficult to generalize, but a number of flies and beetles should be specifically mentioned because they are not really adapted to flowers at all (although the flowers are adapted to them!). These are the carrion, dung, and mushroom flies and beetles that are trapped by various flowers or inflorescences. Species in this group are primarily attracted by smell. Some are looking for food, others are looking for egg-laying sites. In either case, they are tricked by the flower odor into thinking that they have found their normal prey. They enter the flower, eventually figure out that they have been fooled, then move on.

Common traits of the flowers that use such pollinators include dull colors, often large, open flowers, (although some species instead have enclosures, which trap the pollinator for a time), and distinct odors, which are sometimes quite unpleasant to humans. The names of some of these flowers are can be equally unattractive.

The world's largest "flower" (really it's an inflorescence) is the stinking corpse lily (Raflesia sp.).

The suborder Nematocera consists of at least 12 families known to contain anthophilous taxa. In most of these families the mouthparts are short (generally a millimeter or two long) and the flower-visiting taxa are thus restricted to visiting either flat or bowl-shaped blossoms (in which the nectar is well exposed and the stamens are very short), or very small tubular blossoms in which the nectar is easily accessible. According to Willis and Burkill (1895–1908), flower-visiting Nematocera are chiefly nectarivorous although pollen-collecting species have been reported in the Bibionidae, Mycetophilidae, and Scatopsidae. The Culicidae are exceptional among the Nematocera in that most taxa possess the piercing-and -sucking type of elongate mouthpart, which characterizes the typical "proboscis" of the true mosquitoes. It has only recently been realized that mosquitoes are very frequent blossom visitors with both sexes of many, perhaps all, species feeding on sugary substances such as honey-dew or nectar (Faegri and van der Pijl 1966). The most important dipteran suborder in relation to pollination is the Brachycera exhibiting a gradual transition from very simple to more highly evolved blossom visitors, such as the Syrphidae, Conopidae, and Bombyliidae.

Gibernau et al. (1999) studied the pollination of *Philodendron solimoesense* (subgenus *Meconostigma*) in four populations of French Guiana and found that numerous insects visit *Philodendron* inflorescences, but the main pollinator seems to be *Cyclocephala colasi* (Scarabaeidae, Dynastinae). The pollination process displays aspects typical of beetle pollination: the production of heat and of a strong odor, the presence of a food reward (stigmatic secretion and sterile male flowers), and the presence of a copulation chamber. Flower heat production is important (ca. 117°C above the ambient air) and may help to volatilize the fragrance. Attraction and choice-test experiments showed that *C. colasi* is not likely to depend on chemical information (such as pheromone) to localize conspecifics but may rely instead on stimuli produced by the inflorescences in order to meet mating partners. Beetles can be reliable and specific pollinators in the Tropics (Gottsberger 1977, 1986, 1990; Henderson 1986; Irvine and Amstrong 1990; Momose et al. 1998). Flower adaptations to beetle pollination, as typified in *Philodendron solimoesense*, include the following: a 2-day flowering period, heat production plus emission of an unpleasant odor, presence of a floral chamber in which pollinators copulate and shelter during one night and day, protogynous inflorescences, offering of food rewards (stigmatic secretions, male sterile flowers), and closure of the inflorescences with pollinator extrusion. Nevertheless, the two other *Philodendron* species previously studied, *Philodendron selloum* and *Philodendron bipinnatifidum* (both of the subgenus *Meconostigma*), have 3- and 4-day flowering cycles, respectively (Gottsberger and Amaral 1984).

9.2.9 Ants and Pollination (Myrmecophily)

More than 15,000 species of the Formicidae are known in the World. Although these insects are commonly anthophilous, many behavioural and general morphological characteristics preclude them from effectively participating in the pollination process. Pollen does not adhere readily to their hard and generally smooth bodies, and the diminutive size of these creatures allows them to avoid contact with the anthers and stigmas when they visit flowers in search of nectar. Also, the flightless worker ants are unlikely to facilitate cross-pollination, because most of their foraging time is spent crawling from one blossom to another on the same plant. Until recently, no beneficial role in pollination was attributed to ants: they were considered to be just thieves of nectar and pollen. At best, certain investigators were willing to concede that an "ant guard," provided with food by the plant in the form of extrafloral nectar, might keep potential flower robbers at bay. However, it is now recognized that there is a genuine ant-pollination syndrome. Because worker ants do not fly and therefore do not expend many calories on traveling, the whole system is low-energy. The nectaries are small and produce a quantity of nectar so modest that larger insects are not interested. The flowers, likewise, are small, sessile, and close to the ground, and exhibit minimal visual attractions. They produce only small quantities of sticky pollen grains, so the ants are not forced into intensive self-cleaning activities that would remove the pollen from their bodies. Outbreeding is promoted because on each plant only a few flowers are open at the same time and also because these low-growing plants occur in groups with their branches closely intertwining. It is believed that this syndrome is most often found in hot, dry habitats, which are certainly among those favored by ants.

Jones (1972) observed numerous "black jumper" ants (*Myrmecia pilosula*) on the inflorescences of *Prasophyllum alpinum* (Orchidaceae) (a species pollinated by the wasp *Pterocormus promissorius* (Ichneumonidae)); although pollinia were often observed on the jaws of these ants, their habit of cleaning their mandibles on the vegetative parts of the plant, before proceeding to other nectar-rich blossoms, prevented pollen exchange.

A genuine case of ant pollination, in the Australian flora, has been reported in *Microtis parviflora* (Orchidaceae). Jones (1975a) observed worker ants of three different genera (*Iridomyrmex* sp. (Dolichoderinae), *Meranops* sp. (Myrmeciinae); and *Rhytidoponera tasmaniensis* (Ponerinae)) feeding on the abundant nectar secreted by the labellum of this orchid species. All three ant species effectively pollinate the *Microtis* blossoms, but *Iridomyrmex* sp. is the most frequent pollinia-bearing visitor.

Although *Microtis parviflora* is an autogamous species, 75% of the flowers are ant pollinated within 3 days of anthesis (Jones 1975). Bates (1979) recently recorded a case of pseudocopulatory pollination in the South Australian orchid *Leporella fimbriata,* by winged male ants of the genus (*Myrmecia iurens* group).

9.2.10 Pollination by Wasps (Sphecophily)

Wasps possess unspecialized mouth-parts and hence are generally restricted to allophilic blossoms (Faegri and van der Pijl 1966), with open, easily accessible nectar. In the large genus *Ficus* (Moraceae), a unique situation prevails in which almost every fig species has a different stingless wasp species as a pollinator.

The wasps form a large and highly diversified group. Adults are generally predators or feed on carrion (sometimes just to feed their larvae), and for that reason nectar is important to them only as a source of carbohydrate for their own energy needs. As pollinators, they don't begin to compare to honeybees. In fact, they may exert a strong negative influence on other pollinators by attacking honeybees, other wild bees, and butterflies. The question of whether or not there are flowers adapted specifically to pollination by wasps has been a hotly debated issue.

The one well-known relationship is that of figs and fig wasps. Gall wasps are specialized pollinators of figs (Ficus, of which there are about 700 species, mostly tropical). Female wasps deposit eggs in specialized fig flowers, which are clumped together into an inflorescence. These eggs cause the flowers to change into galls, each with a larva inside. When a male larva matures and hatches, he chews his way out into the fruit, finds himself a female in the same inflorescence "prison," and mates. The female then enlarges the hole the male used to enter, crawls out of her gall, and leaves the fig in which she was born. In doing so, however, she must cross a region of male flowers near the fruit's entrance, which have just opened. Powdered with their pollen, she now makes her way to the young edible figs that have just formed on the same tree or on another one close by. These contain a different type of specialized flowers, which are quite hard and resist the female wasp's attempt to deposit eggs in them, but in the attempt, the flowers are pollinated. This fruit gradually matures and turns into the fleshy fruit we know as figs. Long before, however, the unsuccessful female has left the immature fig to continue her efforts in another fig of about the same developmental stage, but again in vain. She cannot satisfy her urge to deposit eggs in fig flowers until the type of flower in which she hatched again begins to develop in trees. These small, inedible flowers are generally found on the upper branches and are excellent incubators for the eggs and larvae of the female wasp. Thus the cycle starts all over.

Several authors (Ramirez 1974) have indicated that the specificity of the agaonid-fig association ensures that a given fig will produce seed only when its specific agaonid is present. Species of Agaonidae live exclusively in fig inflorescences where they act as pollinating agents. In *Ficus macrophylla* the winged females of *Pleistodontes froggatti* (Agaonidae) are the pollen vectors, whereas the wingless, highly modified males play no part in the pollination process. Scoliid wasps (Scoliidae) pollinate *Calochilus* orchids in eastern Australia (Gumprecht 1977). Jones and Gray (1974) have more recently shown that *Calochilus holtzei* is crosspollinated by male scoliid wasps and that these wasps are involved in pseudocopulatory pollination rather than the pseudoparasitic pollination referred to by van der Pijl and Dodson (1966). Self-pollination mechanisms are also well developed in *Calochilus* orchids (Jones and Gray 1974). Jones and Gray (1974) have noted that the various species will self-pollinate if insect pollination has not occurred within 3 days of anthesis. Thynnid wasps (Thynninae: Tiphiidae) appear to be extensively involved in pseudocopulation in Australian terrestrial orchids (Gumprecht 1977). These parasitic wasps are well represented in Australasia and South America and consist of winged males and smaller, wingless, often ant-like females.

9.3 Pollination by Other Invertebrates

Apart from the major invertebrates already listed, flower-visiting taxa have been recorded amongst the following invertebrate orders in various parts of the world (Muller 1883; Knuth 1895–1905; Faegri and van der Pijl 1966; Proctor and Yeo 1973): Collembola (pollenfeeding), Dermaptera (pollen- and nectar-feeding), Dictyoptera (nectar-feeding), Hemiptera (often recorded at flowers), Mecoptera, Neuroptera, Odonata, Plecoptera (pollen- and nectar-feeding), Psocoptera, Thysanoptera (often found in flowers) and Trichoptera; snail (and slug) pollination (Malacophily) is known, but has not been reported in any Australian plant taxa. The pollinating effectiveness of many of these invertebrate groups is probably negligible and, as Faegri and van der Pijl (1966) state, "one hesitates to accept these allotropic animals as anything more than chance pollinators". Flower visiting amongst "other invertebrates" has rarely been reported in Australia, apart from the following records. COLLEMBOLA: spores and pollen have been found in the gut contents of members of the family Sminthuridae (Wallace and Mackerras 1970). HEMIPTERA: Armstrong (unpublished data) recorded nectar-seeking Lygaeidae on *Aotus lanigera* (Fabaceae), *Nysius clevelandensis* (Lygaeidae) on *Helichrysum* sp. (Asteraceae), and members of the family Miridae on *Astrotricha floccosa* (Araliaceae) and *Dillwynia retorta* (Fabaceae). MECOPTERA: Symmington (1963) noted *Harpobittacus similis* (Bittacidae) visiting *Calectasia cyanea* (Calectasiaceae) blossoms, and Kenneally (1970) observed an undescribed species of *Harpobittacus* seeking nectar from the male flowers of *Diplopeltis huegelii* (Sapindaceae); Riek (1963, 1970) noted//, *australis* obtaining nectar from *Leptospermum* (Myrtaceae) blossoms and Keighery (1974) recorded *H. similis* adults actively foraging in the floral heads of *Eryngium pinnatifldum* (Apiaceae) and *Podolepis lessonii* (Asteraceae). ORTHOPTERA: Clyne (in Key 1974) found that *Zaprochilus* and a closely related undescribed genus of "Zaprochilinae" feed on the pollen and nectar of flowers. THYSANOPTERA: Reed (1970) noted that *Liothrips* (Phlaeothripidae) frequently visits flowers and that *Isoneurothrips australis* (Thripidae), which is commonly found in eucalypt blossoms, probably feeds on nectar; Churchill and Christensen (1970) recorded *Soneurathrips australis* (Thripidae) in *Eucalyptus diversicolor* blossoms; Mound (1974) vaguely noted that the genera *Odontotripiella* (Thripidae) and *Pseudanaphothrips* (Thripidae) are found in the flowers of Australian "herbs and shrubs"; and Endress (1979) recently reported that the genera *Steganthera* and *Wilkiea* (Monimiaceae) show a "normal carpellary pollination by small insects (e.g., Thysanoptera)".

9.3.1 Pollination by Snails

Pollination by snails and slugs (malacophily) is a rare and infrequent phenomenon; so far it has been reported in seven species: *Rohdea japonica*, *Philodendron pinnatifidum*, *Colocasia odora*, *Calla palustris*, *Lemna minor*, *Chrysosplenium alternifolium* and *Phragmipedium caudatum* (Pammel and King 1930; McGregor 1976. Atwood Jr 1982). Prostrate habit of the plant and floral arrangement in which the stigma and anthers do not extend much beyond the corolla, are believed to be conducive to malacophily (Pammel and King 1930). However, some investigators doubt the possibility of snails or slugs being successful pollinators, and consider malacophily to be 'notorious and obscure' (Faegri and van der Pijl 1963) or even 'ridiculous' (Atwood 1982). Snails are usually active at night and also during the day in the rainy season. Sarma et al. (2007) found mass floral foraging by the terrestrial garden garden snail – the Graceful Awlsnail (*Lamellaxis gracile*) on a common garden weed, *Volvulopsis nummularium*, in which flowers open in the morning and close by noon. They clearly established the incidence of snail pollination in *V. nummularium* based on: (i) presence of a large number of snails in soil inhabited by the plants, (ii) foraging pattern of the snails, (iii) presence of pollen load on their body parts, (iv) occurrence of a larger number of pollen grains on the stigma of snail-visited flowers compared to natural autogamy. A snail carried approx. 180 ± 14.2 ($n = 87$) pollen grains on its shell, the average pollen count on the stigma of the snail-visited flowers ($n = 30$) was 95 ± 8.7. 75% ($n = 504$). Nearly 74% of snail-visited flowers developed into fruits, and (v) development of a high proportion of fruits and seeds in snail-visited flowers. Pollination in the family Convolvulaceae is primarily by bees, although there are instances of pollination by moths, birds and bats (Austin 1997). The discovery of malacophily in *V. nummularium* is thus a novel addition to the pollination syndromes prevailing in the family.

9.3.2 Pollination by Vertebrates

It is only in recent years that the importance of vertebrate pollinators in the has been realised. This is probably due to the fact that vertebrates are not known to pollinate blossoms and hence were overlooked as a pollinating group by the classical writers on this subject. The two vertebrate pollination systems are important: ornithophily, involving flower-visiting birds as the pollen vectors, and therophily (Johnson and Briggs 1963) whereby flying or non-flying mammals act as the pollen transporters.

9.3.2.1 The Vertebrate Pollinators Include

Mammals:	Therophily
Birds:	Ornithophily
Marsupials:	Metatherophily
Placentals:	Eutherophily
Bats:	Chiropterophily
Rodents:	Sminthophily

Mammals (Therophily)

Pollination by mammals is called as therophily (Rourke and Wiens 1977). On the basis of functional aspects of pollination biology, two types of mammal pollination occur: nonflying mammal pollination, involving nocturnal marsupials and placental rodents; and flying mammal pollination, involving nectar-seeking placental bats.

Flying Mammals

Pollination by Bats: Bats constitute the order Chiroptera, the only mammals capable of true flight. The family Pteropodidae (suborder: Megachiroptera) contains the flower-visiting chiropterans . The genus *Pteropus* (Pteropodidae) contains the largest number of Australian flower-visiting species . *P. poliocephalus* is the most common fruit observed to feed on the nectar-rich blossoms of the following eucalypt species: *Eucalyptus cloeziana, E. crebra, E.fibrosa* (listed as *E. siderophloia*), *E. grandis, E. intermedia, E. maculata, E. microcorys, E. moluccana, E. pilularis, E. resinifera,* and *E. siderophloia* (listed as *E. drepanophylla*). The spectacled flying-fox (*Pteropus conspicillatus*) is restricted to dense rainforest and swampy habitats regularly visits nectar-rich *Eucalyptus* (Myrtaceae) and *Banksia* (Proteaceae) blossoms and is often seen during the day roosting in trees, close to its blossom sites.

Certain bats have become pure “flower animals” – especially those in the Macroglossinae or “big-tongues,” found in southern Asia and the Pacific. Their protein requirements are met entirely by pollen, which they deliberately collect and consume in great quantities, along with nectar. Several New World species have the same life-style.

Of course, bats are most active at night. They have reasonably good eyesight but appear to be color-blind. They have a keen sense of smell, displaying a preference for odors that humans find definitely unpleasant: mouse- or urine-like, stale, musty or rancid, resembling butryric acid or sweaty feet. The sonar sense of flower-pollinating bats is not as well developed as is that of other bats.

Most flower-pollinating bats are small, sharp-snouted animals with long tongues that can be stuck out very far and have special projections (papillae) and, in some cases, a soft brush-like tip – devices that enable them to rapidly pick up the copious pollen and nectar soup that bat flowers offer. Normally, it is a bat’s head that becomes dusted with pollen, transfer of the precious powder to the pistils of other flowers is no problem. Considering their extreme food specialization, it is not surprising that these bats are usually lacking teeth. The few teeth found in the males are used for fighting and not for eating. While foraging, most macroglossine bats hook themselves into the petals of the flowers (which they probably locate by smell) with their thumb-claws. Several of the New World bats hover like hummingbirds while feeding.

The typical bat flower is large, sturdy, and bell-shaped; has a wide mouth; and is either snow-white or drab in color. The drabness is probably correlated with the lack of color vision in bats, and white makes sense because it is conspicuous by contrast with the darker background. Food is offered in abundance. Bat-flowers have increased pollen production during the process of *Evolution* in two ways: by increasing the number of stamens (up to 2,000 per flower in some species) and by making very large anthers, as in century plants (Agave spp.). Other bat flowers offer their visitors nectar or special food bodies in the form of succulent petals or sweet-tasting bracts.

Another adaptation of bat-pollinated plants is that flowers must be accessible to the relatively large flower bats with poor sonar abilities. To this end, the flowers dangle beneath the crown of trees, or they may be placed on the main trunk or the large limbs. Examples include the white saguaro cactus (Carnegiea) flowers and the century plant, the large flowering spike of which makes the flowers easily accessible high in the air. Some bananas (Musa spp.) are also bat pollinated. Musa fehi, for instance, is found on the Hawaiian Islands. Ethnobotanists have noted that, because bats do not occur in Hawaii, Musa was most probably introduced by man.

Fleming et al. found that a group of plants comprising of 28 orders, 67 families and about 528 species of angiosperms are pollinated by nectar-feeding bats. Two families of bats contain specialized flower visitors, one in the Old World and one in the New World. Adaptation to pollination by bats has evolved independently many times from a variety of ancestral conditions, including insect-, bird- and non-volant mammal-pollination. Bat pollination predominates in very few families but is relatively common in certain angiosperm subfamilies and tribes. flower-visiting bats provide two important benefits to plants: they deposit large amounts of pollen and a variety of pollen genotypes on plant stigmas compared with many other pollinators, they are long-distance pollen dispersers. Bat pollination tends to occur in plants that occur in low densities and in lineages producing large flowers. In highly fragmented tropical habitats, nectar bats play an important role in maintaining the genetic continuity of plant populations and thus have considerable conservation value.

9.4 Bats and Their Flowers

Bats play an important role in pollination as well as in the dispersal of flowering plants (Gardner 1977). Many of the plant species known to be bat-pollinated include the zygomorphic, green-petalled *Lecythis poiteaui* (Lecythidaceae); the long-stamened *Caryocar glabrum* subsp. *glabrum*; the bottle-brush-flowered *Parkia decussata*; and the tubular, light colored flowers of *Markea camponoti*. Although Neotropical bat flowers are diverse in morphology, most bat-pollinated species possess some combination of nocturnal flowers, inflorescences produced free from the foliage thereby providing easier access to the flowers by bats (Pijl 1957), a musky aroma dominated by sulphur-containing compounds (Knudsen and Tollsten 1995), and a relatively dilute nectar rich in hexose sugar (Baker et al. 1998).

Bats comprise one of the important groups of animals that can pollinate plants. Species belonging to about one-third of the bat genera have been observed visiting flowers in darkness, to lap the sugary nectar and eat protein-rich pollen. Nearly all species of these nectarivorous pollinators belong either to family Pteropodidae (the fruit bats and flying foxes, especially in the subfamily of macroglossine bats) or family Phyllostomidae (the leaf-nosed bats, especially in the subfamily of glossophagine bats). Flying from sundown to sunrise, these aerial mammals are able to find appropriate flowers, even on moonless nights. Currently 966 species of bats are recognized, making this the second largest radiation of mammals, after rodents. Most bat species are insectivorous, i.e., they are insect eaters. From insects they obtain protein. It is clear that flower visitation is a derived behavior, having evolved separately, therefore convergently, in the two suborders. Most likely, it developed as a specialization from frugivory, i.e., fruit eating, but possibly a specialization directly from insectivory. Even within suborder Microchiroptera, nectarivory has evolved numerous times. Microbats shifted to visiting flowers instead of catching flying insects to obtain protein and often lipids from pollen, but they gain protein also by consuming insects found on the flower parts and in the nectar. Most nectarivorous species live in the tropics or subtropics; bat pollination does not occur in Europe and temperate North America, nor in South Africa, with the exception of the morning glory *Ipomoea albivena*. Bat pollination is virtually absent in Australia south of Queensland. Nectariferous bats have been observed pollinating species just below the puna vegetation of the high Andes.

Flowers that are pollinated by bats may have a very strong, fruity, nocturnal fragrance or are often described as smell musky or "batty," or like products of fermentation, and nectarivorous bats tend to have a moderate- to well-developed sense of smell. The fruit-eating bats of Megachiroptera, especially, utilize olfaction to locate flowers as well as fruits, and they key on odors of esters, alcohols, aldehydes, and aliphatic acids, particularly butyric acid, as cues for locating food resources. Many microbats use smell to identify prey items; the phyllostomids seem to have the keenest olfactory sense, which is most developed in the flower-visiting spear-nosed bat, *Phyllostomis stenops*.

Bat flowers are firm, large, wide-mouthed, and bell-shaped or dish-shaped. The bat forces its head into the flower through a mass of pollen-bearing anthers, trying to reach a deep nectary with its long tongue. The night-opening flowers of certain giant cacti, such as saguaro (*Carnegiea gigantea*) and organpipe cactus (*Stenocereus thurberi*) in Arizona, and card (*Pachycereus pringlei*) in nearby Sonora, Mexico, are perfect models of this design. These cacti are pollinated by *Leptonycteris curasoae*, a species entirely dependent on nectar and pollen for its existence and feeding on a broad range of plants from Central America through the American Southwest. Such bat flowers are white, cream-colored, or green, but may also be purplish to red or pink. Bats apparently have only rods in their eyes, and hence are considered to be colorblind and therefore are attracted to drab-colored flowers. The animal may hover, but also can perch and then hold onto the strong, sterile parts of the flower while feeding. One evidence of bat visitation is the present the next morning of thumb claw marks on the flower.

Another flower design for chiropterophily (pollination by bats) is termed the brush type, pincushion, or shaving brush type. This may be a large flower with many stamens, as in the African baobab (*Adansonia digitata*), which may have 2,000 stamens, or an inflorescence of many clustered flowers with showy stamens and essentially no corollas (petals), as in the legume *Parkia clappertoniana* in tropical Africa. Many brush-type, bat-pollinated flowers are found among the myrtles (Myrtaceae), sapotes (Sapotaceae), and mimosoid legumes (Mimosaceae), and the bats eat the stamens of these flowers. Some of the chiropterophilous species of *Agave*, which are said to smell somewhat like cabbage, are more like brushes than bell-shaped, and the bat-pollinated feh'i banana (*Musa fehi*), probably originally from New Caledonia and cultivated in the Pacific islands, has bracts that spread apart at night. As you might suspect, not every bat-visited flower fits the syndrome of characteristics.

Bats would have difficulty navigating within cluttered vegetation when flying in the dark at high speeds. Nectarivorous species tend to have a broad wing form with long tips that enable slower travel and even hovering at the face of the flower. Plants that use bats as pollinators most often place flowers in locations where the bat is less likely to be injured. Some bat flowers are formed at the tip of the canopy, as is the case with tall cacti. Some hang below the foliage on long, pendulous inflorescences, a condition termed flagelliflory; examples, among many, are the sausage tree, *Kigelia pinnata*, of Africa and species of the legume *Mucuna* in the American tropics. Some bat flowers are formed on the trunk and large lower branches, a condition termed cauliflory; examples are the species of calabash (*Crescentia*) in the American tropics. Because bats may have difficulty navigating through foliage, some bat flowers are formed when the trees are leafless. Bat-pollinated cacti often have no spines on flowers; spine growth is delayed until after pollination so that the bats are not impaled during their visits.

The well-known ability of bats to navigate adroitly in total darkness has of course been a subject of intense study by biologists, especially since the late 1950s. In the animal kingdom, bats are the quintessential example of a sonar system and echolocation. This requires many ingenious adaptations, including keen audition to detect location and size of prey and to avoid hazards and obstacles while flying. Bats produce and sense loud ultrasonic frequencies that we cannot hear. Such high frequencies cannot be confused with sounds emitted by other animals or with background noises, and the sound waves travel, albeit at 340 m per second, only relatively short distances (meters) as short wavelengths, so they do not interfere with the echolocation of other bats in the vicinity.

The sounds are produced in the larynx as the bat breathes out late in the wing upstroke. The ultrasonic high-pitched sounds, emitted through either the mouth or the nostrils, result when the thorax is compressed. Some evidence suggests that the leaflike nose apparatus on phyllostomid bats focuses sound into a narrow beam, much like an acoustic lens. Emitted sound segments are short bursts at particular amplitudes and duration, consisting of two different classes of sound waves 2–5 ms in length. After emitting the segment, the animal waits for an echo, calculates the distances, and then emits a new set of sound bursts to recalculate the change in position of the nearest prey item or the obstacle. Amazingly, the frequency is adjusted by the individual bat to compensate for the Doppler frequency shift, whereby the sound is distorted depending on whether the individual is moving toward or away from the target. The bat's sound receivers are the enlarged external ears (pinnae), which, like microwave dishes, are a certain size and are oriented (fixed or movable) in such a way as to intercept the returnign echoes. To avoid being deafened by its own emitted ultrasonic sounds, the bat uses a particular muscle to disengage the sound-detecting apparatus in the middle ear (specifically, the stirrup or stapes) when the sound is emitted, and then repositions the bone to interpret the echo. Nectarivorous megabats perch while feeding. They lack echolocation and therefore use only visual and olfactory cues to locate flowers and fruits.

Megabats have substantially larger eyes than do microbats, but even the microbats have very good discrimination of white versus black surfaces and can discern different shapes very precisely at extremely low light levels. Nonetheless, nectarivorous microbats have eyes 10–40 times larger than their insectivorous cousins – an adaptation that results in greater depth of focus for near orientation and discriminating flowers. The nectarivorous microbats seem to utilize sonar echolocation to find flowers at long distance and then visual and olfactory cues to find and choose individuals flowers to visit. Bats also receive sensory information from fine whiskers around the long rostrum (nose) when it is inserted into the flower.

The bat may eat the pollen, anthers, and stamens of the flower, but it also can carry huge loads of pollen on its face and rough fur. So much pollen can attach to a bat during one visit that some of it is bound to be deposited on the next flower. One investigator estimated more than 1.5 million pollen grains per flower of card and an individual bat may visit more than 30 flowers per night! Bats fly relatively long distances swiftly. Thus they can be effective transporters of pollen between widely spaced flowers and thereby perform effective cross pollination in the process. Although local visits are more frequent, bats may forage long distances from their daytime roosts. In some instances, bats travel long distances to a specific plant population; one fruit bat species in Africa flies two and a half hours nightly to visit a particular chiropterophilous plant species.

The nectar reward of bat flowers can be copious, even reaching numerous milligrams for a single flower of balsa (*Ochroma*) in the American tropics. A bat flower contains substantially more nectar than does a flower pollinated by insects. The large quantities of relatively thin nectar are sucrose rich or sucrose dominant in most bat flowers. Birds such as hummingbirds use these flowers when they are open the following morning. The extensible tongues of bats have grooves and minute projections to capture the liquid food. Some bat plants offer other sweet rewards, such as the bracts of *Freycineta insignis*, eaten by fruit bats, and the sweet flower parts of *Madhuca* and *Bassia*. Pollen-feeding bats tend to have fewer teeth than their insect-catching cousins.

No complete worldwide list of bat-pollinated plants has been published, but records exist for more than 40 plant families and species in hundreds of plant genera. Bat pollination is especially important in certain families, such as Old and New World Bombacaceae, including the baobab, kapok, and floss-silk tree species. Classical examples of bat flowers occur in the Bignoniaceae, including the sausage trees and calabash, among others. *Cobaea scandens*, a cultivated vine of the phlox family (Polemoniaceae), has flagelliflory and is bat pollinated in western South America.

9.5 Non-flying Mammals as Pollinators

Carthew and Goldingay (1997) reported that Non-flying mammals such as marsupials, primates and rodents are involved in pollination in Australia, Africa and South and Central America. They found that some plants exhibit traits that have co-evolved with non-flying mammal pollinators. However, much more research is still required to understand the importance of these animals in pollination.

9.6 Monkeys as Pollinators

Prance (1980) reported that the monkeys drink nectar from the flowers of which bats are probably the primary pollinators. Gautier-Hion and Maisels (1994) observed four species of monkey community in a forest of the Zaire Basin intensively lick the nectar of *Daniellia pynaertii* (Caesalpinoideae). The nectar makes up a mean of 20% and a maximum of 50% of monthly plant feeding records resulting up to 8 kg body weight increase in these basically frugivorous primates as an alternative strategy to cope with a shortage of fleshy fruits. This would have been possible due to the high density of the plant species, the synchrony and abundance of its flowering, and the large size of the nectar drop and its nutritional value. Patterns of monkey movements among *Daniellia* trees show that one flowering tree may receive up to 10 species visits and 30 individual visits per day, for a total of up to 141 min. A monkey troop can visit 12 trees in succession over less than 3 h. This suggests that monkeys are able to promote pollen transfer both among flowers of the same tree and between conspecific trees. The individual tree fruiting index is positively correlated with its flowering index and with the amount of visits by monkeys, indicating at least that monkeys do not inhibit the reproductive ability of flowers. These results suggest that monkeys can be considered as a guild of effective pollinators. *D. pynaertii* flowers typically meet the pollination syndrome for attracting large mammals: notably conspicuousness and open morphology of the flowers, nectar colour and abundance. These characteristics suggest that coadaptation between monkeys and plant or at least one-sided adaptation has operated.

9.7 Nonflying Mammals

9.7.1 Nonflying Mammals

A recent review (Rourke and Wiens 1977) documents the extent of our knowledge of the interactions between nonflying mammals and plants. They argue that inflorescences and flowers of certain members of Proteaceae and Myrtaceae in Australia are adapted to pollination by small marsupials, rats and squirrels. Many primates feed on flowers or parts of flowers at times, but the effect on the flowers is usually destructive (Glander 1975). Cebus monkeys may drink water or nectar, or both, from trees of Ochroma pyramidale without destroying the flowers (Oppenheimer 1968) and might participate in their pollination. This is, however, the only well-documented case of an anthropoid which might be acting as an important pollinating agent.

In Madagascar, however, the relation between lemurs and flowering plants appears to be a significant one. All of the diurnal Malagasy lemurs are mainly vegetarian and many spend a small proportion of time feeding on flowers and are destructive to them. In contrast, the six species of nocturnal lemurs viz., *Lemur mongoz., Lepilemur mustelinus., Microcebus murinus., Microcebus coquereli., Cheirogaleus medius., Phaner furcifer* have been observed to feed regularly on flowers during at least a portion of the year, and are therefore of particular interest in terms of their possible significance in pollination systems. In general, nocturnal lemurs do play a significant role in the pollination of certain plant species in Madagascar. Another group of unspecialized nocturnal primates, the bush babies of the mainland of Africa, has been reported to visit the flowers of *Adansonia* for nectar and probably other food material as well without destroying them (Coe and Isaac 1965). The species involved, *Galago crassicaudatus* has also been reported to feed on fruit, insects, and gum (Doyle 1974). A second species of Galago, *G. senegalensis* was reported by Doyle (1974) to visit different flowering trees in succession; whether they were actually seeking insects, as he assumed, remains to be demonstrated.

In summary, certain marsupials in Australia, rodents in Australia and South Africa, lemurs in Madagascar, and galagos in continental Africa regularly visit nectar-rich flowers and lap their nectar as an important source of food, especially during the dry season. Almost all of these animals are nocturnal, and nearly all feed in part on insects, fruits, and, in some cases, gum. In general, they do not appear to compete directly with flower-visiting birds, which are exclusively diurnal, for food (Fenton and Fleming 1976). The living marsupials of South America do not include forms that regularly visit flowers or eat fruits and that might conceivably be implicated in pollination systems. It would be of great interest to know more about food habits of the single nocturnal New World primate, *Aotus*, which night feed on and pollinate flowers. Is There a Class of Flowers Adapted to Pollination by Nonflying Mammals? This question, first raised in a comprehensive manner by Porsch (1936) has been answered in the affirmative, with new evidence, by Rourke and Wiens (1977). The existence of certain species Myrtaceae and Proteaceae of Australia with unusually large, strong flowers or inflorescences, relatively few flowers or inflorescences per plant, strong floral odors, and copious nectar, in areas where bat-pollination is absent or at best sporadic, does point in this direction. For Madagascar, another region where plants that bear flowers with these characteristics exist, and where pollination of flowers by bats is evidently very rare, Jumelle and Perrier de la Bâthie (1910) reported that lemurs regularly visited the nectar-rich flowers of *Symphonia nectarifera*, eating the leathery petals and drinking the nectar. Certainly lemurs may be regular visitors to the largest-flowered of the approximately 16 species of *Symphonia* found in Madagascar (Perrier de la Bathie 1951), and might reasonably be thought to have participated in their *Evolution*. Porsch (1935) considers *Symphonia* in general to be bat-pollinated, but agrees with Perrier de la Bathie about the probability of lemur pollination in these species. He also suggests that some Bombacaceae and Lecythidaceae may be adapted for pollination by nonflying mammals. Other Mascarene plants that have what appear to be suitable characteristics and that have been observed to be visited by lemurs eating portions of the flowers or lapping the nectar include *Adansonia, Brexia madagascariensis, Crateva greveana,* *Delonix floribunda, Rubus roridus, Uapaca sp., and Vaccinium emirnense.* Lemurs have also been observed to feed on nectar from the extrafloral nectaries of the pantropical *Hura crepitans* and to visit and probably efficiently pollinate the flowers of the introduced *Ceiba pentandra*. At the flowers of the normally bird-pollinated and red-flowered *Combretum phaneropetalum* and *Fernandoa madagascariensis* the visits of lemurs were undoubtedly secondary. Bats very often visit normally bird-pollinated plants, such as *Erythrina* (Raven 1977) and *Spathodea* (Ayensu 1974) for nectar. In Madagascar, an island where flower-visiting birds are frequent but flower-visiting bats are rare, there appears to be a strong circumstantial case for the *Evolution* of certain plants with floral characteristics adapted to regular visitation by and consequent pollination by lemurs.

9.8 Contemporary Relationships

Birds, bats, and nonflying mammals visit and pollinate flowers regularly at the present time. Pollination systems involving birds are well developed throughout the tropics and the temperate regions of the Southern Hemisphere; most of the flowers birds visit are brightly colored, usually red, and odorless (Raven 1972). Systems involving bats and nonflying mammals usually include flowers that are dull-colored and odorous; they are almost invariably nocturnal, whereas systems involving birds are always diurnal, as pointed out by Fenton and Fleming (1976). With the exception of the specialized flowers closely adapted for hummingbirds (and the analogous ones visited by hawkmoths), many of the flowers visited by birds are also visited by bats and nonflying mammals in regions where flower-visiting members of these groups are found. Aside from morphological adaptations that presumably evolved to protect the ovules of the plants concerned, the flowers of such plants are generally open, with copious nectar.

Pollination systems involving bats and those which involve nonflying mammals appear to have a reciprocal geographical distribution. Bat-pollination is common and well developed throughout tropical America, Asia, and northern Australasia, reasonably frequent in West Africa, less so in East Africa, and poorly developed on Madagascar. Flower-visiting and fruit-eating bats migrate into temperate regions seasonally, at times reaching temperate Australia and South Africa and the southern borders of the United States and of the Palearctic region. Those systems that appear to involve nonflying mammals, on the other hand, are evidently present in temperate South Africa, temperate Australia, and Madagascar-all regions where flower visiting bats are rare, seasonal, or absent.

Porsch (1934) was the first to suggest that certain Proteaceae and Myrtaceae in Australia were pollinated by mouse-like marsupials; Since then very little new information has come to hand and pollination by non-flying mammals is largely ignored or given the very briefest mention in current summaries of pollination ecology (Faegri and van der Pijl 1966; Proctor and Yeo 1973). To date, no unequivocal evidence for regular pollination by non-flying mammals can be presented and all the available information relating to this phenomenon is, to quote Rourke and Wiens (1977), "either circumstantial, inferential, or anecdotal". The floral features of hooked-styled *Banksia* species appear to be adaptations for more efficient exploitation of both bird and mammal pollen vectors, rather than adaptations for exclusive pollination by mammals as proposed by Carpenter (1978) and others.

9.8.1 Marsupials (Metatherophily)

Australasia is the only region of the world in which marsupial pollination has been reported. The most highly adapted nectar-feeding marsupial is the honey possum (*Tarsipes spencerae*), a species confined in its distribution to the southwestern corner of Western Australia. The long prehensile tail of this mouse-like animal enables it to dangle from one blossom while feeding on another Its extremely etiolated, almost tubular snout is well adapted for nectar collection This new term is based on the name for the mammalian infraclass-Metatheria. and is used to probe nectar-rich blossoms in much plant species: *Adenanthos cuneata, Banksia* the same way as do the long-beaked honeyeating *attenuata, B. baxteri, B. occidentalis, B. sphaero*birds.

9.8.2 Rodents (Sminthophily)

The only rodent known to visit blossoms in Australia is the southern bush rat (*Rattusfuscipes:* Muridae) a shy nocturnal animal that lives on native vegetation, and hides in burrows during the day. Morcombe (1978a, b) was the first to suggest that this animal is attracted to nectar-rich *Banksia* blossoms; recently Carpenter (1978) have verified this suggestion, with their identification *of Banksia ericifolia* and *B. baxteri* pollen on the heads of trapped *Rattus* individuals. Rodents are known to visit blossoms in other parts of the world. In Hawaii, introduced rats are attracted to the fleshy bracts surrounding the flowers of *Freycinetia* (Pandanaceae) (Degener 1945), and in South Africa, the cryptic, geanthous species of *Protea* (Proteaceae) are regularly visited and pollinated by a variety of indigenous rodents (Rourke and Wiens 1977; Wiens and Rourke 1978). Wiens and Rourke (1978) found that that rodent regularly pollinate two Cape *Protea* spp., *Protea amplexicaulis* and *P. humiflora*, and that the flowers are specifically adapted for such pollinators.

9.8.3 Pollination by Squirrels

Nectar robbing by squirrels is reported for the first time in the striped squirrel (*Tamiops swinhoei hainanus*), which was found robbing nectar from ginger plants (*Alpinia kwangsiensis*) in tropical forests of south Yunnan, China (Deng et al. 2004).

Deng et al. 2004 also described the behavior of squirrels visiting inflorescences, and compared the fruit set of inflorescences visited by squirrels with that of inflorescences not subject to nectar robbing by squirrels. Most of the styles of robbed flowers were damaged and the affected plants exhibited reduced fruit set.

9.8.4 Pollination by Lizards

Several species of lizards feed on nectar and fruits of plants. At the same time, it suggests that while consuming these plant materials, lizards could effectively pollinate flowers or disperse seeds to sites away from parent plants. Although this information is valuable to determine the role of lizards in plant reproduction, more studies should be done in order to completely understand the ecological and *Evolution*ary consequences of these interactions. Diet analysis is the subject that has received more attention; however, further research is needed to determine whether lizards are selective feeders that consume plant items in a different proportion to their availability in the environment (Dearing and Schall 1992; van Marken 1993). These studies will permit to address questions related to digestion, energy, and nutrients provided by nectar and fruits in comparison to vegetative structures. Pough et al. (1998) indicate that fruits and flowers have large, energy-rich cells that are easily ruptured and their energy and nutrients are readily accessible to lizards in comparison to leaves. Additionally, information on the selectivity of diet is basic to understand pollination and seed dispersal by lizards because preference for a particular set of plants increases the probability to establish tight interactions. Moreover, biotic interactions between lizards and plants could vary along the distributional ranges of both interactants. Olesen and Valido (2003) have indicated that pollination and seed dispersal by lizards is most common on islands than on mainland. According to these authors, Island lizards reach very high densities and experience lower predation risk, expanding their diets to include nectar and fruits. However, more field studies on the diet of continental lizards are necessary to determine whether these differences really exist or they are only the reflection of insufficient information (Tables 9.8 and 9.9).

From a plants perspective, an effective pollinator must be an abundant and frequent visitor that transports pollen from one flower to another located in the same or different individual. Although the information found on this subject is scarce because only few lizard species have been analyzed with this approach, it suggests that lizards could be considered as effective pollinators of plants. Traveset and Sáez (1997) analyzing the pollination of Euphorbia dendroides (Euphorbiaceae) found that the lacertid Podarcis lilfordi is the true pollinator of this plant because it increases fruit and seed set in comparison to insects. Other species of lizards mainly in the family Gekkonidae could also potentially act as the main pollen vectors of different species of plants. In this regard, Nyhagen et al. (2001) reported that Phelsuma ornata could carry the pollen of up to 80% of all plant species in Ile aux Aigrettes, Mauritius. Similarly, data on the activity patterns of geckos in the genus

Table 9.8 Quantity and quality components of seed dispersal by lizards

Lizard species	Plant species	Quantity	Quality	Reference
Ctenosaura pectinata	*Spondias purpurea*	3	1, 2	Mandujano et al. (1994)
Ctenosaura similis	*Acacia farnesiana*	3	1	Traveset (1990)
Cyclura carinata	*Casasia clusiaefolia* *Coccoloba uvifera* *Eugenia foetida*	–	1	Iverson (1985)
Cyclura rileyi	*Casasia clusiaefolia-* *Coccoloba uvifera* *Eugenia foetida*	1		Iverson (1985)
Gallotia atlantica	*Lycium intrincatum*	3	1	Nogales et al. (1998)
Gallotia galloti	*Lycium intrincatum* *Neochamaelea pulverule* *Opuntia dillenii* *Rubia fruticosa* *Whitania aristata*	3	1	Valido and Nogales (1994)
Liolaemus pictus	*Nertera Granadensis* *Relbunium hypocarpium*	–	1	Willson et al. (1996)
Platysaurus capensis	*Ficus cordata*	2	–	Whiting and Greeff (1997)
Podarcis lilfordi	*Cneorum tricoccon* *Whitania frutescens*	2, 3	1	Traveset (1995), Castilla (1999, 2000)
Teius teyou	*Ziziphus mistol*	–	1, 2	Varela and Bucher (2002)
Tropidurus torquatus	*Erythroxylum ovalifolium* *Melocactus violaceus*	2, 3	1, 2	Fialho (1990) Côrtes et al. (1994)

Quantity: *1* lizard abundance, *2* fruit removal and/or handling time, *3* number of seeds per scat, – not evaluated

Quality: *1* seed germination after gut passage and/or passage time through the digestive tract, *2* habitat use by lizards, – not evaluated

Haplodactylus indicate that their distribution is influenced by the pattern of nectar availability (Eifler 1995). However, more experimental studies related with the analysis of quantity and quality components of pollination are needed, in order to determine whether geckos are effective pollinators. With this information, it will be possible to test an idea proposed by Whitaker (1987) which states that geckos could act as nectar robbers in different species of plants from New Zealand.

Contrary to the information found on pollination, results about seed dispersal indicate that many lizards include a wide variety of fruits in their diets. Thus, species in the families Iguanidae, Lacertidae, Teiidae, Scincidae, and Varanidae could potentially disperse the seeds of different species of plants (van Marken 1993; Mandujano et al. 1994; Willson et al. 1996; Castilla 2000). Seed dispersal is a diffuse co*Evolution*ary process in which a particular animal species interacts with different species of plants. For this reason, it has been suggested that seed dispersers

Table 9.9 Lizard species found in the literature consuming reproductive plant parts

Lizards	N	Fw	Fr	Reference
Family Cordylidae				
Platysaurus capensis			X	Whiting and Greeff (1997)
Family Gekkonidae				
Hoplodactylus duvauceli	X		X	Whitaker (1987), Eifler (1995)
Hoplodactylus granulatus		X		Whitaker (1987)
Hoplodactylus maculates	X		X	Whitaker (1987)
Hoplodactylus pacificus	X	X	X	Whitaker (1987)
Naultinus grayi	X		X	Whitaker (1987)
Phelsuma ornata ornata	X			Nyhagen et al. (2001)
Phelsuma vinsoni	X			Whitaker (1987)
Family Iguanidae				
Ctenosaura pectinata			X	Mandujano et al. (1994)
Ctenosaura similis			X	Traveset (1990)
Cyclura carinata			X	Iverson (1985)
Cyclura rileyi			X	Iverson (1985)
Iguana iguana		X	X	van Marken (1993)
Liolaemus pictus			X	Willson et al. (1996)
Tropidurus torquatus			X	Fialho 1990; Côrtes et al. (1994)
Family Lacertidae				
Gallotia atlantica			X	Nogales et al. (1998)
Gallotia galloti			X	Valido and Nogales (1994)
Lacerta lepida				Hódar et al. (1996)
Podarcis hispanica atrata			X	Castilla and Bauwens (1991)
Podarcis lilfordi	X	X	X	Sáez and Traveset (1995), Pérez-Mellado and Casas (1997)
Podarcis pituyensis			X	Traveset (1995)
Family Scincidae				
Cyclodina alani			X	Whitaker (1987)
Cyclodina oliveri			X	Whitaker (1987)
Cyclodina whitakeri			X	Whitaker (1987)
Leiolopisma fallai			X	Whitaker (1987)
Leiolopisma grande			X	Whitaker (1987)
Leiolopisma nigri*Planta*re			X	Whitaker (1987)
Leiolopisma otagense f. otagense			X	Whitaker (1987)
Leiolopisma otagense f. waimatense			X	Whitaker (1987)
Leiolopisma smithi			X	Whitaker (1987)
Niveoscincus microlepidotus	X	X		Olsson et al. (2000)
Family Teiidae				
Aspidoscelis murinus	X	X	X	Dearing and Schall (1992)
Teius teyou			X	Varela and Bucher (2002)
Family Varanidae				
Varanus olivaceus			X	Corlett (1998)

N nectar, *Fw* flowers, *Fr* fruits

vary in the services provided to plants in terms of the number of seeds deposited in suitable sites and the treatment given to seeds in the gut (Wheelwright and Orians 1982; Schupp 1993). At present, the information related with the effects of lizards on seed germination and seedling establishment is uncertain since studies found in the literature are contradictory (Iverson 1985; Fialho 1990; Côrtes et al. 1994; Mandujano et al. 1994; Valido and Nogales 1994; Willson et al. 1996; Castilla 1999, 2000; Varela and Bucher 2002). Therefore, it is necessary to increase the number of studies on the quality component of seed dispersal (i.e., percentage and rate of seed germination after passage through the digestive tract and deposition site in which seeds were delivered) to properly determine the role of lizards in this mutualistic interaction. Despite this lack of information, some studies have analyzed in a detailed manner the interactions between lizards and plants. Thus, Côrtes et al. (1994) and Vasconcellos-Neto et al. (2000), studying the interaction between the lizard Tropidurus torquatus and the cactus Melocactus violaceus in Brazil, found that the cactus and fruit morphology, the pattern of fruit release, and the germination of seeds may represent a suite of adaptations for dispersal by T. torquatus. Based on these results, it is possible to argue that under some special circumstances lizards could exert selective forces on plants. Field studies with other species of lizards and plants in different habitats may provide evidence about these interactions and their possible *Evolution*ary consequences.

Finally, the information presented in this review suggests that analysis of the mutualistic interactions between lizards and plants is a subject that deserves more attention, in order to completely understand the possible ecological and *Evolution*ary effects of lizards on plant reproduction.

In conclusion, non bee pollinators whose services go unnoticed have a definite role to play in maintaining the diversity of world ecosystems, balance of *Nature* in the context of climatic change and sustaining biodiversity by producing fruits, nuts, berries in forests eaten by animals in wild and providing food security.

References

Anonymous (2003a) Mutualism: lecture 11 outline. Entomology BIOL 4731. http://www.w3.org/TR/REC-html.40

Anonymous (2003b) Bees behavior during foraging, Apiary Fact Sheet # 111. http://agf.gov.bc.ca/apiculture/factsheets/111_forage.html

Atwood J Jr (1982) How is *Paphiopedilum* pollinated? Am Orchid Soc Bull 51:1057–1058

Austin DF (1997) Dissolution of *Ipomoea* series Anisomerae (Convolvulaceae). J Torr Bot Soc 124:140–159

Ayensu ES (1974) Plant and bat interactions in West Africa. Ann Mo Bot Gard 61:702–727

Baker HG, Baker I (1990) The predictive value of nectar chemistry to the recognition of pollinator types. Isr J Bot 39:157–166

Baker HG, Baker I, Hodges SA (1998) Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. Biotropica 30(4):559–586

Bates R (1977) Pollination of South Australian orchids — Part 4. Native Orchid Soc S Aust Newsl 1(6):8

Beynon RM, Struckmeyer HIM, Totterdell JM (1992) Australia – evolution of a continent. Bureau of Mineral Resources Palaeogeographic-Group, Australian Government Publishing Service, Canberra

Bowe LM, Coat G, de Pamphilis C (2000) Phylogeny of seed plants based on all three genomic compartments: extant gymnosperms are monophyletic and Gnetales closest relatives are conifers. Proc Natl Acad Sci USA 97:4092–4097

Carpenter FL (1978) Hooks for mammal pollination? Oecologia 35:123–132

Carthew SM, Goldingay RL (1997) Non-flying mammals as pollinators. Trends Ecol Evol 12(3):104–108

Castilla AM (1999) *Podarcis lilfordi* from the Balearic islands as a potential disperser of the rare Mediterranean plant *Withania frutescens*. Acta Oecologica 20:103–107

Castilla AM (2000) Does passage time through the lizard *Podarcis lilfordi*'s gut affect germination performance in the plant *Withania frutescens*? Acta Oecologica 21:119–124

Castilla AM, Bauwens D (1991) Observations on the natural history, present status, and conservation of the insular lizard *Podarcis hispanica atrata* on the Columbretes Archipelago, Spain. Biol Conserv 58:69–84

Chadwick CE (1993) The roles of *Tranes lyterioides* and *T. sparsus* Boh (Col., Curculionidae) in the pollination of *Macrozamia communis* (Zamiaceae). In: Stevenson DW, Norstog NJ (eds) Proceedings of CYCAD 90, second international conference on Cycad biology. Palm and Cycad Societies of Australia Ltd, Milton, pp 77–80

Chaw SM, Parkinson CL, Cheng Y, Vincent TM, Palmer JD (2000) Seed plant phylogeny inferred from all three plant genomes: monophyly of extant gymnosperms and origin of Gnetales from conifers. Proc Natl Acad Sci USA 97:4086–4091

Churchill DM, Christensen P (1970) Observations on pollen harvesting by brush-tongued lorikeets. Aust J Zool 18:427–437

Clout MN, Hay JR (1989) The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. N Z J Ecol 12(supplement):27–33

Coe MJ, Isaac FM (1965) Pollination of the baobab (Adansonia digitata L.) by the lesser bush baby (Galago crassicaudatus E. Geoffroy). E Afr wildl J 3:123–124

Corlett RT (1998) Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. Biol Rev Camb Philos Soc 73:413–448

Côrtes FJE, Vasconcellos-Neto J, Garcia MA, Teixeira De Souza AL (1994) Saurocory in *Melocactus violaceus* (cactaceae). Biotropica 26:295–301

Cranston PS, Naumann ID (1991) Biogeography. In: CSIRO (ed) The insects of Australia, 2nd edn. Melbourne University Press, Melbourne, pp 180–197

Darwin C (1876) The effects of cross and self fertilisation in the vegetable kingdom. Murray, London

Darwin C (1877) The different forms of flower on plants of the same species. Murray, London

Davies SJ (1999) A new Myrmecophytic Thrip-pollinated species of Macaranga from the highlands of Sarawak. Harv Pap Bot 4:433–437

Dearing DM, Schall JJ (1992) Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorus murinus*. Ecology 73:845–858

Degener O (1945) Plants of Hawaii National park illustrative of plants and customs of the south seas. Edwards, Michigan, 333 pp

Deng X-B, Ren P-Y, Gao J-Y, Li Q-J (2004) The striped squirrel (Tamiops swinhoei hainanus) as a nectar robber of ginger (Alpinia kwangsiensisy). Biotropica 36:633–636

Downes JA (1958) The feeding habits of biting flies and their significance in classification. Annu Rev Entomol 3:249–266

Doyle GA (1974) Behavior of prosimians. In: Schrier AM, Stollnitz F (eds) Behavior of nonhuman primates. Academic, New York, pp 155–353

Eifler DA (1995) Patterns of plant visitation by nectarfeeding lizards. Oecologia 101:228–233

Endress PK (1979) Noncarpellary pollination and 'hyperstigma' in an angiosperm (*Jambourissa religiosa*, Monimiaceae). Experienta 35:45

Faegri K, van der Pijl L (1963) The principles of pollination ecology. Pergamon Press, Oxford

Faegri K, van der pijl L (1966) The principles of pollination ecology. Pergamon Press, London, 248 pp

Faegri K, van der Pijl L (1979) The principles of pollination ecology. Pergamon Press, Oxford

Fenton MB, Fleming TH (1976) Ecological interactions between bats and nocturnal birds. Biotropica 8:104–110

Fialho RF (1990) Seed dispersal by a lizard and a treefrog - effect of dispersal site on seed survivorship. Biotropica 22:423–424

Ford HA, Paton DC, Forde N (1979) Birds as pollinators of Australian plants. N Z J Bot 17:509–519

Forster PI, Machin PJ, Mound LA, Wilson GW (1994) Insects associated with reproductive structures of cycads in Queensland and North-east New South Wales, Australia. Biotropica 26:217–222

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London

Friis EM, Chalconer WG, Crane PR (eds) (1987) The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge

Gardner AL (1977) Feeding habits. In: Baker RJ, Jones JK, Carter DC (eds) Biology of bats of the new world family Phyllostomatidae. Part II. Special Publications. Museum Texas Tech Univ, Lubbock, pp 293–350

Gautier-Hion A, Maisels F (1994) Mutualism between a leguminous tree and large African monkeys as pollinators. Behav Ecol Sociobiol 34(3):203–210

Gibernau M, Barabe D, Cerdan P, Dejean A (1999) Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. Int J Plant Sci 160(6):1135–1143

Glander K (1975) In: Tuttle RH (ed) World anthropology: socioecology and psychology of primates. Mouton, The Hague, pp 37–57

Godley EJ (1979) Flower biology in New Zealand. N Z J Bot 17:441–446

Goldblatt P, Manning JC (2000) The long-proboscid fly pollination system in southern Africa. Ann Mo Bot Gard 87:146–170

Gottsberger G (1977) Some aspects of beetle pollination in the evolution of flowering plants. Plant Syst Evol 1(Suppl):211–226

Gottsberger G (1986) Some pollination strategies in Neotropical savannas and forests. Plant Syst Evol 152:29–45

Gottsberger G (1990) Flowers and beetles in the South American Tropics. Bot Acta 103:360–365

Gottsberger G, Amaral A (1984) Pollination strategies in Brazilian Philodendron species. Ber Dtsch Bot Ges Bd 97S:391–410

Grant V, Grant K (1965) Flower pollination in the phlox family. Columbia University Press, New York, 180 pp

Grimaldi D (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. Ann Mo Bot Gard 86:373–406

Gumprecht R (1977) Seltsame Bestaubungsvorgange bei Orchideen. Die Orchid 3(28):5–23

Henderson A (1986) A review of pollination studies in the Palmae. Bot Rev 52:221–259

Hocking B (1953) The intrinsic range and speed of flight of insects. Trans R Entomol Soc Lond 104:223–345

Hódar JA, Campos F, Rosales BA (1996) Trophic ecology of the Ocellated lizard *Lacerta lepida* in an arid zone of southern Spain: relationships with availability and daily activity of prey. J Arid Environ 33:95–107

Hunter FF, Burgin SG, Woodhouse A (2000) Shattering the folklore: blackflies do not pollinate sweet lowbush blueberry. Can J Zool 78:2051–2054

Ingram M, Nabhan G, Buchmann S (1996) Our forgotten pollinators: protecting the birds and bees. Glob Pest Campaign 6(4):1–8

Ingram M, Nabhan GP, Buchmann SL (with assistance from the Board of Advisors of the Forgotten Pollinators) (1996a) Ten essential reasons to protect the birds and the bees: How an impending pollination crisis threatens plants and the food on your yable. Forgotten Pollinators Campaign, Arizona-Sonora Desert Museum, Tuscon

Irvine AK, Amstrong JE (1990) Beetle pollination in tropical forests of Australia. In: Bawa KS, Hadley M (eds) Reproductive ecology of tropical forest plants, vol 7, Man and the biosphere. UNESCO, Paris, pp 135–149

Iverson JB (1985) Lizards as seed dispersers? J Herpetol 19:292–293

Johnson LAS, Briggs BG (1963) Evolution in the Proteaceae. Aust J Bot 2(1):21–61

Johnson SD, Steiner KE (2000) Generalization versus specialization in plant pollination systems. Trends Ecol Evol 15:140–143

Jones DL (1972) Pollination of *Phrasophyllum alpinum* R. Br. Victorian Nat 89(9):260–263

Jones DL (1975) The pollination of *Microtis parviflora* R. Br. Ann Bot 39:585–589

Jones DL, Gray B (1974) The pollination *of Calochilus holtzei* F. Muell. Am Orchid Soc Bull 43(7):604–606

Jumelle H, Perrier de la Bâthie H (1910) Fragments biologiques de la flore de Madagascar (Dioscorea, Adansonia, Coffea etc.). IV. Les ignames du Nord-Ouest. Musée Colonial de Marseille 8:388–428

Kearns CA (2001) North American dipteran pollinators: assessing their value and conservation status. Conserv Ecol 5(1):5

Keighery GJ (1974) Mecoptera as vectors — a new record. W Aust Nat 13(1):17–19

Keighery GJ (1975a) Pollination of *Hibbertia hypericoides* (Dilleniaceae) and its evolutionary significance. J Nat Hist 9:681–684

Keighery GJ (1975b) Parallel *Evolution* of floral structures in *Darwinia* (Myrtaceae) and *Pimelea* (Thymeleaceae (sic)). J Nat Hist 13:46–50

Keighery GJ (1975c) Breeding systems of the Western Australian Flora I. *Triglochin* L. (Juncaginaceae). W Aust Nat 13(4):811

Kenneally KF (1970) Diplopeltis huegelii Endl. var. huegelii. Unpublished biological flora of Western Australia. Botany Department, University of Western Australia, Perth

Kevan PG (1972) Insect pollination of high arctic flowers. J Ecol 60:831–847

Kevan PG (2001) Pollination: a plinth, pedestal, and pillar for terrestrial productivity. The why, how, and where of pollination protection, conservation and promotion. In: Stubbs CS, Drummond FA (eds) Bees and crop pollination – crisis, crossroads, conservation. Thomas Say publications in entomology. Entomological Society of America, Lanham, pp 7–68

Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annu Rev Entomol 28:407–453

Kevan PG, Tikhmenev EA, Usui M (1993) Insects and plants in the pollination ecology of the boreal zone. Ecol Res 8:247–267

Key KHL (1974) Orthoptera. In: Supplement to the insects of Australia. Melbourne University Press, Carlton, pp 45–47, 146 pp

Kirk WDJ (1997) Feeding. In: Lewis T (ed) Thrips as crop pests. CAB International, Wallingford, pp 119–174

Knox RB, Kenrick J, Bernhardt P, Marginson R, Beresford G, Baker I, Baker HG (1985) Extrafloral nectaries as adaptations for bird pollination in acacia terminalis. Am J Bot 72(8):1185–1196

Knudsen JT, Tollsten L (1995) Floral scent in bat-pollinated plants: a case of convergent evolution. Bot J Linn Soc 119:45–57

Knuth P (1895–1905) Handbuch der Blutenbiologie IIII. Engelmann, Leipzig, 2973 pp

Kukalova-Peck J (1991) Fossil history and the evolution of hexapod structures. In: CSIRO (ed) The insects of Australia, 2nd edn. Melbourne University Press, Melbourne, pp 141–179

Labandeira CC (1998) How old is the flower and the fly? Science 280:57–59

Labendeira CC, Seposki JJ (1993) Insect diversity in the fossil record. Science 261:310–315

Lachance MA, Starmer WT, Rosa CA, Bowles JM, Barker JSF, Janzen DH (2001) Biogeography of the yeasts of ephemeral flowers and their insects. FEMS Yeast Res 1:1–8

Ladd PG, Connell SW (1993) Vicariant *Macrozamia* species in southern Australia? In: Vorster P (ed) Proceedings of the third international conference on cycad biology: conservation through cultivation, vol 3. Cycad Society of South Africa, Stellenbosch, pp 225–240

Larson BMH, Kevan PG, Inouye DW (2001) Flies and flowers: taxonomic diversity of anthophiles and pollinators. Can Entomol 133:439–465

Leppik EE (1956) The form and function of numerical patterns in flowers. Am J Bot 43(7):445–455

Leppik EE (1960) Early evolution of flower types. Lloydia 23:72–92

Levesque CM, Burger JF (1982) Insects (Diptera, Hymenoptera) associated with *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, U.S.A., and their possible role as pollinators. Arctic Alpine Res 14:117–124

Lloyd DG (1985) Progress in understanding the natural history of New Zealand plants. N Z J Bot 23:707–722

Mandujano S, Gallina S, Bullock SH (1994) Frugivory and dispersal of *Spondias purpurea* (Anacardiaceae) in a tropical deciduous forest in Mexico. Rev Biol Trop 42:107–114

Marullo R, Mound LA (1995) Su una classificazione sopra-generica della famiglia Aeolothripidae (Thysanoptera). In: Atti del XVII Congresso Nazionfale Italiano di Entomologia, Udine, pp 87–90

McGregor SE (1976) Pollinating agents and their comparative value. In: Insect pollination of cultivated crop plants, Agriculture handbook, USDA, vol. 496. USDA, Washington, DC, pp 19–23

Mees GF (1967) A note on the pollination of the Kangaroo paw *Anigozanthos manglesii*. W Aust Nat 10(2):149–151

Momose K, Yumoto T, Nagamitsu T, Kato M, Nagamasu H, Sakai S, Harrison RD et al (1998) Pollination biology in a lowland dipterocarp forest in Sarawak. Malaysia. I. Characteristics of the plantpollinator community in a lowland dipterocarp forest. Am J Bot 85:1477–1501

Monteith GB (1973) Entomological notes (Dung Beetles as pollinators of an Arum Lily). News Bull Entomol Soc Qld 97:13

Moog U, Fiala B, Federle W, Maschwitz U (2002) Thrips pollination of the dioecious ant plant Macaranga hullettii (Euphorbiaceae) in Southeast Asia. Am J Bot 89:50–59

Morcombe MK (1978a) Michael Morcombe's Australian marsupials and other native mammals. Summit Books, Paul Hamlyn, Sydney, 100 pp

Morcombe MK (1978b) Michael Morcombe's wild Australia. Summit Books, Paul Hamlyn, Sydney, 112 pp

Mound LA (1974) Thysanoptera. In: Supplement to the insects of Australia. Melbourne University Press, Carlton, pp 57–60, 146 p

Mound LA (1991) The first thrips species (Insecta, Thysanoptera) from cycad male cones and its family level significance. J Nat Hist 25:647–652

Mound LA, Terry I (2001) Pollination of the central Australian cycad, *Macrozamia macdonnellii,* by a new species of basal clade thrips (Thysanoptera). Int J Plant Sci 162:147–154

Mound LA, den Hollander E, den Hollander L (1998) Do thrips help pollinate *Macrozamia* cycads? Vic Entomol 28:86–88

Muller H (1883) The fertilisation of flowers. In:Translated and edited by Thompson DW. Macmillan, London, 669 pp

Nabhan GP, Buchmann SL (1997) Services provided by pollinators. In: Daily G (ed) Nature's services. Island Press, Washington DC, pp 133–150

Nogales M, Delgado JD, Medina FM (1998) Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). J Ecol 86:866–871

Norstog K, Stevenson DW, Niklas KJ (1986) The role of beetles in the pollination of *Zamia furfuracea* L. fil. (Zamiaceae). Biotropica 18:300–306

Nyhagen DF, Kragelund C, Olesen JM, Jones CG (2001) Insular interactions between lizards and flowers: flower visitation by an endemic Mauritian gecko. J Trop Ecol 17:755–761

Oberprieler RG (1995a) The weevils (Coleoptera: Curculionoidea) associated with cycads 1. Classification, relationships and biology. In: Vorster P (ed) Third international conference on cycad biology: conservation through cultivation, vol 3. Cycad Society of South Africa, Stellenbosch, pp 295–365

Oberprieler RG (1995b) The weevils (Coleoptera: Curculionoidea) associated with cycads. 2. Host specificity and implications for cycad taxonomy. In: Vorster P (ed) Third international conference on cycad biology: conservation through cultivation, vol 3. Cycad Society of South Africa, Stellenbosch, pp 335–365

Olesen JM, Valido A (2003) Lizards as pollinators and seed dispersers: an island phenomenon. Trends Ecol Evol 18:177–181

Olsson M, Shine R, Ba'k-Olsson E (2000) Lizards as a plant's 'hired help': letting pollinators in and seeds out. Biol J Linn Soc 71:191–202

Oppenheimer JR (1968) Behavior and ecology of the white-faced capuchins (*Cebus capucinus*) on Barro Colorado Island, Canal Zone. Ph.D. thesis, University of Illinois, Urbana

Pammel LH, King CM (1930) Honey plants of Iowa. Iowa Geol Surv Bull 7:892–894

Paton DC, Ford HA (1977) Pollination by birds of native plants in South Australia. Emu 77:73–85

Pellmyr O (1992) The phylogeny of a mutualism: evolution and coadaptation between Trollius and its seed-parasitic pollinators. Biol J Linn Soc 47:337–365

Pérez-Mellado V, Casas J (1997) Pollination by a lizard on a Mediterranean island. Copeia 1997:593–595

Perrier de la Bathie H (1951) Flore de Madagascar et de Comores. Firmin-Didot, Paris, pp 1–96, 136e famille

Pole M, Douglas B (1999) Plant macrofossils of the Upper Cretaceous Kaitangata Coalfield, New Zealand. Aust Syst Bot 12:331–364

Pont AC (1993) Observations on anthophilous Muscidae and other Diptera in Abisko National Park, Sweden. J Nat Hist 27:631–643

Porsch O (1934) Saugetiere als Blumenausbeuter und die Frage der Saugetierblume. Biol Gen 10:657–685

Porsch O (1935) Saugetiere als Blumenausbeuter und die Frage der Saugetierblume II. Biol Gen 11:171–188

Porsch O (1936) Saugetiere als Blumenausbeuter und die Frage der Saugetierblume HI. Biol Gen 12:1–21

Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, Wells KD (1998) Herpetology. Prentice Hall, New Jersey, xi + 577 pp

Prance GT (1980) A note on the probable pollination of Combretum [lanceolatum] by Cebus monkeys. Biotropica 12(3):239

Prescott-Allen R, Prescott-Allen C (1990) How many plants feed the world. Conserv Biol 4:365–374

Primack RB (1978) Variability in New Zealand montane and alpine pollinator assemblages. N Z J Ecol 1:66–73

Primack RB (1983) Insect pollination in the New Zealand mountain flora. N Z J Bot 21:317–333

Proctor M, Yeo P (1973) The pollination of flowers. Collins, London, 418 pp. Ann Miss Bot Gard 61:770–80

Proctor M, Yeo P, Lack D (1996) The natural history of pollination. Timber Press, Portland

Raju AJS (2005) Passerine bird pollination and seed dispersal in *Woodfordia floribunda* Salisb. (Lythraceae), a common low altitude woody shrub in the Eastern Ghats forests of India. Ornithol Sci 4(2):103–108

Ramirez WB (1974) Coevoution of Ficus and Agaonidae. Ann Mo Bot Gard 61:770–780

Raven PH (1972) Why are bird-visited flowers predom-inantly red? Evolution 26:674

Raven PH (1977) *Erythrina symposium* II. *Erythrina* (Fabaceae: Faboideae): introduction to symposium II. Lloydia 40:401–406

Reed EM (1970) Thysanoptera. In: The insects of Australia. Melbourne University Press, Melbourne, pp 458–464, 1029 pp

Riek EF (1963) Insects of Australia. Jacaranda Pocket Guides, Jacaranda Press, Brisbane, 129 pp

Riek EF (1970) Hymenoptera. In: The insects of Australia. Melbourne University Press, Melbourne, pp 867–959, 1029 pp

Robinson AH (1947) Spinebill honeyeaters and *Dryandra nivea*. W Aust Nat 1:67

Roubik DW (ed) (1995) Pollination of cultivated plants in the tropics. Food and Agricultural Organization of the United Nations, Rome, Bulletin 118

Rourke J, Wiens D (1977) Convergent floral evolution in South African and Australian Proteaceae on pollination by nonflying mammals. Ann Mo Bot Gard 64:1–17

Sáez E, Traveset A (1995) Fruit and nectar feeding by *Podarcis lilfordi* (Lacertidae) on Cabrera Archipielago (Balearic Islands). Herpetol Rev 26:121–123

Sanderson MJ, Doyle JA (2001) Sources of error and confidence intervals in estimating the age of angiosperms from rbcL and 18S rDNA data. Am J Bot 88(8):1499–1516

Sarma K, Tandon R, Shivanna KR, Mohan Ram HY (2007) Snail-pollination in *Volvulopsis nummularium*. Curr Sci 93(6):827–831

Schneider F (1969) Bionomics and physiology of aphidophagous Syrphidae. Annu Rev Entomol 14:103

Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108:15–29

Sun G, Dilcher DL, Zheng S, Zhou Z (1998) In search of the first flower: a Jurassic angiosperm, *archaefructus*, from Northeast China. Science 282(5394):1692–1695

Symmington B (1963) *Calectasia cyanea* R. Br. unpublished biological flora of Western Australia, Botany Department, University of Western Australia

Terry LI (2001) Thrips and weevils as dual, specialist pollinators of the Australian cycad *Macrozamia communis* (Zamiaceae). Int J Plant Sci 162:1293–1305

Thien LB, Azuma S, Kawano S (2000) New perspectives on the pollination biology of basal angiosperms. Int J Plant Sci 161:225–235

Thomas BA, Spicer RA (1987) The evolution and palaeobiology of land plants. Croom Helm, London

Traveset A (1990) *Ctenosaura similis* Gray (Iguanidae) as a seed dispersel in a Central American deciduous forest. Am Midl Nat 123:402–404

Traveset A (1995) Seed dispersal of *Cneorum tricoccon* L. (Cneoraceae) by lizards and mammals in the Balearic islands. Acta Oecol 16:171–178

Traveset A, Sáez E (1997) Pollination of *Euphorbia dendroides* by lizards and insects: spatio-temporal variation in patterns of flower visitation. Oecologia 111:241–248

Valido A, Nogales M (1994) Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. Oikos 70:403–411

van der Pijl L (1957) The dispersal of plants by bats (Cheiropterochory). Acta Bot Ned 6:291–315

Van Der Pijl L, Dodson C (1966) Orchid flowers: their pollination and evolution. University of Miami Press, Coral Gables, 214 p

Van Marken LWD (1993) Optimal foraging of an herbivorous lizard, the green iguana in a seasonal environment. Oecologia 95:246–256

Varela OR, Bucher EH (2002) The lizard *Teius teyou* (Squamata: Teiidae) as a legitimate seed disperser in the dry Chaco Forest of Argentina. Stud Neotrop Fauna Environ 37:115–117

Vasconcellos-Neto J, Alt De Souza M, Guimarāes M, De Faria DM (2000) Effects of color, shape and location on detection of cactus fruits by a lizard. J Herpetol 34:306–309

Vogel S (1954) Blütenbiologische Typen als Elemente der Sippengliederung: dargestellt anhand de Flora Süd Afrikas. Botanische Studien 1:1–338

Wallace MMH, Mackerras IM (1970) The entognathous hexapods. In: The insects of Australia. Melbourne University Press, Melbourne, pp 205–216, 1029

Webber AC, Gottsberger G (1995) Floral biology and pollination of *Bocageopsis multiflora* and *Oxandra euneura* in Central Amazonia, with remarks on the *Evolution* of stamens in Annonaceae. Feddes Repertorium 106:515–524

Wheelwright NJT, Orians GH (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. Am Nat 119:402–413

Whitaker AH (1987) The roles of lizards in New Zealand plant reproductive strategies. N Z Bot 25:315–328

Whiting MJ, Greeff JM (1997) Facultative frugivory in the Cape flat lizard, *Platysaurus capensis* (Sauria: Cordylidae). Copeia 1997:811–818

Wiens D, Rourke JP (1978) Rodent pollination in southern African *Protea* spp. Nature 276(5683):71–73

Williams G, Adams P, Mound LA (2000) Thrips (Thysanoptera) pollination in Australian subtropical rainforests, with particular reference to pollination of Veiny Wilkiea, *Wilkiea huegeliana* (Tul.) A. DC. (Monimiaceae). J Nat Hist 35:1–21

Willis JC, Burkill IH (1895) Flowers and insects in Great Britain. I. Ann Bot 9:227–273

Willson MF, Sabag C, Figueroa JA, Armesto JJ, Caviedes M (1996) Seed dispersal by lizards in Chilean rainforest. Revista Chilena de Historia Natural 69:339–342

Chapter 10
Safety of Pollinators

Abstract The use of pesticides for pest control on the one hand and the role of honeybees (Apis spp.) for crop pollination on the other have become essential components of modern agriculture. Without either of the two, global food production would be seriously impaired. Unfortunately, these two practices are not always compatible, as honeybees are susceptible to many of commonly used pesticides used for the control of insect pests. The major constraint confronting pollinator-plant interaction is the indiscriminate and excessive use of pesticides for controlling insect-pests. The loss of honeybees directly effect beekeeping through loss of honey production and indirectly the crop production due to inadequate pollination. Reduction of population of these beneficial insects due to insecticides, therefore, incurs significant environmental, ecological and economic costs. The safe use of pesticides and prevention of bee death by pesticide poisoning is discussed in this chapter.

10.1 Introduction

Honey bees are required for the pollination of many vegetable and fruit crops. Without adequate populations of bees, the production of these and other crops would be impossible. In a world where people expect and demand more food and fiber each year, all branches of agriculture must continuously adapt and improve to meet this challenge. Farmers now find it essential to annually increase efficiency and production to remain in business and to show a profit. Practically every agricultural crop has insect pests that sometimes require treatment. Unfortunately; beneficial insects such as honeybees are also susceptible to pesticides. The use of pesticides for pest control on the one hand and the role of honeybees (*Apis* spp.) for crop pollination on the other has become essential components of modern agriculture. Without either of the two, global food production would be seriously impaired. Unfortunately, these two practices are not always compatible, as honeybees are susceptible to many of

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commonly used pesticides (Johansen 1977; MacKenzie and Winston 1989; Russell et al. 1998; Cuningham et al. 2002; Sundararaju 2003), used for the control of insect pests (Poehling 1989; Stark et al. 1995). The major constraint confronting pollinator-plant interaction is the indiscriminate and excessive use of pesticides for controlling insect-pests (Bisht et al. 1983; Rana and Goyal 1991; Zhong et al. 2004). The loss of honeybees directly effect beekeeping through loss of honey production and indirectly the crop production due to inadequate pollination. Reduction of population of these beneficial insects due to insecticides, therefore, incurs significant environmental, ecological and economic costs (Bai and Reddy 1977; Pimental et al. 1980; Crane and Walker 1983; Prakash and Kumaraswami 1984).

In India, 50 million hectare of area is under entomophilous crops, cross pollinated by different abiotic and biotic agents. About 90% pollination is carried out by insects, 85% of which comprise the bees (Singh et al. 1989). Honeybees constitute a major group of insect pollinators and their pollinating efficacy is manifested not only through increase in yield but also by the improvement of the crop quality through heterosis breeding (Melnichenko 1976). The bees earn about rupees 10 million to the national exchequer in terms of honey production and beeswax and it is expected that an additional crop yield worth rupees 90 million could be obtained due to pollination of crops (Sorthia and Chari 1985). Levin (1984) estimated that the value of crops in the United States of America that benefited directly from the honeybee pollination approaches 20 billion US Dollars annually. The annual cost of crop loss due to insecticides poisoning of pollinating honeybees has been estimated at 135 million US dollar in the United States of America (Pimental et al. 1980). Not withstanding with the absence of such estimates, the indispensability for a harmonious compromise between pest management and honeybee pollination of crops in India cannot be gainsaid.

Tropical and subtropical climate of India in particular presents suitable conditions for the outbreak and appearance of many pest problems. The pest problems have been further aggravated by the advancement in agricultural technology. Irrigated crops, intensive agriculture, introduction of crops and crop varieties and disturbing the indigenous and primitive cropping patterns have contributed in increasing the pest problem of crops. Reduction in uncultivated land, corners and bunds destroy nesting and hibernating places of wild pollinators and succession of nectar and pollen yielding flowers round the year is destroyed. Weedicides are used to control the weeds and hence lead to starvation of pollinating insects. The advanced agricultural technology has helped to destroy the agriculture cycle through indirect effect. There is also a prominent negative direct factor, i.e., the insect pollinators are killed by pesticidal usage in crop protection. There is increasing use of pesticides for the control of rodents, mites, insects, nematodes and fungal and bacterial diseases of crop plants. The loss by bee kill is direct, i.e., loss of honey production and indirect inadequate pollination of crops resulting in reduced productivity.

Integrated pest management in India has not yet shown desired results and blanket pesticidal applications are given. Most farmers apply large quantities of pesticides at regular intervals and in most cases the pesticides are non-selective coupled with untimely application. Unfortunately honeybees are susceptible to many pesticides used in pest control programmes. This problem is recently overshadowing all other problems in apiculture. Farmers in India have small holdings and hand sprayers/dusters are commonly used for treating small area each day. This results into a continuous threat of chemical poisoning to bees. Moreover, there is no coordination between the beekeepers and the farmers by any Government decree and therefore, measures to save bees cannot be taken.

Large number of killed bees is found in front of the hives or in the fields by insecticidal poisoning. It is not possible to quantify the loss in terms of food production or to assess the financial value of the bees killed. Even more important is the loss in future crop yields because a beekeeper whose bees are killed gives up beekeeping and others too are discouraged to take up beekeeping. Therefore, a balance sheet between the gains in crop yields by control of pests and losses due to decreased pollinator activity and honey production by bee kill should be worked out. While controlling pests the scientists and farmers are looking on to one aspect of the economic considerations in insecticidal applications. Our primary aim should be to assess how crop pests can be kept under control without killing insect pollinators and to ensure optimum pollination by these insects. Widespread destruction of beneficial insects (including pollinators) often occurs as a consequence of irresponsible and improper use of pesticides. It should be accepted that some loss is inevitable in certain circumstances and that a realistic aim should be an acceptably low level of loss rather than complete protection of bees.

Some insecticides have been screened in laboratory in India for their toxicity to bees. First study in this field was carried out by Cherian and Mahadevan with DDT and Gammexane against *Apis cerana indica*. Hameed allowed the worker bees of *Apis mellifera* to forage on cut flowers of mustard to which systemic and contact insecticides had been sprayed. On the basis of safety index Formothion, Vamidothion, Dimethoate and Phosalone were considered to be relatively safer to bees. Contact toxicity to Apis cerana of insecticide applied as sprays was compared with Menazon by Kapil. Taking the LC50 for Menazon as 100, the comparative values for Endosulphan, Eormothion, Methyl demeton, Endrin, Dieldrin, Malathion, Parathion, Phosphamidon, Lindane, Phorate and Mevinphos were 1.17, 1.18, 14.00, 15.70, 17.79, 22.25. 26.01, 28.45, 36.99, 57.96 and 64.24 respectively. Singh tested 15 insecticides and reported that Menazon and Endosulphan were least toxic and were considered nontoxic to *Apis cerana* at their recommended doses. According to Thakur et al. (1981), Fenitrothion and Fenthion were highly toxic as compared to Endosulphan and Trichlorfon and Hinosan were moderately toxic as determined by residue film method. Comparative toxicity of organophosphates, chlorinated hydrocarbons and carbamates was worked out by Bai Attri also assessed the contact and oral toxicities of some insecticides. Toxicity of several organophosphates to *Apis cerana* was determined in the laboratory using topical application method. Determination of the kinetic parameters of the reactions by the authors showed that differences in anticholinesterase activity were due mainly to differences in affinity rather than to different chemical structure of the compounds.

Cholinesterase inhibition by insecticides in Indian honeybee was studied by Dale Bai reported that signs of poisoning in *Apis cerana indica* were first observable when acetylcholinesterase inhibition exceeded 35% and death occurred at 96% or more inhibition.

Reddy reported the inhibition of magnesium activated adenosine triphosphate as the criterion to determine the degree of organochlorine insecticide poisoning to *Apis cerana indica*. Digestive amylase and protease of *Apis cerana indica* were inhibited to the same level by the insecticide poisoning from different groups of insecticides. Studies on the level of ions of amino acids in the haemolymph of worker bees of *Apis cerana indica* treated topically showed pronounced stimulatory effect with organophosphates, a relatively strong inhibitory action with chlorinated hydrocarbons and an intermediary effect with carbamate pesticides.

Bee poisoning or killing of bees from pesticides continuous to be a serious problem for beekeepers. Most bee kill occurs when pesticides are applied or allowed to drift on to blooming crops or weeds (Mayer 2003). Most (99%) bee kills results from bees picking up the pesticides when foraging. The hazards of insecticidal application on flowering crops include- direct mortality, fumigative effects, repellent effect and toxicity of residues present on various floral parts and in nectar to the insect visitor. A highly toxic insecticide generally reduces the field force of a colony within a short period of time. Colonies may be reduced by one third to half in strength within 24–48 h (Eckert and Shaw 1960), thus adversely affecting both the production and marketing segments of the honey and beekeeping industry. Generally, fumigative action of insecticides used under field conditions is of much shorter durations then the effect of contact and stomach poison. A prolong repellent effect will deprive the flowers of pollination benefits of insect visits, while a short repellency will deter the insect pollinators from visiting the treated bloom for a brief period and thereafter, allow them to resume their foraging activity (with minimum residual hazards) without compromising with the yield potential of the crop.

Poisoning of insecticides to honeybees is generally more pronounced because of their long hours of working on the crop flowers for pollen and nectar collection, continuous working *Nature* and long flights with pollen loads. Bee poisoning is more chronic in areas which lack of sufficient wild pollens and nectar plants to sustain the number of colonies required for crop pollination. Most bees are pastured in agricultural areas where they are subjected to killing from pesticides (Mayer and Johansen 1988). The beekeeper has little or no control of when and what pesticides are applied in the areas of his bee forage (Mayer 2003).

Conservation of honeybees for crop pollination is vital to agricultural production (Bisht et al. 1983; Sorthia and Chari 1985; Smirle 1990; Gupta 1994; Dhuley et al. 1996; Russell et al. 1998; Kremen et al. 2002).

Many colonies that are not killed outright may be weakened to such an extent that they are no longer effective as pollinators or honey producers, nor they can be divided to increase the number of colonies. This type of economic loss far exceeds the loss from colonies being killed out right by pesticides. Though the monetary loss to the beekeeping is large, yet the value of the seed and fruit lost through the lack of pollination is estimated to be 50–100 times greater (Atkins 1975).

Pesticides application may also changes the physiology of nectar and pollen producing plants, change in attraction of bees to flowers, affect pollen viability, reduced pollen germination on contaminated stigma (Eaton 1963; Church and Williams 1978; Fell et al. 1983; Kuriachen et al. 1992; Sharma 1993). All these effects of pesticides usages are serious to pollination potential and honey production.

The immature stages of honeybees are vulnerable to insecticidal poisoning that result in hidden damage to honeybee colony (Davis and Shuel 1985; Naumann and Isman 1996). Loss of brood and new bees as result of exposure of insecticides may be more deleterious than the loss of foragers (Abrol and Kumar 2000a, b, 2001; Abrol and Sharma 2007) because the latter could be replaced more quickly and provide less potential value to the colony than the emerging workers

The problem of bee poisoning is an old as about 1870s when Thompson (1881) detected accidentally killed bees by application of Paris green to pear trees in bloom and some sort of bee malady was found around beehives at that time. The intermediary period between 1870 and 1888 contributed further to the knowledge of the toxicity of Paris green and London purple. Brose (1888) demonstrated that these insecticides in sugar syrup repelled the bees to some extent but those fed on syrup were killed in 1–4 h. Troop (1918); Hoskins and Harrison (1934) reported some inorganic compounds like arsenics highly toxic to honeybees. Likewise, Kingsmill (1917) reported accidental killing of bees to a great extend from Paris green and molasses bait mixture. Bourne (1927) reported that blossom treated with a mixture of lead arsenate, lime sulphur and nicotine sulphates were unattractive to bees.

Many major agricultural changes took place in the 1950s, shortly after World War II, when tractors replaced horses, chemical fertilizers replaced organic manure, aerial application of pesticides became common place, and farmers became increasingly conscious of business costs. At the same time, many farmers were encouraged to devote large acreages to the cultivation of a single crop, which necessitated the utilization of large quantities of synthetic fertilizers and pesticides to nourish and protect that crop. Consumers also came to expect all market fruits and vegetables to be completely free from insects and insect damage.

Thus, many growers found it advantageous to apply more and more pesticides each year. Unfortunately, some aspects of this agricultural modernization were not beneficial for beekeepers, whose needs were either frequently forgotten or ignored. Consequently, many honey bees were killed. To compensate, many commercial beekeepers had to keep larger numbers of honey bee colonies in a variety of locations to make up for losses from pesticides and to meet rising operating expenses. This interaction between the needs of crop farmers and the needs of beekeepers, coupled with frequent widespread application of the "newer" insecticides, such as parathion, proved devastating to thousands of colonies.

10.2 Factors Influencing Bee Poisoning

By nature, honey bees from a colony visit flowers over an area of several square miles. The intensity of visitation in any one part of the area is determined by the relative attractiveness of the flowers. The extent of damage to the colony by a pesticide application is influenced not only by the relative toxicity of the material, the number and methods of application, the time of day, and the weather conditions, but also by the number of bees from the colony visiting the flowers in the treated area, the type of food (nectar or pollen) they are collecting, the type of flowers the food is collected from, the season of the year the damage occurs, and even the influence of forage available to the bees for weeks before and after the application. Wild bees are also damaged by pesticides. Poisoning may result from contaminated food as well as from florets, leaves, soil, or other material used by the bees in nesting. The toxicity of a specific insecticide to honey bees and wild bees is not always the same, and even among wild bees some materials are more toxic to one species than to another. Different factors influencing bee poisoning are as given below:

10.2.1 Pesticide Formulation

Dusts are highly hazardous to bees because of their tendency to drift to considerable distance and particles remain adhered to plant surface for long. So is the case with wettable powders which also remain unabsorbed on the plant surface for longer periods than emulsifiable concentrates. The emulsifiable concentrates are relatively safer (Kapil 1970). The granular insecticides are safest. However, granular insecticides with systemic action may contaminate nectar and may result in losses to bees, foraging upon them. The insecticides with fumigant effect may also be hazardous to bees. Microencapsulated granules applied on flowers are sometimes collected by bees and stored in the hives, where they may beaten by adult bees or fed to brood causing high mortality besides causing long term contamination of hive parts and hive products.

10.2.2 Selectivity of Pesticides

There are some insecticides which have little effect on honeybees when applied as sprays e.g. endosulfan, phosalone, pirmicarb, fluvalinate, or trichlorfon. High toxicity of carbamates to honeybees has been considered due to their very low level of phenolase enzymes. It has also been claimed that greater acetylcholinesterase concentration in young enables them to tolerate Malathion. Similarly, high tolerance of trichlorfon by honeybees has been correlated with relatively high pH of the body.

10.2.3 Period of Application

Insecticides when applied to crops in flower may be hazardous to bees or when pesticides are applied to a non – flowering crop but having large number of attractive flowering weeds or hedges in the fields or in the adjoining fields. The bees are also affected if they pass through a field treated or sprayed with pesticides. In mango orchards bees attracted to honey dew secreted by mango hoppers are killed in large numbers when insecticides have been applied to the trees.

10.2.4 Time of Application

Little foraging occurs early in the morning or late in the evening. Application of pesticides during late evening or early morning provides relative safety. This avoid direct deposition of pesticides on the bee body and even residues on the treated surfaces are rendered less harmful, especially in case of short residual pesticides. Species variation has also been noticed. Whereas *Apis cerana* became active at 7–10°C ambient temperature, *Apis mellifera* never became active unless the ambient temperature reached 13–16°C or above.

10.2.5 Attractiveness of Crop

Some crops notably rapeseed and mustard are extremely attractive to bees which will forage from colonies upto 3 km away or more. These crops remain attractive until the very end of flowering. It remains attractive even in cool and dull weather when they not visit other crops.

10.2.6 Weather

Warm and sunny weather is conducive for foraging by bees. When there is a prolonged dull weather the foraging activity is reduced considerably and insecticides can be applied on the crop.

10.2.7 Temperature

Temperature is probably the most significant factor causing differences in the toxicity of pesticides. Immediate effects may be much greater at higher temperatures whereas, residual effects are likely to be less because the toxic materials breaks down more quickly.

10.2.8 Method of Application

Aerial application of pesticides has been regarded as more hazardous than ground application. Bees get less time to escape the drift of insecticides .systemic insecticides applied on the blooming crop may cause hazards to the bees. Fine sprays are safer than coarse sprays.

10.2.9 Colony Strength

Populous colonies always suffer greater losses than small colonies, because more foragers are exposed to insecticides.

10.2.10 Age and Body Size of Honeybees

Newly emerged bees are more susceptible to insecticides than older bees. smaller bees likewise are more susceptible to insecticides because their body surface area is larger in relation to their body weight.

10.2.11 Distance of Colonies

Honeybee mortality is inversely proportional to the distance of colonies from treated fields. Farther is the crop from colony, less likely is to attract large number of foragers.

10.3 How Bees Are Exposed to Pesticidal Hazards

Many of the crop plants need cross-pollination. At the same time they are infested by pests even during flowering causing considerable losses which warrant the application of control measures. The pesticidal applications pose serious danger and eliminates large population of insect pollinators as well. Some of the crops benefiting from bees as well heavily attacked by pests include:

10.3.1 Cotton

It is the most dangerous crop for bees. As many as 15–20 insecticidal applications at shorter and regular intervals are recommended for the control of various cotton pests. The flowering continues for about 2 months and during this period insecticides are regularly applied for the control of many pests like bollworms, aphids, bugs, etc. Foraging bees are killed by these sprays. New generation of bees develop in 3 weeks. Insecticidal applications at shorter intervals than this kill more adult bees than can be replaced and ultimately the colonies die. But co-ordinated application of insecticides can minimize bee kill. (1) Flowering in cotton continues for about 2 months but flowers that set fruit appear within 3–4 weeks. Therefore, use of insecticides during this period should be reduced so that bees can be moved to the crop. (2) Nectar in flowers and extra floral nectaries is exhausted by mid day and very few bees are foraging in the afternoon when insecticides can be applied with reduced hazards to bees. (3) Air spraying has picked up for cotton. In such a situation the colonies should be located away from the flight path of the plane.

10.3.2 Brassica and Vegetable Seed-Crops

These are attacked by aphids, caterpillars and bugs during flowering and pod formation stage. These crops include oilseeds Brassica, seed crops of cauliflower, cabbage, radish, turnip, carrot, fennel and coriander. In these crops too the flowering is greatly extended, lasting for about 1–1½ months. These crops need insecticidal applications during flowering periods. But all these crops are also enthusiastically foraged by bees which are very useful pollinators of these crops. There is extensive pesticidal poisoning to bees on these crops. There are no specific recommendations to safeguard bees and only general guidelines to reduce bee kill can be followed, though Singh (1969) sprayed Endosulphan on mustard to control aphids at 08:00, 09:00, 16:30 or 17:30 h and found that Apis spp. foraged between 10:30 and 15:30 h without any effect on foraging intensity and no bees were killed.

10.3.3 Sunflower

Its cultivation is gaining importance in India. Bees contribute much in increased crop production by pollination services but bee losses have been reported by insecticidal sprays for the control of aphids and caterpillars. In India Endosulphan was found to be less toxic to honeybees than Fenthion, Carbaryl or Parathion and seed set and yield were not affected since bee activity was not reduced in Endosulphan sprayed plots (Ramakrishna et al. 1974; Bhattacharya et al. 1982). Bees mostly forage in the forenoon and there is limited activity till early afternoon. Therefore, evening or late in the afternoon is appropriate time for chemical control operations.

10.3.4 Sesame

It is automatic self-pollinated but natural cross-pollination also occurs. Honeybees are very active on the flowers of sesame. The crop at flowering stage suffers from the attack of aphids, brown leafhopper, sucking bugs, whiteflies and caterpillars. Chemical application at blossoming would cause hazards to bees also.

10.3.5 Seed Crops

Like lucerne and clovers these are rich bee forages. Under semi-arid tropics the legume flowers usually close in the afternoon and it allows time for safe application of pesticides afterwards against caterpillar pests.

10.3.6 Pulses

Like soybean, cajanus and others are self-pollinated crops but yield increases by bee pollination have been observed. Considerable mortality of honeybees from insecticide poisoning is reported in some countries but lack of knowledge in India is due to non-monitoring of hazards.

10.3.7 Cucurbits

These require the control of fruit flies, pumpkin beetle and aphids when in flowering. Cover sprays of insecticides are given against these pests. Honeybees visit the flowers of melon and other cucurbits. Steps to minimize bee kill from these sprays are required.

10.3.8 Tobacco

In this case self-pollination is normal but honeybees and other insects visit the flowers for nectar, affecting some cross pollination. Aphids, whiteflies, thrips and caterpillars are the pests which may warrant insecticidal application during flowering which consequently would lead to bee hazards. Flowering period in coffee is short and insecticidal applications can be avoided during coffee flowering. Coffee may be attacked by bugs, leaf miner and thrips during flowering. In case of outbreak during flowering, the crop should be treated when bees are not active and less persistent insecticides be used.

10.3.9 Pome and Stone Fruits

Apple, peach, plum, apricot and almond are attacked by caterpillars at blooming time. Insecticidal use has been suggested by economic entomologists against blossom thrips, though economic losses by thrips have not been ascertained. The recommendations are made in ignorance of insecticidal bee hazards. Therefore, caution is important so that the huge benefits from bee pollination are not reduced.

10.3.10 Other Fruit Crops

Insecticides can be applied for pest control at flowering-time in citrus, litchi, olive, grapes, coconut and cocoa. Care should be taken because they are also visited by bees for floral rewards.

10.4 Phtotoxicity to Plants

The effect of an insecticide application may not be confined to damage to the pollinators of a distant crop or elimination of pollinators for the target crop. Another previously overlooked factor associated with the pesticide may be that it can detract from the plants' productiveness. Sedivy (1970) reported that only 10.5% of pollen grains germinated after they were dusted with Melipax (Melipax is a toxaphenelike chlorinated camphene) as compared to 62.1% in the control pollen. When the pollen grains were treated with 0.3% Fribal emulsion, another apparently toxaphenelike compound, only 28.2% germinated as compared to 81.5% of the control pollen. None of the grains treated with 0.7% Fribal emulsion germinated as compared to 79.0% of the control. Gentile et al. (1971) reported that the insecticide naled, at only 100 ppm, completely inhibited germination of both tomato and petunia pollen. They also reported that azinphosmethyl, DDT, dichlorvos, dicofol, endosulfan caused reduction in pollen germination and/or pollen tube elongation. Carbaryl and methomyl had little or no deleterious effect on pollen, and xylene was noninjurious. The separation of the toxic or repelling effect of the presence of the insecticide on the plant from the possible less attractiveness of affected pollen is difficult, but the idea merits further examination, both from the effect of pesticides on the plants and on the pollinating insects.

10.5 Intensity of Damage to Bees by Pesticides

Numerous surveys have been made to determine the extent of the losses of bees from pesticides. Levin (1970) stated that some 500,000 colonies were killed or damaged in the United States in 1967, of which 70,000 were in Arizona and 76,000 in California. Swift (1969) stated that losses in California in 1968 were even greater – 83,000 colonies. Wearne et al. (1970) and Barnes (1972) concluded that the major problem confronting the beekeeping industry was bee losses due to pesticides – with which there is little disagreement by the beekeeping industry. All indications point to an annual loss by the industry in the neighborhood of 10% caused by pesticides alone. Few industries can tolerate such losses and survive. The effect of these losses on the adequacy of crop pollination is unknown.

10.5.1 Indirect Effects of Pesticides on Bees

Pesticide application besides directly killing the bees, indirectly produced several indirect effects.

Reduced foraging due repellency or reduced foraging due to killing of foragers due to poisoning.

Sub lethal doses can also influence other behaviours such as orientation, dance rhythm, dance velocity, walking speed, wing beat frequency.

Physiological injury resulting into reduced longevity.

Pesticide generally accumulate in combs as a result of absorption from stored pollen, honey/nectar and may cause chronic paralysis under stress conditions.

Reduced egg laying and brood rearing due to small doses of pesticides.

Amorphogenic effects on developing brood and delayed and abnormal development.

Pesticide application changes physiology of plants affecting nectar, pollen production, pollen viability, consequently bee behaviour, nectar pollen collection honey storage and pollination.

A schematic model exhibiting direct and indirect of pesticides on bee behaviour, ecosystem and crop productivity is given in Fig. 10.1.

10.6 Pesticides Involved – Basic Types and Classes

The following information is presented to help the beekeeper better understand pesticides and to successfully meet the challenge of pesticides killing honey bees.

10.6.1 Classes of Pesticides

The need of human beings to effectively control their environment is most evident in their agricultural pursuits. Modern farming covers large tracts of land under uniform planting, and this has made pest control mandatory. The *Evolution* of pest control agents originated with natural products such as arsenicals, petroleum oils, and toxins derived from plants (nicotine and rotenone, for example). The advent of DDT, which was synthesized in a laboratory, heralded an era in which a mature chemical industry would screen synthetic chemicals for pesticidal activity. This effort spawned an impressive array of insect control agents. The selection of control chemicals is large. However, these materials can be grouped conveniently according to general chemical properties and modes of action.

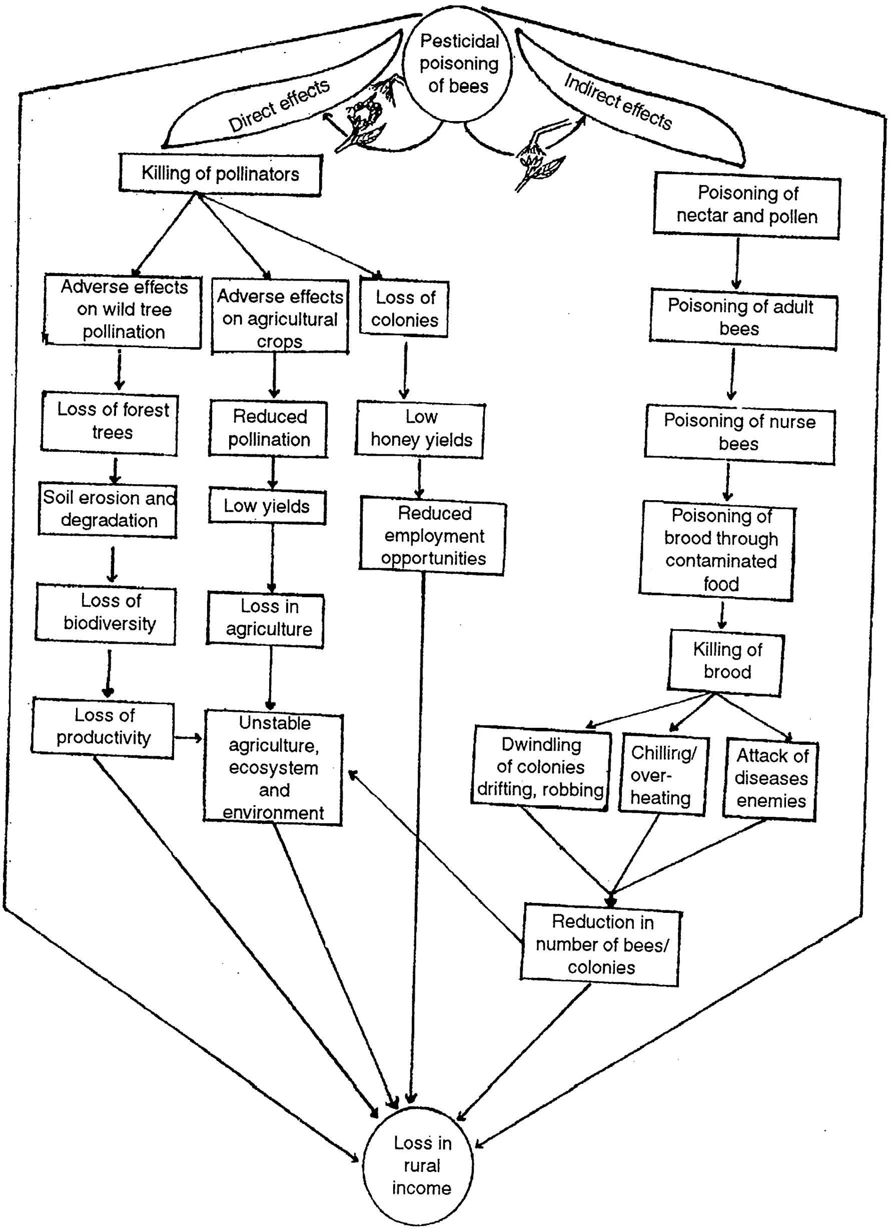

Fig. 10.1 A schematic model exhibiting impact of pesticides on adult honeybees as well as brood

10.6.1.1 Insecticides

Insecticides affect bees in one or more ways as stomach poisons, as contact materials, and as fumigants. Arsenicals are typical stomach poisons, pyrethrum is a typical contact insecticide, and hydrogen cyanide, paradichlorobenzene, and carbon disulfide are examples of fumigants.

Botanicals

Only a small amount of our insecticides are derived from plants. These sources are cube, derris, nicotine, pyrethrins, ryania, sabadilla, and tephrosia. The bulk of this material is used in households and gardens, and, because of its inaccessibility to bees or the relatively minute amount used, it presents no hazards to pollinating insects. Sabadilla dust is sometimes used on citrus where it can create a bee poisoning problem.

Occasionally, bees are poisoned by feeding on nectar or pollen of certain plants, for example, California buckeye (*Aesculus californica* (Spach) Nutt.), locoweed (*Astragalus* spp.), or mountain laurel (*Kalmia latifolia* L.). Reaction of the bees to these plant poisons can usually be differentiated from those caused by most pesticides.

Inorganics

These pesticides include arsenicals, fluorides, mercury compounds, and sulfur. The method and limited use of the mercury compounds precludes their presenting a hazard to bees. Elemental sulfur alone or when used with other insecticides in the field, presents only a slight repelling action, although fumes from burning sulfur are highly toxic to insects. Fluorides are rarely used on a large scale and present no problem. In certain sections of Europe, fluoride compounds from smelters frequently cause bee damage. Whenever arsenicals are used they pose a serious threat to bees.

Organics

The chlorinated hydrocarbons, organophosphates, and carbamates vary in their toxicity to bees from relatively nonhazardous to highly hazardous, depending upon the individual material or combination of materials.

Chlorinated Hydrocarbons

These include such important insecticides as BHC, toxaphene, and chlordane. The chemicals in this group are slowly reactive chemically, thus persistent in the environment. Biological degradation tends to be slow; hence, storage in fatty and muscle tissue causes these materials to become concentrated and enter our food chain. The mode of action of chlorinated hydrocarbons is still a subject of active research. They are classified as neuroactive agents which block the transmission of nerve impulses. Specifically, for example, DDT prevents the normal sodium-potassium exchange in the sheath of the nerve fiber-this exchange being the means by which a message is transmitted along the nerve. Because chemicals such as DDT are not very chemically reactive, it is felt that the mechanism of reaction with the sheath is not chemical, but rather that the size and shape of a DDT molecule may fortuitously permit it to fit into the proteins of the sheath. Such conceptualizations of the toxicological processes have promoted the search for new chemicals with better toxicological and environmental properties.

Organophosphorus Insecticides

These, today, account for about 30% of the registered synthetic insecticides/acaricides in the United States. They possess the common characteristic of inhibiting the enzyme cholinesterase, which mediates the transmission of nerve signals. Hence, organophosphates also are neuroactive agents. As their name implies, these materials contain phosphorus, and as a group they include parathion, Systox, DDVP, and malathion. They are quite reactive chemically and are not regarded as persistent in our environment, unless they are microencapsulated.

Carbamate Insecticides

These also are inhibitors of cholinesterase and feature a nitrogen-containing unit known to chemists as a carbamate function. Members of this class of insecticide include carbaryl (Sevin), baygon, Furadan, landrin, and zectran. For the most part, these materials are easily biodegraded and do not constitute the residual hazard of the chlorinated hydrocarbon class of insecticides. Interestingly, cholinesterase inhibition tends to be reversible for mammals and insects alike. A sublethal dose can bring on the usual symptoms of nerve poisoning (tremors, loss of muscular control, incontinence, vomiting), but the poisoned animal will return to normalcy in a very short time.

Pathogens: Bacteria, Protozoans, and Viruses

None of these that are currently recommended or that have been tested for biological control pose a hazard to bees (Cantwell et al. 1972).

Defoliants, Desiccants, and Herbicides

Most tests have shown this class of materials to be nonhazardous to bees, except for their removal of the food source from the plant; however, Morton et al. (1972)

reported that paraquat, MAA, MSMA, DSMA, hexaflurate, and cacodylic acid were extremely toxic when fed to newly emerged worker honey bees at 100 and 1,000 ppm concentrations. Although newly emerged bees do not forage away from the hive, they consume food that others bring in. MSMA, paraquat, and cacodylic acid were also highly toxic when sprayed onto older bees in small cages (Moffett et al. 1972).

Diluents, Synergists, and Activators

There is little information on the influence of these agents on the toxicity of the primary pesticides on honey bees. Possibly different interpretations of the effects of certain pesticides may have been associated with the materials with which they were applied.

Fungicides

As used, the copper compounds, mercury compounds, pentachlorophenol, sulfur, and zineb have caused no trouble to bees. A wide variety of other synthetic chemicals may be applied to crops on which bees may be foraging. Herbicides and fungicides have bases for their activity which render them relatively much less toxic to honey bees. Still such materials are present in the biosphere of the honey bee, and little information is currently available dealing with the effects of these chemicals in combination with insecticides – a situation which occurs often under normal field conditions. Moreover, such materials as herbicides and nonconventional insecticides (such as insect sex attractants and insect growth regulators) to which bees are being increasingly exposed likely will be transferred to honey and stored pollen with, as yet, incompletely documented results.

10.7 Sex Lures, Attractants, and Other Hormones

These usually cause no problems to bees, and their use near bees is generally welcomed. Occasionally, a few honey bees and bumble bees have been found in traps containing Japanese beetle lures (Hamilton et al. 1972).

10.8 Biological Control Agents (Parasitic and Predatory Insects)

Beekeepers would welcome biological control of harmful insects on crops because the control agents likely to be used would prey on the specific insects without harming bees. This would permit bees to forage with safety and effectively pollinate the crop.

10.9 Nonchemical Control

Along with the beneficial aspects of chemical pesticides come problems such as contamination of the environment and killing of beneficial insects, many of which are honey bees. To reduce agriculture's dependency on pesticides, a new concept of pest control has been developed called integrated pest management (IPM). Under IPM, all techniques and methods that are useful in controlling pests are used, including pesticides. However, a farmer applies a chemical pesticide only as a last resort. Primary reliance is on nonchemical controls, such as insect attractants, repellents, traps, insect-resistant plants, insect pathogens (disease), insect predators and parasites, time of planting, cultivation, time of harvest, sterilized insects, quarantines, and other practices. Not all of these techniques are utilized at the same time in controlling a pest; however, all of the control methods are considered noninjurious to honey bees, except for chemical control. Where possible, beekeepers should encourage farmers to use IPM techniques.

10.10 Toxicity of a Pesticide

The toxicity of a specific pesticide is a composite of its physical and chemical properties, the method of formulation (description follows), and the inherent ability of the honey bee to deal with the material internally. If the pesticide is of high volatility (an example is the fumigant TEPP), then the chemical may be absorbed through the bee's spiracles or respiratory system. The physical properties of an insecticide and especially of its formulation would be largely responsible for the relative hazard from this mode of entry into the bee. Ingestion of contaminated pollen and nectar offers yet another route of entry. The alimentary tract may become altered or paralyzed, making feeding impossible, or the bee's gut may cease to function. The ability of an insecticide to contaminate nectar and pollen would again be a composite of the physical/chemical properties of the material, its formulation, and the time of application of the spray relative to bloom.

10.11 How Bee Poisoning Occurs

Bee poisoning generally occurs after a pesticide has been applied to crops or weeds which contain flowers or are providing secretions attractive to bees, e.g. from extrafloral nectaries.

The pesticide is applied directly onto bees foraging on the crop.

Bees fly to the treated plants and collect contaminated nectar and/or pollen.

Bees collect contaminated water on or near treated plants.

Bees forage on a cover crop associated with the treated crop, e.g. clover in an orchard.

Pollen collecting bees collect pesticide dust and/or contaminated pollen and return these to the hive.

Pesticides drift from their point of application onto flowering plants or across apiaries.

10.12 Symptoms of Bee Poisoning

Bees come in contact with pesticides during foraging. There can be stomach poisoning to bees and also to brood when fed on contaminated pollen. Some pesticides may even cause hazards by fumigant action. After gaining entry to body, different pesticides having different modes of action. Some of the most important and common symptoms of pesticides poisoning in bees are as follows:

Presence of large number of dead bees in front of bee hive (Plate 4). Individual bees that have been poisoned frequently are seen crawling on the ground near the entrance or twirling on their side in a tight circle. Others appear to be weak or paralyzed. These gross symptoms of poisoning vary with the type of pesticide and the degree of exposure. Foraging bees also may die in the field or on the flight back to the hive. Bees become paralytic, lose the power of orientation; legs, wings and digestive tract stop functioning and poisoned bees show unco-ordinated movements.

Abdomen becomes distended.

Dead adult bees typically, but not always, have their wings unhooked and at odd angles to their body, their proboscis fully extended, and their hind pair of legs outstretched behind them.

Plate 4 Dead bees infront of the beehive due to pesticidal poisoning

Workers can get confused, forget their path and could not reach back to hives, hence their number is reduced. Bees may perform abnormal communication dances on the horizontal landing board at the hive entrance while under the influence of insecticide poisoning. Disorganized behavior patterns may lead to lack of recognition of affected field bees by guard bees and may harm them.

Regurgitation of contents of gut is noticed particularly in case of organophosphate insecticidal poisoning. Stupefaction, paralysis, and abnormal activities of bees are commonly caused by chlorinated hydrocarbons and organophosphorus insecticides.

Guard bees are also confused due to toxic effect of pesticides.

Brood chilling can occur due to reduction in the population of adult bees.

Dead brood can be seen inside the colonies if poisoned pollens are stored and fed to the brood.

Sometimes, the queens are also affected. Queens may stop egg laying or lay eggs in irregular pattern, there may be brood in only some of the cells of the, brood area as in case of the colonies suffering from foul brood. Sometimes queenlessness may develop. Queen cells may be raised and queens may be superseded in colonies which survive.

If on crops, gamma-BHC (lindane) and endosulfan etc. from organochlorine group are used, the affected bees can Dot move properly and their legs adversely affected. They appear as though they had been chilled. Most of such bees die away from their hives.

If malathion, Dimethoate and other related insecticides from organophosphate group are used, a watery substance liquid comes out from their mouth due to which whole body of bees becomes wet, swelling of abdomen takes place and both pair of wings stick to the body of bees. The behaviour of such bees also changes and they die near their hives.

If insecticides of carbamate group such as carbaryl, carbofuran etc. are used for insect pest control, the affected bees become more angry and not able to fly properly. Most of the affected bees die near their hives. In such a bee colony, the queen stops egg laying. In extreme cases of pesticide exposure, the house bees also die. When the house bees die, the brood will show signs of neglect or poisoning and many, or all, immature bees still in the cells may die. Some pesticides, particularly systemic pesticides, have a less noticeable, but debilitating effect, resulting in an overall weakening of the colony. Signs are reduction in adult bee numbers and stages of the brood cycle or complete brood cycles missing. In severe cases, when insufficient numbers of adult bees remain, temperature and humidity control in the brood area is lost and brood is not fed. Brood die from chilling, overheating or starvation.

By observing symptoms one can find out the group of insecticides sprayed on the crop in the vicinity of the apiary. In addition to this a scientist or a bee-keeper as well as farmers should also know the degree of toxicity of different insecticides to the bees so that a person can spray such an insecticide which is quite effective against pests but least toxic to the bees.

10.13 Groups of Insecticides Based on Their Toxicity to Bees

Toxicity is life property of a substance (insecticides) that causes any adverse effect in an organism. The toxicity may be due to single short term exposure period (acute toxicity) or due to repeated/continuous exposure within less than half life time of that animal (sub-acute toxicity) or repeated exposure over a period of at least half the life time of that organism (chronic toxicity). On the basis of toxicity to bees, the insecticides can be grouped into the following three Categories:

10.13.1 More Toxic Insecticides

The insecticides which have adverse effect on bees even after 90 h (about 4 days) comes under this category. Such insecticides are carbofuran, dichlorvos fenthion, monocrotophos, fenitrothion, lindane, malathion, carbaryl, methl-parathion, chlorpyrifos, dimethoate, phosphamidon, diazinon etc.

10.13.2 Less Toxic Insecticides

Those insecticides whose residues is less persistent in *Nature* and remain toxic to bees upto 90 h (Less than 4 days) fan in this category. Such insecticides are endosulfan and phosalone etc. Besides this, all systemic insecticides also fan in this category if used properly. These insecticides should be sprayed after 3 PM and next day morning allow bees to go a little bit late in the fields on crop plants so that by that time most of the toxicant enters inside the plant system being systemic in *Nature* resulting in minimum harm ten the bees.

10.13.3 Non-toxic Insecticides

There are some chemicals which are very effective for control of insect pests but DOD-toxic to bees. They are some bacteria (B.T. formulations), viruses (NPV) and insect growth regulators etc. Besides this, fungicides, weedicides and some plant growth regulators have also been found safe ten bees.

10.13.4 Relative Toxicity of Pesticides

The kill of bees can be classified as:

<100 per day – normal die off rate
200–400 per day – low kill

500–900 per day – moderate kill
>1,000 per day – high kill

10.13.5 Poisoning and Developmental Stages

Worker bees are those primarily affected by pesticides. The symptoms of poisoning can vary depending on the developmental stage of the individual bee and kind of chemical employed

10.13.6 Development of Adult

It takes worker bees about 21 days to develop from egg to adult. During this process, each individual passes through a larval (feeding) stage followed by a pupal (transformation) stage. The larval stage is the most susceptible to pesticide poisoning during development.

10.13.7 House Bees

These bees are emerged worker adults up to 21 days of age. They care for the brood, process pollen and nectar gathered in the field by older workers, and clean the nest. Eventually, they too will become field bees. House bees are usually poisoned by contaminated pollen which is collected in the field, brought back and stored in the hive. As house bees are killed, there are fewer bees to tend the brood and further decline in population results.

10.13.8 Field Bees

These bees are workers 21 to approximately 42 days of age. There appears to be no greater risk in bee society than to be a field bee. Should the insect avoid all the potential pitfalls due to predators like spiders, toads or skunks, it is still vulnerable at all times to the numerous pesticides applied in commercial agriculture, mosquito control, and home gardens. Most times, field bees are killed by contact with pesticides in the field, but other times they collect contaminated nectar and pollen and contribute to poisoning their sisters in the colony. If field bees are killed, then young bees are forced into the field earlier than normal, disrupting and thus disorienting the colony.

While foraging, field bees may range as far as two to five miles from a colony. They usually seek nectar and pollen systematically, not randomly, and once a food source is found, bees prefer to work that particular source to exhaustion before changing plants. This kind of resource partitioning by bee colonies accounts for the inconsistency observed many times between colonies undergoing pesticide poisoning in the same location. The bees are not all working the same plants and so some are affected more than others. Often it is those bees with established flight patterns located in an area before a pesticide is applied that are most damaged. Those placed in a field immediately after application are less affected by the pesticide because it takes some time for the bees to scout an area and locate food sources.

On the basis of mode of action the insecticides are classified as given below (Table 10.1)

The relative toxicity of different insecticides to honey bees has been given in Tables 10.1–10.9.

LD50 (μg/bee)	Classification
>100	Virtually non toxic
11–100	Slightly toxic
2–10.99	Moderately toxic
<2.0 (i.e., 0.001–1.99 μg/bee)	highly toxic

Application of these pesticides on blooming crops or weeds may cause severe damage to bees. Even after 10 h of spray these pesticides are still very toxic to bees.

Table 10.1 Classification of insecticides on the basis of their mode of action

Group	Subgroup	Example
Physical poisons	–	Heavy mineral oils, inert dusts
Protoplasmic poisons	–	Heavy metals, e.g. Hg, acids
Metabolic inhibitors	Respiratory poisons	HCN, CO, H_2S, rotenone, dinitrophenols
	Inhibitors of mixed-function oxidase	Pyrethrin synergists
	Inhibitors of carbohydrate metabolism	Sodium fluoroacetate
	Inhibitors of amine metabolism	Chlordimeform
	Insect hormones	Juvenile hormone analogues
	Inhibitors of chitin synthesis	Diflubenzuron
Neuroactive agents (nonmetabolic)	Anticholinesterases	Organophosphorus compounds, carbamates
	Effects on ion permeability	DDT analogues, pyrethroid
	Agents for nerve receptors	Ach*nicotinoids, nereistoxin analogues, GABA*cyclodienes, HCH, avermectins(spinosoids), octopamine*formamidines
Hormone mimics	–	Methoprene
Stomach poisons	–	*Bacillus thuringiensis*, toxin, Thiodicarb

Table 10.2 Pesticide risk to bees

Risk rating	Chemicals	Remarks
High risk to bees foraging even 10 h after spraying	Carbaryl, chlorpyrifos, diazinon, dimethoate, omethoate, methomyl, fenthion, methamidophos, methidathion, monochrotophos.	These should never be sprayed on flowering crops especially if bees are active and the crop requires pollination.
Moderate risk with some losses expected 10 h after spraying	Acephate, demeton-s-methyl	
Some risk with low chance of losing bees 3–5 h after spraying	Endosulfan, dicofol, pirimicarb, petroleum oils, most pyrethroid chemicals, trichlorfon.	There is little risk of losing bees if these chemicals are sprayed in the evening when foraging has ceased.
No risk even if sprayed over foraging bees	*Bacillus thuringiensis*, propargite, oxythioquinox	

Table 10.3 Pesticides most toxic to bees (LD50 0.001–1.99 µg/bee)

Acephate fenthion[a]
Aldicarb G (applied 4 weeks before bloom) heptachlor[a]
Aldrin[a] isobenzan
Aminocarb lean arsenate
Azinphosethyl malathion D[a]
Azinphosmethyl malathion ULV
Benzene hexachloridea methamidophos
Bomyl methidathion
Calcium arsenate methiocarb
Carbanolate methomyl D
Carbaryl ULV (over 0.4 kg/ha) methyl-carbophenothion
Carbofuran F methyl parathion[a]
Carbophenothion D mevinphos
Chlorpyrifos[a] mexacarbate
Chlorthion monocrotophos
Colep naled D
Crotoxyphos omethoate
Diazinon[a] paraoxon
Dicapthon parathion[a]
Dichlorvos[a] permethrin
Dicrotophos phenthoate
Dieldrin phosmet
Dimethoate[a] phosphamidon[a]
Dinitrocresol phoxim
Dinoseb propoxur
EPN pydrin (over 0.1 kg/ha)
Ethyl-methyl guthion pyramat
Famphur resmethrin
Fenamiphos sulfotep (p)
Fenitrothion[a] sulprofos
Fensulfothion thionazin

[a] There is an Indian standard for one or more formulations of these pesticides (India Standards Institution 1979)

Table 10.4 Pesticides very toxic to bees[1]

Malathion EC[a]
Naled WP
Phorate EC
Pydrin (0.1 kg/ha or less)

[a] There is an Indian standard for one or more formulations of this pesticide (Indian Standards Institution 1979)

[1] For minimal hazard to honeybees, the insecticides below should be applied only during late evening. Their residual toxicity is usually low with in 8 h

Table 10.5 Pesticides very toxic to bees[1]

Amidithion kroneton
Aramite D larvin
Binapacryl[a] leptophos
Carbaryl ULV (0.5 kg/ha or less) lethane 384 special
Carbophenothion malathion MA
Chlordane[a] malonoben
Chlorfenvinphos menazon
Chlorpyrifos or chlorpyriphos MA methomyl S, SP
Coumaphos methoxychlor
DDD methyl-demeton
DDT[a] Naled EC
Demeton nissol
Dichlorfention or dichlorfenthion oil sprays (superior type)
Dichlorvos MA oxamyl
Dieldrin G oxydemeton-methyl[a]
Dilan phorate G
Dimetilan phosalone[a]
Dinobuton phostex
Dioxathion pirimicarb
Disulfoton EC propoxur MA
Endosulfan[a] Propyl thiopyrophosphate
Endrin[a] rotenone D
Ethion sabadilla
[a]Ethyl-DDD solvigran
Fenchlorphos strobane
Fenthion G or MA temephos[a]
Fonofos TEPP
Formetanate tetrachlorvinphos
Garrathion tetram
Heptachlor G thanite (isobornyl thiocyanate)
Isobornyl thiocyanate thioquinox
Isodrin toxaphene[a]
Isolan tranid
Isopropyl parathion trichlorfon[a]
Malathion EC[a]
Naled WP
Phorate EC
Pydrin (0.1 kg/ha or less)

[a]There is an Indian standard for one or more formulations of this pesticide (Indian Standards Institution 1979)

[1]For minimal hazard to honeybees, the insecticides below should be applied only during late evening. Their residual toxicity is usually low with in 8 h

Table 10.6 Pesticides least toxic to bees[1] (LD50 2.0–10 μg/bee)

Allethrin fenazaflor
Amitraz fenbutatin-oxide
Bromopropylate fenson
Butoxy thiocyanodiethyl ether fensulfothion G
Carbaryl G genite 923 or genitol 923
Carbofuran G hydroprene
Chlorbenside lime-sulphur or lime-sulfur[a]
Chlordecone malathion G
Chlordimeform mirex G
Chlorfenethol nicotine sulphate
Chlorfenson oxythane
Chlorfensulphide propargite
Chlorobenzilate propoxur G
Chloropropylate pyrethrum[a]
Cryolite quinomethionate
Cyhexatin rotenone EC
Dicofol[a] ryania
Dienochlor schradan
Diflubenzuron sodium fluosilicate baits
Dikar sulphenone
Dinex sulphur or sulfur[a]
Dinocap tetradifon
Disulfoton G

[a]There is an Indian standard for one or more formulations of this pesticide (Indian Standards Institution 1979)

[1]The insecticides below can be applied at any time with reasonable safety to honeybees. Their toxicity is usually low with direct application

Table 10.7 Pesticides non-toxic (LD50 above 11 μg/bee)

A. Insecticides and acaricides

Acaraben (chloro-benzilate)
Allethrin
Aramite
Bacillus thuringiensis
Cryolite
Delnav (dioxathion)
Dessin
Dilan
Dylox (trichlorfon)
Eradex
Ethodan
Fundal
Galecron (chlorophenamidine)
Heliothis virus
Kelthane (dicofol)
Kepone
methoxychlor
Mitox (chlorbenside)
Morestan
Nemagon
Neotran nicotine
Omite
OMPA (schradan)
Ovotran (ovey)
Phostex
Phrethrin
Rhothane (TDC)
Rotenone
Ryania
Sabadilla
Sulphenone
Tedion (tetradifon)
Toxaphene

B. Fungicides

Arasan (thiram)
Benlate (benomyl)
Bordeaux mixture
Copper oxychloride sulfate
Copper sulfate (monahydrate)
Cuprous oxide
Cyprex (dodine)
Dexon
Dichlone
Difolatan
Dithane M-45
(Folcid)
Glyoxide (glyodin)
Karathane (dinocap)
Manzate (maneb)
Mylone
Parzate (nabam)
Phaltan (folpet)
Polyram
Sulfur
Thynon (dithianon)
Zerlate (ziram)

C. Herbicides

Amitrol
Ammate (ammonium sulfamate)
Atrazine
Banvel (dicamba)
Betanal (phenmedipham)
Caparol (promytryne)
Casoron (dichlobenil)
Dalapon
DEF
Diquat
Eptam (EPTC)
Folex (merphos)
Herbisan (EXD)
Hyvar (bromacil)
Igran (terbutryne)
IPC
Karmex (diuron)
MCPA
Milogard (propazine)
Monuron
NPA
Paraquat
Picloram
Planavin
Princep (simazine)
Randox (CDAA)
Sinbar (terbacil)
Stem F-34 (propanil)
TOK (nitrofen)
Trysben (2,3,6-TBA)
Vegedex (CDEX)
2,4-D
2,4-DB
2,4,5-T

Table 10.8 Common insecticides and miticides and their relative risk to honey bees[1, a]

Active ingredient	Trade names	Risk class[2]	LD50[3]	Residual[4]
Acephate	Orthene	I	1.2	1 day to >3 days
Aldicarb	Temik	I	0.35	>1 day to >2 days
Azinphos methyl	Guthion	I	0.43	2 days to >5 days
Bacillus thuringiensis	Biobit, Cutlass, Dipel, Javelin, Thuricide	III	NA	<2 h
Carbaryl	Sevin	I	1.5 to 26.5	<2 h to 12 days

(continued)

Table 10.8 (continued)

Active ingredient	Trade names	Risk class[2]	LD50[3]	Residual[4]
Chlorpyrifos	Dursban, Lorsban	I	0.11	5 h to 6 days
Cyhexatin	Plictran	III	NA	<2 h
Cypermethrin	Ammo, Cymbush	III	NA	<2 h to >3 days
Diazinon	Diazinon	I	0.37	<1 day to 2 days
Dicofol	Kelthane	III	NA	<2 h
Dicrotophos	Bidrin	I	0.3	1 day to 1 days
Diflubenzuron	Dimilin	III	NA	<2 h to 6 h
Dimethoate	Cygon, Defend, Rebelate	I 0.19 <2 h to >3 days	I	0.19 <2 h to>3 days
Disulfoton	Di-syston	II	6.12	<2 h to 7 h
Endosulfan	Thiodan	II	7.8	<2 h to 1 day
Ethion	Ethion oil	III	NA	<2 h
Fluvalinate	Mavrik	III	65.8	<2 h
Fonofos	Fonofos Dyfonate	II	8.68	<2 h to 6 h
Formetanate hydrochloride	Carzol	II	9.2	<2 h to 2 h
Lindane	Lindane	I	NA	>2 days
Malathion	Cythion, Malathion	I	0.73	<2 h to 5 days
Methamidophos	Monitor	I	1.37	4 h to 1 day
Methidathion	Supracide	I	0.24	1 day to 3 days
Methomyl	Lannate	I	1.29	<2 h to >1 day
Methoxychlor	Marlate, Methoxychlor	III	NA	<2 h
Methyl parathion	Penncap-M	I	0.11 to 0.24	<1 day to >7 days
Mevinphos	Phosdrin	I	0.3	<2 h to <5 h
Naled	Dibrom	I	0.49	2 h to >1 day
Oxamyl	Vydate	II	10.3	<2 h to 12 h
Oxythioquniox	Morestan	III	NA	<2 h
Parathion	Parathion	I	0.18	10 h to >1 day
Permethrin	Ambush, Permethrin, Pounce	I	0.16 12	<2 h to >3 days
Phorate	Thimet	II	10.25	<2 h to 5 h
Phosmet	Imidan	I	1.13	8 h to >3 days
Profenofos	Curacron	II	3.46	<2 h to 9 h
Propargite	Omite, ornamite	III	NA	<2 h
Sulprofos	Bolstar	II	7.22	<2 h to >1 day
Thiodicarb	Larvin	II	7.08	<2 h
Trichlorfon	Dylox, Proxol	III	NA	<2 h to 6 h

[a] Never spray during bloom periods unless it is absolutely necessary. If treatment is unavoidable, choose a product with a high LD50 and short residual. If a more toxic chemical is required, choose a residual under 8 h and spray at night

[1] Table modified from Johansen and Mayer (1990) and Delaplane (1993)

[2] Risk classes; I = highly toxic to honey bees, II = moderately toxic to honey bees, III = relatively nontoxic to honey bees. The risk class is closely associated with the LD50

[3] LC50 = the Lethal Dose required to kill 50% of the test honey bees, expressed in micrograms per bee. The smaller the LD50, the more toxic the product

[4] Period of residual toxicity to honey bees after application. Evening applications of products with residuals of 8 h or less generally cause only moderate harm to bees, even if the LD50 is small. For example, mevinphos is very toxic to bees, but because it has a short residual, it is fairly safe for early evening applications

Table 10.9 Pesticides recommended as relatively safe for honeybees (Indian Standards Institution 1973)[a]

Pesticide	Use class	Cotton	Maize	*Brassicas*	Vegetables	Fruit	Others
Amidithion	3						X
Carbophenothion	3						X
DDT	3	X			X	X	X
Demeton methyl	3	X	X	X	X	X	X
Disulfoton	3,4						X
Endosulfan	3	X	X		X		X
Endrin	3	X				X	X
Ethion	3						X
Fenchlorphos	3						X
Isolan	3						X
Menazon	3			X	X	X	X
Methoxychlor	3						X
Naled[a]	2,3						X
Phorate	2,3						X
Ryania	4						X
Temephos	3						X
Toxaphene	3		X		X	X	X
Trichlorfon	3		X				X

[a] The recommendations apply to the crop specified, and for time and method of application stated in the publication

The following pesticides should be applied in the late evening when bees are not foraging in the field. Bee hives should not be directly exposed to these insecticides. For minimal hazard to bees, dose, the timing and methods of application are very important.

These can be used around bees with a minimum injury. They should be applied during late evening, night or early morning. These products can be used on fields or near hives with minimum damage to bees; in fact, a few of the listed acaricides can he used to control bee mites within the hive.

10.14 Factors Influencing the Toxicity of Insecticides to Bees

10.14.1 Temperature

Temperature is probably the most significant factor causing differences in the toxicity of pesticides. Immediate effects may be much greater at higher temperatures whereas, residual effects are likely to be less because the toxic materials breaks down more quickly.

10.14.2 Age and Size of the Bees

From the general principles, body size is likely to have a direct effect on the susceptibility of these contact pesticides. Smaller bees have a higher surface to volume ratio and contact poison will be more toxic to them to larger bees.

10.15 Protection of Bees

Several management practices are known that may help protect bees from pesticide-caused mortality.

10.15.1 How Bees Can be Protected from Pesticide Poisoning

Do not apply any insecticide unless the crop is so heavily infested and the insect in question has reached the economic threshold value (ET-value). If necessary, then select the insecticides safer to bees.

10.15.2 Read the Pesticide Label Carefully

Read the pesticide label. Pesticides and formulations which pose a special hazard to bees are required to include a notification on the label.

10.15.3 Use Less Toxic Compounds

Choose an insecticide of low toxicity to bees that will provide the needed pest control.

10.15.4 Types of Formulation and Their Toxicity to Bees

Pesticides vary in their effects on bees. Different formulations, even of the same pesticide, often vary considerably in their toxicity to bees. Dust formulations are typically more hazardous than sprays because they are picked up on bee hairs than solutions or emulsifiable concentrates. Actual damage to bee populations is a function of toxicity and exposure of the compound, in combination with the mode of application. Evidently, proper selection of pesticide formulation can minimize honeybee losses.

10.15.5 Use Less Toxic Formulations

Mostly dust, wettable/water dispersible liquid and granular formulations of insecticides are used to control/insect/pests of various crops. Select the safest formulation of the pesticide that is available for the intended use. "Drifting" of the pesticide from the target pest and/or crop to areas frequented by bees should be minimized.

10.15.6 Dust Formulations

These formulations if used on crop result in maximum toxicity to bees and other pollinators as compared to other formulation. Dusts almost always drift more than other formulations and are generally more dangerous to bees than are sprays or granular application.

10.15.7 W.P./W.D.P. Formulations

These formulations are less toxic to bees as compared to dust formulation but definitely more toxic in comparison to other formulations of insecticides. (iii) Liquid formulations of course liquid formulations are less toxic to bees as compared to dust and wettable or water dispersible powder formulations but they are less toxic as compared to granular formulations. (iii) Granular formulations: Among the insecticidal formulations which are commonly used to control pests of various crops, it is the granular formulation which is least toxic to honey bees visiting flowers to collect nectar and pollen. Further, ground applications are always safer than aerial applications.

10.15.8 Microencapsulated Pesticides

Microencapsulated pesticides present a very distinct and serious threat to honeybees. The particle size of this formulation is very similar to that of pollen, and adult honeybees may carry this pesticide back to the hive, where it will be combined with pollen that is being stored in the hive. This pesticide will not kill the adult bees that collected it, but it will kill the immature stages of the bees and the young adult nurse bees that feed the brood. Bees have little protection from this product.

10.15.9 The Mode of Pesticide Application

The mode of pesticide application is also important, particularly when it comes to drift. Aerial applications are generally more dangerous than applications by ground equipment, because of the location of target pests and/or crops to foraging bees or beehives. Never apply a pesticide directly over beehive.

10.15.10 Do Not Treat Crops in Bloom

Whenever possible, do not treat crops in bloom. If treatments are needed during bloom, choose a short-residual material. Make applications during the evening, when bees are not actively. Honey bees are active primarily during the morning and early afternoon. Many pesticides can be effectively applied in the late afternoon or evening with relative safety to bees. Remove weed blooms in orchard groundcover and in field edges before spraying. Flowering weeds may be removed by mowing or with an herbicide.

10.15.11 Minimize Spray Drift

Minimize spray drift onto adjacent crops or other plants in bloom. Honey bee hives should not be placed next to fields or orchards that are likely to be treated with pesticides toxic to bees. A small number of hives may be protected from pesticides by covering the colonies with wet burlap for a period of 1–2 days. In some cases it may be practical to move hives to a less exposed site. Beekeepers should inform farmers of the location of hives.

10.15.12 Use Pesticides Only When Needed

Foraging honey bees, other pollinators, and insect predators are a natural resource and their intrinsic value must be taken into consideration. Vegetable, fruit, and seed crop yields in nearby fields can be adversely affected by reducing the population of pollinating insects and beneficial insect predators. It is always a good idea to check the field to be treated for populations of both harmful and beneficial insects.

10.15.13 Apply Pesticide When Bees Are Not Flying

Bees fly when the air temperature is above 55–60°F and are most active from 8 a.m. to 5 p.m. Always check a field for bee activity immediately before application. Pesticides hazardous to honey bees must be applied to blooming plants when bees are not working, preferably in the early evening. Evening application allows time for these chemicals to partially or totally decompose during the night.

10.15.14 Do Not Contaminate Water

Bees require water to cool the hive and feed the brood. Never contaminate standing water with pesticides or drain spray tank contents onto the ground, creating puddles.

10.15.15 Identify Attractive Blooms

Bees also visit flowers of some weeds; hence before spraying remove such weeds from fields which might attract bees. In many instances bees have been killed even though the crop being sprayed was not in bloom. Many times these attractive blooms can be mowed or otherwise removed, although mowing can result in destroying other beneficial insect habitat or force destructive insects into the crop being cultivated.

10.15.16 Notify Beekeepers

Notify beekeeper that has beehives near an area to be treated with a pesticide so that they may attempt to protect their bees. If nearby crops or in the crop, bee boxes kept, take them away or cover with jute bags at the time of insecticidal spraying.

10.15.17 Disposing of Unused Pesticides

Follow proper precautions in disposing of unused pesticides and pesticide containers. Be particularly careful not to contaminate was with pesticides, as the water may be collected by bees and result in bee kills.

10.15.18 Use Integrated Pest Management (IPM) to Reduce Pesticide Hazard

IPM is an important approach to controlling insects, mites, weeds and diseases of crops. Whenever possible, it is wise to use such integrated pest management practices viz., recognition of existing biological controls and evaluating their value before applying any pesticides; using pesticides that are less harmful to beneficial organisms; timing pesticide applications so they are less harmful to beneficial organisms. Biological control organisms may be effectively controlling pests even though they are not recognized. Even pests that occur regularly, such as spider mites on field corn or greenbugs on sorghum, may be effectively controlled under some conditions. Before applying pesticides, fields should be examined for the activity of natural enemies. If large numbers are present, pesticide use may be deferred or avoided.

10.15.19 Use of Repellents

Chemical repellents have been studied for many years. The repellent is added to the pesticide before field application and is intended to discourage bees from visiting plant's until the pesticide becomes relatively nontoxic. Field tests showed several compounds to have repellency, but more research is needed before they are used commercially by farmers.

10.15.20 Disposing of Unused Pesticides

Follow proper precautions in disposing of unused pesticides and pesticide containers. Be particularly careful not to contaminate water with pesticides, as the water may be collected by bees and result in bee kills. Pesticide dusts and small granules should not be left open or carelessly thrown any were because bees are likely to collect such dusts during acute pollen dearth period.

10.15.21 Inform Presence of Apiary

If your bees are located in any area where pesticides are commonly used, then identify yourself as a beekeeper to any neighbors who may use pesticides. Explain to growers the importance of your honeybees in the pollination of crops being grown in nearby fields so that they may consider the value of bees in pollination before applying any pesticides that may kill the pollinating insects. Do not place apiaries in areas that are used to grow crops that require heavy and frequent usage of pesticides.

10.15.22 Notify Beekeepers and Inform Presence of Apiary

If your bees are located in any area where pesticides are commonly used, then identify yourself as a beekeeper to any neighbors who may use pesticides. Explain to growers the importance of your honeybees in the pollination of crops being grown in nearby fields so that they may consider the value of bees in pollination before applying any pesticides that may kill the pollinating insects. Do not place apiaries in areas that are used to grow crops that require heavy and frequent usage of pesticides. Notify beekeeper that has beehives near an area to be treated with a pesticide so that they may attempt to protect their bees. In the areas of bee-keeping, there should be good coordination between the bee-keepers and crop/fruit vegetable growers so that the farmers may inform well in advance to the bee-keepers so that either they remove the colonies or should keep the bees confined inside the hive during the application. While confirming the bees, due attention should be paid to the following points :(a) Proper space: While confining the bees in the hive, sufficient and proper space for all the bees including foragers should be made available. (b) Proper ventilation: Proper ventilation must be provided at the top or sides of the hive, Dot only through the entrance, because this may get blocked by deed bees. Ventilation screen should have as large a mesh as possible (c) Shade: Shade is usually provided by the use of local materials. It must not hinder the flow of air past the hives. (d) Covering hives: Covering the hives with wet clothes or gunny bags is very useful because evaporation of water helps to reduce the rise in colony temperature. If pesticides applied from the air, then cover whole of the hive. (e) Water availability: Provide water inside the hives for bees. The bees take it and spread out in the hive where it evaporates and thus reduces the temperature. (f) Minimize period of confinement: The confinement must of course continue as long as the pesticide near the hive retains unacceptable toxicity and its duration can satisfactorily be reduced by application of less persistent insecticide. If there is no store in the hive in that case pollen supplement and sugar syrup may also be provided. If there is adverse effect OD bees including brood due to pesticidal contamination of pollens, in that case bee-keepers can over come this difficulty by prevention of pollen being stored in the hive and provision of a safe pollen supply inside the hive. Provision of pollen cakes in the hive during this period greatly reduces the collection of toxic pollen. Cake of pure pollen were more effective than pollen supplement made with soybean flour.

10.16 Management of Poisoned Colonies

Shift colonies away from foraging range from the source of poisoning Keep bees warm by removing excess supers.

If a pesticide carried by the bees infiltrates the combs and contaminates the nectar or pollen, or both, then the combs may need to be replaced before a colony will recover. Remove contaminated pollen stored in combs by dipping the combs in water and washing by slight shaking or the entire comb melted and replaced with wax foundation. Before washing or melting combs, however, a sample of the pollen, wax, and honey should be analyzed chemically to determine the amount of pesticide residue present, if any.

Provide sugar syrup and pollen substitute. Feed colonies inside the hive with a 1:1 water: sugar syrup until recovered. Loss of field bees results in a lack of fresh nectar and water being brought into the hive. Add frames of sealed brood and adult bees from healthy hives, if require. Moreover, colonies weakened by insecticide treatment should be fed sugar syrup and pollen cake to stimulate brood production as an aid to population recovery. Frequently, weak colonies must be united to save the remaining bees and brood or a queenless package of bees added to the damaged colony to strengthen the population. If above mentioned points are kept in mind, the bee-keepers can protect their bees to a great extent from toxic effects of insecticides.

10.16.1 Managing Pesticide Drift

Serious honeybee poisonings can be caused by pesticide drift. During warm periods, large numbers of honeybees may mass on the outside of the hive to help control hive temperatures. These exposed bees can be destroyed easily by drifting pesticides.

Drift control is vital during every pesticide application. Several techniques can be used to reduce the possibility of drift:

1. Use pesticides that have low volatility;
2. Use formulations that resist drift and volatility;
3. Use low pressures during spraying;
4. Use nozzles which reduce formation of small spray particles;
5. Use high water volumes during application;
6. Apply pesticides close to the crop or soil surface;
7. Avoid applying pesticides when the temperature is high;
8. Avoid applying pesticides during windy conditions;
9. Use drift reducing adjuvants.

Certain formulations of pesticides can help reduce drift. For example, low-volatile acid and amine 2, 4-D formulations have less potential for drift than ester formulations. Dust formulations drift much more readily than most sprays. Granular formulations are relatively less likely to drift.

Droplet size of pesticides during application is extremely important in determining the potential for drift. The ability of particles to drift increases greatly as the particle size decreases (below).

10.16.2 Distance Water Droplets Drift While Falling 10 ft in Winds of 3 Miles Per Hour

Droplet (microns)	Diameter classification	Particle drift distance (ft)
30	Cloud	500
100	Mist	50
200	Drizzle	16
500	Light rain	7

The various spray nozzles and application equipment produce a wide range of droplet sizes. There are several techniques that will reduce the number of the smallest particles while still giving effective coverage.

10.16.3 Application Pressures

Application pressures are important in determining the sizes of droplets that are formed. As pressure increases, the number of fine particles also increases. Drift can be reduced by reducing sprayer pressures during application.

10.16.4 Nozzle Construction

Nozzle construction can also affect the number of small particles that are formed during spraying. Nozzle tips that produce larger droplet sizes help reduce drift. For example, larger nozzles can be used at lower pressures to get the same volume (Gallons per acre, or GPA) as smaller nozzles operated at higher pressures. Use of higher GPA applications are an alternate means of achieving adequate crop coverage with minimal pressures.

10.16.5 "Thickening" or "Drift Control" Adjuvants

"Thickening" or "drift control" adjuvants can be added to the spray mixture to reduce drift. These compounds can increase the percentage of larger droplets which are formed but do not completely eliminate small droplets.

10.16.6 The Weather Conditions

The weather conditions during application have a great effect on pesticide drift. Air movements, both horizontal and vertical, cause pesticides to move away from where you are spraying. The higher the wind speed, the larger the amount of pesticide that will be carried away.

10.16.7 Pesticides Should Never be Applied During High Wind Conditions (Greater than 10 mph)

Pesticides should never be applied during high wind conditions (greater than 10 mph). This is particularly important when wind direction is likely to move drifted pesticides onto nearby sensitive crops or other sensitive areas. Drift to sensitive areas often can be avoided by spraying when the air is moving away from these areas.

Drift may also increase when warming air near the soil rises. Applications should be done at times when air and soil temperatures are most similar, often during early morning and late evening. At this time, vertical air movements are lowest.

If the air near the soil surface is cooler than the air above, an "inversion" exists. Small spray particles remain suspended in the cool air during temperature inversions, and the particles do not settle readily onto soil or plants. Later the suspended particles move out of the crop on winds and drift. Pesticide applications should be avoided during inversions.

10.16.8 Temperature and Humidity

Temperature and humidity can affect pesticide drift. When the temperature is high and humidity low, particles evaporate most rapidly. This evaporation causes droplet sizes to decrease and drift more readily. Volatile pesticides also evaporate more rapidly with high temperatures. Pesticides should be applied when the temperature is cool.

10.16.9 Height and Orientation of Sprayer Nozzles

Height and orientation of sprayer nozzles can also affect drift. Distance and time for spray droplets to reach plants or soil is directly related to the height at which a pesticide is released. Sprays should be released as near the target as will permit adequate coverage. Sprays should also be directed so droplets are propelled downward to reduce the distance of droplet fall. Vapor drift of soil-applied pesticides can be reduced by properly sealing the soil after application. This often involves proper soil incorporation of the pesticides during application.

10.16.10 Avoiding Pollution of Ground and Surface Waters

Contamination of ground and surface waters is an imminent hazard of using pesticides in agriculture. This potential must be a major consideration in planning for pest control on cropland and other agricultural areas. Elements that enter into water pollution by pesticides are:

1. Proximity of the treated area to surface waters;
2. Proximity of the treated area to drinking water wells or aquifers;
3. Depth of the water table at the treated site;
4. Soil conditions that increase the potential for the pesticide to leach into ground water;
5. The hazard of the pesticide as a potential contaminant of ground waters;
6. Conditions during application that affect pesticide drift into surface waters;
7. Crop management practices that minimize pesticide leaching;
8. Precautions during application to avoid leaching or direct ground water contamination.

10.16.11 Irrigate in a Manner that Reduces Pesticide Movement

High rates of irrigation can increase the amount of pesticide leaching. Excessive irrigation can also cause run-off and erosion. Particular care should be given when irrigating shortly after a pesticide application, since the pesticide is in the highest concentration at this time.

10.17 Honey Bee Indemnity Program

Some Governments have enacted national legislation to partially repay each beekeeper for pesticide-killed bees. Beekeepers who exercised reasonable precautions to avoid pesticide damage but still lost bees could apply for indemnity payments after January 1, 1967. The main goal of this program was to aid the bee industry in remaining financially stable and to ensure that enough strong colonies would be available to pollinate agricultural crops nationwide. To accurately access the loss, beekeepers should maintain detailed records of their colonies, noting by date such items as colony condition, population size, syrup and pollen feeding, and honey production. The more detailed the records, the easier it is to establish the true magnitude of a loss and receive reasonable compensation. Be prepared to manage the hives for queen failure or supersedure problems which may occur a number of weeks after the pesticide problem occurred.

10.18 Plant Poisoning

Poisonous plants can be a problem under certain conditions in limited areas. If a plant's nectar is poisonous, the symptoms of plant poisoning are limited to the blooming period of the plant. However, if the poison is in the pollen, the symptoms may linger as long as the pollen remains in the combs. There is no clear-cut method for differentiating between plant poisoning and pesticide poisoning. The effects of plant poisoning are usually more gradual and last longer than the effects of pesticide poisoning. Plant poisoning usually occurs in the same geographical area at the same time each year, whereas pesticide poisoning is indiscriminate. For a good review of poisonous plants, see Barker (1978). Some examples of plant poisoning are listed below and in Table 10.10.

10.19 Purple Brood

Purple Brood Purple brood occurs when adult bees collect and use the pollen and nectar from Cyrilla racemiflora (titi, southern leatherwood). This "disease" is characterized by the blue or purple color of the affected larvae.

10.20 Paralysis

Paralysis Aesculus californica (California buckeye) is probably the best known of the poisonous plants in the United States. Field bees exhibit symptoms similar to those of chronic bee paralysis; i.e., the bees are black and shiny from loss of hair and they tremble. Also, either the eggs do not hatch or the larvae die soon after hatching.

Table 10.10 Comparative symptoms in honey bees poisoned by toxic chemicals and selected plants

Source of poison	Stages most affected	Effect on adult	Effect on brood	Effect on colony
Toxic chemicals	Adult	Field bees die in or near hive. Nurse bees may also die. Queens usually not affected.	Usually few larvae killed. Symptoms of starvation may be evident if adult population reduced severely.	Weakened or killed. Many dead bees near hive.
California buckeye (*Aesculus californica*)	Young brood	Emerging young workers often deformed, pale, some hairless and tremble. Queens lay eggs at reduced rate, cease, or become drone layers.	Eggs normal at outset; later fail to hatch or all are drone eggs. Larvae die soon after hatching and disappear. Little or no capped brood; if present, scattered.	Weakened or killed. May be many dead bees near entrance. Supersedure of queen may fail.
Yellow jessamine (*Gelsemium sempervirens*)	Larva, pupa, and young adult	Young workers affected and soon die. Old adults appear normal.	Pupae die in cells and become mummified.	Slightly to severely weakened.
Loco plants (*Astragalus spp.*)	Adult and pupa	Field bees die. Some become black and tremble. Queen may die.	Many cells contain dried pupae.	Population dwindles. Colony may die.
False hellebore(*Veratrum californicum*)	Adult	Many field bees die between plants and hive. Adults die in curled state. Queens not affected.	No effect	Field population lost.
Southern leatherwood (*Cyrilla racemiflora*)	Larva	No effect.	Many blue or purple larvae die in cells when nearly mature.	Slight to severe weakening.

Source: Modified from Burnside and Vansell (1936)

10.21 Milkweed Pollinia

Milkweed Pollinia The pollen of milkweed (Asciepias species) is produced in pollinia (coherent pollen grains) that are attached in pairs by a slender filament. When removed from a flower, the pollinia resemble a wishbone with pollen masses hanging from the ends. Honey bees become ensnared in the thin pollinia attachment and free themselves by pulling the pollinia from the flower. Honey bees often become seriously encumbered and unable to effectively fly or crawl because of the structures that remain attached to their body parts.

Adey et al. (1986) has given the following guide to minimize bee toxicity

Quick guide to minimize bee toxicity	
↓	
Has the infestation reached the economic injury level?	
↓	
Is there any effective –non chemical method for pest control?	
↓	
Chose the pesticide carefully	
↓	
Read the label in detail	
↓	
Are any plants in bloom in/around the crop to be treated?	
↓	↓
Yes	No
Are bees foraging in /around the crop to treated	
↓	↓
Yes	No
↓	↓
Can the bees be moved prior to treatment? Treat	
↓	↓
Yes	No
↓	
Move bees, treat use non persistent pesticides	
Apply when bees are not foraging	

References

Abrol DP, Kumar R (2000a) Impact of pesticides on the brood rearing activity and foragers of honeybee *Apis mellifera* L. visiting *Brassica campestris* L. var. toria. Indian Bee J 62(1–2):19–27

Abrol DP, Kumar R (2000b) Toxicity of a neem (*Azadirchta Indica* A. Juss.) insecticides to immature stages of honey bee *Apis mellifera* L. Indian Bee J 62(3x4):47–53

Abrol DP, Kumar R (2001) Toxic and morphogenic effects of pesticides on the honeybee *Apis mellifera* L. brood. Korean J Apic 16(2):95–112

Abrol DP, Sharma D (2007) Morphogenic and toxic effects of some pesticides on honeybees, *Apis mellifera* L. brood. J Res SKUAST- J 6(2):144–159

Adey M, Walker P, Walker PT (1986) Pest control safe for bees: a manual and directory for the tropics and subtropics. International Bee Research Association (IBRA), London, pp 224

Atkins EL (1975) Injury to honey bees by poisoning. In: The hive and the honey bee. Dadant and Sons, Hamilton, pp 663–696

Bai ARK, Reddy CC (1977) Laboratory toxicity of some insecticides to *Apis cerana indica*. J Apic Res 16(3):161–162

Barker RJ (1978) Poisoning by plants. In: Morse RA (ed) Honey bee pests, predators, and diseases. Cornell University Press, Ithaca/London, pp 275–296

Barnes G (1972) Beekeepers continue to suffer pesticide losses. Ark Dept Com Apiary Bd Bul 9(1):1–2

Bhattacharyya P, Samui RC, Ghosh MR, Dasgupta SK, Roy A (1982) Sunflower seed yield as influenced by pollination and insect pests. In: Proceedings of tenth international sunflower conference, Sulfers Paradise, Australia, 14–18 Mar 1982, pp 132–134

Bisht DD, Naim M, Mehrotra KN (1983) Studies on the role of honeybees in rapeseed production. In: Proceedings of 2nd international conference of apiculture in tropical climate. Indian Agricultural Research Institute, New Delhi, pp 491–496

Bourne AI (1927) The poisoning of honeybees by orchard sprays. Mass Agric Exp Station Bull 234:74–84

Brose CM (1888) Report of the assistant horticulturist incharge of the apiary. Colo State Coll Exp Station Rep 1:227–235

Burnside CE, Vansell GH (1936) Plant poisoning of bees. E-398, USDA, Bureau of Entomology and Plant Quarantine, Washington, DC

Cantwell GE, Jay EG, Pearman G Jr, Thompson JV (1972) Control of the greater wax moth Gallena mellonella (L.) in comb honey with carbon dioxide. Parts I and II. Am Bee J 112(9): 302–303, 342–344

Church RM, Williams RR (1978) Fungicides toxicity to apple pollen in the another. J Horticultural Sci 53:91–94

Crane E, Walker P (1983) The impact of pest management on bees and pollination. International Bee Research Association, England, pp 107

Cuningham SA, Fitzgibben F, Heard TA (2002) The future of pollinators for Australian agriculture. Agriculture 53(8):893–900

Davis AR, Shuel RW (1985) Invisible damage to honeybees colonies from pesticides. Can Beekeeping 12:60–61

Delaplane KS (1993) Insecticides, miticides and nematicides. In: Georgia pest control handbook, Special Bulletin 28. University of Georgia Cooperative Extension Service, Athens

Dhuley JN, Majumdar SM, Mudumdar AM, Naik SR (1996) Laboratory studies on contact toxicity of aureofongin in *Apis cerana indica* Fabr. Indian Bee J 58(4):207–208

Eaton GW (1963) Germination of apple pollen as influenced by captan sprays. Proc Am Soc Hortic Sci 83:101–106

Eckert JE, Shaw FR (1960) Beekeeping. Macmillan, New York

Fell RD, Rajotte EC, Yoder KS (1983) Effect of fungicides sprays during apple bloom on pollen viability and honeybee foraging. Environ Entomol 12:1572–1575

Gentile AG, Gallagher KJ, Santner Z (1971) Effect of some formulated insecticides on pollen germination in tomato and petunia. J Econ Entomol 64:916–919

Gupta BN (1994) India. In: Non-wood forest products in Asia. Food and Agriculture Organization of the United Nations, Rome

Hoskins WM, Harrison AS (1934) The buffering power of the contents of the ventriculus of the honeybees and its effects upon the toxicity of arsenic. J Econ Entomol 28:924–942

India Standards Institution (1979) Institute of Pesticides Formulation Technology (IPFT) Bureau of Indian Standards Manak Bhavan, 9 Bahadur Shah Zafar Marg, New Delhi 110002

Johansen CA (1977) Pesticides and pollinators. Annu Rev Entomol 22:177–192

Johansen CA, Daniel FM (1990) Pollinator protection: a bee and pesticide handbook. Wicwas Press, Cheshire

Kapil RP (1970) Role of honeybees in argiculture. Indian Bee J 32:53–577

Kingsmill GF (1917) Sweetened poison mixtures. Proceedings Ontario. Bee Keepers Association. Annual Report, 47:61–62

Kremen C, Williams NM, Tharp RW (2002) Crop pollination from native bees at risk from agricultural diversification. Proc Nat Acad Sci USA 99(26):16812–16816

Kuriachen PM, Thomas V, Dave Y (1992) Taxonomic and phylogenetic significance of fruit walls in Asclepiadaceae. Feeds Repertorium 103:179–193

Levin MD (1970) The effects of pesticides on beekeeping in the United States. Am Bee J 110:8–9

Levin MD (1984) Value of honeybee pollination to United States agriculture. Am Bee J 124: 184–186

Mackenzie KE, Winston ML (1989) Effect of sub lethal exposure to diazinon on longevity and temporal division of labour in the honeybee (Hymenoptera: Apidae). J Econ Entomol 82(1):75–82

Mayer DF (2003) Bee kills from pesticides and the expert witness. Am Bee J 143(7):563

Mayer DF, Johansen CA (1988) How to reduce bee poisoning. Washington State cooperative extensions Leaflet No. 15, WREP, pp 12

Melnichenko AN (1976) Role of insect pollinators in increasing yields of agricultural plants. In: Kozin RB (ed) Pollination of entomophilous agricultural crops by bees. Amerind Publishing Company Private Limited, New Delhi, pp331

Moffett JO, Morton HL, Macdonald RH (1972) Toxicity of some herbicidal sprays to honey bees. J Econ Entomol 65:32–36

Morton HI, Moffett JO, Macuonald RH (1972) Toxicity of herbicides to newly emerged honey bees. Environ Entomol 1:102–110

Naumann M, Isman MB (1996) Toxicity of a neem (*Azadirachta indica* A. juss) insecticides to larval honeybees. Am Bee J 96:518–520

Pimental D, Andow D, Dyson-Hudson R, Gallahan D, Jacobson S, Irish M, Kroop S, Moss A, Schreiner I, Shepard M, Thompson T, Vinzant B (1980) Environment and pesticides: a preliminary assessment. Oikos 34(2):126–140

Poehling HM (1989) Selective application strategies for insecticides in agricultural crops. In: Pesticides and non target invertebrates. Intercept, Wimborne, pp 151–175

Prakash R, Kumaraswami J (1984) Toxicity some insecticides of the Indian bee, *Apis cerana* Feb. Indian Bee J 46:15–17

Ramakrishna C, Rajmohan N, Subramaniam TR (1974) Effect of insecticidal sprays on the pollination of sunflower. Madras Agric J 61(6):175–177

Rana BS, Goyal NP (1991) Field toxicity of methyl demeton and dimethoate to the foragers of honeybee (*Apis cerana indica* F.) visitors to *Brassica chinensis* L. Indian Bee J 53(1–4):73–77

Russell D, Meyer D, Bukowski J (1998) Potential impact of micro encapsulated pesticides on New Jersey apiaries. Am Bee J 38(3):207–210

Sedivy J (1970) The influence of toxaphene insecticides on the pollen of lucerne. Ochr Rost 43(3):187–190 [in czech., english summary. aa-805/71]

Sharma P L (1993) Effects of insecticides and insect pollinators activity on seed yield of cauliflower. Ph.D. thesis, YS Parmar University of Horticulture and Forestry, Solan, pp 189 + xviii

Singh JP (1969) Effect of thiodon on foraging honey bees. Indian Bee J 31:9–10

Singh WJK, Singh R, Hameed SF, Singh B (1989) Field toxicity of some insecticides to *Apis cerana indica* Fabr. Indian Bee J 51(4):137

Smirle MJ (1990) The influence of dextofying enzymes in insecticide tolerance in honeybee (Hymenoptera: Apidae). J Econ Entomol 3(3):715

Sorthia BK, Chari MS (1985) Toxicity of some insecticides to honeybees, *Apis florea* F. and *Apis mellifera* L. J Entomol Res 92(2):195–197

Stark DJD, Jepson PC, Mayer DF (1995) Limitation to use of topical toxicity data for production of pesticide side effects in the field. J Econ Entomol 88(5):1081–1088

Sundararaju D (2003) Occurrence of bee fauna and extent of pollination in insecticide sprayed ecosystem of cashew. J Palynol 39:121–125

Swift JE (1969) Unexpected effects from substitute pest control methods. Biological impact of pesticides in the environment. Symposium, Oregon State University, Corvallis, 18–20 August 1969, 16pp

Thakur AK, Kashyap NP, Dogra GS (1981) Relative toxicity of some pesticides against Italian bees *Apis mellifera* L. Indian Bee J 43(4):101–103

Thompson GM (1881) Paris green. Am Bee J 17(1):85

Troop J (1918) Blossom spraying and bee poisoning. J Econ Entomol 11:433

Wearne RA, Bergman P, Gibbs LC, others (1970) Bee losses – the impact on pollination – honey production. U.S. Department Agriculture Extensive Service, 12 pp

Zhong HE, Mark L, Sheve P, Cate B (2004) Minimizing the import if the mosquito adulterine noted or honeybees, *Apis mellifera* (Hymenoptera: Apidae): aerial ultra volume application using a high-pressure nozzle system. J Econ Entomol 97(1):1–7

Chapter 11
Pollination in Cages

Abstract This chapter describes the need for pollination in greenhouses due to its special agro-ecological conditions and unique constraints. The advantages that greenhouses hold for both achieving pollination of particular crops and for safeguarding managed pollinators are compared with open air cultures. The traits of the two main greenhouse pollinators – bumble bees and honey bees – are discussed according to their relevance for pollination in this horticultural system. Finally, some examples of pollination of greenhouse cultures and predictions for the future development of pollination in greenhouses are described. The need for insect pollination of plants in enclosures arises either because the plants must be isolated to produce uncontaminated seed, or because attempts are being made to find whether the species gives increased seed or fruit following insect visits, or because the crop is being produced under artificial heat in a greenhouse. Whichever of these reasons applies similar problems is encountered. During the early stages of plant breeding hand-pollination can produce sufficient seeds but with expanded programmes of breeding and testing this becomes too laborious and time consuming, and bumblebees, honeybees, blowflies, and more recently, solitary bees have been used to pollinate the flowers.

11.1 Introduction

11.1.1 Buzz Pollination

Buzz pollinated crops require vibration in order to release their pollen (Buchmann 1983), and traditionally, pollination of buzz pollinated greenhouse crops was accomplished through the use of hand-held electric vibrators (Verkerk 1957). Because of expense, risk of damage to the flowers and developing fruit, and the time consuming nature of this method (Cribb 1990), there has been interest in developing alternative methods of pollination. The use of bumble bees (*Bombus* spp.) to pollinate certain crops has become common because they are effective pollinators of severai buzz pollinated crops such as

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blueberries (Shaw et al. 1939), cranberries (Kevan and Gadawski 1983) and tomatoes (Pinchinat et al. 1982; van der Sande 1990; van Ravestijn 1990; Banda and Paxton 1991; Kevan et al. 1991; Pressman et al. 1999). Studies in Europe have shown that bumble bees are at least as effective as hand pollinating greenhouse tomato crops (Banda and Paxton 1991; Kevan et al. 1991; van Ravestijn and van der Sande 1991; Straver and Plowright 1991; Asada and Ono 1996; Dogterom et al. 1998; Pressman et al. 1999). Although honey bees (*Apis melfifera* L.) have been tested as pollinator of various greenhouse crops, they have not been found to be very effective on flowers requiring buzz pollination (Banda and Paxton 1991; Kevan et al. 1991). The farm value of greenhouse tomato crops in southern Ontario was estimated at $77.4 million in 1998 (Horticulture crop statistics, Ontario Ministry of Food and Rural Affairs, 1998). Before 1992, virtually all pollination of tomatoes in greenhouses in Ontario was done by hand vibration. As of 1994, all commercial growers in southern Ontario began to use bumble bees (*Bombus impatiens* Cresson) as their sole means of pollination, creating a new multi-million dollar supply business. Although the use of bumble bees as greenhouse pollinators has spread rapidly, very little basic research has been conducted to answer many important questions. Some of the problems that bee suppliers, crop scientists and growers are having include; low bee activity in some greenhouses and loss of bees through the ventilation systems. Both of these problems may contribute to inadequate levels of pollination in some greenhouses. In addition, little research has been done to determine how different levels of bumble bee pollination affect tomato quality.

Green house cultivation of vegetables is a production system that has number of advantages such as year round production with good quality and enhanced yields. Furthermore, this system allows efficient use of water, fertilizers, pesticides and labour. For these reasons protected or green house cultivation acreage has increased worldwide to two million ha (Pardossi et al. 2004). The leading countries in greenhouse or protected cultivation of vegetables include Spain, Turkey Italy followed by France, Israel and Greece. Greenhouse cultivation has also some constraints such as pollination which is necessary to achieve a reasonable fruit weight and quality. Approximately 45% of greenhouse crop production is attributed to pollination (Southwick and Southwick 1992).

The most important plant taxa that are grown in greenhouse for commercial farming include solanaceae (tomato, peppers and egg plant); cucurbtaceae (melons, watermelons, zucchini and cucumbers) Rosaceae (strawberries) and leguminosae (green beans). However, variations in commercial farming occur for one region to another. For instance greenhouse strawberry cultivation is not commercially important in Spain, but they are in Israel and Turkey. Since plants belonging to different families have their peculiar floral biologics which are important when determining the need for pollination in enclosures.

11.2 Impact of Greenhouse Conditions on Bee Behaviour

Bee colonies that are used for pollination in greenhouses meet unfavourable conditions. To warrant optimal pollination activity, colonies should be healthy. Foraging under confined conditions (e.g. greenhouse, netted cage) brings along its own set of difficulties/complications. One of the most common problems is foragers gathering in the top of the enclosure, especially during the first few days after introduction of the hive. These bees are a loss to the colony; when they manage to escape from the enclosure they do not come back, and if no escape is possible they often die of exhaustion and/or overheating (Occhiuzzi 1999; Amano 2004). These bees are probably experienced foragers in search of a known food source. Pilot experiments have shown that transportation of colonies over rough roads increases the incidence of orientation flights, and it would be interesting to see whether (gentle) shaking of closed colonies before introduction in the greenhouse could reduce the problem of forager loss. However, shaking may also cause eggs, which float on top of the larval food, to drown, leading to mortality of young brood.

Although most stingless bee species that have been tried in pollination studies under confined conditions foraged effectively on the crop, some species were reported to not forage on the crop under confined conditions. This may suggest that some species are not suitable for greenhouse pollination. However, lack of foraging may also reflect suboptimal foraging conditions for the given species, such as a low attractiveness of the crop to the species, rather than a species-specific reluctance to forage under confined conditions. Clearly more studies are needed to get a better understanding of which factors attribute to successful foraging in greenhouses.

11.3 Influence of Floral Biology of Greenhouse Plants on Pollinators

Honeybees and bumblebees are the most important pollinators used in greenhouses which are attracted to pollen and nectar and especially to nectar sugars. Some studies have emphasised on the volume of nectar volume, whereas others have under lined the importance of nectar concentration and type of sugars present (Baker and Baker 1983). Nectar contains glucose, fructose and sucrose as the major sugars. However, narabrinose, galactose, mannose, lactose, maltose, melibriose, tretratose, melizitose, raffnose and stachyose may also occur in the nectar of some flowers. In general, nectars can be categorised into: sucrose dominant, glucose and fructose dominant and almost equal amount of glucose, fructose and sucrose. Besides number of other substances such as amino acids, enzymes, minerals, ions and so forth.

Other floral attractants are size of the flower, colour, flower organs, nectar glands on the petals, nectar volume, nectar composite and amount of pollen which affect rotation frequency of honeybees and bumblebees (Dobson et al. 1990; Fahn 1979; Mcgregor 1997). For instance, corolla colour reflectance of Zucchini shows dimorphism between flower gender which may contribute to the selective foraging by bumblebees. Besides, the reflectance of nectar glands might be influenced by the plastic cover of green house because same materials reduce the ultra violet (UV) of the daylight spectrum.

Furthermore, the chemical components constituting to flowers fragrance also play an important role in the attractance of flowers to bees (Henning et al. 1990; Masson et al. 1991; Matile and Altenburger 1998; Pham-Delegue et al. 1989). The chemical composition of flower volatiles may also affect bee behaviour. Olfactory signals afre rapidly leaned indicating that foraging behaviour. Olfactory signals are rapidly learned indicating that foraging behaviour results from the association of plant attachments acting as chemosensory cues for the bees (Pham-Delègue et al. 1990) Moreover, the fact that in some cases bees are more attractants to flowers with a meagre level if nectar than to those with high levels indicates that the olfactory signals may be dominant for controlling bee behaviour therefore, bee behaviour is controlled by the integration of both perceived cues such as colour and or fragrance and the actual amount of reward such as pollen and nectar (Mena Granero et al. 2004, 2005a, b).

11.4 Impact of Physical Properties of Greenhouse on Pollination

The pollinators working in confinement are subject to ecological consequences of greenhouses. Generally green houses are covered with glass or different types of plastic films, such as polyvinylchloride (PVC), polycarbonate (PC) and polyethylene (PE). PE is the most popular of the plastic materials. Besides other aspects, all materials differ in their transmission of UV light (wave length between 300 and 400 nm). UV blocking plastic films help in decreasing the population levels of harmful insects in the crops (Costa et al. 2002). However, UV light is an important component of bee vision and orientation (Peitsch et al. 1992), and the degree of UV transmission through the green house covering affects the behaviour of bees used as pollinator. under glass with UV transmission (upto 80%) bees behave normally. under PVC or PC, With a very low UV transmission (less than 3%), they perform poorly, until atleast they "learn" to cope with the lack of UV vision. a new integrated pest management strategy in green house is to block UV radiation for pest control (Soler et al. 2006). in tomato greenhouse however, reduced radiation interfered with the bees navigation ability and thus reduced their activity (Dag and Eisikowitch 2005). in a bumblebee experiment, different behaviours were noticed depending upon the type of plastic cover (Soler et al. 2006).under UV-absorbing plastic significantly more bumblebees appeared at the nest entrance without flying to forage than was the case under plastic without UV filters. the bumblebees that did fly under UV–absorbing plastic spent more time at the platform nest entrance before flying. Bumble bees that returned from a flight spent more time at the entrance before actually reorienting the nest. Under UV-blocking material, daily activity started slightly later in the day than under material without UV filters.

Morandin and co-workers (2001) compared four types of PE, one with a high degree of UV transmission (called CT), the other three types transmitting only a small fraction (down to 0%) of the UV light. They found that bees under CT plastic made twice as many foraging trips as the bees under three other types. moreover, fewer got lost under the CT plastic (136% more bees remaining after 10 days). Similarly, bumblebee colonies performed better, as measured by foraging visits to flowers under UV – blocking plastics when some normal (UV-containing) daylight entered the greenhouse, for instance through pieces of gauze screen.

Dyer and Chitka (2004) using artificial tomato flowers offered at a distance of 1 m under UV + and UV− conditions, showed that bumblebees indeed detected the presence or absence of UV light. However, the bees were able to find the flowers under both the conditions, presumably after learning to recognize flowers in the absence of UV light.

11.5 Enrichment of Atmosphere with Carbon Dioxide

In modern greenhouse, the CO_2 is artificially increased to stimulate the growth of plants 9 – 3 times the natural level of about 360 ppm. In some cases, measurements of CO_2 close to the gas outlets can be as high as 10,000 ppm. The activity and development of bumblebee colonies placed closed to the outlets are negatively affected at values above 1,000 ppm. Research has shown that from 1,000 ppm upward bees become less active, and at around 5,000 ppm the first larval and adult mortality occur (van Doorn 2006). Colony mortality occurs above 150,000 ppm. Therefore, nest boxes must be placed away from the gas outlets (not underneath them and at least 1 m away from them). Another interesting affect of CO_2 enriched atmosphere was noticed in melons, in which CO_2 levels were found to affect the floral rewards by increasing nectar sugar concentration and possibly honeybee activity (Dag and Eisikowitch 2000a, b).

11.6 Greenhouse Temperature and Humidity

The amount of incoming pollen is influenced not only by the availability of pollen inside the greenhouse but also by bee foraging activity. Bumble bee workers usually do not forage at temperatures below 100°C (Heinrich 1979). However, compared with other bees, including honeybees they forage at relatively low temperatures. For this reason, they are highly esteemed as pollinators of protected crops growing under adverse climatic conditions (Abak et al. 1997a, b; Ercan and Onus 2003, for pepper; Dasgun et al. 2004, for tomato; Abak and Dasgun 2005, for egg plant). The foraging activity of bumblebee is also influenced by high temperature above 30°C. In plastic greenhouses, maximum temperatures often rise above that level (upto around 40°C; Abak and Dasgun 2005). bumblebees limit foraging when the temperature rises above 320°C (Kwon and Saeed 2003 for

Bombus terrestris), although we have observed bumblebee workers foraging at 45°C.they are able to fly at air temperatures up to 35°C but they prefer to stay the nest to ventilate the brood. Above 320°C, bumblebee workers not only stop foraging and start ventilating the brood, but they also stop feeding the larvae (Heinrich 1979; Vogt 1986). Bumblebee larvae can starve for a considerable length of time (upto 2–3 days) before they die; however, a period of starvation results in a more prolonged developmental time (Plowright and Pendrel 1977; Sladen 1989; Suteliffe and Plowright 1990). Nevertheless, because hot days usually are accompanied by periods with moderate temperatures during early morning and late afternoon (Abak and Dasgun 2005),usually the pollination activity and therefore, the pollen intake of the colonies will not be completely blocked at around 40°C bee prevent their own bodies from overheating by becoming inactive and stop fanning. As ling are they are ventilating the nest, they are able to keep the brood temperature equal to, or just above (1–2°C), ambient temperature (Heinrich 1979; Vogt 1986) but at temperatures over 40°C they are not able to cool the brood below ambient temperature, Vogt (1986) suggested that the reason is that little or no evaporative cooling is used. It is well known that some other social insects such as honey bees and wasps, cool the nest by evaporating water that has been collected for that purpose (e.g. Wilson 1971). Although there is no clear agreement on the temperature thresholds limit, it has been indicated that an ambient temperature of 400°C is about the maximum temperature at which bumblebee colonies can survive, on a condition that a sufficient energy supply is available (van Doorn 2006).

Pollen production occurs without any problems in regularly heated greenhouses in cold winter regions, such as in Holland. However, the amount and quality of pollen decrease in regions with mild winter climate (Abak et al. 1997a, b). For example, in Turkey or Spain, heating is used to prevent frost only at particular times. Consequently, there are substantial fluctuations in greenhouse temperatures (at night in winter temperatures are low and in the day time in spring temperatures are high inside the greenhouse) (Abak et al. 1995). other important problems from a climatic point of view are high humidity due to inadequate ventilation and low light permeability due to low quality of plastic covers. both circumstances are limiting for quality fruit production. because of the problems mentioned, greenhouse pollination has gained in relevance for research in the Mediterranean greenhouse region.

A final consideration about temperature and bee behaviour has been recently raised by Dyer et al. (2006) who demonstrated that bees prefer warm nectar to cool nectar and that they are capable of using colour to predict floral temperature before landing. floral colour signals are used by pollinators as predictors of nutritional rewards, such as nectar. but as insect pollinators often need to invest energy to maintain their body temperature above the ambient temperature, floral heat might also be perceived as a reward. Bumble bees (*Bombus terrestris*) prefer to visit warmer flowers and can learn to use colour to predict floral temperature before landing. In what could be a wide spread floral adaptation, plants may modulate their temperature to encourage pollinators to visit.

11.7 Greenhouse Pollination

11.7.1 Caging Effect

A cage may affect the plant growth by influencing its micro and macro and environments. Different types of cages may have a variable effect on the light intensity, Temperature, humidity and wind speed depending upon the weather and climate conditions. The cage designed by Pederson et al. (1950) is commonly used for pollination studies since it has little effect on the environment to which the plants are subjected and id light portable, easily assembled and stored. It consisted of a frame of 1.3 cm diameter electrical conduit which supported a plastic screen cage with five meshes per cm. a zip at each corner of the cage allowed easy access. Probably large cages have little effect on the environment than a small cages. In few crops such as *Brassica alba*, *B. nigra*, *Ribes nigrum* and *Carthamus tinctorius*, caging has been found to reduce the seed yield.

11.7.2 Construction Material for Enclosures

Honeybees forage well in air inflated polythene bubble greenhouses, nylon screen cages erected within the fibre glass greenhouses and inside large polythene tunnels but unable to forage in green houses made of ultraviolet opaque polymethyl methylcylate sheet and fibre glass.

11.8 Type of Bees for Caging

When the colonies ate first caged or put in green houses many of the bees spend much or all of their time trying to escape, fail to return to their hives and die. In green houses the bees are stimulated to excess flight by the unaccustomed heat, and the glass itself also confuses them as they are established foragers. Low height cages (up to 1.5 m) are believed to discourage bees flying against the walls of cage and encourage foraging. The young bees may readily adapt to the cage conditions. the absence of established foragers also reduces the possibility of bees carrying viable pollen into the greenhouses.

11.9 Size of the Colony

Queen right colonies are most efficient pollinators. Colonies with three or four combs of brood and bees adequate for pollination in cages or green houses. Using too large colonies (10,000 bees) in cages may badly damage the anthers, stigmas and corollas. So use of ideal colonies (2,000 bees) is advocated if needed additional frames of emerging bees may be added.

11.10 Sustaining the Caged Conditions

Colonies confined in cages may dwindle in strength owing to scarce forage. An arrangement should be made for bees to fly alternatively in open and into cages on consecutive days or provide artificial food to satiate the requirement of confined bees or locate the colony outside a cage so that it can forage freely and then direct one or two hundred foragers from the colony into it at the beginning of each day. However, this method fails where contamination inside the cages with foreign pollen is to be avoided. Feeding sugar syrup to the colonies inside cages of greenhouses stimulates pollen collection and hence probably results in more pollination. In *Brassica oleracea*, feeding sugar syrup to honeybees reduces the nectar robbers.

11.11 Contamination of Seed Crops

To avoid contamination to pure seed crop (<0.5%), confining bee colonies for 12–48 h have been found suitable in getting viable pollen free bees for pollination in crops like *Brassica oleracea, Medicago sativa, Melilotus alba* and sunflower. the period of confinement of bees depends upon the duration of viability of pollen sticking to the bee's body. In *Brassica oleracea*, the viability of body pollen decreased to 0.5–1.5% after foragers spent 22 h in their colony. foragers that were caged with for 24 h away from the colonies retained more body pollen, 9–20% of which was still viable. Hand collected pollen kept in petridishes for equivalent period was 42% viable.

11.12 Site of Colony Location

To get an even distribution of honeybee foragers on a green house crop, it is better to have a single colony near the centre of a green house than at one end and two or more colonies to have them at diagonally opposite corners or evenly distributed. The hive should be placed in the same relative position in new green house as was in first one.

11.13 Bee Activity and Loss

Anecdotal reports from greenhouse growers and bee suppliers suggest that there is variation among greenhouses in the level of bee activity outside the colonies, and in bee loss through the ventilation systems. Because different types of greenhouse plastic have different transmission spectra, and because bees see within the UV range, variation in plastic type among greenhouses may be responsible for some of the variation in bee activity and loss.

11.14 Bee Vision

Most Hymenoptera, including bumble bees, have trichromatic colour vision (e.g. Mazokhin-Porshniakov 1969; Menzel and Backhaus 1991; Peitsch et al. 1992). The three colour receptors are stimulated by ultraviolet, blue and green wavelengths, with the peak sensitivities at 345, 440, and 550 nm respectively (Kevan and Backhaus 1998; similar to Peitsch et al. 1992). Trichromatic colour vision spans about 300 nm of natural daylight starting at about 310 nm (Kevan and Backhaus 1998). It has been shown that sensitivity to UV in honeybees and other insects is 4–6 times higher than to other parts of the spectrum (Kevan 1970, 1979, 1983; Laughlin 1976; Menzel and Backhaus 1991), suggesting that UV is an important component of insect vision.

Various studies have shown that ultraviolet Light produces a positive phototactic response in many insects, including honeybees (Berthoff 1931; Kaiser et al. 1977; Menzel 1979; Menzel and Greggers 1985), fruit flies (Fischbach 1979), and Diptera (Kevan 1979). It is believed that insects use UV light as an indicator of an open environment (von Hess 1913; Laughlin 1976 – dragonflies; Menzel and Greggers 1985). The polarization pattern of the sky may be used as a celestial compass even under cloudy conditions (Brines and Gould 1982). von Frisch's work (von Frisch 1965) showed that honey bees use polarized light as a means of orientation and navigation. With increasing wavelengths, the polarized pattern becomes subject to atmospheric disturbance (Rozenberg 1966), consequently, it is believed that bees primarily use polarized light within the UV range for orientation. Von Helverson and Edrich (1974) tested the sensitivity of honeybees to different wavelengths of polarized light, and found a maximum sensitivity at 345 nm. They determined that polarized light was detected exclusively by the UV receptors. All three colour receptors in honey bees have been found to be important for large area movements (Kaiser and Liske 1974; Kaiser et al. 1977), as well as foraging behaviour (Thompson 1995). Because bee activity has been found to be affected by various wavelengths of light, evidently, greenhouse plastics that differ in intensity and spectrum of light transmission affect bee activity and bee loss. Because bees use UV light, plastics that transmit more of the UV range may result in greater levels of bee activity. A large spectrum of UV light within a greenhouse may attract more bees to leave the colony, or enable the bees to better orient and navigate, resulting in shorter, more efficient foraging trips. Variation in intensity of transmission and wavelengths transmitted by the plastics may also cause differences in internal temperature, which may affect bee activity, because bee activity increases with increasing temperatures (Lundberg 1980-bumble bees; Abrol 1990 alfalfa pollinating bees; Armbruster and McCormick 1990 euglossine bees; Corbet et al. 1993-honey bees and bumble bees; Abrol 1998-alfalfa-pollinating bees).

Loss of bees through ventilation systems may also be affected by type o greenhouse plastic. The difference in contrast with daylight may be a factor in explaining why bee loss is a serious problem in some greenhouses but not others.

Some of the problems associated with the use of bumble bees as greenhouse pollinators include, loss of bees through the ventilation systems, and variation in levels of bee activity. Anecdotal reports suggest that variation in colony size occurs among greenhouses as a result of loss of bees through cooling vents. Because of the expense of this problem and the effect on pollination levels, it is important to determine what causes the substantial loss of bees in some greenhouses. Greenhouse growers and suppliers have also observed variation in the level of bee activity among greenhouses, leading them to question what factors may be responsible for the variation. Factors that may be responsible for varying levels of bee activity in different greenhouses include greenhouse plastic type, internal greenhouse temperature and humidity, and internal light levels. Various plastic types are used for the different greenhouses. The plastic types have unique transmission spectra, and differ in the amount of UV intensity of light transmitted.

It has been shown that sensitivity to UV in honey bees and other insects is 4–6 times stronger than to other parts of the spectrum, suggesting that UV is an important component of insect vision (Kevan 1970, 1979, 1983; Laughlin 1976; Menzel and Backhaus 1991). Various studies have shown that ultraviolet light produces a positive phototactic response in many insects, including honeybees (Berthoff 1931; Kaiser et al. 1977; Menzel 1979; Menzel and Greggers 1985), fruit flies (Fischbach 1979), and Diptera (Kevan 1979). It is believed that this high responsiveness to UV light results from the insects' taking it as indicator of an open environment (von Hess 1913; Laughlin 1976 Mragonfiies; Menzel and Greggers 1985).

Loss of bees through ventilation systems may also be affected by greenhouse plastics. In greenhouses with plastics that transmit large amounts of UV light, there will be little visual contrast between the open vents and the rest of the roof. In greenhouses with UV blocking plastics, there will be a large visual contrast between the light coming through the open vents and the light coming through the rest of the roof.

It was also believed that daily ambient sunlight levels and internal greenhouse temperature would be positively correlated with bee activity. Because UV light acts as a positive phototaxis for bees (Berthoff 1931; Kaiser et al. 1977; Menzel 1979; Menzel and Greggers 1985), it was expected that there would be greater loss of bees under plastics that transmitted less UV light. Daily activity patterns within greenhouses were also assessed.

Extensive studies by Williams (1940, 1961) and Williams and Osman (1960), on insect activity using trap catches showed that activity increased gradually to a maximum at *2 g°C*; further temperature increases to 34°C resulted in a negative correlation with activity. Many studies have found that bees become more active with increasing temperatures (Lundberg 1980 – bumble bees; Abrol 1990 – alfalfa-pollinating bees; Armbruster and McCormick 1990 – euglossine bees; Corbet et al. 1993 – honeybees and bumble bees; Abrol 1998 – alfalfa-pollinating bees) – A positive correlation between temperature and activity may be a result of deceased thermoregulation costs as temperature increases from 5°C to 25°C (Heinrich 1979). Although few studies have looked at levels of bee activity under very high temperatures, it is believed that they may cease fight (Chappell 1982-carpenter bees), or counter overheating through evaporative cooling (Heinrich 1979-honeybees). Chen and Hsieh (1996), examined bumble bee activity in tomato greenhouses, and found that pollination activity was reduced in the summer as a result of extreme temperatures (up to 40°C). In commercial greenhouses, the highest average daytime greenhouse temperature was 28°C. Because there was no decreased activity up to this point, the observed greenhouse temperatures were apparently within the bees' acceptable temperature range for foraging. Greater bee activity in the CT greenhouse supports the hypothesis that bees are most active when exposed to an extended range of ultraviolet light. Although the hypothesis is supported, the higher internal temperatures in the CT greenhouse may have been partially responsible for the greater activity observed. However, it is unlikely that the 6% higher temperature in the CT greenhouse could have been solely responsible for the fourfold increase in activity in the CT greenhouse over the Patilux greenhouse during the temperature and humidity experiment.

Foraging under confined conditions (e.g. greenhouse, netted cage) brings along its own set of difficulties/complications. One of the most common problems is foragers gathering in the top of the enclosure, especially during the first few days after introduction of the hive. These bees are a loss to the colony; when they manage to escape from the enclosure they do not come back, and if no escape is possible they often die of exhaustion and/or overheating (Occhiuzzi 1999; Amano 2004). These bees are probably experienced foragers in search of a known food source. Pilot experiments have shown that transportation of colonies over rough roads increases the incidence of orientation flights, and it would be interesting to see whether (gentle) shaking of closed colonies before introduction in the greenhouse could reduce the problem of forager loss. However, shaking may also cause eggs, which float on top of the larval food, to drown, leading to mortality of young brood. Although most stingless bee species that have been tried in pollination studies under confined conditions foraged effectively on the crop, some species were reported to not forage on the crop under confined conditions (Table 11.2). This may suggest that some species are not suitable for greenhouse pollination. However, lack of foraging may also reflect suboptimal foraging conditions for the given species, such as a low attractiveness of the crop to the species, rather than a species-specific reluctance to forage under confined conditions.

Clearly more studies are needed to get a better understanding of which factors attribute to successful foraging in greenhouses. Experiments were carried out at the seed company Flora Feliz, Cartago, Costa Rica (9° 43′ 51″N, 83° 54′ 51″ W, altitude 1,388 m). Flower visitors of *S. farinacea* were captured in an open-air patch of 40 plants in December 1995. Pollination experiments were conducted in four netted enclosures ($6 \times 3 \times 3$ m) in April 1996. Each enclosure contained 60 plants that were pollinated by one of the three bee species during 1 month, or were left without pollinators (control). The following bee species were used: *Nannotrigona testaceicornis*, *Tetragonisca angustula*, and *Apis mellifera. N. testaceicornis* is a small robust bee with a body length of 4.1–4.2 mm. Colonies contain a few thousand individuals and the species is quite common in the Neotropics. *T. angustula* is a small, slender bee with a body length of 4.4–4.7 mm. It is the most abundant stingless bee species in Costa Rica with a colony size up to 5,000 individuals. We used a five-frame hive of Africanized *A. mellifera* with approximately 10,000 workers. Bees in the family Apidae were the most common visitors of *S. farinacea* in the open.

11.15 Categories of Insects for Greenhouse Pollination

The different categories of insects which have proved as effective pollinators under controlled conditions include:

Primary insect pollinators are

1. Bumblebees
2. Honey bees
3. Houseflies
4. Blue bottle flies.
5. *Osmia lignaria* or blue orchard bee and *O. cornifrons* or hornfaced bee
6. Alfalfa leafcutter bee or *Megachile rotundata*

11.15.1 Bumblebees

1. Social bee with ca 50 bees/colony
2. Excellent pollinator of many plants
3. Work in rainy, cool (13°C or 55°F), windy weather
4. Active for long hours
5. Rearing is difficult so commercial colonies are used
6. Mildly aggressive
7. Bumblebees are used in ca ten cages per year
8. Used mainly for ornamentals with trumpet shaped flowers as bumblebees have long tongues
9. Used in both field and greenhouse cages
10. Can be purchased year round but availability may be limited by demand
11. Queenright colonies may be too aggressive in working cages with tender or few flowers; Drone colonies are more "mellow"
12. Occasionally we collect "wild" bumblebees for temporary cage use; put 3–5 bees per cage which live ca 5 days

Bumblebees work well in confinement and are especially valuable for use in small enclosures. They can usually be readily obtained from the flowers or by collecting their nests (see Free and Butler 1959). If nests are difficult to find, local advertising usually produces the desired result. Lindhard (1911, 1921) was the first to use bumblebees in cages for pollinating. He enclosed colonies with *Trifolium pratense* plants after first caging them with *Lotus corniculatus* to free them of any viable pollen they might have been carrying. Williams (1925) used bumblebees to pollinate *T. pratense* in small compartments (90 × 90 × 90 cm) of a glasshouse. To ensure that they did not contaminate the selected strains with pollen from elsewhere he captured the bumblebees on flowers other than *T. pratense*, washed them in tepid water, and dried them in isolation for 3–4 h before use. Tests confirmed that this method was effective and, although pollination with pollen that had been immersed in water for only 5 min gave some seed, after it had been dried it was non-viable. Usually only one bumblebee was kept in a cage; they remained active for 12–15 days in favourable weather. When more than one bumblebee was confined in a cage they became lethargic, probably because they were short of food. Pedersen and Bohart (1950) used bumblebees to cross-pollinate *Medicago sativa* clones. They found that a single colony was ideal for pollination in a cage 3.5 × 6.5 × 1.8 m high. The colonies were provided with a gravity feeder containing diluted honey. Because *M. sativa* was the only source of pollen available, a greater proportion than usual of bees of some species visited the flowers for pollen.

Bumblebees have also been used to pollinate in small cages containing *Brassica oleracea*, *B. napus*, *Cichorium endivia*, *Raphanus sativus* or *Cichorium intybus* (Priestley 1954; Kraai 1958). Recent successful methods of producing bumblebee colonies in captivity (page 80) will no doubt encourage their use in enclosures for the pollination of many crop species, especially *Lycospersicon esculentum*, tomato.

The bumblebees work well in confinement and are especially suitable for use in small enclosures. They can work at low temperature at which honeybees cannot. Lindhard 1911 was try he first to use bumblebees in cages in *Trifolium pretense.* Later, William (1925) used them in small glass compartments (90×90×90cm) *T. pretense.* Washing and drying of bees prior to release in cages was found effective in getting pollen free bees.

In *medicago sativa* one colony in cage of 3.5×6.5×1.8 m high was found ideal for pollination. The bumblebees have been reported to be suitable for pollination in cages in crops like *B. oleracea*, *B. napus*, *Cichorium endivia*, *Raphanus sativus*, *Lycopersicon esculentum etc.*

Rearing of bumblebees bees in captivity (artificial domiciles) became possible when the queens of *Bombus terrrestris* could be stimulated and helped to establish colonies by the presence of a few newly emerged honeybee workers (Ptacek 1983). the diapauses in queens can be broken by exposing them to carbon dioxide so that overwintering could be avoided. A colony with 80 worker strength is strong enough to be used for pollination. The use of distinguishing colours for different boxes has been found helpful in smooth functioning of various bumblebee colonies. Protection of bumblebees against their enemies especially parasitic bumblebees (*Psithyrus spp.*) and the nematode, *Sphaerularia bombi* should be provided.

11.15.2 Honeybees

Honey bees

1. Social bee with 2–4,000 bees/cage
2. Traditionally used to pollinate many different plants
3. Forage best from 15°C to 32°C (60–90°F); don’t fly when wind speeds exceed 25 MPH
4. Rearing well established but costly due to equipment and regular care required
5. Aggressive, sting

Honey bee use

Major insect pollinator utilized

1. Placed in ca 800 cages per year
2. Can be used year round
3. Used in both field and greenhouse cages
4. Used to replace *Osmia* in *Brassica* cages
5. Used in conjunction with flies in umbels

The following are the important commercial green house crops where honeybees are used to pollinate: *Lycopersicon esculentum: Prunus persica: P. domestica: Cucumis sativa: C. melo* and many ornamentals. Because of the ease with which they can be obtained, honeybees are usually preferred to bumblebees for pollination in large cages or greenhouses. Using honeybees to pollinate fruit, vegetables and ornamental flowers in greenhouses has increased considerably of late. In Japan about three-quarters of the honeybee colonies used for pollination are concentrated on strawberry production in greenhouses (Sakai and Matsuka 1982, 1988).

Cages of many types of construction and material have been used for pollination work. Early ones often consisted of a wooden or metal framework, covered with muslin, wire mesh, or perforated zinc.

Many of these were cumbersome and difficult to transport and the first field cage that was light, portable, easily assembled and stored was designed and used by Pedersen et al. (1950). Cages based on its design are now commonly used in pollination studies and have been adapted to cover large areas of crop (see Farrar (1963)). It consisted of a framework of 1.3 cm diameter electrical conduit, which supported a plastic screen cage with five meshes per centimetre. A zip at each corner of the cage allowed easy access.

Inevitably, a cage influences the light intensity, temperature, humidity and wind speed to which the plants inside are subjected; but the extent to which it does so varies with different weather and climatic conditions and with different types of cage; the effect of these differences on plant growth also depends on the plant species concerned. The cage designed by Pedersen et al. (1950) had little effect on the environment to which the plants were subjected, compared to cages of an earlier design with walls of metal screen or cloth; the relative humidity, light and wind speed inside were slightly reduced, but the temperature inside and outside was the same. Probably large cages have less effect than small ones. Palmer-Jones et al. (1962) found that large cages had little effect on the growth of *Trifolium repens*, but others have found that cages have a pronounced influence on plant growth. For example: Free and Spencer-Booth (1963b) found that *Brassica alba* and *B. nigra* plants caged with bees became etiolated and produced less seed than in the open; caging has also been found to diminish the yield of *Ribes nigrum* (Hughes 1966) and *Carthamus tinctorius* (Rubis et al. 1966). Free (1966b) obtained evidence that in some conditions the adverse effect of caging on *Vicia faba* seed production was so great that it tended to minimize the beneficial effect of honeybee pollination (see also pages 6 and 7).

Because colonies confined without much forage inevitably dwindle in strength, arrangements have sometimes been made for them to fly alternately in the open and into cages on consecutive days (Butler and Haigh 1956). However, there is a controversy as to the value of such a procedure; some workers (e.g. Scriven et al. (1961) and National Agricultural Advisory Service, Derby, 1962) reported that under such alternating conditions, few bees appear to settle to forage in the cages and that a high mortality occurs on days the bees are confined, whereas Nye (1962) stated that the mortality rate was greater when colonies were confined continuously rather than intermittently. To preserve colony strength without providing artificial food, it is possible to obtain sufficient pollination by locating a colony outside a cage so it can forage freely, and then to direct one or two hundred foragers from the colony into it at the beginning of each day. However, this method is of no use when it is necessary to avoid contaminating the plants inside the cage with foreign pollen. Although bees leaving their hives carry viable pollen on their bodies (Free and Durrant 1966) this pollen loses its viability after several hours. When Butler and Haigh (1956) allowed bees to fly into a cage and outside the cage on alternate days, the change-over was made after flying had ceased for the day, and the *Brassica oleracea* and *Raphanus sativus* cultivars in the cage produced pure seed although other cultivars of each species were growing just outside. Kraai (1962) kept honeybees with cultivars of *B. oleracea* (cabbage, kale, sprouts), *R. sativus*, *Begonia* spp. *Cheiranthus cheiri* or *Centaurea cyanus* that had dominant characters, and then either isolated the bees or confined them to their hives for a minimum of 10 h, and finally put them with cultivars of the same species that had recessive characters. There was no contamination of the recessive cultivars with pollen from the dominant. Hence, it would seem safe to transfer a honeybee colony between cages containing cross-compatible cultivars without danger of contamination, after confining the bees to their hives overnight. Haslbachova et al. (1986) also demonstrated that after 12 h isolation the same pollinating colonies of honeybees could be used for pollinating different but generally related *Brassica* plants without the risk of undesired pollination. In a more intensive study Kubisova and Haslbachova (1990) found that after *Brassica oleracea* foragers had spent the night in their colony, their bodies had fewer pollen grains than when caught on *B. oleracea* flowers. The viability of the body pollen decreased to 0.5–1.5% after the foragers had spent 22 h in their colony. Foragers that were caged for 24 h away from colonies retained more body pollen, 9–20% of which was still viable. Hand collected pollen kept in petri dishes for the equivalent period was 42% viable.

Pankiw and Bolton (1965) and Pankiw and Goplen (1967) showed that when honeybee colonies had been isolated from a contaminating source of *Medicago sativa*, *Melilotus alba* or *Melilotus officinalis* for 2 days the bees no longer carried viable pollen from it. Confining honeybee colonies for 12 and 36 h before introducing them to a cage containing sunflowers reduced contamination of seed to 0.35% and 0.20% respectively (Wilson 1989). To obtain pure seed of a range of crop species Ellis et al. (1981) arranged for colonies, used to pollinate in cages, to fly in the open on alternate days. They considered that pollen contamination was unlikely to occur with this method and showed that no crossing occurred between cucumbers grown inside and just outside the cages. Pollination every other day provided adequate pollination and good seed set. A few bees often remained in the cage overnight and so performed some pollination on the ‘out’ days.

Experience has shown that using honeybees to pollinate early flowering crops in greenhouses is particularly likely to harm the colonies. Sometimes this is difficult to avoid, particularly when the flowering season is a long one. Consequently, efforts are often made to use colonies whose destruction will be no great loss. The presence of a queen stimulates foraging (pages 49, 71) and Goplen and Pankiw (1961) reported that queenless colonies were not as efficient as queenright colonies for pollinating *Melilotus alba* in cages. However, queenless colonies may provide sufficient foraging for some purposes. Kraai (1954) found that small colonies of two or three combs, which were queenless but contained plenty of brood, were suitable for greenhouse compartments 3×5×2 m. For smaller compartments (0.8×0.8×2 m) he used very small colonies in miniature hives. These hives, which had walls 1.5 cm thick were of two compartments; the larger front compartment had two miniature combs and the smaller rear compartment contained sugar syrup and dry sugar. The two compartments were connected by a small round hole and the larger front compartment had two additional holes; one served as a hive entrance and the other covered with wire gauze as a ventilator. Each hive was given 400–500 bees initially and 100 newly emerged bees were added later. These small colonies survived an average of 25 days in the glasshouse compartments and a few lived 112 days. Kraai successfully used his small colonies to self- and crosspollinate selected strains of *B. oleracea* (cabbage, winter and summer cauliflower), *R. sativus*, *Brassica rapa*, *Cichorium endivia*, *C. intybus*, *Tragopogon porrifolius*, *Daucus carota*, *Apium graveolens*, *Asparagus officinalis* and *Fragaria* × *ananassa.* Obviously honeybee colonies of such a small size are not viable and can only be used in heated greenhouses and to pollinate relatively few plants.

For most circumstances colonies containing three or four combs of brood and bees are adequate for pollination in cages or greenhouses (e.g. Steuckardt 1963; Cooper and Emmett 1977; Matsuka and Sakai 1988). It can be disadvantageous to use colonies that are too large for the areas needing pollination. Weaver (1956) put colonies of about 10,000 bees into cages of *Vicia villosa* and found that the anthers, stigmas, and corollas were badly damaged by such an excess of insects; he largely eliminated this trouble by replacing the colonies with ones containing less than 2,000 bees. Should the colonies become weakened, combs of emerging bees can be introduced to them. When the combs do not contain sufficient pollen to maintain brood rearing a supply of pollen or pollen substitute should be made available. The bees should be provided with a source of sugar and, if dry sugar or candy is given, it is essential to give water also. Water may also be needed by the bees to regulate the temperature of their colonies. In addition to providing food for the colony, feeding sugar syrup stimulates pollen collection and hence probably results in more pollination; Free and Racey (1966) found that pollen-gatherers were more valuable pollinators of *Freesia refracta* in greenhouses than nectar-gatherers and their numbers could be increased by feeding their colonies with sugar syrup. This may well also apply to other greenhouse crops especially *Actinidia chenensis*, Kiwi fruit (see page 114). Feeding sugar syrup to honeybee colonies caged with *Brassica oleracea*, Brussels sprout plants, greatly diminished the proportion of bees that were robbing the flowers of nectar and failing to pollinate (Free and Williams 1973a, b, c).

It is usually found that when colonies are first caged or put in greenhouses many of the bees spend much or all of their time trying to escape, fail to return to their hives and die. This seems to be particularly true in greenhouses, and is perhaps partly because the bees are stimulated to excess flight by the unaccustomed heat, and partly because the glass itself confuses them. However, it is usually found that the proportion of bees trying to escape soon decreases, probably because the bees concerned are established foragers and soon die. Scriven et al. (1961) and Hawkins (1968) allowed the foragers of small colonies that they had prepared for pollination work to fly back to their original hives so that the small colonies consisted of young bees only, which quickly adapted to cage conditions. The absence of established foragers also reduced the possibility of the bees carrying viable pollen into the greenhouse. Rothenbuhler et al. (1968) found that, when colonies composed entirely of young bees without previous flight experience were used in cages, the bees orientated when they left their hives and nearly all of them returned. However, it is not always possible to prepare colonies of young bees only, or colonies of bees without foraging experience, particularly in the winter or spring. The use of a synthetic Nasanov lure (see Free (1987)) at the hive entrance may help the bees return to their hives. Hitchings (1941) and Cuypers (1968) reported that releasing colonies in greenhouses after dark reduced the subsequent tendency of bees to fly against the glass; this tendency was also reduced when the sky was overcast during the first few days the bees were in the greenhouse, and the greatest loss was likely to occur on the first sunny day. The cages used by Ellis et al. (1981) were only 1.5 m high; there, was little space between the canopy of most crops and the cage roof, which allowed very little free-flying room. They believed this discouraged flying against the cage walls and encouraged foraging.

Free and Racey (1968), who used honeybees to pollinate an early crop of *Phaseolus multiflorus* in a greenhouse, put the colonies just inside the open doorways so the bees : could also fly outside; under these conditions few, if any, of the bees became lost in the greenhouse and the flowers were adequately pollinated. When conditions in a greenhouse are too unfavourable for honeybee colonies in the spring or summer, they may be kept outside and allowed access to the greenhouse through tunnels connected to their hive entrances. Sorokin (1958) and Shemetkov (1960) used hive entrances which allowed access to both a *Cucumis sativus* greenhouse and the open air; bees that started to work in the greenhouse continued to do so but in order to ensure sufficient recruits to maintain the greenhouse population, the part of the hive entrance leading to the outside was closed until 10.00 h each day. Honeybees seem unable to forage in greenhouses made of ultra-violet opaque polymethyl methacrylate sheet (perspex) and fibre-glass (Moffett and Spangler 1974; Cooper and Emmett 1977).

The latter reported that ultra-violet transparent grades of these materials were available and that bee flight can be improved in existing structures by inserting glass panels. Moffett and Caddel (1985) overcame the problem by confining the bees to nylon screen cages erected within fibre-glass greenhouses. Honeybees appear to forage and pollinate satisfactorily in large polyethylene tunnels commonly used for growing strawberries in England. Most honeybees forage for nectar in them and those collecting pollen are able to obtain only small loads. Probably the polyethylene allows sufficient light, including ultra-violet light, to enter. Honeybees also forage well in air-inflated polyethylene 'bubble' greenhouses (Cooper and Emmett 1977; Moffett and Spangler 1974). Certainly, under the right conditions, when they receive adequate food, and are not subject to sudden temperature fluctuations, honeybees appear to forage as normally in a greenhouse as when visiting a crop in the open. For example, in large greenhouses containing *C. sativus* Hitchings (1941) and Shemetkov (1960) found that the flight period of the bees was adjusted to the times of presentation of pollen by the flowers, and Lecomte (1955) observed that when a choice of species is present, individual honeybees tend to keep to one only.

The site at which colonies are located in a greenhouse is important. Shemetkov (1960) discovered that individual bees kept to one row only of *C. sativus* in a greenhouse. Free and Racey (1966) found that when colonies were located at one end of greenhouses 50 m long containing *Freesia refracta* the number of bees on the flowers became fewer as the distance from the hives increased and the bees tended to work along rather than across rows. D'Aguilar et al. (1967) reported that when a colony was placed at one end of a greenhouse containing *C. melo* comparatively few bees foraged on the plants most distant from their hive. Hence, to get an even distribution of honeybee foragers on a greenhouse crop, it would be better to have a single colony near the centre of a greenhouse than at one end, and with two or more colonies to have them at diagonally opposite corners or evenly distributed. When a hive is moved from one greenhouse to another, it should be placed in the same relative position in the second house as in the first and its hive entrance should face in the same direction to avoid disorientation of the bees; it has been found that keeping hives clear of walls and sloping glass roofs also helps the bees to orientate. Commercial greenhouse crops that honeybees are commonly used to pollinate include *Fragaria × ananassa*, *Lycopersicon esculentum*, *Prunus persica*, *P. domestica*, *Cucumis sativus*, *C. melo* and various ornamental flowers.

Honeybees (*Apis mellifera*) and three species of blowflies (*Calliphora vomitoria*, *Lucilia caesar* and *L. sericata*) were observed on mass-pollinated populations of onions (*Allium cepa*) in 4.4 × 3.6 m × 2–2.5 m cages in June-August 1977. Pollination activity at temperatures from 14°C to 28°C was compared on the basis of mean time per flower touched on each umbel visit. Honeybees did not forage below 16°C. Above 16°C their mean time per flower was short (1.4 s) and varied little with temperature. For blowflies, it decreased markedly from 12.1 s at 14–15.5°C to 2.7 s at 26°C and above, largely because at low temperatures flies spent long periods quiescent or grooming rather than actively feeding. When flowering was not completely synchronous between cultivars, honeybees were more selective than blowflies, but where flowering was synchronous, both types of pollinator visited the two cultivars at random. For the size of cage used, neither type of insect had a distinct advantage as a pollinator of onions, despite their different behaviour patterns (Table 11.4).

Gatoria et al. (2008) conducted pollination studies on radish caging the crop with bee hive, led to the decline in the foraging activity of *Apis mellifera* Linnaeus on radish blooms in the cages. However, providing an additional entrance at the rear of the caged bee hive so that it opened outside the cage resulted in normalizing the foraging activity of the honey bee inside the cages to some extent. It is, thus, suggested that while conducting pollination experiments under caged conditions, an additional entrance at the rear of the bee hive, opening outside the cage should be included.

11.15.3 Solitary Bees

11.15.3.1 ***Osmia***

1. Solitary bee; ca 40 bees per cage
2. *O. cornifrons* brought from Japan in 1977, *O. lignaria* native to U.S.
3. Excellent for early season plants (*Brassica* and fruit trees)
4. Will work 10–32°C (50–90°F) during the spring
5. Rearing is established; cannot be manipulated further
6. Cannot relocate domiciles from original placement during pollination season
7. Non-aggressive

Osmia Domiciles

Domicile is PVC pipe (5 or 7.6 cm diameter) suspended via eye-bolts from 1.25 m metal rod bent at 45° angle ca 1 m from bottom

1. PVC end cap placed on back; front of pipe is cut at an angle to reduce weather damage to straws inside
2. Small domiciles for germplasm cages contain four filled straws (ca 32 bee pupae) in bundle of 16 cardboard tubes
3. Large domiciles for bee increase contain five filled straws (ca 40 bee pupae) in total of 23 cardboard tubes; front of domicile covered with mesh screen to protect from predators
4. Bees need a source of mud for forming walls between cells in nesting straws. Osmia domiciles are collected in early July and stored at 26°C (80°F)
5. Domiciles must be handled carefully to prevent dislodging developing larvae from pollen balls within the nesting straws
6. Nest straws will be invaded by a variety of Hymenoptera
7. Mid-November straws are removed from domiciles and examined for bee pupae before winter storage at 4°C (40°)
8. In March straws are placed into new domiciles ready for springtime use
9. Used in ca 200 field cages of *Brassica* annually from April – June
10. Can be used in cool greenhouse cages beginning in April
11. Used for some miscellaneous umbels and ornamentals

Plant breeders use *Megachile rotundata* for pollination in cages and greenhouses. Bohart and Pedersen (1963) found that these bees were suitable pollinators of

Medicago saliva in 6 m^2 cages in the field (about 50 female bees per cage), and in 1.2 × 1.2 × 0.9 m cages enclosing plants on a greenhouse bench. The bees nested and foraged readily in the cages, although in the greenhouse natural light was supplemented with artificial light on overcast days, and the temperature was maintained above 28°C. They pointed out that either emerging bees or bees collected in the field can be put in the cages, although to avoid possible contamination in the latter circumstances they should be collected from species other than those they are required to pollinate. Because *M. rotundata* is apparently more susceptible to insecticides than the honeybee they recommended that use of insecticides should be terminated several days before the bees are introduced. Heinrichs (1967) used 100 incubated cells, from which adults were beginning to emerge, per growth chamber (1.8 × 2.7 m) containing *Medicago sativa* plants. The chambers were subject to 16 h of continuous light per day (48,000 cd/m^2) and the temperature of 20°C maintained during darkness was increased to 27°C during the light period. The bees did not become active until the temperature exceeded 23°C. The females readily accepted the artificial domiciles provided and pollinated the flowers. In three successive tests 30 plants produced 324, 321 and 282 g seed. He calculated that, by carefully arranging for the emergence of the bees to coincide with flowering, a growth chamber could be used for the pollination of eight successive batches of *M. sativa* plants per year. *Megachile rotundata* has been exported from N. America to be used for plant breeding and greenhouse pollination in other countries (e.g. England, Aubury and Rogers 1971: Japan, Maeta et al. 1973).

Contamination of alfalfa grown for pure seed by *M. rotundata* that had previously visited other alfalfa lines has been measured. Isolating the bees overnight or for periods of less than 16 h were inadequate and could give rise to about *2%* crossing. Contamination could be avoided by giving the bees access to flowering plants of a different species for 24 h prior to reintroducing them to alfalfa (Johansen and Holm 1971; Strachan and Ellis 1984).

Holm (1964) reported that *M. rotundata* was an efficient pollinator of both diploid and tetraploid.

Trifolium pratense, as well as *M. sativa*, and worked more readily in greenhouses than honeybees. Szabo and Smith (1970) found *M. rotundata* useful for pollinating *Lotus corniculatus* and *Cucumis sativus* in greenhouses and to be especially valuable in small cages in which honeybees will not forage. The bees readily collected artificial supplies of nectar and pollen to supplement the insufficient supplies from the flowers. However, they were extremely sensitive to light intensity in such conditions preferring the upper part of *C. sativus* vines and because they did not accept *C. sativus* leaves for cell building, other plants had to be provided. Richards (1991) reported that *M. rotundata* pollinated birdsfoot trefoil, red clover and sainfoin in cages and the yields compared favourably with open fields.

A few comparisons have been made of the pollinating efficiency in cages of solitary bees and honeybees. Johansen and Holm (1971) observed that *M. rotundata* tripped about 95% of alfalfa flowers they visited in cages, but cross-pollinated only 25–47% of the flowers compared to 63–85% by honeybees and bumblebees. Ptacek et al. (1984) found that both *M. rotundata* and bumblebees gave good yields of alfalfa in cages and in greenhouses. Currie et al. (1990) compared *M. rotundata* and honeybees visiting caged plants of *Faba* bean. In different years 40–65% of honeybees entered the flowers and contacted the stigmas; *M. rotundata* did so initially but after 2 days foraged mostly on the extra floral nectaries, and below 17°C ceased to forage while honeybees continued to do so. Waller et al. (1985a, b) compared the carpenter bee, *Xylocopa varipuncta* with the honeybee at pollinating male sterile and male fertile cotton plants in cages. There was either one honeybee colony per cage or seven carpenter bees with suitable nest material. Both treatments gave similar yields from the male sterile plants, but honeybees gave more seed from male fertile plants, more cotton bolls and more cotton seed. They concluded that seven carpenter bees provided adequate pollination and considered that capturing carpenter bees and sending them by mail for pollination of male sterile cotton in cages should be economically feasible.

The solitary bees forage in small cages where honeybees do not. Use of Megachile rotundata for pollination in enclosures has been found successful in several crops like *Medicago sativa, Lotus corniculatus, T. pretense and Cucumis sativa*. In hybrid, cotton, *Xylocopa varipuncta* (seven bees/cage) gave good results.

To manage solitary bees for pollination in enclosures either introduce emerging bees or collect the adults from the field. To avoid contamination collect bees from the species other than those required to pollinate. Provide artificial nesting material inside the enclosures. These bees are extremely sensitive to light intensity so artificial light (48,000 candles/m^2) should be given. The greenhouse temperature should be maintained above 280°C and the use of insecticides should be stopped well in advance.

11.15.3.2 Alfalfa Leafcutter Bee

Why use ALC?

1. Pollinator to supplement honey bees
2. Wanted insect easy to rear with established management
3. Non-stinging preferred
4. Largest unmet pollination demands:
    (a) Wild cucumis in GH cages
    (b) Late-blooming wild-type sunflowers

Traits of Alfalfa leafcutter bee

Solitary bee; use 20–40 bees per cage, replaced ca every other week

1. Introduced to U.S. from Europe ca 1930
2. Traditionally used for pollination of forage legumes and blueberries
3. Work at 26°C (80°F) or above but not frequently in cool cloudy or rainy weather, prefer dry sunny climate
4. Rearing is established; bees are low cost ($100/gal) and require little care
5. Non-aggressive but will bite if squeezed

ALC can be used as greenhouse pollinator in winter/spring

1. Early emergence of bees from cells is possible, but bees will not live for an extended time until a springtime "trigger" occurs
2. Continuous incubation allows for weekly replacement of bees
3. Extended emergence test (into fall) is underway now
4. Parasitoids (tiny wasps, ca 3 species) are a problem/concern
5. We can release a known number of bees per cage

ALC management

1. Cool (4°C or 40°F) storage and pre-incubation at room temperature
2. Cell depth should not exceed 3.8 cm (1.5 in.) for reduced mortality
3. Pre-incubation at 23–24°C (73–75°F) for several days prior to warm incubation

ALC management: warm incubation and bee collection

1. Cells incubated for 30 days at 30°C (86°F) for complete bee emergence
2. First 2 weeks incubated in dark, then placed in chamber with limited light period
3. Bees collected daily; provided wood nest cell and sucrose soaked wicks
4. Retrieved ca 43 sets of bees (20 bees/set) from ca 2,400 cells
5. Parasitoids are controlled with 24 h black-light/water trap
6. Domiciles seem important in extending life span and activity level of ALC bees
7. Female bees carry pollen; providing domicile encourages them to work flowers in order to nest
8. Cut disks from leaves and petals for nest cells
9. Manmade domiciles have evolved from wood to styrofoam blocks; some models we tried in 2005 field and GH
10. ALC seem to be most effective at pollinating small to medium sized flowers of a "flat" nature
    (a) *Angelica*
    (b) *Brassica napus*
    (c) *Cucumis*
    (d) *Daucus*
    (e) *Helianthus* (wild-type heads)
    (f) *Melilotus*
    (g) *Ocimum*
    (h) *Potentilla*

11.15.4 Blowflies

Houseflies and blue bottle flies

1. Place ca 200 flies per cage each week
2. "Incidental" pollinators
3. Work at average temperatures

4. Rearing is well established; pupae are low cost, cost varies per number of pupae purchased
5. Require pre-conditioning of pupae prior to cage release for good emergence; no care required for adults
6. Non-aggressive but may be considered “irritating”
7. Flies are used primarily for pollination of *Daucus* and other umbels
8. May use as “fill in” pollinator for other crops (e.g. *Erysimum, Crambe*) when bees unavailable
9. Used in ca 40 greenhouse cages in the winter and ca 20 GH cages in the spring/summer
10. Used in ca 80 field cages in the summer
11. Flies are replenished in cages weekly due to their short life span; live 2–3 weeks
12. Using two species of flies together or flies along with HB has been shown to increase seed quantity and quality

For an insect to be used as a pollinator either by a plant breeder or in the production of a commercial crop, it should be easily handled and readily available in large numbers; so far, apart from bees, only Diptera, especially blowflies, have filled these criteria. Firms supplying blowfly maggots for fishbait are also a source of pupae which can be introduced to cages or greenhouses.

Blowflies were first used in California by Jones and Emsweller (1933) who found they were more suitable than honeybees for cross-pollinating selected lines of *Allium cepa* in cages (1× 1 × 2 m high) and more efficient than hand pollination. Later, Jones et al. (1934) used blowflies to pollinate *A. cepa* flower heads enclosed in pairs in small wire cages covered with muslin. Borthwick and Emsweller (1933) enclosed umbels of *Daucus carota*, with blowflies inside muslin cages with wire frameworks which were fastened to stakes driven in the ground; when there were ten flies per cage a good set was obtained. Faulkner (1962) found blowflies were as effective as honeybees in pollinating *Brassica* crops in cages and more effective than hand pollination. He recommended growers to put about 500 adults, produced within a few days from pupae kept at 15–21°C in a cage containing 25 plants soon after flowering begins; and every 4 or 5 days thereafter during flowering, to put an additional handful of pupae on the floor of the cage and lightly cover with soil. He found that blowflies lived 2–3 weeks in the cages provided sufficient nectar was available; within limits the amount of pollination increased with the number of flies present (Fig. 11.1).

Wiering (1964) made extensive tests of the efficiency of blowflies (*Phormia terra-novae*), honeybees and bumblebees in pollinating *Brassica oleracea* (Brussels sprouts, kale and cabbage) in plant-breeding work. He found that small isolation cages, which enclosed two plants only, were too small for honeybees and bumblebees which soon died in them, but blowflies gave sufficient cross-pollination and seed. Even when caged with an isolated single plant, pollination by blowflies resulted in a small amount of seed which was sufficient to maintain inbred lines, whereas when plants were isolated without flies a much smaller and often insufficient amount of seed was produced. It seems that blowflies are especially suitable

Fig. 11.1 Sarson (*Brassica campestris var. toria*) and *Allium cepa*, onion, flowers enclosed in small cages with blowflies to pollinate them

for use in small cages or greenhouse compartments; their other main advantages are that they are easy to handle, do not sting and can be used in small numbers. In large cages, blowflies, honeybees and bumblebees produced similar amounts of seed and cross-pollination. Wiering pointed out that pollination was normally needed in early spring, when worker bumblebees are not available and the low temperature often encountered deterred foraging by honeybees but not by blowflies. However, honeybees moved more freely from plant to plant, especially when the plants were separated by more than 50 cm and he suggested that preference should be given to honeybees when uniform pollination of a larger group of plants is needed.

Attempts have also been made to compare the efficiency of honeybees and blowflies as onion pollinators in enclosed spaces. Meer and Bennekom (1972) discovered that honeybees were more likely than blowflies to cross-pollinate in greenhouses (56–82% for honeybees; 29–54% for blowflies) but neither gave as much cross-pollination as in the open field (73–92%). They pointed out that onion breeders would prefer honeybees as insufficient cross-pollination could lead to substantial inbreeding depression. Currah and Ockenden (1983, 1984) compared the foraging behaviour of the two pollinators. When flowering of two cultivars present was not completely synchronous, honeybees were more selective than blowflies, but when flowering was synchronous both species visited the two cultivars at random. Blowflies collected nectar only; all honeybees collected nectar and some collected pollen also. Blowflies spent longer per flower than bees and so were more likely to self-pollinate when bees did not discriminate between cultivars. It seemed that neither species was distinctly advantageous as a pollinator, and this was reflected in their findings that the amount of seed produced and cross-pollination by each was similar. Schiavi et al. (1984) also found that honeybees and blowflies cross-pollinated to a similar extent but honeybees gave more seed. However, honeybees were found by Dowker et al. (1985) to be greatly superior in producing hybrid seed in 16 × 5 m polyethylene tunnels. In tunnels where honeybees were present the male sterile and male fertile plants produced averages of 3.6 and 7.0 g/seed/plant respectively but when blowflies were present only 0.3 and 1.9 g/seed/plant. Male sterile flowers had a mean of 3.5 pollen tubes at the base of the style in tunnels with honeybees but only 0.6 in tunnels with blowflies.

Other crops that blowflies have been used to pollinate include *Pastinaca sativa*, *Apium graveolens*, *Brassica napus*, *Fragaria* × *ananassa*, *Rheum rhaponticum*, *Scorzonera* spp. and *Angelica* spp. (Gaag 1955). However, their short tongues will probably restrict their use to open flowers with readily accessible nectaries; they failed to pollinate *Phaseolus multiflqrus* which have long corolla tubes (Free and Racey 1968). Perhaps smaller flies (e.g. *Musca domestica, M. autumnalis* and *Fannia canicularis*), which could more easily enter long corolla tubes, could be used with advantage for some flower species but a necessary prerequisite is that the insects can be easily bred. Watts (1958) attempted to use hoverflies to pollinate *Lactuca sativa* in muslin bags but without success as the hoverflies made continuous efforts to escape and died within 36 h. However, *Eristalis cerealis* is used for pollinating strawberries and for hybrid seed production in Japan. Growers purchase packages of about 200 pupae that emerge within a week and the adults live for 20 days (Matsuka and Sakai 1988).

Besides honeybees, only diptera (blow flies) qualify the criteria of being large population. The blowflies were first used in onion by Jones and Emusweller as early as 1933 in California. Blow flies *Phormia terranove* are especially suitable for use in small cages or greenhouse compartments, though can also be used for large cages.

They are especially useful inbreeding work where small number of plants is to be grown in cages. Pollination with blow flies is better than hand pollination. The blow flies are easy to handle, do not sting and can be easily used in small numbers. They are useful in pollination of *Daucus carota, Brassica oleracea*, *B. napus, Pastinaca sativa, Apium graveolens, Rheum rhaponticum* and onion (*Allium cepa*). However, in hybrid seed production of onion green houses and polythene tunnels, honeybees are more suitable.

In Japan *Eristalis cerealis* is available commercially and used for pollinating strawberries and for hybrid seed production. In *Brassica* crops for cages containing 25 plants, 500 adults emerged from pupae released soon after initiation of flowering. Place additional pupae on the floor of the cages and lightly cover with soil after every 4–5 days during flowering.

11.15.4.1 Pollination of Cross-Pollinating Species Using Blowflies

Research has been performed to study the use of honey bees and blowflies for pollination of cross pollinating crops such as cabbages (Boukema et al. 1988). Blowflies are used to cross pollinate crops in isolation cages. These flies are purchased, as larvae, from a commercial producer of larvae used as live-bait for fishing, or as insect pollinators. The firm produces mixtures of different types of larvae, of which the flies are either active under warm conditions (up to 35°C), or under colder conditions. Depending on demand, 10–20 l of larvae (in sawdust) are purchased per week. After 3–4 days in a dry room at 25°C, pupae develop. These can be kept for ±1 month at 2°C. The pupae for immediate use are put in containers with a gauze lid and are kept at 25–30°C and 60–70% RH, to produce adults in ±8 days. The flies inside these containers are fed a mixture of sugar and water. Three times a week, upon demand some 200 flies are released in the isolation rooms (±4×4×2 m). Sometimes bumblebees are used for the pollination of cross pollinating crops (Table 11.1).

Table 11.1 Regeneration of crops

Crop	Breeding system	Pollination mechanism	Isolation	Number of plants
Onion and leek	Mostly CP	Insects	Gauze cages	80–150[b]
Barley	SP	–	–[a]	± 200[b]
Cole crops	Mostly CP	Insects	Gauze cages	80–150[b]
Tomato	SP	–	–	7 or more
Pepper	SP	–	–	7 or more
Melon	Mostly CP	Hand pollination	Pollinating–insects free greenhouse	10 or more
Cucumber	Mostly CP	Hand pollination	Pollinating–insects free greenhouse	10 or more
Eggplant	SP	–	–	7 or more
Clover	CP	Insects	*Triticale* fields	± 50
Lettuce	SP	–	–	8–16
Flax	SP	–	–	± 2000[b]
Miscellaneous crucifers	Mostly CP	Insects	*Triticale fields*	50–100
Faba beans	Often CP	Insects	*Triticale* fields	100
Miscellaneous grasses	Mostly CP	Wind	*Triticale* fields	± 70
Lupin	CP	Insect	*Triticale* fields	100
Maize	Mostly CP	Wind	Bagging	100
Oats	SP	–	–	± 200
Peas	SP	–	–	50
Spinach	Mostly CP	Wind	Greenhouse compartments	80
Poa	Apomictic	–	–	± 25
Wheat	SP	–	–[a]	± 200[b]
Potato	Mostly CP	Insects	*Triticale* fields	20–25

CP Cross pollinating; *SP* (Predominantly) self pollinating
[a] Only wild species in greenhouse
[b] Less plants for wild species

11.15.5 Stingless Bees

Stingless bees are considered to be very important pollinators in the tropics, and they are known to effectively pollinate at least nine crops (Amano 2004). Nevertheless, they are seldomly used for commercial pollination. To our knowledge, only one study has been published using stingless bees for crop pollination (Amano et al. 2000). In that study, *Nannotrigona testaceicornis* was used successfully to pollinate strawberries in a greenhouse in Japan. There are several advantages that might make stingless bees more suitable for the pollination of certain crops than the commonly used honeybee (Amano 2004; Asiko 2004). The fact that they lack a functional sting makes them especially suitable for pollination in enclosures. In our study, we compared the pollinating activity between two species of sting-less bees and honeybees on the ornamental plant *Salvia farinacea* var. strata (Lamiaceae) in enclosures.

S. farinacea is an ornamental herbaceous plant, with small (ca. 1 cm) purple and white flowers. It is commercially grown for seed export, usually in enclosures to ensure the production of pure seeds (Tables 11.2 and 11.3).

Slaa et al. (2000a, b) found that Both *A. mellifera* and *T. angustula*, visited *S. farinacea* in good numbers (20% and 23% of all bees, respectively). Pollination by all tested pollinators resulted in the production of good quality seeds with seed weight (953–1,176 seeds/g) and germination rate (61–71%) similar among the enclosures. This study shows that stingless bees can be effective pollinators in enclosures and can therefore be a valuable alternative to honeybees for commercial crop pollination. Currah and Ockendon (1984) found that Honeybees (*Apis mellifera*) and three species of blowflies (*Calliphora vomitoria*, *Lucilia caesar* and *L. sericata*) were observed on mass-pollinated populations of onions (*Allium cepa*) in 4·4 × 3·6 m × 2–2.5 m cages in June-August 1977. Pollination activity at temperatures from 14°C to 28°C was compared on the basis of mean time per flower touched on each umbel visit. Honeybees did not forage below 16°C. Above 16°C their mean time per flower was short (1.4 s) and varied little with temperature. For blowflies, it decreased markedly from 12.1 s at 14–15.5°C to 2.7 s at 26°C and above, largely because at low temperatures flies spent long periods quiescent or grooming rather than actively feeding. When flowering was not completely synchronous between cultivars, honeybees were more selective than blowflies, but where flowering was synchronous, both types of pollinator visited the two cultivars at random. For the size of cage used, neither type of insect had a distinct advantage as a pollinator of onions, despite their different behaviour patterns.

Malagodi-Braga (2002) studied the impact of *T. angustula* pollination on strawberry ('Sweet Charlie' cultivar) production in greenhouses and found that fruits produced under greenhouse conditions were heavier in weight and well developed compared to control (Table 11.4).

Calin et al. (2008) studied the use of honeybees in the seed production of three hybrids in Cornichon type of *Cucumis sativus* ('Cornisa', 'Cornibac', and 'Cornirom'). Honey-bees are very efficient in pollination of cucumber flowers, resulting in an increase of seed quantities per fruit ranging from 150% ('Cornirom') to 214% ('Cornisa'), as compared to hand pollination (Table 11.5).

Ladurner et al. (2002) tested *Osmia cornuta* as a pollinator of caged hybrid red rape for seed production in comparison to *A. mellifera*. *Osmia cornuta* readily visited red rape flowers, and pollinated them successfully. The *O. cornuta* cages produced a 1.5-fold increase in seed yield compared to *A. mellifera* cages. Seed quality was similar in *O. cornuta* and *A. mellifera* cages. The "no pollinator" cage produced few seeds, and of low quality. Red rape seems to be a suitable plant on which to rear *O. cornuta*, since the *O. cornuta* population released was increased by 1.2-fold.

In the production of hybrid varieties, the standards for purity are extremely high. To prevent contamination by external pollen sources, plants of the parent lines are often isolated in cages (Brantjes 2000). Small colonies of honey bees, *Apis mellifera* L., in three-frame-boxes (nuclei) containing 5,000–6,000 bees, are usually used for pollination. However, confinement in cages for more than 1 month causes severe bee worker losses. Confined honey bee workers often show aggressive behaviour, difficulting work within the seed production cages.

Table 11.2 Two stingless bee species that have been reported to forage under confined conditions and those that have been reported not to forage under confined conditions

Species	Crop	Foraging	Greenhouse size (l×w×h)	Location	Reference
Melipona favosa	Sweet pepper	Yes	9×6×4 m	The Netherlands	Meeuwsen (2000)
M. quadrifasciata	Tomato	Yes	234 m^2, 3 m high	Brazil	Santos et al. (2004a); Sarto et al. (2005)
M. subnitida	Sweet pepper	Yes	83 m^2	Brazil	Cruz et al. (2004)
Nannotrigona perilampoides	Tomato	Yes	4×4×3.5 m	Mexico	Cauich et al. (2004)
	Salvia farinacea	Yes	6×3×3 m	Costa Rica	Slaa et al. (2000a, b)
	Salvia splendens	No	6×3×2.5 m	Costa Rica	Bustamante (1998)
	Broccoli Rape Endive Chicory Leek Carrot	Yes	5×5×2 m	The Netherlands	Fonseca and Picado (2000)
N. testaceicornis	Strawberry	Yes	4.2×8.1×2.4 m	Japan	Maeta et al. (1992)
	Cucumber	Yes	86.4 m^2	Brazil	Santos et al. (2004b)
Plebeia tobagoensis	Strawberry	Yes	9×6×4 m	The Netherlands	Asiko (2004); Lalama (2001)
Scaptotrigona bipunctata	Strawberry	Yes	No 8×25 m	Brazil	Malagodi-Braga (2002)
	Cucumber	Yes	10 m high	Japan	Amano (2004)
	Eggplant	Yes	10 m high		
	Paprika	Yes	10 m high		
	Red pepper Yes 10 m high				
S. aff. *depilis*	Cucumber	Yes	86.4 m^2	Brazil	Santos et al. (2004b)
S. mexicana	Rambutan	Yes	16×16×4 m	Mexico	Roubik (1995)
S. quadripunctata	Strawberry	Yes	No 8×25 m	Brazil	Malagodi-Braga (2002)

Tetragonisca angustula	*S. farinacea*	Yes	6×3×3 m	Costa Rica	Slaa et al. (2000a, b); Sánchez et al. (2002)
	Strawberry	Yes	8×25 m	Brazil	Malagodi-Braga and Kleinert (2004)
	Rambutan	Yes	16×16×4 m	Mexico.	Roubik (1995)
	Broccoli	Yes	5×5×2 m		Fonseca and Picado (2000)
	Rape	Yes		The Netherlands	
	Chicory	Yes			
	Leek	Yes			
	Radish	Yes			
	Sweet pepper	Yes			
Trigona carbonaria	White clover	Yes	0.2 ha	Japan	Amano (2004)
	Tomato	Yes	0.2 ha		
	Cucumber	Yes	10 m high		
	Eggplant	Yes	10 m high		
	Paprika	Yes	10 m high		
	Red pepper	Yes	10 m high		
	Sweet pepper	Yes	3×5×4 m	Australia	Occhiuzzi (1999)
T. fuscipennis	*S. splendens*	No	6×3×2.5 m	Costa Rica	Bustamante (1998)
T. minangkabau	Strawberry	Yes	4.2×8.1 m	Japan	Kakutani et al. (1993)

Table 11.3 Crops effectively pollinated by stingless bees under enclosed conditions

Scientific name	Common name	Stingless bee	Reference
Fragaria × ananassa	Strawberry	*Plebeia tobagoensis* *Trigona minangkabau* *Nannotrigona testaceicornis* *Tetragonisca angustula*	Asiko (2004), Lalama (2001), Kakutani et al. (1993), Maeta et al. (1992), Malagodi-Braga and Kleinert (2004)
Nephelium lappaceum	Rambutan	*Scaptotrigona mexicana + Tetragonisca angustula*	Rabanales et al. (unpublished)
Capsicum annuum	Sweet pepper	*Melipona favosa* *Melipona subnitida* *Trigona carbonaria* *Melipona favosa*	Meeuwsen (2000), Cruz et al. (2004), Occhiuzzi (2000) Meeuwsen (2000)
Lycopersicon esculentum	Tomato	*Melipona quadrifasciata* *Nannotrigona perilampoides*	Santos et al. (2004a), Sarto et al. (2005), Cauich et al. (2004)
Cucumis sativus	Cucumber	*Scaptotrigona* aff. *depilis, Nannotrigona testaceicornis*	Santos et al. (2004b)
Salvia farinacea		*Nannotrigona perilampoides, Tetragonisca angustula*	Slaa et al. (2000a, b)

Table 11.4 The effect of *T. angustula* pollination on strawberry ('Sweet Charlie' cultivar) production in greenhouses

	T. angustula	Control	T-test
Fruit number	490 ± 48	519 ± 84	NS
% deformed fruit	6.9 ± 2.2	50.1 ± 12.9	t = 15.1, df = 40, $P = 0.0001$
Fruit weight (g)	9.6 ± 0.7	8.4 ± 1.2	t = 3.9, df = 40, $P = 0.0003$

Given are the mean ± SD for various fruit measurements. Each greenhouse contained either one colony of *T. angustula* or no bee colonies (control). In the latter treatment the parcels were covered to prevent flower visitation by bees. After Malagodi-Braga (2002)

Table 11.5 Comparison of honeybees and hand pollination for hybrid seed production of three hybrid cultivars: 'Cornirom', 'Cornibac' and 'Cornisa'

Character	Honey bees	Hand pollination
'Cornirom'		
Number of seeds per fruit Quantity of seeds/fruit (g)	227 7.5	155.2 5.0
'Cornibac'		
Number of seeds per fruit Quantity of seeds/fruit (g)	258.9 8.5	124.8 4.2
'Cornisa'		
Number of seeds per fruit Quantity of seeds/fruit (g)	56.3 9.1	119.9 4.3

Table 11.6 Seed yield, percentage of germination after 5 and 7 days, and seed weight in red rape cages with various pollinators[a]

Pollination treatment	Seed yield (g) (mean ± sd)	Germination after 5 days (%) (mean ± sd)	Germination after 7 days (%) mean ± sd)	Seed weight (g) (mean ± sd)
A. mellifera	290.0 ± 87.6 (a)	96.3 ± 1.0 (a)	97.5 ± 0.6 (a)	4.3 ± 0.1 (a)
O. cornuta	430.0 ± 39.2 (b)	94.8 ± 1.0 (a)	97.8 ± 0.5 (a)	4.3 ± 0.1 (a)
No insects	30.0	78.0	81.0	3.9

[a] Different letters indicate significant statistical differences (one-way ANOVA: $p < 0.05$)

Furthermore, in Northern Italy, red rape, *Brassica rapa* L. (Brassicaceae), blooms in early spring and honey bee pollination may be curtailed due to adverse climatic conditions. For these reasons, a mason bee, *Osmia cornuta* (Latreille), was tested as a red rape pollinator in cages (Ladurner et al. 2000). Because of its foraging behaviour and capacity to fly under less favourable weather conditions, *O. cornuta* has already been shown to be a more efficient pollinator than *A. mellifera* on almond and apple (Bosch and Blas 1994; Vicens and Bosch 2000a, b). Preliminary investigations, carried out in 1999, indicated that *O. cornuta* may be an interesting alternative pollinator for red rape (Ladurner et al. 2000). Pollen gathering activity was performed by *O. cornuta* females even under damp and cool weather conditions. As few as nine *O. cornuta* females provided better pollination than a nucleus colony of honey bees (Ladurner et al. 2000). Moreover, as with other solitary bee species tried in cages, *O. cornuta* require less maintenance than honey bees (Cox et al. 1996; Wilson et al. 1999). Seed yields, germination percentages and seed weights in cages with *O. cornuta, A. mellifera* and no pollinators, respectively, are reported in Table 11.6. Cages pollinated by *O. cornuta* yielded 32.5% more seed than those pollinated by *A. mellifera*. For all the other parameters analysed, i.e. percentage of germination after 5 and 7 days and seed weight, no significant differences emerged: seed quality on plants pollinated by mason bees was comparable to that on plants pollinated by honey bees.

The contribution of self- and/or wind pollination (cage with no pollinators) was very low (Table 11.5). The control cage also yielded the lowest germination percentages and seed weight of all nine cages. The *O. cornuta* nesting materials recovered contained 195 cells with live adults and 84 cells with dead immatures. Most mortality occurred in pre-defecating larval stages. Evidently, *O. cornuta* is a more efficient pollinator than *A. mellifera* on red rape in confined environment. The significant increase in seed yield in *O. cornuta* cages is not only due to *O. cornuta*'s greater tolerance to inclement weather (Vicens and Bosch 2000b), as might be concluded from previous results (Ladurner et al. 2000), but also to *O. cornuta*'s foraging behaviour. As on almond and apple (Bosch and Blas 1994; Vicens and Bosch 2000a), *O. cornuta* females systematically landed on the reproductive organs of red rape flowers. They introduced their head through the stamens to reach the nectaries with simultaneous scrabbling movements of the legs against the anthers to detach the pollen. Honey bees, conversely, visited red rape flowers mostly for nectar, reaching the nectarines from the side by introducing their proboscis through the basis of the petals, without contacting the stigmas or getting dusted with pollen (side-working behaviour) (Robinson 1979). Furthermore, *O. cornuta* females were observed visiting fewer flowers per red rape plant, and changed rows more often than honey bees, thus enhancing cross-pollination. Similar results have been observed on fruit trees (Bosch and Blas 1994; Vicens and Bosch 2000a). In previous cage studies (Ladurner et al. 2000), *O. cornuta* population increase on red rape was 2.9-fold. In 2000, all adult progeny obtained survived the winter. Thus, a 1.2-fold population increase was obtained, despite the high larval progeny mortality recorded (30.1%). A possible reason for this high larval mortality are pesticides, sprayed against aphids and fungi on May.

Further studies should determine the number of *O. cornuta* visits per flower necessary to achieve maximum seed set on red rape. Red rape appears to be a suitable plant on which to rear *O. cornuta*. Red rape produces abundant pollen and nectar, and blooms for longer (over 1 month in our study) than most commercial fruit tree orchards. *Osmia cornuta* larvae of this and our previous study (Ladurner et al. 2000) developed into adults on provisions containing exclusively red rape pollen. By being able to maintain or increase *O. cornuta* populations on caged red rape, seed producers could minimize the risk of sting incidents, frequent when honey bees are used in confinement, as *O. cornuta* is not aggressive to humans.

Controlled pollination of individual accessions helps retain the original genetic diversity of the plant populations. Some plants are more effectively pollinated by insects than by hand. In addition, insects may be more economical than hand pollination of some crops. Insect pollinators are added to caged accessions of *Brassica*, miscellaneous umbels, sunflowers, and vegetables, as well as some ornamental and medicinal species.

11.16 Pollination of Tomato

The tomato plant, *Lycopersicon esculentum* Miller, has poricidial dehiscent flowers; the anthers need to be shaken to release their pollen through apical pores (McGregor 1976; Buchmann 1983). In open areas, shaking by wind is usually sufficient to trigger this pollen release, promoting self-fertilization (Free 1993). In the absence of wind, however, as is the case in greenhouses, successful pollination of cultivated tomato flowers is difficult. Artificial mechanical vibration, using hand-held electrical shakers, is commercially employed for the pollination of tomato flowers in greenhouses. This method, however, although resulting in tomatoes of higher quality than fruits derived from self-fertilization (Banda and Paxton 1991), is expensive and risks damaging the flowers (Banda and Paxton 1991; Roubik 1995). Alternatively, or in addition to such artificial vibration, bees have been used as pollinators to increase the production of greenhouse tomatoes. Traditionally, bumble bees (Apidae, Bombini) have been used for pollinating greenhouse tomatoes with great success (Plath 1925; Banda and Paxton 1991; Kevan et al. 1991; Asada and Ono 1997; Dogterom et al. 1998; Estay et al. 2001; Al-Attal et al. 2003). These bees are capable of vibrating the anthers of poricidial dehiscent flowers by producing strong thoracic vibrations, which are transmitted through the bees' legs to the flowers (the so-called "buzz pollination") (Buchmann 1983). Bumble bees, particularly *Bombus terrestris*, have been exported worldwide for greenhouse tomato pollination; unfortunately, such exports pose a considerable risk to the indigenous bee fauna in those countries where they are not native (Hingston and McQuillan 1998; Goulson 2003; Hingston 2005). Hence, in recent years there has been an increasing interest in finding alternative, native bee species that have a pollination efficiency that is equal to or at least similar to that of bumble bees. In Australia, solitary bees that perform buzz pollination, such as *Amegilla chlorocyanea* and *A.* (*Zonamegilla*) *holmesi* (Anthophoridae), and *Lestis aeratus* and *L. bombylans* (Apidae, Xylocopinae) have been found to be very efficient in pollinating greenhouse tomatoes (Hogendoorn et al. 2000, 2006; Bell et al. 2006). In Latin America, stingless bees (Apidae, Meliponini) have received increasing attention as crop pollinators during the past few years. These highly eusocial bees live in perennial colonies, are easily domesticated and show various behavioral traits (such as recruitment of foragers (Lindauer and Kerr 1960), high flower constancy, great diet-breadth, and easy adaptation to new plant species) that make them promising candidates as pollinators of commercial crops (Roubik et al. 1986; Ramalho et al. 1994; Nogueira-Neto 1997; Heard 1999).

Bombus working on brinjal flowers

Tomato quality

Tomatoes that bumble bees pollinate have a higher percent fruit set, larger size and heavier fruit and more seeds per fruit than those pollinated manually or by honey bees (Banda and Paxton 1991; Kevan et al. 1991; van Ravestijn and van der Sande 1991). The quality of a tomato is also a result of the number of pollinator visits to the flower. Too few visits by bees may result in a low number of ovules being fertilized, and substandard tomatoes (Verkerk 1957; Straver and Plowtight 1991; van Ravestijn and van der Sande 1991; Pressman et al. 1998). Too much bee activity on a flower may cause damage to the reproductive organs, premature loss of the flower, and no fruit development (Cribb 1990). Fletcher and Gregg (1907) showed that within limits, the size of the tomato was positively correlated with **how** much pollen was transferred to the stigma. Verkerk (1957) found that the more often flowers were manually pollinated-up to a total of four times-the greater percent fruit set and the higher the number of seeds per fruit. He also found that more pollen on the stigma resulted in faster fruit development and therefore an earlier and more profitable crop.

11.17 Pollination Levels

Various methods have been used to assess levels of pollination of greenhouse tomatoes by bumble bees. Bin and Sonessi (1973) observed that pollination of tomato **flowers** by bumble bees caused necrotic spots **on** the anther cone. In European greenhouses, van Ravestijn and van der Sande (1991) assessed the number of tomato flowers that had been pollinated by bumble bees **(*Bombus terrestris*)** by observing the **brown** discolouration of the anther cone caused by pollination visits. By following bumble bees and recording flower handling time, they also estimated that a single active worker could pollinate at least 500 tomato 10–15 colonies per hectare was more than enough for sufficient pollination.

Bispo dos Santos et al. (2009) compared the efficiency of two eusocial bee species, the most common commercial crop pollinator, the honey bee *Apis mellifera* (Sabara and Winston 2003; Higo et al. 2004) and the native stingless bee, *Melipona quadrifasciata* (Del Sarto et al. 2005) in subtropical climate of the Ribeirão Preto SP, Brazil. They found that the largest number of fruits (1,414 tomatoes), the heaviest and largest tomatoes, and the ones with the most seed were collected from the greenhouse with stingless bees. Fruits cultivated in the greenhouse with honey bees had the same weight and size as those produced in one of the control greenhouses. The stingless bee, *M. quadrifasciata*, was significantly more efficient than honey bees in pollinating greenhouse tomatoes. Several recent studies have also shown that *Melipona* spp are efficient pollinators of economically important crops, including sweet pepper (Cruz et al. 2005) and tomatoes (Del Sarto et al. 2005). These bees easily adapt to greenhouses (Cruz et al. 2004; Del Sarto et al. 2005), and there are well-established techniques for multiplying the colonies (Nogueira-Neto 1997), further increasing the potential economic value of these bees as crop pollinators. Honey bees (*A. mellifera*) are often used as pollinators of crops in order to increase or improve production, such as in arrowleaf clover (*Trifolium vesiculosum*) seed production (Camacho et al. 1999). Though these bees do not efficiently vibrate greenhouse tomato flowers, some benefit from honey bee pollination has been reported (Banda and Paxton 1991; Sabara and Winston 2003; Higo et al. 2004). Bispo dos Santos et al. (2009) found that fruit quality (weight, seed number and size) in this plots caged with honeybees was similar to that in greenhouse D, which had no bee/insect visitors. This could be due to the fact that the nectar secretion of tomato flowers is of little, if any, value for bee visitors (McGregor 1976). Furthermore, not all insects are capable of vibrating flowers. Most efficient pollinators of greenhouse tomatoes are buzz-pollinators [*M. quadrifasciata*: Del Sarto et al. 2005; *Bombus terrestris*: Kevan et al. 1991; Banda and Paxton 1991; Pressman et al. 1999; *B. hypocrite hypocrite* and *ignutos*: Asada and Ono 1997; *B. vosnesenskii*: Dogterom et al. 1998; *B. dahlbomii*: Estay et al. 2001; *Amegilla* (*Zonamegilla*) *holmesi*: Bell et al. 2006; *Amegilla chlorocyanea* and *Xylocopa* (*Lestis*) *aeratus*: Hogendoorn et al. 2000, 2006]. The fact that *A. mellifera* is not capable of performing buzz-pollination would explain the finding that these bees are less efficient pollinators of greenhouse tomatoes than are *Melipona* bees or bumble bees (*M. quadrifasciata*: present study; *B. terrestris*: Banda and Paxton 1991).

11.18 Conclusions and Future Strategies

Increasing awareness for greenhouse pollination technique and studies has occurred over the past years, many of them inspired by the introduction of new cultures in greenhouses, such as triploid watermelons. Greenhouse cultivation is highly advantageous due to high income generated by extra–early horticulture crops. New and more thrilling events are yet to come, such as the search for new pollinators. Generally speaking, greenhouse culture is expanding all over the world and together with the use of pollinators, real advances in IPM practices are growing, which gives a very positive and hopeful scenario for thus particular corner of agriculture.

References

Abak K, Dasgan HY (2005) Efficiency of bumblebees as pollinators in unheaded or anti frost heated greenhouses. In: Guera Sanz JM, Roldán Serrano A, Mena Granero A (eds) First short course on pollination of horticultural plants. CIFA La Mojonera (IFAPA), Almería, pp 19–29

Abak K, Sari N, Paksoy M, Kaftnoglu O, Yeninar H (1995) Efficiency of bumblebees on the yield of egg plant and tomato grown in unheated greenhouses. Acta Hortic 412:268–274

Abak K, Sari N, Büyükalaca S, Derin K, Tunali C (1997a) Effects of pollen irradiation on pollen viability and germination in some cucurbit crops. In: Abstract of the 1st Balkan botanical congress, Thessaloniki-Greece, 19–22 Sept 1997, p 137

Abak K, Dasgun HY, Ikiz O, Uygon N, Kaftnoglu O, Yeninar H (1997b) Pollen production and quality in pepper grown in antifrost heated greenhouses during winter and the effects of bumblebee (*Bombus terrestris*) pollination on fruit yield and quality. Acta Hortic 437:303–307

Abrol DP (1990) Pollination activity of alfalfa-pollinating subtropical bees *Megachile* nana and *Megachile flavipes* (Hymenoptera: Megachilidae). Trop Ecol 31(1):106–115

Abrol DP (1998) Foraging ecology and behaviour of the alfalfa pollinating bee species *Megachiie* nana (Hymenoptera: Megachilidae). Entomol Generalis 22(3–4):233–237

Al-Attal YZ, Kasrawi MA, Nazer IK (2003) Influence of pollination technique on greenhouse tomato production. Agric Mar Sci 8:21–26

Amano K (2004) Attempts to introduce stingless bees for the pollination of crops under greenhouse conditions in Japan, Food and Fertilizer Technology Center. http://www.fftc.agnet.org/library/article/tb167.html. Accessed 6 Mar 2006

Amano K, Nemoto T, Heard TA (2000) What are stingless bees, and why and how to use them as crop pollinators? – a review. JARQ 34:183–190

Armbruster WS, McCormick KD (1990) Diel foraging patterns of male Euglossine bees: ecological causes and evolutionary response. Biotropica 22(2):160–171

Asada S, Ono M (1996) Crop pollination by Japanese bumblebees, *Bombus* spp. (Hymenoptera: Apidae): tomato foraging behavior and pollination efkiency. Appl Entomol Zool 31(4):581–586

Asada S, Ono M (1997) Tomato pollination with Japanese native bumblebees (*Bombus* spp.). Acta Hotic 437:289–292

Asiko AG (2004) The effect of total visitation time and number of visits by pollinators (*Plebeia* sp. and *Apis mellifera*) on the strawberry, M.Sc. thesis, Utrecht University, Utrecht

Aubury RG, Rogers HH (1971) The use of *Megachile rotundata* F. as a pollinator of lucerne in glasshouses. J Br Grassl Soc 26:91–94

Baker HG, Baker I (1983) Floral nectar sugars constituents in relation to pollinator type. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold Co., New York, pp 117–141

Banda HJ, Paxton RJ (1991) Pollination of greenhouse tomatoes by bees. Acta Hortic 288: 194–198

Bell MC, Spooner-Hart RN, Haigh AM (2006) Pollination of greenhouse tomatoes by the Australian bluebanded bee *Amegilla* (*Zonamegilla*) *holmesi* (Hymenoptera: Apidae). J Econ Entomol 99:437–442

Berthoff LM (1931) Reactions of the honey bee to light. J Agric Res 42:379–419

Bin F, Sonessi GP (1973) Pollinating insects and the production of hybrid tomato seed. Genet Agraria 27(1):35–74

Bispo dos Santos SA, Roselino AC, Hrncir M, Bego LR (2009) Pollination of tomatoes by the stingless bee *Melipona quadrifasciata* and the honey bee *Apis mellifera* (Hymenoptera, Apidae). Genet Mol Res 8(2):751–757

Bohart GE, Pedersen MW (1963) The alfalfa leaf-cutting bee, *Megachile rotundata* F., for pollination of alfalfa in cages. Crop Sci 3:183–184

Borthwick HA, Emsweller SL (1933) Carrot breeding experiments. Proc Am Soc Hortic Sci 30:531–533

Bosch J, Blas M (1994) Foraging behaviour and pollinating efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera: Megachilidae, Apidae). Appl Entomol Zool 29:1–9

Boukema IW, Dotinga FD, de Groot EC (1988) Pollination of cole crops by honey bees or blow flies? Cruciferae Newsl (13):132–133

Brantjes NBM (2000) Insect pollination in plant breeding. In: Sommeijer MJ, de Ruijter A (eds) Insect pollination in greenhouses: proceedings of the specialists' meeting, Universiteit Utrecht, Soesterberg, 30 Sept–2 Oct 1999

Brines ML, Gould JL (1982) Skylight polarization patterns and animal orientation. J Exp Biol 96:69–91

Buchmann SL (1983) Buzz pollination in angiosperms. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp 73–113

Bustamante M (1998) Polinización de Salvia splendens Sello utilizando cuatro especies de abejas bajo condicones de invernadero en Cartago, Costa Rica, M.Sc. thesis, Universidad Nacional, Heredia, Costa Rica

Butler CG, Haigh JC (1956) A note on the use of honeybees as pollinating agents in cages. J Hortic Sci 31:295–297

Calin M, Ambarus S, Cristea TO, Falticeanu M, Stoian L, Popa CM, Dumbrava MM (2008) The utilization of honey-bees for the production of seeds of cucumber Cornichon type1 Cucurbitaceae 2008. In: Pitrat M (ed) Proceedings of the IXth EUCARPIA meeting on genetics and breeding of Cucurbitaceae, INRA, Avignon, 21–24 May 2008

Camacho JCB, Monks PL, Silva JB (1999) A polinização entomófila na produção e qualidade germinativa de sementes de trevo vesiculoso (*Trifolium vesiculosum* Savi) cv. Embrapa-28 "Santa Tecla". [Entomophilous pollination and its effect on arrowleaf clover (*Trifolium vesiculosum* Savi) cv. Embrapa-28 "Santa Tecla"]. Rev Bras Agrocienc 5:114–119

Cauich O, Quezada-Euán JJG, Macias-Macias JO, Reyes-Oregel V, Medina-Peralta S, Parra-Tabla V (2004) Behavior and pollination efficiency of *Nannotrigona perilampoides* (Hymenoptera: Meliponini) on greenhouse tomatoes (*Lycopersicum esculentum*) in Subtropical México. Hortic Entomol 97:475–481

Chappell MA (1982) Temperature regulation of carpenter bees (Xylocopa californica) foraging in the Colorado desert of Southern California. Physiol Zool 55:267–280

Chen CT, Hsieh FK (1996) Evaluation of pollination efficiency of the bumblebee (*Bombus terestris* L.) on greenhouse tomatoes. Zhonghua Kunchong 16(3):167–175

Cooper BA, Emmett BJ (1977) Hive management in captivity. A crop pollination technique. Ministry of Agriculture, Fisheries and Food: Entomology Leaflet 16

Corbet AA, Fussell RA, Fraser A, Gunson C, Savage A, Smith K (1993) Temperature and the pollinating activity of social bees. Ecol Entomol 18(1):7–30

Costa HS, Robb KL, Wilen CA (2002) Field trials measuring the effects of ultraviolet absorbing greenhouse plastic films on insect populations. J Econ Entomol 95:113–120

Cox RL, Craig A, Gustavson E (1996) A novel use of bees: controlled pollination of germplasm collections. Am Bee J 136(10):709–712

Cribb D (1990) Pollination of tomato crops by honeybees. Bee Craft 72(8):228–231

Cruz D de O, Freitas BM, da Silva LA, da Silva SEM, Bomfim IGA (2004) Use of the stingless bee *Melipona subnitida* to pollinate sweet pepper (*Capsicum annuum* L.) flowers in greenhouse. In: Proceedings of the 8th IBRA international conference on tropical bees and VI Encontro sobre Abelhas, Ribeirão Preto, 2004, p 661

Cruz DO, Freitas BM, Silva LA, Silva EMS et al (2005) Pollination efficiency of the stingless bee *Melipona subnitida* on greenhouse sweet pepper. Pesq Agropec Bras 40:1197–1201

Currah L, Ockendon DJ (1984) Pollination activity by blowflies and honeybees on onions in breeders' cages. Ann Appl Biol 105:167–176

Currie RW, Jay SC, Wright D (1990) The effects of honeybees (*Apis mellifera* L.) and leafcutter bees (*Megachile rotundata* F.) on out-crossing between different cultivars of beans (*Viciafaba* L.) in caged plots. J Agric Res 29:68–74

Cuypers J (1968) Using honeybees for pollinating crops under glass. Bee World 49:72–76

D'Aguilar I, Delia Giustina W, Lecomte J (1967) Problems de pollinisation des cultures sous abri. Bull Tech Inf Ingrs Servs Agric 217:185–188

Dag A, Eisikowitch D (2000b) The effect of environmental conditions on bee pollination activity in greenhouses. In: Abstract of the thirty-ninth apimondia international apicultural congress, Dublin, 2001, p 65

Dag A, Eisikowitch D (2000b) The effect of carbon dioxide enrichmebnt on nectar production in melon under greenhouse conditions. J Apic Res 39:88–89

Dag A, Eisikowitch D (2005) The effect of environmental conditions on bee pollination activity in greenhouses. In: Book of abstracts, 39th Apimondia. International apicultural congress, Dublin, 2005, pp 65

Del Sarto MC, Peruquetti RC, Campos LA (2005) Evaluation of the neotropical stingless bee *Melipona quadrifasciata* (Hymenoptera: Apidae) as pollinator of greenhouse tomatoes. J Econ Entomol 98:260–266

Dobson HEM, Bergstrom G, Groth I (1990) Differences in fragrance chemistry between flower parts of *Rosa rugosa* Thunb. (Rosaceae). Isr J Bot 39:143–156

Dogterom MH, Matteoni JA, Plowright RC (1998) Pollination of greenhouse tomatoes by the North American *Bombus vosnesenskii* (Hymenoptera: Apidae). J Econ Entomol 91:71–75

Dowker BD, Currah L, Horobin JF, Jackson JC, Faulkner GJ (1985) Seed production of an F, hybrid onion in polyethylene tunnels. J Hortic Sci 60:251–256

Dyer AG, Chitka L (2004) Bumblebee search time without ultraviolet light. J Exp Biol 207: 1683–1688

Dyer AG, Whitney HM, Arnold SEJ, Glover BJ, Chitka L (2006) Bees associate warmth with floral colour. Nature 442:525

Ellis MD, Jackson GS, Skrdla WH, Spencer HC (1981) Use of honey bees for controlled interpollination of plant germplasm collections. Hortic Sci 16:488–491

Ercan N, Onus AN (2003) The effect of bumblebees (*Bombus terrestris* L.) on fruit quality of pepper (*Capsicum annuum* L.) grown in an unheated greenhouse. Isr J Plant Sci 51:275–283

Estay P, Wagner A, Escaff M (2001) Evaluación de *Bombus dahlbomii* (Guér.) como agente de flores de tomate (*Lycopersicon esculentum* (Mill)), bajo condiciones de invernadero. [Evaluation of *Bombus dahlbomii* (Guér.) as a pollinating agent for tomato (*Lycopersicon esculentum* (Mill.)) flowers under greenhouse conditions]. Agric Tec 61:113–119

Fahn A (1979) Ultrastructure of nectaries in relation to nectar secretion. Am J Bot 66(8):977–985

Farrar CL (1963) Large cage design for insect and plant research. U.S. Department of Agriculture, Agricultural Research Service (ARS), pp 33–77

Faulkner GJ (1962) Blowflies as pollinators of brassica crops. Comml Grow 3457:807–809

Fischbach K-F (1979) Simultaneous and successive colour contrast expressed in "slow" phototactic behaviour of walking *Drosophila melanogaster*. J Comp Physiol 130:161–171

Fletcher SW, Gregg OI (1907) Pollination of forced tomatoes. Spec Bull Mich Agric Exp Stn 39(2–10):294–301

Fonseca A, Picado A (2000) The use of the stingless bees for pollination in production of vegetables seeds, Report, Faculty of Biology, Utrecht University, The Netherlands

Free JB (1966) The pollination requirements of broad beans and field beans (*Viciafaba*). J Agric Sci Camb 66:395–397

Free JB (1987) Pheromones of social bees. Chapman and Hall, London

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London

Free JB, Butler CG (1959) Bumblebees. Collins, London

Free JB, Racey PA (1966) Hie pollination of *Freesia refracta* in glasshouses. J Apic Res 5:177–182

Free JB, Durrant AJ (1966) The transport of pollen by honeybees from one foraging trip to the next. J Hon Sci 41:87–89

Free JB, Racey PA (1968) The pollination of runner beans (Phaseolus multiflorus Willd.) in a glasshouse. J Apic Res 7:67–69

Free JB, Spencer-Booth Y (1963) The foraging areas of honey-bee colonies in fruit orchards. J Hon Sci 38:129–137

Free JB, Williams IH (1973a) Genetic determination of honeybee (*Apis mellifera* L.) foraging preferences. Ann Appl Biol 73:137–141

Free JB, Williams IH (1973b) The pollination of hybrid kale (*Brassica oleraceae* L.). J Agric Sci 81:557–559

Free JB, Williams IH (1973c) The foraging behaviour of honeybees (*Apis mellifera* L.) on Brussels sprout (*Brassica oleracea* L.). J Appl Ecol 10:489–499

Gatoria GS, Brar PK, Chhuneja Pardeep K (2008) Impact of pollination cages and number of entrances in hive the foraging activity of the bee on radish (*Raphanus sativus* L.). Indian J Crop Sci 3(1):22–25

Goplen BP, Pankiw P (1961) Note on a greenhouse technique for crossing legumes by honey bees. Can J Pl Sci 41:679–682

Goulson D (2003) Effects of introduced bees on native ecosystems. Annu Rev Ecol Evol Syst 34:1–26

Haslbachova H, Kubisova S, Matejik T, Smrhova O (1986) Studie o pfenosu pyly vcelami po casove izolaci. Sbomik UVTIZ Zahradnictvi 13:299–306

Hawkins RP (1968) Honeybees as pollinators in greenhouses. J Apic Res 49:157

Heard TA (1999) The role of stingless bees in crop pollination. Annu Rev Entomol 44:183–206

Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge

Heinrichs DH (1967) Seed increase of alfalfa in growth chambers with *Megachile rotundata* F. Can J Pl Sci 47:691–694

Helverson Ovon, Edrich W (1974) The spectral sensitivity of polarized light orientation in the honeybee. J Comp Physiol 94:33–47

Henning J, Thomassin P, Baker L (1990) Financing organic agriculture: a survey of the experiences of farm lending institutions and organic producers in Quebec. Report to Agriculture Canada, Department of Agricultural Economics, McGill University, Quebec

Higo HA, Rice ND, Winston ML, Lewis B (2004) Honey bee (Hymenoptera: Apidae) distribution and potential for supplementary pollination in commercial tomato greenhouses during winter. J Econ Entomol 97:163–170

Hingston AB (2005) Does the introduced bumblebee, *Bombus terrestris* (Apidae), prefer flowers of introduced or native plants in Australia? Aust J Zool 53:29–34

Hingston AB, McQuillan PB (1998) Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? Aust J Ecol 23:539–549

Hitchings JM (1941) Observations on bee behaviour in a cucumber greenhouse. Rep St Apiarist Iowa 1940:76–81

Hogendoorn K, Steen Z, Schwarz MP (2000) Native Australian carpenter bees as a potential alternative to introducing bumble bees for tomato pollination in greenhouses. J Apic Res 39:67–74

Hogendoorn K, Gross CL, Sedgley M, Keller MA (2006) Increased tomato yield through pollination by native Australian *Amegilla chlorocyanea* (Hymenoptera: Anthophoridae). J Econ Entomol 99:828–833

Holm SN (1964) Bladskaerebien (*Megachile rotundatd)*. Ugeskr Landm 109:719–721

Hughes HM (1966) Investigations on the pollination of blackcurrants var. Baldwin Expl Hortic 14:13–17

Johansen BR, Holm SN (1971) Cross-fertilization in lucerne in cages and the risk of interpopulation pollen transfer by bees. Royal Veterinary and Agricultural University Copenhagen, Denmark, Yearbook 1971, pp 20–34.

Jones HA, Bailey SF, Emsweller SL (1934) Thrips resistance in the onion. Hilgardia 8:215–232

Kaiser W, Liske E (1974) Optomotor reactions of stationary fiying bees during stimulation with spectral light. J Comp Physiol 89:391–408

Kaiser W, Seidl R, Vollrnar J (1977) Spectral sensitivities of behavioural patterns in honey bees. J Comp Physiol 122:27–44

Kakutani T, Inoue T, Tezuka T, Maeta Y (1993) Pollination of strawberry by the stingless bee, *Trigona minangkabau*, and the honey bee, *Apis mellifera*: an experimental study of fertilization efficiency. Res Popul Ecol 35:95–111

Kevan PG (1970) High Arctic insect fiower relations: the inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, N.W.T., Canada. Ph.D. dissertation, University of Alberta, Edmonton

Kevan PG (1979) Vegetation and floral colors revealed by ultraviolet light: interpretational difficulties for functional significance. Am J Bot 66:749–751

Kevan PG (1983) Floral colours through the insect eye: what they are and what they mean. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Scientific and academic editions. Van Nostrand and Company, New York, pp 3–25, Chapter 1

Kevan PG, Backhaus WGK (1998) Color vision: ecology and evolution in making the best of the photic environment. In: Backhaus WGK, Kiiegl R, Werner JS (eds) Color vision: perspectives from different disciplines. Walter de Gruyter, New York, pp 163–183, Chapter 9

Kevan PG, Gadawski RM (1983) Pollination of cranberries *Vaccfiium macrocarpon,* on cultivated marshes in Ontario. Proc Entomol Soc Ontario 1(14):45–53

Kevan PG, Straver WA, Offer M, Laverty M (1991) Pollination of greenhouse tomatoes by bumble bees in Ontario. Proc Entomol Soc Ontario 122:15–19

Kraai A (1954) Het gebruik van bijen bij het veredelingswerk. Zaadbelangen 8:121–122, 132–133, 144–146

Kraai A (1958) Bijen en hommels bij het veredelingswerk. Meded Dir Tuinb 21:291–297

Kraai A (1962) How long do honeybees carry germinable pollen on them? Euphytica 11:53–56

Kubisova S, Haslbachova H (1990) Pollenkorner am Bienenkorper nach der Bestaubung verschiedener Kohlsorten (*Brassica oleracea*). Apidologie 21:1–10

Kwon YJ, Saeed S (2003) Effect of temperature on the foraging activity of Bombus terrestris L. (Hymenoptera: Apidae) on greenhouse hot pepper (Capsicum annuum L.). Appl Entomol Zool 38:275–280

Ladurner E, Maccagnani B, Santi F, Felicioli A (2000) Preliminary investigation on *Osmia cornuta* Latr. (Hymenoptera, Megachilidae) for controlled pollination in hybrid seed production of selected Brassicaceae (red cabbage). In: Sommeijer MJ, de Ruijter A (eds) Insect pollination in greenhouses: proceedings of the specialists' meeting, Universiteit Utrecht, Soesterberg, 30 Sept–2 Oct 1999, pp 203–207

Ladurner E, Santi F, Maccagnani B, Maini S (2002) Pollination of caged hybrid seed red rape with *Osmia cornuta* and *Apis mellifera* (Hymenoptera Megachilidae and Apidae). Bull Insectol 55(1–2):9–11

Lalama K (2001) Pollination effectiveness and efficiency of the stingless bee *Plebeia sp.* and the honeybee *Apis mellifera* on strawberry *Fragaria×ananassa* in a greenhouse, M.Sc. thesis, Utrecht University, Utrecht

Laughlin SB (1976) The sensitivities of dragonfly photoreceptors and the voltage gain of transduction. J Comp Physiol 111:221–247

Lecomte J (1955) Observations sur le comportement d'abeilles vivant en serres chaudes Durant l'hiver. Apiculteur (Sect. sci.) 99:39–42

Lindauer M, Kerr WE (1960) Communication between the workers of stingless bees. Bee World 41:65–71

Lindhard E (1911) Om R0dkl0verens Best0vning og de Humlebiarter, sorn herved er virk somme. Tidsskr Landbr PlAvl 18:719–737

Lindhard E (1921) Der Rotklee, Trifolium pratense L. bei natiirlicher und kiinstlicher Zuch tawahl. Z PflZucht 8:95–120

Lundberg H (1980) Effects of weather on foraging-fights of bumblebees (Hymenoptera, Apidae) in a subalpinefalpine area. Holarct Ecol 3:104–110

Maeta Y, Maki Y, Hayakawa R (1973) Studies on the seed production of alfalfa by using the wild bees. I. Nest structure of *Megachile* (*Eutricharaea*) *rotundata* (Fabricius) and damage of leaf cuttings by the founding bees. J Jpn Soc Grassl Sci 19:161–170

Maeta Y, Tezuka T, Nadano H, Suzuki K (1992) Utilization of the Brazilian stingless bee, Nannotrigona testaceicornis, as a pollinator of strawberries. Honeybee Sci 13:71–78 (in Japanese)

Malagodi-Braga KS (2002) *Tetragonisca angustula* as strawberry pollinator in greenhouses, Ph.D. thesis, Brazil

Malagodi-Braga KS, Kleinert AMP (2004) Could *Tetragonisca angustula* Latreille (Apinae, Meliponini) be used as strawberry pollinator in greenhouses? Aust J Agric Res 55:771–773

Masson J, Tremblay N, Gosselin A (1991) Effects of nitrogen fertilization and HPS supplementary lighting on vegetable transplants production. J Am Hortic Sci 116:594–598

Matile P, Altenburger R (1988) Rhythms of fragrance emission in flowers. Planta 174:242–247

Matsuka M, Sakai T (1988) Bee pollination in Japan with special reference to strawberry production in greenhouses. In: 2nd Australian and international beekeeping congress 1988. Federal Council of Australia Apiarists' Association, Gold Coast, 1988

Mazokhin-Porshniakov GA (1969) Insect vision. Translated from Russian by Roberto and Liliana Masironi. Translation editor: Timothy H. Goldsmith. Plenum Press, New York, xiv, 306 pp

McGregor SE (1976) Insect pollination of cultivated crop plants. Agricultural Research Service, Washington DC

Mcgregor R (1997) Host feeding and ovipositor by parasitoids: value of egg load. J Ins Behav 10:451–462

Meeuwsen FJAJ (2000) Stingless bees for pollination purposes in greenhouses. In: Sommeijer MJ, Ruijter A de (eds) Insect pollination in greenhouses: proceeding of the specialists' meeting, Soesterberg, 2000, pp 143–147

Mena Granero A, Egea González FJ, Garrido Frenich A, Guerra Sanz JM, Martínez Vidal JL (2004) Single step determination of fragrances in Cucurbita flowers by coupling headspace solid-phase microextraction low-pressure gas chromatography–tandem mass spectrometry. J Chromatogr A 1045(1–2):173–179

Mena Granero A, Egea González FJ, Guerra Sanz JM, Martínez Vidal JL (2005a) Analysis of biogenic volatile organic compounds in zucchini flowers: identification of scent sources. J Chem Ecol 31(10):2309–2322

Mena Granero AM, Sanz JMG, Gonzalez FJE, Vidal JLM, Dornhaus A, Ghani J, Serrano AR, Chittka L (2005b) Chemical compounds of the foraging recruitment pheromone in bumblebees. Naturwissenschaften 92(8):371–374

Menzel R (1979) Spectral sensitivity and colour vision in invertebrates. In: Autrum H (ed) Invertebrate photoreceptors, vol VI, V6A handbook of sensory physiology. Springer, Berlin/Heidelberg/New York, pp 503–580

Menzel R, Greggers U (1985) Natural phototaxis and its relationship to colour vision in honey bees. J Comp Physiol 141:389–393

Menzel, R. and, Backhaus, W. (1991). Colour vision in insects. In: Gouras P (ed) Vision and Vvisual Ddysfunction: Tthe Pperception of Ccolour. (ed. P. Gouras), pp. 262-288. London: MacMillan Press, London., pp. 262–288

Moffett JO, Caddel JL (1985) Using honey bees to pollinate greenhouse alfalfa. Am Bee J 125:835–837

Moffett JTO, Spangler HG (1974) Honey bees flew and visited flowers satisfactorily in polyethylene greenhouses. Am Bee J 114:62–63

Morandin LA, Laverty TM, Kevan PG, Khosla S, Shipp L (2001) Bumble bee (Hymenoptera: Apidae) activity and loss in commercial tomato greenhouses. Can Entomol 133:331–341

National Agricultural Advisory Service (1962) Honeybee management in pollination cage experiments. Bee Craft 44:61–62, 73

Nogueira-Neto P (1997) Vida e Criação de Abelha sem Ferrão. Editora Nogueirapis, São Paulo

Nye WP (1962) Management of honeybee colonies for pollination in cages. Bee World 43: 37–40

Occhiuzzi P (1999) Stingless bees thrive in glasshouse trial, Aussie Bee 12:8–11, Australian Nature Bee Research Centre, North Richmond

Occhiuzzi P (2000) Stingless bees pollinate greenhouse Capsicum. Aussie Bee 13:15. Published by Australian Native Bee Research Centre, North Richmond

Palmer-Jones T, Forster IW, Jeffery GL (1962) Observations on the role of the honey bee and bumble bee as pollinators of white clover (*Trifolium repens* Linn.), in the Timaru district and Mackenzie country. *N.Z.* J Agric Res 5:318–325

Pankiw P, Bolton JL (1965) Note on a floral mutant of alfalfa. Can J Pl Sci 45:228

Pankiw P, Goplen BP (1967) The confinement period required to rid honeybees of foreign sweet-clover pollen. Can J Pl Sci 47:653–656

Pardossi A, Tognoni F, Incrocci L (2004) Mediterranean greenhouse technology. Chronic Hortic 44(2):28–34

Pedersen MW, Bohart GE (1950) Using bumblebees in cages as pollinators for small seed plots. Agron J 42:523

Pedersen MW, Todd FE, Lieberman FV (1950) A portable field cage. U.S Bur Ent, ET-289

Peitsch D, Fietz A, Hertel H, De Souza J, Ventura DF, Menzel R (1992) The spectral input systems of hymenopteran insects and their receptorbased colour vision. J Comp Physiol A 17:23–40

Pham-Delegue MH, Etievant P, Guichard E, Masson C (1989) Sunflower volatiles involved in honeybee discrimination among genotypes and flowering stages. J Chem Ecol 15:329–343

Pham-Delègue MH, Etievant P, Guichard E, Marilleau R, Douault P, Chauffaille J, Masson C (1990) Chemicals involved in honeybee-sunflower relationship. J Chem Ecol 16:3053–3065

Pinchinat B, Bilinski M, Ruzkowski A (1982) Possibilities for applying bumble bees as pollen vectors in tomato FI hybrid seed production, Michigan Agrïcultural Experimental Station Special Miscellaneous Publication 1:73–90

Plath OE (1925) The role of bumblebees in the pollination of certain cultivated plants. Am Nat 59:441–451

Plowright RC, Pendrel BA (1977) Larval growth in bumble bees (Hymenoptera: Apidae). Can Entomol 109:967–973

Pressman E, Shaked R, Rosenfeld K, Hefetz A (1998) A comparative study of the efficiency of burnble bees and an electric bee in pollinating unheated greenhouse tomatoes. J Hortic Sci Biotechnol 74:101–104

Pressman E, Shaked R, Rosenfeld K, Hefetz A (1999) A comparative study of the efficiency of bumble bees and an electric bee in pollinating unheated greenhouse tomatoes. J Hortic Sci Biotechnol 74:101–104

Priestley G (1954) Use of honey bees as pollinators in unheated glasshouses. NZ J Sci Tech A 36:232–236

Ptacek V (1983) Indukce plodovánísamiček čmeláků (Hymenoptera, Bombidae) pomocíkontaktusevčelami medonosnými (Apis melliferaL.). (Předběžnésdělení) (Induction of bumblebee queens to egg laying by means of their contact with honey bees. The pilot study). Sborník věd pracíVŠÚP Troubsko 8:157–161

Ptacek V, Krejci F, Babinec J (1984) Pollinators in breeding lucerne. In: Proceedings of Eucarpia, group Medicago sativa, Brno, 1984

Ramalho M, Giannini TC, Malagodi-Braga KS, Imperatriz-Fonseca VL (1994) Pollen harvest by stingless bee foragers (Hymenoptera, Apidae, Meliponinae). Grana 33:239–244

Richards KW (1991) Effectiveness of the alfalfa leafcutter bee as a pollinator of legume forage crops. In: The 6th international symposium on pollination, Tilburg, Aug 1990

Robinson WS (1979) Effect of apple cultivar on foraging behavior and pollen transfer by honey bees. J Am Soc Hortic Sci 104:596–598

Rothenbuhler WC, Thompson VC, McDermott JJ (1968) Control of the environment of honeybee observation colonies by the use of hive-shelters and flight cages. J Apic Res 7:151–155

Roubik DW (1995) Stingless bee colonies for pollination. In: Roubik DW (ed) Pollination of cultivated plants in the tropics, FAO Agricultural Services Bulletin 118, Rome, pp 150–154

Roubik DW, Moreno JE, Vergara C, Wittmann D (1986) Sporadic food competition with the African honey bee: projected impact on neotropical social bees. J Trop Ecol 2:97–111

Rozenberg GV (1966) Twighlight. A study in atmospheric optics. Plenum Press, New York

Rubis DD, Levin MD, McGregor SE (1966) Effects of honey bee activity and cages on attributes of thin-hull and normal safflower lines. Crop Sci 6:11–14

Sabara HA, Winston ML (2003) Managing honey bees (Hymenoptera: Apidae) for greenhouse tomato pollination. J Econ Entomol 96:547–554

Sakai T, Matsuka M (1982) Beekeeping and honey resources in Japan. Bee World 63:63–71

Sánchez LA, Picado A, Sommeijer MJ, Slaa EJ (2002) Floral biology, pollination ecology and seed production of the ornamental plant *Salvia splendens* Sello. J Hort Sci Biotech 77:498–501

Santos SAB dos (2004b) Pollination of cucumber – *Cucumis sativus* – by stingless bees (Hymenoptera, Meliponini). In: Proceedings of the 8th IBRA international conference on tropical bees and VI Encontro sobre Abelhas, Ribeirão Preto, 2004, p 689

Santos SAB dos, Bego LR, Roselino AC (2004a) Pollination in tomatoes, *Lycopersicon esculentum*, by *Melipona quadrifasciata anthidioides* and *Apis mellifera* (Hymenoptera, Apinae). In: Proceedings of 8th IBRA international conference tropical bees and VI Encontro sobre Abelhas, Ribeirão Preto, 2004, p 688

Schiavi M, Masera R, Nervo G, Mazzola P, Soressi GP (1984) Different efficiency of blow-flies and honey bees in controlled pollination of onion (Allium cepa L.). In: Abstract of the 3rd Eucarpia Allium symposium, Institute for Horticultural Plant Breeding, Wageningen, 1984, p 115

Scriven WA, Cooper BA, Allen H (1961) Pollination of field beans. Outl Agric 3:69–75

Shaw FR, Bailey JS, Boume A (1939) The comparative value of honeybees in the pollination of cultivated blueberries. J Econ Entomol 32:872–874

Shemetkov MF (1960) Pollinating activity of bees in greenhouses. Pchelovodstvo Mosk 37:28–31

Slaa EJ, Sánchez LA, Sandî M, Salzar W (2000a) Pollination of an ornamental plant (*Salvia farinacea*: Labiatae) by two species of stingless bees and Africanised honey bees (Hymenoptera: Apidae). In: Sommeijer MJ, Ruijter A de (eds) Insect pollination in greenhouses: proceeding of the specialists' meeting, Soesterberg, 2000, pp 209–215

Slaa EJ, Sánchez LA, Sandî M, Salzar W (2000b) A scientific note on the use of stingless bees for commercial pollination in enclosures. Apidologie 31:141–142

Sladen EWL (1989) The Bumble-bee, its life-history and how to domesticate it. Logaston Press, Woonton

Soler A, Vander Blom J, Lopez JC, Cabello T (2006) The effect of the UV plastic on the behaviour of *Bombus terrestris* in greenhouses: results of a bioassay. In: Guerra-Sanz JM, Roldan Serrano A, Mena Granero A (eds) Second short course on pollination of horticulture plants. CIFA La Majonera, Almeria, pp 258–261

Sorokin V (1958) Pollination by bees in greenhouses. Sad Ogorod 96:24–25

Southwick EE, Southwick L Jr (1992) Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. J Econ Entomol 85:621–633

Steuckardt R (1963) Der Einsatz von Honigbienen bei diallelen Kreuzungen insektenblutiger Fremdbefuchter. Z PflZucht 49:161–172

Strachan CM, Ellis TJ (1984) Lucerne pollen contamination by leafcutter bees in greenhouse cages. In: Viands DR, Elgin JH (eds) Report of the twenty-ninth alfalfa improved conference, Lethbridge, 1984

Straver WA, Plowright RC (1991) Pollination of greenhouse tomatoes by bumblebees. Greenhouse Canada 11:10–12

Suteliffe GH, Plowright RC (1990) The effects of pollen availability on development time in the bumble bee *Bombus terricola* K. (Hymenoptera: Apidae). Can J Zool 68:1120–1123

Szabo TI, Smith MV (1970) The use of *Megachile rotundata* for the pollination of greenhouse cucumbers. In the indispensable pollinators. A report of the 9th pollination conference, The University of Arkansas Agricultural Extension Service, Hot Springs, Arkansas, 1970, pp 95–103

Thompson E (1995) Colour vision: a study in cognitive science and the philosophy of perception. Routledge, London/New York, 354 pp

van der Gaag HC (1955) Het kweken en het gebruiken van vleesoliegen bij het verdelingswerk. Zaadbelangen 9:233–236

van der Meer QP, van Bennekom JL (1972) Influence of the environment on the percentage of self-fertilisation in onions and some consequences for breeding. Euphytica 21:450–453

van der Sande J (1990) Bumble bees are a good alternative to tmss vibration for beefsteak tornatoes. Hortic Abstr 60(6):506

van Doorn A (2006) Factors influencing the performance of bumblebee colonies in the greenhouse. In: Guerra-Sanz JM, Roldan Serrano A, Mena Granero A (eds) Second short course on pollination of horticulture plants. CIFA La Majonera, Almeria, pp 258–261

van Ravestijn W (1990) Bumble bees are good alternatives to tmss vibration in round tomatoes. Hortic Abstr 60(6):506–510

van Ravestijn W, van der Sande J (1991) Use of bumblebees for the pollination of glasshouse tomatoes. Acta Hortic 288:204–212

Verkerk K (1957) The pollination of tomatoes. Neth J Agric Sci 5:37–54

Vicens N, Bosch J (2000a) Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera Megachilidae, Apidae) on ‘Red Delicious’ Apple. Environ Entomol 29(2):235–240

Vicens N, Bosch J (2000b) Weather-dependent pollinator activity in an apple orchard, with special reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera Megachilidae and Apidae). Environ Entomol 29(3):413–420

Vogt FD (1986) Thermoregulation in bumblebee colonies. 1. Thermoregulatory versus brood – maintenance behaviours during acute changes in ambient temperature. Physiol Zool 59:55–59

von Frisch K (1965) Tanzsprache und Orientierung der Bienen. Springer, Berlin/Heidelberg/-New York

von Hess V (1913) Experimentelle Untersuchungen uber den angeblichen Farbensinn der Bienen. Zoologisches Jahrbuch (Physiologie) 34:81–106

Waller GD, Moffett JO, Loper GH, Martin JH (1985a) An evaluation of honey bee foraging activity and pollination efficacy for male-sterile cotton. Crop Sci 25:211–214

Waller GD, Vaissiere BE, Moffett JO, Martin JH (1985b) Comparison of carpenter bees (*Xylocopa varipuncta* Patton) (Hymenoptera: Anthopheridae) and honey bees (*Apis mellifera* L.) (Hymenoptera: Apidae) as pollinators of male-sterile cotton in cages. J Econ Entomol 78:558–561

Watts LE (1958) Natural cross-pollination in lettuce, *Lactuca sativa* L. Nat Lond 181:1084

Weaver N (1956) The foraging behaviour of honeybees on hairy vetch. I. Foraging methods and learning to forage. Insectes Soc 3:537–549

Wiering D (1964) The use of insects for pollinating *Brassica* crops in small isolation cages. Euphytica 13:24–28

Williams RD (1925) Studies concerning the pollination, fertilization and breeding of red clover. Welsh Plant Breeding Station, Aberystwyth

Williams CB (1940) The analysis of four years captures of insects in a light trap. Part 2. The effed of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population. Trans R Entomol Soc Lond 90:227–306

Williams CB (1961) Studies in the effect of weather conditions on the activity and abundance of insect populations. Philos Trans 8(244):331–378

Williams CB, Osman MFH (1960) A new approach to the problem of the optimum temperature for insect activity. J Anim Ecol 29:187–190

Wilson EO (1971) The insect societies. Belknap, Cambridge, 548 p

Wilson RL (1989) Minimizing extraneous transfer of sunflower pollen by honey bees (Hymenoptera: Apidae) in field cages. J Kansas Entomol Soc 62:387–391

Wilson RL, Abel CA, Luhman RL (1999) Comparing three bee species for controlled pollination of selected Brassicaceae. J Iowa Acad Sci 106(1):1–3, Italy

Chapter 12
Pollination for Hybrid Seed Production

Abstract Production of hybrids to obtain higher yields is newer breeding method. To produce hybrid seed, the flowers on the male-sterile lines must be visited by nectar seeking pollen coated insects that have earlier visited the flowers of male-fertile plants. Now-a-days there is an increasing demand for hybrid seed of various crops. For hybrid seed production, parental cultivars are selected and crossed to produce off-spring of increased size, uniform volume, quality in earliness or resistance to unfavourable environmental factors when grown commercially. The production of these hybrid seed crops needs special techniques to prevent self-pollination and encourage cross-pollination favourable by insects.

12.1 Introduction

Production of hybrids to obtain higher yields is newer breeding method. To produce hybrid seed, the flowers on the male-sterile lines must be visited by nectar seeking pollen coated insects that have earlier visited the flowers of male-fertile plants. Now-a-days there is an increasing demand for hybrid seed of various crops. For hybrid seed production, parental cultivars are selected and crossed to produce off-spring of increased size, uniform volume, quality in earliness or resistance to unfavourable environmental factors when grown commercially. The production of these hybrid seed crops needs special techniques to prevent self-pollination and encourage cross-pollination favourable by insects. The techniques include:-

1. **Production of male sterile lines**: Two types of male sterility have become economically significant-cytoplasmic male sterility and genetic male sterility. Use of chemical sprays to create pollen slerility is also in practice. When male-sterility is bred into one of the cultivars to be crossed (e.g. carrot, cotton, faba bean, onion, sunflower) insects pollinate only when they transfer pollen from a male-fertile flower to a male sterile flower. The male-fertile and male-sterile lines are planed in such a way that sufficient movement of bees occurs between them.

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2. **Crossing self-incompatible lines**: Self-incompatibility is employed for producing hybrid seed in cauliflower, Brussels sprout, kale, red clover etc. by using suitable combiner. Sufficient pollinating insects are required to the pollen to compatible flowers.
3. **Selection of line** for low pollen fertility combined with delayed anther dehiscence e.g. safflower.

12.2 Heterostyly

In this case long styled plants that remain in the 'female' rows after removing short-styled plants from them are pollinated by short styled plants of the 'male' cultivars e.g. buckwheat. There are some problems encountered in the use of honeybees for hybrid seed production. There is a tendency of bees to discriminate between the two parental lines and not to readily corss-poolinate between them. The problem is aggravated when female parent (male-sterile line) secretes more nectar. These problems can be solved by selecting parental lines/cultivars that are equally attractive to honeybees, have synchronized flowering periods and provide floral rewards of equal value. The details of hybrid seed production with the role of honeybees and specific problems encountered are given for some important crops as below.

12.3 Pollination Problems in Different Crops

12.3.1 Onion (Allium Cepa L.)

The flowers of male-sterile onion plants normal female parts but no viable pollen. How completely male-sterile plants are cross-pollinated depends on the number and type of insect pollinators present, frequency with which they move and carry pollen from male-fertile to male-sterile plants, the proportion of flowering male-fertile plants and their distribution on the crop. It is necessary to supply honeybees to ensure sufficient and rapid pollen transfer because both the of onion pollen to germinate and the receptivity of stigma diminishes with age. Moreover 1ofl pollen is sticky and pollination by wind is of no avail.

Seed growers generally plant 4–24 rows of a male-sterile variety alternating with 1–4 rows of a male-fertile variety. Currah (1981) concluded that plantings of two male-fertile to eight male. sterile lines were the most common but emphasized on the need for synchronization of flowering of the different cultivars and the need for the pollen to be made available throughout prior to the flowering of male-sterile line to reduce contamination and ensure a good set. Plant row ratio compatible with the foraging pattern of pollinators and the movement of pollen by them is important (Franklin 1958). Woyke and Dudex (1984) found no differences between rows, in the number of honeybees on A-lines as these were observed in the 12th row at 5.4 m, from the C-line on a sunny day. However, Williams and Free (1974) and Woyke (1981) have confirmed that about twice as many honeybees occur on male-fertile rows and visited about twice as many umbels before moving to another row. In general, honeybees with and without pollen loads moved quite freely between male-sterile and male-fertile rows and carried sufficient pollen to fertilize the male-sterile flowers; any unattractiveness of male-sterile plants to pollen gatherers would not seem to limit hybrid seed production. In another study, planting of A-and B-lines did not increase bee visits as 7.5% bees were found foraging on male-fertile lines (Waters 1985), which have higher nectar concentration (Lederhouse et al. 1968). As soon as the flowering starts, placement of 3–5 colonies per acre is recommended.

12.3.2 Safflower (Carthamus tinctorius L.)

In this crop the female parent line used is not male-sterile but is functionally female due to selection for low pollen fertility, combined with delayed anther dehiscence. Its florets elongate normally and the stigmas emerge free of pollen but need to receive pollen from the chosen male line before their own pollen matures (930–1,000 h) and their anthers are ruptured by foraging bees. Hence high population of pollinating insects is needed early in the day. To achieve maximum pollination by honeybees, male and female lines should be planted in alternate rows.

12.3.3 Sunflower (Helianthus annus L.)

Cytoplasmic male-sterility is used to produce hybrid seed in this crop. In addition to being equally attractive, the male-fertile cultivars used must provide pollen throughout the flowering period of the male-sterile lines. Frank and Farkes (1979) reported that seed production (5.7 g per plant) is very low when A and B lines are raised without bees as compared to when bees were allowed to pollinate (52–13 1 g per plant). Honeybee visits are more on male-fertile than on male-sterile heads. A seed set of 59.1% occurred in open male-sterile heads with 36 bee visits per head, whereas the respective values were 92.4 and 460 in open pollen bearing heads (Radford and Rhodes 1980). Furgala (1974) found that less than 25% of bees crossed over from male- fertile to male-sterile rows.

To produce hybrid seed, blocks of male-fertile rows should alternate with blocks of male-sterile rows. Ideally, the seed producing fields should contain as many rows as possible of the male- sterile line from which seeds are harvested, without diminishing set due to reduced pollination because there are insufficient non-productive male-fertile rows. Satyanarayana and Seetharam (1982) in India found that in a hybrid seed crop, planted with one male-fertile to blocks of five male- sterile rows, the number of *Apis cerana* and A. dorsata foragers was greatest on the male-fertile rows, and decreased towards the central rows of the male-sterile blocks. They obtained greater seed yields from plots planted with 1:3 and 1:4 ratio of male-fertile: male-sterile rows than from a 1:5 ration. There were no differences in seed set between strips containing 4, 8 or 12 female rows, alternated with two male rows (Delaude et al. 1979). Increasing the ratio of female: male rows to at least 5:1 increased the yield of hybrid seed without affecting bee activity or seed productivity (Drane et al. 1982). Bee activity and seed yield fell beyond 9-Il rows distance from nearest male rows.

The relative attractiveness of the male-fertile and male-sterile lines has varied with the cultivars concerned Shein et al. (1980) found that the number of honeybees foraging on flowers of different genotypes was negatively correlated with corolla tube length and darkness of the stigmatic pigmentation. When the corolla tubes were relatively dark and long, relatively few foragers visited. To provide sufficient pollination for hybrid seed production atleast one bee per sunflower head is recognized as necessary in Australia (Jones 1988). In India, A cerana is only a pollen gatherer but do not collect nectar from female lines, therefore is an inefficient pollinator. However, A. mellfera foragers collect both nectar and pollen and visit both the hybrid lines. Therefore, presence of A. mellfera near the hybrid sunflower crop ensures good seed setting.

Plants produced from hybrid seed tend to possess greater self-compatibility than the traditional cultivars and sometimes the need for the cross-pollination has been reduced. However, there is considerable variation in the need for cross-pollination among different cultivars. Pollination is a problem in sunflower and this is due to morphological characteristics of flower types and colouration of ray and disc florets. Stigma colouration, corolla tube length and diameter of disc florets influence the availability of nectar to pollinators (Fick 1978; Shein et al. 1980). Genetic variation for nectar production has been found to influence the bee visits (Tepedino and Parker 1982). Thus discrimination of flowers by honeybees due to lack of attractiveness would act as a limiting factor in pollination. Therefore, Drane et al. (1982) suggested that essential factors for attractiveness to bees should be studied and incorporated into new hybrid system.

12.3.4 Brussels Sprout, Cabbage, Cauliflower (Brassica oleracea L.)

In the pollination of Brussels sprout to produce hybrid seed, individual honeybees tended to remain in each line and not readily cross over to another. Faulkner (1976) pointed out that plant height and flower colour were important aspects of discrimination and that honeybees not only differentiated between distinct colour differences but between different shades of yellow.

In cabbage, planting two self-incompatible cultivars as alternate plants in the same row instead of in separate alternate rows caused honeybees to move between cultivars twice as often but the seed yield did not differ much. So for convenience of cultivation and harvesting, planting in separate rows was recommended (Kubisova et al. 1987).

In cauliflower, Woyke (1989) found that alternating two male rows with ten female rows was satisfactory However, honeybees were 3.5 times more on female as on the male line probably due to greater nectar production by female line. Differences in nectar production by different lines of cauliflower have been reported by Gupta et al. (1984). It is suggested that breeders should use such – and B- lines that secrete more amount of nectar. To ensure a sufficient movement of honeybees between cultivars in the open, a large bee population than usual is needed.

12.3.5 Cotton (Gossypiuni species)

Honeybees are reckoned as the most important pollinators of cotton in many parts of the world. They work on cotton from 700 to 2,000 h daily but are most abundant near mid-day when the amount and concentration of nectar is greatest, and thus perform little pollination in the afternoon. The behaviour of honeybees (A. mell and A. cerana) on this crop is such that they seldom touch the stigmas on leaving the flower so it favours cross pollination (Tanda and Goyal 1979). They further observed that both the Apis spp. while collecting pollen brushed past the stigmas in 60–70% of their floral visits, respectively and so cross-pollinated before scrabbling over the anthers to collect pollen loads. The amount of cross-pollination in cotton and the distance over which it occurs is of interest both from the point of view of preventing intracultivar contamination and producing hybrid cotton. For this, distribution of pollen within a crop can be determined by using a technique involving methylene blue dye.

Commercial production of hybrid cotton seed became possible with the development of a cytoplasmic male-sterile genotypes of Gossypium hirsutum. Honeybees are the most important pollinators of male-sterile cotton flowers (Moffett et al 1976). According to Mc Gregor (1976), 50 pollen grains per stigma are enough for fertilization, however number of bee visits required to set all the seeds on a male-fertile flower have not been determined. On an average, ten bees per 100 flowers are sufficient to practically coat all stigma with pollen. Wailer et al. (1985) reported 0.4–1.7 bee visits on A- line and 0.1–1.2 visits on B- line per 100 flowers in 2: 2 planting ratio. About 12 colonies per hectare are sufficient for hybrid seed production. It is generally accepted that bee population of one per 100 flowers is enough for pollination. Honeybees showed 5:3 preference for male-sterile (A-line) flowers over male-fertile (8-line) flowers but crossed over readily between A- and B- lines. Effective hybrid seed production depends upon the arrangement of male-fertile and male-sterile rows. Knowledge of most appropriate ratios of B-line to A- line rows is essential for hybrid seed production. Bee foragers are more in number on male-sterile flowers closer to male-fertile rows as compared to those farther away. All foragers on male-sterile flowers had some pollen on their bodies (Degrandi-Hoffman and Morales 1989). Moffett et al. (1980) found that when only 4 or 6 of the male-sterile rows were planted together, alternating with two male fertile rows, the two centre male-sterile rows produced the same amount of seed as the two outer rows, honeybees moved readily between the male-sterile and male-fertile flowers, on an average every fourth flower visit. They moved less readily when there was a skip row between the two genotypes. Wailer et al. (1985) observed that even when honeybees readily cross between the two genotypes in a field, they usually prefer the male-sterile line to the male-fertile line by a ratio of about 2:1. A correlation between the honeybee population in different plots and hybrid seed produced showed that a population of 0.5–1.0 honeybee per 100 flowers is adequate for pollination and increasing it did not increase seed set and seed production. Attractiveness of honeybees to cotton genotypes depends largely on the sugar concentration of nectar; genotypes with 10% or more sugar concentration attracted twice as many honeybees and decreased with decrease in sugar concentration. Pairing of seed parents based on measured compatibility of pollinator foraging cues viz., nectar, aroma, colour, flower morphometrics etc. has also been suggested Some other problems are also faced for effective pollination of hybrid cotton. With the looming of other more rewarding crops in the vicinity, the honeybees shift from cotton. At other times, honeybees visit only extra-floral nectarines. Higher gossypol content, although good for insect-pest resistance, may affect the foraging behaviour of bees. Heavy pesticide schedule for pest control is also a great problem due to bee poisoning losses and this is more aggravated in case 0 use of pesticides.

12.3.6 Soybean (Glycine max (L.) Mess.)

The hybrid seed in soybean is produced by using genetic male-sterility. The presence of honeybees greatly increased the yield of male-sterile plants and gave upto 62% cross-pollination (Sadanaga and Grindeland 1981). Nelson and Bernard (1984) concluded that the best way to obtain commercial crop was to grow male-sterile plants 10 m apart in every third row rather than to grow male-sterile plants in small blocks surrounded by male-fertile plants. It was emphasized that for efficient production of hybrid soybean seed, plant breeders must ensure that the cultivars to be crossed are equally attractive to honeybees.

12.3.7 Broad or Field Bean (Viciafaba L.)

Plants from hybrid seed of faba bean have special advantage compared to other crops in that the hybrids will produce seed more readily than inbreeds by auto-pollination and so give greater yield in the absence of bee pollination (Bond 1987). The foraging behaviour of honeybees on this crop is such that the pollen collecting honeybees are attracted mostly by male fertile lines and visit the male sterile plants only by mistake and therefore, honeybees are of little use in hybrid seed production unless used at an uneconomical concentration. Bond and Hawkins (1967) suggested that to increase the pollination of male-sterile beans the crops should be grown in areas where beneficial species of bumble bees are normally abundant, and male-fertile and male-sterile lines should be planted in alternate single rows or the seed of the two lines even mixed at random during sowing to increase the frequency of chance visits to the male-sterile lines by bees.

12.3.8 Carrot (Daucus carota L.)

The flowers are generally portentous; self-pollination is largely absent and crop depends upon insect-pollination for seed production. Honeybees are the most important pollinators in carrot. Anther dehiscence occurs during 1st and 2nd day after anthesis. The stigma becomes receptive on the third or fourth day and remains receptive for a week or more. Honeybees discriminate between carrot phenotypes and genotypes. Erickson and Peterson (1979a, b) observed marked honeybee discrimination between different lines and this non-random foraging resulted in wide differences in the amount of seed set by different lines. They found that cross over from male-fertile to male-sterile lines was only 19.7% and concluded that male-sterile lines competed poorly for the attention of pollinators, because they flowered later and produced smaller amounts of nectar. Furthermore, five distinctly different aromas were noted among sterile lines, and a single aroma was typical of nearly all male-fertile lines. Hence, bees could readily differentiate and become conditioned to the male-fertile line. Galuszka and Tegrek (1987) concluded that to facilitate crossing, the distance between male-fertile and male-sterile lines should not exceed 3 in and reported that a 6:1 ratio of male-sterile to male-fertile rows gave homogeneous seed production. However, Rodet et al. (1991) concluded that in cages when the distance between male-fertile and male-sterile rows was less than 1 m, bees were more readily diverted to cross-over the rows and the harvest per row was greater and more homogeneous.

Bohart and Nye (1960) concluded that on carrot, in general, bees were most numerous towards the middle of the flowering period when pollen was most abundant, whereas syxphids were most numerous towards the end of flowering when flowers with fallen anthers were still secreting nectar. According to them, although honeybees are effective pollinators of carrots and their population can readily be increased, they do not seem to be especially attracted to carrot flowers, thus taking their colonies to carrot crops may not be particularly useful when there are more attractive crops in the nearby. If possible, carrot fields should not be located near competing crops but should be in areas with varied habitats capable of supporting many kinds of pollinators.

12.3.9 Cucumber (Cucumis saliva L.)

When producing hybrid seeds in cucumber, plants of the ‘female’ type having any male flowers are to be removed. Sometimes it is necessary to plant the two parents of the hybrid at different dates to ensure that plenty of pollen is available when the female flowers open. Higher ratio of ‘female’ and ‘male plants should be used. In Poland, the yield of hybrid seed of plants in field cages pollinated by honeybees, bumble bees (Bombus terrertris or B. ruderarius) and Megachile rotundata was equivalent to 301, 295 and 47 kg/ha, respectively (Uszkowaski and Bilinski 1984). For producing hybrid crops in a green house, the presence of a male-fertile plant as every 10th plant in every row has been found to provide sufficient pollen (Pettinga and Hensels 1984).

12.3.10 Tomato (Lycopersicon e.sculenius Mill.)

Only a few insect species, especially wild bees, visit the tomato flowers. There is not much importance of insect pollinators in hybrid seed production of tomato. But some primitive species of family Solanaceae produce floral nectar and transferring of the characteristic into male-sterile lines can be a good approach.

12.3.11 Buckwheat (Fagopyrum esculentum Moench)

In this crop, heterostyly is made use of in the production of pure hybrid seed. The cultivars to be crossed are sown in alternate rows and the short-styled plants removed from the ‘female’ cultivar; hence all the long styled plants that remain in the ‘female’ rows will be pollinated by short styled plants of the ‘male’ cultivars (Elagin 1976). Selection for increased proportions of long styled plants of the ‘female’ cultivar will reduce the necessity of removing short styled plants. Honeybees are important pollinators of this crop and increase the yield by 57–96%.

12.3.12 Rape Seed-Mustard (Brassica spp.)

Restorer lines are not available in Brassica spp., except in B. napus. The male-fertile flowers of B. napus are more attractive to honeybees than male-sterile plants (Mesquida and Renard 1979a).

According to Mesquida and Renard (1979b), by using one strip of male-fertile plants with 1, 2, 3, 4, or 5 female strips, considerable overlapping of flowering periods of two lines occurred and it was suggested that pollination with bees was more effective with two rows of male line for 14 rows of female line. There was a marked pollination gradient across the female rows when two rows of male plants were sown with 7–10 rows of female plants on each side. Seed set was about 70% in rows next to male rows and decreased to 25–50% in outer female rows (Mesquida 1983).

Mesquida and Renard (1981) investigated the pollination of B. napus for hybrid seed production. Plots containing both male-fertile and cytoplasmically male-sterile lines were caged with bees, without bees or left uncaged. In general, bee pollination significantly increased the yield, number of seeds per pod and number of pods in the male-sterile plants. Renard and Mesquida (1987) studied the distribution of honeybees on different lines and their effect on pod set and concluded that the percentage pod set decreased more rapidly with distance from male fertile rows and plots with 10 or 20% female lines gave best results in Brassica napus L.

According to Dhsawa and Nawal (1988), a pollen parent to seed plant row ratio of 1:3 was suitable for hybrid seed production with syrphid fly (Eristalis cerealis) as pollinator in cages. More flies visit pollen parent than CMS parent. A CMS line in B. napus, with small anthers, short filaments and narrow petals has been found to be least attractive to honeybees (Mc Vetty et al.; 1989). Therefore, floral characteristics which are important for attracting the pollinators should be kept in view while breeding CMS lines.

12.4 Pollination in Green Houses/Cages

Honeybees, bumble bees, solitary bees, syrphids and blowflies have been used to pollinate flowers in the greenhouses, glasshouses or cages. Bumble bees are valuable for use in small enclosures and can be readily obtained from flowers or by collecting from their nests. They forage at low temperatures at which honeybee activity is limited. These bees have been used to pollinate Brassica oleracea, B. napus, Cichorium intybus, Raphanus sativus, Lycopersicon esculentum etc. Although solitary bees are valuable pollinators of certain crops (e.g. Medicago saliva. Trifolium prazense, Cucumis sativus etc.) but their usefulness is limited because their numbers fluctuate greatly from year to year and from place to place. So, in general, they cannot be relied upon. Attempts have been made to increase the population of solitary bees by inducing them to occupy artificial nests. Megachile rotundata, Nomia melanderi, Osmia spp., Anthophoro spp. have been reared by providing artificial nesting sites and managed for pollination of different crops in various parts of the world.

Blowflies can be easily handled and are readily available in large numbers. These can be effectively used inside small isolation cages. However, use of these flies is restricted to crops with open flowers with readily accessible nectarines because of the short tongues of these flies. These flies have been used to pollinate Brassica oleracea (Brussels sprout, Kale and Cabbage), Allium cepa, B. napus and Daucus carota etc.

Among honeybees, bumble bees, solitary bees and blowflies, the honeybees are usually preferred because of the ease with which they can be obtained and managed. Use of honeybees to pollinates fruit, vegetable and ornamental flowers in greenhouses has increased Considerably. They have been used to pollinate strawberry, brussels sprout, muskmelons, onion, runner bean, tomatoes etc. in greenhouses or in large pollination cages. In Japan about three quarters of the honey colonies used for pollination are concentrated on strawberry production in greenhouse (Sakai and Matsuka 1982; Matsuka and Sakai 1988).

Pollination by honeybees inside the greenhouses/glasshouses or cages depend upon:

12.5 Type of Material Used for Constructing Green Houses/Cages

A cage influences the light intensity, temperature, humidity and wind speed to which plants inside are subjected. However, the extent to which it does so varies with different weather and climatic conditions and with different types of cages. Honeybees seem unable to forage in greenhouse made of ultraviolet opaque polymethyl methacylate sheet (perspec) and fibre glass, but foraged well in air inflated polyethylene “bubble” greenhouses (Cooper and Emmett 1977), nylon screen cages erected within fibre-glass greenhouses and inside large polyethylene tunnels (Moffett and Caddel 1985).

12.6 Size of Colonies and Their Management

For most circumstances, colonies containing three or four combs of brood and bees are adequate for pollination in cages or greenhouses (Matsuka and Sakai 1988). It can be disadvantageous to use colonies that are too large for the areas needing pollination. More bees inside pollination cage can badly damage the anthers, stigmas and corollas. Strength of bees should be according to the size of the cage. If the colonies inside the cage become weakened, combs of emerging bees can be introduced to them. When the combs do not contain sufficient pollen to maintain brood rearing a supply of pollen or pollen substitute should be made available. The bees should be provided with source of sugar and if dry sugar or candy is given, it is essential to give water also. Feeding sugar syrup to honeybee colonies, caged with Brassica oleracea, and brussels sprout plants greatly diminished the proportion of bees that were robbing the flowers of nectar and failing to pollinate (Free and Williams 1973). Under the right conditions when bees receive adequate food and are not subject to sudden temperature fluctuations, honeybees appear to forage as normally in greenhouse as when visiting a crop in the open. When conditions inside the greenhouse are too unfavourable for honeybee colonies in the spring or summer, they may be kept outside and allowed to the greenhouse through tunnels connected to their hive entrances. To get even distribution of honeybee foragers on a greenhouse crop, it would be better to have a single colony near the centre of a greenhouse than at one end, and with two or more colonies to have them at diagonally opposite corners or evenly distributed. When a hive is moved from one greenhouse to another, it should be placed in the same relative position in the second house as in the first and its entrance should face in the same direction to avoid disorientation of the bees. Generally, using honeybees to pollinate early flowering crops in greenhouses harms the colonies. For this, efforts should be made to use colonies whose destruction will be of no great loss.

12.7 Use of Honeybees for Pollination of Some Important Crops in Greenhouses/Cages

12.7.1 Strawberries (Fragaria spp.)

There has been an increasing use of honeybees to pollinate strawberry in greenhouses and so avoid the need for hand labour. Mommers (1961) enclosed strawberry plants growing in greenhouses in two cages and put a honeybee colony in one cage. The cages with and without bees produced mean of 86.9 kg and 74.0 kg of well formed fruit. In Romania, plants in greenhouses isolated from honeybee had 50–59% set compared to more than 80% set when honeybees were present and the final yield of plants visited by honeybees was 107% greater (Cirnu et al. 1978). In Italy, the presence of honeybees in greenhouses gave 2% increase in fruit set and 74% increase in fruit yield (Priore and Sannino 1979). Ahn et al. (1989) demonstrated the value of honeybees in strawberry production in greenhouse and obtained negative correlation between the presence of honeybee colonies and the production of malformed fruits.

12.7.2 Onion (Allium cepa L.)

Walsh (1965) found that honeybees were more efficient than house flies in pollinating caged onion plants, and extensive tests indicate that honeybees are to be preferred to blow flies especially for hybrid seed production in cages. Kumar et al. (1989) found that there was a greater s and yield and better seed generation from plots caged with bees (*Apis cerana*) than from plots caged without bees and in open plots. Estimated seed yields of 275, 73 and 95 kg/ha was obtained from plots caged with honeybees, caged without honeybees and not caged, respectively.

12.7.3 Runner Bean (Phaseolus coccineus L.)

Free and Racey (1968) compared the ability of honeybees, bumble bees and blow flies to pollinate runner beans enclosed in cages in a glasshouse. Blow flies were ineffective as pollinators, probably because their tongues were too short to obtain nectar and plants caged with them produced only a few more pods than plants from which insects were excluded. Pod formation on plants enclosed with bumble bees was no better than on plants enclosed with honeybees. Thus there seems to be no disadvantage in using honeybees to pollinate runner beans in greenhouses so as to facilitate the production of an earlier and more profitable crop. The pollinating efficiency of honeybess may be much greater in a greenhouse or cage than in the field, as bumble bees with short tongues obtain nectar through holes they bite in the bases of corolla tubes and honeybees also obtain nectar through these holes although they cannot make them.

12.7.4 Tomatoes (Lycopersicon esculentum Mill.)

In Belgium, a technique was developed to induce bumble bee queens to produce their colonies in captivity and consequently colonies were available to pollinate tomato crops in greenhouses throughout the year. In the Netherlands, it was common practice to vibrate stems or trusses two or three times a week. Honeybees could only be used to replace hand pollination from the beginning of January to mid-April when greenhouse windows were closed, but thereafter the honeybees forsook ‘the tomato plants inside the greenhouses and flew outside to crops that were more attractive to them. No such problems are encountered with bumble bees which forage consistently on tomato flowers in greenhouses Ravestijn and Sande (1991) on the basis of ‘buzz pollination calculated 10-IS bumble bee colonies per hectare of greenhouse to be adequate. Bumble bee pollination has been found to produce most first class fruits (79%) and least Waste fruit (9%) (Banda and Paxton 1991).

Now-a-days there is an increasing demand for hybrid seed production of various crops and their production has been facilitated with the development of various techniques viz; male-sterility, self-Incompatibility and heterostyly etc. Hybrid seed production is feasible only when pollen is transferred from one line to another. Honeybees being potential agents of pollen transfer are effectively used for pollination and production of hybrids, both us the open fields and in greenhouses/cages Honeybees should be managed as efficiently as possible for their effective use in pollination of crops.

The parental lines (male-sterile/fertile or self-incompatible lines) are used presently for hybrid seed production in various crops. But these lines are not equally attractive to honeybees; bees tend to remain on one or the other line and cross-over is very less. Therefore, research should be oriented to select/breed lines that are equally attractive to honeybees, have synchronized flowering and provide floral rewards of equal value.

Honeybees are being used for pollination of various crops in the greenhouses/cages However, pollination results are not that satisfactory due to the difference in environment inside and outside the greenhouses/cages Therefore, large number of materials which can be used for making greenhouses/cages need to be screened, so that the bees, forage inside as if they were working in the open. The management of bees inside the greenhouses/cages needs attention.

References

Ahn SB, Kim IS, Cho WS, Choi KM (1989) Survey on the use of honeybee pollination of strawberries grown in plastic greenhouses. Korean J Apic 4:1–8

Banda HJ Paxton RJ (1991) Pollination of greenhouse tomatoes by bees. In: The 6th international symposium on pollination, Tilburg, Aug 1990. Acta Horticulture 288:194

Bohart GE, Nye WP (1960) Insect pollinators of carrots in Utah Bul. Utah Agric Exp St 41:1–16

Bond DA (1987) Recent developments in breeding field beans (*Vicia faba* L.). Plant Breed 99:1–26

Bond DA, Hawkins RP (1967) Behaviour of bees visiting male sterile field beans (*Vicia faba*). J Agric Sci (Camb) 68:243–247

Cirnu I, Fata O, Grosu B (1978) Rezultate privind polenizarea cu ajutorul albinelor a culturilor de capsuni (*Fragarga* sp.) in solarii. Apiculture in Romania 53:12–14

Cooper BA, Emmett B (1977) Hive management in captivity. A crop pollination technique. Ministry of Agriculture Fisheries and Food: Entomology leaflet No. l6

Currah L (1981) Onion flowering and seed production. Sci Hart 32:25–46

Degrandi G, Morales F (1989) Identification and distribution of pollinating honeybees (Hymenoptera: Apidae) on sterile male cotton. J Econ Entomol 82(2):580–583

Delaude A, Tasei JN, Rollier M (1979) Pollinator insects of sunflower (Helianihus annus L.) in France. Pollination of male-sterile lines for hybrid seed production. In: Proceedings of the 4th international symposium on pollination, Maryland, 1979, pp 29–40

Dhsawa R, Nawal H (1988) Cross pollination efficiency of insect pollinators. J Breed 38(1): 91–102

Drane D, Mac Pherson R, White K (1982) Pollination studies in hybrid sunflower seed production. In: Proceedings of the 10th international sunflower conference, Surfers Paradise, 1982

Elagin IN (1976) Role of bees in increasing yield and improving seed germination and crop qualities of F hybrid buckwheat seed. In: Kozin RB (ed) Pollination of entomophilous agricultural crops by bees. Amerind Publishing Co, New Delhi, pp 31–36

Erickson EH, Peterson CE (1979a) Asynchrony of floral events and other differences in pollinator foraging stimuli between male fertile and male sterile carrot inbreds. J Am Soc Hortic Sci 104:639–643

Erickson, EH, Peterson CE (1979b) Problems encountered in the pollination of cytoplasmically male- sterile hybrid carrot seed parents. In: Proceedings of the 4th international symposium on pollination, Maryland, 1978, pp 59–63

Faulkner GJ (1976) Honeybee behaviour as affected by plant height and flower colour in Brussels sprouts. J Apic Res 5:15–18

Fick ON (1978) Breeding and genetics. In: Sunflower science and technology. American Society of Agronomy and Crop Science of America, Madison, pp 279–339

Frank J, Farkas I (1979) Pollination of sunflower hybrids by honeybees. In: Proceedings of the 4th international symposium on pollination, Maryland, 1979, pp 41–43

Franklin DF (1958) Effects of hybrid seed production using different ratios of male-sterile and pollen rows. Proc Am Soc Hortic Sci 71:435–439

Free JB, Racey PA (1968) The pollination of runner beans (Phaseolus multiflorus willd.) in a glass house. J Apic Res 7:67–69

Free JB, Williams IH (1973) Genetic determination of honeybee (*Apis mell* L.) foraging preferences. Ann Appl Biol 73:137–141

Free JB, Paxton R, Waghchoure ES (1991) Increasing the amount of foreign pollen carried by honeybee foragers. J Apic Res 30:132–136

Furgala B (1974) Honeybee pollination of sunflowers; Evaluation of limiting factors, cooperative project between University of Minnesota and USDA, 17 p

Galuszka H, Tegrek K (1987) Honeybee (*Apis mellifera* L.) foraging in seed plantations of hybrid carrot (*Daucus carrota* 1). In: The 31st international apiculture congress, Apiomondia, 1987. Apimondia Publishing House,Buckharest, pp 334–336

Gupta JK, Mishra RC, Kumar I (1984) Nectar sugar production and honeybee foraging activity in different cultivars of cauliflower, brassica oleracea var botrytis. Indian Bee J 46:21–22

Jones WA (1988) A pollination study into relative self-compatibility levels of 25 sunflower oilseed cultivars. In: 2nd Australian and international beekeeping congress, Surfers Paradise, 1988. Federal Council of Australian Apiarist's Association, Gold Coast

Kubisova S, Haslbachova H, Janderkova J (1987) Efektivnost prace vcel pri autoinkom-patibilnich Iinii zeli (*Brassica oleracea* var. capitata L.). Sb UVTIZ Zahradnictvi 14:300–308

Kumar J, Mishra RC, Gupta JK (1989) Effect of honeybee pollination on onion (*Allium cepa* L.) seed praduction. Indian Bee J 51:3–5

Lederhouse RC, Caron M, Morse RA (1968) Onion pollination in New York's. Food Life Soc 1:8–9

Matsuka M, Sakai I (1988) Bee pollination in Japan with special reference to strawberry production in greenhouses. In: 2nd Australian and international beekeeping congress, Surfers Paradise, 1988. Federal Coucil of Australia Apiarists' Association, Gold Coast

Mc Gregor SE (1976) Insect-pollination of cultivated crop plants. Agriculture handbook no. 496. Agricultural Research Service, United States Department of Agriculture, Washington, DC, VIII + 4ii pp

Mc Vetty PBE, Minnisch R, Scarth R (1989) The significance of floral characteristics in seed production of four summer rape cultivar A-line with Pol cytoplasm. Can J Plant Sci 69(3): 915–918

Mesquida J (1983) Studies of factors involved in the pollination of male-sterile rape and of methods for the production of F_1 hybrid seed in different regions of France. Bull Tech Apicole 10(4):189–196

Mesquida J, Renard M (1979a) Entomophilous pollination of male sterile strains of winter rape seed (*Brassica napus* L.) Metzger var. oleifera and a preliminary study of alternating devices. In: Proceedings of the 4th international symposium on pollination, Maryland, 1979, pp 49–57

Mesquida J, Renard M (1979b) Preliminary results on the pollination of male-sterile winter rape and methods for the production of hybrid seed. Information techniques No. 65, pp 3–14. INRA, France

Mesquida J, Renard M (1981) Pollinisation du colza d' hiver male-fertale et male sterile (*Brassica napus* L var. ole Metzger) per l'abeille domestique (*Apis mell* L.) effects sur la phenologie et le rendement. Apidologie 12:345–362

Moffett JO, Caddel JL (1985) Using honeybees to pollinate greenhouse alfalfa. Am Bee J 125:835–837

Moffett JO, Cobb HR Rummer DR (1980) Bees of potential value as pollinators in the production of hybrid cotton seed on the high plains of Texas. In: Proceedings of the beltwide cotton research conference, St. Louis, 1980

Moffett JO, Stitch LS, Burkhardt CC, Shipman CW (1976) Nectar secretion in cotton flowers and its relation to floral visits by honeybees. Am Bee J 116(32–34):36

Mommers J (1961) De bestuiving van ardbeien onder glas. Meded Dir Tuinb 24:353–355

Nelson RR, Bernard RL (1984) Production and performance of hybrid soybeans. Crop Sci 24:550–553

Pettinga II Hensels LGM (1984) Pollination of gherkins in glasshouses. In: 5th international pollination symposium, Versailles, 1983, pp 297–299

Priore R, Sannino O (1979) Ruolo dell' ape (*Apis mellifera*) nella coltura della frogola sotto serra. Apicoltore Mod 70:115–119

Radford B, Rhodes W (1980) Effect of honeybee activity on the cross-pollination of male-sterile sunflowers. Aust Beekeeper 81(8):167–170

Ravestijn W, van Sande Van der (1991) Use of bubble bees for the pollination of glasshouse tomatoes. In: The 6th international symposium on pollination, Tilburg, Aug 1990. Ada Hon 288:204–212

Renard M, Mesquida J (1987) Etude Preliminaire sur Ia pollinisation entomophile du colza male-sterile dans un systeme de culture 'mixte' renfermant des proportions variable de plantes pollinisatrices. Bull Tech Apicole 14:99–104

Rodet O, Grosse JPT, Bonnet A (1991) Foraging behaviour of *Apis mell* L. on male-sterile and male-fertile inbred lines of carrot (*Daucus carota* L.) in gridded enclosures. In: The 6th international symposium on pollination, Tilburg, August 1990. Ada Hort 288:371–375

Sadanaga K, Grindeland R (1981) Natural cross-pollination in diploid and autotetraploid soybeans. Crop Sci 21:503–506

Sakai T, Matsuka M (1982) Beekeeping and honey resources in Japan. Bee World 63:63–71

Satyanaryana AR, Seetharam A (1982) Studies on the method of hybrid seed production in oilseed sunflower (1-lelianthus annus). 3. Role and activity of insect visitors in pollination and seed set. Seed Sci Technol 10:13–17

Shein SE Sargent S Miko J (1980) An evolution of differential attractiveness of sunflower genotypes to honeybees. In: Proceedings of the 9th international sunflower conference, Torremolinos, 1980, pp 216–220

Tanda AS, Goyal NP (1979) Insect pollination in Asiatic cotton. J Apic Res 18:64–72

Tepedino VJ, Parker FD (1982) Interspecific differences in the relative importance of pollon and nectar to bee species foraging on sunflower. Environ Entomol 11(1):246–250

Uszkowaski A, Bilinski M (1984) Proba wykorzystania trzmiek (Bombus Later) i miesiarki lucemowki (*Magachile rotundata* F.) dozaphlania materialu hodowlanego ogorkow. Pszczelnicze Zeszyty Naukowe 28:175–184

Wailer GD, Moffeft JO, Loper GH, Martini H (1985) An evaluation of honeybee foraging activity and pollination efficacy for male-sterile cotton. Crop Sci 25:2111–2214

Walsh RS (1965) Pollination of onion plants by honeybees. Newzealand Beekeeper 27:18–20

Waters ND (1985) Pollination problems in hybrid onion seed production using honeybees. In: Proceedings of the 4th international symposium on pollination, Maryland, 1985, pp 65–72

Williams IH, Free IB (1974) The pollination of onion (*Alliuni cepa* L.) to produce hybrid seed. J Appl Ecol 11:409–418

Woyke HW (1981) Some aspects of the role of the honeybee in onion seed production in Poland. Ada Hart III:91–98

Woyke HW (1989) Honeybee foraging on the flowers of cauliflower Ft cultivar components. In: Proceedings of the XXXIst congress of apiculture, Warsaw, 19–25 Aug 1987. Apimondia Publishir'g House, Bucharest, pp 360–364

Woyke HW, Dudex MM (1984) The influence of distance between male sterile and male fertile rows on the number of honeybees visiting flowers and on the seed yield of hybrid onion. In: Proceedings of the 5th international symposium on pollination, Versailles, 1984, pp 123–28

Chapter 13
Biochemical Basis of Plant-Pollination Interaction

Abstract Plants use chemical components to attract potential pollinators to visit flowers and facilitate the efficient transfer of pollen The Evolution of plant volatile production in pollination ecology and in pollinator-plant relationships has been discussed in this chapter. When insects, birds and bats visit flowers for nectar and pollen, they usually pollinate flowers thereby benefitting from the mutualistic interaction. This interrelationship between the two is governed by biochemical factors such as scent, colour and nutritional value of nectar and pollen. For example, the faecal-smelling indole of Arum maculatum is also produced, surprisingly, in the blossoms of Cucurbita (Cucurbitaceae), where the pollinators are diabroticite beetles. Indole acts synergistically with 1, 2, 4-trimethoxybenzene and **(***E***)-** cinnamaldehyde to attract the beetles to the flowers for pollination. In visiting flowers to collect their food, bees may come into contact with toxic constituents. Alkaloids, for example, are known to be present in certain nectars. The apparent reliance on one or a few floral scent constituents as attractants and few and specific pollinators may indicate co-evolution.

13.1 Introduction

When insects, bats and birds visit flowers to feed on (or collect for future consumption) the nectar and pollen, they usually pollinate the flowers in the process, so that both partners clearly benefit from this mutuality association. There are three biochemical factors in this interrelationship; scent and colour of the flower and the nutritional value of nectar and pollen. As a pollinating animal approaches a flowering plant, one of the signals it receives is an olfactory one, from the flower scent. Animals live in a world of chemical communication, of pheromones, and they are undoubtedly able to detect the terpenes and other volatiles of flower odour at some distance. As the pollinator arrives near the plant, it also receives a visual signal, in the contrasting colour of the flower against the general green leafy background.

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As it alights on the flower, it may be drawn to the nectar by visual honey guides on the petal, derived from the differential distribution of pigments within the flower tissue. Finally, as it transfers the pollen from anther to stigma, it gains its reward, a nutritional one, based on the sugar and other constituents of nectar and pollen.

In spite of the great amount written on pollination ecology (e.g. Faegri and van der Pijl 1979; Kevan and Baker 1983; Proctor and Yeo 1973; Real 1983; Richards 1978), biochemical aspects have rarely been explored in any detail. The present account is an attempt to gather most of the available information on this ecological topic. The subject of pollination biology is vast, largely because this interaction between plant and animal is such a complex and suitable one and also because almost every group of plants has its own method of attracting pollinators and there are an enormous number of morphological, adaptations to the various animal pollinators available to plants. Some brief introduction to the subject is needed here, particularly regarding the range of animal pollinators, the varying roles of animal visitors in relationship to flower pollinating processes and the phenomenon of flower constancy.

To the casual observer in a flower garden in temperate latitudes, the pollination of the flowers would largely appear during daylight hours to be the province of the very active bumble and hive bee, with some help being provided by a few smaller insects. This ignores, of course, the much wider range of active pollinators in tropical habitats: the humming birds, an enormous variety of large tropical butterflies, the wasps and the beetles. In addition, some flowers are only pollinated at night by bats or moths. Also, there is occasional pollination by rodents, e.g. by mice and shrews in Protea spp. of South Africa and by bushrats in certain Banksia spp. in Australia. Finally, there are many smaller fauna, different kinds of flies and fleas, some of which are only apparent as pollinators to the most acute observer. The problem of determining which pollinator or pollinators are active on a particular plant species is difficult, requiring much time-consuming observation by the field naturalist. Some animals may visit flowers for other reasons than pollination also they may be able to ‘steal’ the nectar, without carrying out the pollination necessary to the plant. Ants, for example, are well-known nectar thieves and are often so small that they sneak in and out of blossoms without touching the reproductive organs. They do, however, act as genuine pollinators in some cases. Hickman (1974) has shown that the small self-incompatible annual *Polygonum cascadense* is cross-pollinated by the ant *Formica argentea*. Reports of ant-pollinated plant species are, however, still few and far between (Beattie 1991).

The need of a plant to attract animals to visit it for purposes of pollination depends quite naturally on its sexual system and floral structure. There are some groups, e.g. the grasses, where pollination is by wind and animal visitations to the inflorescences would be superfluous. However, such angiospermous plant groups are relatively few the majority of plants clearly require animals to achieve their pollination. This is obvious in plants with single sex flowers, particularly those that are dioecious, i.e. where the male and female flowers are on different plants. It is also obvious in self-incompatible hermaphrodite plants, which account for the majority of angiosperms. Self-incompatibility is essentially a system which ensures out-crossing and hence genetic variability and vigour within a plant population. There are immunological barriers to self pollination and such plants depend on cross-pollination, i.e. insects travelling from flower to flower and unwittingly transferring pollen from the anther of one plant to the stigma of a second, in order to achieve seed set.

The evolution of the sexual system in the angiosperms has generally progressed from it compatibility to self-compatibility (Crowe 1964). However, even in those self-compatible species with large, coloured flowers (e.g. the sweet pea) where the floral morphology is such that self-pollination can occur without animal visitors, it is generally agreed that insects are beneficial in increasing seed set. This may be because pollinators increase the amount of self-pollen transferred to the stigma or because, when cross-pollen is available, it grows faster down the style than self-pollen. Evidently, the theory that many self-pollinated species still gain an advantage from animal pollinators explains why many such plants continue to produce large and brightly coloured petals and fragrant flower scents which attract bees and other visitors,

Finally, there is the phenomenon of flower constancy, a factor of great significance in the co-*Evolution* of angiosperms and their animal partners. It represents the fidelity of a pollinator to regularly visit only a limited number of plant species and in extreme cases, only one. Such fidelity is guided by floral morphology, odour and petal colour. lndeed many plants through *Evolution* of their floral parts have deliberately restricted them-selves to pollination by one type of vector so that they have what are called bee-flowers' (with short, wide corollas), 'butterfly-flowers' (with medium-length, narrow corollas) or 'humming bird-flowers' (with long, narrow corollas). Animals on their part, within the range of plants they are capable of pollinating, become restrictive and dependent on a small number of species and eventually even a single plant. This may be because of a special blossom fragrance, a richness in nectar or some other lure. This mutual co- *Evolution* has many benefits to both plant and animal. In extreme form, it can be seen in the fig genus, *Ficus*, where almost every species has its own species of chalcid wasp to pollinate it. Similarly, one finds examples in the Orchidaceae, where individual species of *Ophrys* depend on a single pollinator, an *Andrena* bee, to pollinate them. The case of the bee orchids will be considered in more detail in a later section.

13.2 Role of Flower Colour

Sprengel and Darwin were the first and most prominent researchers pointing out many examples of floral traits which have coevolved with their corresponding pollinators' morphological and physiological traits (for reviews see: Faegri and van der Pijl 1979; Jones and Little 1983; Paulus 1988; Cohen and Shmida 1993; Dafni et al. 1997; Chittka et al. 2001; Waser and Ollerton 2006). One of the most striking traits is the floral colouration, which evolved as an advertisement for pollinators.

13.2.1 Colour Preferences of Pollinators

Largely due to the work of von Frisch (1950) and others, much information is available about the colour preferences of bees. They are known to prefer what to us appear as blue and yellow colours. They can also discern differences in absorption in the UV region of the spectrum and are sensitive to the intensely UV-absorbing flavones and flavonols. Which are present as such in practically all white flowers and also occur as co-pigments in cyanic flowers. Although bees are insensitive to red colours, they still visit some red-flowered species (e.g. red poppies) guided by the presence of UV-absorbing flavones, which are also present in these blooms.

Hive bees (*Apis mellifera*) are very catholic in the flowers they visit. They do, however, visit some plant families more than others. Families which have many species with typical bee blossoms include the Labiatae, Scrophulariaceae and Leguminosae; blue and yellow flower colour are common in these groups. Honey bees are also regular pollinators of Compositae, a family in which yellow is the dominant flower colour. Other types of bee are more restricted in their choice of flowers, notably those of the genus *Andrena*, which mainly visit orchids such as *Ophnys*.

Hive bees exhibit their colour preferences by visiting blue- and yellow-blossomed flowers if given a choice of other colours as well. Clearly, when nectar is in short supply, bees will visit flowers with other colours (assuming the nectar is available to them) but such plants are at a selective disadvantage, e.g. in a bad summer when bee activity is limited. The operation of natural selection for bee colour can be seen in blue-flowered species (e.g. *Delphinium nelsonii*) which give rise to the white mutant forms ii natural populations. Such mutants are unable to maintain themselves, seed set and viability being poor, because they are discriminated against by their pollinators (Waser and Price 1981). In the case of the larkspur, D. *nelsonii*, discrimination occurs because white flowers have inferior nectar guides and therefore it takes longer for the pollinators to locate the nectar. The pollinators thus experience lower net rates of energy intake than al blue flowers, a sufficient reason for undervisitation by optimally-foraging animals (Waser and Price 1983).

The colour preferences of other pollinators have been less well studied; present available data are collected in Table 13.1. Humming birds are sensitive to red and their preferences for bright scarlet blooms as in *Hibiscus* is well known. Tropical members of the Bignoniaceae, Gesneriaceae and Labiatae all have characteristic humming bird blossoms with red, orange-red or yellow-red colours. These birds do, on occasion, visit plants with white blooms in special habitats, e.g. in the Hawaiian forests. Some humming birds have brilliant scarlet plumage resembling the colour of the flower they pollinate. This is seen in the flower paraqueet *Loriculus* which feeds from scarlet *Erythrina* blossoms. This is a clear case of protective colouring, since these birds are most vulnerable to predators when hovering by the flower to collect nectar. Other birds which pollinate flowers, e.g. sun-birds and honey-birds, appear to have similar colour preferences as humming birds.

Table 13.1 Colour preferences of different pollinators

Animal	Flower colour preferences	Comments
Bats	White or drab colours, e.g. greens and pale purples	Mostly colour-blind
Bees	Yellow and blue intense colours, also white	Can see in UV, but not sensitive to red
Beetles	Dull, cream or greenish	Poor colour sense
Birds	Vivid scarlets, also bicolours (red-yellow)	Sensitive to red
Butterflies (Rhoalocera)	Vivid colours, including reds and purples	
Moths (Heterocera)	Reds and purples, white or pale pinks	Mostly pollinate at night
Flies	Dull, brown, purple or green,	Chequered pattern may be present
Mice	Whitish interiors, surrounded by dark reddish bracts	Pollination occurs at night time
Wasps	Browns	

The other classes of pollinator (Table 13.1) show less sensitivity to flower colour. While Butterflies are actively attracted to brightly coloured blossoms, moths and wasps prefer chill and drab colours. Finally, there are the beetles and bats, which are visually colour blind, and which depend mainly on other sorts of signal to draw them to their host plants.

The colour preferences listed in Table 2.1 are only a very general guide to which pollinators are likely to visit a particular plant species. The adaptive significance of certain colours may not be directly attributable to the major pollinator of a species but rather to selection pressures exerted by other floral visitors. For example, it is possible that the scarlet red colour of hummingbird flowers originally evolved as a mechanism to diminish visits by bees, which are insensitive to red colours (Wyatt 1983).

13.2.2 *Chemical Basis of Flower Colour*

13.2.2.1 Role of Pigments

Flower colour is largely due to the presence of pigments present in chromoplasts or cell vacuoles of floral tissues. Colours produced by the reflection and refraction of light from cell surfaces, so important in the animal kingdom, are not apparent in plants. Flower pigments have been widely studied, particularly from the genetical viewpoint and much information is now available about them (Goodwin 1988).

Table 13.2 Chemical basis of flower colour in angiosperms

Colour	Pigments responsible	Examples
White, ivory, cream	Flavones (e.g. luteolin) and/or flavonols (e.g. quercetin)	95% of white flowered spp.
Yellow	(a) Carotenoid alone	Majority of yellows
	(b) Yellow flavonol alone	Primula, Gossypium
	(c) Anthochlor alone	Linaria, Oxalis, Dahlia
	(d) Carotenoid + yellow flavonoid	Coreopsis, Rudbeckia
Orange	(a) Carotenoid alone	Calendula, Lilium
	(b) Pelagonidin + aurone	Antirrhinum
Scarlet	(a) Pure pelagonidin	Many inc, Salvia
	(b) Cyanidin + carotenoid	Tulipa
Brown	Cyanidin on carotenoid	Cheiranthus, many orchidaceae
Magenta, crimson	Pure cyanidin	Most reds, inc, Rosa
Pink	Pure peonidin	Peony Rosa rugosa
Mauve, violet	Pure delphinidin	Many, inc, Verbena
Blue	(a) Cyanidin + co-pigment/metal	Centaurea
	(b) Delphinidin + co-pigment/metal	Most blues, Gentiana
Black (purple black)	Delphinidin at high concentration	Black, tulip pansy
Green	Chlorophylls	Helleborus

Harborne and Smith (1978a, b) found that anthocyanins pigment type in the flowers is broadly correlated with pollination ecology. They found that hummingbird pollinated species such as *Ipomopsis aggregata* generally contain pelargonidin sometimes with cyanidin, while bee and beefly pollinated species (e.g. *Gilia latiflora*) contain mainly delphinidin. On the other hand, lepidopteran species such as *Leptodactylon californicum* have cyanidin or mixtures of cyanidin with delphinidin. The above three anthocyanidins occur usually as the 3-glucoside, 3,5-diglucoside, 3-(*p*-coumarylglucoside) and 3-(*p*-coumarylglucoside)-5-glucoside, although other types are occasionally found. The distribution of glycosidic types and of acylation, unlike that of the anthocyanidins, is more closely correlated with systematic position than with pollinating vectors. In autogamous species where animal pollination is absent or unimportant, anthocyanin pigmentation in the flowers retains the complexity present in related animal-pollinated taxa. Anthocyanins were also identified in hummingbird pollinated plants from two related families and pelargonidin derivatives were detected.

The most important group of flower pigments are the flavonoids, since they contribute cyanic colours (orange, red to blue) as well as yellow and white (Harborne 1967, 1988). The only other major group are the carotenoids, which provide principally yellow colours, with some oranges and reds. Other classes of much less importance in relation to flower pigmentation are chlorophylls (greens), quinones (occasional reds and yellows), and betalain alkaloids (giving yellow, red and purple colours in Centrospermae). A brief summary of the chemical basis of flower colour is presented in Table 13.2 together with some indication of frequency and importance of the different pigment types.

Table 13.3 Factors controlling cyanic colour in flowers

1[a]	Hydroxylation pattern of the anthocyanidins (i.e. based on pelargondin, cyanidin or delphindin)
2	Pigment concentration
3	Presence of flavone or flavonol co-pigment (may have blueing effect)
4	Presence of chelating metal (blueing effect)
5	Presence of aromatic acyl substituent (blueing effect)
6	Presence of sugar on B-ring hydroxyl (reddening effect)
7	Methylation of anthocyanidins (small reddening effect)
8	Presence of other types of pigment (carotenoids have browining effect)i

[a]In approximate order of importance. there are other minor factors, including pH, physical phenomenon etc

In the case of cyanic colour, the chemical basis is simple. There are three main pigments, all members of the class of flavonoids known as anthocyanidins: pelargonidin (Pg) (orange-red), cyanidin (Cy) (magenta) and delphinidin (Dp) (mauve). These differ in structure only in the number (one, two or three) of hydroxyl groups in the B-ring. These three chromophores occur, usually singly or occasionally as mixtures, in angiosperm flowers and provide the whole range of colour from orange, pink, scarlet and red to mauve, purple and blue. Essentially, all pink, scarlet and orange-red flowers contain pelargonidin, all crimson and magenta flowers cyanidin and all mauve and blue flowers delphinidin.

A rare change in hydroxylation pattern is loss of the 3-hydroxyl. This happens infrequently, but when it does, it causes significant shifts to shorter wavelengths. Two such pigments are known, luteolinidin (3-desoxycyanidin) and apigeninidin (3-desoxy- pelargonidin) which are orange-yellow and yellow respectively. These compounds occur in the New World Gesneriaceae (see p. 47) but hardly anywhere else.

A number of other chemical factors modify the basic anthocyanidin colours (Table 13.3); this is one of the reasons why such a variety of different shades and hues can be found in flowering plants. One of the modifying factors is methylation of one or more of the free hydroxyl groups in the three basic pigments. Only three methylated pigments are at all common: peonidin, petunidin and malvidin. While methylation has only a small reddening effect on colour, it is probably important in improving the ‘In the table and elsewhere. anthocyanidins are referred to as pigment chromophores; these pigments actually cur in pica as glycosides (anthocyanins). The *Nature* of the sugar, however, usually has little effect on colour. One group often families in the Centroapermac differ from all other higher plants in having alkaloidal beta- sins as their yellow and purple pigmentation.’ ‘For details of the species concerned, see the text or Goodwin (1988).

Stability of the anthocyanidin chromophore; methylated pigments are relatively common in the more highly specialized plant families. All anthocyanidins occur in vivo as glycosides (anthocyanins) and have sugars attached to the 3- or 3- and 5-hydroxyl groups. Sugar attachment is probably important (as is methylation) for pigment stability but generally has little effect on flower colour per se since glycosylation is the rule rather than the exception. In rare cases, sugar attachment at the B-ring hydroxyls of the anthocyanidin has been observed, giving, for example, cyanidin 3,5,3′-triglucoside which occurs Ar many bromeliads. This substitution does produce a small colour shift towards shorter wavelengths (Saito and Harborne 1983).

One of the factors modifying cyanic colour (Table 2.3) needs special mention – sence of flavone and/or flavonol co-pigment. For many years, it was thought that co-pigmentation was a special effect, restricted to plants with blue flowers. The co-pigments were present to form weak complexes with the anthocyanidin, shifting the mauve or purple delphinidin colour to pure shades of blue. However, research (Asen et al. 1972) has now demonstrated that for the hill expression of the colour of all three common anthocyanidins – Pg, Cy and Dp – flavones or flavonols are needed to stabilize the pigment chromophore at the pH of the flower cell sap (around 4.5). This explains why, in fact, all cyanic flowers, not just those which are blue, contain both anthocyanidin and flavone or flavonol (as glycosides). Then, the blueing effect of flavones in blue flowers is simply due to art increase in the concentration of flavone; i.e. the anthocyanin/flavone ratio is decreased from that in mauve blooms. That this is so has been confirmed by directly comparing the spectra of pigments and co-pigments mixed in the test tube with those given by the pigments in the living flower. Not surprisingly, flavone copigments are located with the anthocyanins in viva, usually in the cells of the petal epidermis (Kay et al. 1981).

Other chemical features which are important in providing blue flower colour are the presence of aromatic acylation and the presence of chelating metal. It is now possible o recognize two forms of co-pigmentation, inter- and intramolecular, the first involving a loosely bound flavone, as in Fuchsia, and the second the presence of an aromatic hydroxycinnamic acid attached covalently through sugar to the anthocyanidin, as in ipornoea. The acyl group is so arranged that it protects the anthocyanidin chromophore from hydrolytic attack in the same way as the hydrogen-bonded flavone co-pigment (Fig. 2.2). In addition to having co-pigments. some blue pigments occur in oivo associated with metal ions; in *Commelina communis*, the metal is magnesium, while in *Hydrangea* flowers it is aluminium.

There are a variety of ways that yellow colour may be produced in flowers (see Table 2.2). Most are due to carotenoids; almost all yellow and lemon-yellow carotenoidcontaining flowers have mainly xanthophylls, such as zeaxanthin and its 5,8-epoxides auroxanthin and flavoxanihin. Deep orange flowers may have large amounts of β-carotene (e.g. the orange fringes of *Narcissus majalis*) or alternatively lycopene (*Calendula*) (for carotenoid structures, see Fig. 2.3). The carotenoids in petals are concentrated in the chromoplasts and may be present in bound form linked to protein or esterified with fatty acids.

Flavonoids make minor contributions to yellow colour, through three groups of pigmenh yellow flavonols, chalcones and aurones (Fig. 2.4). Yellow flavonols such as gossy petin, quercetagetin and their derivatives provide colour in cotton flower *Gossypium hirsutum*, in the primrose *Primula vulgaris* and in various composites, e.g. *Chrysanthemum segetum*. Yellow flavonols owe their colours to the presence of an extra hydroxyl (or methoxyl) group in the 6- or 3-position of the aromatic A-ring of their structures. The related flavonols without this Feature, e.g. quercetin (Fig. 2.5), are more or less colourless. Chalcones and auxones occur especially frequently in another group of composites, including Coreopsis and Dahlia, but do also occur sporadically in nine other plant families. They are distinguished from other types of yellow pigment in that when petals containing them are fumed with ammonia (or the basic smoke of a cigar) there is a colour change from yellow to red. Chalcones and aurones often occur together in flower petals and are collectively known as anthochlor pigments.

One other class of water-soluble yellow pigment needs to be mentioned; those based on alkaloids. The well-known base berberine, for example, contributes yellow colour *Berberis* tissues. One important class of yellow alkaloids are the betaxanthins of the Centrospennae. Within this order, alt yellows are given by pigments such as indicaxanthin (Fig. 2.4) a betaxanthin based on the amino acid proline linked to a betatarnic acid moiety. Eight other betaxanthins are known in the Centrospermae with aliphatic amino acids other than proline as part of their structures (Piattelli 1976).

One final point may be made about yellow colour. Mixtures of two unrelated classes of yellow pigment are not infrequent in petals, especially of carotenoids and yellow flavonoids in members of the Compositae. It seems peculiarly wasteful in terms of biosynthetic potential for plants to produce two classes of compound to carry out the same function. However, the explanation for this apparent profligacy has been uncovered in relation to guide marks in petals, as will be discussed in a later section.

Finally, there are the compounds which occur in white flowers. They are scarcely colours to human eyes, appearing as pale cream or ivory in the petal. However, as already mentioned, they are clearly discernible by bees and other insects, which can perceive differences in absorption in the UV range of the spectrum. There are two classes: flavones such as luteolin and apigenin, and flavonols such as kaempferol and quercetin (see Fig. 2.5). There seems to be no particular advantage of one over the other, although the flavonols absorb at slightly longer wavelengths (at c. 360–380 instead of at 330–350 nm) than the flavones. In fact, flavones are more widely found in the flowers of more advanced plant families than are flavonols.

13.3 Evolution of Flower Colour

The distribution of cyanic coloration in angiosperms is by no means haphazard. There is a pattern in the relative frequency of delphinidin (Up), cyanidin (Cy) and pelargonidin (Pg) types. The frequencies vary according to the flora sampled, and there is clear evidence of natural selection for particular colours in different environments, according to the most active pollinators which are present. Analyses of the results of pigment surveys show that selection has worked in two directions, from cyanidin as the basic or more primitive type. Loss mutations in tropical

Table 13.4 Differences in pigment chemistry of subfamilies of Gesnerioidae

Subfamily[a]	Desoxyanthocyanin	Presence of yellow pigments		
New world Gesnerioidae	Present in 29/36 spp.	+	−	+
Old world Cyrtandrioidae	Absent from 0/50 spp.	−	+	+

Data from Harborne (1967)

[a] Generic coverage 74%

habitats produce scarlet and orange colours favoured by humming birds; by contrast, gain mutations in temperate climates produce blue colours favoured by bees.

Evidence that cyanidin is the most primitive pigment type is based on a variety of observations. It is the most common type in the ancestors of angiosperms, i.e. the gymnosperms. It is the major pigment of wind-pollinated groups such as the grasses, where clearly selection for flower colour will not operate. It is also the most common pigment found in tissues more primitive than the flower such as the leaf.

Evidence that pelargonidin is advanced over Cy is based on its regular occurrence in tropical plants and almost complete absence from temperate floras. The further loss mutation to give the 3-desoxyanthocyanidins luteolinidin and apigeninidin only appears in very advanced angiosperm families, such as the Gesneriaceae and Bignoniaceae. In the former family, 3-desoxyanthocyanidins are clearly restricted to the tropical American New World species and are completely absent from the Old World taxa in the family. This difference in cyanic pigmentation is also (Table 13.4).

Finally, evidence that delphinidin and its derivatives are advanced over cyanidin is drawn from distribution patterns in the angiosperms and especially the frequent presence of Op in advanced bee families, such as the Scrophulariaceae, Boraginaceae, Hydrophyllaceae and Polemoniaceae.

The situation illustrated is only an evolutionary trend and clearly there will be some exceptions. The position of Cy itself is to some extent ambiguous since with suitable modifying factors it can under different circumstances provide the basis of scarlet colours (e.g. in Tulipa, or the basis of blue colours, as in the cornflower, Centaurea cyanus). However, if one takes the other two pigment types, Pg and Up, it seems that humming bird flowers almost never have delphinidin, and bee flowers almost never have pelargonidin; such cases, if they exist in *Nature*, are very rare.

The effects of the evolutionary trends portrayed can be gauged also, by comparing the frequencies of Pg, Cy and Op types in various floras. In the Australian flora, the relative frequencies based on analyses of wild plant species are Op 63%, Cy 47% and Pg 2%. The remarkable scarcity of Pg types is presumably due at least in part to the infrequency of species with bird-pollinating mechanisms in the flowers. Also the bird fauna of Australia is \different from that in tropical America and there may be different colour preferences. Where bird pollination occurs, the mechanism is often distinctive as in those species of the Myrtaceae which have bright red inflorescences arranged like the bristles of a bottlebrush. On the other hand, the high figure for Op suggests that pollination by insects attracted to mauve and blue colours must be especially common.

Table 13.5 Correlation between anthocyanidin type flower colour and pollinator in polemoniaceae

Plants	Flower colour	Petal anthocyanin
Humming bird pollinated plant species		
Cantua buxifloia	Scarlet	Cy
Loeselia mexicana	Orange-red	Pg
Ipomopsis aggregata ssp. aggregate	Bright red	Pg
I. aggregata ssp. bridgesii	Red to magenta	Pg, Cy
I. rubra	Scarlet	Pg
Collomia rawsoniana	Orange red	Cy
Bee pollinated species		
Polemonium caeruleum	Blue	Dp
Gilia capitata	Blue-violet	Dp
G. latiflora	Violet	Dp/Cy
Eriastrum densifolium	Blue	Dp
Langloisia mathewsii	Pink	Dp/Cy
Lianthus liniflorus	Liliac	Dp/Cy
Lepidoptera pollinated species		
Phlox diffusa	Pink to liliac	Dp/Cy
P. drummondii	Pink to violet	Dp/Cy(Pg)
Ipomopsis thurberi	Violet	Dp
Leptodactylon californicum	Bright rose	Dp/Cy
L. pungens	Pink to purple	Dp/Cy
Linanthus dichotomus	Reddish-brown	Cy

Key: *Pg* pelargonidan; *Cy* cyanidin; *Dp* delphinidin

Figures from the contrasting tropical flora of the West Indies are also available. Here a sampling based on both wild and introduced species (and hence not entirely representative of the natural habitat) gave the results of Dp 47%, Cy 70% and Pg 17%. The high figure for Pg and to some extent that of Cy is undoubtedly because bird pollination is a widespread feature in this flora (van der Pijl 1961).

The dichotomous *Nature* of *Evolutionary* trends in cyanic colours can also be seen at work in families which have both tropical and temperate members. One of the best examples here is the Polemoniaceae, a family restricted to the New World but present both in northern temperate areas as well as central tropical habitats. The animal pollinators of these plants have been exhaustively studied by Grant and Grant (1965). In their monograph on the family, these authors include two colour plates of typical Polemoniaceae species pollinated by humming birds and by bees respectively. There is a remarkable contrast in colour and flower shape in these plates. The humming bird flowers have long, narrow corollas, mostly scarlet. The bee flowers have wide open short corollas, nearly all blue in colour.

Yet other flowers in the family (not illustrated) have shorter narrow corollas, mauve or pink in colour and are butterfly pollinated. Analyses of the anthocyanidins present in petals of 18 representative members of the Polemoniaceae (Table 13.5) show a clear-cut correlation between flower colour, anthocyanidin type and pollinator

(Harborne and Smith 1978a). Thus humming bird species all have pelargonidin, with but one exception, while bee- or bee/fly-pollinated species all have delphinidin. On the other hand, lepidopteran species are intermediate in containing mainly cyanidin or mixtures of cyanidin and delphinidin.

Similar differences in flower colour types have been observed between tropical and temperate members of the Labiatae. Pelargonidin was found in all six scarlet-flowered species surveyed, cyanidin in 17 species with red-purple flowers and delphinidin in 26 species with violet or blue flowers which are bee pollinated (Saito and Harborne 1992). The results with the Gesneriaceae, where the main geographical difference is Old World/New World, have already been given in Table 13.4.

Evolutionary changes in flower colours can also be observed at the species level. Plants may have to switch their flower colours within a generation or two in order to adapt to changes in pollinators. Baker and Hurd (1968) have pointed out the considerable differences in dominant flower colour that can exist between two habitats adjacent to each other. In the northem Californian flora, herbaceous species growing in the open prairie are pollinated by bees and have yellow flowers. Close by in the dark Redwood forest, the plants are pollinated by moths and have white or pale pink flowers. Any species migrating across the border from one habitat to another would have to switch flower colour rapidly in order to adapt to the new environment. Species known to be variable in their flower colour (e.g. members of the Viola genus) are presumably in a better position than most to achieve emigration from one contrasting habitat to another in this way.

Undoubtedly plant species have considerable flexibility in being able to cease, modify or re-establish anthocyanin synthesis in the flowers depending on what pollinators are present or whether any pollinators are available. In this respect, it is significant that two autogamous species of Polemoniaceae that were analysed, Allophyllum gilioides and Microsteris gracilis (Harborne and Smith 1978a), retained the anthocyanin pigments of their out-breeding relatives, in spite of the fact that animal pollination is not needed in these self-compatible species. Thus, the possibility remains in the make-up of these plants of returning to out-breeding in some future generation.

The ability of plants to respond rapidly to changing pollinators is nicely illustrated in another polemoniad, the scarlet gilia *Ipomopsis aggregata*. In populations growing near Flagstaff, Arizona, it has been observed that a minority of plants shift in flower colour during the season from red, through shades of pink to white (Paige and Whitham 1985). The shift is correlated precisely with the coincident southern emigration of humming birds, which are primary pollinators in mid-July and the need to be attractive to the remaining pollinator, a hawkmoth *Hyies lincata*. Colour shifting, which can occur within the same inflorescence, involves diluting the amount of anthocyanin formed in the petal (see Table 2.5) and eventually turning off anthocyanin synthesis altogether.

Colour shifting in ipomopsis provides a mechanism for ensuring that the pollinators present at a particular time are most effectively attracted to visit the flower. Another plant which benefits from the visits of two pollinators is Pedicularis (Scrophulariaceae) (Macior 1986). Here the flower has scarlet corollas to attract humming birds and magenta calyces and bracts with high UV-reflective hairs which attract bumble bees. While younger flowers are bee pollinated, the older flowers are bird pollinated. Instead of a shift in colour, there is an increase in nectar sugar (from 15% to 25%) as the flower ages, which correlates with the change in pollinator.

One way that flower colour may be modified is by hybridization, but this may not always be advantageous. In Pensfemon for example, there is a red humming bird pollinated species which will hybridize with a blue carpenter bee-pollinated species when growing sympatrically (see Grant 1971). The hybrid is purple flowered and attract yet another pollinator, a wasp. The purple intermediate is pigmented by the same delphinidin as the blue form, but with less co-pigment being present; deiphinidin would be expected to be dominant to the pelargonidin present in the red-flowering species (Beale 1941). Such a purple hybrid may not always be fortunate enough as in this ca to attract its own pollinator. It clearly could be at a selective disadvantage, since may not be able to attract either of the pollinators of the parental plants. In other situations, it might then have to revert back quickly to the flower colour of one or other parent. This could dearly be a limiting factor in the success of hybrids in evolving populations.

Flowers may change colour after being pollinated, e.g. from yellow (carotenoid) to (anthocyanin) as occurs in Lantana camara. This is triggered by the removal of nectar from the nectary by the pollinator (Eisikowitch and Lazar 1987). Such colour changes are beneficial to both parties. Thus, they direct the pollinator towards the unvisited (yellow) flowers and improve the efficiency of pollination and nectar gathering. Equally the retention of the pollinated (red) flowers in the inflorescence increases the attractiveness of flowers from a distance. These colour changes have now been recorded in at least angiosperm families and the majority of insect pollinators readily discriminate between the different floral colours at close range (Weiss 1991). Although colour changes may be of several kinds, the biochemistry of the switch in pigment synthesis has yet to be investigated.

13.4 Honey Guides

Honey guides or guide marks are part of the pigment patternning in flowers, heir object being to guide pollinating insects to the centre, where the sex organs and nectar are present. They are particularly prominent in bee flowers and take a variety of forms. Many an visible to the human eye and may be a colour contrast – a yellow spot on the lip of an otherwise blue flower, as in *Cymbalaria muralis*. They also may take the form of colonied dots or lines on the corolla tube. Recent research has shown that some honey guides in yellow flowers are invisible to the human eye, but can be detected by insects due to their intense absorption in the UV; this work has created a new impetus in the study of honey guides in flowering plants.

Visible honey guides are often produced by the local concentration of anthocyanin pigmentation in particular areas of the corolla. This is true in the foxglove, *Digitalis purpurea*, which has a pink bell-shaped corolla, pigmented by cyanidin, with a series of concentrated areas of the same pigment in the inside of the bell drawing the insect to the stigma and style. In Sire ptocarpzs species, a similar situation exists except that the honey guides take the form of lines of pigment inside the tubular corolla.

A slightly different situation holds in the genus Pa paver where honey guides generally take the form of pigment blotches on the petals (Fig. 2.8). In this case, the pigment in the blotch (cyanidin as the 3-glucoside) is different from that present in the rest of the petal, which is cyanidin as the 3-sophoroside (in P. i-hoe-as or pelargonidin as the 3-sophoroside in P. orientate).

The first biochemical evidence that honey guides invisible to the human eye occur in flowers was provided by Thompson et al. (1972) in a variety of Rudbeckin hirta called Slack Eyed Susan. In daylight the petals of this composite are uniformly yellow. However, in VV light, the outer parts of the ray are UV-reflecting and bright, while the inner parts are dark-absorbing. Chemical analyses reveal that carotenoid pigment is responsible for the UV reflection of the outer ray and also that this lipid pigment is uniformly distributed throughout the ray. In the inner dark-absorbing zones of the ray, there is a different kind of pigment. In fact, three water-soluble yellow flavonols are present, including especially a derivative of patuletin.

Thus, in Rudheckia, there is separation of function of the two types of yellow pigment present. The carotenoid provides the general yellow flower colour in the plant, in order to attract the bee from a distance. On the other hand, the water-soluble yellow flavonols, differentially present only in the inner ray, act as a UV honey guide, directing the UV sensitive bee once it has landed on the flower head to the nectar in the centre of the blossom. This explains why many highly evolved plant species tend to have two types of yellow pigment in the flower; the two types clearly have different functions.

Invisible honey guides can be readily detected in yellow-flowering species by looking at flower heads under UV light and then by confirming the result by photography, using an appropriate filter. Such detection can actually be done on plants from herbarium sheets. However, it is also vital to actually identify that both carotenoids and yellow flavonoids are present in the flower and this can only be done on fresh flowers. Herbarium surveys have shown that UV guides probably occur in a number of other yellow-flowering composites, particularly those in Heliantheae, the same tribe as Rudheckia (Eisner et al. 1973). Honey guides have been confirmed in Eriophyllum and Helian thus spp. by pigment analyses (Harborne and Smith 1978b). Detection of both yellow carotenoid and yellow flavonoid in a flower does not a priori mean that UV guides are present. We have found that in another tribe of the Compositae, in the Anthemideae, there are many yellow-flowered species with both carotenoid and yellow flavonols (Harborne et al. 1976) but there is no evidence of honey guides in them.

Other types of yellow flavonoid can contribute to honey guides. In Oenofhera (Onagraceae), Dement and Raven (1974) have shown that the chalcone isosalipurposide is responsible for UV honey guides in these flowers. Similarly, Scogin and Zakar (1976) have found that both chalcones and aurones provide UV absorption patterns in flowers of Bidens (Compositae). These patterns are not universally present but occur in five of the seven sections of the genus; there is also variation in how far along the ray the absorbing pigments extend.

There is no necessity for the flavonoids in such flowers to be visibly yellow (although it is obviously a more efficient mechanism), since all flavonoids, irrespective of their visible absorption characteristics, absorb strongly in the UV. Indeed, colourless flavonol glycosides have recently been recognized to provide patterning in some species. Thus in yellow flowers of Coronilla (Leguminosae), yellow gossypetin derivatives provide differential LJV absorption in the wings of the petal of C. ualenfina, but kaempferol and quercetin glycosides take over this role in the wings of C. emerus (Harborne and Boardley 1983). Similarly, in petals of Potentilla (Rosaceae), the yellow chalcone isosalipurposide provides honey guides in six species, while quercetin glycosides are responsible for UV patterning in eight other species (Harborne and Nash 1983). Honey guides have also been observed in some white flowers (Horovitz and Cohen 1972) and in such cases there may well be differential distribution of colourless flavonols in these petals too.

13.5 Role of Flower Scent

13.5.1 Types of Scent

13.5.1.1 Floral Volatiles and Pollination

The evolution of plant volatile production in pollination ecology and in insect-plant relationships has been reviewed by Harrewijn et al. (1995). The floral volatiles play an important role in attracting pollinators to the plant (Harborne 2001). They may attract a pollinating bee or wasp from a distance of several metres. Fruity or aminoid odours are attractive to beetles, sweet smells to bees, moths, and butterflies, musty or fruity odours to bats, and fecal odours to dung-flies. Research using headspace analysis has indicated the major floral volatiles in a representative sample of flowering plants (Table 13.6).

The chemistry of aroid odours has been somewhat controversial in that simple amines such as hexylamine were earlier reported from *Arum maculatum* and several related species. A reinvestigation of *A. maculatum* failed to indicate any amines in the headspace. Instead, indole, *p*-cresol, germacrene B (Pass et al. 1998) and heptan-2-one were detected as major constituents. The plant is pollinated by females of the owl midge, *Psychoda phalaenoides*, which otherwise feeds on cow dung. Both indole and *p*-cresol were detected in the headspace of the dung, so these two compounds appear to be the most important attractants (Kite 1995). Incidentally, indole and skatole are the major "distasteful" odours of another aroid plant, the voodoo lily *Sauromatum guttatum*. Odours unpleasant to the human nose are also dominant in bat-pollinated flowers, and a series of methyl sulfides (Table 13.1) have been identified in *Crescentia cujeta* and several other bat-pollinated plants (Knudsen and Tollsten 1995).

Table 13.6 Floral volatiles of bat-, bee-, beetle-, butterfly-, moth-, and fly-pollinated plants

Floral volatiles[a]	Plant species	Pollinator
Dimethyl trisulfide (24.3%), dimethyl disulfide, dimethyl tetrasulfide, *etc*.	*Crescentia cujeta*	Bat
Squalene (26.5%) nerol, geraniol, hydrocarbons	*Dactylanthus taylorii*	Bat
Geraniol, citral, farnesol, *etc*.	*Ophrys* spp.	*Andrena* male bee
Carvone oxide	*Catasetum maculatum*	*Eulaema* male bee
Linalool (95%) – its oxides	*Daphne mezereum*	*Colletes* bee
Indole, 1,2,4-trimethoxybenzene, cinnamaldehyde	*Cucurbita* spp.	Diabroticite beetle
Methyl anthranilate and isoeugenol	*Cimifuga simplex*	Butterfly
Methyl benzoate (25%), linalool (50%), geraniol (12%)	*Platanthera chlorantha*	Moth
Ethyl acetate, monoterpenes, and aliphatics	*Zygogymum* spp.	Moth
trans-Ocimene (50) (46%), 1,8-cineole (12%)[b]	*Brugmansia* × *candida*	Hawkmoth
Heptan-2-one (16%), indole (16%), germacrene B (49) (18%), *p*-cresol (3%)	*Arum maculatum*	Dung-fly

[a] Only major components are listed: values in parentheses are average percentages of total floral odour

[b] Tropane alkaloids, thought to be present, could not be detected

Many species with carrion smells produce mixtures of dimethyl oligosulfides. Kite and Hetterschieid (1997) analysed by headspace techniques the inflorescence odours of 18 *Amorphophallus* and two *Pseudodracontium* species. Fourteen of these species had nauseating odours based on dimethyl disulfide and dimethyl trisulfide. *A. brachyphyllus* with an anise-like odour contained trimethylamine, while *A. elatus* with a cheese smell produced isocaproic acid. A parallel investigation of 11 bat-pollinated species by Bestmann et al. (1997) showed that 6 of the 11 were sulfide producers. Nine sulfur-based volatiles were variously detected. Not all bat-pollinated species, however, necessarily produce such vilesmelling compounds and the remaining five species surveyed contained more expectable aliphatic, monoterpenoid and sesquiterpenoid volatiles. One other fetid-smelling plant species to be investigated is *Senecio articulatus* (Compositae), which is fly-pollinated. The flower of this plant produces 3-methylbutanoic acid, with minor amounts of linalool and its oxides (Kite and Smith 1997).

Turning to plants with fragrant odours, it may be mentioned that pleasant-smelling species can be found in families such as the Araceae, where nauseous odours dominate. Investigation of five *Anthurium* species showed none with sulfides present. In fact, all of them yielded terpenoids such as α- and β-pinenes, limonene, 1,8-cineole and linalool and the odours were characterized as floral, minty, pine and sweet (Kuanprasert et al. 1998).

In sweet-smelling plants, individual constituents may dominate (*e.g.* linalool in *Daphne mezereum*), but more usually there are several components, which act synergistically to attract the pollinator (*e.g.* as in the moth-pollinated *Platanthera*) (Table 13.12). The floral scent is usually released at the right time of day for the particular pollinator, *e.g.* during the day for beepollinated flowers. For moth-pollinated species, it may be at dusk or even later in the night. Thus, ocimene (Eschler et al. 2000) is released from flowers of *Mirabilis jalara* at night between 6.00 and 8.00 p.m. Different parts of the flower may have slightly different odours. This is true in *Rosa rugosa* and *R. canina*, where bees can select out pollen for collection from the rest of the flower. The compound geranylacetone (Lindroth and Weisbrod 1991), for example, is specific to the pollen and is not found in the floral odour (Dobson et al. 1987). In the distinctive pollination of orchid flowers of the genus *Ophrys* by male bees of the genus *Andrena*, a large number of scent constituents are involved. Pseudocopulation of the flower by the male bee depends on the flower having the same shape, same scent, and same colour as the female bee. In *Ophrys lutea*, for example, octan-1-ol, decyl acetate, and linalool are common to the floral volatiles and to the pheromonal odour of the female bee. Studies on the *Ophrys–Andrena* volatiles were described by Borg-Karlson et al. (1993).

The pleasant floral volatiles of *Ligustrum japonicum* were investigated to see which of the odour molecules were particularly attractive to the foraging adult small white butterfly, *Pieris rapae*. Five of the 30 volatiles were implicated: phenylacetaldehyde, 2-phenylethanol, 6-methylhept-5-en-2-one, benzaldehyde and methyl phenylacetate. These substances acted synergistically to attract the insect to feed on the nectar (Honda et al. 1998).

A survey of floral fragrances in nine species of *Narcissus* native to southern Spain divided them into two groups. One group of species pollinated by butterflies and moths have fragrances typical of moth-pollination, *i.e.* indole and aromatic esters. The second group pollinated by bees and flies have monoterpenoids but lack the components of moth-pollination. One species, *Narcissus assoanus*, is unusual in having both fragrance chemotypes and is pollinated by both moths and solitary bees (Dobson et al. 1997). A strange discovery is the presence of the moth-repellent naphthalene (Palto et al. 1993) in *Magnolia* flowers (Azuma et al. 1996).

It occurs in petals, gynoecia and leaves of five out of nine species surveyed. Its role in beetle pollination is not clear. Is it an attractant or does it stop beetles from chewing the petals? Its function deserves further investigation. Otherwise, *Magnolia* flowers contain more expectable pleasant-smelling volatiles; a range of terpenoids, benzenoids and fatty acid esters have been characterized variously in flowers of Magnoliaceae (Azuma et al. 1999).

The odour or scent of a flower often plays a major role as attractant to pollinating insects in the angiosperms. Bees are especially responsive to flower scents which we would describe as fragrant or ‘heady’ and many bee flowers are scented, e.g. the garden violet and other Viola species. Odour is of special importance in night-flying insects and other animals, where visual stimulus is practically absent; bat-pollinated and moth-pollinated flowers are generally strong smelling.

Because of the sensitivity of insects to small concentrations of volatile chemicals, flower odours are probably effective at relatively low concentrations. Many species which do not appear to be strongly scented to human senses may, in fact, produce sufficient odour to attract bees or butterflies. In many species, maximum scent production is co-ordinated with the time when the pollen is ripe and the flower is ready for pollination. Diurnal variations in production also occur so that scent is produced for day-time pollinators at noon, for night-time pollinators at dusk.

Floral scent may attract a pollinator to the flower for other purposes than food, as happens in the case of the primitive angiosperms Zygogynum and Exospermum, which are pollinated by a moth of the genus Sabatinca. These moths use the flowers, which blossom for only a few days, as a mating site. The fragrance, a mixture of terpenes and aliphatics (see Fig. 2.10), also contains large quantities of ethyl acetate, with its peardrop odour. This latter compound appears to improve the effectiveness of pollination by making the moth drowsy (Thien et al. 1985).

Other plant tissues besides the petals give off scents. Indeed, many labiates and other plants have special scent glands on the leaf surfaces which are full of volatile oils. It is not dear in such cases whether leaf odours contribute at all to the attraction of pollinating vectors. Certainly higher animals may be sensitive to leaf odours of the Liabiatae – witness the well-known attraction of the domestic cat for the catmint, Nepeta cataria.

From the viewpoint of the human observer, Rower scents broadly fall into two classes: those that are pleasant, fragrant or fruity; and those that are distinctly unpleasant or aminoid. While we can make such a classification for our own benefit the pollinator concerned is clearly attracted to the scent whatever its particular quality to the human nose. Pleasant odours are generally contained in the ‘essential oil’ fraction of the Rower, that part which can be separated by steam distillation or ether extraction and is volatile. Within the essential oils, a range of organic compounds may be present, the majority being mono- or sesquiterpenes. Volatile aromatic substances may be present, as well as simple aliphatic alcohols, ketones and esters. Typical structures of some Rower odoriferous principles are illustrated in Fig. 2.10. In some cases, a major constituent may be responsible for a particular flower scent but, more usually, a mixture of components provide the scent. An important factor in scent production is that one component may reinforce the effectiveness of a second and third in producing a characteristic odour.

Monoamines	
CH_3NH_2	Methylamine
$CH_3CH_2NH_2$	Ethylamine
$CH_3(CH_2)_2NH_{22}$	Propylamine
$CH_3(CH_2)_3NH_2$	Butylamine
$CH_3(CH_2)_4NH_2$	Amylamine
$CH_3(CH_2)_5NH_2$	Hexylamine
Diamines	
$NH_2–(CH_2)_4–NH_2$	Putrescine
$NH_2–(CH_2)_5–NH_2$	Cadaverine

Flower scents have, of course, been utilized for many years in human society as perfume. While most modern perfumes are synthetic in origin, natural Rower scent extracts still have an importance for boosting the effectiveness of synthetic mixtures. Roses are still cultivated in Bulgaria for their scent. Modem research by perfumers has shown that even the simplest flower scent may have many, indeed a hundred or more, constituents. In view ol this complexity, the way in which many plant species have recognizably different Rower scents may readily be appreciated. Some idea of the range of substances detected in flower scents can be gathered from the recent monograph by Kaiser (1993) on orchid volatiles.

Unpleasant aminoid odours in plants have, perhaps not unnaturally, been poorly studied. Our knowledge of the chemistry of highly repulsive and distasteful plant odours is therefore limited. Three typical plants with obnoxious odours are the hogweed. Heracleurn sphondyhurn, stinking hellebore, Hellehorus foetidus, and cuckoo pint, Aruni maculaturn. Other examples occur in the families to which these species belong, especially the Umbelliferae and Araceae. Unpleasant smells, in fact, represent a chemical mimicry by which the plant produces the smell of decaying protein or faeces to persuade carrion and dung insects to transfer their attention to the Rower heads. Indeed, the chemicals produced are very similar to those given off by carrion or dung.

Major constituents of aminoid plant odours are monoamines, which have unpleasant fishy smells. They are fairly volatile and range from methylamine to hexylamine (Fig. 2.11). Some free ammonia may also be present. Even more offensive to some are the two diamines, putrescine and cadaverine, which as their names imply are characteristicbreakdown products of decaying protein. Putrescine and the monoamine isobutylamine have, for example, been reported in Arurr floral odours. Other unpleasant compounds that may be present are skatole and indole (which have faecal odours) and odd-chain auphatic organic acids, such as isobutyric acid with its rancid smell.

The way by which plants use such smells as a trap for insects has been investigated in some detail (see Faegri and van der PijI 1979). In Arum nigrurn and A. vnacu1aum, for example, the bright purple spathe opens overnight to reveal the spadix in which respiration is unusually rapid and temperatures of 30°C have been measured (Fig. 2.12). The heat thus generated in the spadix aids the volatilization of the amine into the objectionable odours which are then released. Dung beetles and flies attracted by the amines alight on the spadix, and fall into the bottom of the flower, where they are happed. The insects cannot escape because of the slippery surface of the inner spathe and are kept prisoner for 24 h, during which time they transfer pollen to the receptive styles; rapid anatomical changes then occur (including wrinkling of the spathe surface) and the insect is eventually released. The generation of heat in the spadix is a truly remarkable feature of these plants and it must increase the effectiveness of the faecal odours. The rapid respiration that occurs uses up a quantity of starch in the process but presumably this is offset in terms of metabolic efficiency by the fact that only small amounts of nitrogen compounds are needed in the scent.

In the related voodoo lily, Sauromalum guftahon, the trigger for heat production and volatilization of the aminoids has been identified as salicylic acid (2-hydroxybenzoic acid), the concentration of which rises 100-fold in the upper spadix some 12 h beforehand (Raskin et al. 1987). Production of heat and faecal stench reaches a maximum between 3 and 5 h after dawn on the day of pollination and drops back to normal by late afternoon. A second heating phase in the following night, also triggered by salicylic acid, stimulates the flies trapped in the floral chamber to carry out the pollination (Diamond 1989).

The floral scent of eight bat-pollinated plant species has been found to be based primarily on sulfur compounds. Besides dimethyl sulfide, dimethyl disulfide and dimethyl trisulfide, irregular sulfides are present such as 2,4-dithiapentane and 2,3,5-trithiahexane. Three species contained mushroomsmelling fatty acid derivatives with a C, skeleton. The presence of closely similar sulfur compounds in seven out of the eight species, which all belong to different families, suggest that this is a case of convergent *Evolution* in scent composition (Kundsen andTollsten 1995). A further bat-pollinated species, *Dactylanthus taylorii*, a member of the Balanophoraceae, has unexpectedly yielded squalene as a major floral constituent. Also present are C_{21} to C_{31} hydrocarbons, fatty acid esters and typical fragrance chemicals such as nerol and geraniol. Although the plant is bat pollinated, the nectar is attractive to possums and ship rats, who browse on the flowers without pollinating them. As a result, this species is threatened with extinction (Ecroyd et al. 1995).

Two of the sulfur compounds reported in bat-pollinated flowers have been found in the odour of the voodoo lily flower, *Sauromatum guttatum*: dimethyldisulfide and dimethyltrisulfide. 128 The same two compounds are incidentally responsible for the foul odour released by the mushroom, *Phallus impudicus* (Borg-Karlson et al. 1994). A reinvestigation of the well known aroid *Arum maculatum* failed to reveal any of the simple amines that were earlier recorded in the volatiles. Instead, the analysis showed the presence of heptan-2-one (8–23% of total volatiles), indole (8–23%), germacrene B (10–14%) and p-cresol (O.2–6%). The major pollinators were confirmed as females of the dung fly *Psychoda phalaenoides* and a comparison of floral odours with those produced by cow dung identified p-cresol as the main common component (Kite 1995). The faecal-smelling indole of *Arum maculatum* is also produced, surprisingly, in the blossoms of *Cucurbita* (Cucurbitaceae), where the pollinators are diabroticite beetles. Indole acts synergistically with 1,2,4-trimethoxybenzene and ***(E)*-**cinnamaldehyde to attract the beetles to the flowers for pollination. Beetle species vary in their responses to indole and it appears that the indole receptor in the beetles has been conserved over 30 million years during diabroticite *Evolution* (Metcalf et al. 1995). In the hawkmoth-pollinated *Brugmansia* × *candida* (syn. *Datura candida*), it was suggested that tropane alkaloids were present in the volatiles which intoxicated the moths during pollinating visits. A reinvestigation by Kite and Leon, 13′ however, failed to uncover any alkaloids in the floral odours. The dominant components are trans-ocimene (3,842%) and 1,8-cineole (5–19% of total). The leaf odour also lacked any alkaloid, but contained perillene (1,425%) and dendrolosin.

Three forms of the orchid *Ophrys insectifera* are pollinated by male bees, who carry out pseudo-copulation with the flowers which resemble the female bees in morphology, colour and scent. Different species of male bees were involved, suggesting that there might be differences in floral odours. Indeed, analysis showed both quantitative differences in aliphatic hydrocarbons, methyl esters and aliphatic alcohols and qualitative differences in the nine terpenoids that were present (Borg-Karlson et al. 1993). In moth-pollinated orchids of the genus *Platanthera*, similar differences were observed in the scent volatiles in individuals and in different populations (Tollston and Bergstrom 1993). Again, in the bee-pollinated plant *Pyrola grandzyora*, populational variation in scent production was apparent, with either benzaldehyde or methoxybenzenes dominating (Knudsen 1994). Analysis of the floral fragrance of the early flowering shrub *Daphne mezereun* revealed a remarkably simple pattern, with (*S*)-(+)-linalool as 95% of the total. Linalool oxide isomers made up the remainder of the By contrast, the floral odours of *Jacquinia macrocarpa* in the Theophrastaceae have a range of sesquiterpenes, aliphatic alcohols and esters, pyrazines and benzenoids. Additionally, there are several cyclohexane derivatives (*e.g.* P-cyclocitral), which could be formed by degradation of the carotenoids present in the corolla (Knudsen and Stahl 1994).

The visually-distinctive umbell-shaped flowers of the Umbelliferae are unusual in attracting a great assemblage of diverse insect species to feed on and pollinate the flowers.

This would suggest the absence of species-specific cues in the volatile fraction, but that the odours would attract groups of different insects. Chemical analysis has borne this out, in that there are many components present. Monoterpene hydrocarbons dominate in several species, but nitrogenous compounds, aliphatic short-chain esters and linalool are also present (Borg-Karlson et al. 1994; Tollsten et al. 1994).

In visiting flowers to collect their food, bees may come into contact with toxic constituents. Alkaloids, for example, are known to be present in certain nectars. Detzel and Wink139 therefore tested 63 allelochemicals on the feeding behaviour of *Apis mellifera* and found that they were not especially adapted to plant defence chemicals. Some 17 of the chemicals proved to be fatal to the bees at concentrations between 0.003% and 0.6%. Bees are thus at risk from visiting *Atropa belladonna* flowers, where the tropane alkaloid levels in the nectar reach 273 yg g – 'fresh wt. By contrast, they are safer on tobacco flowers, where the nicotine levels are only 0.17 pg g –' fresh wt.

Vereecken and Schiestl (2009) reported that sexually deceptive orchids achieve cross-pollination by mimicking the mating signals **of** female insects, generally hymenopterans. This pollination mechanism is **of**ten highly specific as it is based primarily on the mimicry **of** mating signals, especially the female sex pheromones **of** the targeted pollinator. Like many deceptive orchids, the Mediterranean species *Ophrys arachnitiformis* shows high levels **of** floral trait variation, especially in the colour **of** the perianth, which is either green or white/pinkinsh within populations. Floral colour polymorphism in *O. arachnitiformis* is not subjected to selection imposed by *C. cunicularius* males, and an interplay between different non-adaptive processes may be responsible for the maintenance of floral colour polymorphism both within and among populations. The adaptive significance of perianth colour polymorphism and its influence on pollinator visitation rates in sexually deceptive orchids remain obscure.

13.5.2 Insect Pheromones and Flower Scents

Insect behaviour is known to be controlled by chemical signals, which take the form of volatile organic constituents released by one insect to affect another. These substances are active in very small amounts and have been termed 'pheromones', to indicate their relationship to hormones. Pheromones are involved in almost every aspect of insect life: feeding, sex, aggregation, oviposition, defence and laying trails. Chemically, many of the pheromones are simple aliphatic alcohols, acids or esters; others are closely related to the plant scents in being terpenoid in nature. Pheromones will be discussed inter a/ia in several later chapters of this book. Mention of them here is pertinent, since the action of a flower in producing a fragrant scent to attract a pollinator can be a similar signal to that of a pheromone released by one insect to attract another. Indeed the signals may sometimes get crossed, with interesting results, as will be mentioned below.

Because insects depend on volatile compounds for social communication, they can clearly become sensitive to similar molecules which may be present in flower scents. Plants may occasionally deceive insects by producing attractive odours to trap them (see above) or to draw them away from more rewarding pursuits (e.g. feeding). Insects 'learn' to recognize the smells of individual flowers and it is this factor, perhaps more than any other, which is responsible for the phenomenon of flower constancy, where insects limit their attention to a few or only one plant species. It has even been suggested that some plants produce hallucinogenic or narcotic substances in their scents, so that insects become 'hooked' on them and a close symbiotic relationship may develop. Such a floral reward appears to operate in Datum maria, where the nectar presumably contains the typical hallucinogenic tropane alkaloids of this genus. Grant and Grant (1983) have observed that the hawkmoth pollinators are erratic in flight after visiting the flowers at dusk and show all the signs of being hooked on this 'fix'.

Three examples will now be given where pheromones and flower scents have become interwoven in insect behaviour. The first refers to the oriental fruit fly, Dacus dorsalis, which has the phenylpropanoid eugenol methyl ether (see Fig. 2.10) as sex pheromone. Pheromonal activity is exhibited both in feeding and in male aggregation. This same compound is produced in the blossoms of several plants, especially in the golden shower tree Cassia fistulosa (Leguminosae), where its prime purpose is to attract pollinators. Methyleugenol is also incidentally produced in the volatile leaf oils of other species, and in Zieria srnithii (Rutaceae) it constitutes as much as 85% of the total essential oil. Because of the striking attraction of this chemical to the fruit fly, it has been proposed that Cassia blossoms or Zieria leaves be employed in insect traps, e.g. when Dacus develops to pest proportions in fruit orchards.

This fruit fly is perhaps unusually sensitive to this flower or leaf scent. As little as 0.01 jig methyleugenol will produce a response from a single fly in a cage. The structure is highly specific; synthesis of 34 analogues failed to produce another compound as active and most analogues were essentially inactive. Its pheromonal effect in the male fly is in part to stimulate feeding and this can have drastic effects if wrongly applied. Thus in laboratory experiments, adult fruit flies continuously exposed to traces of methyleugenol will engorge so much food that they will actually die from overfeeding.

The second example of pheromone – flower scent interaction is taken from studies on bee orchids by Kullenberg and Bergstrom (1975). The specific way that certain wild solitary bees of the genus *Andrena* are attracted to orchid flowers of the genus Ophrys for purposes of pollination has been appreciated for some time. The shape and colour of the orchid flower closely resemble that of the female bee of the species and the male descends on the plant, performing what is termed 'pseudocopulation', and pollinating the flower in the process. What has not been realized before (Kullenberg 1952) is that the visual lure of the orchid flower shape is closely associated with an olfactory attraction and that the orchid scent, in fact, mimics the sexual odours of the female bee, thus ensuring the presence of the male bee to trigger orchid pollination. Significantly, the orchid flower does not offer any nectar for the insect and neither does the female bee visit it.

Following from these field observations, the scent of Ophrys has been analysed. The major constituents are short chain aliphatic compounds, monoterpenes and some bicyclic sesquiterpenes of the cadinene series. Both (-I-)- and (—)-7-cadinene have been identified and it is interesting that it can be shown in laboratory experiments that the male bee is excited by the (—)-isomer, but not by the (+)-form. Thus only compounds with the right stereochemistry produce maximal behavioural response in these insects.

The odour glands of the female *Andrena* bees have also been extracted and examined. Their 'Dufour's gland' secretions contain open chain mono- and sesquiterpene esters. (E)Farnesyl and geranyl hexanoates are the major substances in five And rena species; the corresponding octanoates occur in a sixth species. The mandibular gland secretions are species-specific and are composed of fatty acid derivatives, especially short to medium chain alcohols and esters, and monoterpenes. Some of these, like octanol, decyl acetate and linalool, are present also in the Ophrys perfumes and help to 'fool' the male bee into thinking he is approaching a real female.

The co-evolution between these orchids and bees is fairly complex in terms of the species involved. Pseudocopulation takes place in at least 15 Opiirys species or forms and several genera of bees, including *Andrena* and Colletes, and sphecid wasps are concemed. Pollination is decidedly assortative in that different orchid species or species groups are preferentially visited by different aculeate hymenopteran species or species groups. However, a considerable number of different volatiles have been variously detected in the orchid flower scents and in the cephalic glands of the female bees (Bergstrom 1978), sufficient at least to account for the specific interactions that have been observed in nature. Ophrys lutea appears to differ from other related species in producing a much wider range of scent compounds and then benefits by receiving visits from males of more than one Andrena species. Among the 150 scent constituents of 0. lidea are several which are present in the gland secretions of the corresponding female bees, so that the plant is directly mimicking the female pheromones (Borg-Karlson et al. 1985).

A special feature of the odour compounds in the *Andrena* female bee secretions is that they have to perform two functions. Not only do they provide a sex pheromone, but also they are employed as a nest-lining material during the egg-laying process. The active constituents of the Dufour's gland in two other bee genera, Colleies and Halictus, have also been studied and characterized as macrocyclic lactones, which have distinctive musky odours. One such compound is 18-octadecanolide. Again, these substances are dual-purpose. It is appropriate here to mention that very similar lactones have sex attract- ant properties in mammals, for example civetone and muscone, the active odour compounds of the civet cat, Viverra civetta, and of the musk deer, Moschus moschiferus, respectively.

A further twist in the story of the *Andrena* female bee secretions has been discovered by Tengo and Bergstrom (1977). It is that the Dufour's gland compounds are utilized by yet other bees (of the genus Nomada), which parasitize *Andrena* nests, as chemical cues to specifically locate the nests. The Nomada female lays her egg in the next cell, and the larva which hatches then kills the host egg and consumes its food supply. In spite of the harm caused by this parasite in the nest of the Andrew bee, an encounter between females of the two very different species never apparently provokes any aggressive behaviour. This lack of aggression, however, is readily understandable when it is realized that the Nomada females smell the same as their Andrea hosts. Very remarkably, the odour compounds of the *Andrena* female – farnesyl hexanoate or geranyl octanoate – are manufactured by the male Novnada bee, who sprays his mate with them during copulation. The chemical links in this co-evolutionary adaptation are almost as striking as those of the original orchid – *Andrena* interaction.

A final, third example, also taken from the bee orchid literature, records a case where male bees make use of flower scents as their sex pheromones. This happens with male euglossine bees which live in the tropical forests of Central and South America. These bees are highly unusual in their mating behaviour; the males are brilliantly coloured and during mating congregate together into small swarms or 'leks' in order to attract the females to them. The orchids which are pollinated by them have evolved a wide range of different floral scents, as part of their extensive speciation in the neotropics. At least 60 chemically distinct fragrances have been recognized in these plants. While pollinating the orchids, several species of Euluema bees collect the odour fragrances in their hind legs and use them to attract other males of the same species. They then form into swarms or leks, and when this is done, the Females are attracted by visual means and mating takes place. Orchid compounds used in this way include eugenol, vanillin, cineole, benzyl acetate and methyl cinnamate. Different bee species are differentially attracted by only some of these odours. Thus, isolation mechanisms preventing different bee species from mating may be due to varying preferences for orchid scent compounds (Dodson 1975).

A close co-evolutionary relationship between bees and orchids has been observed in central Panama, where 11 orchid species are assortatively pollinated by five species of Eu/aetna and three species of Eug/ossa male bees. The chemical link is the major floral volatile carvone epoxide, which is collected by the males and used in lek formation. What is remarkable here is that there is a single species of Euphorbiaceae, Dalechampia spat ku/ala, in the same habi tat which produces the same floral reward as the orchids and is pollinated by the same bees. Thus, through biochemical convergence in floral odours, an unrelated euphorb has managed to break into the orchid – bee pollination syndrome (Whitten et al. 1986). In a similar way, through visual mimicry, Cavnpanula rubra growing in southern Sweden resembles a red helleborine orchid in order to persuade male solitary bees away from the orchid to pollinate it (Nilsson 1983).

That plant scents and odors have been recognized as valuable chemotaxonomic markers is well established (Harborne 1993). However, for pollination ecology studies, the focus is often centered on the role that flower morphology and flower color play in pollination ecology with scent recognized as a secondary player.

Floral scent is an important component in the reproductive biology of many flowering plants (Harborne 1993). Scents will serve as attractants in plants pollinated by a variety of fauna: birds, bats, beetles, butterflies, moths, bees and wasps. Scent will advertise the presence of awards to foraging pollinators, such as nectar or pollen, or temporary protection from predators. Research in floral scent ecology has important implications for studies in population ecology, pollen dispersal, pollination ecology, plant speciation, insect behavior, and pest management (Raguso and Pellmyr 1998). Further, Pellmyr and Thien (Pellmyr and Thien 1986) suggest that pollination systems between insects and extant archaic angiosperms evolved primarily through the meshing of the sexual life cycles of phytophagous insects with flowers.

In light of the recognition that floral scent plays a key role in pollination ecology, much recent research has been focused on the pollination ecology of those plant species that emit arbitrarily unpleasant odors, often likened with the odors of decaying tissues and fecal material. The composition of these odors serves as important ecological cues for insects within the Coleoptera and Diptera. Beetle-pollinated flowers, for example, often provide the pollinators with a space to protect them from predators, and/or produce relatively large amounts of pollen and sometimes special nutritive tissues to provide nutrition for the pollinators (Beach 1982; Gottsberger 1990). In addition to cueing for the presence of pollinator awards (nectar, pollen) and protection, these odor compounds will also often cue for mating and oviposition sites which can result in an exercise of deceit pollination where the pollinator leaves the plant often without benefit of reward. Additionally, these pollination systems may have evolved for plants which inhabit areas which are unsuitable for hymenopteran and lepidopteran species, such as the littoral layers of forests or in rocky and treeless areas with few flowering plant species.

13.5.3 Odoriferous Chemical Compounds in Plants

Foul and fetid odors produced by plants are generally associated with a pollination syndrome known as sapromyophily, or pollination by insects that breed or feed on decaying matter or fungi (Kite and Smith 1997). In most beetle-and some fly-pollination schemes, scent acts as the primary attractant (Gottsberger 1990). Recent work on odoriferous compounds suggest that the chemical cues emitted from *Sauromatum guttatum* (Araceae), for example, may be more important to these insects than the visual cues (Skubatz et al. 1996). More precisely, the physiological features of the plant that actually produce the scent (described below) are capable of dispersing the scent over long distances.

The *Sauromatum* appendix was found to emit a complex blend of terpenes, fatty acid derivatives, phenolic, sulphur and nitrogenous compounds (Skubatz et al. 1996). Indole and 30 other nitrogenous compounds were identified, to which over 30 insect species, many of which were species of Coleoptera and Diptera, were attracted (Skubatz et al. 1996). Among these were compounds from at least nine different chemical classes. The major group in those compounds released were terpenes (mono- and sesquiterpenes), with monoterpenes accounting for approximately 70% of the mixture, and sesquiterpenes accounting for about 6% of the mixture. As a group, fatty acids, alcohols, ketones and aldehydes accounted for about 20% of the mixture. Those compounds responsible for the characteristic fetid odor of the plant, indole and sulphur compounds were found in 0.2% and trace amounts, respectively (Skubatz et al. 1996). The nitrogen and the sulphur-containing compounds provide the distinctive vile aroma of the appendix. For example, indole is pungent and dimethyl disulphide is intensely foul (Skubatz et al. 1996).

The foul odor produced by these plants is apparently attractive to many species of Coleoptera and Diptera that are associated with the ecological recycling of dung and carrion (Skubatz et al. 1996). The affinity these insects have for these compounds released by the plant is not surprising since the same volatiles which are released from *Sauromatum guttatum* are also the same as those liberated from decomposing tissue and wastes through microbial oxidation of lipids and decarboxylation of amino acids. Interestingly, terpenes, which are the prevalent pleasant-smelling compounds in the majority of flowering species, are also found in the *Sauromatum guttatum* appendix. However, their presence is masked (to the human nose) by the presence of the malodorous compounds which are detectable at very low concentrations due in part to their volatility and compact molecular structures (Skubatz et al. 1996).

Another foul-smelling plant, *Arum maculatum* (Araceae) possesses an odor described as foul and urinous which is produced by the presence of indole and additionally *p*-cresol. The combination of these two compounds in *Arum maculatum* mimics the pollinator's food and oviposition sites resulting in deception (Kite and Smith 1997). The primary pollinator for *Arum maculatum* is a dipteran *Psychoda phalaenoids* (Psychodidae) which in field observations breeds exclusively in cow dung (Kite 1995).

Deceit pollination has also been observed in *Orchidantha inouei* (Lowiaceae: Zingerbales) was recently discovered in Malaysia (Sakai and Inoue 1999). This pollination system is believed to be an oddity in this particular group of plants, as many members of this family exhibit fascinating mutual relationships with their pollinators. *Orchidantha inouei* attracts two genera of dung beetle (Coleoptera: Scarabaeidae), only one of which was observed to actually pollinate this orchid, although the orchid itself does not offer any nutritional reward nor offer protection, hence the observation that this is deceit pollination (Sakai and Inoue 1999).

13.5.4 The Role of Thermogenecity in the Release of Odors

All known flowers contain metabolic biochemical activity, the by-product of which is heat (Seymour and Schultze-Motel 1997). However, in most flower-producing plants, the reaction to produce heat is slow and therefore the heat dissipates slowly. The plants technically classified as "thermogenic", however, produce an unusually large amount of heat over a very short period of time. This significant heat production is assumed to not be a by-product of metabolic activity, but produced rather for the sake of completing some ecological need or function (Seymour and Schultze-Motel 1997). This episodic heat production in these plants usually corresponds with the period when the female flower parts are most receptive to pollination and the floral scent is the strongest (Seymour and Schultze-Motel 1997).

Sauromatum guttatum also undergoes a heat-producing stage which aids in liberating the volatiles coinciding with the female flower's receptivity to pollinators attracted to the appendix by the odor that is emitted (Skubatz et al. 1996). Gottsberger (1990) reports that pollination occurs by large dynastid scarab beetles of the genus *Cyclocephala* in two plants, *Annona coriacea* (Annonaceae) and *Philodendron selloum* (Araceae). Gottsberger further states that although the two plant species are widely separated phylogenetically, their pollination biologies are very similar, which indicates that their adaptations to pollination by beetles is the result of convergent *Evolution*ary developments.

Annona coriacea possesses a thermogenetic function in order to attract its beetle pollinator *Cyclocephala atricapilla* (Coleoptera: Dynastidae) (Gottsberger 1990). Apparently this plant will produce a functional flower that warms to 34°C, which may be as much as 15°C above ambient air temperature. Again, the purpose of this thermogenesis is to volatilize a characteristic spicy odor which attracts the beetle for pollination. This takes place over the course two days. The flowers, which are protogynous, have the male and female phases of the flower distinct from one another so that self-pollination is unlikely. During the first evening, the flower enters its female phase, attracting its beetle pollinators over long distance through its thermogenetic function. The flower's petals will close off the entrance, effectively trapping the beetles in the chamber for approximately 24 h. The next evening, the stamens will detach from the receptacle and shed pollen grains, which cover the body of the beetle. As the petals drop, the floral chamber is opened, and the beetles are liberated. These pollen-covered beetles fly off and then enter a newly opened odoriferous flower in the female stage to successfully induce pollination. The *Annona* provides for its pollinator rewards such as comestibles, mating and protection sites (Gottsberger 1990).

Philodendron selloum (Araceae) also possesses a thermogenetic function (Gottsberger 1990). Thermogenesis occurs in the evening hours, and may reach temperatures of 46°C, which may be as much as 30°C more than ambient temperature. *Philodendron selloum*, however, is one of the few plant species known which has lipid oxidation during the main heating phase, insect of normal starch utilization. This very distinct respiration process, with its accompanying heat production, causes an accentuated volatilization of odor components, attracting its representative beetle pollinator, *Erioscelis emarginata* (Dynastidae), over long distances. The attractivity of the inflorescence is often so intense that 50, 100 or even 200 beetles may be observed approaching a single inflorescence simultaneously (Gottsberger 1990).

In another thermogenetic example, the Amazon water lily, *Victoria amazonica*, heat-production is combined with a change in petal color during a 2-day sequence, presumably to control the behavior of its scarab beetle pollinators of the genus *Cyclocephala* (Seymour and Schultze-Motel 1997). These flowers on the first day, floresce during the evening hours, when these beetles are the most active. *Cyclocephala* beetles fly to the petals, crowd the floral chamber, and eat a nutritious starchy material provided by the lily. Later, the petals will close around the beetles, effectively trapping them for approximately 24 h. The next evening, the petals reopen, allowing escape of the now pollen-covered beetles to fly to the next series of first-day flowers. The flower of escape is no longer attractive to the beetles, as the scent no longer lingers, neither the flowers are white (Seymour and Schultze-Motel 1997).

13.6 Timing of Inflorescence and Pollination

Variation in the diurnal and seasonal production of floral scents is also of key importance to successful pollination of odor producing flora, and correlate well with daily and seasonal insect activity.

Amorphophallus johnsonii flowers during April in the main rainy season (Beath 1996). Anthesis of this plant commences at dusk when emission of a strong aminoid odor takes place. Large numbers of carrion beetles of the crepuscular species *Phaeochrous amplus* begin to arrive just after dark and become trapped in the lower spathe overnight and remain in the appendix of the inflorescence for approximately 24 h. At this time the anthers produce long threads of sticky pollen, which adhere to the beetles as they finally make their escape, and fly to the next aminoid-emitting inflorescence, perhaps now in its female stage, resulting in pollination of the next flower.

Experiments with *Phaeochrous amplus* beetles and pollination of *Amorphallus johnsonii* demonstrated that beetles traveled from male phase blooms to female phase blooms on the same day, and were even observed up to 3 days later, with distances traveled by marked beetles of 8–37 m (Beath 1996). The number of successfully fertilized flowers observed in this manner was given about a 40% success rate.

The reason for the success of certain flowers over others was found to be that successful fertilization only occurred when the female phase blooms were visited by beetles coming from a bloom in the male phase on the same evening (Beath 1996).

Senecio articulatus produces an odor that is described as rather repugnant and fetid, which is more noticeable during the morning hours (Kite and Smith 1997). Although actual pollination of *Senecio articulatus* has not been directly observed in the field, insects associated with they recycling of nutrients have been observed to visit the inflorescences, including calliphorid flies (Kite and Smith 1997), which are known to be active during the daylight hours.

The timing and release of 3-methylbutanoic acid from *Senecio articulatus* suggests that the responsible pollinators are active during the day, which supports the assumption that calliphorid flies are presumably the pollinators (Kite and Smith 1997).

Similarly *Arum maculatum* (Araceae) inflorescences usually open mid to late morning and temporarily trap small flies, the majority of which are diurnally active *Psychoda phalaenoides* (Diptera: Psychodidae), which are attracted to the dung-like scent emitted by the thermogenic inflorescence (Ollerton and Diaz 1999).

13.7 Evolutionary Significance and Ecological Functions of Thermogenecity and Chemoattractants

Evolutionarily speaking, the significance of thermogenesis for beetle pollination is apparent in several ways (Seymour and Schultze-Motel 1997). First, it is apparent that thermogenic flowers are always protogynous and the spike of heat production occurs with the period of female flower receptivity. Second, the morphology of the flowers is well-suited for beetle pollination. The flowers are generally large in size, and provide broad landing platforms for clumsy fliers (beetles). Third, the floral scents often mimic those scents that beetles associate with places to feed, mate, or lay eggs, and it is believe that the fragrances have co-evolved with the beetles to induce specific activities (Seymour and Schultze-Motel 1997). Lastly, there is evidence for correlation between the thermal requirements of beetles and the temperatures maintained inside the thermogenic flowers (Seymour and Schultze-Motel 1997). Most beetles are endothermic and require high temperatures for activity such as flight, mate competition, and feeding. Higher and non-lethal temperatures therefore reduce the energy expenditures by beetles required by the plants for pollination. It is significant to note that the temperatures often found in thermogenic flowers are in the same range preferred by active beetles (Seymour and Schultze-Motel 1997).

One ecological explanation for the very high temperature reached in *Philodendron selloum* (highest temperature measured in plants to date), for example, may be found in its population structure (Gottsberger 1990). Apparently, *Philodendron* *selloum* inhabits semi-dry forests on the Brazilian plateau, quite in contrast with other members of the genus, which are found to inhabit humid rain forests. Therefore, suitable habitat for *Philodendron selloum* is scarce, and so its population density is sparse, and individual plants are often found far from one another. It seems certain that the need for such highly specialized floral biology to successfully attract pollinators over such long distances contributes to its success as a species.

Dung beetles have been observed to be excellent searchers for dung material, and many species will fly for long distances in search of a particular type of dung. Dung beetles, therefore, are suggested by Sakai and Inoue (1999) to provide long-distance pollen transfer. The interest here is that many plant species of Zingerbales specialize in long-distance yet costly (in terms of protection and nutritional rewards) pollination tactics through pollinators such as bees, birds and bats. One species within this group, *Orchidantha inouei* does not offer such costly rewards for pollination, and is presumed to be an energy saver (Sakai and Inoue 1999). *Orchidantha inouei* (Zingerbales) attracts two genera of dung beetles, *Onthophagus* and *Paragymnopleurus* (Sakai and Inoue 1999). However, *Onthophagus*, being the smaller of the two genera, was the only one observed to actually carry pollen as it left the flower, and through this particular study, is identified as the major pollinator of *Orchidantha inouei*. Although several individuals of *Paragymnopleurus* were observed to aggregate around the base of the plant, pollen on the bodies of individuals was observed rarely (2 out of 27). This was possibly because *Paragymnopleurus* beetles are too large to reach the anthers located in the narrow, innermost part of the corolla of the flower, as was facilitated by *Onthophagus'* smaller body size (observed pollen carriers 18 of 30 cases). However, the odor produced in *Orchidantha inouei* was not observed to attract dung or carrion flies within the dipteran families Muscidae, Calliphoridae or Scatophagidae (Sakai and Inoue 1999). It is suggested by these observations that the odor is not a precise imitation of dung or carrion, and so do not always function to attract specific pollinators.

On the other hand, the chemical composition of foul *Amorphophallus* plant odors (a cocktail of amines and indole compounds volatilized by thermogenesis) do attract distinct species of pollinators. Each species of *Amorphophallus* studied has revealed a characteristic chemical compound and are presumed to have evolved thusly to each attract a specific pollinator (Beath 1996). Selecting for specific pollinators increases pollen discrimination between simultaneously blooming plants and reduces the likelihood of production of wasted gametes through mixing of pollen between incompatible plants species.

Additionally, fly pollinated plants which produce a variety of odor-producing compounds can potentially exploit different aspects of a dipteran pollinator's behavior through production of different odors conforming to various chemical types (Kite and Smith 1997). Calliphorid flies, for example, are known to be able to perceive differences in the odor compositions of decaying meat and flowers through different antennal receptors (Kite and Smith 1997). Therefore, production of various odoriferous compounds to exploit the perception of the calliphorids will increase the likelihood that the plant will successfully attract the fly for pollination among individuals of its species.

13.8 Role of Nectar and Pollen

13.8.1 Sugars of Nectar

One of the main reasons why animals visit flowers is to obtain the nectar and its nutritional properties are important to most pollinators, especially those who do not obtain nourishment in any other form (e.g. butterflies). Nectar clearly has no other function in the angiosperm flower other than to attract pollinating animals.

The majority of nectars that have been examined consist simply of a solution of sugars. Most are very sweet to taste, varying in sugar content from 15% to 75% by weight. The compounds present are the three common sugars of plant metabolism: glucose, fructose and sucrose (Fig. 2.14). Oligosaccharides also occur, usually in traces, in a number of plant nectars. Of these, the trisaccharide raffinose (6G-α-galactosylsucrose) is the most frequent, occurring in nectars of Ranunculaceae, Berberidaceae and related families. Other sugars reported on occasion are the disaccharides maltose (glucosyl-α 1 4-glucose), trehalose (α-glucosyl-α-glucose) and melibiose (galactosyl-α 1 6-glucose) and the trisaccharide melezitose (2F-α-glucosylsucrose).

The distribution of the three common sugars in nectars has been surveyed in over 900 species (Percival 1961) and it has been found that there are distinct quantitative differences between species. Indeed, angiosperm nectars can be divided into three broad groups: those in which sucrose is dominant (e.g. *Berberis*, *Helleborus*); those in which all three sugars occur in about equal amounts (Abutilon); and those in which glucose and fructose are dominant (crucifers, umbellifers, some composites). From these results, it could be concluded that there is an evolutionary trend within the angiosperms from nectars with mainly sucrose to those with mainly glucose and fructose. The advantage of this to the pollinator would be the more readily assimilable sugar mixture, i.e. sucrose has to be broken down to glucose and fructose since it cannot be absorbed directly into the blood.

An analysis of nectar types by Baker and Baker (1990) suggests that there is a relationship between the ratio of sugars present and the type of pollinator that visits the flower (Table 13.7). This is particularly striking in the genus Erythrina, where flowers pollinated by passerine (perching) birds are uniformly high in glucose and fructose whereas flowers pollinated by humming birds are high in sucrose.

Table 13.7 Relationship between nectar classes and pollinator types

Sugar ratio[a]	Pollinators
High sucrose (>0.5)[a], e.g. average for 27 species of passerine bird-pollinated Erythrina = 1.3	Big bees Humming birds Lepidoptera
Low sucrose (>0.5)[a], e.g. average for 23 species of passerine bird-pollinated Erythrina = 0.04	Small bees Passerine birds Neotropical bats

[a] Ratio by weight of sucrose to hexose sugars, glucose and fructose

In favourable cases, such correlations can be used to predict the likely pollinator of a plant. Thus Lue flea specsosa, which grows in Costa Rica, has a low sucrose value (Table 2.6) and predictably could be bat pollinated, although no records were available in that country. Subsequent observations of the same plant in Brazil showed indeed that it was visited by bats.

A remarkable feature of these quantitative variations in nectar sugars is that the groupings remain consistent within the species and are not subject to diurnal or seasonal variations. Since sucrose is readily converted to glucose and fructose via enzymic reaction with invertase, one might expect considerable changes with age. Although invertase has been detected in nectars, it is presumably not present in sufficient quantity or sufficiently frequently or not present at the right time to change the patterns seriously. A survey of nectars for proteins (Baker and Baker 1975) showed them to be generally absent, detectable amounts only being present in 14% of the sample.

13.8.2 Nectar and Pollen Constituents

Nectar is an important source of food for most animal pollinators. Nectar chemistry does vary within certain limits and it is possible to suggest that many plant species modify the nectar components, through natural selection, to suit the needs of particular pollinators. The major components of nectars are simple sugars in solution, the sugar content varying from 15% to 75% by weight. The three common sugars are glucose, fructose, and sucrose, but traces of various oligosaccharides (*e.g.* raffinose) are sometimes present. There are distinct quantitative differences in the proportions of the three common sugars and angiosperm species can be divided into three groups, according to whether sucrose is dominant, glucose and fructose are dominant, or all three sugars occur in equal amounts. There is thus an evolutionary trend from nectar that is mainly sucrose, to nectar that is mainly glucose and fructose. Such a trend would correspond to some extent to the sugar preferences of the particular pollinators which vary from butterflies and bees to flies and bats.

Lipid is an alternative source of energy to sugar, and lipid bodies replace nectar sugar in some 49 genera of the Scrophulariaceae, Iridaceae, Krameriaceae, Malpighiaceae, and Orchidaceae. These are all bee-pollinated and the oil is mainly used by the bees for feeding their young. These lipids appear to be chemically distinct from the triglyceride seed oils. Indeed, in species of *Krameria*, free fatty acids have been characterised. These are all saturated acids with chain lengths C16 and C22 and all have an acetate substituent in the β-position (Simpson et al. 1977).

Small amounts of protein amino acids are also present in nearly all nectars. The ten amino acids essential for insect nutrition are often present and there is no doubt that nectars are a useful source of nitrogen, especially to insects such as butterflies, which have few other ways of acquiring amino acids at the adult stage. It is much less important for bird pollinators and there are indications that amino acid concentrations are related to the needs of the different pollinating vectors (Baker and Baker 1986).

Table 13.8 Toxins of plant nectars

Class	Compound	Plant nectar
Alkaloid	Hyoscyamine	*Atropa belladonna*
Phenolic	Arbutin	*Arbutus unedo*
Alkaloid	Hyoscyamine	*Brugmansia aurea*
Alkaloid	Pyrrolizidines	*Eupatorium* spp.
Alkaloid	Quinolizidines	*Lupinus polyphyllus*
Alkaloid	Nicotine	*Nicotiana tabacum*
Iridoids	Catalpol	*Catalpa speciosa*
Diterpenoid	Acetylandromedol[a]	*Rhododendron ponticum*
Alkaloid	Pyrrolizidines[a]	*Senecio jacobaea* and other spp.
Alkaloid	Quinolizidines	*Sophora microphylla*
Sugar	Mannose[b]	*Tilia cordata*

[a] These toxins are carried through from nectar to the honey stored by bees in their hives

[b] Toxic to bees, since they are unable to metabolise it

Plant nectars may contain toxins, which are presumably derived from their synthesis in other plant parts. Alkaloids have been most frequently detected, but several other classes have also been noted (Table 13.8). The alkaloid content may vary from the traces (0.106 μg g_1 fresh weight) in the tobacco plant nectar to as much as 273 μg g_1 fresh weight of tropane alkaloids in the deadly nightshade, *Atropa belladonna* (Detzel and Wink 1993).

The purpose of toxin accumulation in nectars is still uncertain, although a defensive role aganst herbivores or an undesirable animal visitor is certainly possible. The formation of iridoids in the nectar of the plant *Catalpa speciosa* is apparently to protect the plant from ants, which are nectar thieves (Stephenson 1982).

Occasionally, the toxins in the nectar may be collected during the process of pollination by certain butterflies. This is true of adult Ithomiines and Danaids, which have a requirement for pyrrolizidine alkaloids both for defence and for pheromone production. These alkaloids are obtained from nectar of *Eupatorium* and *Senecio* species, which are grown in their respective habitats. Pollen, like nectar, is largely nutritional and is collected and eaten by bees and beetles. Carotenoids are present in many pollens, providing yellow colour, and function in improving pollen detection by the pollinator. All pollens also contain small amounts of flavonol glycosides, particularly such compounds as kaempferol 3-sophoroside (Sunnerheim-Sjoberg and Knutsson 1995) and isorhamnetin 3-sophoroside (Reichards et al. 1990).

Until recently, the occurrence of these flavonol glycosides was obscure. However, there is now evidence in the *Petunia* flower that the pollen flavonol (Sunnerheim-Sjoberg and Knutsson 1995) has an essential role in assisting the germination of the pollen when it lands on the stigma. During the process, a specific β-glycosidase removes the protecting sugars to release the free aglycone. The kaempferol formed is probably a growth promoter and at the same time prevents the introduction of pathogens into the pistil (Vogt et al. 1994).

Table 13.9 Amino acid concentration of nectars according to plant family

Relative advancement	Plant family	Total amino acid on histidine scale[a]
More	Asclepidaceae	8.4
	Liliaceae	7.4
	Campanulaceae	7.0
	Leguminosae	6.9
	Amaryllidaceae	6.9
	Compositae	6.3
Less	Rosaceae	3.9
	Myrtaceae	3.1
	Saxifragaceae	2.7
	Caprifoliaceae	2.2

Source: Baker and Baker (1973b)

[a] Ninhydrin colour on paper of single drops of nectar compared with some colours of histidine solutions. A score of 2 corresponds to a 98 um solution , of 4–391 um, of 6–1.56 mM and of 8–6.25 mM (=c.1 mg/ml)

13.8.3 Amino Acids of Nectar

It is curious that until recently, the presence of amino acids in plant nectars lay largely undetected. Apart from a few earlier isolated reports (Ziegler 1956), clear-cut proof that amino acids are regular constituents of nectars did not appear until 1973 (Baker and Baker 1973a, b). These two authors found them in minor but significant amount in 260 of 266 plant nectars surveyed.

The Bakers first looked for amino acids following the logical argument that certain pollinators, especially higher butterflies, were almost ompletely dependent on nectar for their nutrition; since they survived as adults for several months, they must clearly need nitrogen as well as sugar. These authors were also guided in their search by a number of naturalist observations, all indicating that these same butterflies took advantage of any nitrogen that might be available to them. Thus, tropical forest butterflies have been known to feed both on decaying crocodiles on the banks of the Amazon and on rotting, putrescent fruit of tropical legume trees. They have even been observed to absorb human sweat for its nitrogen content. There is an authenticated story of a hiker in Arctic Canada who took off his boots, while resting at midday, only to be invaded by a swarm of butterflies collecting around his sweaty feet and socks.

The amounts of amino acid present in most nectars, although small, are sufficient to provide insects with a useful nitrogen supply. Thus 0.4 ml of a butterfly flower nectar contains about 840 nmol of amino acid, a daily intake of which would probably be sufficient to meet the nitrogen requirements. Baker and Baker (1973b), in their quantitative analyses of nectar nitrogen, noted significant variations in different angiosperms. Indeed, increase in amino acid content was correlated with increasing *Evolution*ary advancement, woody primitive families tending to have lower amino acid scores than advanced herbaceous groups (Table 13.9). This is also correlated with the fact that the lower scoring families tend to be pollinated by bees, insects

Table 13.10 Amount of amino acid in nectars of plants with different animal visitors

Animal group	Amount of amino acid on histidine scale	Other sources of nitrogen
Carrion and dung flies	9.0	None, flowers mimic carrion or dung
Butterflies	5.4[a]	[a]Pollen not eaten
Settling moths	5.4[a]	
Wasps	5.2[a]	
Bees	4.6	
Hawkmoths	4.4	
Birds		Pollen eaten
	3.9	Ingest large amounts of nectar
Bats	3.6	Insects eaten

[a] Source: Baker and Baker (1986)

which can obtain nitrogen from other sources (e.g. pollen). By contrast, the higher scoring families have significantly more taxa which are pollinated by butterflies and, to a lesser extent, by moths. It thus appears almost as if plants have evolved to produce larger amounts of (Table 13.10).

All the common protein amino acids are present in nectars (Baker and Baker 1975). There is considerable qualitative variation and the number in easily detectable amounts may vary from 1 to 12. The ten amino acids essential for insect nutrition (arginine, histidine, lysine, tryptophan, phenylalanine, methionine, threonine, leucine, isoleucine and valine) are better represented than others; glutamic and aspartic acids are also frequent. The variation in detectable amino acids between species is consistent and may be useful as a chemotaxonomic character (Baker and Baker 1976). Nectars of hybrids between species with different amino acid profiles contain all the amino acids of the two parents; inheritance of nectar nitrogen is thus additive.

Gardener and Gillman (2008) reported that the amino acids are the second most abundant class of compound (after sugars) to be found in nectar which play an important role in determining the foraging preferences of pollinators. Although amino acids are detectable by insects, little work has focussed on the role of taste in the ecology of pollination. Gardener and Gillman (2008) based on the idea that different amino acids elicit different responses in insect taste receptors characterized nectar samples from 65 plant species from a wide range of families according to their amino acid profile and found that there is a wide range of taste profiles with most plant species having their own characteristic taste value. How nectar tastes to pollinating insects is of great importance in understanding the foraging choices of insect

Baker (1977) reported that nectars in flowers pollinated by settling moths, butterflies and many wasps which, as adults, do not have alternative sources of protein-building materials were found to be richer in richer in amino acids. Whereas in the cases of flowers pollinated by bees and bats (which utilize pollen as a Table 13.11).

Flower-visiting bats in tropical countries make use of fruit-juices and pollen as sources of protein-building materials and those that belong to the neotropical

Table 13.11 Average amino acid concentrations in floral nectars, grouped according to principal pollinators

Principal pollinators	Number of determinations	Amino acids in micromolecules per ml
Bees	515	0.702
Wasps	38	0.975
Butterflies	124	1.186
Settling moths	65	1.178
Hawk moths	59	0.550
Flies (general)	89	0.573
Carrion and dung flies	9	12.500
Old world birds	21	0.255
Humming birds	104	0.452
Bats	19	0.302

Source: Baker (1977)

Microchiroptera also catch some insects (Baker 1973, 1978). The nectars that they take are weak in amino acids. Hummingbirds are avid insect-catchers; flowers could hardly provide them with a significant alternative supply of protein-building materials-and they do not.

Hawkmoths (Sphingidae) imbibe large quantities of nectar each night and the amino acid concentration in these nectars is low; nevertheless, the total amount ingested may be high. Another anomaly is provided by the nectar of flowers (e.g. *Stapelia grandiflora*) that lure fesmale dung and carrion flies to oviposit on them instead of on faeces and decaying flesh. The allurement of these insects is provided by color (often brownish-purple), smell (unpleasant to the human nose) and an extremely high amino acid content of the nectar when this is provided.

On the other hand, nectars from generalized; fly flowers have relatively low amino acid contents. The conclusion that we may draw is that for the settling moths, butterflies and wasps, the amino acids may perform a nutritive function (Baker and Baker 1973a, b, 1975). This is further suggested by feeding experiments with Colias butterflies (Watt et al. 1974) and butterflies of several species (Arms et al. 1974).

Even in those cases where the concentration of amino acids is too low for them to be likely to be of direct nutritional significance, it is probable that their presence, proportions and concentrations have significance for the animal that drinks the nectar. Even to the human palate, some nectars are sweet, some are sour and some are bitter. Shiraishi and Kuwabara (1970) have shown that some insect chemoreceptors react differentially to similar groups of amino acids. Consequently, we may believe that amino acids in particular combinations may affect the; taste ; of nectar and, along with the sugars, may reinforce the morphology, color and scent of flowers in enabling the flower visitor to build a relationship with a particular flower species. If this function is to be performed, it is important that the amino acid complement of each species' nectar be under tight genetic control, and remain constant in the face of environmental variation. That this is true to a remarkable extent has been shown by Baker and Baker (1976a, b, 1977).

13.9 Lipids in Nectar

On a weight basis, lipids and their component fatty acids are more energy rich than sugars so that there may be some advantage to a plant in using this nutritional attractant rather than sugar since less need be made. Such a substitution has occurred during angiosperm *Evolution* but it appears to have been a rather infrequent event. Indeed, lipids were only recognized recently to be nectar components, after their discovery by Vogel (1969) in a few bee-pollinated members of the Scrophulariaceae. Subsequently, lipids have been recognized in species of 49 genera from five Families. Besides the Scrophulariaceae, these are the Iridaceae, Krameriaceae, Malpighiaceae and Orchidaceae (Vogel 1974).

Lipid production appears to be closely related to certain species of solitary bee of the Anthophoridae which act as pollinators to the above plants. The oil is mainly used by the bees for feeding their young, although its consumption by adult males has been recorded. In Centris spp., it is collected exclusively by the female, who carries it back to the nest, mixes it with pollen and places an egg on the mixture. The young hatch out and have a special lipid-rich diet to develop on. These lipids thus play a role in the co-*Evolution*ary relationship between plant and pollinator. The bees benefit from an energy-rich diet, the plants through fidelity of pollination by these bees.

Chemical studies of lipid-containing nectars have been few and it is not yet clear whether they are generally of the common triglyceride type. In the few cases where analyses have been carried out, the oils have been found to be unusual. The oil is usually located within the flower in trichomes and the exudates of these trichomes in Calceolaria pavonii were examined by Vogel (1976), who identified the major . component as a diglyceride ol acetic acid and 3-acetoxystearic acid. The oils of Krameria spp. have proved to be even more unusual in consisting of free fatty acids (Simpson et al. 1977). The fatty acids were all saturated with chain lengths between C_{16} and C_{22} and all contained an acetate substitution at the β -position. One is β-acetoxystearic acid, $CH_3(CH_2)_{14}CHOA_cCH_2CO_2H$, as in Calceolaria. Not only are free fatty acids rare in plants, but these particular β-acetoxy acids seem to be unique to floral nectars. It will be interesting to see if subsequent studies confirm the special *Nature* of the oils present in other plants which have lipid-based insect lures.

13.9.1 *Nectar Toxins*

Occasionally, nectars contain toxins, presumably derived initially from other plant parts. Honey produced by bees foraging on unusual plant sources is sometimes tainted by such compounds. The toxic diterpene acetylandromedol has actually been characterized in the nectars of Rhododendron. Alkaloids also occasionally appear and in the case of the nectar of Sophora micro phylla, have been present in sufficient concentration to cause toxicity to the honey bees (Clinch et al. 1972).

Alkaloid toxicity may be more serious as a possible hazard to humans consuming the honey. Bees feeding on the ragwort Senecio jacobaea are known to produce honey contaminated with the pyrrolizidine alkaloids present in the plant nectar (Deinzer et al. 1977). The alkaloid concentration in the honey may vary From 0.3 to 3.9 ppm. Fortunately such honey has a bitter taste and is off-colour so that it is normally avoided.

There is also the other side of the coin: substances which are harmless to man may be toxic to bees. The glucoside arbutin from Arbutus unedo honey is apparently harmful to bees (Pryce-jones 1944). Also, the simple sugar galactose has been detected in the stigmata 1 exudates of tulip flowers and is toxic to bees (Barker and Lehner 1976). Again, the toxicity of Tilia nectar and pollen to bees is attributable to the presence of the sugar man- nose. In this case, it is known that the insects cannot fully metabolize it. They lack the enzyme mannose phosphate isomerase so that mannose 6-phosphate accumulates, causing paralysis (Vogel 1978).

The presence of nectar toxins, of course, may occasionally be advantageous to the pollinator. Adult lthomiine butterflies in South America have a requirement for pyrrolizidine alkaloids, which are used for pheromone production. This can be met by sucking withered borage leaves but also in part by collecting nectar from the flowers of those Eupatorium species which secrete these alkaloids in their nectar.

13.9.2 Extrafloral Nectaries

Extrafloral nectaries are sugar-producing glands which occur on the bracts, leaves, petioles or stems of a significant number of angiosperm plants. In families like the Leguminosae, Orchidaceae and Passifloraceae, they are found with some frequency. Although these nectaries are very similar to floral nectaries and attract many insect visitors, they are not normally concerned at all in pollination. Indeed their function has for a long time remained unclear and controversial. However, recent biochemical analyses have indicated that they contain very similar nutrients to those of the flowers, with the same sugars and amino acids being present. Thus, they represent an important source of food to insects. Furthermore, they do seem to have a purpose. There is increasing ecological evidence that they have value to the plant in attracting particular ant species, the colonies of which then provide the plant with antiherbivore defence (Bentley 1977). The mutual interaction that occurs is therefore not all that different from the more widespread plant – pollinator system.

In ant-Acacia species, the beneficial interactions between plant and ant are highly developed, the ants being particularly vicious in their attack on any animal visitors to the plant. The ecological importance of nectar-feeding ant colonies may, however, vary from plant to plant. In lpomoea leptophylla, for example, there are both foliar and sepal nectaries fed on by ants. Here, however, the ants' protective role is to save the plant from seed loss due to bruchid beetle activity and from flower damage by grasshoppers (Keeler 1980). The extrafloral nectaries thus make an indirect positive contribution to pollination biology by keeping away harmful visitors.

In general, plants with extrafloral nectaries continue to secrete sugars and amino acids irrespective of any mutual association with a colony of ants. This apparently wasteful process was one of the reasons why the ecological significance of these organs was not appreciated until recently. Physiologists argued that the flow of sugar from such nectaries simply represented a method of shedding excess sugar during periods of growth when sugar synthesis was at its maximum. In fact, there is now evidence that certain plants can actually restrict the secretion of food in such organs to times that active insect association is present.

It has been observed, for example, in the plant Piper cenociadum, which has a beneficial relationship with the ant Phoidole bicornis, that the production of food bodies is directly linked with the presence of ants. If ants are removed, the food, which contains protein and lipid as well as sugar, is no longer produced (Risch and Rickson 1981). Food bodies in this plant are exactly equivalent to extrafloral nectaries in other species, so that it is likely that a range of these plants may exercise a similar economy in producing nutrients only when their associated ants are in residence.

13.9.3 Nutritive Value of Pollen

Any account of the nutritional benefit gained by animal pollinators from plants would be incomplete without some mention of pollen. The pollen is usually more accessible than the nectar and is collected and used by many flower visitors. Pollen is particularly fed on by beetles, who have to chew it in order to break open the tough pollen walls. Bees benefit enormously from pollen, which they are able to digest. Pollen occasionally becomes mixed with the nectar, and in such conditions, the nutritional benefits may be available to animals (e.g. 1-leliconius butterflies) which feed solely on the nectar.

The chemistry of pollens has been exhaustively investigated (Barbier 1970; Stanley and Linskens 1974). Nutritionally, pollen is a rich source of food with 16–30% protein, 1–7% starch, 0–15% free sugar and 3–10% fat. Trace constituents present include various vitamins and inorganic salts. There are also varying amounts of secondary substances. Pollen is often coloured, especially by carotenoid but also by flavonoids, and this is probably a signal to indicate its availability to insect feeders. The carotenoids of pollen are usually α- and β-carotene, lutein, zeaxanthin and their various epoxides. Deep red and purple pollens often have anthocyanidin for pigmentation (e.g. Anemone). Other flavonoids, especially the flavonol isorhamnetin, are frequently present in pollens and contribute to pale yellow colours.

Pollen has primary importance as the carrier of the male gametophytes, so that all use of pollen by animals for feeding is secondary and represents pollen theft' as far as the plant is concerned. Competition between the two contrasting uses of pollen is rarely a problem, since the majority of angiosperms are overabundant in pollen production. If insects did not capitalize on the excess pollen available to them, it would go to waste in other ways.

There is plenty of evidence that pollen is deliberately provided by some plants to their pollinators as a reward. That animals can 'home in' on plant pollen is apparent from the fact that pollens produce characteristic odours which are often different from the scents of the flowers. Furthermore, honey and solitary bees are able to discriminate between plant species on the basis of pollen odours. That pollens differ in their volatile constituents has been confirmed in the case of Rosa rugosa and I?. canina where 31 terpenoids, aliphatics and aromatics were variously detected (Dobson et al. 1987).

13.10 Conclusions

In this chapter, the different biochemical aspects of plant pollination have been considered in turn: the role of flower colour, flower scent, nectar and pollen. In the field, all these factors may come together in particular plant-pollinator interactions (Table 13.12). One or other biochemical factor may dominate in a particular interaction, whereas in others, flower colour, odour and nectar may all be required to attract a particular pollinator.

While the main purpose of flower colour, scent and floral reward is to attract an available pollinator, it is worth remembering that plants have also to protect themselves from animal visitors which may steal the floral reward without pollinating the flower.

Table 13.12 Plant-pollinator interactions and their biochemical features

Plant and family	Major pollinator(s)	Biochemical factors
Delphinium nelsonii Ranunculaceae	Bumble bee and humming bird	Blue flower colour essential; mutation to white leads to pollinator neglect
Rechsteineria macrorhiza Gesneriaceae	Humming bird	Desoxyanthocyanin provides scarlet-orange flower colour
Ipomopsis aggregata Polemoniaceae	Humming bird and Hawkmoth	Colour shift from red to white in response to availability of pollinator
Rudheckia hirta Compositae	Bee	UV patterning by patuletin increases efficiency of pollination
Arum maculatum Araceae	Dungfly	Skatole in scent attracts fly away from dungheap
Datura moxie Solanaceae	Hawkmoth	Alkaloids in nectar act as addictive drug to pollinator
Ophrys spp. Orchidaceae	Andrena male bee	Flowers resemble female bees in shape, colour and odour
Catasetum spp. Orchidaceae	Euglossine male bee	Flower scent collected by male to use as pheromone
Calceo/aria pavonii Scrophulariaceae	Solitary bee	Energy-rich lipid nectar used by female to feed the young
Passiflora spp. Passlfloraceae	Heliconiad butterfly	Pollen mixed with nectar increases N content of floral reward

Thus, biochemical (and structural) features may be important in repelling visitors as well as for attracting them. For example, bees are not generally attracted to red flowers, because they are insensitive to this colour, and likewise they will avoid plants which have sugars (e.g. mannose) in the nectar which they cannot metabolize.

One final point, illustrated here by several examples, is the dynamic *Nature* of the association between flower and pollinator. The situation is continually changing with *Evolution*ary time and some associations which seem to be tightly knit (e.g. bee – orchid and wasp – orchid associations) may be open to variation. Witness the ability of members of the Euphorbiaceae and Campanulaceae (Section IIIB) to mimic orchids biochemically in order to be visited by their highly specific male bee pollinators. Members of the Orchidaceae provide a rich source of bizarre variations in plant – pollinator interactions and biochemical studies of further orchids are bound to be rewarding.

References

Arms K, Feeny P, Lederhouse RC (1974) Sodium: stimulus for puddling behavior by tiger swallowtail butterflies, papilio glaucus. Science 185:372–374

Asen S, Stewart RN, Norris KH (1972) Co-pigmentation of anthocyanins in plant tissue and its effect on color. Phytochemistry 11:1139–1144

Azuma H, Toyota M, Asakawa Y, Kawano S (1996) Naphthalene – a constituent of magnolia flowers. Phytochemistry 42:999–1004

Azuma H, Thien LB, Kawano S (1999) Floral scents, leaf volatiles and thermogenic flowers in magnoliaceae. Plant Species Biol 14:121–127

Baker HG (1973) Evolutionary relationships between flowering plants and animals in American and African forests. In: Meggers BJ, Ayensu ES, Duckworth WD (eds) Tropical forest ecosystems in Africa and south America: a comparative review. Smithsonian Institution Press, Washington, DC, pp 145–159, Chap. 11

Baker HG (1977) Non-sugar non-sugar chemical constituents of nectar. Apidologie 8(4): 349–356

Baker HG (1978) Chemical aspects of the pollination biology of woody plants in the tropics. In: Tomlinson PB, Zimmermann M (eds) Tropical tress as living systems. Cambridge University Press, New York

Baker HG, Baker I (1973a) Amino acids in nectar and their evolutionary significance. Nature (London) 241:543–545

Baker HG, Baker I (1973b) Some anthecological aspects of the evolution of nectarproducing flowers, particularly amino acid production in nectar. In: Heywood VH (ed) Taxonomy and ecology. Academic, London, pp 243–264, Chap. 12

Baker HG, Baker I (1975) Studies of nectar-constitution and pollinator-plant coevolution. In: Gilbert LE, Raven PH (eds) Coevolution of animals and plants. University of Texas Press, Austin, pp 100–140

Baker I, Baker HG (1976a) Analyses of amino acids in flower nectars of hybrids and their parents, with phylogenetic implications. New Phytol 76:87–98

Baker L, Baker HG (1976b) Analysis of amino acids in nectar. Phytochem Bull 9:4–7

Baker HG, Baker L (1977) Intraspecific constancy of floral nectar amino acid complements. Bot Gaz 138:183–191

Baker HG, Baker I (1986) The occurrence and significance of amino acids in floral nectar. Plant Syst Evol 151:175–186

Baker HC, Baker I (1990) The predictive value of nectar chemistry to the recognition of pollinator types. Israel J Bot 39:157–166

Baker HC, Hurd PD (1968) Intrafloral ecology. Annu Rev Entornol 13:385–414

Barbier M (1970) Chemistry and biochemistry of pollens. In: Reinhold L, Lipschitz I (eds) Progress in phytochemistry, vol 2. Wiley, London, pp 1–34

Barker RJ, Lehner Y (1976) Galactose, a sugar toxic to honey bees, found in exudate of tulip flowers. Apidologie 7:109–111

Beach JH (1982) Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). Am J Bot 69:1074–1081

Beale GH (1941) Gene relations and synthetic processes. J Genet 42:197–214

Beath DDN (1996) Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaeochrous amplus*) in a Ghanaian rain forest. J Trop Ecol 12:409–418

Beattie AJ (1991) Problems outstanding in ant–plant interaction research. In: Huxley CR, Cutler DF (eds) Ant–plant interactions. Oxford Science, Oxford, pp 559–576

Bentley BL (1977) Extrafloral nectaries and protection by pugnacious bodyguards. Annu Rev Ecol Syst 8:407–427

Bergström G (1978) Role of volatile chemicals in ophrys-pollinator interactions. In: Harborne G (ed) Biochemical aspects of plant and animal coevolution. Academic, New York, pp 207–230

Bestmann HJ, Winkler L, von Helversen O (1997) Headspace analysis of flower scent constituents of bat-pollinated plants. Phytochemistry 46:1169–1172

Borg-Karlson A-K, Bergström G, Groth I (1985) I. Volatile compounds of *Ophrys lutea* and *O. fusca* as insect mimetic attractants/excitants. Chem Scripta 25:283–294

Borg-Karlson A-K, Groth I, Ågren L, Kullenberg B (1993) Evidence of sympatric speciation? Chemoecology 4(1):39–45

Borg-Karlson AK, Valtorova I, Nilsson LA (1994) Volatile compounds from flowers of 6 species in the family apiaceae – bouquets for different pollinators. Phytochemistry 35(1):111–119

Chittka L, Spaethe J, Schmidt A, Heckelsberger A (2001) Adaptation, constraint, and chance in the evolution of flower colour and pollinator colour vision. In: Chittka L, Thompson JD (eds) Cognitive ecology of pollination. Cambridge University Press, Cambridge, pp 106–126

Clinch PG, Palmer-Jones T, Forster IW (1972) Effect on honey bees of nectar from the yellow kowhai (*Sophora microphylla* Ait.). N Z J Agr Res 15:194–201

Cohen D, Shmida A (1993) The evolution of flower display and reward. Evol Biol 27:197–243

Crowe L (1964) Evolution of outbreeding in plants. I. The angiosperms. Heredity 19:435–457

Dafni A, Lehrer M, Kevan PG (1997) Spatial flower parameters and insect spatial vision. Biol Rev 72:239–282

Deinzer ML, Thomson PA, Burgett DM, Isaacson DL (1977) Pyrrolizidine alkaloids: their occurrence in honey from tansy ragwort (*Senecio jacobaea* L.). Science 195:497–499

Dement WA, Raven PH (1974) Pigments responsible for ultraviolet patterns in flowers of *Oenothera* (Onagraceae). Nature (London) 252:705–706

Detzel A, Wink M (1993) Attraction, deterrence or intoxication of bees (*Apis mellifera*) by plant allelochemicals. Chemoecology 4:8–18

Diamond JM (1989) Hot sex in Voodo lilies. Nature (London) 339:258–259

Dobson HEM, Bergström J, Bergström G, Groth I (1987) Pollen and flower volatiles in two *Rosa* species. Phytochemistry 26:3171–3173

Dobson HEM, Arroyo J, Bergstrom G, Groth I (1997) Interspecific variation in floral. Biochem Syst Ecol 25:685–706

Dodson CH (1975) Coevolution of orchids and bees. In: Gilbert LE, Raven PH (eds) Coevolution of animals and plants. Texas University Press, Austin, pp 91–99

Ecroyd CE, Franich RA, Kroese HW, Steward D (1995) Volatile constituents of Cactylanthus. Phytochemistry 40:1387–1389

Eisikowitch D, Lazar Z (1987) Flower change in *Oenolhera drummondii* Hooker as a response to pollinators' visits. Bot J Linn Soc 95:101–111

Eisner T, Eisner M, Hyypio PA, Aneshansley ID, Silbersgleid RE (1973) Plant taxonomy: ultraviolet patterns of flowers visible as fluorescent patterns of flowers. Science 179:486

Eschler BM, Pass DM, Willis R, Foley W (2000) Distribution of foliar formylated phloroglucinol derivatives amongst *Eucalyptus* species. Biochem Syst Ecol 28:813–824

Faegri K, van der PijI L (1979) Principles of pollination ecology, 3rd edn. Pergamon Press, Oxford

Gardener MC, Gillman MP (2008) The taste of nectar – a neglected area of pollination ecology. Oikos 98(3):552–557

Goodwin TW (ed) (1988) Plant pigments. Academic, London

Gottsberger G (1990) Flowers and beetles in the South-American tropics. Bot Acta 103(4):360–365

Grant V (1971) Plant speciation. Columbia University Press, New York, 435 pp

Grant V, Grant KA (1965) Flower pollination in the phlox family. Columbia University Press, New York

Grant V, Grant KA (1983) Behavior of hawkmoths on flowers of *Datura metaloides*. Bot Gaz 144:280–284

Harborne JB (1967) Comparative biochemistry of the flavonoids. Academic, London, 383 pp

Harborne JB (1988) The flavonoids: recent advances. In: Goodwin TW (ed) Plant pigments. Academic, London, pp 299–344

Harborne JB (1993) Introduction to ecological biochemistry, 4th edn. Academic, London

Harborne JB (2001) Twenty-five years of chemical ecology. Nat Prod Rep 18:361–379, 361

Harborne JB, Boardley M (1983) Identification of two gossypetin monomethyl ethers as yellow flower pigments in the Rutaceae. Z Naturforsch 38c:148–150

Harborne JB, Nash RJ (1983) Flavonoid pigments responsible for ultraviolet patterning in petals of the genus potentilla. Biochem Syst Ecol 12:315–319

Harborne JB, Smith DM (1978a) Correlations between anthocyanin chemistry and pollination ecology in the polemoniaceae. Biochem Syst Ecol 6(2):127–130

Harborne JB, Smith DM (1978b) Anthochlors and other flavonoids as honey guides in the Compositae. Biochem Syst Ecol 6:287–291

Harborne JB, Heywood VF-I, King L (1976) Flavonoid sulphates in the umbelliferae. Biochem Syst Ecol 4:111–115

Harrewijn P, Minks KA, Mollema C (1995) Evolution of plant volatile production in insect-plant relationships. Chemoecology 5/6:55–74

Hickman JC (1974) Pollination by ants – a low energy system. Science 184:1290

Honda K, Omura H, Hayashi N (1998) Identification of floral volatiles from *Ligustrum japonicum* that stimulate flower-visiting by cabbage butterfly, *Pieris rapa*. J Chem Ecol 24:2167–2180

Horovitz A, Cohen Y (1972) Ultraviolet reflectance characteristics in flowers of crucifers. Am J Bot 59:706–713

Jakobsen HB, Friis P, Nielsen JK, Olsen CE (1994) Emission of volatiles from flowers and leaves of *Brassica napus* in situ. Phytochemistry 37:695–699

Jones CE, Little RJ (1983) Handbook of experimental pollination biology. Scientific and Academic Editions, New York, pp 558

Kaiser R (1993) The scent of orchids: olfactory and chemical investigations. Elsevier, Amsterdam

Kay QON, Daoud HS, Stirton CH (1981) Pigment distribution, light reflection and cell structure in petals. Bot J Linn Soc 83:57–84

Keeler KH (1980) The extrafloral nectaries of *Ipomoea leptophylla*. (Convolvulaceae). Am J Bot 67:216–222

Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annu Rev Enlomol 28:407–453

Kite GC (1995) The floral odour of *Arum maculatum*. Biochem Syst Ecol 23(4):343–354

Kite GC, Hetterschieid WLA (1997) Inflorescence odours of *Amorphophallus* and *Pseudodracontium* (Araceae). Phytochemistry 46:1169–1172

Kite GC, Smith SAL (1997) Inflorescence odour of senecio articulatus: temporal variation in isovaleric acid levels. Phytochemistry 45(6):1135–1138

Knudsen JT (1994) Floral scent composition in *Pyrola rotundifolia* complex in Scandinavia and Western Greenland. Nord J Bot 14:277–282

Knudsen JT, Stahl B (1994) Floral odours in the Theophrastaceae. Biochem Syst Ecol 22:259–268

Knudsen JT, Tollsten L (1995) Floral scent in bat-pollinated plants: a case of convergent evolution. Bot J Linn Soc 119:45–57

Kuanprasert N, Kuehnle AR, Tang CS (1998) Floral fragrance compounds of *Anthurium* (Araceae) species and hybrids. Phytochemistry 49:521

Kullenberg B (1952) Recherches sur la bio- logie florale des Ophrys. Bull Soc Hist Nat Afrique Nord 43:53–62

Kullenberg B, Bergstrom G (1975) Chemical communication between living organisms. Endeavour 34:59–66

Lindroth RL, Weisbrod AV (1991) Genetic variation in response of the gypsy moth to aspen phenolic glycosides. Biochem Syst Ecol 19:97–103

Macior LW (1986) Floral resource sharing by bumblebees and hummingbirds in pedicularis (Scrophulariaceae) pollination. Bull Torrey Bot Club 113:101–109

Metcalf RL, Lampman RL, Deem-Dickson L (1995) Indole as an olfactory synergist for volatile kairomones for diabroticite beetles. J Chem Ecol 21:1149–1162

Nilsson LA (1983) Mimesis of bellflower (Campanula) by the red helleborine orchid *Cephalanthera rubra*. Nature 305:799–800

Ollerton J, Diaz A (1999) Evidence for stabilising selection acting on flowering time in *Arum maculatum* (Araceae): the influence of phylogeny on adaptation. Oecologia 119(3): 340–348

Paige KN, Whitham TG (1985) Individual and population shifts in flower color by scarlet gilia: a mechanism for pollinator. Science 227:315–317

Palto RJ, Anderson SK, Iason G (1993) Niche separation in two species of hare. Metabolic costs of plant phenolics. Chemoecology 4:153

Pass DM, Foley WJ, Bowden B (1998) Vertebrate herbivory on Eucalyptus – identification of specific feeding deterrents for common ringtail possums (*Pseudocheirus peregrinus*) by bioas-say-guided fractionation of *Eucalyptus ovata* foliage. J Chem Ecol 24:1513–1527

Paulus HF (1988) Co-evolution and unilateral adaptations in flower-pollinator systems: pollinators as pacemakers in the evolution of flowers. Verh Dtsch Zoologischen Ges 81:25–46

Pellmyr O, Thien LB (1986) Insect reproduction and floral fragrances: keys to the evolution of the angiosperms? Taxon 35(1):76–85

Percival MS (1961) Types of nectar in angiosperms. New Phytol 60:235–281

Piattelli M (1976) Betalains. In: Goodwin TW (ed) Chemistry and biochemistry of plant pigments, 2nd edn. Academic, London, pp 560–596

Proctor M, Yeo P (1973) The pollination of flowers. Collins, London

Pryce-Jones J (1944) Some problems associated with nectar, pollen and honey. Proc Linn Soc Lond 1944:129–174

Raguso RA, Pellmyr O (1998) Dynamic headspace analysis of floral volatiles: a comparison of methods. Oikos 81(2):238–254

Raskin I, Ehmann A, Melander WR, Meeuse BJD (1987) Salicylic acid: a natural inducer of heat production in Arum lilies. Science 237:1601–1602

Real L (ed) (1983) Pollination biology. Academic, Orlando, 338 pp

Reichardt PB, Bryant JP, Mattes BR, Clausen TP, Chapin FS, Meyer M (1990) Winter chemical defense of Alaskan balsam poplar against snowshoe hares. J Chem Ecol 16:1941–1959

Richards AI (ed) (1978) The pollination of flowers by insects. Academic, London, 213 pp

Risch SJ, Rickson FR (1981) Mutualism in which ants must be present before plants produce food bodies. Nature 291:149–150

Saito N, Harborne JB (1983) A cyanidin glycoside giving scarlet coloration in plants of the Bromeliaceae. Phytochemistry 22(8):1735–1740

Saito N, Harborne JB (1992) Correlations between anthocyanin type, pollinator and flower colour in the Labiatae. Phytochemistry 31:3009–3015

Sakai S, Inoue T (1999) A new pollination system: dung-beetle pollination discovered in *Orchidantha inouei* (Lowiaceae, Zingiberales) in Sarawak, Malaysia. Am J Bot 86(1): 56–61

Scogin R, Zakar K (1976) Anthochlor pigments and floral UV patterns in the genus Bidens. Biochem Syst Ecol 4:165–167, 190. Scott, A. I. 1964

Seymour RS, Schultze-Motel P (1997) Heat-producing flowers. Endeavour 21(3):125–129

Shisaisai A, Kuwabara M (1970) The effect of amino acids on the labellar hair chemosensory cells of the fly. J Gen Physiol 56:768–782

Simpson BB, Neff JL, Seigler D (1977) Krameria, freefatty acids and oil-collecting bees. Nature 267:150–151

Skubatz H, Kunkel DD, Howald WN, Trenkle R, Mookhergee B (1996) The *Sauromatum guttatum* appendix as an osmophore: excretory pathways, composition of volatiles and attractiveness to insects. New Phytol 134(4):631–640

Stanley G, Linskens HF (1974) Pollen: biology biochemistry and management. Springer, Berlin, 307 pp

Stephenson AG (1982) Toxic nectar deters nectar thieves of Catalpa speciosa … speciosa are unpalatable to nectar thieves. J Chem Ecol 8:1025–1034

Stránský K, Valterová I (1999) Release of volatiles during the flowering period of *Hydrosome rivieri* (Araceae). Phytochemistry 52(8):1387–1390

Sunnerheim-Sjoberg K, Knutsson P-G (1995) Platyphylloside: metabolism and digestibility reduction in vitro. J Chem Ecol 21:1339–1348

Tengo J, Bergstrom G (1977) Cleptoparasitism and odor mimetism in bees: do Nomada males imitate the odor of Andrena females? Science 196:1117–1119

Thien L, Bemhardt P, Gibbs CW, Pellmyr O, Bergstrom G, Groth I, McPherson G (1985) The pollination of Zygogynum (Winteraceae) by a moth, Sabatinca (Micropterigidae): an ancient association? Science 227:540

Thompson WR, Meinwald J, Aneshanslet D, Eisner T (1972) Flavonols: pigments responsible for ultraviolet absorption in nectar guide of flower. Science 177:528–530

Tollsten L, Knudsen JT, Bergström LG (1994) Floral scent in generalistic Angelica (Apiaceae): an adaptive character? Biochem Syst Ecol 22:161–169

Tollston L, Bergstrom G (1993) Fragrance chemotypes of Platanthera (Orchidaceae): the result of adaptation to pollinating moths. Nord J Bot 13:607–613

van der Pijl L (1961) Ecological aspects of flower evolution. II. Zoophilous flower classes. Evolution 15:44–59

Vereecken NJ, Schiestl FP (2009) On the roles of colour and scent in a specialized floral mimicry system. Ann Bot 104(6):1077–1084

Vogel S (1969) Flowers offering fatty oil instead of nectar. In: Abstracts, XI. International botanical congress, Seattle, p 229

Vogel S (1974) Olblumen und 6lsammelnde Biene. Trop Subtrop Pflanzenw 7:283–547

Vogel S (1976a) Lysimachia: Olblumen der Holarktis. Naturwissenschaften 63:44–45

Vogel S (1976b) Oil collecting bees of the old world and their flowers. Naturwissenschaften 67:627–628, 84

Vogel S (1978) Floral ecology report on the years 1974 (73) to 1978. Prog Bot 40:453–481

Vogt T, Pollak P, Tarlyn N, Taylor LP (1994) Pollination- or wound-induced kaempferol accumulation in petunia stigmas enhances seed production. Plant Cell 6:11–23

von Frisch K (1950) Bees, their vision, chemical senses and language. Cornell, Ithaca

Waser NM, Ollerton J (2006) Plant-pollinator interactions from specialization to generalization. University of Chicago Press, Chicago, pp 488

Waser NM, Price MV (1981) Pollinator choice and stabilizing selection for flower color in *Delphinium nelsonii*. Evolution 35:376–390

Waser NM, Price MV (1983) Pollinator behaviour and natural selection for flower colour in *Delphinium nelsonii*. Nature 302:422–424

Watt WB, Hoch PC, Mills SG (1974) Nectar resource use by colias butterflies: chemical and visual aspects. Oecologia (Berl) 14:353–374

Weiss MR (1991) Floral colour changes as cues for pollinators. Nature 354:227–229

Whitten WM, Williams NH, Armbruster WS, Battiste MA, Strekowski L, Lindquist N (1986) Carvone oxide: an example of convergent evolution in euglossine pollinated plants. Syst Bot 11(1):222–228

Wyatt R (1983) Pollinator–plant interactions and the evolution of breeding systems. In: Real L (ed) Pollination biology. Academic, Orlando, pp 51–96

Zeigler H (1956) Untersuchungen fiber die Leitung und Sekretion der Assimilate. Planta (Berl) 47:447–500

Chapter 14
Pollination Energetics

Abstract Nectar from flowers provides nourishment for animals ranging in size from mites to man. Pollinator-plant interaction is governed by the energy needs and pay off as the basic plan. The pollinators are highly selective in their floral visits and are shown to choose those flowers which best meet their energetic needs. The energy needs and foraging dynamics of pollinators are dependent upon prevailing weather conditions which regulate the schedule of activities thus influencing the energy budget. In this chapter, the role of energetics in pollinator-plant interaction, the current and future lines of research for the understanding of pollination biology are discussed.

14.1 Introduction

The pollinators are highly selective in their floral visits and are shown to choose those flowers which best meet their energetic needs. The energy needs and foraging dynamics of pollinators are dependent upon prevailing weather conditions which regulate the schedule of activities thus influencing the energy budget. The pollinators are highly sensitive to variations in nectar rewards and alter their foraging behaviour patterns with change in floral rewards.

Heinrich and Raven's (1972) feature article in 'science' emphasized the role of energetics pollinator-plant interaction. Their ideas dealt with the study of energetic strategy a plant should evolve to secure the services of a particular pollinator. In pollinator-plant interaction. The publication of this article stimulated researchers all over the world to discover and test hypotheses governing.

The flower must provide sufficient energetic reward to be attractive to the potential pollinator to restrict the latter to a single plant species. In most plants, pollinators' visits (and hence outcrossing) results only if the food rewards of the flowers are in balance with the energy needs of the pollinators.

The flowers of a plant species must provide sufficient food to be competitive with other concurrently blooming flowers that the pollinators could potentially visit. Mismatches in energy needs of pollinators and energy availability in flowers may

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result in inadequate pollination. Since 1972, several studies pertinent to their ideas have emerged. This paper addresses to the question how the energy requirement of pollinators and energy availability in flowers may result in inadequate pollination and influence their foraging strategies.

14.2 Energy Requirement-Reward System and Pollinator-Plant Interaction

Plant pollinator interaction, besides biological and physical features such as colour, shape and odour of the flowers, is governed by the energy needs and pay-offs as its basic components. The pollinators differ in their energy requirements from low (such as in ants and flies) to high (e.g. in endothermic groups like mammals and birds) (Heinrich 1975a, b, c, 1977, 1979, 1981, 1983; Hickman 1974; Abrol 1992a, 1993a, 1997, 2000). Rewarding system developed by the flowers enable pollinators to discriminate between the closely related plant species or ecotypes. This has resulted in a co-partnership between the flowers and their pollen vectors. Co-*Evolution* has brought a close correlation between pollinator needs and floral energy expenditures (Heinrich 1975a, b). Though pollen is an important food reward but its importance in pollination energetics is less than nectar due to its being a protein source, in bees mainly used for egg maturation and larval development? Pollen is relatively more important food for solitary bees than the social bees. The latter need continuous influx of energy for heating the nest which accelerates the brood development. The major sources of energy are the nectar sugars which make a basis of the pollinator-plant interaction. The plant species which are pollinated regularly by animals with high energy requirements must provide large amounts of nectar if cross-pollination is to be accomplished.

The intake of energy and profitability depend upon the quality and quantity of floral rewards (Heinrich 1975a, b, 1976, 1979, 1983; Sihag and Kapil 1983; Helverson and Reyer 1984; Abrol 1986a; Alm et al. 1990; Abrol and Kapil 1991; Comba-Livio et al. 1999; Nicolson 2007; Fleming et al. 2004, 2008; Barrera and Nobel 2004; Johnson and Nicolson 2008; Mitchell et al. 2009; Brandenburg et al. 2009). These functions in turn are under the key control of physical environment which interact in complex ways influencing not only the physiology of the plants but also that of pollinators in a manner that functional activities of both of them synchronize (Corbet 1978a, b, c, 1990). The various parameters determining energy intake and expenditure are detailed below:

14.2.1 Energy Intake

Nectar is a complex mixture of substances belonging to diverse biochemical classes and its chemical composition is highly variable (Brandenburg et al. 2009). Both quality and quantity of nectar are important in determining the pollinator-plant interaction.

Since the characterization of nectar as an attractant, many workers have recognised the importance of quality and quantity of nectar that influence abundance of floral visitors (Butler 1945; Mommers 1977; Corbet 1978a, b, c; Corbet et al. 1993; Kapil and Brar 1971; Southwick et al. 1981; Sihag and Kapil 1983; Southwick and Southwick 1986; Abrol and Kapil 1991; Abrol 1990a, b, 1992a, b, 1995, 2010, 2011). Whereas some workers stressed more on the predominance of quality of nectar in attracting bees (Sihag and Kapil 1983; Alm et al. 1990; Abrol and Kapil 1991), others have failed to establish such relationship. It has been emphasized in general that high nectar sugar concentration is desirable for attracting the honeybees (Moffett et al. 1976). The feeding studies have shown that intake of sugar syrup in bees is a function of threshold of acceptance of total sugars, that ranged between 5% and 40% (Frisch 1950), while a few others specified that the acceptance range lies in between 30% and 50% (Jamieson and Austin 1956; Waller 1972), and bees rejected solution with sugar concentration less than 20%. It has also been reported that honeybees can discriminate a sugar solution with a difference of 5% concentration (Jamieson and Austin 1956).

A wide variety of floral types acceptable to honeybees exist in various parts of the world and many among them are rich sources of honey due to the production of good quality of nectar. Large variations have been reported to occur in both the quality and quantity of nectar in different flower sources at inter- and intra-specific levels (Simidchiev 1977; Real 1981, 1983; Sihag and Kapil 1983; Crane et al. 1985). Various workers in a variety of plant species recorded sugar concentration ranging between 4% and 87% (Shaw 1953; Deodikar et al. 1957; Sharma 1958). Percival (1965) reported nectar sugar concentration variations from 5% to 74% in plants from Britain. Rowley (1976) observed 2–95% from Philippines, Sihag and Kapil (1983) reported 24–62% from Hisar (India). Considerable variations have been reported in sugar concentrations of even the same crop. For example, the nectar sugar concentrations of alfalfa have been reported to vary between 38% and 55% (Cirnu et al. 1977); 20–81% (Pederson and Bohart 1953) and 63–68% (Loper and Waller 1970). In *Brassica* crops also, variable amounts of nectar-sugar concentrations have been reported. In general, nectar sugar concentration has been reported in the range of 33–71% at different geographical locations by various workers (Kapil and Brar 1971; Sihag and Kapil 1983). The difference in nectar sugar concentration may be due to varietal differences and/or due to geographical locations (Teuber and Barnes 1978). Pernal and Currie (1998) found that in case of oilseed rape significant differences in nectar sugar content were also found in relation to the bloom phenology of the cultivars. Cultivars produced the greatest amount of sugar per flower during the first 2 weeks of the bloom period, and then sugar production decreased in the third and fourth weeks.

14.2.2 Energy Reward and the Competition for Food

Silva and Dean (2000) found that in onion flowers the average amount of nectar produced by both the umbels and the individual florets was significantly positively correlated with the number of bee visits. Evidently, selection of flowers with high nectar production may lead to a higher rate of pollination of the onion seed crop. Ish-Am and Eisikowitch (1998) reported that at the beginning of the blooming season, the avocado flowers competed for nectar-foraging bees mainly with flowers of *Citrus* spp., and for pollen foragers with Brassicaceae and Fabaceae, all of which were more attractive to the bees. However, toward the end of its blooming season, the avocado competed with Poaceae, Asteraceae and Apiaceae flowers, and its relative attractiveness increased. Wilms and Wiechers (1997) reported that niche overlap between *Melipona* bees and *A. mellifera* was more evident for nectar than for pollen. Goulson et al. (1998) found that both honey bees and bumblebees, *Bombus* spp., can mark rewarding flowers with scent marks that promote probing by conspecifics. Goulson-Dave et al. (2001) obtained evidence for direct detection of reward levels in two bee species: *Agapostemon nasutus* was able to detect directly pollen availability in flowers with exposed anthers, while *Apis mellifera* appeared to be able to detect nectar levels of tubular flowers. A third species, *Trigona fulviventris*, avoided flowers that had recently been visited by conspecifics, regardless of reward levels, probably by using scent marks. This can be interpreted as indirect evidence of actual competition for food. Page et al. (1998) tested honeybee foragers for their proboscis extension response (PER) to water and varying solutions of sucrose. They found that responses were related to nectar and water reward perception of foragers.

14.2.3 Nectar Sugar Concentration Fluctuations

Sugar concentration in nectar changes from hour to hour and day to day. These changes, in turn, are reflected in the spectrum of flower visitors (Heinrich and Raven 1972; Corbet 1978a, b, c; Corbet et al. 1979, 1993; Teuber and Barnes 1979). Changes in nectar sugars reflect a situation that is complicated by the interaction of a number of factors that influence the amount and concentration of nectar present in a flower at a time. These may be due to the activity of nectaries (secretion or reabsorption), equilibration with humidity of the air (evaporation and condensation) and removal of nectar by flower visitors.

Insect activities influence the total yield of nectar in flowers. Boetius (1948) and Raw (1953) found that flowers from which nectar is periodically removed yield, in total, more nectar (containing more sugar) than do flowers which have not been disturbed over the same period. In almonds, following intermittent rains, honeybees rejected nectar of about 9–15% concentration and collected pollen exclusively till the nectar concentration rose to 25% (Abrol 1993a). Energetically, the dilute nectars provide very low calories and bees are exposed to the extra load of water to be removed through evaporation. Kleiber (1935) found that honeybees stopped visiting lime flowers when the nectar dried up in the afternoon but resumed their visits when nectar became more dilute in the evening. This clearly indicates the importance of relative humidity on nectar concentration and insect visits. On a humid day the pattern of change in nectar would be quite different, and because of the effects of weather and nectar concentration on insect visits, the pattern of change in nectar

Table 14.1 Preferred nectar-sugar concentration ranges of different flower visitors (Percival 1965)

Visitor type	Preferred sugar concentration ranges (%) in nectar
Moth	8–18
Bat	14–16
Bird	13–40
Butterfly	21–48
Honeybee + bumble bees	10–74
Short tongued flies	(Higher)
Long tongued flies	(Still higher)

volume and sugar contents would be quite different too. Weather, therefore, also affects post secretory changes in the nectar as well as insect visits.

14.2.4 Feeding Niches of Pollinators in Relation to Their Preferred Nectar Concentration Ranges

The concentration of sugar in nectar influences the visits of nectarivorous animals to flowers. There are some evidences that different groups of flower visitors differ in their choices of nectar concentration groups ranges (Percival 1965, Table 14.1). The lower value in each case represents the dilute nectars. If the more concentrated nectars are included in the table then the sequence will end with short tongued flies, because the viscous solutions cannot be sucked by insects with long tongues. Betts (1930) has shown that sucking rate of honeybees declines markedly when the concentration of sugar syrup on which they feed exceeds 50–60%.

Simpson (1964) showed that honeybees taking up such concentrated solutions diluted them to very few percent by spitting into them only watery saliva from their labial glands. Lepidopterans can make concentrated solutions more easily potable by spitting labial gland secretion into the drink. Both lepidopterans and bees seem to feed on only moderately concentrated nectars in the field. Short tongued flies on the other hand take nectar at high concentrations (Elton 1966) and readily feed on crystalline sugar. They do this by spitting on their food and lapping up the solution. This spit and lap mechanism enables flies to exploit dry nectar abandoned by bees in the heat of the day (Hansen-Bay 1976).

14.2.5 Nectar Secretion Pattern and Its Influence on Pollinator-Plant Interaction

Time sense in honeybees as well as rhythmicity in nectar secretion in flower types has been of great significance in the pollination of various entomophilous plants. The bees have been found to anticipate seasonal and diurnal changes in the caloric reward of their host plants (Frankie et al. 1976) and adjust their collection activities to the rhythms of nectar production (Corbet 1978a, b, c; Sihag and Abrol 1986). When a plant has two peaks, the bee activity may coincide accordingly. Bimodal pattern of nectar secretion has been observed in most of the plants (Corbet et al. 1979; Real 1981; Lack 1982; Pelmenev et al. 1984; Abrol 1986b, 1987). However, more than two peaks may occur in some plants depending upon genus or sub-family (Pesti 1976). Nunez (1977) found that flight activity of honeybees collecting nectar coincides with the nectar secretion pattern of host plants. The coincidence pattern of nectar secretion and pollinator visitation has an *Evolution*ary significance. Plants produce nectar when their potential pollen vectors are available. The pollinators also avoid visiting flowers at times when rewards are not available. This strategy on the parts of the plants and pollinators has brought a co*Evolution* of the diagonally apart, yet mutually linked organisms.

14.2.6 Nectar Composition and Caloric Content – Their Influence on Pollinator-Plant Interaction

Considering the diversity of pollinators and their different energy needs, nectars are highly variable in sugar composition, concentration and caloric content. The caloric rewards available in flowers of different plant species in Central America varies from less than 0.03 mg to approximately 1,800 mg – a difference of 60,000 times (Hainsworth and Wolf 1972a, b; Heithaus et al. 1974; Stiles 1975). The amount of sugar in “bee flowers” may be<1 mg per floret whereas in “bird flowers” and “bat flowers” it is appreciably higher (Shaw 1953; Percival 1965; Hainsworth 1973; Heinrich 1975b; Stiles 1975; Baker 1979). Bat flowers contain some of the largest amount of sugar. Up to 15 ml of nectar is produced per flower per night by some bat pollinated flowers in West Africa (Baker and Haris 1957) and Costa Rica (Heithaus et al. 1974). Whether a given caloric reward is presented as dilute or concentrated solution is important in the energetics of foraging. It is assumed that 1 mg of sugar, regardless of type; yield about 4.0 cal, probably a reasonable estimate for most ecological questions.

The most common sugars in the nectar are a disaccharide: sucrose, and two monosaccharides: glucose and fructose. Sucrose predominates in most of the flowers with tubular corolla and its hydrates, glucose and fructose, in open flowers (Wyke 1953; Bailey et al. 1954; Percival 1961; Stiles 1975; Corbet 1978b).

Majority of the plant species investigated by Rowley (1976) in Philippines had the dominance of sucrose. Sihag and Kapil (1983) studied nectar sugars of 44 plant species in subtropical Hisar (India) and found that sucrose dominated in 13, glucose in 24 and the rest contained equi-proportioned glucose (G), fructose (F) and sucrose (S). Bahadur et al. (1986) found that SGF type of sugar composition was the most common occurring in 56 out of 100 species investigated. In a later study, Baker and Baker (1983) found that out of 765 plant species examined, sucrose, glucose and fructose combination was most common (649 plants) followed by glucose and fructose (78 plants); Sucrose and fructose (29 plants); sucrose alone (seven plants) and glucose alone (two plants); whereas sucrose + fructose or only fructose was not detected in any of the plant species. Abrol and Kapil (1991) found sucrose, glucose and fructose as the main components of nectar in most of the agricultural crop plants. *Parkinsonia aculeata* L. and *Pongamia glabra* L. contained traces of maltose also. Abrol and Kapil (1991) further found that total caloric reward matters more to the pollinators than the proportion of consequent sugars. Generally, pollinators with high energy requirements foraged on sucrose rich flowers whereas those with low energy requirements relied on glucose or fructose rich flowers. They also explained the relative attractiveness of different sugar components to different pollinators in relation to energy needs and the possible origin of maltose.

Different nectar feeders have been reported to vary in their preferences (Baker and Baker 1979, 1982a, b). Small bees preferred broad spectrum nectar; big bees, lepidopterans and humming birds preferred sucrose rich; and flies, passerine birds and bats preferred sucrose poor nectars. This partitioning of resources reduces competition and ensures the co-existence of several nectar feeding animals in a community.

Nectar sugars vary in their taste to bees, and consequently in their attractiveness too. Frisch (1950) categorised the nectar sugars into following different classes:

(i) Nectar sugars sweet to bees: sucrose, maltose, glucose, fructose, trehalose and melizitose;
(ii) Nectar sugars tasteless to bees: lactose, melibiose, raffinose, xylose and arabinose;
(iii) Nectar sugars toxic to bees: mannose and galactose; and
(iv) Nectar sugars repellent to bees: cellobiose and gentibiose.

Wyke (1952a, b) concluded that honeybee prefers a "balanced nectar" with roughly equal amounts of glucose, fructose and sucrose. Percival (1961) in his extensive nectar survey studies revealed that balanced nectars are very uncommon in plants. Waller (1972) disputed Wyke's claim and showed that honeybees preferred sucrose rich liquids. Sihag and Kapil (1983) and Abrol and Kapil (1991) also supported the Waller's contention but stated that the bees preferred nectar with one dominant sugar and not the equi-proportioned sugars as has earlier been reported by Wyke (1952a, b).

However, birds have been reported to show a different pattern of nectar preferences. Hainsworth and Wolf (1976) found that birds preferred nectar sugars in the order: $SFG = SF > S > FG > SG > F > G$. However, Stiles (1975) found a different order of nectar preference which was $S > G > F$ (where $S =$ sucrose, $F =$ fructose and $G =$ glucose). Nearly all birds rejected fructose in any comparison test. Van Ripper (1960) also found that broad tailed hummingbird (*Selasphorus platycerus*) preferred sucrose and glucose. Josens et al. (1998) found that in case of nectar feeding ant, *Camponotus mus* both sucrose concentration and viscosity of the ingested solution modulate feeding mechanics as well as workers decision about the load size to be collected before leaving the source. In a similar study, Josens and Roces (2000) found that responsiveness of foragers of nectar feeding ant, *Camponotus mus*, determined by the nutritional state of the colony, influenced both foraging decisions and the dynamics of fluid intake.

The presence of certain amino acids in nectars have been considered of *Evolution*ary significance. Baker and Baker (1973a, b, 1975, 1977) and Baker et al. (1978) concluded that occurrence of amino acids in floral nectars is a universal phenomenon and reported amino acids in the nectars of 260 out of 266 plants studied. They also pointed out that amino acids in nectar may be important in the nutrition of nectar feeding insects, as well as contributing to taste and feeding stimulus, although their amounts are small in comparison to the concentration of sugars.

14.2.7 Floral Visits in Relation to Quality of Food

Köhler et al. (2009) reported that animals commonly experience variation in both food quality and metabolic requirements, and must regulate their food intake to maintain energy balance. They found that captive white bellied (*Cinnyris talatala*) and amethyst (*Chalcomitra amethystina*) sunbirds (Nectariniidae) exposed to different nectar sugar concentrations (0.25, 0.5 and 1 M sucrose), i.e. food qualities, and ambient temperatures (5°C, 15°C and 25°C), compensated for decreased dietary sugar concentration by increasing food intake. In a further study, Köhler et al. (2010) found that floral nectars of bird-pollinated plants are relatively dilute. Nectar ingestion rate is determined by viscosity; however, total food intake is mainly modulated by sugar concentration. Similar effects of food viscosity have been observed in insects that suck nectar.

14.3 Measurement of Energy Costs

The energy costs of foraging pollinators must be less than the energy gains. The profits must be sufficient for long term energy balance. Different methods for measurement of foraging energetics vary depending upon the conditions as follows:

1. Direct measurement of food consumption, particularly when foods are chemically defined as sugars from nectar, can be reliable indicators of energy expenditure especially in honeybees and humming birds that presumably not accumulate far reserves. Rapid utilization of sugars by these animals has made it possible to compute 24/h energy budgets on the basis of food intake.
2. The standard and most reliable indicator of energy expenditure is the rate of either oxygen consumption or carbon dioxide emission. Animals feeding on nectar sugars generally have respiratory quotient close to 1.0 and every milliliter oxygen consumed or carbon dioxide liberated is equivalent to an energy expenditure of 5.0 cal or 83.70 J. By far the greatest bulk of food stuffs in nectar is sugar, which yields about 4 cal per milligram. Hymenoptera and Diptera have

respiratory quotient (RQ) equal to 1.0 indicating that their flight muscles use primarily carbohydrates. The method has some limitations that the natural conditions are difficult to be obtained in animals confined to respirometers. However, when combined with careful field observations the measurements can be a powerful tool to infer energy budgets. Morrant et al. (2009) developed the Methods for sampling and storing nectar from the flowers of species with low floral nectar volumes (<1 μL) using the flowers of *Eucalyptus* species. They recommended the washing for nectar collection from flowers with low nectar volumes in the field (with the understanding that one wash underestimates the amounts of sugars present in a flower), as is immediate analysis of sugar mass.

3. Energy budgets can also be determined by the use of isotope-labelled water. Monitoring the amount of isotope in the blood after a given amount has been injected provides an indication of the amount of energy expended during the time between injection and sampling. The isotope labeling method is ideal for social insects because these animals can be recaptured in the field after a given interval (Mullen 1971; Utter 1973).
4. Body temperature is possibly the most reliable indicator of "instantaneous" energy expenditure of free living animals in which discrete activity states are not apparent through visual inspection. At least 80% of an animal's energy expenditure is degraded to heat, due to inefficiency at biochemical and mechanical levels of organisation (WeisFogh 1972). An increase in heat production is usually accompanied by an increase in body temperature (Heinrich 1974a, b, 1975c, d). The method has been useful for determining the energy expenditure of flying birds and insects (bumblebees) (Weis-Fogh 1972; Heinrich 1972).

14.4 Energy Expenditure

Pollinators conform to energy expenditure relationship similar to those of other animals and may restrict their foraging activity to short periods when their host flowers present nectar. Flower visiting insects are the most extravagant utilizers of energy on weight-specific basis (Heinrich and Raven 1972; Abrol 1986a, 1992c). However, large expenditure is often required to make small profits.

Energy expenditure of some insects while thermoregulating depends upon the body size. On the basis of whole body weight, the metabolic rate of a bumblebee while incubating is 170 cal $(g\ h)^{-1}$ at 0°C. A hummingbird weighing 10 times more than the bee has a weight specific respiratory rate 2–4 times less than that of the bee, and a bat weighing 10 times more than the bird has a respiratory rate at the same temperature 2.8 times less than that of the bird (Heinrich 1975d). The smaller the animal, the greater is the energetic barrier to activity at low ambient temperature. Bartholomew (1968) pointed out that as long as small animals maintain high body temperature, they are never more than a few hours from death by starvation, particularly at low ambient temperatures. Hill-Peggy et al. (2001) observed that foraging decisions are based on a suite of choices that include energetics physiological constraints. Although traveling farther to harvest a greater net energetic reward is beneficial, many animals opt for a smaller net reward that requires less travel.

The state of activity of rest and ambient temperature have great influence on energy expenditure. For example, a hummingbird weighing 8 g may increase its metabolic rate from about 9.0 to 65 cal (g h)$^{-1}$ at 0°C (Hainsworth and Wolf 1972b). A stationary bumblebee weighing approximately 0.5 g increases the metabolic rate of its thoracic muscles from 85 to 850 cal (g h)$^{-1}$ over the same range of ambient temperatures while incubating brood (Heinrich 1974a).

Many pollinators have evolved mechanisms to overcome periods of severe energy problems. Since many flowers bloom only for short durations, the high energy demanding pollinators face acute problems. Some insects during this period undergo torpidity. Social insects such as bumblebees avoid this torpidity by storing food energy in the nest. A queen bumblebee may use the entire contents of her honey pot in a single night (Heinrich 1974a, 1975d). When all the available food has been utilized, the bee enters torpor (Heinrich 1972). When at 0°C, a torpid bumblebee has a metabolic rate 1,000–2,000 times less than when it is regulating its body temperature (Heinrich 1974a, b; Kammer and Heinrich 1978). Thus, these energy saving mechanisms help the pollinators to overcome unfavourable or dearth conditions.

The rates of increase in the body temperature are strongly size dependent (Pereboom and Biesmeijer 2003). For example, a bumblebee weighing 0.6 g may warm at 12°C in 1 min (Heinrich 1975d) but an animal weighing 300 g warms up about 120 times less rapidly (Pearson 1960; Bartholomew et al. 1970). The energy costs for warm up are nearly unfavourable for large animals. For example, a bumblebee weighing 0.5 g costs 7.5 cal to warm up from 13.5°C to 38.0°C (Heinrich 1974b) which is equivalent to the energy expenditure during 3.0 min of flight. A sphinx moth weighing 2.0 g requires 30 cal to warm up from 15°C which is equivalent to the energy expended during approximately 3.7 min of flight (Heinrich 1971a, b; Heinrich and Casey 1973). A small bat or hummingbird expends 114 cal during a warm up from 10°C, corresponding to approximately 1.2% of the total energy budget for 24 h. In contrast, a 200 kg bear would need as much energy to warm up as it uses during an entire 24 h activity period (Pearson 1960).

The highest energy costs, other than thermoregulation, are those of locomotion. Flight, particularly hovering (Tucker 1968; Weis-Fogh 1972), is a metabolically the most expensive mode of locomotion, although for a given distance of travel it can be energetically less costly than waling (Tucker 1968; Weis-Fogh 1972; Hainsworth and Wolf 1972b; Epting and Casey 1973). For insects and birds, the energetic cost of flight has been shown to vary markedly with load (Berger and Hart 1974; independent of ambient temperature (Betts 1930; Hart and Berger 1972; Heinrich and Casey 1973; Heinrich 1975d).

The oxygen consumption rates during flight represent 100–150 fold increase over the resting rates. Hovering flight imposes heavy demands of energy on small birds and bats as well as insects (Weis-Fogh 1972), and thus it is the mode of locomotion and not the systematic position of the animal that demands high metabolic rates. The large range in measured metabolic rates reflect the intrinsic differences among species as well as conditions of measurement. The metabolic rates during flight may be influenced by the ambient temperature, weight and speed of flight (Kammer and Heinrich 1978; Cooper et al. 1985). In some insects, however, which can regulate their body temperature behaviourally or physiologically, the metabolic rate will be relatively independent of the ambient temperature. In a number of species of sphinx moths (Heinrich 1971a; Heinrich and Casey 1973; Casey 1976); syrphid flies and bumblebees (Heinrich and Pantle 1975; Kwon and Saeed 2003); *Xylocopa californica* (Chappell 1982); *X. capitata* (Louw and Nicolson 1983); *X. fenestrata, X. pubescens, Megachile cephalotes, A. mellifera and A. dorsata* (Abrol 1992c) muscle temperature is stabilized during flight over a relatively wide range of ambient temperatures. In these insects, the metabolic rate is independent of the ambient temperature but energy is expended prior to flight to raise the thoracic temperature to a level at which flight is possible. In case of small insects or some large uninsulated ones, body temperature probably equals or parallels ambient temperature during flight (Sotavalta 1954; Kammer and Heinrich 1978; Abrol 1992c). For example, in *A. florea and Pithitis smaragdula* oxygen consumption paralleled ambient temperature during flight (Abrol 1992c).

These physiological measurements of metabolic rates and economics of foraging costs provides a suitable tool for inferring energy budget of the pollinators (Abrol 1986c).

14.5 Cost-Benefit Analysis and Pollinator Behaviour

Energy requirements of pollinators govern their foraging relationship with flowers. The interdependence of pollinators and flowers depends upon the balance sheet they share with each other. Each pollinator moulds its efforts in such a way that it can maximize the reward. Energy intake and expenditure depend upon the allocation of time into various daily activities e.g. rest, flight and hovering etc. Time energy budgets have extensively been studied in birds especially nectarivores (Gill and Wolf 1975a, b; Wolf and Hainsworth 1971; Wolf et al. 1972, 1975; Wolf 1975), solitary bees (Abrol 1986a, 1989, 1993b), honeybees and solitary bees (Abrol 1992a) and dragon flies (Fried and May 1983). Abrol (1986a, 1989, 1992a, 1993b) studied the time budgets of honeybees and solitary bees and categorized their daily activities into foraging, active and resting periods etc. Wolf (1975) studied the time budgets of *Nectarina famosa* males and allocated their activities into sitting., fly catching and chasing. Likewise time energy budgets of *Apis florea, A. dorsata Megachile cephalotes, M. lanata, Xylocopa fenestrata, Pithitis smaragdula* (Abrol 1992a), *Andrena ilerda, A. leaena* (Abrol 1989) and *Megachile femorata* (Abrol 1993b) have been worked out.

In general, honeybees need continual influx of energy for thermoregulation which accelerates the brood development and hence work for larger durations in the field than the solitary bees. The latter because of their individual nesting habits could dispense with such an energy expenditure and require resources just sufficient to meet their own energy demands and as such worked for smaller durations in the field (Abrol 1992a).

Co-evolution has brought a close correlation between pollinator needs and expenditures of food energy. Each pollinator modifies its behaviour in such a way that maximizes its net energy gains. Thus the foraging strategies vary accordingly (Faegri 1978; Abrol 1986a, 1989, 1992a, 1993b; Moffatt-Luciano 2001; Cakmak-Ibrahim and Wells-Harrington 2001). Environmental factors such as atmospheric temperature, relative humidity, light intensity, solar radiation and time of the day influence the energy relationship of pollinators with flowers (Riessberger and Crailsheim 1997; Abrol 1998a, b). The complex interactions of various weather parameters determine the schedule of activities, time budgets and energy intake of pollinators. According to Abrol (1992a) the energy requirement of different bee species varies amongst seasons and crop which depends, in all probability, one the existing set of environmental conditions in a unit time influencing the physiology of both the plants and their pollen vectors.

Energy budget balance indicated that bees with higher energy requirements do not forage on the flowers providing low caloric rewards (Abrol 1992a., Klinkhamer and Jong 1993; Marden and Waddington 1981). The carpenter bee, *X. fenestrata* with higher energetic requirement rarely visited *Medicago sativa*, *Trifolium alaxandrinum, Coriandrum sativum, Foeniculum vulgare, Daucus carota, Allium cepa and Brassica* group of crops which provide low caloric reward inadequate to meet its higher energy demands. Another factor limiting the visit of *X. fenestrata* to these crops is the poor correlation between the morphology of the flowers and the bee which makes its landing on these flowers difficult. In general, size of the flower and caloric reward in relation to the size of the visitor and energy demands seem to be the determinants for resource partitioning among various species of bees and permitting thus co-existence under similar ecological conditions (Abrol 1992a). The population of certain species of pollinators visiting certain flowers was found to be a function of their own size as well as the size of the flowers, since the feeding pattern of many animals differ as a function of trophic apparatus (Harder 1985). *X. fenestrata* visited *Cajanus cajan, Parkinsonia aculeata, Pongamia glabra* and *Luffa cylindrica* flowers (Abrol 1992a). The flowers of these crops are relatively large, suitable for landing and provide sufficient caloric reward. The bee can handle these flowers efficiently and maximize obtainable gain as net energy. Similarly, flowers of *F. vulgare, C. sativum, D. carota, A. cepa. Trigonella foenumgraecum* var Kasuri and *Mangifera indica* were not attractive to *A. dorsata* because the bee could make no profit from these crops. However, *A. dorsata* collected pollen from these flowers by treating the inflorescences as a single unit and walked over the massed florets. Though *Brassica* crop were intermediate to umbelliferous and leguminous crops in energetic rewards, *A. dorsata* visited in the early hours of the day when the flowers had peak periods of nectar production, and then the foraging populations shifted to other high rewarding crops. However, *A. florea* with small energetic needs commenced activity between 1,000 and 1,100 h and dominated on the later crops throughout the day. The latter bee species with its smaller size and body weight is physiologically and morphologically better adapted to extract maximum reward from these flowers. Because of relatively low energy requirements, the bee is still able to maintain an energy balance and visited these crops in large numbers. Sihag and Kapil (1983) reported that *A. florea* visited *Brassica* crops in larger numbers than *A. dorsata.* They attributed this to a differential response of bees to their energy demands. In *Brassica* crops, exceptions were *B. juncea* and *B. carinata* where foraging populations of *A. dorsata* were also large. Interesting situation was observed in case of *M. sativa* and *T. alexandrinum* which bloom simultaneously and compete for pollinators. *M. sativa* has comparatively higher caloric reward than *T. alexandrinum.* The honey bees (*Apis* sp.) were attracted to *M. sativa* during early hours of the day at peak periods of nectar production but after 1,100 h onward foraging populations shifted to *T. alexandrium* due to reduction in quantity of available rewards from *M. sativa.* Evidently, pollinators even prefer low rewarding flowers, when high floral rewards are not available or the nearly resources are depleted. *A. florea* visited flowers with low caloric rewards whereas *A. dorsata* preferred those with high rewards. This behaviour was largely guided by their energy demands. Sunflower (*Helianthus annuus*) attracted almost all type of pollinators. Though the caloric reward per flower is low yet each bee species including *X. fenesterata* and *A. dorsata* are able to maintain energy balance. Since flower head with plateform provides no barrier for the landing of foragers, the energetic cost is reduced due to temporarily suspension of hovering flight, and large number of flowers can be visited in rapid succession. Generally, the smaller flowers with little nectar are unattractive to large hovering animals such as hummingbirds and sphinx moth which probably cannot suffice their energetic demands. However, insects such as bumblebees, which land on inflorescences of *Spiraea latifolia* L. (Rosaceae) and *Solidago canadensis* L. (Asteraceae) are still able to maintain an energy balance despite minute amount of nectar in florets, because the energy expended in walking from one flower to another is 100 times less than an equivalent period of flight and because the flowers can be visited in rapid succession (Heinrich and Raven 1972). Similarly, *Luffa cylindrica* flowers were visited by almost all kinds of bee pollinators because the flowers are large with open nectaries and easily accessible to each type of pollinator irrespective of the body size.

The solitary bees in contrast to social bees have far less energy demands as they need not to incubate brood or support nestmates. However, it is essential for solitary bees that foraging profit should exceed some minimum threshold value. Furthermore, emergence pattern of solitary bees was synchronized with their specific host plants (Sihag 1983, 1984). The emergence of *Megachile lanata* synchronizes with the blooming of *Cajanus cajan*, which is highly profitable for all the bees. Similarly *L. cylindrica* is visited by all the solitary and social bees and is highly profitable. During March-May, solitary bees mostly forage on *M. sativa*, *P. aculeata*, *P. glabra*, *H. annuus* and *C. cajan.* Foraging on these crops is also highly profitable for all the bees excepting *X. fenesterata* which rarely visited *M. sativa* flowers. In general, solitary bees were adapted behaviourally, morphologically and physiologically to their specific host plants (Linsley et al. 1963; Strickler 1979; Sihag 1988). Interestingly, *M. sativa* has to compete with *P. aculeata* for pollinators (Sihag 1982). The pollinators are more attracted to *P. aculeata* and because the latter provides relatively more caloric rewards. Further, ultra violet reflectance pattern of *P. aculeata* flowers is more attractive to bees (Jones and Buchmann 1974). However, the contention of Jain and Kapil (1980) that attraction of pollinators to the latter plant is due to the presence of maltose in their nectar does not find a support, because according to Rowley (1976) it is not a primary product of nectar yielding plants but mainly arises due to glucophilic enzymes introduced by the insects or by fungal/bacterial contamination. Therefore, to assign the floral attractiveness to this foreign agent seems to be inappropriate.

14.6 Conclusion

Thus, in conclusion, it can be said that energy-budget balance enables the characterization of pollinators with their plants on diurnal and seasonal basis and provides a clue for their management. Ecological factors such as temperature, light, wind etc. influence the activity of both bees and production of nectar, thereby influencing time budgets in the form of energy costs and gains from the flowers. However, much is needed to be known about the energetics of nectar production in plants, the variability of nectar production among plants and the correlation of seed to nectar and pollen production in order to accurately assess the plant's options. More attention is needed to determine the individual areas, if examined in detail, are likely to shed light on some important aspects of pollination biology.

References

Abrol DP (1986a) Time and energy budgets of alfalfa pollinating bee, *Megachile nana* Bingh and *M. flavipes* Spinola (Hymenoptera: Megachilidae). Proc Indian Acad Sci (Anim Sci) 95: 579–586

Abrol DP (1986b) Ecophysiological adaptations between pollinating bees and their flowers. Environ Ecol 4:161

Abrol DP (1986c) Metabolic expenditures of *Megachile nana* Bingh and *M. flavipes* Spinola (Hymenoptera: Megachilidae). J Anim Morphol Physiol 33:107–112

Abrol DP (1987) Activity time budgets and pollination potential of *Apis cerana indica* workers. Environ Ecol 5(4):707–709

Abrol DP (1989) Energy intake and expenditure in *Andrena ilerda* and *A. leaena* (Hymenoptera: Andrenidae). Korean J Apic 4:41–47

Abrol DP (1990a) Energetics of nectar production in some apple cultivars as a predictor of floral choice by honeybees. Trop Ecol 31(1):116–122

Abrol DP (1990b) Energy intake and expenditure in *Xylocopa fenestrata* F. and *X. pubescens* Spinola (Hymenoptera: Anthophoridae). In: Veeresh GK, Malik B, Virakthamath CA (eds) Social insects and the environment, Proceedings of the 11th international congress of IUSSI, Bangalore, August 1990. Oxford and IBH Publishing Co., New Delhi, pp 574

Abrol DP (1992a) Bioenergetics in bee flower interrelationship – an analysis of foraging behaviour. Korean J Apic 7(1):39–66

Abrol DP (1992b) Energetics of nectar production in some strawberry cultivars as a predictor of floral choice by honeybees. J Biosci 17(1):41–44

Abrol DP (1992c) Oxygen consumption of foraging bees. J Anim Morphol Physiol 39:27–42

Abrol DP (1993a) Intervarietal differences in nectar production affecting pollinator attractiveness and fruit set in almond. In: Veeresh GK, Uma Shankar R, Ganeshaiah KN (eds) Pollination in tropics. IUSSI Indian Chapter, Bangalore, pp 120–122

Abrol DP (1993b) Energy intake and expenditure in *Megachile femorata* Smith (Hymenoptera: Megachilidae). Trop Ecol 34(2):173–180

Abrol DP (1995) Energetics of nectar production in some almond cultivars as a predictor of floral choice by honeybees *Apis cerana indica* F. and *A. mellifera* L. (Hymenoptera: Apidae). Proc Indian Natn Sci Acad B 57(2):127–132

Abrol DP (1997) Bees and beekeeping in India. Kalyani Publishers, Ludhiana, 450p

Abrol DP (1998a) Environmental factors influencing flight activity in honeybees *Apis cerana* Fab. and *Apis mellifera* L. (Hymenoptera: Apidae). Indian Bee J 60:71–75

Abrol DP (1998b) Food acquisition efficiency as a determinant of honeybees foraging decisions. Indian Bee J 60(3):133–136

Abrol DP (2000) Energy budget versus plant pollinator interactions. J Palynol 36:17–36

Abrol DP (2010) Energy requirement and its harvest as determinant of foraging decisions of bees abstract no MP-002. Paper presented in 10th Asian Apicultural Association Conference & Api Expo held at Bexco Busan South Korea between 4th and 7th Nov 2010

Abrol DP (2011) Foraging. In: Hepburn HR, Radloff SE (eds) Honeybees of Asia. Springer, Berlin, pp 257–292

Abrol DP, Kapil RP (1991) Foraging strategies of honeybees and solitary bees as determined by nectar sugar components. Proc Indian Natl Sci Acad B57(2):127–132

Alm J, Ohnemeiss TE, Lanza J, Verizenia L (1990) Preference of white cabbage butterflies and honeybees for nectar that contains amino acids. Oecologia 84(1):51–57

Bahadur B, Chaturvedi A, Ramaswamy N (1986) Nectar types in Indian plants. Proc Indian Acad Sci (Plant Sci) 96:41–48

Bailey ME, Feiger EA, Oertel E (1954) Paper chromatographic analysis of some southern nectars. Glean Bee Cult 82:401–403

Baker HG, Baker I (1973a) Amino-acids in nectar and their evolutionary significance. Nature 241:543–545

Baker HG, Baker I (1973b) Some anthecological aspects of the evolution of nectar-producing flowers, particularly amino acid production in nectar. In: Heywood VH (ed) Taxonomy and ecology. Academic, London, pp 243–264

Baker HG, Baker I (1975) Studies of nectar-constitution and pollinator-plant coevolution. In: Gilbert LE, Raven PH (eds) Coevolution of animals and plants. University of Texas Press, Austin, pp 100–140

Baker HG, Baker I (1977) Intraspecific constancy of floral nectar amino acid compliments. Bot Gaz 138:183–191

Baker HG, Baker I (1979) Chemical constituents of the nectars of two *Erythrina* species and their hybrids. Ann Missouri Bot Gard 66:446–450

Baker HG, Baker I (1982a) Chemical constituents of nectar in relation to pollination mechanisms and phylogeny. In: Nitecki MH (ed) Biochemical aspects of evolutionary biology. The University of Chicago Press, Chicago, pp 131–171

Baker HG, Baker I (1982b) Some chemical constituents of floral nectars of *Erythrina* in relation to pollinators and systematics. Allertonia 3:25–38

Baker HG, Baker I (1983) A brief historical review of the chemistry of floral nectar. In: Bentley B, Elias T (eds) The biology of nectarines. Columbia University Press, New York, pp 126–152

Baker HG, Haris BJ (1957) The pollination of *Parkia* by bats and its attendant *Evolution*ary problems. Evolution 11:449–460

Baker HG, Opler PA, Baker I (1978) A comparison of the amino acid complements of floral and extrafloral nectars. Bot Gaz 139:322–332

Barker HG (1979) Two cases of bat pollination in Central America. Rev Biol Trop 17:187–197

Bartholomew GA (1968) Body temperature and energy metabolism. In: Gordon MS (ed) Animal functions: principles and adaptarins. Macmillan, New York, pp 348

Bartholomew GA, Dawson WR, Laslewski RC (1970) Thermoregulation and heterothermy in some of the smaller flying foxes (Megachiroptera) of New Guinea. Z Verg Physiol 70:196–209

Berger M, Hart JS (1974) Physiology and energetics of flight. In: Farner DS, King JR (eds) Avian biology, vol 4. Academic, New York, pp 415–477

Betts AD (1930) The ingestion of syrup by the honeybees. Bee Wld 11:85–90

Boetius J (1948) Uber den verlaufder Nekarabsandering einiger Blutenpflanzen. Bethefie Zur Schweizerischen Bienzeitum 2:257–317

Brandenburg A, Dell'Olivo A, Bshary R, Kuhlemeier C (2009) The sweetest thing. Recent advances in nectar research. Curr Opin Plant Biol 12:486–490

Butler CG (1945) The influence of various physical and biological factors of environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance. J Exp Biol 21:5–12

Cakmak I, Wells H (2001) Reward frequency: effects on flower choices made by different honeybee races in Turkey. Turk J Zool 25(3):169–176

Casey TH (1976) Flight energetics of sphinx moths; power input during hovering flight. J Exp Biol 64:529–543

Chappell MA (1982) Temperature regulation of carpenter bee (*Xylocopa californica*) foraging in the Colorado desert of Southern California. Physiol Zool 55:267–280

Cirnu I, Harnaj A, Lucescu A, Fota H, Grosu E (1977) New criteria and elements to classify and estimate beekeeping economic contribution of honey plants. In: Honey plant basis of apiculture; international symposium on melliferous flora, Budapest, 1976, pp 191–194

Comba L, Corbet SA, Barron A, Bird A, Collinge S, Miyazaki N (1999) Garden flowers: insect visits and the floral reward of horticulturally – modified variants. Ann Bot 83(1):73–86

Cooper PD, Schaffer WM, Buchmann SL (1985) Temperature regulation of honeybees (*Apis mellifera* L.) foraging in the Sonovan desert. J Exp Biol 114:1–7

Corbet SA (1978a) A bee's view of nectar. Bee World 59:25–32

Corbet SA (1978b) Bees and nectar of *Echium vulgare*. In: Richards AJ (ed) The pollination of flowers by insects. Academic, London, pp 21–30

Corbet SA (1978c) Bee visits and nectar of *Echium vulgare* L. and *Sinapsis alba* L. Ecol Ent 3:25–27

Corbet SA (1990) Pollination and weather. Israel J Bot 39:13–30

Corbet SA, Unwin DM, Pryce-Jones OE (1979) Humidity, nectar and insect visits to flowers with special reference to *Crategues. Tilia* and *Echium*. Ecol Ent 4:9–12

Corbet SA, Fussel M, Ake R, Fraser A, Gunsen E, Salvage A, Smith K (1993) Temperature and the pollinating activity of social bees. Ecol Entomol 18:17–30

Crane E, Walker P, Day R (1985) Directory of important world honey sources. International Bee Research Association, London, 384p

de la Barrera E, Nobel PS (2004) Nectar: properties, floral aspects, and speculations on origin. Trends Plant Sci 9:65–69

Deodikar GB, Thakur CV, Phadke RP (1957) High nectar concentration in floral nectaries of silver oak, *Grevillea robusta*. Indian Bee J 19:84–85

Elton CS (1966) The pattern of animal communities. Mathuen, London

Epting RJ, Casey TM (1973) Power output and wing-disc loading in hovering hummingbirds. Am Nat 107:761–765

Faegri K (1978) Trends in research on pollination ecology. In: Richards AJ (ed) The pollination of flowers by insects. Academic, London, pp 5–12

Fleming PA, Hartman Bakken B, Lotz CN, Nicolson SW (2004) Concentration and temperature effects on sugar intake and preferences in a sunbird and a hummingbird. Funct Ecol 18: 223–232

Fleming PA, Xie S, Napier K, McWorther TJ, Nicolson SW (2008) Nectar concentration affects sugar preferences in two Australian honeyeaters and a lorikeet. Funct Ecol 22:509–605

Frankie GW, Opler PA, Bawa KS (1976) Foraging behaviour of solitary bees: implications for outcrossing of a neotropical forest tree species. J Ecol 64:1049–1057

Fried CS, May ML (1983) Energy expenditure and intake of territorial male of *Pachydiplax longipennis* (Odonata: Libellulidae). Ecol Ent 8:283–292

Gill FB, Wolf LL (1975a) Economics of feeding territoriality in the golden winged sunbird. Ecology 56:333–345

Gill FB, Wolf LL (1975b) Foraging strategies and energetics of African sunbirds at mistletoe flowers. Am Nat 109:491–510

Goulson D, Chapman JW, Hughes-William OH (2001) Discrimination of unrewarding flowers by bees; direct detection of rewards and use of repellent scent marks. J Insect Behav 14(5):669–678

Goulson D, Hawson SA, Stout JC (1998) Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. Anim Behav 55(1):199–206

Hainsworth FR (1973) On the tongue of a hummingbird; its role in the rate and energetics of feeding. Comp Biochem Physiol A 46:65–78

Hainsworth FR, Wolf LL (1972a) Energetics of nectar extraction in a small high altitude, tropical hummingbird. J Comp Physiol 80:377–387

Hainsworth FR, Wolf LL (1972b) Power hovering flight in relation to body size in hummingbirds. Am Nat 160:589–596

Hainsworth FR, Wolf LL (1976) Nectar characteristics and food selection by hummingbirds. Oecologia (Berl) 25:101–113

Hansen-Bay CM (1976) Secretary control mechanism in salivary glands of adult *Calliphora.* Ph.D. thesis*,* University of Cambridge, Cambridge

Harder LD (1985) Morphology as a predictor of floral choice by bumblebees. Ecology 66: 190–210

Hart JS, Berger M (1972) Energetics, water economy and temperature regulation during flight. In: Proceedings of the 15th international ornithological congress, the Hague, pp 189–199

Heinrich B (1971a) Temperature regulation of sphinx moth *Manduca sexta.* I. Flight energetics and body temperature during free and tethered flight. J Exp Biol 54:141–152

Heinrich B (1971b) Temperature regulation of sphinx moth *Manduca sexta.* II. Regulation of heat loss by control of blood circulation. J Exp Biol 54:153–166

Heinrich B (1972) Patterns of endothermy in bumblebee queens, drones and workers. J Comp Physiol 77:65–79

Heinrich B (1974a) Thermoregulation in bumblebees: I. Brood incubation by *Bombus vosnesenskii* queens. J Comp Physiol 8:129–140

Heinrich B (1974b) Thermoregulation in endothermic insects. Science 185:747–755

Heinrich B (1975a) Energetics of pollination. Ann Rev Ecol Syst 6:139–170

Heinrich B (1975b) The role of energetics in bumble bee flower interrelationships. In: Gilbert LE, Raven PH (eds) CoEvolution of animals and plants. University Texas Press, Austin, pp 141–158

Heinrich B (1975c) Thermoregulation and flight energetics of desert insects. In: Hagley N (ed) Environmental physiology of desert animals. Academic, London

Heinrich B (1975d) Thermoregulation in bumblebees. II. Energetics of warm-up and free flight. J Comp Physiol 96:155–166

Heinrich B (1976) Foraging specialization of individual bumblebees. Ecol Monogr 46:105–128

Heinrich B (1977) Pollination energetics: an ecosystem approach. In: Matton WJ (ed) The role of arthropods in forest ecosystem. Springer, New York, pp 41–46

Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge, London

Heinrich B (1981) Energetics of pollination. Ann Missouri Bot Gard 68:370–378

Heinrich B (1983) Insect foraging energetics. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Academic, New York, pp 187–215

Heinrich B, Casey TM (1973) Metabolic rate and endothermy in sphinx moths. J Comp Physiol 82:195–206

Heinrich B, Pantle C (1975) Thermoregulation in small flies (*Syrphus* sp.): basking and shivering. J Exp Biol 62:599–610

Heinrich B, Raven PH (1972) Energetics and pollination ecology. Science 176:497–602

Heithaus ER, Opler PA, Baker HG (1974) Bat activity and pollination of *Bauhinia pauletia*: plant pollinator co*Evolution*. Ecology 55:412–419

Helversen OV, Reyer HU (1984) Nectar intake and energy expenditure in a flower visiting bat. Oecologia 63:178–184

Hickman JC (1974) Pollination by ants: a low energy system. Science 184:1290–1292

Hill-Peggy SM, Hollis J, Harrington W (2001) Foraging decisions in nectarivores: unexpected interactions between flower constancy and energetic rewards. Anim Behav 62(4):729–737

Ish-Am G, Eisikowitch D (1998) Low attractiveness of avocado (*Persea americana* Mill.) flowers to honeybees (*Apis mellifera* L.) limits fruit set in Israel. J Hort Sci Biotechnol 73(2): 195–204

Jain KL, Kapil RP (1980) Foraging rhythm of Megachild bees in relation the flowering of *Medicago sativa* L. and *Parkinsonia aculeata* L. Indian Bee J 42:35–38

Jamieson CA, Austin GH (1956) Preferences of honeybees for sugar solutions. In: Proceedings of the 10th international congress on entomology. Montreal, 1956, vol 4, pp 1059–1062

Johnson SD, Nicolson SW (2008) Evolutionary associations between nectar properties and specificity in bird pollination systems. Biol Lett 4:49–52

Jones CE, Buchmann SL (1974) Ultraviolet floral patterns as functional orientation cues in hymenopterous pollination systems. Anim Behav 22:481–485

Josens RB, Roces F (2000) Foraging in the ant Camponotus mus: nectar intake rate and crop filling depend on colony starvation. J Insect Physiol 46:1103–1110

Josens RB, Farina WM, Roces F (1998) Nectar feeding by the ant *Camponotus mus*: intake rate and crop filling as a function of sucrose concentration. J Insect Physiol 44:579–584

Kammer AE, Heinrich B (1978) Insect flight metabolism. Adv Insect Physiol 13:113–228

Kapil RP, Brar HS (1971) Foraging behavior of *Apis florea* F. in relation to *Brassica campestris* var. toria. L. In: Proceedings of 22nd international apicultural congress, Moscow, 1971, pp 335–339

Kleiber E (1935) Hat des Zeitzedachtis der Bienen biologische Bedeutung. Z.Vergl. Physiology 22:221–262

Klinkhamer GL, De Jong TJ (1993) Attractiveness to pollinators – a plants dilemma. Oikos 66:180–184

Köhler VL, McWhorter TJ, Nicolson SW (2009) Energy management on a nectar diet: can sunbirds meet the challenges of low temperature and dilute food? Funct Ecol 24(6):1241–1251

Köhler A, Carolina D, Leseigneur C, Verburgt L, Nicolson SW (2010) Dilute bird nectars: viscosity constrains food intake by licking in a sunbird. Am J Physiol Reg Integr Comp Physiol 299(4):1068–1074

Kwon YJ, Saeed S (2003) Effect of temperature on the foraging activity of Bombus terrestris L. (Hymenoptera: Apidae) on greenhouse hot pepper (*Capsicum annuum* L.). Appl Entomol Zool 38(3):275–280

Lack AJ (1982) Competition for pollination in the ecology of *Centaurea scabiosa* L. and *Centaurea nigra* L. II. Observations on nectar production. New Phytol 91:309–320

Linsley EG, MacSwain JB, Raven PH (1963) Comparative behaviour of bees on onagraceae. Univ Calif Pub Ent 33:1–58

Loper GM, Waller GD (1970) Alfalfa flower aroma and flower selection by honeybees. Crop Sci 10:66–68

Louw GN, Nicolson SW (1983) Thermal energetic and nutritional considerations of the carpenter bee, *Xylocopa capitata*. J Ent Soc South Africa 46(2):227–240

Marden JH, Waddington KD (1981) Floral choice by honeybees in relation to the relative distances to flowers. Physiol Entomol 6:431–435

Mitchell RJ, Irwin RE, Flanagan RJ, Karron JD (2009) Ecology and evolution of plant-pollinator interactions. Ann Bot 103:1355–1363

Moffatt L (2001) Metabolic rate and thermal stability during honeybee foraging at different reward rates. J Exp Biol 204(4):759–766

Moffett JO, Smith LS, Burkhardt CC, Shipman CW (1976) Nectar secretion in cotton flowers and its relation to honeybee. Am Bee J 116:32, 34, 36

Mommers J (1977) The concentration and composition of nectar in relation to honeybee visits to fruit trees. Apidologie 8:357–361

Morrant DS, Schumann R, Petit S (2009) Field methods for sampling and storing nectar from flowers with low nectar volumes. Ann Bot 103(3):533–542

Mullen RR (1971) Respiratory metabolism and body water turn over rates of two species of free living Kangaroo rats *Dipodamys merriami* and *D. microps.*. Comp Biochem Physiol A 39: 279–290

Nicolson SW (2007) Nectar consumers. In: Nicolson SW, Nepi M, Pacini E (eds) Nectaries and nectar. Springer, Dordrecht, pp 293–346

Nunez JA (1977) Nectar flow by melliferous flora and gathering flow by *Apis mellifera ligustica*. J Insect Physiol 23:265–276

Page RE Jr, Erber J, Fondrk MK (1998) The effect of genotype on response thresholds to sucrose and foraging behavior of honey bees (*Apis mellifera* L.). J Comp Physiol Sens Neural Behav Physiol 182(4):489–500

Pearson OP (1960) Torpidity in birds. Bull Mus Com Zool Harv Univ 24:93–103

Pederson MW, Bohart CE (1953) Factors responsible for the attractiveness of various clones of alfalfa to pollen collecting bumblebees. Agron J 45:548–551

Pelmenev VK, Korshenevskaya NI, Kharitonova NF (1984) Flowering, nectar secretion and significance as a fodder crop of *Rhanonticum carthamoides* introduced in the Leningrad oblash (USSR). Rastitelinye Resursv 17:62–68

Percival MS (1961) Types of nectars in angiosperms. New Phytol 60:236–281

Percival MS (1965) Floral biology. Pergamon Press, New York

Pereboom JJM, Biesmeijer JC (2003) Thermal constraints for stingless bee foragers: the importance of body size and coloration. Oecologia 137(1):42–50

Pernal SF, Currie RW (1998) Nectar quality in open-pollinated, pol CMS hybrid, and dominant SI hybrid oilseed summer rape. Can J Plant Sci 78(1):79–89

Pesti J (1976) Daily fluctuations in the sugar content of nectar and periodicity of secretion of nectar in the composition. Acta Agron Acad Sci Hungarica 25:5–17

Raw GR (1953) The effect on nectar secretion of removing nectar from flowers. Bee World 34: 23–25

Real LA (1981) Nectar availability and bee foraging in flowers of *Ipomoea* and *Aniseia* (Convolvulaceae). Ecology 51:1061–1067

Real LA (ed) (1983) Pollination biology. Academic, London

Riessberger U, Crailsheim K (1997) Short-term effect of different weather conditions upon the behaviour of forager and nurse honey bees (*Apis mellifera carnica* Pollmann). Apidologie 28(6):411–426

Rowley FA (1976) The sugars of some common Philippines nectars. J Apic Res 15:19–21

Sharma PL (1958) Sugar concentration of nectar of some Punjab honey plants. Indian Bee J 20(7): 86–91

Shaw RW (1953) The sugar concentration of nectar of some New England honey plants. Glean Bee Cult 81:88–89

Sihag RC (1982) Effect of competition with *Parkinsonia aculeata* L on pollination and seed production in Medicago sativa L. Indian Bee J 44:89–90

Sihag RC (1983) Life cycle pattern, seasonal mortality, problem of parasitization and sex ratio pattern in alfalfa pollinating Megachilid bees. Z Ang Entomol 96:191–203

Sihag RC (1984) Role of temperature in the *Evolution* of bee- plant mutualism. Indian Bee J 46: 28–32

Sihag RC (1988) Characterization of the pollinators of cruciferous and leguminous crops of subtropical Hisar (India). Bee World 69(4):153–158

Sihag RC, Abrol DP (1986) Correlation and path-coefficient analysis of environmental factors influencing flight activity of *Apis florea* F. J Apic Res 25:202–208

Sihag RC, Kapil RP (1983) Foraging strategies of honeybees as determined by quality and quantity of nectar. In: Proceedings of the 5th international symposium on pollination, Versailles, 1983, pp 51–59

Silva EM, Dean BB (2000) Effect of nectar composition and nectar concentration on honey bee (Hymenoptera: Apidae) visitations to hybrid onion flowers. J Econ Entomol 93(4):1216–1221

Simidchiev (1977) Pollen and nectar production of sunflower (*Helianthus annuus* L.) In: Honey plants basis of apiculture: international symposium on melliferous flora, Budapest, Bucharest, Romania, 1977; Apimondia Publishing House, pp 125–135

Simpson J (1964) Dilution by honeybees of solid and liquid food containing sugar. J Apic Res 3: 37–40

Sotavalta O (1954) On the fuel consumption of honeybees (*Apis mellifera* L.) in flight experiments. Ann Zool Soc Fenn Vanamo 16:1–27

Southwick EE, Southwick AK (1986) Nectar characteristic and phenology of spring bee plants in Northwestern New York. Agri Ecosyst Environ 16:55–62

Southwick EE, Loper GM, Sadwick SE (1981) Nectar production, composition, energetics and pollinator attractiveness in spring flowers of western New York. Am J Bot 68(7):994–1002

Stiles FG (1975) Ecology, flowering and humming bird pollination in some Costa Rican *Heliconia species*. Ecology 56:285–301

Strickler K (1979) Specialization and foraging efficiency of solitary bees. Ecology 60:998–1009

Teuber LR, Barnes DK (1979) Environmental and genetic influence on alfalfa nectar. Crop Sci 19:874–879

Teuber LR, Barnes DK (1978). Breeding alfalfa for increased nectar production. In: Proceedings of the IVth international symposium on pollination, Maryland Agricultural and Experimental Station Special Miscellaneous, Publication 1, pp 109–116

Tucker VA (1968) Respiratory exchange and evaporative water loss in the flying Budgerigar. J Exp Biol 48:67–87

Utter JM (1973) Daily energy expenditure of purple Martins (*Progne subis*) during the breeding season, estimates using D2O18 and time budget methods. Ecology 54:597–604

Van Ripper W (1960) Does a hummingbird find nectar through its sense of smell? Sci Am 202:157–160

von Frisch K (1950) Bees. Their vision, chemical senses and language. Cornell University Press, Ithaca

Waller GD (1972) Evaluating responses of honeybees to sugar solutions using an artificial flower feeder. Ann Ent Soc Am 65:857–862

Weis-Fogh T (1972) Energetics of hovering flight in hummingbird and *Drosophila*. J Exp Biol 56:79–104

Wilms W, Wiechers B (1997) Floral resource partitioning between native Melipona bees and the introduced Africanized honey bee in the Brazilian Atlantic rain forest. Apidologie 28(6): 339–355

Wolf LD (1975) Energy intake and expenditure in a nectar feeding sunbird. Ecology 56:92–102

Wolf LL, Hainsworth FR (1971) Time and energy budgets of territorial humming birds. Ecology 52:980–988

Wolf LL, Hainsworth FR, Stiles FG (1972) Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. Science 176:1351–1352

Wolf LL, Hainsworth FR, Gill FB (1975) Foraging efficiencies and time budgets in nectar feeding birds. Ecology 56:117–128

Wyke GR (1952a) An investigation of sugars present in the nectar of flowers of various species. New Phytol 51:210–215

Wyke GR (1952b) The preferences of honeybees for solutions of various sugars which occur in nectar. J Exp Biol 29:511–528

Wyke GR (1953) The sugar content of nectars. Biochem J 53:294–296

Chapter 15
Climate Change and Pollinators

Abstract This chapter describes how the climate change is potentially the most severe threat to pollinator biodiversity. Mounting evidence demonstrates that there have already been biotic responses to the relatively small climate changes that have occurred this century. Pollinators such as birds, bees, butterflies, moths, flies, wasps, beetles bats and even mosquitoes are essential for food production because they transfer pollen between seed plants-impacting 35% of the world's crops. Along with providing an essential service to human populations, pollinators also have a key role in maintaining other ecosystem services including ensuring biodiversity and helping Nature to adjust to external threats such as climate change. The "pollination crisis" that is evident in declines of honeybees and native bees worldwide is due to disruption of critical balance between the two mutually interacting organisms. Anthropogenic climate change is widely expected to drive species extinct by hampering individual survival and reproduction, by reducing the amount and accessibility of suitable habitat, or by eliminating other organisms that are essential to the species in question. The potential disruption of a ubiquitous mutualistic interaction of terrestrial habitats, that between plants and their animal pollinators, via climate change is at risk.

15.1 Introduction

Pollination of flowers is an essential step in the sexual reproduction of angiosperms. Most angiosperm species rely on insects or other animals, rather than wind, for transfer of pollen among individual plants. The pollinators in turn benefit by obtaining floral resources such as nectar or pollen. Pollination is not only mutually beneficial to the interacting plants and animals, but also serves humanity directly through the yield of many crops, and indirectly by contributing to the healthy functioning of unmanaged terrestrial ecosystems (Costanza et al. 1997; Nabhan and Buchmann 1997; Klein et al. 2007; Abrol 2007, 2008). Unfortunately, plant and pollinator species are increasingly at risk of local and global extinction from human

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activities, including habitat loss, altered land use, introduction of alien species and climate change (Kearns et al. 1998; Biesmeijer et al. 2006). Furthermore, some anthropogenic changes directly threaten pollination interactions themselves. The most obvious example is climate change, which may disrupt the overlap in seasonal timing (i.e. phenology) of flower production and of pollinator flight activity, thus altering the opportunity for interaction between the plants and animals (Harrison 2000; Wall et al. 2003).

The major aspect of climate change, increase in mean global temperature, is associated with an average advancement in the phenology of life history events, including migration and reproduction, in many species. Plants and their pollinators appear to follow this pattern. Over the past century, global warming has advanced the first flowering date of plants, and the seasonal flight activity of some pollinating insects, by c. 4 days/°C on average in temperate zones. However, the responses of individual species vary around these averages, so that while most phenologies have been advanced, the degree of advancement has varied, and some phenologies have remained essentially unchanged or have even been retarded.

Anthropogenic changes in habitats and climates have resulted in substantial reductions in biodiversity and evidence has been accumulating that insect biodiversity is at risk as well. Of particular concern is the pollinators and the plants that are linked to one another within communities show coincident declines. Many agricultural crops and natural plant populations are dependent on pollination and often on the services provided by wild, unmanaged, pollinator communities. Despite widespread concern about declines in pollination services, little is known about the patterns of change in most pollinator assemblages. Depending on the assemblage and location, pollinator declines were most frequent in habitat and flower specialists, in univoltine species, and/or in non migrants. In conjunction with this evidence, outcrossing plant species that are reliant on the declining pollinators have themselves declined relative to other plant species.

Approximately one-third of the global food supply relies on insect pollination of which bees, especially domesticated Western honey bees, are largely responsible for. If we think the global food supply is in trouble now, imagine what the world would be like if bees ceased to exist. Without bees to pollinate flowers and crops – the honey bee pollinates more than 90 commercial crops without which over half of the world's population would starve to death.

No other group of insects are of more benefit to humans than bees. Most of the crops that require pollination to set seeds and fruits, to produce meat and dairy products rely on bees for pollination of clover and Lucerne (Abrol 1988, 1991, 1993; Free 1993). Crops relying on bee pollination include apple, citrus, tomato, melon, strawberry, apricot, peach, cherry, mango, grape, olive, carrot, potato, onion, pumpkin, bean, cucumber, sunflower, various nuts, a range of herbs, cotton, alfalfa and lavender. The worldwide annual economic value of the pollination service provided by insect pollinators, has been estimated to be €153 billion Euros in 2005 for the main crops that feed the world. This figure amounted to 9.5% of the total value of the world agricultural food production. The study also determined that pollinator disappearance would translate into a consumer surplus loss estimated between €190 to €310 billion (Helmholtz Centre for Environmental Research 2008). The results of this study on the economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Among biodiversity concerns, the decline of pollinators has become a major issue, but its impact remains an open question. Even crops that do not require pollination for harvesting, such as those producing fibre or timber, still require pollination to produce further generations, and crops such as cotton that do not require pollination to produce seeds, provide greater yields when pollinators are available (Allen-Wardell et al. 1998). The European honeybee (*Apis mellifera*) dominates crop pollination worldwide, but local native bee species also play their part.

15.2 Pollinators an Essential Component for Ecosystem Functioning

Crop-associated biodiversity (CAB) refers to biodiversity that supports the functioning of ecosystem services necessary for agriculture, as well as contributing to the maintenance of ecosystem health and resilience. CAB is an intrinsic and important part of agricultural ecosystems, and includes components such as pollinators. Pollinators contribute to the maintenance of biodiversity, and ensure the survival of plant species including plants that provide food security to innumerable rural households. Pollination is an essential ecosystem service that enables plant reproduction and food production for humans and animals (fruits and seeds also impacting on the quality and yield) that depend, to a large extent, on the symbiosis between species, i.e., the pollinated and the pollinator. The reduction and/or loss of either will affect the survival of both.

Pollinator diversity is directly dependent on plant diversity and vice-versa – no other natural phenomenon illustrates more vividly the principle that conservation measures must be directed at ecological processes, and not just individual species. Indeed, pollination, a fundamental step for plant reproduction, is an ecological service that cannot be taken for granted. Plants are the primary producers in terrestrial ecosystems and direct providers of many ecosystem services such as carbon sequestration, prevention of soil erosion, nitrogen fixation, maintenance of water tables, greenhouse gas absorption, and food and habitat providers for most other terrestrial and many aquatic life forms. Pollinators, through facilitating plant reproduction, thus play a crucial role in the maintenance of ecosystem services. Pollination requires pollinating agents which themselves require resources for nesting, feeding and reproduction in the form of vegetation, prey, and certain habitat conditions, as well as the application of pollinator-friendly land-use management practices to ensuring their survival.

15.2.1 The Pollinators

Over 75% of the major world crops and 80% of all flowering plant species rely on animal pollinators (Nabhan and Buchmann 1997). Of the 100 or so animal-pollinated crops which make up most of the world's food supply, 15% are pollinated by domestic bees, while at least 80% are pollinated by wild bee species and other wildlife (Ingram et al. 1996). Diversity among species, including agricultural crops, depends on animal pollination. Thus, pollinators are essential for diet diversity, biodiversity, and the maintenance of natural resources.

15.2.2 Diversity of Pollinators

The principle pollinators are bees. The diversity of pollinators and pollination systems is striking. Most of the 25,000–30,000 species of bees (Hymenoptera: Apidae) are effective pollinators, and together with moths, flies, wasps, beetles and butterflies, make up the majority of pollinating species. Vertebrate pollinators include bats, non-flying mammals (several species of monkey, rodents, lemur and tree squirrels etc.) and birds (hummingbirds, sunbirds, honeycreepers and some parrot species). Current understanding of the pollination process shows that, while interesting specialized relationships exist between plants and their pollinators, healthy pollination services are best ensured by an abundance and diversity of pollinators. Approximately 73% of the world's cultivated crops, such as cashews, squash, mangoes, cocoa, cranberries and blueberries, are pollinated by some variety of bees, 19% by flies, 6.5% by bats, 5% by wasps, 5% by beetles, 4% by birds, and 4% by butterflies and moths. Of the 100 principal crops that make up most of the worlds food supply, only 15% are pollinated by domestic bees (mostly honey bees, bumble bees and alfalfa leafcutter bees), while at least 80% are pollinated by wild bees and other wildlife. The 25,000 different species of bees differ significantly in size and habit requirements, and diverge accordingly in the plants they visit and pollinate. Though bees form the most important group of pollinators, other animals, such as bats, birds, butterflies, moths, flies and beetles also play key roles in pollination. Both the diversity of wild plants and the variability of food crops depend on this diversity. Pollination is a complicated process with some pollinators being generalists and others being species-specific. Likewise, many different pollinators visit some plants, while other plants have species-specific pollinator requirements. Given this complexity, managing pollination as an ecosystem service requires a comprehensive understanding of the pollination process and the application of that knowledge in the design and implementation of intricate management practices. In most cases, there is limited knowledge about the exact relations between individual plant species and their pollinators. "Pollinators also play a vital role in sustaining wildlife and ecosystem health, both as part of the complex food chain and in the reproduction of plants. Evidently, measures are needed to ensure that our native and managed pollinator population is maintained and protected."

Agricultural biodiversity is often understood as crop genetic resources, yet agroecosystems hold a wide diversity of other organisms that contribute toward their productivity and sustainability. Amongst these are pollinators, being animals that carry pollen from the male to the female parts of plants and thus ensure that fruit or seeds are formed. Over the past decade, the international community has increasingly recognised the importance of pollinators as an element of agricultural diversity supporting human livelihoods. Yet mounting evidence points to a potentially serious decline in populations of pollinators. Maintaining and increasing yields in horticultural crops, seeds and pastures through better conservation and management of pollinators is critically important to health, nutrition, food security and better farm incomes for poor farmers.

15.2.3 Pollination and Ecosystem Functions

In *Nature*, the vast majority of flowering plant species only produce seeds if animal pollinators move pollen from the anthers to the stigmas of their flowers. Without this service, many interconnected species and processes functioning within an ecosystem would collapse. With well over 200,000 flowering plant species dependent on pollination from over 100,000 other species, pollination is critical to the overall maintenance of biodiversity. Approximately 80% of all flowering plant species are specialized for pollination by animals, mostly insects. The dependence of ecosystems on animal pollinators is even stronger in the tropics than the global average: less than 3% of all tropical lowland plants rely on wind for pollination. Arid and mountain ecosystems often have highly diverse pollinator communities as well, with finely tuned adaptations to ensure that pollination is effective even when climatic conditions are erratic. Not only are tropical areas of the world more dependent on animal pollinators, but they may also be more susceptible to pollinator loss.

15.2.4 Contribution of Pollination to Food Security

In agro-ecosystems, pollinators are essential for orchard, horticultural and forage production, as well as the production of seed for many root and fibre crops. Pollinators such as bees, birds and bats affect 35% of the world's crop production, increasing outputs of 87 of the leading food crops worldwide, plus many plant-derived medicines in our pharmacies. Food security, food diversity, human nutrition and food prices all rely strongly on animal pollinators. This is particularly the case of horticultural crops. Diversification into horticultural crops is becoming an avenue to poverty alleviation amongst many farmers around the world. The trade in horticultural crops accounts for over 20% of developing countries' agricultural exports, more than double that of cereal crops. Unlike the historical increase in cereal production, the expansion of production in fruits and vegetables has come primarily from increases in the area cropped, not from yield increases. The consequences of pollinator declines are likely to impact the production and costs of vitamin-rich crops like fruits and vegetables, leading to increasingly unbalanced diets and health problems. Thus, maintaining and increasing yields in horticultural crops under

Table 15.1 Population decline of honeybees in world scenario

Country	% age decline	Duration
Germany	57	Last 15 year
U.K	61	Last 10 year
U.S.A.	>50	Last 20 year
Poland	>35	Last 15 year
India	>40	Last 25 year
Brazil	>53	Last 15 year
Netherland	58–65	Last 25 year
China	>50	Last 20 year

Compiled from different sources

Table 15.2 Pollinators decline in U.S.A

Pollinators	% Loss in population
Honey bees	>50
Bumble bees	36
Solitary bees	30
Bats	14
Humming birds	16
Monarch butterflies	28

Compiled from different sources

agricultural development is critically important to health, nutrition, food security and better farm incomes for poor farmers.

The efforts of insects are largely forgotten in today's agri-business world, but the bottom line shows just how important their contribution is. The world honey production is worth around £380,000,000, but the value of insect pollinated agriculture is worth somewhere in the region of £800,000,000,000, one must remember that this includes the contribution of all insect pollinators, not just honey bees.

15.2.5 Decline of Pollinators

Pollinators are products of millions of years of *Evolution* and eroding at fast rate from the globe. During the last few years honey bees have been dying across the globe in unprecedented numbers and, no one seemed to be able to prove beyond a reasonable doubt what the cause may have been (Tables 15.1 and 15.2). Bees fly off to collect pollen, but never return – or simply weaken and die in the hives. Beyond the larger effects on the food chain, the economic implications of these deaths are immediate because honey bees are integral to the pollination of tens of millions of dollars of cash crops in the world (Gallai et al. 2008).

Despite much of the world's agriculture relying on pollination by European Honeybees, their numbers have declined worldwide. In the USA, Mexico and Canada, both feral and managed honeybees declined by 25% between 1990 and 1998 (Allen-Wardell et al. 1998). In Europe, particularly France and Germany, the same species declined by about 10% between 1992 and 2002.Similar declines have been reported from Indian subcontinent (Abrol 2008). Among wild pollinators, patterns of population change are clearest for large, warm-blooded species such as Bats. Declines in bat populations have been so dramatic that two of the three U.S. pollen-feeding species are now listed as endangered under the terms of the U.S. Endangered Species Act. It is generally believed that bat populations have declined worldwide in recent decades (Gillette and Kimbrough 1970). Bats seem to have evolved as moderately long-lived (e.g., 5–30 years), intelligent creatures that are acutely in synchrony with global climates. Many tropical species are dependent on nectar, pollen, and flowers and fruits of plants and are known to "track" the development of the plant resources upon which they depend. They are important pollinators of plants, especially in tropical areas and on island ecosystems in the Pacific. Disturbances to climate that interrupt or alter the phenology of plants, or greatly alter plant species occurrence or distribution, can be expected to affect bats. Similarly, other species of bats, especially in temperate zones, are insectivorous and collectively consume large quantities of insects. Just as pollinating activities of bats are important to plant ecology, the insectivorous food habits of bats play an important role in maintaining a balance among insect populations. Changes in worldwide insect population occurrence or distribution can be expected to affect numbers and species diversity of bats. Bats restricted to cooler climates, either latitudinally or altitudinally, may be jeopardized by global warming and if unable to adapt or persist will become extinct. Bats already adapted to warm climates may increase both in numbers and geographic ranges. To the extent that global warming alters the zonation of plants and animals (especially insects) around the world, we can expect bats to respond to such forces.

Among the cold-blooded pollinators, aesthetically pleasing butterflies, e.g., constitute the majority of listed endangered insects. Because butterflies have long attracted the attention of both the scientific and lay communities, they have been the focus of the majority of long-term monitoring efforts in the U.S. that have documented distribution changes, declines, and local extinctions. In one California study, a 29-year census of butterfly species showed nearly a 40% decline in species diversity. Moths, which are generally nocturnal and drab, outnumber butterflies in the U.S. by a substantial margin but are outnumbered on the endangered species list by their more colorful relatives. Moths are important pollinators in a variety of plant communities; within southwestern U.S. deserts, hawk moths are principal pollinators of many plants, including night-blooming cacti, desert lilies, evening primroses, and wild tobacco.

Many other pollinators such as digger bees, sweat bees, alkali bees, squash bees, leafcutter bees, carpenter bees, mason bees, and shaggy fuzzy foot bees could well be in decline, but data providing unambiguous documentation of trends are simply not available. Alkali bees can pollinate onions, mint, and celery, carpenter bees pollinate canola and pepper, leafcutter bees contribute to pollinating the alfalfa that provides forage for dairy and beef cattle, mason bees can pollinate apples and cherries, squash bees can pollinate pumpkins, and shaggy fuzzfoot bees can pollinate apples and blueberries. Their contribution to pollination of native plant communities is likely indispensable but for most species no evidence of population decline exists because their abundance has never been measured over time.

Among native bees, bumble bees are exceptional in that there are some indications of significant declines. The native long-tongued bumble bees pollinate a diversity of wild plants, particularly those with deep, tubular flowers, and serve as complementary pollinators for crops such as watermelon, cucumber, berries and sunflowers. Global climate change also poses a real threat to bumble bees; anecdotal evidence has suggested that some of the bumble bee species adapted to cool temperatures are in decline, whereas warmer adapted species are expanding their ranges. Baseline data and long term monitoring are needed to better understand the true impact of climate change on bumble bees. Similarly, in Europe extensive studies show unambiguous patterns of decline in species richness and distribution of many bees, particularly long-tongued species. Flies are especially important pollinators in alpine habitats. Fly pollination is agriculturally important as well; they are the sole pollinators of cacao, the source of all things chocolate, and also contribute to the pollination of several minor crops, including onions. Although data are insufficient to document population declines in flower-visiting flies but there is a clear indication of their decline.

In Britain more than two-thirds of the nation's larger moth species have declined over the past four decades. "Moths represent the hidden wealth of wildlife on all doorsteps. Without moths, plants would not be pollinated and garden birds would go hungry." it was suggested that the main suspects were habitat destruction, pesticides, pollution and climate change.

15.2.6 The Impact of Declining Pollinator Populations on Agriculture

It is recognized that agricultural production, agro-ecosystem diversity and biodiversity are threatened by declining populations of pollinators. Many pollinator population densities are being reduced below levels at which they can sustain pollination services in agroecosystems, natural ecosystems, and for the maintenance of wild plant reproductive capacity. Ecological dangers of pollinator decline include the loss of essential ecosystem services (particularly agro-ecosystem services) and functions that pollinators provide. Ecosystem services in their turn have their own value not only biophysical, but also economic. For example, for the entire biosphere, the value of ecological services (most of which outside the market) was estimated to be in the range of US$16–54 trillion per year, with an average of US$33 trillion per year (Costanza et al. 1987). The value of the annual global contribution of pollinators to the major pollinator-dependant crops is estimated to exceed US$ 54 billion. In the Canadian prairies, the value of pollinators to the alfalfa seed industry has been placed at about CAD six million per year (Kevan and Phillips 2001).

Examples from Asia (e.g. northern Pakistan, parts of China) show linkages between declining natural insect populations and decreasing crop yields – as a result, people have begun to manage the crop-associated biodiversity (i.e. pollinators) in order to maintain their crop yields and quality. For example, farmers in Himachal Pradesh (in northwestern India) are using honeybees to pollinate their apples (Partap and Partrap 2002). Due to declining pollinator populations and changing cultivation practices, an increasing number of farmers around the world are now paying for pollination services and are importing and raising non-native pollinators to ensure crop production. In many developing countries, however, external pollination services are not available and rural communities have to live with reduced quantity, quality, and diversity of foods. In fruit orchards in Western China, the decline of useful insect populations has led farmers to pollinating by hand, acting as human bees (Partap and Partap 2002). Despite a general recognition of the impact of declining pollinator populations on ecosystem functioning, and despite the examples of the ecological and economic impacts as well as examples of where this is occurring, bottlenecks and constraints hinder the conservation and management of pollinators in sustainable agriculture.

15.2.7 Consequences of Decline

To estimate the economic and ecological value of wild pollinators and predict the consequences of their losses in natural communities is considerably more challenging. Such calculations are complicated both by the enormous number of species involved and the paucity of information available for most of those species. Although many species may visit a particular flower, only a small proportion of visitors may have the capacity to pick up and deliver pollen to the appropriate stigma. In some studies, fewer than one-quarter of insect species visiting a particular plant proved to be competent pollinators.

As to the effects of losing the pollination services of individual species, most ecosystems depend on pollinators for food web stability. Few plant species rely on a single pollinator and many are visited by different suites of pollinator species over the course of a season. When entire suites decline, as has been the case for long-tongued bees in Europe, significant losses within the wild flora dependent upon these suites are likely. Unfortunately, missing markets make it difficult to estimate the economic value of changes to pollination services in natural communities. The economic cost of complete loss of all pollination services cannot be estimated because ecological and human adjustments to such extreme change would be radical.

One indicator of the ecological consequences of pollinator decline is pollen limitation of seed set – the failure of plants to produce the maximum number of seeds due to inadequate supplies of pollen. Pollen limitation is common in wild plants; surveys demonstrate that it is more common in plants with fewer pollinator species. In the absence of adequate pollinator populations, some plant populations, particularly those that are small, may become more vulnerable to extinction because of the elevated risks incurred by small population size, including genetic erosion, decreased reproductive success, and greater susceptibility to random catastrophic events.

Perhaps the principal reason that estimating the ecological impact of pollinator decline is difficult is that in many natural communities pollinators are keystone species. Just as a keystone maintains the integrity of a stone arch, a keystone species maintains the integrity of an ecological community; the removal of a keystone in either case can result in a collapse of the entire structure. Identifying a keystone in a stone arch follows predictable architectural principles, but identifying a keystone species requires a vast amount of ecological information about many interacting species. Figs, for example, are considered keystone species in tropical communities around the world; in the New World tropics the fruits provide food for a broad diversity of birds, including toucans, hornbills, parrots, and pigeons, as well as bats and monkeys and even fish in nearby rivers, the foliage supports an array of insects, including larvae of butterflies, and the tree itself provides habitat for a diversity of invertebrates, rodents, reptiles and amphibians. Fig trees, however, are entirely dependent on a group of tiny wasps that are the only known pollinators capable of negotiating the complex tangle of reproductive organs inside the fig flower; throughout the world, most fig species depend on one or sometimes two specific species of fig wasp. The entire food web, with its conspicuous, colorful, and charismatic birds, bats, and primates, thus rests on the tiny shoulders (or prothorax) of an insect averaging less than 0.1 in. in length. A cascade of ecological consequences may result from the loss or decline of a particular plant in a community, with the loss of roots, stems, leaves, flowers, fruits, and seeds that are resources for herbivores, which in turn are resources for parasites and predators.

In estimating the ecological consequences of pollinator decline, it is important to keep in mind that pollinator species play multiple roles in food webs. Most pollinating species are insects that undergo complete metamorphosis, with immature stages engaging in lifestyles bearing little or no resemblance to those exhibited by pollinating adults. Grubs, maggots and caterpillars live in different worlds, consuming entirely different foods, than do parental bees, flies, and butterflies. Moreover, pollinating adults have resource needs unrelated to the flowers they pollinate. Many require specific building materials for nests, including clay, sand, mud, bark, or plant fibers. Bumble bees often build nests in abandoned mouse burrows and some mason bees nest in beetle burrows or even vacant snail shells.

15.2.8 Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions

The status of pollinators is a matter of national interest because the lives of over 200,000 plant species worldwide depend on pollination, the process by which pollen grains, containing male sex cells, are transferred to stigmas, or female floral parts, to bring about fertilization, a necessary step in producing seeds. Pollen delivery presents a challenge to flowering plants, most of which spend their lives rooted to the ground, and approximately three-fourths of them rely on mobile animal partners – pollinators – to achieve this end. Beyond its other attractions, sexual reproduction provides opportunities for producing genetic variability, which allows organisms to adjust to changing environmental conditions. As ecological interactions go, animal-mediated pollination tends to be rapid, intermittent, and easily overlooked; that animals can serve as pollinators was not even widely recognized by the scientific community until the nineteenth century.

15.2.9 Causes of Decline

Threats to pollinators and the services they provide are perceived to be increasing around the world and are largely man-made in origin (Kearns et al. 1998; Cane 2001). Declines in pollinators have been reported in several regions of the world (Williams 1986; Rasmont 1988; Westrich 1989; Corbet et al. 1991; Osborne et al. 1991; Day 1991; Falk 1991; O'Toole 1994; Banaszak 1995; Williams 1996; Pekkarinen et al. 1987; Luig and Maavara 1998; Pekkarinen 1998; Söderman and Leinonen 2003; Gärdenfors 2000; Rassi et al. 2001) and the main drivers of pollinator loss can be grouped as follows:

1. Changing land use practices (habitat loss through mechanical destruction, fragmentation, fire, overgrazing, and recreation etc.)
2. Agrochemicals and other pollutants herbicides (loss of food plants)
3. Parasites and Diseases
4. Competition between species and individuals induced by man
5. Climate change

Climate change could be a major factor in weakening the bees and has affected the pollination of crops in many agricultural areas. It could be the result of various factors combined, but historical records show that there are fluctuations with beehives every 7 or 8 years that are affected by weather conditions and crop yields. Climate change has the potential to affect the distribution of pollinators and the plants they pollinate, as well as the timing of flowering and migration. For migratory pollinators, such as bats, hummingbirds, and the monarch butterfly, the identification and protection of nectar corridors is important (Allen-Wardell et al. 1998). If nectar is unavailable anywhere along their migratory route at the time of migration, it could result in the death of part of the population (Buchmann and Nabhan 1996).

Climate change is one of the biggest challenges we will face in the future. The effects of climate change can already be observed and are projected to become more pronounced, in terms of impacts on natural ecosystems, biodiversity, human health and water resources. Climate change will have profound effects on the way we go about our daily lives. The latest Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2007) projects that global average temperatures in 2100 will be between 1.8°C and 4.0°C higher than the 1980–2000 average. Sea levels are projected to rise 0.18/0.59 m by 2100, based on observed rates of ice flow from Greenland and Antarctica. More frequent and intense extreme weather events, including drought and flooding, are also expected.

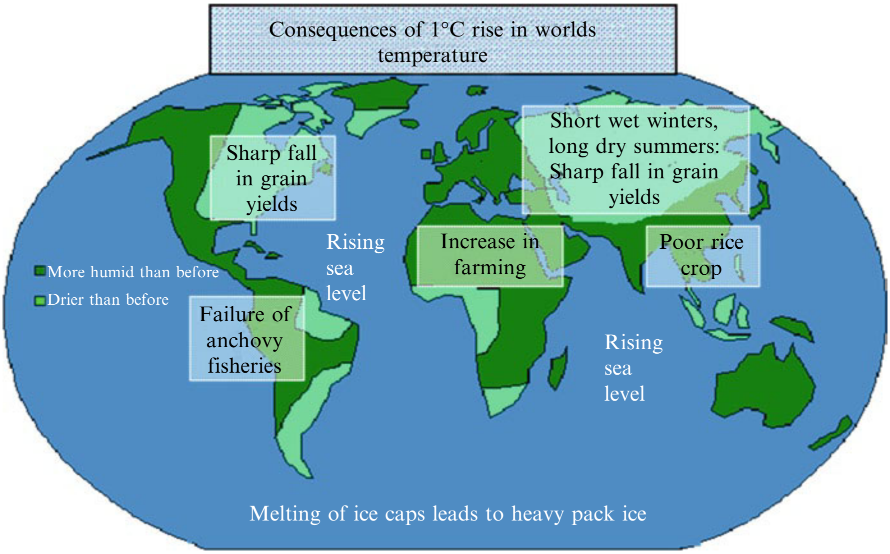

Fig. 15.1 Impact of climate change on world environment (Source: Adapted from University of Southampton 2000)

The climate is warming in most parts of the world. The global average temperature has increased by about 0.7°C and the European average by about 0.95°C in the last 100 years. It is estimated that temperature will increase by 1.4–5.8°C globally and 2.0–6.3°C in Europe by 2100. Precipitation patterns are more varied. In the last 100 years northern Europe has become 10–40% wetter and southern Europe up to 20% drier. These changes are projected to continue (IPCC 2007). The Intergovernmental Panel on Climate Change (IPCC 2007) states that 'the risk of water shortage is projected to increase particularly in southern Europe…. Climate change is likely to widen water resource differences between northern and southern Europe.' Environment (Fig. 15.1).

Biodiversity is inextricably linked to climate. Changes in climate affect biodiversity and changes to natural ecosystems affect climate. Climate change may lead to a sharp increase in rates of extinction. Thomas et al. (2004) studied five regions of the world, and predicted that if the present rate of climate change continues, 24% of species in these regions will be on their way to extinction by 2050. This study indicated that for many species, climate change poses a greater threat to their survival than the destruction of their natural habitat. Evidence directly linking climate change and species extinction is difficult to procure, but at least one species: the golden toad of Costa Rica, may have become extinct due to climate change (Pounds et al. 1999). Global extinction rate of species are accelerating at an alarming rate (Table 15.3). Wilson (1988) estimated that 0.2–0.3% of all species are lost every year. Range of 5–10% of the tropical forest species may become extinct within the next 30 years (UNEP 1993). It is estimated that 60,000 species will be eliminated in the foreseeable future and 50,000 species will be at risk of extinction in the next half of the century (Willis et al. 2008).

Table 15.3 Estimate loss of species on earth (Wilson 1988)

SN	Species loss	Global loss per decade (%)
1	1 million species (1975–2000)	4
2	15–20% of species (1980–2000)	8
3	25% of species (1985–2015)	9

15.3 Climate Change and Pollinators

As climate changes, the habitats suitable for supporting pollinators may change with some areas being lost and others being newly created. When a habitat disappears, or the pollinator is unable to move to a new habitat, then local extinction can occur (Travis 2003; Hill et al. 2002). Climate change may also disrupt the synchrony between the flowering period of plants and the activity season of pollinators (Price and Waser 1998; Wall et al. 2003).

15.3.1 The Consequences of Pollinator Population Declines

One consequence of pollinator decline may be an increased vulnerability of some plant species to extinction, although consequences are difficult to define in nonagricultural systems. In the event of declining pollinator populations, some plant populations that are dependent on affected pollinators for reproduction could become more vulnerable to an extinction vortex – the interacting factors that serve to progressively reduce small populations – because of the demographic and genetic consequences of small population size. The effects of pollinator decline on rare plant species or on those with small populations should be given special attention.

Bee colonies are very much influenced by frequent extreme temperature and rainfall conditions (drought period, unusually intensive precipitations, especially during August) because of impact on honey pastures. The honey pastures decreasing will result in over wintering decreasing and finally end of bee colony. Decreasing of bee population in environment resulted in less effective pollination of native plant species and also decreasing of crop yields up to 30%, especially oleaginous plants. Climate changes have impact on native pollinators in agroecosystems, especially bumble bees and solitary bees and their decreasing is in close connection to plant species extinction (Luig and Maavara 1998; Stefanescu et al. 2003).

15.3.2 Climate Change and Butterfly Species Richness

Climate change may potentially be one of the most severe threats to pollinator biodiversity (Kerr 2001). Substantial distribution changes are predicted for groups such as butterflies (Cowley et al. 1999). Kerr (2001) reported that the human influence on climate is surprisingly pervasive. For example, continental declines in precipitation in industrialized regions can be attributed to an increase in atmospheric particulate matter that inhibits raindrop nucleation (Rosenfeld 2000). Storm timing and frequency are influenced by industrial aerosols on the Atlantic seaboard of North America (Balling and Cerveny 1998). Most significantly, the global climate has been changing as a result of increasing greenhouse gas emissions since the beginning of the industrial r*evolution*. The potential negative consequences of shifts in temperature, precipitation, and seasonality are sweeping and might easily become catastrophic over the next several decades. Regional shifts in species distributions observed in Europe and North America offer strong circumstantial evidence that climate change is already affecting pollinator taxa. Recent evidence suggests that the northern distributional limits of many species in Europe have extended northward in conjunction with climate changes that took place during the 1900s (Parmesan 1996; Parmesan et al. 1999), a predictable result considering the climatic tolerances of these species (Kukal et al. 1991). However, the argument that climate change has already affected species ranges is considerably strengthened by complementary studies that demonstrate similar phenomena among birds (Thomas and Lennon 1999) and *Euphydryas editha*, a butterfly in the western USA (Parmesan 1996). Damage caused to biotic communities of non pollinator taxa by climate change has also been documented. For example, precipitous declines in high-altitude amphibian communities in a Costa Rican cloud-forest habitat would appear to coincide with recent climatic changes (Pounds et al. 1999).

There is some early evidence that butterfly diversity in Canada is responding to climate changes that have occurred during the last few decades. At least two species, the Gorgone checkerspot (*Chlosyne gorgone*) and the Delaware skipper (*Anatrytone logan*), recently established breeding populations near Ottawa, Ontario, well beyond the previous northern limits of their respective ranges. These butterflies are conspicuous, and their new localities are frequently surveyed by specialists, so there is little likelihood that these populations have been long established. Additional support for the circumstantial case that climatic changes have caused this range expansion northward is provided by the finding that a third species, the Tawny-edged skipper (*Polites themistocles*), from an area near Ottawa, now has a second generation during the longer warm periods in the region. These intriguing observations are consistent with other observations of range shifts from North America (Parmesan 1996), and with discoveries of extensive butterfly distribution shifts in Europe (Parmesan et al. 1999). Earlier studies of lepidopterans (Turner et al. 1987; Kerr et al. 1998) demonstrated that contemporary climate was important in determining spatial patterns of butterfly diversity in Canada, so there is reason to believe that further shifts in butterfly species distributions will occur because of the effects of climate change.

A few other studies document shifts in pollinator species ranges that can be attributed to anthropogenic climate change. Bryant et al. (1997) considered it likely that two nymphalid butterflies had shifted their ranges because of recent climate change, but most studies tend to focus on the anticipated biotic consequences of future changes (Sparks and Yates 1997). Few species or higher taxa, even in the UK where most taxa have been painstakingly documented, have been monitored over a long enough period or so intensively that observed range shifts can be attributed to recent climate changes. Changes in the distribution of a taxon are more often attributed to habitat loss, or perhaps to habitat fragmentation (Cane 2001). In most cases, this is probably the correct diagnosis (Swengel 1998a; Kerr et al. 2000). As climate change becomes increasingly obvious, it will more frequently be considered as a possible cause of shifts in the distribution of organisms (Pollard et al. 1996; Mikkola 1997; Tarrier and Leestmans 1997; Fleishman et al. 1998).

The direct effects of elevated atmospheric carbon dioxide concentrations on pollinators and their mutualistic plant hosts are also difficult to predict. Indirectly, elevated atmospheric CO_2 is expected to modify ratios of carbon and nitrogen in plant tissues (Bazzaz 1998; Bazzaz and Sombroek 1996), possibly leading to changes in patterns of herbivory by organisms such as butterfly larvae (Rusterholz and Erhardt 1998). How this might affect communities of pollinators is uncertain. Furthermore, increasing concentrations of CO_2 in the atmosphere will probably lead to changes in plant community structure, particularly in the proportions of C_3 and C_4 plants in a given habitat (Bazzaz 1998). It is too early to say whether these effects will influence the conservation status of particular pollinator species. However, stresses to ecosystems that are caused by climate change will act synergistically with other forms of human perturbation (Myers 1992), and the results of such synergisms cannot yet be predicted.

A thorough understanding of why species richness varies through space is useful when attempting to predict how it will respond to climate change or other perturbations (Kerr and Packer 1999). Thousands of studies have investigated the basis for spatial variation in species richness (Currie et al. 1999), but relatively few of these involve invertebrates (Kerr 1999), and an even smaller number focus on pollinator taxa (Kerr et al. 1998). The preponderance of empirical evidence suggests that regional variability in species richness is related to aspects of climatic energy (Wright 1983; Currie 1991; Wright et al. 1993), with additional influences of habitat heterogeneity (Kerr and Packer 1997; Fraser 1998). In general, climatic energy is able to explain 60–90% of the variability in species richness in cold and temperate areas, a finding of obvious importance in view of ongoing climatic change. Although it may be possible to predict the effects of climate change on the numbers of species in a region (Bazzaz 1998; Kerr and Packer 1998), it will be much harder to predict how individual species may respond; this will require detailed study of butterfly communities across geographical gradients (Swengel 1998a, b).

15.3.3 Climate Change Threatens Pollination Timing of Flowering

Global warming could disrupt the timing of pollination with serious negative impacts to both plants and pollinators. One of the most insidious impacts of global warming will be changes in the timing of flowering in high altitudes, potentially resulting in reduced reproductive success and possible extinctions (Inouye and Wielgolaski 2003; Wielgolaski and Inouye 2003). Inouye et al. (2003) reported that global warming could disrupt the timing of pollination in alpine environments, with serious negative impacts on both plants and pollinators. "High altitudes are one of the habitats where it seems that climate change is having dramatic effects. According to them, the timing of flowering has become earlier, particularly, the abundance of some flowers has changed, and the synchrony of plants and pollinators may be changing." Inouye et al. (2003) reported that flowering time for plants in the Rocky Mountains is determined by when the snow melts, which is likely to change in response to global warming. There is already some evidence that plants and pollinators are responding differently to climate change.

The impact of global warming on 'phenology' – the timing of climate-sensitive biological events – including flowering, insect emergence, and bird feeding behavior has been reported by several investigators (Inouye 2000; Inouye et al. 2000; Saavedra et al. 2003). They also reported predictions of how time-sensitive ecological relationships will change in response to global warming. As a result, animals exposed to earlier warm weather may exit hibernation earlier and birds responding to earlier spring weather in their wintering grounds may flock north to find several feet of snow on the ground, risking starvation. Already the difference in timing between seasonal events at low and high altitudes has negatively influenced migratory pollinators, such as hummingbirds, which hibernate at lower altitudes and latitudes (Inouye et al. 2000). If climate change disturbs the timing of flowering and the behaviour of pollinators such as butterflies, bumblebees, flies and even mosquitoes, then the intimate relationships between plants and pollinators that have co-evolved over thousands of years will be irrevocably altered (Inouye et al. 2003).

It is well documented that plant and animal phenology is changing in response to recent climate warming in the Palaearctic. However, during these last decades, insect phenology showed a steeper advance than plant phenology, suggesting an increase of decoupling of some plant-insect interactions, such as those between pollinators and flowers or herbivorous insects and their plant resources (Wielgolaski and Inouye 2003).

15.3.4 Phenology and Climate Change

The timing of phenological events such as flowering are often related to environmental variables such as temperature. Changing environments are therefore expected to lead to changes in life cycle events, and these have been recorded for many species of plants (Parmesan and Yohe 2003). These changes have the potential to lead to the asynchrony between species, or to change competition between plants. Flowering times in British plants for example have changed, leading to annual plants flowering earlier than perennials, and insect pollinated plants flowering earlier than wind pollinated plants; with potential ecological consequences (Fitter and Fitter 2002; Willis et al. 2008).

Climate change is affecting the timing and intensity of the seasons thereby affecting the phenology. Across the entire northern hemisphere, spring is arriving earlier at a pace of approximately 1.2 days per decade. Land surfaces are also retaining more heat during the summer, leading to persistent summer temperatures that linger into the fall. Thus, with regard to the temperatures that permit plants to grow, an earlier spring and a persisting summer means that the growing season is expanding (whether plants will receive enough rainfall to take advantage of these warmer temperatures is an unresolved question of great concern). Across Europe, for example, the growing season expanded 10.8 days during the period 1960–1999 (6 days toward an earlier spring, 4.8 days toward a persisting summer). While these might seem like small changes, the natural world is actually responding in observable, dramatic, predictable, and potentially problematic ways. Summarizing more than 29,000 observational data series that demonstrate significant changes in physical and biological systems, the IPCC reported in 2007 that more than 89% (25,810) of those changes are in the direction expected as a response to climate change. In the biosphere, these changes tend to fall into two categories: responses in space and in time.

15.3.5 Geographic Responses to Climate Change

On a spatial scale, many species of animals and plants have expanded their geographic ranges poleward in latitude (northward in the northern hemisphere; southward in the southern hemisphere) and upward in elevation over the last century, following shifting temperatures. As higher elevations experience more mild winters, for example, species from lower elevations may expand their range towards higher elevations because they can now tolerate the winters there. The same may be true across latitudes; species from lower latitudes (i.e., closer to the equator) may expand their range toward higher, or poleward, latitudes. These "range expansions" can be advantageous for species that can disperse easily, but they can threaten the existence of less mobile or more sensitive species.

Migration into new territory is often impossible, as habitat fragmentation due to human activities (such as the building of housing developments, golf courses, highways, or shopping malls) or the existence of natural barriers such as rivers or mountain ranges can prevent the movement (or dispersal) of seeds and fruits, and of young, pregnant or nursing animals.

15.3.6 Temporal Responses to Climate Change

On a temporal scale, living organisms respond to the expanding or shifting growing season by changing their phenological schedules. Thousands of biological records spanning both the globe and the twentieth century indicate a nearly ubiquitous shift in spring phenology toward earlier calendar dates. Organisms are tracking an earlier start to the growing season by emerging from dormancy earlier (mammals, insects), migrating earlier (birds, insects, mammals), developing new leaves and stems earlier (plants), and breeding earlier (mammals, insects, birds, plants). Not surprisingly, similar delays in autumn phenology are occurring due to a persisting summer – deciduous trees are shedding their leaves later than they used to, and birds and mammals are migrating later in the autumn than they used to. As you can imagine, the consequences of phenological shifts will depend on the level of biological organization that we investigate. For a long-lived *individual* tree, for example, leafing out several days earlier each spring may allow it to get a rapid head start in its annual growth, especially if neighboring trees remain leafless, which would allow its leaves to receive a great deal of sunlight. On the other hand, if it produces its leaves earlier than any of the other members of its population, it may be particularly vulnerable to leaf-eating insects (e.g., moth and butterfly larvae, leaf miners, and leaf-cutting ants) simply because it will be a rare and limited resource for them.

The effects of a phenological shift on a given *population* of a species will also depend on whether the other species on which it relies – for food, pollination, or seed dispersal – change with it. For example, if populations that benefit from each other respond differently to climate change (e.g., if a plant population flowers on average 5 days earlier but its pollinators haven't arrived), then one or both of them may exhibit population declines. On the other hand, if a population flowers early enough to "escape" one or more of its "natural enemies" (e.g., flower bud-eating beetle larvae), it may reap the benefits of high flower and fruit production.

At the community level, well, predictions are highly elusive. We've learned from radio-tracking and bird-banding efforts that birds are returning to spring and summer breeding grounds earlier and earlier, but the effects of these altered migration patterns on both the birds and the species with which they interact (as predators or as seed dispersers) are likely to be highly species- and community-specific. Nevertheless, there are several rules of thumb that probably apply.

First, the more specialized the relationship between species, the more vulnerable each of them are likely to be to the phenological effects of climate change. For example, plant species that are pollinated by only one species of pollinator are more vulnerable to losing these pollinator services than are species that are visited by a wide range of pollinator species. Similarly, insects that rely on a single plant species as their food source may experience severe population declines if their emergence times are mismatched with the growing or flowering season of their host plant.

Second, animals that habitually migrate between geographically distant biomes to complete distinct portions of their life cycles (e.g., growth and sexual maturation vs. breeding) are particularly vulnerable to the phenological effects of climate change simply because there are more inter-specific interactions that may be disrupted. Such species must continue to exhibit a phenological schedule that is viable given the co-occuring species and the climate in each of their "home" habitats. For example, species of birds that migrate over long distances must co-occur with their food sources (while avoiding their enemies) in the biome in which they grow and reach sexual maturity, and then, following migration to their breeding grounds, they must be in synchrony with the food sources that they feed to their newborns.

Migratory animals must meet these demands while also avoiding the natural enemies that destroy them.

These shifts in spatial and temporal range what scientists call the “fingerprint of climate change.” Phenological schedules are changing rapidly and at different rates for co-dependent species such as plants and pollinators. There is an increasing number of reports in recent years of population crashes in the wild due to such asynchronous responses to climate change among co-dependent species, but scientists are only beginning to learn how widespread they are and in how many different kinds of organisms they occur.

Phenological cues are critical in the life cycle of many species. When global warming alters the climate, certain phenological events generally shift accordingly. If a phenological change in one species does not match linked changes in an interdependent species, an *ecological mismatch* can occur (Visser and Both 2005) For example, if certain trees bloom earlier in response to warmer springs, but pollinators do not hatch earlier, disruptions (e.g., failed or inadequate pollination) may occur. The mismatches caused by climate change can disrupt the reproductive cycle of many species. In one example, variability in precipitation, linked to regional climate change, is considered as the cause of the extinction of two populations of checkerspot butterflies in California (John McLaughlin et al. 2002). Changing levels of precipitation were found to alter the relationship between butterfly larvae and host plants. In very wet or dry years, larvae do not get the opportunity to feed on host plants before the plants die. These lost opportunities for successful reproduction cause variation in butterfly abundance, which eventually may lead to their extinction. Because of their close ecological ties, when either the pollinator or the plant declines, the other is adversely affected. For example, the lesser long-nosed bat is the primary night pollinator of the saguaro and the organ pipe cactus, two important cacti of the Sonoran desert ecosystem. The timing of the migration of the bats from Mexico closely corresponds to the timing of the blooming of the cactus flowers. Blossom and bat are closely adapted to each other: the flower provides food in the form of nectar and the bats consume it. In the process, the bats pollinate the flowers. Research has shown that in recent years the time of blooming in some species has changed significantly, likely due to changing temperatures. These changes may disrupt the plant-pollinator relationships, jeopardizing both species. Some other endangered and threatened pollinator species include the Karner Blue Butterfly in Wisconsin and the Hawaiian crested honeycreeper bird. Tedeschini et al. (2006) studied the effects of climatic change on *Platanus* spp. pollination in different areas of Italy and Spain, characterized by different climate. A previous start of pollination (−0.66; −1.21; days/year) is reported in both Italian stations where the temperatures have significantly increased and a delay of 0.2–0.8 days/year in Spanish stations where a different trend of temperature is recorded. The study revealed that pollen release was more gradual with higher temperatures or faster under colder conditions.

Miller-Rushing et al. (2007) reported that climate change is affecting plant phenology worldwide. Phenological responses vary among species, but it is not clear how responses differ among closely related species. They examined a 25-year record (1981–2005) of flowering times for 97 trees, representing 17 species and hybrids of cherry (*Cerasus* sp. or *Prunus* sp.) grown at Mt. Takao, in Tokyo, Japan and found that the cherry trees flowered earlier over time, by an average of 5.5 day over the 25-year study. This was attributed to 1.8°C increase in February–March mean monthly temperatures. Most species and hybrids flowered 3–5 day earlier for each 1°C increase in temperature, but early-flowering taxa flowered as much as 9 day earlier for each 1°C increase in temperature. Flowering durations and differences in flowering times among species were greater in warm years than in cold years. Species and individual trees also flowered longer in warm years. These results show that the flowering times of closely related species may change similarly in response to climate change, but that early-flowering species may diverge from the overall trend in a predictable way. Such changes in flowering may affect gene flow and pollination as the length of the flowering season increases. Memmott et al. (2007) studied the network of interactions between 1,420 pollinator and 429 plant species and found that as a consequences of the phenological shifts that can be expected with a doubling of atmospheric CO_2 there was reduction of floral resources available to 17–50% of all pollinator species, by reducing availability of flowers during the pollinators' flight seasons. Reduced overlap between plants and pollinators also decreased diet breadth of the pollinators. Climate change is also causing shifts in the reproductive cycles and growing seasons of certain species. Research by Parmesan and Yohe (2003) on the timing of spring events, such as egg laying by birds or flowering by plants, showed that in 61 studies, the timing had shifted earlier by an average of 5.1 days per decade over the last half century. Likewise, Root et al. (2003) found that out of 1,700 species reviewed, 87% of observed shifts in phenology were in the direction expected by climate change. In Europe, phenological data shows an increase in the length of the growing season by about 10 days from 1962 to 1995 (Menzel and Fabian 1999).

15.3.7 Changes in Species Interactions

The impact that climate change will have on many of the more complex interactions (predation, competition, pollination and disease) that constitute functioning ecosystems remains largely unknown. Mismatches in timing between interdependent species may occur, especially when changes in some species are cued by day length, and others by temperature (Hughes 2000). Small variations in weather caused by climate change could affect the water, nectar and pollen the bees rely on. In the 1940s, there were an estimated five million managed bee colonies in North America but now there are just over two million. Adverse weather conditions and hurricanes have also contributed to the heavy losses of bee colonies in recent years. Climate change could also be a factor in weakening the bees and has affected the pollination of crops in many agricultural areas. Historical records that show that there had been fluctuations with beehives every 7 or 8 years that are affected by weather conditions and crop yields.

15.3.8 Bees and Flowers Are Disappearing Together

The diversity of bees and of the flowers they pollinate has declined significantly in Britain and the Netherlands over the last 25 years according to research led by the University of Leeds and published in Science (Biesmeijer et al. 2006)**.** The paper is the first evidence of a widespread decline in bee diversity. Concerns have been raised for years about the loss of pollination services, but until recently most of the evidence has been restricted to a few key species or a few focal sites. Biesmeijer et al. (2006) compiled biodiversity records for 100 sites, and found that bee diversity fell in almost 80% of them. Many bee species are declining or have become extinct in the UK.

15.3.8.1 Examples of Declining Bees and Plants

Scabious bees and field Scabious are declining Field scabious (*Knautia arvensis*) provides pollen and nectar to a wide range of insects. One visitor, the scabious bee, *Andrena hattorfiana*, raises her young exclusively on pollen from this plant. Our study shows (Biesmeijer et al. 2006) that both species have recently declined in Britain and the Netherlands. Field scabious is still common, but much less so than several decades ago. In addition, grazing and early cutting of hay meadows makes that field scabious often does not reaches the flowering stage. This may be a major cause of the decline of the scabious bee. The absence of the bee may also play a role in the decline of the plant. The bee has been shown, in a Swedish study, to be a more effective pollinator of field scabious than other bees and hoverfly visitors. The good news is that adequate habitat management can help the declining bee and its food plant. Bees specialized on wild peas are having a hard time. It has been suggested that the decline of various bumblebee species has been caused, in part, by the decreased use members of the pea family as fodder for farm animals. The other species of wild bees that specialize on pollen collection from wild peas are also declining. As an example, the longhorn bees (*Eucera nigrescens, Eucera longicornis*) have all but disappeared. *Eucera nigrescens* has become extinct in the UK and is very rare in the Netherlands. This may be a result of a decline in some of their food plants (vetches, vetchlings and clovers).

Studies conducted by Biesmeijer et al. (2006) comparing records from before and after 1980 in Britain and the Netherlands have showed bee diversity had declined consistently in both countries, whereas the diversity of hoverflies stayed roughly constant in Britain, but increased in the Netherlands. Loss of bee diversity in itself might not be too worrying, so long as other surviving insect pollinators are similar, and capable of pollinating the same flower species. However, this is not the case. The research found for both bees and hoverflies, the “winners” and “losers” were consistently different; insects which pollinate a limited range of flower species or which have specialized habitat needs were most often lost. Overall, a small number of common generalist pollinators are replacing a larger number of rarer specialist species. There have been parallel shifts in the plant world, with the plants that depend on pollination by bees disappearing too. In Britain, where bee diversity has fallen and hoverflies have at best held steady, there have been declines in 70% of the wildflowers that require insects for pollination. In conjunction with this evidence, outcrossing plant species that are reliant on the declining pollinators have themselves declined relative to other plant species.

15.4 Impact of Climatic Change on Pollinators and Agriculture

During April 2007 farmers in Taiwan reported heavy losses in bees "for no reason", bee boxes had been emptied". While the exact reason for the exodus is unknown, experts say "volatile weather" may be to blame. The temperature recently swung from 20°C to 30°C over a few days, and this may have done for the bees. "You can see climate change really clearly these days in Taiwan." The impact of the bees' absence has yet to be felt, although it could have a serious effect on pollination.

In India, during 2007, mango trees in Andhra Pradesh flowered 3 months early because of the rising heat. A few years ago, bees in the Himalayas were impacted by similar erratic flowering patterns, leading to a big drop in the honey supply and pollination of almonds. Normally almond flowering occurs in Kashmir in the third week of February but during 2000 flowering occurred during December when no pollinating bees were active leading to total a loss of the crop. Climate change during the past 8 years has played a critical role in apple pollination failure. There are rains during the flowering season which affect pollination by wind and insects. Low temperatures also adversely affect fruit set in apple (Abrol unpublished data). Weather has impacted not just birds, ladybirds, butterflies across the country and soon mammals will be next." the effect of climate on agriculture is related to variabilities in local climates rather than in global climate patterns.

In 2002, India and the United States suffered sharp harvest reductions because of record temperatures and drought (Attri 2001). In 2003 Europe suffered very low rainfall throughout spring and summer, and a record level of heat damaged most crops from the United Kingdom and France in the Western Europe through Ukraine in the East. Low lying areas such as Bangladesh, India and Vietnam will experience major loss of rice crop if sea levels are expected to rise by the end of the century.

15.5 Pollination as a Tool in Adaptation to Changing Environments and Minimising Risk

Climate change is causing changes in the distribution of many species. There is an interest in identifying crop genetic resources that help crops adapt to climate change. Pollinators, however, will largely respond by contracting or expanding their ranges according to new climatic patterns. Thus the possibility of crops losing key pollinating species, or mismatches in the ranges of crops and their pollinators, is a real threat. Such effects have already been felt in the seed industry of India. Since seed production requires a certain degree of chilling to induce seed formation in temperate crops, many vegetable seed farms are located in mountainous regions, such as the Hindu-Kush Himalayas. While mountainous regions can provide such a climate, they also make farmers increasingly vulnerable to the effects of climate change. Farmers in the Kullu valley of Himachal Pradesh state in India are finding that overall temperatures have been rising, while rains have become more unpredictable, leading to several crop failures. Vegetable seed yields have been decreasing, yet the challenge of ensuring sufficient natural pollination under changing climatic conditions has not been addressed by researchers, much less farming communities (Sharma 2006).

15.6 Global Warming May be Partly to Blame for Honeybee Deaths

Biologists also wonder if global warming may be exaggerating the growth rates of pathogens such as the mites, viruses and fungi that are known to take their toll on bee colonies. The unusual hot-and-cold winter weather fluctuations in recent years, also blamed on global warming, may also be wreaking havoc on bee populations accustomed to more consistent seasonal weather patterns.

15.7 How to Overcome Climate Change for Better Pollination

Crops produce optimally with a suite of pollinators possibly including, but not limited to managed honeybees. Different pollinators become most active at different times of the day or under different weather conditions, and even between years the most abundant and effective pollinators of a crop may shift from one pollinator to another (Inouye et al. 2002; Kremen et al. 2000; Inouye 2008). A diverse assemblage of pollinators, with different traits and responses to ambient conditions, is one of the best ways of minimizing risks due to climatic change. The “insurance” provided by a diversity of pollinators ensures that there are effective pollinators not just for current conditions, but for future conditions as well. A biodiverse agroecosystem, with many more facilitative interactions between crops and crop-associated biodiversity, may also contribute significantly to carbon sequestration (Hajjar et al. 2008).

15.8 Sustainable Agriculture Mitigates Climate Change and Has Climate Adaptation Potential

Sustainable agriculture, by its very definition, reduces harm to the environment, for example through the reduction or elimination of polluting substances such as pesticides and nitrogen fertilisers, water conservation practices, soil conservation practices, restoration of soil fertility, maintenance of agricultural biodiversity and biodiversity etc. (Wilson 1988). Importantly, sustainable agriculture practices can also mitigate climate change. There are a variety of sustainable farming practices that can reduce agriculture's contribution to climate change, which are easy to implement. These include crop rotations and improved farming design, improved cropland management, nutrient and manure management, grazing-land and livestock management, maintaining fertile soils and restoration of degraded land, improved water and rice management, and set-asides, land use change and agroforestry (Bellarby et al. 2008).

15.9 Plant Reproductive Biology Studies Crucial for Conservation

Successful fertilization is dependent on effective pollination. Pollination studies alone can provide a gamut of information about the loss of many species, because pollination is the fundamental step in plant reproduction (Inouye and Barr 2006; Moza and Bhatnagar 2007). Successful pollination is an essential pre-requisite for survival of plants in natural communities and is dependent on many biotic and abiotic factors. Plants have coevolved with their pollinators and large ecological changes can decouple their coinciding flowering and breeding cycles. Conservationists need to focus on the pollinators and their biology as well while framing any conservation strategy. The decline of many ornithophilous and entomophilous plants has been assigned to unsuccessful pollination because of loss of their pollinators. For outcrossing of entomophilous plants, population size and plant density are closely associated with the attraction and activity of pollinators. Because small populations may be less attractive to pollinators, the reduction in population size results in decreased fruit or seed production because of insufficient pollen transfer. Some plants have narrow amplitude in which these can flower and fruit. The conditions must be favourable for plants to produce flowers. A study conducted by a reproductive biology group in Italy on *Rhus aculeatus,* an evergreen shrub, has yielded some interesting results. On the RET list the plant is threatened because of unsuccessful pollination. Information was gathered in the laboratory by observing the absence of pollen grains on the stigmatic surface of 80 flowers in anthesis samples randomly in field during the flowering period. Studies on the reproductive biology of *Lactoris fernanndeziana*, an endemic plant of an island in Chile belonging to a monotypic family Lactoridaceae, have helped in conserving the species.

15.10 Conclusions

These usually small and often unobtrusive creatures such as pollinators do not come immediately to mind when we think of Wildlife System. However, pollinators can be considered guardians of the biological integrity of ecosystems. They ensure the biological integrity, diversity, and environmental health of the ecosystem." Addressing their needs often has broader implications related to managing for biodiversity and biological integrity in general. Though we often think of birds as the indicators of environmental conditions, yet pollinators may be a far better way to measure whether an ecosystem is intact and healthy. When pollinators are in trouble, ecosystems are in trouble.

Likewise, as a critical component to ecosystem sustainability, pollinators are important to the nation's economy. Many of our fruits, vegetables, and nuts, as well as other food products rely on pollinators for reproduction or to increase crop yields. While the importance of a healthy pollinator population to agriculture is readily apparent, it is just as important to sustaining the food supply for fish and wildlife. For example, the diet of many migratory birds includes berries, fruits, or seeds that require pollination.

The public does not recognize the magnitude of the threat that these mysterious events present but we should be more than alarmed. Scientists have been observing how one species after another is disappearing from our planet but never before has one with such a direct bearing on food production been threatened. Extinction of a species doesn't just affect the group that disappears – it tends to alter much more. Bees do make excellent biological geiger counters. They are especially valuable perennial mobile biomonitors of the local environment. Thus, with their wide foraging range and collecting activities, they are natural monitoring agents for investigating the ebb and flow of floral resources and toxic substances within the environment. The cost of conserving biodiversity is far less than the penalty of allowing its degradation.

Anthropogenic activities may be detrimental to some species but beneficial to others, with sometimes subtle and counter intuitive causal linkages (Thomas and Jones 1993; Benedek 1996). It is essential to recognize that pollination is not a free service, and that investment and stewardship are required to protect and sustain it. Economic assessments of agricultural productivity should account for the "cost" of sustaining wild and managed pollinator populations (Ingram et al. 1996). There is a need for well-documented cases of specific pollinator declines notwithstanding, rapid extrapolation from our current knowledge to imply worldwide pollinator and crop production crises might be inappropriate and premature, much uncertainty remains regarding pollinator-pollination declines (Ghazoul 2005). As Albert Einstein put it bluntly, "If the bee disappeared off the surface of the globe then man would only have 4 years of life left. No more bees, no more pollination, no more plants, no more animals, no more man." The bee is the basis for life on this earth."

References

Abrol DP (1988) Environmental factors influencing pollination activity of *Apis mellifera* L. on *Brassica campestris* L. var toria. J Indian Inst Sci (Biol Sci) 68:49–52

Abrol DP (1991) Conservation of pollinators for promotion of agricultural production in India. J Anim Morphol Physiol 38(1/2):123–139

Abrol DP (1993) Insect pollination and crop production in Jammu and Kashmir. Curr Sci 65:265–269

Abrol DP (2007) Honeybee and rapeseed – a pollinator plant interaction. In: Dr Gupta SK (ed) Advances in botanical research: rapeseed breeding, vol 45. Elsevier, London, pp 339–367

Abrol D (2008) Bees and beekeeping in India, 2nd edn. Kalyani Publishers, Ludhiana, 720p

Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, Cox PA, Dalton V, Feinsinger P, Ingram M, Inouye D, Jones CE, Kennedy K, Kevan P, Koopowitz H, Medellin R, Medellin-Morales S, Nabhan GP, Pavlik B, Tepedino V, Torchio P, Walker S (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conserv Biol 12(1):8–17

Attri SD (2001) Status of climate change in India. In: Dash SK, Rao P (eds) Assessment climate change in India and mitigation policies. WWF, New Delhi, pp 10–17

Balling RC, Cerveny RS (1998) Weekly cycles of air pollutants, precipitation and tropical cyclones in the coastal NW Atlantic region. Nature 394:561–563

Banaszak J (1995) Changes in fauna of wild bees in Europe. Pedagogical University, Bydgoszcz

Bazzaz FA (1998) Tropical forests in a future climate: changes in the biological diversity and impact on the global carbon cycle. Clim Chang 39:317–336

Bazzaz F, Sombroek W (eds) (1996) Global climate change and agricultural production. Direct and indirect effects of changing hydrological, pedological and plant physiological processes. FAO/Wiley, Rome/Baffins Lane

Bellarby J, Foereid B, Hastings A, Smith P (2008) Cool farming: climate impacts of agriculture and mitigation potential. Greenpeace International, Amsterdam

Benedek P (1996) Structure and density of lucerne pollinating wild bee populations as affected by changing agriculture. Acta Hortic 437:353–357

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313(5785): 351–354

Bryant SR, Thomas CD, Bale JS (1997) Nettle-feeding nymphalid butterflies: temperature, development and distribution. Ecol Entomol 22:390–398

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington, DC

Cane JH (2001) Habitat fragmentation and native bees: a premature verdict? Conserv Ecol 5(1):3

Corbet SA, Williams IH, Osborne JL (1991) Bees and the pollination of crops and wild flowers in the European Community. Bee World 72:47–59

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1987) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Costanza R, d' Arge R, de Groot R, Farber S, Grasso M, Hannon B et al (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Cowley MJR, Thomas CD, Thomas JA, Warren MS (1999) Flight areas of British butterflies: assessing species status and decline. Proc R Soc Lond B 266:1587–1592

Currie DJ (1991) Energy and large-scale patterns of animal and plant species richness. Am Nat 137:27–49

Currie DJ, Kerr JT, Francis AP (1999) Some general propositions about the study of spatial patterns of species richness. Ecoscience 6:392–399

Day MC (1991) Towards the conservation of Aculeate Hymenoptera in Europe. Convention on the conservation of European wildlife and natural habitats, *Nature and Environment Series* 51. Council of Europe Press, Strasbourg

Falk S (1991) A review of scarce and threatened bees, wasp and ants of Great Britain. Research and survey in nature conservation no 35, Nature Conservancy Council, Peterborough, UK

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. Science 296:1689–1691

Fleishman EG, Austin T, Weiss AD (1998) An empirical test of Rapoport's rule: elevational gradients in montane butterfly communities. Ecology 79:2482–2493

Fraser RH (1998) Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. Glob Ecol Biogeogr 7:215–220

Free JB (1993) Insect pollination of crops. Academic, London, 684 pp

Gallai N, Sallas JM, Settele J, Vaissiere BE (2008) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68:810–821

Gärdenfors U (ed) (2000) Rödlistade arter i Sverige 2000 – the 2000 red list of Swedish species. ArtDatabanken SLU, Uppsala, 397 pp

Ghazoul J (2005) Buzziness as usual? questioning the global pollination crisis. Trends Ecol Evol 20(7):15–17

Gillette DD, Kimbrough JD (1970) Chiropteran mortality. In: Slaughter BH, Walton DW (eds) About bats: a chiropteran biology symposium. Southern Methodist University Press, Dallas, pp 262–283, 339 pp

Hajjar R, Jarvis DI, Gemmill-Herren B (2008) The utility of crop genetic diversity in maintaining ecosystem services. Agric Ecosys Environ 123:261–270

Harrison RD (2000) Repercussions of El Nin˜o: drought causes extinction and the breakdown of mutualism in Borneo. Proc R Soc Lond B 267:911–915

Helmholtz Centre for Environmental Research (UFZ) (2008) Economic value of insect pollination worldwide estimated at 153 billion Euros. Ecological economics, Press release, 15 Sept 2008

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to twentieth century climate warming: implications for future changes. Proc R Soc Lond B 269:2163–2171

Hughes MJ (1996) Commercial rearing of bumblebees. In: Matheson A (ed) Bumblebees for pleasure and profit. International Bee Research Association, Cardiff, pp 40–47

Ingram M, Nabhan G, Stephen B (1996) Our forgotten pollinators: protecting the birds and bees. Glob Pest Campaign 6(4):123–125

Inouye DW (2000) The ecological and Evolutionary significance of frost in the context of climate change. Ecol Lett 3(5):457–463

Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362

Inouye D, Barr B (2006) Consequences of abrupt climate change for hibernating animals and perennial wildflowers at high altitude in the Colorado Rocky Mountains, USA. In: Price MF (ed) Global change in mountain regions. Sapiens Publishing, London, pp 166–168

Inouye DW, Wielgolaski FE (2003) Phenology of high-altitude climates. In: Schwartz MD (ed) Phenology: an integrative environmental science. Kluwer Academic Publishers, Dordrecht, pp 195–214

Inouye DW, Barr WA, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. Proc Natl Acad Sci 97(4):1630–1633

Inouye DW, Morales M, Dodge G (2002) Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. Oecologia 130:543–550

Inouye DW, Saavedra F, Lee-Yang W (2003) Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* L. (Primulaceae). Am J Bot 90(6): 905–910

IPCC (2007) Climate change 2007: synthesis report. In: Pachauri RK, Reisinger A (eds) Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team]. IPCC, Geneva, 104 pp

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. Annu Rev Ecol Syst 29:83–112

Kerr JT (1999) Weak links: "Rapoport's rule" and large-scale species richness patterns. Glob Ecol Biogeogr 8:47–54

Kerr JT (2001) Butterfly species richness patterns in Canada: energy, heterogeneity and the potential consequences of climate change. Conserv Ecol 5:1–18

Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high energy regions. Nature 385:252–254

Kerr JT, Packer L (1998) The impact of climate change on mammal diversity in Canada. Environ Model Assess 49:263–270

Kerr JT, Packer L (1999) Epicauta species richness patterns in North America: the importance of energy. Biodivers Conserv 8:617–628

Kerr JT, Vincent RL, Currie DJ (1998) Determinants of Lepidoptera richness in North America. Ecoscience 5:448–453

Kerr JT, Sugar A, Packer L (2000) Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. Conserv Biol 14:1726–1734

Kevan PG, Phillips T (2001) The economics of pollinator declines: assessing the consequences. Conserv Ecol 5(1):8

Klein AM, Vaissie`re BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C et al (2007) Importance of pollinators in changing landscapes for world crops. Proc R Soc Lond B 274:303–313

Kremen C, Williams NM, Thorp RW (2000) Crop pollination from native bees at risk from agricultural intensification. PNAS 99:16812–16816

Kukal O, Ayres MP, Scriber JM (1991) Cold tolerance of the pupae in relation to the distribution of swallowtail butterflies. Can J Zool 69:3028–3037

Luig J, Maavara V (1998) Kiletiivalised, *Hymenoptera*. – Rmt: V.Lilleleht (koostaja). Eesti Punane Raamat. Ohustatud seened taimed ja loomad, lk. 103–106

McLaughlin J et al (2002) Climate change hastens population extinctions. Proc Natl Acad Sci 99(9):6070–6074

Memmott J, Craze PG, Waser NM, Price MV (2007) Global warming and the disruption of plant-pollinator interactions. Ecol Lett 10:710–717

Menzel A, Fabian P (1999) Growing season extended in Europe. Nature 397:659

Mikkola K (1997) Population trends of Finnish Lepidoptera during 1961–1996. Entomol Fennica 8:121–143

Miller-Rushing Abraham J, Katsuki T, Primack RB, Ishii Y, Lee SD, Higuchi H (2007) Impact of global warming on a group of related species and their hybrids: cherry tree (Rosaceae) flowering at Mt. Takao, Japan. Am J Bot 94:1470–1478

Moza MK, Bhatnagar AK (2007) Plant reproductive biology studies crucial for conservation. Curr Sci 92(9):1206–1207

Myers N (1992) Synergisms: joint effects of climate change and other forms of habitat destruction. In: Peters RL, Lovejoy TE (eds) Global warming and biological diversity. Yale University Press, New Haven, pp 344–354

Nabhan GP, Buchmann SL (1997) Services provided by pollinators. In: Daily GC (ed) Nature's services: societal dependence on natural ecosystems. Island Press, Washington, DC, pp 133–150

O'Toole C (1994) Who cares for solitary bees? In: Metheson A (ed) Forage for bees in an agricultural landscape. International Bee Research Association, Cardiff, pp 47–56

Osborne JL, Williams IH, Corbet SA (1991) Bees, pollination and habitat change in the European community. Bee World 72:99–116

Parmesan C (1996) Climate and species' range. Nature 382:765–766

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Parmesan C, Ryrholm N, Steganescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583

Partap U, Partap T (2002) Warning signal from the apple valley of the HKH: productivity concerns and pollination problems. ICIMOD, Kathmandu

Pekkarinen A (1998) Oligolectic bee species in Northern Europe (Hymenoptera, Apoidea). Entomol Fennica 8:205–214

Pekkarinen A, Teräs H, Wuorenrinne H (1987) Suomen myrkkypistiäislajien taantuminen ja uhanalaisuus. Luonnon Tutkija 91:124–129

Pollard E, Rothery P, Yates TJ (1996) Annual growth rates in newly established populations of the butterfly *Pararge aegeria*. Ecol Entomol 21:365–369

Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. Nature 398:611–615

Price MV, Waser NM (1998) Effects of experimental warming on plant reproductive phenology in a subalpine meadow. Ecology 79:1261–1271

Rasmont P (1988) Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae). PhD thesis, Faculté des Sciences Agronomique de l'Etat, Gembloux, Belgium

Rassi P, Alanen A, Kanerva T, Mannerkoski I (toim.) (2001) Suomen lajien uhanalaisuus 2000. – Ympäristöministeriö and Suomen ympäristökeskus, Helsinki, 432 pp

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Rosenfeld D (2000) Suppression of rain and snow by urban and industrial air pollution. Science 287:1793–1796

Rusterholz HP, Erhardt A (1998) Effects of elevated CO_2 on flowering phenology and nectar production of nectar plants important for butterflies of calcareous grasslands. Oecologia 113:341–349

Saavedra F, Inouye DW, Price MV, Harte J (2003) Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. Glob Chang Biol 9:885–894

Sharma HK (2006) Cash crops farming in the Himalayas: the importance of pollinators and pollination in vegetable seed production in Kullu valley Of Himachal Pradesh, India. FAO. Case study submitted for Rapid Assessment of Pollinators' Status Report. Available (http://www.fao.org/ag/AGP/AGPS/Default.htm – then go to C-CAB Group>Pollinators>Case studies on pollinators and pollination)

Söderman G, Leinonen R (2003) Suomen mesipistiäiset ja niiden uhanalaisuus. Tremex Press Oy, Helsinki, 420 pp

Sparks TH, Yates TJ (1997) The effect of spring temperature on the appearance dates of British butterflies, 1883–1993. Ecography 20:368–374

Stefanescu C, Pen˜uelas J, Fililla I (2003) Effects of climate change on the phenology of butterflies in the northwest Mediterranean basin. Glob Chang Biol 9:1494–1506

Swengel AB (1998a) Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biol Conserv 83:77–89

Swengel AB (1998b) Comparisons of butterfly richness and abundance measures in prairie and barrens. Biodivers Conserv 7:1639–1659

Tarrier M, Leestmans R (1997) Losses and acquisitions probably linked to the effects of global climatic warming on western Mediterranean lepidopteran fauna (Lepidoptera, Papilionoidea). Linneana Belgica 16:23–36

Tedeschini E, Rodriguez-Rajo FJ, Caramiello R, Jato V, Frenguelli G (2006) The influence of climate changes in *Platanus* spp. pollination in Spain and Italy. Grana 45(3):222–229

Thomas CD, Jones TM (1993) Partial recovery of a skipper butterfly (Hesperia comma) from population refuges: lessons for conservation in a fragmented landscape. J Anim Ecol 62: 472–481

Thomas CD, Lennon JJ (1999) Birds extend their range northwards. Nature 399:213

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC et al (2004) Extinction risk from climate change. Nature 427:145–148

Travis MJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc R Soc Lond B 270:467–473

Turner JRG, Gatehouse CM, Corey CA (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. Oikos 48:195–205

UNEP (1993) Global biodiversity. UNEP, Nerobi

University of Southampton (2000) Credit: National Oceanography Centre, Southampton, University of Southampton

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. Proc R Soc Lond B 272:2561–2569

Wall MA, Timmerman-Erskine M, Boyd RS (2003) Conservation impact of climatic variability on pollination of the federally endangered plant, *Clematis socialis* (Ranunculaceae). Southeast Nat 2:11–24

Westrich P (1989) Die Wildbienen Baden-Württembergs. Ulmer, Stuttgart

Wielgolaski FE, Inouye DW (2003) Phenology of high-latitude climates. In: Schwartz MD (ed) Phenology: an integrative environmental science. Kluwer Academic Publishers, Dordrecht, pp 175–194

Williams PH (1986) Environmental change and the distributions of British bumble bees (Bombus Latr.). Bee World 67:50–61

Williams IH (1996) Aspects of bee diversity and crop pollination in the European Union. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) The conservation of bees, Linnaean Society symposium series 18. Academic Press, London, pp 210–226

Willis JK, Chambers DP, Nerem RS (2008) Assessing the globally averaged sea level budget on seasonal to interannual time scales. J Geophys Res 113:C06015. doi:10.1029/2007JC004517

Wilson EO (1988) The current state of biodiversity. In: Wilson EO, Peter FM (eds) Biodiversity. National Academic Press, Washington DC, pp 3–18

Wright DH (1983) Species-energy theory: an extension of species-area theory. Oikos 41:496–506

Wright DH, Currie DJ, Maurer BA (1993) Energy supply and patterns of species richness on local and regional scales. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. University of Chicago Press, Chicago, pp 66–74

Chapter 16
Pollinators as Bioindicators of Ecosystem Functioning

Abstract Pollinators and pollination are crucial in the functioning of almost all terrestrial ecosystems and serve as valuable bioindicators of ecosystem health and can be used to monitor environmental stress brought about by introduced competitors, diseases, parasites, predators as well as by chemical and physical factors, particularly pesticides and habitat modification. Honeybees are useful as samplers of the environments because they indicate the chemical impairment of the environment they live in and have been used to assess atmospheric and other types of pollution. Pollinator guilds offer new means of assessing ecosystemic health because the species diversity and abundance relationship is changed from the log-normal standard expected from ecological principles and niche theory.

16.1 Introduction

Pollination plays a dominant role in maintaining the biodiversity of the world's dominant flora, through insect and flower relationships (Kevan 1984b; Willemstein 1987). Both have co evolved in the course of *Evolutionary* history spanning over more than 400 million years. The vital roles of pollinators and flowers are no less important in remote wildernesses of the Arctic and deserts than in highly managed farming systems, thereby clearly indicating that pollination is central to all human beings, livestock, and wildlife. More- over, the ecological roles of non-pollinating flower visitors provide benefits, and sometimes problems which are essential to other aspects of ecosystemic function.

The pollinators and other flower visiting animals serve as most important bioindicators, organisms that, by their presence, abundance, and activities can reveal something about the state of the ecosystem in which they are found. Whether in a state of deterioration or amelioration, they can suggest that ecosystemic processes are operating according to expectations within normal bounds. In the latter case, the species used may be indicators of ecosystemic health. Thus, pollinators can be used as bioindicators of ecosystemic processes in three ways: (1) as individuals since

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their activities are affected or as they sample their environments, (2) as populations of species as affected by environmental change, and (3) as species assemblages, guilds or taxocenes, interacting with each other and their environment.

Most research on pollinators as bioindicators has been at the population level and has focused mainly on honeybees. Likewise, research on individual pollinators as bioindicators has dealt almost exclusively with honeybees. The value of pollinator assemblages as bioindicators of ecosystemic stress has only recently been rigorously demonstrated. As the size of pollinator populations, the 'pollinator force' (Kevan et al. 1986), is generally thought to be most important to plant reproduction, especially through crop production, this aspect of their role as bioindicators is reviewed first followed by individual pollinators or pollinator colonies (as in bee hives) are very useful in special contexts. The problems associated with declining diversity of pollinators and conservation, with special reference to agricultural productivity, provides insights into failures and inefficiencies in disturbed ecosystemic processes is discussed elsewhere (Richards and Myers 1995).

Anthophiles or flower visitors are animals which feed at flowers and serve as best bioindicators as they sample the environment for pollen, nectar, oil or floral tissue to satisfy their nutritional needs (Kevan and Baker 1983, 1998). Pollen provides protein, lipid, carbohydrate, vitamins and minerals in various amounts depending on the plant species. Nectar is mostly a sugary solution and provides energy for locomotion, mostly flight. It also contains other compounds, some probably involved in nutrition, in trace amounts. Oil is provided by some specialized flowers as the reward for their specialized pollinators.

Floral tissue is thought to have been the original resource sought by primitive, herbivorous anthophiles, the beetles (Coleoptera) (Bernhardt and Thien 1987). Pollinators are anthophiles which bring about pollination. Not all anthophiles are effective pollinators; some are floral larcenists that remove the resources sought by pollinators or eat pollen needed in abiotic pollination (Inouye 1980); others may be innocuous and merely rest in flowers or glean residual resources after pollination is over. Although pollinators are vital to plant reproduction, non pollinating (or poorly pollinating) anthophiles may also be important in ecosystemic function. For example, many insects that are useful in biocontrol of pests require florally derived food to mate, find hosts, oviposit and complete their life cycles (Jervis et al. 1993; Ruppert 1993). There are also anthophiles that use floral sites for capturing prey (Kevan and Baker 1983; Greco and Kevan 1994).

The diversity of anthophiles probably numbers in the millions of species. Most species of bees and wasps, many ants (Hymenoptera), true flies (Diptera), moths and butterflies (Lepidoptera), and some families of beetles (Coleoptera) visit flowers. There are other insect orders in which anthophily is common, as in thrips (Thysanoptera), and others where it is quite specialized, as in the Zaprochilidae (Orthoptera) or sporadic, as in the springtails (Collembola). Among the vertebrates, some groups of birds e.g., hummingbirds (Trochilidae), flowerpeckers (Dicaeidae), honeyeaters (Meliphagidae), honeycreepers (Coerebidae), sunbirds (Nectariniidae), and lories (Loriinae), and bats (fruit bats or flying foxes (Pteropidae) of the old world Tropics and leafnosed bats (Phyllostomatidae) of the Neotropics) are notorious as anthophiles and pollinators (Arita and Martinez 1990). In the South Pacific, conservation issues loom for flying foxes and the plants they pollinate (Cox et al. 1991). There are even a few other specialized gliding and scansorial mammals that are important pollinators, especially in Australia and Africa (see Proctor et al. 1996). Even primates are important as pollinators in some places, e.g., Madagascar (Kress et al. 1994). Thus, almost all groups include examples of bioindicators. Demonstrating that an anthophile is a pollinator requires care. First it is necessary to establish that the plant in question requires a pollinating agent; some plants set fruit and seed without the intervention of pollinators and some can do so even without fertilization (Richards 1986). Thus, it is not sufficient that the anthophile is commonly encountered on flowers of the plant; the particular anthophile may be a floral larcenist on some plant species but the true pollinator of another; the larceny may be vital to the anthophile and thereby vital to the plant which it truly pollinates. A pollinator must visit the flower in such a way, and within such a period, that viable pollen is transferred from anther to stigma. Associated with these requirements are the anatomical and behavioural fit of the pollinator and the flower, the appropriateness of the floral advertisement to the pollinator's sensory capabilities, and the floral resources and the pollinators' needs. Taken together, floral characteristics can be combined into 'syndromes' that suggest the *Nature* of the pollinator, and the characteristics of the pollinator may suggest what sorts of flowers they are best suited to pollinate (Faegri and van der Pijl 1979; Whitehead et al. 1987). The harmonies between floral and pollinator characteristics can be taken as evidence for the long period of co-*Evolution* between flowering plants and pollinators (Kevan 1984b; Willemstein 1987). Nevertheless, there are many flowers that are effectively pollinated by a wide diversity of animals (Waser et al. 1996) along with many that are special, with restricted assemblages of potential pollinators (Grant and Grant 1965, 1968; Hurd and Linsley 1975; Faegri and van der Pijl 1979; Vogel 1990; Proctor et al. 1996). Very few species of plants appear to be pollinated by single species of pollinators. Honeybees are the most valuable pollinators in agriculture. Their biology is well known and they can be managed in easily transportable boxes for pollination of many agricultural crops (Free 1993). The diversity of beekeeping practices goes beyond that represented by hives of European races and hybrids of honeybees (*Apis mellifera* spp. *ligustica, caucasica,* and *carnica* or the Italian, Caucasian, and Carniolan honeybees). Nevertheless, those bees are the best understood and easily managed for pollination and hive products (Crane 1990; Graham 1992). Throughout Africa and the Middle East, other indigenous races are kept. The so-called 'killer bee', better referred to as the Africanized bee (a hybrid between European and African races), has spread from Brazil throughout the tropical and subtropical Americas since the introduction there of the African parent stock of *A. scutellata* from southeastern Africa in 1956. It is notoriously defensive and easily provoked to attack intruders, be they beekeepers or innocent passers-by (Espina 1986). *A. mellifera* is genetically and behaviourally diverse (FAO 1986; Ruttner 1988).

In Asia, other species of honeybees are kept or encouraged for human exploitation. The most important is the Asiatic hive bee (*A. cerana*) which probably comprises as much racial biodiversity as does *A. mellifera* (see Ruttner 1988; Verma 1995). The Asiatic hive bee has been maligned as difficult to manage but recently more attention has been paid to its potential (see Verma 1990; Punchihewa 1994; Kevan 1995). Also, the wisdom of transplanting European honeybees into Asia has been seriously questioned (Kevan 1995). In tropical and subtropical Asia, other species of honeybees, *A. dorsata* and related species and *A. florea* are used commercially (Crane 1990). In the tropical and subtropical Americas where there are no indigenous *Apis*, stingless bees (Meliponinae) have been traditionally kept since pre Columbian times. This practice, called meliponiculture, is enjoying some resurgence with the encouragement and recognition of non-European cultural values. Meliponine bees occur throughout the world's tropics and present immense potential for managed pollination in agriculture. However, little attention has been paid to their biology as pollinators (see Roubik 1988, 1995) although, they have been shown to be valuable in cucurbit farming (Meléndez-Ramírez 1997).

Nevertheless, honeybees are not the best pollinators for all crops (Bohart 1972; Westerkamp 1991; Williams 1996). Other bees that do not produce harvestable quantities of honey, if any at all, can be are managed or have potential for management as pollinators of particular crops. Crane (1990) lists about 50 species of bees that have been managed commercially (very few) or experimentally for pollination. There are several particularly important and proven pollinators that can be used commercially and be relied upon to consistently pollinate some crops more efficiently than honey bees (Martin and McGregor 1973; Kevan 1989b; Richards 1993; Torchio 1994; Williams 1996). Bumblebees (*Bombus* spp.) are the pollinators of choice for red clover which has corolla tubes that are usually too deep to allow honeybees access to nectar (Free 1993). Willmer et al. (1994) have noted the superiority of bumble bees as pollinators of raspberry, vis à vis honey bees which serve the crop not quite as well. The importance of the forage, pollen or nectar, sought by pollinators, in relation to pollination success is beginning to be recognized and in some crop plants, especially those with specialized floral forms (e.g., blueberry, cranberry), bees foraging for pollen are more effective than nectar foragers (Cane and Payne 1988; MacKenzie 1994). On these crops, honeybees are often poor pollinators because of the small proportion of pollen foragers in their colonies and their inability to 'buzz-pollinate' to obtain the pollen they seek (Buchmann 1983). Some crop plants that require or benefit from insect pollination do not produce nectar and rely solely on pollen-foraging insects. Among these are kiwi-fruit, tomato, and perhaps pomegranate. Lupine also produces only pollen but is automatically self-pollinating. Pollen-foraging honeybees are thought to be better pollinators than nectar foragers even for apples and other such crops that produce relatively open flowers (Free 1993). For pollination of pome fruits, orchard bees (*Osmia* spp.) show greater efficiencies and start foraging at lower temperatures than do honeybees (Torchio 1987, 1991). Alfalfa leaf-cutting bees (*Megachile rotundata* and other species) are the primary pollinators for alfalfa and other leguminous crops (Richards 1993). Bumblebees are now used for pollination of tomatoes and other solanaceous crops in greenhouses (Banda and Paxton 1991; Kevan et al. 1991b) and of some leguminous crops. The use of the blueberry bee (*Habropoda laboriosa*) is being encouraged for blueberries (Cane and Payne 1988, 1990), and the hoary squash bee (*Peponapis pruinosa*) has similar potential for use on squash and pumpkin (Willis and Kevan 1995). In Malaysia, carpenter bees (*Xylocopa* spp.) have recently been managed by providing nesting material for pollination of passion fruit with flowers too large to be pollinated by honeybees (Mardan et al. 1991, 1993).

Pollination of some crops is not effected at all by bees but by other pollinators. Oil palm is now effectively pollinated in Malaysia by the recently introduced weevil, *Elaeidobius kamerunicus* Faust (Curculionidae). It is the natural pollinator of oil palm and was introduced from West Africa, the original home of the oil palm, to Malaysia for pollination (Syed et al. 1982; Kevan et al. 1986). Various annonaceous fruit crops are pollinated by beetles but relatively little information is available on the pollinators most adapted to these plants (see Roubik 1995). Cacao is pollinated by midges (Diptera: Ceratopogonidae) (Free 1993; Roubik 1995) and mango mostly by an assemblage of flies and other insects (Free 1993; Roubik 1995). Durian, an important fruit crop of tropical Asia, is bat-pollinated (Roubik 1995) and represents an even more extreme example of the need to consider alternative pollinators for many crops. In the Tropics, issues regarding pollination are especially important because the natural pollination mechanisms of many plants (crops and others) are not known (Kevan 1984a, 1995; Mbaya and Kevan 1995; Roubik 1995).

Expanded and continued evaluation and development of management practices for non-honeybee pollinators will ensure adequate and economical pollination for a diversity of crops and other plant species. The value of 'pollinating bees in a box' cannot be discounted wherever agriculture is practiced (Free 1993; Kevan 1995; Roubik 1995) but as Roubik (1995) points out, the age of 'designer pollination' is beginning, as pollination technology diversifies. Recently, conservation concerns for pollination have started to take on a greater profile than ever before (Kevan 1974, 1975a, b, 1986, 1989a, 1990, 1993; Parker et al. 1987; Kevan et al. 1990a, b, 1991a; Torchio 1990, 1991, 1994; Corbet et al. 1991; Osborne et al. 1991; Williams et al. 1991; Ellis and Ellis-Adam 1993; Kingsmill 1993; Richards 1993; Watanabe 1994; Buchmann and Nabhan 1996; Matheson et al. 1996; Kearns and Inouye 1997). Some of this concern has resulted from the recognized value of pollination to agriculture. Figures calculated for the USA, Canada, and Australia, mostly with regard to honeybees, show that the value of pollination far exceeds that of hive products (Southwick and Southwick 1992). The European Economic Community commissioned the study by Corbet and coworkers (noted above) as a result of its recognition of the international scope of the problem. Nevertheless, the economics of animal pollination in agriculture in any one country are complex and difficult to assess (Southwick and Southwick 1992). That notwithstanding, agriculture cannot do without a variety of pollinators including the most important, honeybees. The total value of animal pollination to world agriculture has not been estimated, and the value to world ecosystemic health is beyond measure! Pollinators need more recognition as bioindicators because of their diversity, the importance of their population and activities of individuals, and their central place in agricultural and natural productivity.

Other flower visiting insects are also invaluable, especially predators and parasitoids which are important in controlling populations of otherwise pestiferous insects in all environments. Although new and more environmentally sensitive approaches to agriculture and forestry recognize and encourage these biocontrol agents (Altieri 1987), the crucial place of floral resources in their livelihoods is often not considered (for examples, see below). Biocontrol agents represent a particularly valuable group of insects in agroecosystems. Leius (1960, 1967) showed that the incidence of ichneumonoid parasitism of codling moth in apple orchards was greater if floral resources such as those of weeds were available in the orchards.

Syme (1975) noted the importance of floral resources for biocontrol agents in forests as well. In fact, long ago it was suggested that the failure to establish potentially useful biocontrol agents against Japanese beetles was caused, at least partially, by lack of floral resources (King and Holloway 1930). Certainly, some of the successes reported regarding the high incidence of natural biocontrol agents of pestiferous insects in low-input agricultural systems (Altieri and Whitcomb 1979; Altieri 1987) should be ascribed to the availability of floral resources (see Kevan 1986).

Most of the foregoing has concerned pollinators but the plants' side of the equation should not be ignored. The huge diversity of crop plants that are pollinated by insects is well explored in Free (1993) account of insect pollination of crops, and recently Roubik (1995) has edited a treatise on tropical plants alone. These books list literally hundreds of crop plants and their pollination requirements so far as they are known. The value of non-crop forage plants, often regarded as weeds to pollinators of crops and other anthophiles is also high. In situations where such alternative forage which would normally be available before, during or after the bloom of the crop, has been eliminated or reduced in abundance, the natural assemblages of pollinators have suffered and so have crop yields. This situation has arisen in blueberry heaths in eastern Canada and Maine, USA (Kevan et al. 1997). In Europe there is growing awareness of the need to maintain or create flower-rich field borders to stimulate populations of beneficial insects like aphidophagous hoverflies (Syrphidae), ladybird beetles (Coccinellidae) and parasitoid Hymenoptera (Molthan and Ruppert 1988; Weiss and Stettmer 1991; Schmid 1992).

16.2 Inhibiting Factors in Pollinator Build Up

Populations of anthophiles suffer from pesticides, diseases, parasites, predators, pollution, habitat destruction, and competitive interactions. Serious losses of pollinators and sometimes, concomitant reductions in crops, have been attributed to pesticides, a few diseases, and parasitic mites of honeybees. Predators seem to be a minor problem, although serious for beekeeping in some places. Honeybees are excellent as samplers of environmental pollution and thus, serve as bioindicators, although non-pesticide pollutants seem to have only a minor influence on pollinator populations and diversity. Habitat destruction is a major issue, especially in the decline of wild pollinators.

16.2.1 Pesticides

The dangers of pesticides, especially insecticides, to pollinators are well documented and understood (Johansen and Mayer 1990; Sihag 1995). Most studies on pesticide toxicity and hazards to pollinators have dealt with honeybees, but these are poor bioindicators for effects on other pollinators, even bees (Johansen and Mayer 1990; Kevan and Plowright 1995). Less understood, and often overlooked, is the problem of sublethal effects which reduce longevity and adversely affect foraging, memory and navigational abilities of some bees (see MacKenzie 1993; Kevan and Plowright 1995). Piles of dead honeybees in front of hives and behavioural abnormalities are bioindicators of serious environmental problems. Although most mass mortalities of honeybees stem from accidents and careless application, occasionally deliberate misuse of pesticides despite label warnings and recommendations have caused major pollinator kills. Mosquito control programmes have been associated with major losses of honeybees in Canada and the USA. In Manitoba, efforts to combat outbreaks of western equine encephalitis by controlling its mosquito vectors resulted in damage to colonies of honeybees totalling $90,000 in 1981 and $850,000 in 1983 (Dixon and Fingler 1982, 1984). Although not measured, the effects of these programmes on populations of native pollinators would have been expected to be extremely severe. The problem of pesticide poisonings of other managed pollinators is serious wherever pesticides are used. In general, guidelines borrowed from the literature on honeybees are used to assess the effects of pesticides but as has been noted, these are not reliable. There are records of evaluated losses of alfalfa leaf cutting bees caused by pesticides in the western USA (Johansen 1977; Richards 1984) but by and large there is little information relating specifically to the effects of pesticides on managed non-honeybee pollinators. Issues of pesticides in non-agricultural settings and agroforestry are more complex because of the importance of a wider diversity of pollinators. The most well understood situation is in eastern Canada where fenitrothion, sprayed against spruce budworms (*Choristoneura fumiferana*) defoliating forest trees, had devastating side effects on wild, native pollinators of commercial blueberry fields and on the pollinators servicing the sexual reproductive needs of some of the native flora. A number of plant species of the forest and forest margins suffered reduced fruit and seed set which in turn would be expected to impact wildlife by depriving them of natural quantities of food (Kevan and Plowright 1989, 1995). The ecosystemic ramifications of the decline of populations and diversity of native forest bees had been predicted before they were documented (Kevan 1975a), illustrating the potential of pollinators as sensitive bioindicators.

16.2.2 Pollution

Apart from that produced by agricultural chemicals, pollution seems to have exerted a minor influence on pollinators. Nevertheless, honeybees have been investigated as bioindicators to monitor pollutants. Honey or pollen or both may become contaminated with various industrial pollutants. The release of arsenic and cadmium may cause mass killings of honeybees and contaminate pollen, but not nectar (Krunic’ et al. 1989). The accumulation of radioisotopes in honey and pollen following the Chernobyl disaster in April 1986 illustrates the value of honeybee colonies as samplers of local, regional, and global environmental quality (Bunzl et al. 1988; Ford et al. 1988). They also sample fluorides (Dewey 1973), heavy metals (Stein and Umland 1987) and organic compounds (e.g., PCBs and pesticides) (Anderson and Wojtas 1986; Morse et al. 1987) through floral nectar, pollen, and their own bodies. They have been advocated as bioindicators in natural, agricultural, industrial and urban milieus (Celli et al. 1975; Celli and Porrini 1987; Rousseau 1972; Drescher 1982; Celli et al. 1989; Bromenshenk et al. 1985; Stein and Umland 1987) yet, despite their proven worth, programmes for their use as biomonitors do not seem to have been instituted.

Bromenshenk et al. (1991) addressed the problem of population dynamics in honeybees with respect to pollution and so expanded concern for the health of pollinators beyond pesticide hazards. Little information is available on the effects of pollutants on other pollinators. Dewey (1973) showed that the highest levels of fluoride, associated with an aluminium reduction plant, were found in flower-visiting insects (from bumblebees to butterflies and hoverflies). Sulphur dioxide reduces activity of pollinators including honeybees and male sweat bees (*Lasioglossum zephrum*) but may not kill them (Ginevan et al. 1980).

Although, the actual species differ between continents, latitudes, altitudes, and biomes, some general remarks about pollinators as bioindicators can be made. In urban environments, many people value flower visiting insects, and various publications are available for encouraging butterflies in gardens. In Europe, several studies have been made on bees in cities (Haeseler 1982; Jacob-Remacle 1984; Kratochwil and Klatt 1989; Torres et al. 1989; Sauer 1996) and other highly anthropogenic environments (Haeseler 1972) studied the effects of artificial domiciles in encouraging urban populations of bumblebees in Liège, Belgium. These studies exemplify the amazing adaptability of some species of pollinators to persist and thrive in small enclaves of highly disturbed vegetation and to contribute to human well-being by their presence and through pollinating various ruderal, encouraged, and cultivated plants (Edwards 1996; Klemm 1996).

Landscapes dominated by annual crops (e.g., grains and oil seeds) are among the most intensively managed and most highly disturbed monocultures. Such high levels of disturbance hamper the establishment of pollinator populations (Ellis and Ellis-Adam 1995) and most annual crops do not depend on insects for pollination. Cereals are wind-pollinated or set seed asexually, most beans are self-pollinating and many other crops do not require pollination because the harvests are roots, stems, leaves, and immature flowers. Nevertheless, some crops, such as canola, flax, safflower, sunflower, tomatoes, peppers, and strawberries require, or at least benefit from, insect pollination (Free 1993). A few field cucurbits (melons, cucumbers, squash, gourds, and pumpkins), some cole crops (some canola varieties, mustard, and oil seed radish) and some annual forage legumes require insect pollination and honeybees are the pollinators of choice.

However, for squash, gourds, and pumpkins the specialized bee, *P. pruinosa* (Say), is more efficient and becomes well established where these crops are grown year after year (Kevan et al. 1988; Willis and Kevan 1995). In areas of intensive farming, field margins, headlands or turn-rows, fence-lines, road, rail, and utility rights of way, public lands, and so forth are important refuges for many pollinators, yet, the value of these areas to agricultural productivity is unknown, denigrated, and not researched. Long-term set aside lands are being recognized for their value in the conservation of biodiversity in mostly agricultural settings, and pollinators are benefitting (Corbet 1995). All such areas support much rural wildlife, mammals, birds, and insects that depend on pollination of wild plants for sustenance.

16.3 Ecosystemic Stress and Health

As the ideas in this review have unfolded, emphasis has moved from specific pollinators and specific problems to landscape issues and broader scale conservation problems. The importance of assemblages of pollinators and pollination interactions to the functioning of ecosystems (Rathke 1983, 1988; Frankie et al. 1990; Vogel and Westerkamp 1991) logically follows but is only recently being considered in terms of how the interactions can serve as bioindicators. The idea that concepts of health can be applied to ecosystems has had difficulty in practicality and acceptance because there are problems as to how such a form of health might be measured. The measures of ecosystemic health that have been proposed are not satisfactory to scientific ecologists. Some have been based on natural processes which are not necessarily indicative of ill-health (e.g., eutrophication and succession), some suites of symptoms comprise different measures of the same ecosystemic processes, others are anthropocentrically derived (Costanza 1992; Rapport 1992; Callicott 1995; Jamieson 1995). Nevertheless, the concepts of health and ecosystemic conditions can be juxtaposed through rigorously applied ecological principles. If ecology is defined as the study of the distribution, abundance, and activity of organisms, then these three facets of life must be included in ecosystemic analyses, including those aimed at health. Two unifying concepts in ecology are competitive exclusion and niche hierarchies. Sugihara (1980) has argued that because the species in complex communities of organisms occupy a hierarchy of niches with partial overlaps, the relationship between diversity and abundance is log-normal. Pollinator diversities and abundances follow log-normality in various habitats, from cropped fields in Mexico to old fields in Canada (MacKay and Knerer 1979; Tepedino and Stanton 1981; Meléndez-Ramírez 1997). Under extraordinary environmental stress, it is generally thought that the log-normal relationship would not apply. These ideas were validated on blueberry fields in south central New Brunswick, Canada.

It is known that Fenitrothion has reduced levels of pollinators and pollination on blueberry fields and in forests, causing ecosystemic dysfunction (Kevan and Plowright 1995; Kevan et al. 1997) and that agricultural productivity has been adversely affected (Kevan and Oppermann 1980). The hypothesis that the log-normal relationship of diversity and abundance could be used as a standard for health was tested with data from east, central, and west southern New Brunswick and in two periods; the years when the insecticide Fenitrothion was being applied in the central part of the area, and the years following the cessation of its application. Almost all data sets were log-normal; the exceptions were those from central New Brunswick taken during the years of Fentitrothion applications. Lack of log-normality in the one data set was taken as indicative of ill-health (Kevan et al. 1997).

16.3.1 Butterflies

Butterflies (Lepidoptera) are one of several guilds that are used as a potential ecological indicator of forest condition. Indicator species are thought to either signal the presence/abundance of other species, or to signal chemical/physical changes in the environment through changes in their own presence or abundance (Landres et al. 1988; Simberloff 1998). In many regions of the world, Lepidoptera are widely accepted as ecological indicators of ecosystem health (Rosenberg et al. 1986; New et al. 1995; Beccaloni and Gaston 1995; Oostermeijer and van Swaay 1998), Hilty and Merenlender (2000). Butterflies have a fairly clear taxonomy, and their life history and biology are well defined (Nelson and Anderson 1994; Wood and Gillman 1998). Many of their physiological tolerances, such as light, temperature, and habitat requirements, have been quantified (Warren 1985; Thomas and Harrison 1992; Greatorex-Davies et al. 1993; Sparks et al. 1996; Oostermeijer and van Swaay 1998; Pollard et al. 1998), and correlations with changes in ecosystem conditions have been demonstrated (Bowman et al. 1990; Thomas and Harrison 1992; Hill et al. 1995; Pullin 1996; Sparks et al. 1996; Spitzer et al. 1997; Pollard et al. 1998; Schultz 1998; Swengel 1998). In addition, butterflies are small, have high reproductive rates, and are at a low trophic level that allow them to quickly respond to environmental stress. Many butterflies specialize on a specific plant species for oviposition or in areas with high climatic variability, as changes detected in their abundance may be in response to a climatic condition instead of ecosystem structure (Pollard et al. 1975; Pollard and Yates 1993).

16.3.2 Honeybees as Bio-Indicators

Honeybees are good biological indicators because they indicate the chemical impairment of the environment they live in through two signals viz pesticides residues present in their bodies or in the bee hive products and or other contaminants like heavy metals and radionuclides that may be detected by means of suitable laboratory analyses. Several ecological and morphological factors make the honey bee a reliable ecological detector: it is an easy to breed, almost ubiquitous organism, with modest food requirements; its body is covered with hairs which make it particularly suitable to hold the materials and substances it comes into contact with; it is highly sensitive to most plant protection products, revealing when they are improperly spread through the environment (e.g. during flowering during wind etc.); its very high rate of reproduction and relatively short average life span, causes the colony to undergo rapid, continuous regeneration ; its great mobility and flying range allows a vast area to be monitored. Furthermore, almost all environmental sectors (soil, vegetation, water, air) are sampled by honeybees (numerous inspections per day). A variety of materials are brought by honeybees into the hive through foraging (nectar, pollen, honeydew, propolis and water) and stored. Porrini et al. (2002) at the university of Bologna has been studying the use of honeybees as bioindicators to detect pesticides, heavy metals, and radionuclides in many areas.

16.4 Monitoring of Pesticides

Honeybees are highly sensitive to pesticides. The number of dead bees in front of the hive is the most important variable to be considered for these contaminants. Many bees directly stuck by the insecticides will not have the enough strength to return and die in the field or during their return flight. In case of dangerous compounds, the insect act as an indirect indicator i.e. not sensitive but exposed, and will provide us with the information in the form of residues. Other bees marginally hit gathering nectar pollen will eventually die in front of the hive. Heavy metals present in the atmosphere can deposit on the hairy bodies of bees and be brought back to the hive with pollen, or they may be absorbed together with the nectar of flowers or through the water or honeydew. The lead in the urban environment was found in higher quantities inside the bee than on the bee's surface.

Monitoring of pesticides with honey bees, is an extremely important technique not only for proving potential bee poisoning risks by the use of pesticides, but also for determining the degree of environmental contamination due to plant protection products. In fact, because of its morphological and ethological features (such as its wide area of patrol and its intense foraging activity), the honey bee can be considered an excellent bioindicator. In many cases, pollution caused by abuse or by erroneous application of pesticides could not be proven without the help of honey bees (Porrini et al. 2002).

Monitoring techniques, chemical and palynological analyses, and data processing enable us to characterize areas, to indicate periods of major bee poisoning risk, and to identify the most frequently used pesticides and the crops treated. The studies with honey bees reveal the type of plant protection management applied to the area under investigation and allow us to prove the application of molecules not permitted under certain circumstances or even forbidden. Between 1983 and 1986 in particular, the analysis of 581 dead bee samples revealed which compounds were most widely used in that period in cultivated fields, above all in northern Italy (Celli et al. 1988a, b).

In those years, bee poisoning incidents were caused primarily by treatments carried out in orchards, vineyards, on seed crops and by pollution due to drift on spontaneous plants. The most frequently found pesticides were phosphorganics (dimethoate, parathion, azinphos- methyl, methyl-parathion, omethoate and metamidophos), followed by carbamates (carbaryl) and clororganics (endosulfan). Dithiocarbamates were almost always found in the dead bees samples, together with other products, insecticides for the most, which were the ones to blame for the bees' death. These include dimethoate, a compound serving a huge variety of purposes but often misused. Pollution by pesticides can be detected promptly and continuously at low costs by using bees as bioindicators, since they are able to signal immediately and unambiguously the incorrect use of pesticides. Anyway, some of the new insecticides do not induce high bee mortality but, even at low doses, they may cause severe behavioural changes, which could damage the entire family. They are also difficult to detect with chemical analysis and thus our tools (mortality and residues) are not always able to reveal them.

Brood and adult bees are directly or indirectly (through the process of royal jelly secretion by hypopharyngeal glands) fed with bee bread and can be exposed to pesticide residues for various times. Many research teams have worked on quantifying the amount of pollen needed to rear a bee larva. It mainly depends on season, pollen species, and conditions under which the larvae are reared. For example, it has been shown that worker honey bee larvae needed 86 mg of maize pollen for their complete development (Babendreier et al. 2004).

Pollen supply also is involved in bee resistance to pesticide exposure. Amount and quality of pollen ingested in the first days of life affected the pesticide sensitivity of young and older bees (Wahl and Ulm 1983). The most frequent residues (i.e., imidacloprid, 6-chloronicotinic acid, and fipronil) were searched with very low LODs compared with other pesticides.

The main question to be addressed remains, are the doses found in pollen dangerous for bees? Let us consider this question for imidacloprid. We would like to know how much contaminated pollen an adult bee should eat to reach the LD_{50} quantity. If we rely on the average content, we have found in this study (1.2 g/kg) that the consumption of 33 g of pollen by one individual would be needed to meet the oral LD50 (0.04 g per bee). A certain amount of time would be needed for one worker to eat this quantity of pollen, which then would be stocked in cells in the form of bee bread. Our lack of knowledge on active ingredient fate and interactions between molecules stocked into hives remains unexplored.

Moreover, it has been shown that LD50 values would not be sufficient to assess the adverse effects of a pesticide. Very small quantities of active ingredients can lead to subtle effects at various levels of bee physiology and behavior. These effects are more difficult to detect, but they also may affect bee populations.

Contamination by pesticides ranged from 50% to 0%. Coumaphos and tau-fluvalinate residues were the most concentrated of all residues (mean concentrations were 925.0 and 487.2 g/kg, respectively). Fipronil and metabolite contents were superior to the limit of detection in 16 samples. Residues of fipronil were found in ten samples. Nine samples contained the sulfone compound, and three samples contained the desulphonyl compound. Residues of imidacloprid and 6-chloronicotinic acid were found in 69% of samples. Imidacloprid contents were quantified in 11 samples with values ranging from 1.1 to 5.7 g/kg. 6-Chloronicotinic acid content was superior to the limit of quantification in 28 samples with values ranging from 0.6 to 9.3 g/kg).

The use of honey bee *Apis mellifera* L. (Hymenoptera: Apidae), as a tool for monitoring environmental pollution is founded upon several ethological features such as high rate of reproduction, great mobility, large flying range, and numerous flower inspections per day. It is also founded on morphological characteristics: the honey bee body is covered with hairs that collect various particles and increase by this means the contact of the insect with its environment (Porrini et al. 2002). Apicultural matrix analysis such as honey, wax, bees themselves, or pollen can provide useful indications of the diffusion of pesticides within the environment.

Wax and honey bees also have been subjected to various analyses to detect different types of contamination. Chemical contamination through *Varroa* treatments (*Varroa destructor* Anderson and Trueman [Acari: Mesostigmata]) has been found to be a route of wax contamination by coumaphos (Tremolada et al. 2004), bromopropylate (Hansen and Petersen 1988), and fluvalinate (Tsigouri et al. 2004).

In addition, numerous studies have reported the use of honey bees to monitor environmental radionuclide contamination (Haarmann 1997; Barisic et al. 2002) or heavy metal contamination (Porrini et al. 2002). Less commonly, honey bees have been used as bioindicators to detect the presence of phytopathogenic microorganism in the environment (Porrini et al. 2002). There are three main purposes for monitoring bee products: consumer health protection, international commercial competition, and better product quality (Yakobson 1996). Although pollen loads are a product for human consumption, they currently are subject to no legislation, leading to very limited data. For experimental purposes, pollen loads collected from traps set on honey bee colonies have occasionally been used to monitor environmental pollution: radioactive contamination after the Chernobyl accident (Barisic et al. 1994) or new insecticide used for particular crops, such as sweet corn (Erickson et al. 1998) or oilseed rape (Kevan et al. 1984; Fries and Wibran 1987). Pollen also has often been analyzed for the presence of pesticide residues in bee mortalities (Johansen and Brown 1972; Waller et al. 1984; Kubik et al. 1995). Samples were either collected with the aid of pollen traps or more often by hand, directly from flowers. The new agriculture which we so much hope for, will have to strive for that the application of these molecules in our cultivated fields will decrease and, for this purpose, the honey bee can be of great help. In any case, let us remember that the honey bee is killed by pesticides when they are incorrectly diffused in the environment (cultivated fields or private gardens) either in a qualitatively or quantitatively wrong way, that is by not applying the recommended dosage or by not obeying the accepted technical norms of use (culling of spontaneous plants, absence of wind, absence of honeydew).

16.4.1 Monitoring of Radionuclide

Tonelli et al. (1990) analyzed the samples of honeybees, wax and pollen after the Chernobyl incident and demonstrated that pollen was the most efficient indicator of atmosphere radionuclide contamination. On a typical day, bees from a hive containing about 10,000 bees make more than 200,000 trips a day.

16.4.1.1 Honeybees and Landmines

Honeybees are being trained to serve us in still another quite remarkable way to locate land mines. Trained bees can act as biological detectors of these explosive devices, and lidar is being investigated as a way to pinpoint the location of the insects as they momentarily hover over and thereby mark a land mine.

One of the saddest leftovers from warfare is the wide distribution of landmines. Worldwide, thousands of innocent civilians are killed each year by these mines; still more are crippled. In Cambodia alone today there are an estimated 35,000 amputees who were injured by mines, many of them innocent children. The mines are also a continuing daily threat in Afghanistan, Angola, Bosnia, Chechnya, Croatia, Iraq, Mozambique, Nicaragua, Somalia, and dozens of other countries. More than 90 countries, unfortunately including the United States, have manufactured and distributed 200 million antipersonnel landmines in the last 25 years. Land mines are inexpensive weapons, but their cost to the world community is much higher. As many as 20,000 people a year are killed or injured by land mines. Mines can render roads, farms and other land useless. They sometimes remain active decades after a military conflict has ended. The United Nations estimates there are more than 100 million active mines and new mines are buried more quickly than old ones are safely unearthed.

Identifying and clearing minefields is itself a life-threatening activity and a wide range of techniques is being implemented. Although humans with metal detectors remain a common method, huge machines, chain mats dragged by helicopters and trained dogs have also been employed. And here is where the bees come in. They don't have noses, but they do have a strong sense of smell. A group of entomologists at the University of Montana led by Jerry Bromenshenk have spent several years developing techniques to employ honeybees in landmine and biological weapon detection. According to Bromenshenk, "A honeybee's body has branched hairs that develop a static electricity charge, making it an extremely effective collector of chemical and biological particles, including pollutants, biological warfare agents and explosives. They also inhale large quantities of air and bring back water for evaporative cooling of the hive." Thus an individual hive has tens of thousands of foragers out sampling local air, soil, water and vegetation. Examination by the scientific team of a number of returning bees provides initial information about areas where materials of concern are to be found and appropriate relocation of hives can further zero in to areas of a few 100 m. But even this detection is now being refined.

The scientists have devised methods to train the bees by the same kind of reward techniques (formally called operant conditioning) that are employed by dog trainers. The reward provided the bee is food which is associated with the particular target being sought – the smell of the chemicals in land mine explosives in this instance. Again from the Bromenshank report: Bees follow "vapor plumes toward and over the source or target. We have observed that bees detect the vapor plume several meters from the source, then navigate up the plume to the source. We then map the density of bees over an area, using visual, camera or laser-assisted counts." In the summer of 2003 field trials were conducted at Fort Leonard Wood in Missouri. Ten full-size bee colonies were conditioned to search for explosive vapors and the hives were placed in the test area.

The trial results were spectacular: The detection equipment worked over hundreds of meters with location to within a few centimeters. Bees found both individual mines and clusters of mines. The bees even made a surprise detection of a site contaminated with left-over TNT where none was expected. The researchers are now exploring ways to make their procedures simple enough to be used by local beekeepers anywhere in the world. Here is still another reason to appreciate these wonderful insects.

Scientists at Sandia National Laboratory in New Mexico and University of Montana have discovered that bees foraging for pollen and nectar pick up dust, soil and other particles on their bodies and bring them back to the hive. Those particles can include explosives such as TNT, a primary ingredient in many land mines. “All land mines leak explosives into the environment. If you can get bees to go into that area they’ll then collect the explosive signatures that are coming off the mines, and bring it back to the hive which can be detected using various chemical sensors.” Bees bring pollen back to the hive on their back legs which can help detection of land mines. Samples of the plants can also reveal how much explosive is actually coming out of the mine and getting into the environment.

In addition the free-roaming bees bring back samples of other hazardous materials and can be connected in their hives by an electronic network which alerts beekeepers to changing field conditions. Bees from monitored hives visit an area up to a half mile in radius on the post. They bring back traces of metals, toxic organics, and even volatile chemicals along with the pollen stuck to their bodies. When computers detect erratic behaviors among the bees, such as queens walking outside the hive, built-in hive monitors collect air samples for laboratory testing. Heavy metals are determined by analyzing the collected bee pollen and the bodies of the bees themselves. Some of the compounds successfully detected include: PCE, carbon tetrachloride, TCE, diesel fuels and gasoline, benzene, *p*-dichlorobenzene, naphthalene, and acetophenone. Limonene and other components of the hive itself are ignored. Mustard gas itself has not yet been detected, perhaps because much of it is converted into thiodiglycol which then percolates into groundwater.

Bromenshenk measured the amounts of inorganic elements, such as arsenic, cadmium, lead, zinc, copper, and fluoride, in the bees’ bodies. Using the results of the tests, he mapped out patterns of metal contamination in the area. They corresponded well to similar maps that local agencies had drawn by analyzing soil samples. On a typical day in Montana, the counters register 200,000 trips a day from a hive containing about 10,000 bees. “Our ultimate goal is to use the bee behavior as a tip-off to the existence of a chemical problem. Running a beehive is fairly inexpensive, compared with doing ongoing chemical sampling. To sample the same mile wide area with [conventional] samplers would just be unfeasible.” The researchers look forward to the day when the technique moves beyond assessing normal events, such as weather, and can warn them of chemical changes in the environment as they happen. Then, the busy bees will be working not only for their brothers and sisters in the hive but also for the humans watch.

16.4.1.2 Use of Wasps

Wasps and bees are buzzing all over the place and sniffing up a storm. An unusual device that uses trained wasps, rather than trained dogs, to detect specific chemical odors could 1 day be used to find hidden explosives, plant diseases, illegal drugs, cancer and even buried bodies. Besides detecting plant diseases, the device has a wide variety of other potential applications. In previous studies, the researchers demonstrated that they also could train the wasps to detect 2,4-dinitrotoluene (2,4-DNT), a chemical used in certain explosives. The wasps can also be used to detect chemical odors that are associated with certain human diseases, including lung cancer, skin cancer and stomach ulcers, they say. More recently, their group has been looking into the possibility of using the wasps to detect odors associated with hidden bodies, from murder victims to victims of disasters.

16.4.1.3 Passive Sampling

Bromohensk and his team at the University of Montana (UM) began sending out bees to explore and sample environments of interest, as a way of collecting and mapping data over large areas within a 2–4 km radius of the hive. A honey bee's body has branched hairs that develop a static electricity charge, making them an extremely effective collector of chemical and biological particles, including pollutants, biological warfare agents and explosives. They also inhale large quantities of air and bring back water for evaporative cooling of the hive. As such, bees sample all media (air, soil, water and vegetation) and all chemical forms (gaseous, liquid and particulate). With proper colony placement and sampling, gradient maps of the distribution of chemical or biological materials can be produced.

Given an appropriate sampling design, bees can quickly provide samples of materials in the vicinity of each hive, since the foragers from each colony will make tens to hundreds of thousands of foraging forays or flights each day, with each forager returning to its home hive by nightfall. This passive collection to determine environmental presence of chemical and biological threats can provide an initial survey of landscapes. It generally identifies regions where materials of concern can be found and, with appropriate re-location of hives and re-sampling, can help narrow down the search to areas of a few 100 m.

16.4.1.4 Active Training and Search

Bees have an acute sense of smell and can be trained to find explosives, bombs and landmines, as well as other chemicals of interest, including drugs and even decomposing bodies. Bees are trained in much the same way as dogs, using traditional operant conditioning methods. The reward is food, which is associated with the odor of the chemical of interest. Like dogs, bees can detect suites of chemicals, such as 2,4-DNT, 2,6-DNT, TNT, and RDX over a wide range of concentrations. Bees indicate the presence of an odor by the numbers of bees following vapor plumes toward and over the source or target. We have observed that bees detect the vapor plume several meters from the source, then navigate up the plume to the source. Numbers of bees over odor sources are integrated over time and compared to those over the rest of the area. In other words, we map the density of bees over an area, using visual, camera or laser-assisted counts. Like dogs, bees are able to recognize multiple substances concurrently at very low concentrations. As with any vapor sensing system, bees cannot find a mine that is not leaking. Therefore there is a the need for additional research to define the performance of mine-detecting bees, taking into consideration environmental factors that influence the amount of chemical signatures.

Since 1962, the bee has increasingly been employed to monitor environmental pollution by heavy metals in territorial and urban surveys, pesticides in rural areas and also radionuclide presence in the environment (Celli and Maccagnani 2003). The bee as biological indicator possesses several important morphological, ecological and behavioural requisites, and man's beekeeping assures an unlimited supply. The bee acts as a detector of environmental pollution in two ways, as it signals either via high mortality rates the presence of toxic molecules, or via the residues in honey, pollen, and larvae the presence of heavy metals, fungicides and herbicides that are harmless to it. Bee monitoring also contributes to the ecological impact statement by culminating in the charting of environmental health maps, which include such data as mortality rates, apicide number, type and risk-level of molecules detected, and so forth.

In general terms each organism, and its home, form a mirrored pair, and it is not possible to deal separately with them. It is precisely this mirror-image of the living being and its biotope which enables us to resort to certain organisms in their capacity as biological indicators. The idea of employing the bee in environmental monitoring is not a new one. It dates back to J. Svoboda, who in 1935 (Crane 1984) felt that this insect could provide us with valuable data on the environmental impact of certain industries in given areas; 25 years later he and his co-workers reported via bee-monitoring an increase of the radionuclide strontium 90 in the environment – the result in all likelihood of atmospheric nuclear testing (Svoboda 1962). Since 1970, the bee has increasingly been employed to monitor environmental pollution heavy metals in territorial and urban surveys (Cavalchi and Fornaciari 1983; Crane 1984; Accorti and Persano Oddo 1986; Celli et al. 1987; Stein and Umland 1987; Celli et al. 1988b) and pesticides in rural areas (Atkins et al. 1981; Celli 1983; Mayer and Lunden 1986; Mayer et al. 1987; Celli et al. 1988c; Celli and Porrini 1991; Celli et al. 1991; Porrini et al. 1996) as well as radionuclides (Wallwork-Barker et al. 1982; Gattavecchia et al. 1987; Tonelli et al. 1990) (for a review on the state of the research on these topics in Italy see Porrini et al. 2002).

The bee as biological indicator possesses several important requisites. First, man's beekeeping assures an unlimited supply. Then, the bee is active throughout the area surrounding the hive: for, although an opportunist in the sense that it prefers to gather pollen in the flowered fields nearby, the bee can range over long distances, even up to 10 km under exceptional circumstances: a hive can keep an area of 7 km^2 "under its control" (Crane 1984). And the number of bees in a given area is considerable. A quarter or 10,000, of the 40,000 bees in a normal hive are active pollinators. It should be borne in mind that each one completes 12–15 flights a day, and that it takes about a 100 apple flowers to fill the honey stomach and 80 or so pear flowers to lord the pollen basket. The bee ethogram described above shows it to be an especially apt monitoring instrument: it issues from the hive and flies about the surrounding area casually picking up airborne particles with its body hairs, while busily harvesting plant and flowers. In other words, it takes samples for us, gathering nectar and pollen from flowers, propolis from the buds of various botanic species, especially poplars, honeydew from the aphids of infested plant and water from wells and irrigation ditches. All of which leads to the truly crucial moment of the bee's return to the hive with is precious cargo. The nectar an pollen are stored, honey is made, the propolis is used in the hive and the larvae are fed. These latter, which in certain cases accumulate residues in their bodies, can thus become biological indicators by stockpiling given contaminants via a nutritional body balance whose input is grater than its output. These indicators accumulators constitute a special category that not only takes samples but highlights residues, thereby facilitating their determination.

Bee monitoring also contributes to the ecological impact statement on pesticides by culminating in the charting of environmental health maps, which include such data as mortality rates, apicide number, type and risk-level of molecules detected, and so forth. In Forlì Province (Emilia Romagna region, Northern Italy), where our work began over 20 years ago, we were able to draw up an historical atlas, so to speak, of environmental health maps. They chart the *Evolution* – for the better, as it turns out – of the impact of synthetic molecules on farmland and, hence, covering most of the province itself (Celli and Porrini 1991). The environment monitoring through the bee allowed us to register also local, critical situations without the risk of a significant alteration of the general "depict" of environmental health made by the complex of the monitoring stations. In 1995, in the Ravenna Province (nearby the Forlì Province) a particular worrisome situation came to light with the discovery of lindane in two inhabited areas of the town where the use of this substance could not be justified by the local conditions. Dangerous and obsolete molecules such as parathion and Endosulfan also indicated the difficulty of local agriculture in relinquishing the old methods of protection cultivation, even .in an overall medium-low level of contamination of the investigated area (Porrini et al. 1998).

For some time now in the Romagna Region both integrated pest management, which seeks to limit the use of pesticides and at the same time to combine their use with alternative methods, and biological pest control, which strives towards the complete elimination of synthetic compounds, have been in operation, and the bees have probably registered the resulting, first few ecological benefits.

16.4.2 Birds as Bioindicators

Birds are useful biological indicators (Gregory et al. 2005), especially at the edges of urban areas, because they are ecologically versatile and can be monitored relatively easily and cheaply (Koskimies 1989). They are also highly mobile and therefore can respond rapidly to changes in their habitat (Fuller et al. 1995a, b; Louette et al. 1995). It is at the edges of urban areas, where habitat structure is often highly fragmented, that relationships between humans and bird assemblages are easiest to study (Cody 1985). Thus, birds have long been used as both environmental (e.g. Kushlan (1993), Alleva et al. (2006)) and biodiversity indicators (Reynaud and Thioulouse 2000).

16.4.3 Bats as Bioindicators

Indicators that represent responses over a range of trophic levels (e.g. insectivores and insect prey, pollinators and pollinated plants) can represent the effects of environmental degradation on specific ecological processes, and bats can thus have important roles as ecological indicators. Bats can also be important environmental indicators because they are sensitive to a wide range of environmental stresses to which they respond in predictable ways. Additionally, the wide range of food sources exploited by bats allows them to be used as indicators for a wide range of environmental stressors. The earth is now subject to climate change and habitat deterioration on unprecedented scales. Monitoring climate change and habitat loss alone is insufficient if we are to understand the effects of these factors on complex biological communities. It is therefore important to identify bioindicator taxa that show measurable responses to climate change and habitat loss and that reflect wider-scale impacts on the biota of interest. Bats have enormous potential as bioindicators: they show taxonomic stability, trends in their populations can be monitored, short- and long term effects on populations can be measured and they are distributed widely around the globe. Because insectivorous bats occupy high trophic levels, they are sensitive to accumulations of pesticides and other toxins, and changes in their abundance may reflect changes in populations of arthropod prey species. Bats provide several ecosystem services, and hence reflect the status of the plant populations on which they feed and pollinate as well as the productivity of insect communities. Bat populations are affected by a wide range of stressors that affect many other taxa. In particular, changes in bat numbers or activity can be related to climate change (including extremes of drought, heat, cold and precipitation, cyclones and sea level rise), deterioration of water quality, agricultural intensification, loss and fragmentation of forests, fatalities at wind turbines, disease, pesticide use and overhunting. There is an urgent need to implement a global network for monitoring bat populations so their role as bioindicators can be used to its full potential.

16.4.3.1 Why Bats?

Bats are excellent indicator taxa that have been used as ecological indicators of habitat quality (Wickramasinghe et al. 2003; Kalcounis-Rueppell et al. 2007).They are also sensitive to human-induced changes to ecosystems (Fenton et al. 1992; Estrada et al. 1993a, b; Medellín et al. 2000; Moreno and Halffter 2000, 2001; Estrada and Coates-Estrada 2001a, b; Clarke et al. 2005a, b; Hayes and Loeb 2007; Kunz et al. 2007). Insectivorous bats occupy higher trophic levels and would be excellent indicators owing to the relationship between contaminant and/or environmental disturbance and trophic levels (Alleva et al. 2006). Dietary accumulation and metabolic capacity increases at higher positions in the food chain, and insectivorous bats are likely to show the consequences of pollutants before organisms at lower trophic levels such as herbivorous insects or birds. The slow reproductive rates of bats mean that populations take a long time to recover from declines, and although population declines take longer to detect, trends are less subject to noise that may confound patterns in short-term studies of fast reproducing taxa such as insects. Although bat populations can be monitored directly to assess longterm population changes (Walsh et al. 2001), short term impacts on insectivorous bats can be quantified by monitoring ‘feeding buzzes’ – increases in the rate of emission of echolocation calls as bats home in on insect prey (Griffin et al. 1960).

With respect to other criteria that make groups of species suitable indicators, the taxonomy of bats is mostly stable, at least at the species level. Although the genera of some bat species have been changed (Kearney et al. 2002; Simmons 2005), relatively few species names have been altered. However, several new cryptic species have recently been discovered (Jones and Van Parijs 1993; Kingston et al. 2001; Mayer and von Helversen 2001; Kiefer et al. 2002; Kingston and Rossiter 2004; Jacobs et al. 2006) and there are likely to be more as bat research increases. However, this problem is relatively minor (compared to insects or birds with their greater diversity) and is easily circumvented by the careful choice of indicator species. Cost-effectiveness can be an important criterion in determining the practical feasibility of long-term surveys of potential indicator taxa (Gardner et al. 2008). However, many frugivorous and nectar-feeding taxa, involve low-cost trapping methods such as the use of mist-nets and harp traps (Kunz et al. 2009b).

16.4.3.2 The Importance of Bats in Ecosystems

The extensive taxonomic and functional diversity of bats makes them well suited as bioindicators (Patterson et al. 2003; Simmons and Conway 2003). Indeed, bats are among the most diverse and geographically dispersed group of living mammals. They form some of the largest non-human aggregations of mammals, and may be among the most abundant groups of mammals when measured in numbers of individuals (Kunz 2003; O’Shea and Bogan 2003). Powered flight sets bats apart from other mammals, and this most likely has been an important factor contributing to their widespread distribution and diversity (Kunz and Fenton 2003). Living bats are known from all continents except Antarctica and their distribution ranges from the southern tip of South America to northern Scandinavia (Kunz and Pierson 1994; Willig et al. 2003). They are absent only from Polar Regions and some isolated oceanic islands. Powered flight has also contributed to their extraordinary feeding and roosting habits, reproductive strategies and social behaviours (Patterson et al. 2003; Simmons and Conway 2003). Roosting habitats include foliage, caves, rock crevices, hollow trees, crevices beneath exfoliating bark and an assortment of man-made structures (Kunz 1982; Kunz and Lumsden 2003; Kunz and Reynolds 2003). Their rich dietary diversity, which includes insects, fruits, leaves, flowers, nectar, pollen, seeds, fish, frogs, other vertebrates and blood, is unparaleled among the orders of living mammals (Kunz and Pierson 1994; Patterson et al. 2003; Simmons and Conway 2003).

Bats are important in terms of their ecological and economic roles. Because bats fill such a wide array of ecological niches, they offer an important multisensory role in assessing ecosystem health. Old World pteropodids and New World phyllostomids are important pollinators and seed dispersers for a number of ecologically and economically important plants (Fujita and Tuttle 1991; Kunz and Pierson 1994; Kunz 1996; Hodgkinson et al. 2003). The New World plant-visiting bat *Leptonycteris curasoae* appears to be the major pollinator of two primary cactus species of the Sonoran Desert, the cardon and organ pipe cactuses (Fleming et al. 2001; Fleming et al. 1996; Molina-Freaner et al. 2004). The Old World bats *Rousettus aegypticaus*, *Epomophorus wahlbergi* and *Eidolon helvum* pollinate flowers of the baobab tree, an economically important species in the African savannah (Kunz 1996). On faunally depauperate oceanic islands, pteropodids are often the sole pollinators of plants that are known to have multiple pollinators on mainland areas, and they are often the only vertebrates large enough to carry large-seeded fruits (Fleming and Racey 2009).

Thus, in these assemblages, plant-visiting bats may fulfill keystone roles in structuring local forest communities. As frequent dispersers of pioneer species such as *Solanum* and *Piper*, bats are important for the revegetation of cleared areas (Kelm et al. 2008). Over 186 paleotropical plant species utilized by flying foxes (*Pteropus*) have been identified as being of economic importance to people for a variety of products, including food, medicines, dyes, fibers, ornamental plants, and timber (Fujita and Tuttle 1991). For example, pteropodids are the primary pollinators of two plant species that are extremely important to the local economies of Southeast Asia, durian *Durio zibethinus* and petai *Parkia speciosa* and *P. javanica*, and thus play vital roles in both pollination and seed dispersal of a number of valuable timber species (Start and Marshall 1976).

Insectivorous species are the primary consumers of nocturnal insects. Given the relatively large volumes consumed (up to 100% of body mass per night, e.g. Kurta et al. 1989a, b) and the long distances travelled (several km per night), these bats are thought to play a major role in suppressing nocturnal insect populations and transporting nutrients across the landscape, particularly from stream corridors to tree roosts (Pierson 1998). Indeed, experiments show that bat exclusion reduces the numbers of arthropods and hence limits herbivory more than bird exclusion in Neotropical forests (Kalka et al. 2008). Similar exclusions also show that bats significantly reduce arthropod numbers in coffee *Plantations*, especially during the wet season (Williams-Guillén et al. 2008). Although mosquitoes are often touted as an important dietary item of some insectivorous bats, the overwhelming numbers and diversity of insects eaten by bats are represented by other groups, namely lepidopterans, coleopterans, homopterans, hemipterans and trichopterans (Anthony and Kunz 1977; Whitaker 1993, 1995; Agosta 2002; Agosta and Morton 2003). Bats are predators on a number of economically important insects, including cucumber beetles, June bugs, corn earworm moths, cotton bollworm moths, tobacco budworm moths and Jerusalem crickets (Whitaker 1995; Lee and McCracken 2005), which are important agricultural pests on such crops as corn, cotton and potatoes (Whitaker 1993; Cleveland et al. 2006). Extrapolations based on data from the Winter Garden region of south-central Texas suggest that the presence of large numbers of Brazilian free-tailed bats *Tadarida brasiliensis* can reduce the influence of insect herbivory from cotton boll worms and corn earworms on a transcontinental scale. With a few exceptions, the model suggests that both genetically engineered (Bt) and conventional cotton production is more profitable when large numbers of insectivorous bats are present (Cleveland et al. 2006; Federico et al. 2008).

Bats are taxonomically and functionally diverse, often abundant, global in distribution and provide key ecosystem services. Population declines suggest that bats are affected by environmental stressors, and that monitoring of their populations may give insight into the importance of these stressors in a more general context. We now review specific case studies that illustrate the potentially important roles that bats can play as bioindicators, emphasizing mechanisms that might drive population declines.

In conclusion, Bats are excellent indicators of human-induced changes in climate and habitat quality. They show functional and taxonomic diversity and are widely distributed. Many bats fulfill vital ecosystem services, and declines in bat populations often reflect features of habitat deterioration that have impacts on a wide range of taxa. Bat populations show responses to environmental stressors ranging from alterations in habitat quality to climate change as well as direct exploitation. They are reservoirs of a wide range of diseases whose spread and spillover may be related to habitat deterioration and climate change. Bats have taxonomic stability, and can be monitored by a range of methods (Kunz and Parsons 2009). The importance of bats as bioindicators is already being recognised. For example, in May 2008 the UK government adopted bats into their suite of biodiversity indicators of the sustainability of lifestyles to meet targets under the Convention on Biological Diversity. EUROBATS has a ‘Bats as Indicators’ Intersessional Working Group that aims to take forward opportunities to use bats as biodiversity indicators. It is now time to ‘seize the night’ and to develop a global monitoring programme for bat populations, involving standardised methodology that can be applied in both New and Old World situations, so that the value of bats as bioindicators can be fully realised (Fleming et al. 2009).

16.4.4 Euglossine as Biological Indicators

Biological indicators are used as measurable surrogates for monitoring environmental health. According to Noss (1990), reliable indicators should be: sensitive to provide an early warning of change; distributed over a broad geographic area; provide a continuous assessment over a wide range of states; independent of sample size; easy and effective to measure and collect; and able to differentiate between natural cycles or trends and those induced by anthropogenic stress. As suggested by Roubik and Hanson (2004), male orchid bees serve as potential biological indicators of tropical ecosystems, specifically the ecosystems of organic and conventional coffee *Plantations*. They are long distance pollinators of low to middle- elevation plants across mainland tropical America, comprising 20–30% of the bee community’s species in lowland forests (Ackerman 1983; Roubik and Hanson 2004). According to Dressler (1982), large numbers of males may be collected without seriously affecting the reproduction and survival of the population. Male euglossine bees possess a highly sensitive sense of smell (Schiestl and Roubik 2003) that may allow them to detect chemical disruptions in their habitat such as synthetic pesticides and herbicides. They are highly attracted to perfumes of plants other than orchids, which they collect on specialized hairs on their forelegs and hind tibias for unknown use (Roubik and Hanson 2004). They have a memory for scents relative to their location and can trace the origin of an odor from up to 1 km away (Dressler 1982). According to a study by Ackerman (1983) in central Panama, species richness and bee abundance are correlated; both fluctuate seasonally and peak in the early wet season. Individuals are known to fly long distances, up to 2.5 km, in response to a perfume bait (Dressler 1968), and according to Janzen (1981), will seek a variety of resources in different and distant habitats when their original habitat becomes seasonally severe. Under ordinary circumstances, every orchid bee can cover an area of over 1,000 km^2 a day (Roubik and Hanson 2004). Janzen (1981) suggests that distances in excess of 20 km are normal for foraging, and greater distances are feasible when resources become scarce. However, according to Ackerman (1983), species composition, evenness, and dominance ranks were virtually non-seasonal, so the male euglossine bee community seems to have some structural continuity. The orchid bees may serve as viable biological indicators of ecosystem health because they exhibit many of the aforementioned qualities of biological indicators. variables such as seasonality has been taken into account to project the most effective conditions for using euglossine bees as a biological indicator of agricultural ecosystem health.

16.5 Conclusions

Pollinators are key to global sustainable terrestrial productivity. They are a bellwether for environmental stress as individuals and as colonies. Moreover, their populations and diversity also serve as bioindicators of the state of many environments and their productivities. Honeybee keeping stands at the threshold of major changes as mite parasitism in Europe, the Americas and Asia has stimulated intensive research in bee breeding for resistance and tolerance, in honeybee protection by synthetic and natural biocides, and in sophisticated management. Certainly, agriculture cannot function efficiently without honeybees and the potential for diversifying stocks within the genus is great (Rinderer 1995; Sylvester 1995). There is increasing recognition of the importance of non-honeybees as crop pollinators (Bohart 1972; Kevan 1987, 1990; Parker et al. 1987; Torchio 1987, 1990, 1991, 1994; Kevan et al. 1990a; Richards 1987, 1993; Roubik 1995; Matheson et al. 1996). Nevertheless, pollinator populations seem to be declining world wide though the effects of pesticides, habitat (Kunz et al. 1977) destruction, spread of diseases and parasites, and competition from introduced flower visitors. The protection of native pollinators is critical (Bailey and Ball 1991; Kevan 1991, 1993; Krell 1995). It would thus be prudent to set aside areas for native pollinators in agroecosystems and to encourage their populations by providing forage and nesting sites for their conservation (Corbet 1995). Krell (1995) and (Corbet 1995; Kunz et al. 2008, 2009) discuss the importance of hedges, field margins, riparian forests, rights of way, road-sides, copses, successional growth, and home gardens as places where native pollinators can thrive. Several recent publications (Banaszak 1995a, b; Kevan 1995; Buchmann and Nabhan 1996; Matheson et al. 1996; Kearns and Inouye 1997) have alerted the general public, policy makers and planners, and politicians to the importance of pollination and pollinators, the seriousness of their demise, and the urgency for their conservation.

References

Accorti M, Persano OL (1986) Un servizio di monitoraggio ambientale urbano: "Apincittà". Informatore Agrario 42:39–41

Ackerman JD (1983) Diversity and seasonality of male euglossine bees (Hymenoptera: Apidae) in Central Panama. Ecology 64:274–283

Agosta SJ (2002) Habitat use, diet, and roost selection by the big brown bat (*Eptesicus fuscus*) in North America: a case for conserving an abundant species. Mammal Rev 32:179–198

Agosta SJ, Morton D (2003) Diet of the big brown bat, *Eptesicus fuscus*, from Pennsylvania and western Maryland. Northeast Nat 10:89–104

Alleva E, Francia N, Pandolfi M, De Marinis AM, Chiarotti F, Santucci D (2006) Organochlorine and heavy-metal contaminants in wild mammals and birds of Urbino-Pesaro Province, Italy: an analytic overview for potential bioindicators. Arch Environ Contam Toxicol 51:123–134

Altieri MA (1987) Agroecology: scientific basis of alternative agriculture. Westview Press, Boulder, 227 pp

Altieri MA, Whitcomb WH (1979) The potential use of weeds in the manipulation of beneficial insects. Hortic Sci 14:12–18

Anderson JF, Wojtas MA (1986) Honey bees (Hymenoptera: Apidae) contaminated with pesticides and polychlorinated biphenyls. J Econ Entomol 79:1200–1205

Anthony ELP, Kunz TH (1977) Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 58:775–786

Arita HT, Martinez C (1990) Interacciones Flor-Murcielago: Un Enfoque Zoocentrico. Universidad Nacional Autonoma de Mexico, Mexico

Atkins EL, Kellum D, Atkins KW (1981) Reducing pesticides hazard to honey bees: mortality prediction techniques and integrated management strategies. Division of Agricultural Sciences, University of California, Leaf. 2883, 22 pp (with: Supplemental list to leaflet 2883 (1981) compiled by E Atkins Nov 1990)

Babendreier D, Kalberer N, Romeis J, Fluri P, Bigler F (2004) Pollen consumption in honey bee larvae: a step forward in the risk assessment of transgenic plants. Apidologie 35:293–300

Bailey L, Ball BV (1991) Honey bee pathology, 2nd edn. Academic Press, London, 193 pp

Banaszak J (ed) (1995a) Changes in the fauna of wild bees in Europe. Pedagogical University, Bydgoszcz, 220 pp

Banaszak J (ed) (1995b) Natural resources of wild bees in Poland. Pedagogical University, Bydgoszcz, 174 pp

Banda HJ, Paxton RJ (1991) Pollination of greenhouse tomatoes by bees. Acta Hortic 288:194–198

Barisic D, Lazaric K, Lulic S, Vertacnik A, Drazic M, Kezic N (1994) ^{40}K, ^{134}Cs and ^{137}Cs in ollen, honey and soil surface layer in Croatia. Apidologie 25(6):585–595

Barišic D, Bromenshenk JJ, Keziæ N, Vertaènik A (2002) The role of honey bees in environmental monitoring in Croatia. In: Devillers J, Pham-Delègue MH (eds) Honey bees: estimating the environmental impact of chemicals. Taylor & Francis, London/New York, pp. 160–185

Beccaloni GW, Gaston KJ (1995) Predicting the species richness of Neotropical forest butterflies: Ithominae (Lepidoptera: Nymphalidae) as indicators. Biol Conserv 71:77–86

Bernhardt P, Thien LB (1987) Self-isolation and insect pollination in primitive angiosperms: new evaluations of older hypotheses. Plant Syst Evol 156:159–176

Bohart GE (1972) Management of wild bees for pollination of crops. Annu Rev Entomol 17:287–312

Bowman DM, Woinarski JC, Sands DP, Wells A, McSHane VJ (1990) Slash and burn agriculture in the wet coastal lowlands of Papua New Guinea: response of birds, butterflies and reptiles. J Biogeogr 17:227–239

Bromenshenk JJ, Carlson SR, Simpson JC, Thomas JM (1985) Pollution monitoring of puget sound with honey bees. Science 227:632–634

Bromenshenk JJ, Gudatis JL, Carlson SR, Thomas JM, Simmons MA (1991) Population dynamics of honey bee nucleus colonies exposed to industrial pollutants. Apidologie 22:359–369

Buchmann SE (1983) Buzz pollination in angiosperms. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp 73–113

Buchmann SE, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington, DC, 292 pp

Bunzl K, Kracke W, Vorwohl G (1988) Transfer of Chernobyl-derived 134Cs, 137Cs, 131I, and 103Ru from flowers to honey, and 103Ru from flowers to honey and pollen. J Environ Radioact 6:261–269

Callicott JB (1995) A review of some problems with the concept of ecosystem health. Ecosyst Health 1:101–112

Cane JH, Payne JA (1988) Foraging ecology of *Habropoda laboriosa* (Hymenoptera: Anthophoridae), and oligolege of blueberries (Ericaceae: *Vaccinium*) in southeastern United States. Ann Entomol Soc Am 81:419–427

Cane JH, Payne JA (1990) Native bee pollinates rabbiteye blueberry: highlights in agricultural research. Alabama Agric Res Sta 37(4):4

Cavalchi B, Fornaciari S (1983) Api, miele, polline e propoli come possibili indicatori di un inquinamento da piombo e fluoro – Una esperienza di monitoraggio biologic nel comprensorio ceramico di Sassuolo-Scandiano. In: Manzini P, Spaggiari R (eds) Atti del seminario di studi "i biologi e l'ambiente" Nuove esperienze per la sorveglianza ecologica. Reggio Emilia, 17–18 Febbraio 1983, pp 275–300

Celli G (1983) L'ape come insetto test della salute di un territorio. In: Arzone A, ContiM, Currado I, Marletto F, Pagiano G, Ugolini A, Vidano C (eds) Atti XIII Congresso Nazionale Italiano Ento139 mologia, Sestriere – Torino, pp 637–644

Celli G, Maccagnani B (2003) Honey bees as bioindicators of environmental pollution. Bull Insectol 56(1):137–139

Celli G, Porrini C (1987) Apicidi e residui di pesticide nelle api e nell'alveare in Italia (1983–1986). Bollettin dell'Istituto di Entomologia "Guido Grandi" dell'Università degli Studi di Bologna 42:75–86

Celli G, Porrini C (1991) L'ape, un efficace bioindicatore dei pesticidi. Le Scienze 274:42–54

Celli G, Poggiali F, Giordani G (1975) Inquinamento del nettare dei fiori di melo da endosulfan in rapporto a ripercussioni nocive sulle api bottinanti. In: Goidanich G, Stupazzoni G, Foschi S (eds) Atti Giornate Fitopatologiche, Torino, pp 117–120

Celli G, Porrini C, Frediani D, Pinzauti M (1987) Api e piombo in città (nota preventiva). In: Bufalari V (ed) Atti del convegno: "Qualità dell'aria indicatori biologici api e piante", Firenze, 19 Mar 1987, pp 11–45

Celli G, Porrini C, Raboni F (1988a) Monitoraggio con api della presenza dei Ditiocarbammati nell'ambiente (1983–1986). Bollettino dell'Istituto di Entomologia "Guido Grandi" dell'Università degli Studi di Bologna 43:195–205

Celli G, Porrini C, Siligardi G, Mazzali P (1988b) Le calibrage de l'instrument abeille par rapport au plomb. In: Proceedings XVIII international congress of entomology, Vancouver, 3–9 Aug 1988, p 467

Celli G, Porrini C, Tiraferri S, (1988c) Il problema degli apicidi in rapporto ai principi attivi responsabili (1983–1986). In: Brunelli A, Foschi S (eds) Atti Giornate Fitopatologiche, vol 2. Lecce, pp 257–268

Celli G, Porrini C, Balesstra V, Menozzi R (1989) Monitoraggio di inquinanti atmosferici urbani mediante api. Giornate di Studio su Salute e Ambiente, Cagliari, Italia 27–28 maggio 1989, pp 73–85

Celli G, Porrini C, Baldi M, Ghigli E (1991) Pesticides in Ferrara Province: two years' monitoring with honey bees (1987–1988). Ethol Ecol Evol Spec Issue 1:111–115

Clarke FM, Pio DV, Racey PA (2005a) A comparison of logging systems and bat diversity in the neotropics. Conserv Biol 19:1194–1204

Clarke FM, Rostant LV, Racey PA (2005b) Life after logging: post-logging recovery of a neotropical bat community. J Appl Ecol 42:409–420

Cleveland CJ, Frank JD, Federico P, Gomez I et al (2006) Economic value of the pest control service provided by Brazilian free-tailed bat in south-central Texas. Front Ecol Environ 4:238–243

Cody ML (1985) An introduction to habitat selection in birds. In: Cody ML (ed) Habitat selection in birds. Academic, Orlando, pp 4–56

Corbet SA (1995) Insects, plants and succession: advantages of long-term set-aside. Agric Ecosyst Environ 53:201–217

Corbet SA, Williams IH, Osborne JL (1991) Bees and the pollination of crops and wild flowers in the European Community. Bee World 72:47–59

Costanza R (1992) Towards an operational definition of ecosystem health 1. Measuring ecosystem health. In: Constanza R, Norton BG, Haskel BD (eds) Ecosystem health: new goals for environmental management. Island Press, Washington, DC, pp 239–256

Cox PA, Elmquist T, Pierson E, Rainey WE (1991) Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. Conserv Biol 5:448–454

Crane E (1984) Bees, honey and pollen as indicators of metals in the environment. Bee World 55:47–49

Crane E (1990) Bees and beekeeping: science, practice and world resources. Heinemann, Oxford, 614 pp

Dewey JE (1973) Accumulation of fluorides by insects near an emission source in western Montana. Environ Entomol 2:179–182

Dixon DP, Fingler BG (1982) The effects of the 1981 Manitoba emergency mosquito control program on honey bees. In: Western equine encephalitis in Manitoba. Government of Manitoba, Winnipeg, pp 243–247

Dixon DP, Fingler BG (1984) The effects of the mosquito control program on bees. In: Final technical report volume, environmental monitoring program for the 1983, aerial spraying of malathion to combat western equine encephalitis. Environmental Management Division, Manitoba Department of Environment, Workplace Safety and Health, Winnipeg, pp 101–121

Drescher W (1982) Die Eignung der Bienen als Indikatoren für Umweltbelastungen. Decheniana 26:171–177

Dressler RL (1968) Pollination by euglossine bees. Evolution 22:202–210

Dressler RL (1982) Biology of the orchid bees (Euglossini). Annu Rev Ecol Syst 13:373–394

Edwards M (1996) Optimizing habitats for bees in the United Kingdom: a review of recent conservation action. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) The conservation of bees, vol 18, Linnean social symposium series. Academic, London, pp 35–47

Ellis WN, Ellis-Adam AC (1993) To make a meadow it takes a clover and a bee: the entomophilous flora of northwestern Europe and its insects. Bijdragen tot de Dierkunde 63:193–220

Ellis WN, Ellis-Adam AC (1995) Flower visitation, plant's life forms, plant's life forms and ecological characteristics (Syrphidae, Parasitica). Proc Sec Appl Entomol Neth Entomol Soc (NEV) 6:53–58

Erickson EH, Atmowidjojo AH, Hines L (1998) Can we produce *Varroa*-tolerant honeybees in the United States? Am Bee J 138(11):828–832

Espina D (1986) Beekeeping of the assassin bees. Editorial Tecnologica de Costa Rica, San Juan, 170 pp

Estrada A, Coates-Estrada R (2001a) Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. Ecography 24:94–102

Estrada A, Coates-Estrada R (2001b) Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. J Trop Ecol 17:627–646

Estrada A, Coates-Estrada R, Merrit D Jr (1993a) Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography 16:309–318

Estrada A, Coates-Estrada R, Merrit D, Montiel S, Curiel D (1993b) Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. In: Fleming TH, Estrada A (eds) Frugivores and seed dispersal: ecological and evolutionary aspects. Kluwer, Dordrecht, pp 245–257

Faegri K, van der Pijl L (1979) The principles of pollination ecology. Pergamon Press, Oxford, 244 pp

FAO (1986) Tropical and subtropical apiculture. Bull. No. 68. Agricultural Service, FAO, Rome, 283 pp

Federico P, Hallam TG, McCracken GF, Purucker ST et al (2008) Brazilian free-tailed bats (*Tadarida brasiliensis*) as insect predators in transgenic and conventional cotton crops. Ecol Appl 18:826–837

Fenton MB, Acharya L, Audet D, Hickey MBC, Merriman C, Obrist MK, Syme DM (1992) Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica 24:440–446

Fleming TH, Racey PA (2009) An introduction to Island bats. In: Fleming TH, Racey PA (eds) Island bats: ecology, evolution, and conservation. University of Chicago Press, Chicago, pp 1–14

Fleming TH, Tuttle MD, Horner MA (1996) Pollination biology and relative importance of nocturnal and diurnal pollinatorsin three species of Sonoran desert columnar cacti. Southwest Nat 41:257–269

Fleming TH, Sahley CT, Holland JN, Nason JD, Hamrick JL (2001) Sonoran desert columnar cacti and the evolution of generalized pollination systems. Ecol Monogr 71:511–530

Fleming TH, Geiselman C, Kress WJ (2009) The evolution of bat pollination: a phylogenetic perspective. Ann Bot 104(6):1017–1043

Ford BC, Jester WA, Griffith SM, Morse RA, Zall RR, Burgett DM, Bodyfelt FW, Lisk DJ (1988) Cesium-134 and Cesium-137 in honey bees and cheese samples collected in the US after the Chernobyl accident. Chemosphere 17:1153–1157

Frankie GW, Vinson SB, Newstrom LE, Barthell JF, Haber WA, Frankie JK (1990) Plant phenology, pollination ecology, pollinator behavior and conservation of pollinators in neotropical dry forest. In: Bawa KS, Hadley M (eds) Reproductive ecology of tropical forest plants, vol 7, Man and the biosphere series. Parthenon, Carnforth, pp 37–47

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London, 684 pp

Fries I, Wibran K (1987) Effects on honey-bee colonies following application of the pyrethroids cypermethrin and PP 321 in flowering oilseed rape. Am Bee J 127:266–269

Fujita MS, Tuttle MD (1991) Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. Conserv Biol 5:455–463

Fuller RJ, Gough SJ, Marchant JH (1995a) Bird populations in new lowland woods: landscape, design and management perspectives. In: Ferris-Kaan R (ed) The ecology of woodland creation. Wiley, London, pp 163–182

Fuller RJ, Gregory RD, Gibbons DW, Marchant JH, Wilson JH, Baillie JD, Carter SR (1995b) Population declines and range contractions among lowland farmland birds in Britain. Conserv Biol 9:1425–1441

Gardner TA, Barlow J, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes MIM, Hernandez MIM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Sontos R, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, da Silva MNF, da Silva Motta C, Peres CA (2008) The cost effectiveness of biodiversity surveys in tropical forests. Ecol Lett 11:139–150

Gattavecchia E, Ghini S, Tonelli D, Porrini C (1987) Il miele italiano dopo Chernobyl. L'ape nostra Amica 9(5):27

Ginevan ME, Lane DD, Greenberg L (1980) Ambient air concentration of sulfur dioxide affects flight activity in bees. Proc Natl Acad Sci USA 77:5631–5633

Graham JM (ed) (1992) The hive and the honey bee. Dadant and Sons, Hamilton, 1324 pp

Grant V, Grant KA (1965) Flower pollination in the phlox family. Columbia University Press, New York, 179 pp

Grant KA, Grant V (1968) Hummingbirds and their flowers. Columbia University Press, New York, 115 pp

Greatorex-Davies JN, Sparks TH, Hall ML, Marrs RH (1993) The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. Biol Conserv 63:31–41

Greco CF, Kevan PG (1994) Contrasting patch choosing by anthophilous ambush predators: vegetation and floral cues for decisions by a crab spider (*Misumena vatia*) and males and females of an ambush bug (*Phymata americana*). Can J Zool 72:1580–1588

Gregory RD, van Strein A, Vorisek P, Gmelig Meyling AM, Noble DG, Foppen RPB, Gibbons DW (2005) Developing indicators for European birds. Proc R Soc Lond Ser B Biol Sci 360: 269–288

Griffin DR, Webster FA, Michael CR (1960) The echolocation of flying insects by bats. Anim Behav 8:141–154

Haarmann TK (1997) Honey bees as indicators of radionuclide contamination: exploring sample consistency and temporal contaminant accumulation. J Apic Res 36(2):77–87

Haarmann TK (2000) Honey bees as indicators of radionuclide contamination: a truly useful biomonitor? In: Devillers J, Minh-H, Pham-Delègue M (eds) Honey bees estimating the environmental impact of chemicals. CRC Press, London/New York, pp 132–150

Haeseler V (1972) Man-made habitats (deforested area, gravel pit, city gardens, city gardens and parks) as refuges for insects. Hym Aculeata Zoologische Jahrbuch für Systematik 99:133–212

Haeseler V (1982) Ameisen, Wespen und Bienen als Bewohner gepflasterter Bügersteige, Parkplätze und Strassen (Hymenoptera: Aculeata). Drosera 82:17–32

Hansen H, Petersen JH (1988) Residues in honey and wax after treatment of honeybee colonies with brompropylate. Danish J Plant Soil Sci 92:1–6

Hayes JP, Loeb SC (2007) The influences of forest management on bats in North America. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, pp. 207–235

Hill JK, Hamer KC, Lace LA, Banham WMT (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. J Appl Ecol 32:754–760

Hilty J, Merenlender A (2000) Faunal indicator taxa selection for monitoring ecosystem health. Biol Conserv 92:185–197

Hodgkinson R, Balding ST, Zubaid A, Kunz TH (2003) Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in lowland Malaysian rain forest. Biotropica 35:491–502

Hurd PD Jr, Linsley EG (1975) The principle Larrea bees of the southwestern United States. Smithson Contr Zool 193:1–74

Inouye DW (1980) The terminology of floral larceny. Ecology 61:1251–1253

Jacob-Remacle A (1984) Étude écologique du peuplement d'hyménoptères aculéates survivant dans la zone la plus urbinisée de la ville de Liège. Bull Annu Soc R Belge Entomol 120: 241–262

Jacobs DS, Eick GN, Schoeman MC, Matthee CA (2006) Cryptic species in an insectivorous bat *Scotophilus dinganii*. J Mammal 87:161–170

Jamieson D (1995) Ecosystem health: some preventative medicine. Environ Values 4:333–350

Janzen DH (1981) Bee arrival at two Costa Rican female *Catasetum* orchid inflorescences, and a hypothesis on euglossine population structure. Oikos 36:177–183

Jervis MA, Kidd NAC, Fitton MG, Huddleston T, Dawah HA (1993) Flower-visiting by Hymenoptera parasitoids. J Nat Hist 27:67–105

Johansen CA (1977) Pesticides and pollination. Annu Rev Entomol 22:177–192

Johansen CA, Brown FC (1972) Toxicity of carbaryl – contaminated pollen collected by honeybees. Environ Entomol 1:385–386

Johansen CA, Mayer DF (1990) Pollinator protection. A bee and pesticide handbook. Wicwas Press, Cheshire, 212 pp

Jones G, van Parijs SM (1993) Bimodal echolocation in pipistrelle bats: are cryptic species present? Proc R Soc Lond Ser B 251:119–125

Kalcounis-Rueppell MC, Payne VH, Huff SR, Boyko AL (2007) Effects of wastewater treatment plant effluent on bat foraging activity in an urban stream system. Biol Conserv 138:120–130

Kalka MB, Smith AR, Kalko EKV (2008) Bats limit arthropods and herbivory in a tropical forest. Science 320:71

Kearney C, Volleth M, Contrafatto G, Taylor PJ (2002) Systematic implications of chromosome GTG-band and bacula morphology for southern African *Eptesicus* and *Pipistrellus* and several other species of Vespertilioninae (Chiroptera: Vespertilionidae). Acta Chiropt 4:55–76

Kearns CA, Inouye DW (1997) Pollinators, flowering plants, and conservation biology. BioScience 47:297–307

Kelm DH, Wiesner KR, von Helversen O (2008) Effects of artificial roosts for frugivores bats on seed dispersal in a Neotropical forest pasture mosaic. Conserv Biol 22:733–741

Kevan PG (1974) Pollination, pesticides, and environmental quality. BioScience 24:198–199

Kevan PG (1975a) Pollination and environmental conservation. Environ Conserv 2:293–298

Kevan PG (1975b) Forest application of the insecticide Fenitrothion and its effects on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in southern New Brunswick, Canada. Biol Conserv 7:301–309

Kevan PG (1984a) Insect pollination of economically important plants of tropical and sub-tropical Asia. In: Expert consultation on beekeeping with *Apis mellifera* in tropical and sub-tropical Asia. Bangkok and Chiang Mai, Thailand. Food and Agriculture Organization of the United Nations, Rome, pp 77–85

Kevan PG (1984b) Pollination by animals and angiosperm biosystematics. In: Grant WF (ed) Plant biosystematics. Academic, Toronto, pp 271–292

Kevan PG (1986) Pollinating and flower visiting insects and the management of beneficial and harmful insects and plants. In: Hussein MY, Ibrahim AG (eds) Biological control in the Tropics: proceedings of the "First Regional Symposium on Biological Control" held at Universiti Pertanian Malaysia, Serdang from 4–6 Sep 1985, Universiti Pertanian Malaysia, Serdang, Selangor, pp 439–452

Kevan P (1987) Alternative pollinators for Ontario's crops. Proc Entomol Soc Ont 118:109–170

Kevan PG (1989a) Recent Canadian progress on the biology, management and protection of native pollinators:ca.1983–1988. In: National workshop on bee and pollination research, Winnipeg, Agriculture Canada, Ottawa, pp 63–72, 4–5 Apr 1989

Kevan PG (1989b) Commodity-oriented pollination. In: National workshop on bee and pollination research, Winnipeg, 4–5 Apr 1989. Agriculture Canada, Ottawa, pp 168–171

Kevan PG (1990) Beekeeping and pollination at the crossroads. III alternative pollinators. Can Beekeep 16(1):8–11

Kevan PG (1991) Pollination: keystone process in sustainable global productivity. Acta Hortic 288:103–110

Kevan PG (1993) Conservation and management of pollinators: an issue in sustainable global productivity. In: Conner LJ, Rinderer T, Sylvester A, Wongsiri S (eds) Asian apiculture. Wicwas Press, Cheshire, pp 281–288

Kevan PG (1995) Applied pollination in Asia. In: Roubik DW (ed) Pollination of cultivated crops in the tropics. Food and Agriculture Organization of the United Nations, Bulletin Number 118, Rome

Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annu Rev Entomol 28:407–453

Kevan PG, Baker HG (1998) Insects on flowers: pollination and floral visitations. In: Huffaker CB, Gutierrez RC (eds) Insect ecology, 2nd edn. Wiley, New York, pp 607–631

Kevan PG, Oppermann EB (1980) Nova Scotia and Maine: a reply to Wood et al. Can J Agric Econ 28:81–84

Kevan PG, Plowright RC (1989) Fenitrothion and insect pollination. In: Ernst WR, Pearce PA, Pollock TL (eds) Environmental effects of fenitrothion use in forestry: impacts on insect pollinators, songbirds, and aquatic organisms. Environment Canada, Dartmouth, pp 13–42

Kevan PG, Plowright RC (1995) Forest insect pests in Canada. In: Armstrong JA, Ives WGH (eds) Natural resources Canada. Canadian Forest Services, Ottawa, pp 607–618, Chapter 59

Kevan PG, Gadawski RM, Kevan SD, Gadawski SE (1984) Pollination of cranberries, *Vaccinium macrocarpon*, on cultivated marshes in Ontario. Proc Entomol Soc Ont 114:45–53

Kevan PG, Hussein NY, Hussey N, Wahid MB (1986) Modelling the use of *Elaeidobius kamerunicus* for pollination of oil palm. Planter 62:89–99

Kevan PG, Mohr NA, Offer M, Offer D, Kemp JR (1988) The squash and gourd bee, *Peponapis pruinosa* (Hymenoptera: Anthophoridae) in Ontario, Canada. Proc Entomol Soc Ont 119:9–15

Kevan PG, Clark EA, Thomas VG (1990a) Insect pollinators and sustainable agriculture. Am J Altern Agric 5:13–22

Kevan PG, Clark EA, Thomas VG (1990b) Pollination: a crucial ecological and mutualistic link in agroforestry and sustainable agriculture. Proc Entomol Soc Ont 121:43–48

Kevan PG, Clark EA, Thomas VG (1991a) Pollination: a crucial link in agroforestry and sustainable agriculture. In: Proceedings of 1st conference agroforestry in North America. Ontario Ministry of Agriculture and Food, Guelph, pp 242–248

Kevan PG, StraverWA, Offer M, Laverty TM (1991b) Pollination of greenhouse tomatoes by bumblebees in Ontario. Proc Entomol Soc Ont 122:15–19

Kevan PG, Greco CF, Belaoussoff S (1997) Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths. J Appl Ecol 34:1122–1136

Kiefer A, Mayer F, Kosuch J, von Helversen O, Veith M (2002) Conflicting molecular phylogenies of European long-eared bats (*Plecotus*) can be explained by cryptic diversity. Mol Phylogenet Evol 25(3):557–566

King JL, Holloway JK (1930) *Tiphia popilliavora* Rohwer, a parasite of the Japanese beetle. US Department of Agriculture Circular No. 145, p 11

Kingsmill S (1993) Pollinators in peril. Nat Can 22(2):15–23

Kingston T, Rossiter SJ (2004) Harmonic-hopping in Wallacea's bats. Nature 429:654–657

Kingston T, Lara MC, Jones G, Akbar Z, Schneider CJ, Kunz TH (2001) Acoustic divergence in two cryptic Hipposideros species: a role for social selection? Proc R Soc Lond Ser B 268:1381–1386

Klemm M (1996) Man-made bee habitats in the anthropogenous landscape of central Europe: substitutes for threatened or destroyed riverine habitats? In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) The conservation of bees, vol 18, Linnean social symposium series. Academic, London, pp 17–34

Koskimies P (1989) Birds as a tool in environmental monitoring. Ann Zool Fenn 26:153–166

Kratochwil A, Klatt M (1989) Bee species of ruderal sites in the city of Freiburg: Br (FRG) submediterrenean elements in mosaic habitats with high persistence. Zoologische Jahrbuch für Systematik 116:379–389

Krell R (1995) Alternatives to artificial pollinator populations (Part 1.6 pp 74–84) and Successful pollination with enhanced pollinator populations (Part 2.1 pp 93–100). In: Roubik DW (ed) Pollination of cultivated plants in the tropics, vol 118, FAO agricultural service bulletin. FAO, Rome, 196 pp

Kress WJ, Schatz GE, Andrianifahanana M, Morland HS (1994) Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic coevolutionary system. Am J Bot 81:542–551

Krunic' MD, Terzic' LR, Kulinc evic' JM (1989) Honey resistance to air contamination with arsenic from a copper processing plant. Apidologie 20:251–255

Kubik M, Nowacki J, Michalczuk L, Pidek A, Marcinkowski J (1995) Penetration of fluvalinate into bee-products. J Fruit Ornam Plant Res 1:13–22

Kunz TH (1982) Roosting ecology of bats. In: Kunz TH (ed) Ecology of bats. Plenum Press, New York, pp 1–55

Kunz TH (1996) Obligate and opportunistic interactions of Old World tropical bats and plants. In: Hasan ZA, Zubaid A (eds) Conservation and faunal biodiversity in Malaysia. Penerbit Universiti Kebangsaan Malaysia, Kuala Lumpur, pp 37–65

Kunz TH (2003) Censusing bats: challenges, solutions, and sampling biases. In: O'Shea TJ, Bogan MA (eds) Monitoring trends in bat populations of the United States and territories: problems and prospects. US Geological Survey, Biological Resources Division, Information and Technology Report, USGS/BRD/ITR-2003-003, Washington, DC, pp 9–20

Kunz TH, Fenton MB (2003) Bat ecology. University of Chicago Press, Chicago

Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 3–89

Kunz TH, Parsons S (eds) (2009) Ecological and behavioral methods for the study of bats. Johns Hopkins University Press, Baltimore

Kunz TH, Pierson ED (1994) Bats of the world: an introduction. In: Nowak RW (ed) Walker's bats of the world. Johns Hopkins University Press, Baltimore, pp 1–46

Kunz TH, Reynolds DS (2003) Bat colonies in buildings. In: O'Shea TJ, Bogan MA (eds) Monitoring trends in bat populations of the United States and territories: problems and prospects. US Geological Survey, Biological Resources Division, Information and Technology Report, USGS/ BRD/ITR-2003-003, Washington, DC, pp 91–102

Kunz TH, Anthony ELP, Rumage WT (1977) Mortality of little brown bats following multiple pesticide applications. J Wildl Manag 41:476–483

Kunz TH, Arnett EB, Erickson WP, Johnson GD et al (2007) Ecological impacts of wind energy development on bats: questions, hypotheses, and research needs. Front Ecol Environ 5:315–324

Kunz TH, Gauthreaux SA Jr, Hristov NI, Horn JW et al (2008) Aeroecology: probing and modeling the aerosphere. Integr Comp Biol 48:1–11

Kunz TH, Betke M, Hristov NI, Vonhof M (2009a) Methods for assessing colony size, population size, and relative abundance of bats. In: Kunz TH, Parsons S (eds) Ecological and behavioral methods for the study of bats, 2nd edn. Johns Hopkins University Press, Baltimore (in press)

Kunz TH, Hodkison R, Weise C (2009b) Methods of capturing and handling bats. In: Kunz TH, Parsons S (eds) Ecological and behavioral methods for the study of bats, 2nd edn. Johns Hopkins University Press, Baltimore (in press)

Kurta A, Bell GP, Nagy KA, Kunz TH (1989a) Energetics of pregnancy and lactation in free-ranging little brown bats (Myotis lucifugus). Physiol Zool 62:804–818

Kurta A, Bell GP, Nagy KA, Kunz TH (1989b) Water balance of free ranging little brown bats (myotis lucifugus) during pregnancy and lactation. Can J Zool 67:2468–2472

Kushlan JM (1993) Colonial waterbirds as bioindicators of environmental change. Colon Waterbird 16:223–225

Landres PB, Verner J, Thomas JW (1988) Ecological uses of vertebrate indicator species: a critique. Conserv Biol 2(4):316–328

Lee YF, McCracken GF (2005) Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. J Mammal 86:67–96

Leius K (1960) Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. Can Entomol 92:369–376

Leius K (1967) Influence of wild flowers on parasitism of tent caterpillar and codling moth. Can Entomol 99:444–446

Louette M, Bijnens L, Upoki Agenong'a D, Fotso RC (1995) The utility of birds as bioindicators: case-studies in Equatorial Africa. Belg J Zool 125:157–165

MacKay PA, Knerer G (1979) Seasonal occurrence and abundance in a community of wild bees from an old field habitat in southern Ontario. Can Entomol 111:365–376

MacKenzie KE (1993) Honey bees and pesticides: a complex problem. Vector Contr Bull North Central States 1(2):123–136

MacKenzie KE (1994) Pollination of two Ericaceous berry crops, the highbush blueberry (*Vaccinium corymbosum* L.) and the American cranberry (*Vaccinium macrocarpon* Ait.). PhD dissertation, Cornell University, Ithaca

Mardan M, Yatim IM, Khalid MR (1991) Nesting biology and foraging activity of carpenter bee on passion fruit. Acta Hortic 288:127–132

Mardan M, Jaafar ASU, Yatim IM (1993) Investigations on the plant pollinator compatibility between introduced passion fruit and an indigenous large carpenter bee. In: Connor LJ, Rinderer

T, Sylvester HA, Wongsiri S (eds) Asian apiculture. Proceedings of the 1st international conference Asian Honeybees and Bee Mites, Wicwas Press, Cheshire, pp 384–390

Martin EC, McGregor SE (1973) Changing trends in insect pollination of commercial crops. Annu Rev Entomol 18:207–226

Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) (1996) The conservation of bees, vol 18, Linnean social symposium. Academic, London, 252 pp

Mayer DF, Lunden JD (1986) Toxicity of fungicides and an acaricide to honey bees (Hymenoptera: Apidae) and their effects on bee foraging behavior and pollen viability on blooming apples and pears. Environ Entomol 15:1047–1049

Mayer F, von Helversen O (2001) Cryptic diversity in European bats. Proc R Soc Ser B Biol Sci 268:1825–1832

Mayer DF, Johansen CA, Lunden JD, Rathbone L (1987) Bee hazard of insecticides combined with chemical stickers. Am Bee J 127(7):493–495

Mbaya JKS, Kevan PG (1995) Applied pollination in Africa. In: Roubik DW (ed) Pollination of cultivated crops in the tropics. Food and Agriculture Organization of the United Nations, Rome

Medellín R, Equihua M, Amín MA (2000) Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. Conserv Biol 14:1666–1675

Meléndez-Ramírez V (1997) Polinización y biodiversidad de abejas nativas asociadas a cultivos hortícolas en el estado de Yucatán, México. M. Sc. Tesis, Facultad de Medicina Veterinaria y Zootecnia, Universidad Autonoma de Yucatán, Mérida

Molina-Freaner F, Rojas-Martinez A, Fleming TH, Valiente- Banuet A (2004) Pollination biology of the columnar cactus *Pachycereus pecten-aboriginum* in north-western Mexico. J Arid Environ 56:117–127

Molthan J, Ruppert V (1988) Zur Beteutung blühender Wildkräuter in Feldrainen und Äckern für Blütenbesuchendeden Nutzinsekten. Mitteilungen aus der biologischen Bundesanstalt für Land- und Forstwirtschaft 247:85–99

Moreno CE, Halffter G (2000) Assessing the completeness of bat biodiversity using species accumulation curves. J Appl Ecol 37:149–158

Moreno CE, Halffter G (2001) Spatial and temporal analysis of α, β and γ diversities of bats in a fragmented landscape. Biodivers Conserv 10:367–382

Morse RA, Culiney TW, Gutenmann WH, Litman CB, Lisk DJ (1987) Polychlorinated biphenyls in honeys. Bull Environ Contam Toxicol 38:271–276

Nelson SM, Anderson DC (1994) An assessment of riparian environmental quality by using butterflies and disturbance susceptibility scores. Southwest Nat 39:137–142

New TR, Pyle RM, Thomas JA, Thomas CD, Hammond PC (1995) Butterfly conservation management. Annu Rev Entomol 40:57–83

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Cons Biol 4: 355–364

Oostermeijer JGB, van Swaay CAM (1998) The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. Biol Conserv 86:271–280

Osborne JL, Williams IH, Corbet SA (1991) Bees, pollination and habitat change in the European community. Bee World 72:99–116

O'Shea TJ, Bogan MA (eds) Monitoring trends in bat populations of the United States and territories: problems and prospects. U.S. Geological Survey, Information and Technology Report, USGS/ BRD/ITR--2003–0003, 264 p

Parker FD, Batra SWT, Tepedino V (1987) New pollinators for our crops. Agric Zool Rev 2:279–304

Patterson BD, Willig MR, Stevens RD (2003) Trophic strategies, niche partitioning, and patterns of ecological organization. In: IKunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp 536–579

Pierson ED (1998) Tall trees, deep holes, and scarred landscapes: conservation biology and North American bats. In: Kunz TH, Racey PA (eds) Bat biology and conservation. Smithsonian Institution Press, Washington, DC, pp 309–325

Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme. Chapman and Hill, London

Pollard E, Elias DO, Skelton MJ, Thomas JA (1975) A method of assessing the abundance of butterflies in Monks Wood National Nature Reserve in 1973. Entomol Gaz 26:79–88

Pollard E, Woiwod IP, Greatorex-Davies JN, Yates TJ, Welch RC (1998) The spread of coarse grasses and changes in numbers of Lepidoptera in a woodland nature reserve. Biol Conserv 84:17–24

Porrini C, Colombo V, Celli G (1996) The honey bee (*Apis mellifera* L.) as pesticide bioindicator. Evaluation of the degree of pollution by means of environmental hazard indexes. In: Proceedings XX international congress of entomology, Firenze, 25–31 Aug 1996, p 444

Porrini C, Celli G, Radeghieri P (1998) Monitoring of pesticides through the use of honeybees as bioindicators of the Emilia-Romagna coastline (1995–1996). Ann Chim 88:243–252

Porrini C, Ghini S, Girotti S, Sabatini AG, Gattavecchia E, Celli G (2002) Use of honey bees as bioindicators of environmental pollution in Italy. In: Devillers J, Pham-Delègue M (eds) Honey bees: estimating the environmental impact of chemicals. Taylor & Francis, London/New York, pp 186–247

Proctor M, Yeo P, Lack A (1996) The natural history of pollination. Harper Collins, London, 479 pp

Pullin AS (1996) Restoration of butterfly populations in Britain. Restor Ecol 4:71–81

Punchihewa RWK (1994) Beekeeping for honey production in Sri Lanka: management of Asiatic hive honeybee *Apis cerana* in its natural tropical monsoonal environment. Sri Lanka Department of Agriculture, Peredeniya, 232 pp

Rapport DJ (1992) What is clinical ecology? In: Constanza R, Norton BG, Haskel BD (eds) Ecosystem health: new goals for environmental management. Island Press, Washington, DC, pp 144–156

Rathke B (1983) Competition and facilitation among plants for pollination. In: Real L (ed) Pollination biology. Academic, New York, pp 305–329

Rathke B (1988) Interactions for pollination among coflowering shrubs. Ecology 69:446–457

Reynaud PA, Thioulouse J (2000) Identification of birds as biological markers along a neotropical urban–rural gradient (Cayenne, French Guiana), using co-inertia analysis. J Environ Manag 59:121–140

Richards KW (1984) Alfalfa leafcutter bee management in western Canada. Publication No. 1495E, Agriculture Canada, p 30

Richards AJ (1986) Plant breeding systems. George Allen and Unwin, London, 529 pp

Richards KW (1987) Alfalfa leafcutter bee management in Canada. Bee World 68:168–178

Richards KW (1993) Non-Apis bees as crop pollinators. Rev Suisse Zool 100:807–822

Richards KW, Myers TW (1995) Effects of lifestock gazing on bumble bee and native flowering plant populations. In: Proceedings of the 4th Prairie conservation and endangered species workshop ‘Sharing the Prairies, Sustainable Use of a Vulnerable Landscape’, Lethbridge, 23–26 Feb 1995 (abstract in press)

Rinderer TE (1995) Honeybee genetics. In: Kevan PG (ed) The Asiatic hive bee: apiculture, biology, and role in sustainable development in tropical and subtropical Asia. Enviroquest Ltd, Cambridge, pp 81–86

Rosenberg DM, Danks HV, Lehmkuhl DM (1986) Importance of insects in environmental impact assessment. Environ Manag 10:773–783

Roubik DW (1988) An overview of Africanized honey-bee populations: reproduction, diet, and competition. In: Needham GR, Page RE, Delfinado-Baker M, Bowman CE (eds) Africanized honeybees and bee mites. Ellis Horwood, Chichester, pp 45–54

Roubik DW (ed) (1995) Pollination of cultivated plants in the tropics, vol 118, FAO Agriculture service bulletin. FAO, Rome, 196 pp

Roubik DW, Hanson PE (2004) Orchid bees of tropical America: biology and field guide. Instituto Nacional de Biodiversidad (INBio), Heredia, 370 p

Rousseau M (1972) Les abeilles domestiques et la pollution de l’environnement. Bull Office Int Epizooites 77:1473–1480

Ruppert V(1993) Einflusz blutenreicher feldrandstrukturenauf die dichte blutenbessuchender nutzinsekten insbesondere der Syrphinae(Diptera:Syrphidae). Agrarokologie 8:1–49

Ruttner F (1988) Biogeography and taxonomy of honeybees. Springer, Berlin, 284 pp

Sauer C (1996) Urban habitats for bees: the example of the city of Berlin. In: Matheson A, Buchmann SL, O’Toole C, Westrich P, Williams IH (eds) The conservation of bees, vol 18, Linnean social symposium. Academic, London, pp 47–54

Schiestl FP, Roubik DW (2003) Odor compound detection in male euglossine bees. J Chem Ecol 19(1):253–257

Schmid A (1992) Untersuchungen zur Attraktivität von Ackerwildkräuten für aphidophage Marienkäfer (Coleoptera, Coccinellidae). Agrarökologie 5:1–122

Schultz CB (1998) Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. Conserv Biol 12:248–292

Sihag RC (1995) Pollination biology: pollination, plant reproduction and crop seed production. Rajendra Scientific Publishers, Hisar

Simberloff D (1998) Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biol Conserv 83:247–257

Simmons NB (2005) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore, 312–529

Simmons NB, Conway T (2003) Evolution of ecological diversity in bats. In: Kunz T, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 493–535

Southwick EE, Southwick L (1992) Estimating the economic value of honeybees (Hymenoptera: Apidae) as agricultural pollinators in the United States. J Econ Entomol 85:621–633

Sparks TH, Greatorex-Davies JN, Mountford JO, Hall ML, Marrs RH (1996) The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. For Ecol Manag 80:197–207

Spitzer K, Jaros J, Havelka J, Leps J (1997) Effects of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. Biol Conserv 80:9–15

Start AN, Marshall AG (1976) Nectarivorous bats as pollinators of trees in West Malaysia. In: Burley J, Styles BT (eds) Tropical trees, vol 2, Linnean society symposium. Academic, London

Stein K, Umland F (1987) Mobile und immobile Probensammlung mit Hilfe von Bienen und Birken. Fresenius Zeitschrift für Analytische Chemie 327:132–141

Sugihara G (1980) Minimal community structure: an explanation of species abundance patterns. Am Nat 116:770–787

Svoboda J (1962) Teneur en strontium 90 dans les abeilles et dans leurs produits. Bull Apicole 5:101–103

Swengel AB (1998) Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biol Conserv 83:77–89

Syed RA, Law IH, Corley RHV (1982) Insect pollination of oil palm: introduction, establishment and pollinating efficiency of *Elaeidobius kamerunicus* in Malaysia. Planter 58:547–561

Sylvester HA (1995) Biotechnological potential of *Apis cerana*. In: Kevan PG (ed) The Asiatic hive bee: apiculture, biology, and role in sustainable development in tropical and subtropical Asia. Enviroquest Ltd, Cambridge, pp 87–96

Syme PD (1975) The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. Environ Entomol 4:337–346

Tepedino VJ, Stanton NL (1981) Diversity and competition in bee-plant communities on short grass prairie. Oikos 36:35–44

Thomas CD, Harrison S (1992) Spatial dynamics of a patchily distributed butterfly species. J Anim Ecol 61:437–446

Tonelli D, Gattavecchia E, Ghini S, Porrini C, Celli G, Mercuri AM (1990) Honey bees and their products as indicators of environmental radioactive pollution. J Radioanal Nucl Chem Artic 141(2):427–436

Torchio PF (1987) Use of non-honey bee species as pollinators of crops. Proc Entomol Soc Ont 118:111–124

Torchio PF (1990) Diversification of pollination strategies for US crops. Environ Entomol 19:1649–1656

Torchio PF (1991) Bees as crop pollinators and the role of solitary species in changing environments. Acta Hortic 288:49–61

Torchio PF (1994) The present status and future prospects of non-social bees as crop pollinators. Bee World 75:49–53

Torres F, Guyabo SF, Asensio E (1989) Effects de la presion urbana sobre abejas y avispas en Salamura. V Sperfamilia Apoidea. Communo Instituto Nacional de Investigatigaciones Agraria. Series Recursos Naturales 52:1–49

Tremolada P, Bernardinelli I, Colombo M, Spreafico M, Vighi M (2004) Coumophos distribution in the hive ecosystem: case study for modelling applications. Ecotoxicology 13:589–601

Tsigouri A, Passaloglou-Katrali M, Sabatakou O (2004). Palynological characteristics of different unifloral honeys from Greece. Grana 43:122–128

Verma LR (1990) Beekeeping in integrated mountain development: economic and scientific perspectives. Oxford & IBH, New Delhi, 367 pp

Verma LR (1995) *Apis cerana*: biometric, genetic and behavioural aspects. In: Kevan PG (ed) The Asiatic hive bee: apiculture, biology, and role in sustainable development in tropical and subtropical Asia. Enviroquest Ltd, Cambridge, pp 41–54

Vogel S (1990) The role of scent glands in pollination: on the structure and function of osmophores. A. A. Balkema, Rotterdam, 202 pp

Vogel S, Westerkamp C (1991) Pollination: an integrating factor in biocoenoses. In: Seitz A, Loeschke V (eds) Species conservation: a population-biological approach. Birkhauser, Basel, pp 159–170

Wahl O, Ulm K (1983) Influence of pollen feeding and physiological condition on pesticide sensitivity of the honeybee Apis mellifera carnica. Oecologia 59:106–128

Waller GD, Erickson BJ, Harvey J, Martin JH (1984) Effects of dimethoate on honey bees (Hymenoptera: Apidae) when applied to flowering lemons. J Econ Entomol 77:70–74

Wallowork-Barber AK, Ferenbaugh RW, Gladney ES (1982) The use of honey bees as monitors of environmental pollution. Am Bee J 122(11):770–772

Walsh A, Catto C, Hutson T, Racey P, Richardson P, Langton S (2001) The UK's national bat monitoring programme, Final report 2001. Bat Conservation Trust, UK

Warren MS (1985) The influence of shade on butterfly numbers in woodland rides with special reference to the wood white Leptidea sinapis. Biol Conserv 33:147–164

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043–1060

Watanabe ME (1994) Pollination worries rise as honey bees decline. Science 265:1170

Weiss E, Stettmer C (1991) Unkräuter in der Agrarlandschaft locken blütenbesuchende *Nutzinsekten an*. Agrarökologie 4:1–104

Westerkamp CW (1991) Honeybees are poor pollinators – why? Plant Syst Evol 177:71–75

Whitaker JO Jr (1993) Bats, beetles, and bugs. Bats 11(1):23

Whitaker JO Jr (1995) Food of the big brown bat, *Eptesicus fuscus*, from maternity colonies in Indiana and Illinois. Am Midl Nat 134:346–360

Whitehead VB, Giliomee JH, Rebelo AG (1987) Insect pollination of the Cape flora. In: Rebelo AG (ed) A preliminary synthesis of pollination biology in the Cape flora. South African National Scientific Programs Report No. 141, pp 52–82

Wickramasinghe LP, Harris S, Jones G, Vaughan N (2003) Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. J Appl Ecol 40:984–993

Willemstein SC (1987) An evolutionary basis for pollination ecology, vol 10, Reiden botanical series. Leiden University Press, Leiden, 425 pp

Williams IH (1996) Aspects of bee diversity and crop pollination in the European union. In: Matheson A, Buchmann SL, Toole CO', Westrich P, Williams IH (eds) The conservation of bees, Linnaean Society symposium series, vol 18. Academic Press, London, pp 63–80

Williams IH, Corbet SA, Osborne JL (1991) Beekeeping, wild bees, wild bees and pollination in the European Community. Bee World 72:170–180

Williams-Guillén K, Perfecto I, Vandermeer J (2008) Bats limit insects in a Neotropical agroforestry system. Science 320:70–70

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309

Willis DS, Kevan PG (1995) Foraging dynamics of *Peponapis pruinosa* on pumpkin (*Cucurbita pepo*) in southern Ontario. Can Entomol 127:167–175

Willmer PG, Bataw AAM, Hughes JP (1994) The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. Ecol Entomol 19:271–284

Wood B, Gillman MP (1998) The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. Biodivers Conserv 7:597–616

Yakobson BA (1996) The monitoring of possible biological and chemical contaminants in bee products. In: Proceedings of international conference on bee products: applications and Apitherapy. Tel –Aviv, isarael, pp 227–230

Chapter 17
Decline in Pollinators

Abstract Pollinators are a key component of global biodiversity, providing vital ecosystem services to crops and wild plants. There is clear evidence of recent declines in both wild and domesticated pollinators, and parallel declines in the plants that rely upon them. Birds, bees, bats and other species that pollinate plants life are declining at alarming rate which has threatened the existence of plant life and this downward trend could damage dozens of commercially important crops. A decline in pollinator populations is one form of global change that actually has credible potential to alter the shape and structure of terrestrial ecosystems. The decline in pollinator population and diversity presents a serious threat to agricultural production and conservation and maintenance of biodiversity in many parts of the world. Pollinator declines can result in loss of pollination services which have important negative ecological and economic impacts that could significantly affect the maintenance of wild plant diversity, wider ecosystem stability, crop production, food security and human welfare. This paper discusses the world scenario on the causes of pollinator decline, including habitat loss and fragmentation, agrochemicals, pathogens, alien species, climate change and the interactions between them and future strategies to overcome the impending crisis.

17.1 Introduction

Sexual reproduction of many crops and the majority of wild plants is dependent on animal pollination through insects, birds, bats and others, with insects playing the major role. Among the insect pollinators, solitary and social bees provide most pollination in both managed and natural ecosystems. Most of the world's staple foods, including wheat, corn, and rice reproduce without insect pollination. These crops account for 65% of global food production, still leaving as much as 35% depending on pollinating animals (Klein et al. 2007). In part due to the massive scale and homogeneity of modern agriculture, the majority of crops requiring pollination are dependent on managed pollinators, and especially on managed honeybees (Aizen et al. 2008).

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No other group of insects are of more benefit to humans than bees. More than one third of the world's crops require pollination to set seeds and fruits, and most meat and dairy industries rely on bees for pollination of clover and lucerne (Dias et al. 1999). Crops relying on bee pollination include apple, citrus, tomato, melon, strawberry, apricot, peach, cherry, mango, grape, olive, carrot, potato, onion, pumpkin, bean, cucumber, sunflower, various nuts, a range of herbs, cotton, alfalfa and lavender. The annual value of this service is estimated at US$ 112 billion worldwide (Southwick and Southwick 1992). Even crops that do not require pollination for harvesting, such as those producing fibre or timber, still require pollination to produce further generations, and crops such as cotton that do not require pollination to produce seeds, provide greater yields when pollinators are available (Allen-Wardell et al. 1998). The European honeybee (*Apis mellifera*) dominates crop pollination worldwide, but local native bee species also play their part.

17.2 The Pollinators

Over 75% of the major world crops and 80% of all flowering plant species rely on animal pollinators (Nabhan and Buchmann 1997b; Kevan and Imperatriz-Fonseca 2002). Of the hundred or so animal-pollinated crops which make up most of the world's food supply, 15% are pollinated by domestic bees, while at least 80% are pollinated by wild bee species and other wildlife (Prescott-Allen and Prescott-Allen 1990; Ingram et al. 1996). Diversity among species, including agricultural crops, depends on animal pollination. Thus, pollinators are essential for diet diversity, biodiversity, and the maintenance of natural resources. The principle pollinators are bees. Approximately 73% of the world's cultivated crops, such as cashews, squash, mangoes, cocoa, cranberries and blueberries, are pollinated by some variety of bees, 19% by flies, 6.5% by bats, 5% by wasps, 5% by beetles, 4% by birds, and 4% by butterflies and moths (Free 1993).

The economic value of animal pollination to world agriculture has been estimated to be 200 billion US dollars per year. More than one lakh different animal species play roles in pollinating the 250,000 kinds of wild flowering plants on our planet. In addition to bees, wasps, moths, butterflies, flies and beetles, as many as 1,500 species of birds and mammals serve as pollinators. Hummingbirds are the best known wildlife pollinators in the Americas, but perching birds, flying foxes, fruit bats, snails, slugs, possums, lemurs and even a gecko function as effective pollinators elsewhere in the world. Many crops of commercial importance (almond, cherry, pear, apple, coffee, sunflower, turnip rape, water melon, cucumber, melon, avocado, alfalfa, etc.) rely on pollination by insects, and of these insects, bees are by far the most important.

17.2.1 Pollinators and Ecosystem Functioning

Crop-associated biodiversity (CAB) refers to biodiversity that supports the functioning of ecosystem services necessary for agriculture, as well as contributing to the maintenance of ecosystem health and resilience. Indeed, pollination, a fundamental step for plant reproduction, is an ecological service that cannot be taken for granted. Plants are the primary producers in terrestrial ecosystems and direct providers of many ecosystem services such as carbon sequestration, prevention of soil erosion, nitrogen fixation, maintenance of water tables, greenhouse gas absorption, and food and habitat providers for most other terrestrial and many aquatic life forms. Pollinators, through facilitating plant reproduction, thus play a crucial role in the maintenance of ecosystem services. Pollination requires pollinating agents which themselves require resources for nesting, feeding and reproduction in the form of vegetation, prey, and certain habitat conditions, as well as the application of pollinator-friendly land-use management practices to ensuring their survival.

17.2.2 Pollinator Decline: Importance

Concerns have been raised that invertebrate pollinators of crops and wild plants are in decline as a result of modern agricultural practices, habitat degradation, and introduced pests and diseases. This has led to demands for a response by land managers, conservationists and political decision makers to the impending ‘global pollinator crisis’. In questioning this crisis, it becomes apparent that perceptions of a pollinator crisis are driven mainly by reported declines of crop-pollinating honeybees in North America, and bumblebees and butterflies in Europe, whereas native pollinator communities elsewhere show mixed responses to environmental change. Additionally, few staple food crops depend on pollinator services, and most crops that do are grown at small scales in diversified agro-ecosystems that are likely to support healthy pollinator communities, or in highly managed systems that are largely independent of wild pollinators. Consequently, justifying conservation action on the basis of deteriorating pollinator services might be misplaced. Nevertheless, existing initiatives to monitor pollinators are well founded, given the uncertainty about the dynamics of pollinator populations.

Pollinators play an important functional role in most terrestrial ecosystems and represent a key ecosystem service that is vital to the maintenance of both wild plant communities (Ashman et al. 2004; Aguilar et al. 2006) and agricultural productivity (Klein et al. 2007; Ricketts et al. 2008). Insects, particularly bees, are the primary pollinators of most agricultural crops and wild plants. Pollination services depend on both domesticated and wild pollinator populations, both of which might be affected by a range of recent and projected environmental changes, such as habitat loss and climate change, with unknown consequences for pollination service delivery. Growing concern about the fate of both domesticated and wild pollinators has resulted in the establishment of special initiatives by the Convention on Biological Diversity (International Pollinator Initiative) and several continental, national and regional programmes to tackle the issues of pollinator declines.

However, whether substantial evidence exists for widespread declines and negative impacts on pollination services was recently questioned (Ghazoul 2005a, b), although since then published literature on the subject has greatly expanded. In this chapter an attempt has been made to understand current status and trends of pollinators and how pollinator declines and associated loss of pollination services impact floral biodiversity and human livelihoods. Furthermore, information has been assembled to address the question of what are the actual drivers of observed pollinator declines and what the consequences are. Finally, we identify the most important future research directions.

The presumption of ample honey bees for crop and ecosystem pollination has been severely challenged in the past several years by enigmatic declines of honey bee colonies (Aizen and Harder 2009; vanEngelsdorp et al. 2007). These losses are defined by a rapid loss of adult worker bees in colonies and the lack of apparent symptoms, leading to the nebulous label of ‘Colony Collapse Disorder’ (CCD). CCD is distinct from other forms of colony collapse described that dead bees cannot be found in the vicinity of the hive, and food stores are not touched by robbing bees or honey bee comb for several weeks after the collapse. This disorder is not universal and, in fact, global populations of honey bee populations are increasing (Aizen and Harder 2009). Further, similar episodes are apparent for specific geographic regions over much of the recorded history of beekeeping (vanEnglesdorp and Meixner 2010). Nevertheless, this phenomenon has triggered an aggressive search for abiotic and biological causes, including pathogens.

Due to the link between animal pollinators and global food security, any decline of managed honeybees and the loss of wild pollinators are of increasing concern. Although there is an ongoing discussion of whether or not we are facing a ‘global pollinator crisis’ (Allsopp et al. 2008; Ghazoul 2005a, b; Steffan-Dewenter et al. 2005) there is no question that many solitary and social bees are declining (Ghazoul 2005a, b; Steffan-Dewenter et al. 2005). Given the increasing dependence on honeybee pollination in North America and Europe (Aizen et al. 2008), the unquestioned decline in managed honeybee colonies in these regions is alarming. Undoubtedly, the global health of honeybees is at risk. Honeybee well being is negatively affected by the intensive use of pesticides and fungicides in agriculture (Barnett et al. 2007; Desneux et al. 2007; Karise 2007) and the chronic exposure to acaricides needed to combat the parasitic mite *Varroa destructor*. Furthermore, destruction and fragmentation of natural and semi-natural habitats as well as land-use intensification in agricultural landscapes have significant negative effects on honeybees and other pollinators (Kremen et al. 2007; Rathcke and Jules 1993; Steffan-Dewenter and Westphal 2008; Tscharntke et al. 2005). In addition and perhaps most importantly, honeybees are attacked by parasitic mites (*Varroa destructor*, *Acarapis woodi*, *Tropilaelaps* spp.), fungi (*Nosema* spp., *Ascosphaera apis*), bacteria (*Paenibacillus* larvae, *Melissococcus plutonius*), numerous viruses, and scavengers (from beetles and mice to bears) during any life stage. For some of these parasites and pathogens the consequences for individual bees and colonies are known, while for others they remain elusive. Still, it is clear that they all in one way or another reduce the fitness of their honeybee hosts.

We are currently enduring the 6th mass extinction, losing between 1% and 10% of biodiversity per decade, mostly as a result of habitat loss, pest invasion (exotics), pollution, over harvesting and disease. Why care? Biodiversity losses aren’t only affecting natural ecosystems but also the services they provided and some of them are vital for human societies amongst other the presence of oxygen into the atmosphere, renewing of soils (from bacteria, worms) and pollination – the transfer of pollen from oneflower to another – is critical to fruit and seed production, and is often provided by insects and other animals on the hunt for nectar, pollen or other floral rewards.

Until very recently, most farmers considered pollination as one of *Nature*'s many "free services", so taken for granted that it has rarely figured as an "agricultural input" or even as a subject in agricultural science courses. This assumption has apparently become obsolete as these changes are already being illustrated, need to be monitored and mitigated in the near future, posing threats to the integrity of biodiversity, global food webs and even ultimately to human health.

17.3 Historical Perspectives

17.3.1 Do Pollination Deficits Exist in Agroecosystems?

The oldest recorded examples of pollination and pollination deficit in crops are for sycomore (also known as sycamore) figs, *Ficus sycomorus* (Amos ca. 760 B.C.) and for date palm, *Phoenix dactylifera*, and Smyrna figs, *Ficus carica* (Herodotus 485–425 B.C.). Although the sycomore fig is native to central eastern Africa and Yemen, it is also widely cultivated in Egypt and Mediterranean countries, where its pollinators (*Ceratosolen arabicus*: Hymenoptera: Agaonidae) are absent (Galil and Eisikowitch 1968, 1969a, b, 1974). (Theophrastus 372–287 B.C.) recorded the lack of seeds in Egyptian figs, and Galil (1967) noted that there were no wasps associated with figs from ancient tombs. How the plant spread beyond the reaches of its pollinators is unknown, but its range included Egypt by at least 3000 B.C. (Galil 1967). For the unfertilized fruit to develop, it must be scraped in the manner described by (Theophrastus 372–287 B.C.) and Galil (1967), often with a special knife (Henslow 1892, 1902; Keimer 1928). Depending on the translation, Amos (760 B.C.) describes himself variously as a fig scraper, piercer, dresser, or gatherer. Nevertheless, whatever his occupational designation, he clearly understood how to produce sycomore figs without pollinators.

The date palm is dioecious and appears to be pollinated by wind and bees (Free 1993; Roubik 1995). Because male palms are not fruitful in the sense of agricultural production, only female palms have been retained. The result, even about 3,000 years ago in Mesopotamia, was that hand pollination using male inflorescences taken to the female trees was necessary (Tylor 1889; Meeuse 1981). Herodotus (485–425 B.C.) also described this practice; however, he was under the impression that it also involved a gall fly, and he mixed the techniques used for the anthropogenic pollination of dates and *F. carica.* Pollination was probably associated with festivals of spring and fertility in the region at the time of the Prophet Mohammed, who reportedly discouraged such festivals and only reluctantly recognized the need to hand-pollinate dates (Margoliouth 1905, p. 230; Fraser 1935: II: 25, V: 281). The best pollination results today are obtained by tying dehiscent staminate inflorescences into the pistillate inflorescences of female palms (McGregor 1976; Mbaya and Kevan 1995), or by other artificial means.

The need for caprification in Smyrna figs, i.e., providing production trees with a pollinating wasp containing caprifigs, was known in ancient Greece (Herodotus 485–425 B.C.) and Turkey (Condit 1920; Goor 1965). In addition, both Herodotus (485–425 B.C.) and Aristotle (350 B.C.) had some understanding of the role of wasps in pollination, although they referred to the insects involved as gall flies and psene, respectively. By the mid-eighteenth century, the process of pollination was better understood in figs according to Knuth (1909: III: 372), who reported that even Linnaeus spoke of a special "messenger of love" needed to fertilize Smyrna figs. However, this concept was vociferously ridiculed in Europe (Reasoner 1891) and California (Condit and Swingle 1947) in the mid- and late 1800s, so it is not hard to understand why the Smyrna figs introduced into California in the late 1800s failed to bear fruit. It was not until Eisen (1891) introduced the wasps into California that fruit set was achieved.

At about the same time as the fig pollination problem was being resolved in California, the shortage of pollinators for seed production of red clover, *Trifolium pratense*, in New Zealand prompted the introduction of bumble bees, *Bombus* spp., from Europe (Belt 1876; Dunning 1886; Hopkins 1914). Their establishment was successful, although New Zealand has still not solved its on-going problems with regard to the pollination of kiwifruit, *Actinidia deliciosa* (Free 1993; Roubik 1995).

More recently, Malaysia, where labor costs for hand pollination are rising sharply, found a solution to its shortage of pollinators for oil palm, *Elaeis guineensis*. Syed (1979) studied the pollination of this important crop plant in its native West Africa and worked out the relationship between the pollinating weevils, *Elaeidobius* spp., and the inflorescences of the male and female palms. After careful screening and quarantine, *Elaeidobius kamerunicus* was released in Malaysian oil palm *Planta*tions, where it rapidly became established and spread (Syed et al. 1982). The result continues to be the sustainable and sufficient pollination of crops whose harvests exceed those previously produced by hand pollination, with savings of millions of U.S. dollars per year (Kevan et al. 1986).

Another example of placing pollinators into a novel habitat to enhance crop production is the introduction of bumble bees into hot houses to pollinate tomatos, *Lycopersicon esculentum*, in Europe (Banda and Paxton 1991) and North America (Kevan et al. 1991). Artificial pollination with electric vibrators (Kerr and Kribs 1955) is a costly method that is no longer used, whereas buzz pollination (Buchmann 1983) by bumble bees produces superior fruit (Banda and Paxton 1991; Kevan et al. 1991). Morandin (2000) describes the efforts being made to solve the remaining technological problems related to hothouse pollination. The value of "bombiculture" for producing hothouse tomatos and other fruit has not been assessed, but must amount to millions of dollars worldwide. Although it may be argued that these examples are special cases and that the pollinator deficits were artificial, they serve to illustrate that, when pollinator forces are insufficient, there may be inexpensive, effective alternative methods of solving problems related to pollinator deficits.

The success story of the alfalfa leaf-cutter bee (*Megachile rotundata*) and its culture for the pollination of alfalfa (*Medicago sativa*), both exotic organisms in North America, is well known. The pioneering work of Bohart (1972) and Hobbs (1967) has given rise to the multimillion-dollar industry of "megachileculture," whose huge economic benefits are described by Olmstead and Woolen (1987). Bohart (1957) also recognized the problem of providing adequate pollination to alfalfa seed production fields, which led to the commercial development of practices for encouraging and maintaining pollinators other than honey bees, especially the alkali bee (*Nomia melanderia*). On the Canadian prairie, problems with alfalfa pollination and concomitant seed yield declines can be attributed to the expanding agriculture. As a result of the subsequent reduction in nesting habitat, there were too few native pollinators to provide pollination for any plants except those at the peripheries of large fields (Peck and Bolton 1946; Stephens 1955). In Manitoba, Stephens (1955) recorded yields of 1,000 kg/ha from small fields, but only 15 kg/ha from large fields. In Ontario, the contemporaneous decline of alfalfa seed production has been attributed to changing agricultural practices, including the use of insecticides.

Habitat destruction has also been a problem in the pollination of cacao (*Theobroma cacao*). Overly fastidious management of *Plantations* included the removal of rotting vegetation, the substrate in which the pollinating midges undergo larval development (Winder 1977), and yield reductions ensued. By purposely placing appropriate plant material such as banana (Young 1982) or palm trunks (Ismail and Ibrahim 1986), adequate pollinator forces can be encouraged and maintained. The destruction of Brazilian habitat for pollinators of Brazil nuts (*Bertholletia excelsa*) has been even more detrimental to production (Maués 2002). Brazil nuts are pollinated by an assemblage of large bees whose nesting habitats have been severely curtailed or even eliminated (Sutton and Collins 1991). The vicious cycle of habitat destruction or pollution, paucity of pollinators, and failures in plant reproduction, recruitment, and regeneration has been well described (Janzen 1974; Kevan 1974, 1975a).

The catastrophic effects of recently introduced parasitic mites on honey bees have changed the face of apiculture in North America. Colony mortality and intensive management have made it more expensive to keep bees. The number of beekeepers has declined, as has the number of colonies being kept all over North America. Other pests also threaten to make beekeeping more costly and difficult. Pollination has been adversely affected, and growers have reported difficulties in obtaining services for crops such as blueberries in Maine, pome fruit in the northeastern United States and Canada, almonds in California, field cucumbers in the eastern United States and Canada, and hybrid seed production in western Canada. Economic analyses of the effects of parasitic mites are much needed for beekeeping per se and for the ancillary benefits of pollination (Morse and Calderone 2000). Although the epidemic of *Nosema* that reportedly swept through the cultures of *Bombus occidentalis* used in hothouse tomato pollination on the Pacific coast of North America has had major repercussions, the economic consequences have not been analyzed.

The adverse effects of pesticides on pollinators are well understood, especially from a toxicological viewpoint (Johansen and Mayer 1990), although less is known about their impact on crop reductions. Several works (Kevan 1975b, 1977; Kevan and LaBerge 1979; Kevan and Oppermann 1980; Kevan and Plowright 1995) explore the effects of applications of the organophosphorous pesticide Fenitrothion on nontarget habitat and on blueberry pollinators in New Brunswick, Canada. The demise of the pollinators resulted in such severe declines in the blueberry crop in the affected regions that provincial yields were significantly below those of neighboring Nova Scotia and Maine (Kevan 1977; Kevan and Oppermann 1980; Kevan and Plowright 1995), with an annual harvest loss of about 0.75×10^6 kg. Intensity of agricultural activities has also been shown to correlate with lower (by about 50%) populations and diversity of pollinators in apple orchards in British Columbia (Scott-Dupree and Winston 1987) and berry production areas (MacKenzie and Winston 1984). Kevan (1999) presents more details about these and other examples, but crop yields have rarely been included in such studies.

Although the economic impacts of pollinator declines have not been well recorded, it can, however, be safely assumed that many local economies are being affected. Examples of available studies of this type include Siebert (1980), who provides an estimate of the revenue losses to both almond growers and honey producers in California resulting from a pesticide-induced decline in the numbers of pollinators; Olmstead and Woolen (1987), who document the historical and economic effects of the addition of pollinators on the production of alfalfa seed; and Cox et al. (1991), who show that the demise of fruit bats (Megachiroptera) through overhunting in South Pacific islands has reduced the pollination and fruit yields of some traditional harvests. No matter what their cause, would we expect anything different to result from pollinator declines elsewhere?

Although several works have attempted to illustrate the severity of pollinator declines (Buchmann and Nathan 1996; Matheson et al. 1996; Kearns et al. 1998; Kevan 1999), the problem has generally been ignored. For this reason, it is appropriate to ask the following questions from the point of view of documentation: “Are pollinator declines real?” and “Do they have economic consequences for agriculture?” We would not only answer both questions in the affirmative, but we also believe that the problem is extremely serious, with far-reaching consequences for agriculture and global food production. However, even the most obvious example of honey bee pests and diseases should be carefully examined. The previous example of the demise of pollinators on lowbush blueberry heaths in New Brunswick shows how the basic pollination biology of crops is linked, through production agriculture and ecosystem health, to economic impacts on consumers (Belaoussoff and Kevan 1998). Issues of scale are important. For example, even though the demise of pollinators on lowbush blueberry production fields in New Brunswick adversely affected yields, farm-gate income, and other aspects of the local economy (casual employment), it did not affect the overall market price for blueberries because that was set elsewhere by broader, regional effects (Kevan and Oppermann 1980). Below we explore the broader context of inter-regional or international trade.

Table 17.1 Estimate loss of species on earth

SN	Species loss	Global loss per decade (%)
1	One million species (1975–2000)	4
2	15–20% of species (1980–2000)	8
3	25% of species (1985–2015)	9

17.3.2 Status of Pollinators Decline

Pollinators are products of millions of years of *Evolution* and eroding at fast rate from the globe. The ecological consequence of contemporary agriculture can be viewed from various angles analyzing each component of agriculture- deforestation for expanding agriculture, soil, irrigation, fertilizer, pesticide, and agronomic practices with their influence on the environment of plants and thereby pollinators.

17.3.3 Declining Biodiversity

Decline biodiversity results decline in pollinators as well. About 75% of the genetic diversity of agricultural crops lost since the beginning of twentieth century from the earth and 25% of the world's species present in the mid 1980 will be lost by 2015 (FAO 1993). Over 85% of the 7,000 or so apple varieties grown in last century are now extinct in the USA (FAO 1993). In 1970, genetic uniformity of maize in USA, caused almost $ 1,000 million loss and yield reduced by as much as 50%. Similarly, the broad breast turkey accounting for 90% of all turkeys in the US today would be extinct without AI. In Europe, half of the breeds of domestic animals that existed in the beginning of the century have been extinct and one third of remaining in danger. Irish potato famine in 1840s is the result of genetic uniformity causing million people to die and million more to immigrate. Rice, one of the most important cereal crops in south east Asia, only ten varieties cover third fourth of rice area, over 30,000 grown before in the same areas in India. The word biodiversity is often spelled out by many people but pollinators are quite new to this theme. The cost of conserving biodiversity is far less than the penalty of allowing its degradation. Global extinction rate of species are accelerating at an alarming rate (Table 17.1). Wilson (1999) estimated that 0.2–0.3% of all species are lost every year. Range of 5–10% of the tropical forest species may become extinct within the next 30 years (UNEP 1993). It is estimated that 60,000 species will be eliminated in the foreseeable future and 50,000 species will be at risk of extinction in the next half of the century.

Globally, the pollinator that is predominantly managed to enhance agricultural production is the honey bee (*Apis mellifera*), although other species of bee are used in specialist contexts (e.g. the leafcutter bee *Megachile rotundata*) (Natural Research Council 2006). The honey bee, which has been well studied compared to other bee species, has been documented to be capable of increasing yield in 96% of animal-pollinated crops (Klein et al. 2007). The honey bee also provides pollination services to many wild plants, but the amount they contribute is not always well supported by empirical data, and the contribution of wild pollinators might be higher than previously acknowledged (Klein et al. 2007). There is clear evidence for severe regional declines in domestic honey bee stocks in the USA (59% loss of colonies between 1947 and 2005) (National Research Council 2007; vanEngelsdorp et al. 2008) and Europe (25% loss of colonies in central Europe between 1985 and 2005 making the dependence of agricultural crops, and possibly wild plants, on a single species worrisome (Potts et al. 2010a, b). Substantial concerns have been raised about the future availability of honeybee pollination services. Indeed, owing to the ectoparasitic mite *Varroa destructor*, an invasive species from Asia (Sammataro et al. 2000), most wild and feral honey bee colonies in Europe and the USA have vanished, leaving only those kept by beekeepers (Kraus and Page 1995; Moritz et al. 2007; Jaffée et al. 2010). Unfortunately, in recent decades beekeeping has been an industry in decline in the USA (National Research Council 2007; vanEngelsdorp et al. 2008) and most European countries (Potts et al. 2010a, b). Despite these regional losses, worldwide the number of honey bee hives have increased by 45% since 1961, however, the proportion of agricultural crops depending on pollinators is increasing much more rapidly (>300%) so that the demand for pollination services could outstrip the increase in hive numbers (Aizen and Harder 2009). Honey bee population shifts are poorly documented, but even less is known about recent changes in wild pollinator populations and communities. Until recently there was little firm evidence of geographically widespread declines for most groups (Ghazoul 2005a, b). Among bees, the best documented group are the bumblebees (*Bombus* sp.), which have shown evidence of an ongoing decline in diversity over much of Belgium and the UK (Rasmont and Mersch 1988; Goulson et al. 2008). For example, in the UK 6 of the 16 non-parasitic bumblebees have declined considerably (including *B. subterraneus* which has become extinct), 4 might be declining and 6 are stable or increasing (Williams and Osborne 2009). With the exception of butterflies (Settele et al. 2008), data for other pollinators, including other bee species, are fragmentary because of the lack of coordinated monitoring programmes. Consequently, scientists have had to rely on data collected in less standardized ways to test for changes in the pollinator community, such as comparing recording frequencies between time periods or comparing species richness (Biesmeijer et al. 2006).

Indirect evidence of pollinator loss comes from studies of pollinator communities along gradients of agricultural intensification and habitat fragmentation as proxies for temporal change (Kremen et al. 2002). Quantitative syntheses of these local-scale studies suggest a widespread pattern of loss of pollinator richness and abundance as a result of agricultural intensification and habitat loss (Winfree et al. 2009). As most natural landscapes around the world have been anthropogenically modified, it is likely that pollinator abundance and richness has declined in many parts of the world. There is also evidence that pollinator losses are biased towards species with particular traits: for example, bumblebees with narrow pollen specialisation (Kleijn and Raemakers 2008), and dietary and habitat specialists among pollinators in general (Biesmeijer et al. 2006). Such biased extinctions raise concerns that important functional roles, such as long-distance pollen dispersal, will be lost, reducing the resilience of pollination services across species, time and space (Larsen et al. 2005).

The population of both wild and managed pollinators is declining at alarming rates owing to alteration in their food and nesting habitats, shrinkage in natural ecosystems, i.e. forests and grassland ecosystems, pesticide poisoning, diseases and pests, over-collecting, smuggling and trading in certain rare and endangered species. Insects (butterflies, moths, bees, wasps, ants, beetles, etc.) numbering about 500 species are an important supplementary source of calories and proteins in many regions of the world. Honeybees, economically the most important crop pollinator worldwide, are in decline. The number of commercial U.S. bee colonies had fallen from 5.9 million in the late 1940s to 2.7 million in 1995. The loss of one quarter of all managed honeybee colonies since 1990 signals one of the most severe declines U.S. agriculture has ever experienced in such a short period. An estimated 20% of all losses of honeybee colonies involve some degree of pesticide exposure. Some pesticides highly toxic to bees and birds are: aldrin, carbaryl, carbofuran, diazinon, dieldrin, endosulfan, EPN, fenthion, heptachlor, malathion, monocrotophos, parathion, phosmet, etc. In a recent field study at Cornell University in the USA, it was found that monarch butterfly caterpillars eating Bt corn toxic pollen blown on to milkweed plants near Bt corn fields had suffered significant adverse effects leading to death of nearly 20% of the caterpillars. These chemicals and toxins can eliminate nectar sources for pollination, destroy or adversely affect larval host plants for moths and butterflies, and deplete nesting materials for bees. Gardeners, orchard growers, farmers and urban dwellers can switch to more pollinator-friendly organic methods of cultivation to reduce wildlife exposures to insecticides, herbicides and fungicide.

There are over 1,500 species of butterflies in the Indian subcontinent, but their population is dwindling because of the indiscriminate use of insecticides and chemical weed-killers as well as atmospheric pollution. Many other manmade environmental changes like deforestation, extension of farming and unrestricted urbanization are also threatening some species of butterflies to extinction by destruction or disturbance of their larval as well as adult food plants, feeding grounds and shelters. The Travancore Evening Brown, the Malabar Tree Nymph, Bhutan Glory and Kaiser-I-Hind Butterfly are listed as endangered due to the wanton destruction of habitats in various parts of the subcontinent. Many of the most spectacular and endangered species have various levels of protection under local legislation. However, there is a major trade in the spectacular tropical species for incorporation in ornaments and souvenirs. The international demand for insects is greater than most people realize. Next to bees and moths only, butterflies are most efficient pollinators of flowers to help turn them into food crops, fruits and seeds so essential for the survival of man and animals. Wildlife farming, based on sustainable exploiting wild creatures, can help to save endangered species like butterflies and their habitats.

Among the bird functional groups nectarivores pollinate many plant species which have important consequences for plant populations and community dynamics.

Declines in pollination (Robertson et al. 1999) as a result of bird extinctions may lead to extinctions of dependent plant species (Cardoso da Silva and Tabarelli 2000). Three pollinating bats, including *Leptonycteris curasoae* and *L. nivalis* are threatened or endangered in the U.S. and Mexico. The cause of their decline appears to be destruction of critical cave roosting areas due to tourism and agricultural development.

Over the past decade, farmers in the Himalayan region have been complaining about decline in apple production and quality due to pollination-related problems. Apart from habitat alteration from highly diverse natural ecosystems far less diverse agro-systems, indiscriminate use of pesticides, and the over-harvesting of honey through traditional honey-hunting methods have contributed to the extermination of both the diversity and abundance of pollinating insects. The general observation of farmers is that, in the past, there used to be a lot of insects such as wild bees, butterflies and moths during the apple flowering season but now they have all disappeared. The scarcity of natural insect pollinators has, therefore, become a critical factor in inadequate pollination. The solution lies in supplementing populations of crop pollinators such as honeybees, bumblebees, sting less bees, solitary bees, etc. Farmers in Himachal Pradesh are using honeybee colonies of *Apis mellifera* and *A. cerana* for pollination. Hand pollination of apples is a common practice in Maoxian County of Sichuan, China. Awareness about the value of honeybees as crop pollinators has to be raised at all levels among planners, policy makers, beekeepers or farmers. In western countries, farmers are already using honeybees and solitary bees (species of *Osmia*, *Megachille*, *Nomia*, *Xylocopa*, etc.) for pollination of different crops. The focus of beekeeping needs to change from conventional honey production to crop pollination.

17.3.4 Ecological and Economic Consequences of Pollinator Declines

Pollinator loss will impact two broad groups of pollinator dependent flowering plants: wild flowers and cultivated crops.

17.3.4.1 Impacts of Pollinator Declines on Wild Flower Pollination

The decline in pollinator diversity and abundance can bring with it a decline in pollination services for wild plant populations, potentially affecting populations of animal pollinated plants (and thus potentially further reducing floral resources for the pollinators). Most wild plant species (80%) are directly dependent on insect pollination for fruit and seed set, and many (62–73%) of the plant populations investigated showed pollination limitation, at least some of the time (Burd 1994), although this may vary markedly between sites and seasons. Obligate outcrossing animal-pollinated plants are particularly vulnerable to declines in pollination services (Aguilar et al. 2006), and such species have generally declined in parallel with their pollinators (at least in Western Europe Biesmeijer et al. 2006). Such correlative approaches should ideally be backed up by more mechanistic evidence, but there are few studies that have explored the consequences of pollen limitation on plant survival and plant community composition (Fontaine et al. 2006; Hegland and Totland 2008). Although there might be many ways for short-term compensation for poor pollination (e.g. clonal propagation), this cannot compensate in the long-term for a chronic loss of pollination services (Bond 1994): in a meta-analysis of 54 studies (covering 89 plant species), the most frequent proximate cause of reproductive impairment of wild plant populations in fragmented habitats was pollination limitation (Aguilar et al. 2006). Among animal-pollinated species, those with the most specialised pollination requirements might be expected to be most at risk, but there is little evidence of this (Aguilar et al. 2006); it may be that the redundancy that is built in to most plant–pollinator networks can provide some buffering capacity against pollinator species losses. Usually, plant–pollinator interactions are asymmetric and generally nested (Bascompte et al. 2006), with a core set of generalist species having key roles and specialist pollinators often relying on generalist plants and specialist plants often relying on generalist pollinators (Bascompte et al. 2003). Since generalist species are often less vulnerable to change than specialist species (e.g. Biesmeijer et al. 2006), they might partly sustain network structure under changed conditions. However, generalist species are still vulnerable. For example, local extinction of the supergeneralist honeybee as a result of disease is not unlikely and could lead to considerable species loss of plants (Memmott et al. 2004). Asymmetric and nested network patterns are widespread and largely independent of community composition, geographic location and other factors (Bascompte et al. 2006); asymmetric networks are also suggested to have a high level of redundancy (Memmott et al. 2004) making them relatively robust to the loss of species and interactions. However, ongoing global change affects not only species occurrences, but also species interactions and interaction pathways (Hegland and Totland 2008). Thus, in the face of severe disturbance, plant–pollinator networks could also reach a tipping point and collapse despite their seemingly robust structure (Fortuna and Bascompte 2006).

17.3.4.2 Impacts of Pollinator Declines on Crop Production

Insect pollination, mostly by bees, is necessary for 75% of all crops that are used directly for human food worldwide (Klein et al. 2007). Although many of the highest volume crops (e.g. rice and wheat) are wind-pollinated (Ghazoul 2005a, b), a large proportion of fruit crops (e.g. apple, melon and berry) are potentially vulnerable to declines in apiculture and wild pollinator stocks. The cultivation of pollinator-dependent crops steadily increased between 1961 and 2006 (Aizen et al. 2008). Although the average yield increase over time is no lower than for pollinator-independent crops (Aizen et al. 2008), a more detailed analysis has revealed that a large proportion of this annual yield increase can be explained by the use of commercial pollinators (usually honey bees) or hand pollination (a relatively rare practice) (Garibaldi et al. 2009). Until now, most growers have either matched their pollinator needs by renting honey bees, or utilized the 'free' services of wild bee species foraging in farm fields, a component of pollination services that has largely been overlooked in economic calculations (Losey and Vaughan 2006). Despite the importance of pollination for crop production, there is still a lack of basic information about how species diversity, and the abundance and community composition of pollinating insects, contributes to seed and fruit yield and quality in most crops (but see Hoehn et al. 2008; Winfree and Kremen 2009). The global annual economic value of insect pollination was estimated to be s153 billion during 2005 (i.e. 9.5% of the total economic value of world agricultural output considering only crops that are used directly for human food (Gallai et al. 2009). Complete pollinator loss would translate into a production deficit over current consumption levels of −12% for fruits and −6% for vegetables (Gallai et al. 2009). Although this scenario is unrealistic, the purpose of such calculations is to demonstrate the relative importance of insect pollination as an important agricultural input. This calculation takes into account the fact that production of most crops is only partially reduced in the absence of insect pollinators, and a pollinator dependence ratio compiled in Klein et al. (2007) was utilized to derive calculations of economic value (Gallai et al. 2009). Different crop varieties can have different yield responses to changes in animal pollination, but little information exists on these differences (Klein et al. 2007). Accordingly, global economic calculations of the value of pollination services could change substantially if the true dependencies associated with each variety, and the area cultivated per variety, were accounted for.

17.4 Honey Bee Colony Losses

17.4.1 The Decline of European Honeybees

Despite much of the world's agriculture relying on pollination by European Honeybees, their numbers worldwide have declined due to a range of natural and human mediated causes. In the USA, Mexico and Canada, both feral and managed honeybees declined by 25% between 1990 and 1998 (Allen-Wardell et al. 1998; Loper 1995). In Europe, particularly France and Germany, the same species declined by about 10% between 1992 and 2002. Honeybee "specialists consider all countries will become seriously affected" by this decline, which is expected to continue for at least the next few years (Dias et al. 1999).

Apiculture has been in decline in both Europe and the USA over recent decades, as is shown by the decreasing numbers of managed honeybee (*Apis mellifera* L.) colonies (Ellis et al. 2010; Potts et al. 2010a, b). Apart from socio-economic factors, which can only be addressed by politicians, sudden losses of honey bee colonies have occurred, and received considerable public attention. Indeed, in the last few years,

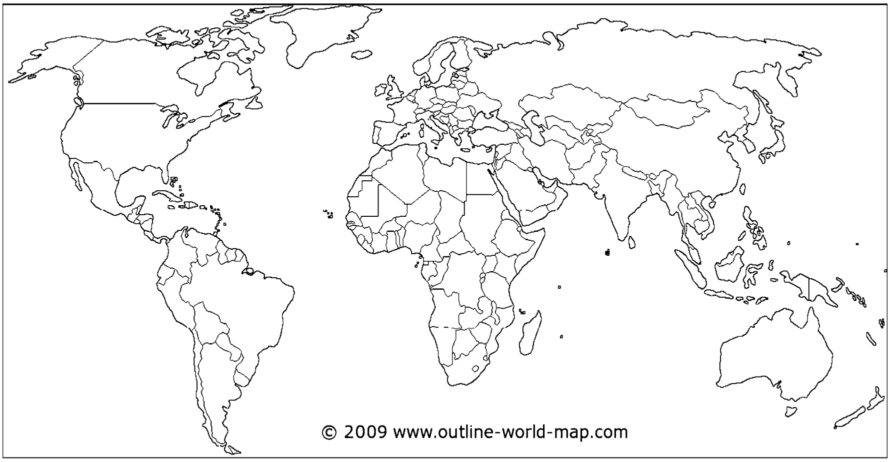

Fig. 17.1 Colony losses due to *Varroa destructor* across the global colony. Elevated colony losses have recently been reported from Europe (Crailsheim et al. 2009), the USA (vanEngelsdorp et al. 2009; 2010), the Middle East (Haddad et al. 2009; Soroker et al. 2009), and Japan (Gutierrez 2009), but not from South America, Africa and Australia. Colonies of African honey bees and Africanized honey bees in South America survive without *V. destructor* treatment, whilst the mite has not yet been introduced into Australia. This global picture indicates a central role of this particular ectoparasitic mite for colony losses

the world's press has been full of eye catching but often uninformative headlines proclaiming the dramatic demise of the honey bee, a world pollinator crisis and the spectre of mass human starvation. "Colony Collapse Disorder" (CCD) in the USA has attracted great attention, and scientists there and in Europe are working hard to provide explanations for these extensive colony losses. Colony losses have also occurred elsewhere (Fig. 17.1), but examination of the historical record shows that such extensive losses are not unusual (vanEngelsdorp and Meixner 2009).

Almost exactly a century ago, in 1906, beekeepers on the Isle of Wight, a small island off the south coast of England, noticed that many of their honey bee colonies were dying, with numerous bees crawling from the hive, unable to fly. Despite some skeptical beekeepers suggesting that this was "paralysis", a condition which had long been known, the colony losses were widely reported in the media, and beekeepers became convinced that the cause was a novel and highly infectious disease, and the condition was soon reported from all parts of Britain. Within a few years, all losses of bees in Britain, from whatever cause, were ascribed to "Isle of Wight Disease" (Bailey and Ball 1991; Bailey 2002).

The response of the scientific community was instructive. Initially, the UK Government sent the eminent entomologist A. D. Imms to the Isle of Wight, but being unfamiliar with bees, he was unable to throw much light on the problem (Bailey and Ball 1991). Other scientists soon made suggestions. By 1912, Fantham and Porter became convinced that the cause was the microsporidium *Nosema apis*, but this view was overshadowed by the discovery in 1919 of the tracheal mite Acarapis woodi (Rennie et al. 1921). Conventional wisdom and beekeeping text books soon accepted that this impressive mite was the cause of the "Isle of Wight Disease", yet close examination of the original paper shows that this could not be so. Rennie et al.'s experimental results clearly demonstrated that some bees heavily infested with the mite were able to fly normally, yet other crawling bees, exhibiting the symptoms of the disease, contained no mites. One can only conclude that carried away by the excitement of their new discovery, they had failed to test Koch's Postulates, and had jumped to conclusions. Sober reassessment of the "Isle of Wight Disease" many years later (Bailey and Ball 1991; Bailey 2002) led to the conclusion that the disease had been due to a combination of factors, in particular, infection by chronic bee paralysis virus (completely unknown at the time), together with poor weather which inhibited foraging, and an excess of bee colonies being kept for the amount of forage available. The recent concern over CCD has much in common with the historical "Isle of Wight Disease" episode, and many lessons can be learned. Initial concern about colony losses in one particular area, the USA, has led to global media attention. Moreover, colony losses throughout the world are being ascribed to CCD, yet that term was specifically coined to describe a precisely defined set of symptoms (vanEngelsdorp et al. 2009) and not colony losses per se. Indeed, honey bee colonies can die in many ways, and CCD is just one of them (vanEngelsdorp et al. 2010). Finally, since both honey bee host and pathogens are genetically diverse, the symptoms and causes of colony losses may well be different in different regions.

Many well intentioned suggestions as to the possible causes of colony losses, including such improbable ideas as mobile telephones, genetically modified crops and nanotechnology, have perhaps overshadowed much more likely explanations such as pests and diseases, pesticides, loss of forage and beekeeping practices. For example, the long known major pest of *A. mellifera* apiculture, the ectoparasitic mite *Varroa destructor* has recently received comparatively little attention, but is certainly involved. Indeed, the broad patterns of CCD coincide with continents with different pressures from *V. destructor* (Fig. 17.1). Since African and Africanized honey bees survive without treatment for *V. destructor* (Martin and Medina 2004), and the mite has not yet been discovered in Australia, this supports a central role of *V. destructor* for the current colony losses. In fact, data by Dahle (2010) strongly support this view, showing that regions with established mite populations had consistently higher losses than those without. After the development and dissemination of adequate mite control methods, however, losses due to *V. destructor* remained at tolerable limits until recently, suggesting that the mite alone cannot explain all of the recent losses.

Despite comprehensive recent research efforts on these colony losses, no single driver has yet emerged as the definitive cause of the phenomenon. Instead, interactions between multiple drivers are the most probable explanation for elevated over-wintering mortality, similar to the conclusions for the Isle of Wight disease (Bailey 2002).

At a global scale, most managed *A. mellifera* colonies are infested by *V. destructor*, facilitating the potential interaction between this factor and multiple other potential drivers almost anywhere in the world. Moreover, many other prominent honey bee pathogens are now also almost globally distributed, for example *Nosema*

Table 17.2 Colony losses due to *Varroa destructor* in different parts of globe

1	USA	~30% losses
2	Europe	1.8–53%
3	Middle East	10–85%
4	Japan	25% beekeepers sudden losses
5	South America	No reports of high losses
6	Africa	No reports of high losses
7	Australia	No reports of high losses

spp. and several viruses (Allen and Ball 1996; Ellis and Munn 2005; Maori et al. 2007; Fries 2009). Multiple infections with pathogens and also interactions between pathogens and other suspected drivers of honey bee loss are therefore almost inevitable, at least in areas with established mite populations. Whilst the list of these other potential drivers is not novel, the evidence of such interactive effects, although limited, is important and growing. These interactions are particularly worrying, as sub-lethal effects of one driver could make another one more lethal; for example a combination of pesticides and pathogens.

Ascribing a definitive cause to losses has also been made much more difficult because of differing pathogen virulence and different host susceptibility in different regions, and different methods used by scientists in previous surveys and experiments. In order to eliminate this latter variability, an international standardisation of methods is urgently required (Nguyen et al. 2010). Moreover, the complex interactions between individual drivers of colony mortality and the high number of interacting factors easily exceed the research facilities of individual bee laboratories or even entire countries. Thus, efforts by individual countries to reveal the drivers of colony losses are probably doomed. The international COLOSS network (Prevention of honey bee COlony LOSSes) has therefore been created to coordinate efforts to explain and prevent large scale losses of honey bee colonies at a global scale. For that purpose, international standards will be developed for monitoring and research in the form of an online BEE BOOK, analogous to the RED BOOK of the Drosophila community (Lindsley and Zimm 1992). Only this will enable collaborative large scale international research efforts to identify the underlying factors and mechanisms, such as global ring tests conducted to ensure common practices across diagnostic laboratories. These efforts appear critical for the development of adequate emergency measures and sustainable management strategies. Only if we succeed in bridging the gap between bee science and apiculture will we achieve sustainable progress in the prevention of colony losses at a global scale. So far, elevated colony losses have recently been reported from Europe (Crailsheim et al. 2009), the USA (vanEngelsdorp et al. 2009, 2010), the Middle East (Haddad et al. 2009; Soroker et al. 2009), and Japan (Gutierrez 2009), but not from South America, Africa and Australia. Colonies of African honey bees and Africanized honey bees in South America survive without *V. destructor* treatment, whilst the mite has not yet been introduced into Australia. This global picture (Table 17.2; Fig. 17.1) indicates a Central role of this particular ectoparasitic mite for colony losses as given below.

Recent colony losses in Europe have been reported by several investigators in different countries viz. Austria (Brodschneider et al. 2010); Bulgaria (Ivanova and Petrov 2010); Croatia (Gajger et al. 2010); Denmark (Vejsnæs and Kryger 2010); England (Aston 2010); Greece (Hatjina et al. 2010); Italy (Mutinelli et al. 2010); Norway (Dahle 2010); Scotland (Gray et al. 2010); Switzerland (Charrière and Neumann 2010).

Journal of Apicultural Research in a special issue addresses the subject of colony losses. The possible causes of honey bee colony losses include: viruses (Berthoud et al. 2010; Carreck et al. 2010a, b; Martin et al. 2010); *Nosema ceranae* (Paxton 2010; Santrac et al. 2010); *Varroa destructor* (Carreck et al. 2010b; Dahle 2010; Martin et al. 2010); pesticides (Chauzat et al. 2010b; Medrzycki et al. 2010); the effects of acaricides (Harz et al. 2010); the loss of genetic diversity (Meixner et al. 2010); and loss of habitats (Potts et al. 2010a, b). In addition, gathered together for the first time in one place, a group of papers report on colony losses and possible causes in 16 individual countries: Austria (Brodschneider and Crailsheim 2010; Brodschneider et al. 2010); Bosnia and Herzegovia (Santrac et al. 2010); Bulgaria (Ivanova and Petrov 2010); Canada (Currie et al. 2010); Croatia (Gajger et al. 2010); Denmark (Vejsnæs and Kryger 2010); England (Aston 2010); France (Chauzat et al. 2010a, c); Greece (Hatjina et al. 2010); Italy (Mutinelli et al. 2010); the Netherlands (Van der Zee 2010); Norway (Dahle 2010); Poland (Topolska et al. 2010); Scotland (Gray et al. 2010); Switzerland (Charrière and Neumann 2010); and the USA (Ellis et al. 2010; vanEnglesdorp et al. 2010). Finally, two further papers consider the general status of both managed honey bees (Potts et al. 2010a, b) and non-Apis bees (Roberts and Potts 2010) in Europe. Biesmeijer and colleagues (2006) analyzed species diversity change in Britain and the Netherlands and found that, in both countries, bee diversity has fallen significantly in most landscapes (pre- versus post-1980), whereas hoverfly diversity increased in the Netherlands, with a mixed response in the UK. However, in the Netherlands, where bee diversity declines were accompanied by increased hoverfly richness, only bee-pollinated plants declined; plants pollinated by hoverflies and other pollinators have continued to thrive.

17.4.1.1 Pollinator Decline *Apis cerana*

Despite its economic usefulness, biodiversity of Asian hive bee *Apis cerana* is suffering precipitous decline and is threatened with extinction in its entire native habitat. For example, in Japan, beekeeping with this native bee species has been completely replaced by European honeybee, *Apis mellifera* and only a few beekeepers and research institutes are raising *Apis cerana* colonies (Sakai 1992). In China, out of more than 8.5 million colonies of bees kept in modern hive, 70% are exotic *Apis mellifera* (Zhen-Ming et.al. 1992). Similarly, in South Korea, only 16% beekeeping is with native *Apis cerana* and remaining has been replaced by exotic *Apis mellifera* (Choi 1984). In Jammu and Kashmir India, 95% of the beekeeping is done with exotic bee *Apis mellifera and Apis cerana* is confined to higher altitudes only (Abrol 2009).

In Hindu Kush Himalayan range, beekeeping with *Apis cerana* is being replaced by *Apis mellifera* at such a fast rate that populations of native *Apis cerana* is declining to a level that is no longer viable. These countries include Afghanistan, Bhutan, Myanmar, Nepal, India, Bangladesh and Pakistan (Verma 1990, 1992a, b, 1993). A visit of some mountain areas of north-west Frontier province of Pakistan in 1989 led by Eva Crane to conclude that *Apis cerana* populations may soon become an endangered species Crane (1992). Thus, the existing centuries old and long established craft of beekeeping with *Apis cerana* has now almost got destroyed in its entire native habitat.

Apis cerana remains till now a forgotten and completely ignored species. Therefore, from biodiversity conservation point of view, it will be disastrous to leave this important genetic resource at its own and definitely require research and development interventions for its conservation and sustainable uses both in natural and agricultural eco-systems.

17.4.1.2 Causes and Consequences of Declining *Apis cerana* Diversity

In seeking ways to conserve genetic diversity of *Apis cerana*, it is necessary to have a clear understanding of the major threats which this bee species is facing in its own native habitat. Like any other threatened biological resources, decline in *Apis cerana* population is also being threatened by human mismanagement, misguided scientific and economic policies and faulty institutions. Major threats include the following: There are many potential drivers that affect biodiversity in general and pollinator abundance and diversity in particular (Natural Research Council 2006), and different environmental drivers rarely act in isolation (e.g. Didham et al. 2007). Interactive, non-additive effects, where one sub-lethal driver increases the severity of another driver, can help explain ongoing declines in wild and managed pollinators (Settele et al. 2008; Le Conte and Navajas 2008; Oldroyd 2007). However, while awareness of the importance of interacting drivers is increasing (Tylianakis et al. 2008), most studies have analysed the impacts of specific drivers in isolation, and therefore evidence of interactive effects is scant (Schweiger et al. 2008). Among the most important drivers are land-use change with the consequent loss and fragmentation of habitats (Goulson et al. 2008; Winfree et al. 2009; Steffan-Dewenter et al. 2002; Hendrickx et al. 2007); increasing pesticide application and environmental pollution (Kevan et al. 1997a, b; Rortais et al. (2005); decreased resource diversity; alien species (Thomson 2006; Stout and Morales 2009)); the spread of pathogens (Cox-Foster et al. 2007; Neumann and Carreck 2010); and climate change (Williams et al.2007; Dormann et al. 2008).

17.5 Reasons for Pollinator Decline

There are number of causes responsible for pollinator decline. Pollinator decline has been a global issue for many decades as natural ecosystems were cleared to make way for agricultural systems, particularly monocultures. This decline has accelerated dramatically in recent years because, in addition, a number of factors such as climate change, the spread of bee parasites and diseases, the overuse of pesticides, the spread of Africanised bees and other invasive species, and the introduction of GMOs appear to have compounded the situation.

17.5.1 Habitat Fragmentation

Habitat loss is generally thought to be the most important factor driving bee declines (Brown and Paxton 2009). Winfree et al. (2009) found a significant, but relatively small, negative effect, of various types of disturbance on wild bee abundances and species richness, of which habitat loss and/or fragmentation was the most important contributor. Similarly, Ricketts et al. (2008) found a strongly significant negative effect of distance from natural habitat on the richness and abundance of wild bees. In summary, the bulk of evidence from quantitative synthesis supports the hypothesis that habitat loss reduces bee diversity and abundance (Cane et al. 2006; Winfree et al. 2007; Carré et al. 2009).

Habitat fragmentation is also postulated to negatively affect wild pollinator populations, but to date; relatively few studies exist on effects of fragmentation on pollination (Winfree et al. 2009; Steffan-Dewenter et al. 2006; Brosi et al. 2008). Habitat degradation might affect bee species primarily by the loss of floral and nesting resources, and the introduction of insecticides with lethal or sub-lethal effects. To date, studies of drivers potentially leading to habitat degradation (grazing, fire, urbanization, agricultural intensification) are few, and findings from a recent meta-analysis did not find these disturbances to have an overall significant impact on bees, although this might simply reflect low statistical power (Winfree et al. 2009). However, we know that agricultural intensification has increased the use of agrochemicals, resulting in potential habitat degradation within agricultural areas. Insecticides can cause mortality by direct intoxication and can result in local shifts in wild bee diversity and abundance (Brittain et al. 2010), whereas herbicides and fertilisers can affect pollinators indirectly by decreasing floral resource availability (Gabriel and Tscharntke 2007; Holzschuh et al. 2008). Risk assessment procedures for pesticides usually only consider effects on honey bees even though the effects of pesticide exposure varies between pollinator taxa (Thompson and Hunt 1999). Sub-lethal effects of pesticides have been demonstrated (Morandin et al. 2005) with implications for the longer term survival of populations. A comparison of fallow strips next to organic versus conventional wheat fields found that both adjacency to organic fields and the proportion of the landscape that was farmed organically significantly increased bee diversity and abundance (Holzschuh et al. 2008). In addition, the effects of agrochemicals might not be restricted to agricultural lands themselves because agrochemicals can drift into semi-natural habitats where pollinators nest and forage.

Plant biodiversity in most regions of the world has also undergone rapid change in recent decades (Lavergne et al. 2006). Local plant diversity appears to have declined in most sites and most habitats and these declines seem to have affected obligately outcrossing animal-pollinated plant populations in particular as they rely entirely on insect pollen vectors, suggesting a general decline in floral resources for pollinators (Biesmeijer et al. 2006). Indeed, in the UK, there is evidence that 76% of forage plants used by bumblebees declined in frequency between 1978 and 1998 (Carvell et al. 2006). Recent research has begun linking these floral shifts to pollinator dynamics, both in controlled experiments (Fontaine et al. 2006) and in the field (Kleijn and Raemakers 2008; Carvell et al. 2006). If wild floral resources have decreased, the planting of mass-flowering crops such as oilseed rape and sunflowers could provide valuable resources for pollinators (Westphal et al. 2003). However, such superabundant resources are only available for brief periods of time and as a consequence they might have little effect in sustaining viable pollinator populations (Kremen et al. 2007).

17.5.2 Habitat Alteration

In developing countries of south and south-east Asia, habitat alteration (especially due to deforestation) from a highly diverse natural ecosystems to far less diverse (often monocultures) agro-ecosystems is adversely affecting native bee populations in the region. This is one of the most important threats often related to land-use changes on a regional scale that involve great reduction in the area of natural vegetation. Such habitat destruction could lead to loss of different types of flowering plants and bee flora. Scarcity of bee flora due to environmental degradation not only leads to decline in colony numbers but also creates “stress conditions” for living bee colonies and increases their vulnerability to the pests and diseases, hunting and random population changes. Recent incidence of Thai sac brood virus disease and European foul brood in *Apis cerana* might have arisen due to the stress conditions created by environmental degradation.

Destruction of forest habitat for growing agricultural and horticultural crops adversely affects the availability of floral resources because many of the staple crops such as rice, wheat, barley, potato, etc. are of little or no value to honeybees. Due to increasing dearth of bee floral resources, colonies in the spring would not be able to build their own populations rapidly and this might force them to forego swarming or cause them cast smaller swarms that would reduce the probability of survival. In either case, the result would be an eventual decline in colony numbers.

Habitat destruction greatly limit the choice of honeybees to carefully choose a particular micro-habitat in which to build nests and rear off-spring and thus protect itself from the attacks of predators. In the absence of dense vegetation, nest sites are often visible from a long distance and colonies are not able to defend themselves effectively from the predators and they become more prone to absconding.

17.5.3 Habitat Loss

Natural forests that play a vital role in maintaining ecological balance, providing energy, animal fodder and timber and recharging water tables, are being degraded day by day causing habitat loss of other life system and ultimately threatening biodiversity and associated pollinators. A constant rise in the population, higher rate of deforestation, and over-exploitation of resources with expansion of farm lands for agriculture and rearing livestock, cause a continuous depletion of the forest resources. The lowland and mid-hill fauna are more endangered than mountain fauna. Kaiser -I-Hind is the rear species of butterfly listed in IUCN Red Book. This is mainly due to greater human activity in lowland and mid-hills. Since 1945, 17% of the earth's vegetative land (1.2 billion ha) degraded, to an area equivalent to China and India together. To meet the need, the agriculture is expanding and pollinators' habitat is being lost so rapidly that sustainable agriculture is in jeopardy.

17.5.4 Habitat Changes

One of the major causes of native pollinator decline around the world is changes to habitat. This may include habitat loss and reduction, particularly in areas where natural ecosystems are replaced with agricultural systems; habitat fragmentation, where natural ecosystems survive but in patches too small to support sustainable pollinator populations; and habitat disturbances, where human activities disrupt pollination systems even when the habitat itself remains intact (Kremen and Ricketts 2000). An additional complication is the replacement of natural habitat with monocultures. Even for bee species that will feed on the crop and effectively pollinate it, the bees may be unable to find suitable nesting sites or alternative flowers when the monoculture is not in flower (Dias et al. 1999).

Degradation and fragmentation are the main causes of pollinator decline as illustrated below:

1. Hedgerows, field margins, embankments, and other "waste places" provide nesting habitat for some native bees. Removal of these often unappreciated habitats has been associated with dramatic declines in Germany's native bee fauna since the 1960s.
2. Fragmentation and habitat destruction can add to the rate of genetic erosion by reducing gene flow between demes (locally interbreeding group within a geographic population), and increases the likelihood that populations and species will become extinct.
3. When large habitats are fragmented into small isolated patches, it is not long before some of the animal residents decline in numbers to the point that they no longer provide effective ecological services beneficial to plants. Because some wild pollinators need undisturbed habitat for nesting, roosting and foraging, they are very susceptible to habitat degradation and fragmentation.
4. Urbanisation not only removes habitat directly but also isolates and fragments much of the land that it does not degrade or assimilate.
5. Reduction of food sources.
6. Fewer sites for mating, nesting and migration.
7. Over grazing and early cutting of hay meadows results in plants not reaching the flowering stage. However, forest clearing has opened up previously shaded,

humid habitats for many sun-loving pollinators and their plants. Roadsides, with their partially compacted soils, are frequently favoured nesting sites for bees and wasps.

17.5.5 Introduction of Alien Species: Plants, Pollinators, Pests and Pathogens

There is empirical evidence that entomophilous alien plants are readily integrated into native plant–pollinator networks, and can act as additional pollen and nectar sources (Stout and Morales 2009). In this case alien plants can buffer against potential shortages in nectar (and pollen) supply under environmental change (Schweiger et al. 2008). For instance, the alien plant *Impatiens glandulifera* facilitated the survival of native bumblebees when native nectar sources were scarce (Kleijn and Raemakers 2008). Therefore, alien plants with showy floral displays and/or large rewards decrease the dependence of native bees on native plants. In Europe, a significant proportion of entomophilous alien plants are ornamentals with long flowering seasons, appealing scent or showy flowers (Lambdon et al. 2008) and so facilitate interactions with native bees. However, the positive effects of alien plants might be limited to generalist pollinators, and indirect effects can disrupt native plant–pollinator interactions. For instance, competitive displacement of the preferred hosts of native pollinators can lead to declines in native pollinator populations, particularly specialist species (Traveset and Richardson 2006). Invasive plant species, often not requiring pollination to reproduce, are able to move in and displace native plant species, disrupting the ecology of both local plants and their pollinators. This is particularly destructive on small islands. Invasive animal species may impact the pollinators through competition with or predation on local pollinators (Kremen and Ricketts 2000).

Introduction of managed pollinators for crop pollination and honey production can impact on native pollinators (Thomson 2006) through competition for resources or direct interaction. A high level of overlap in plant use (up to 90%) was reported for alien *Apis mellifera* and native *Bombus* species in the USA (Thomson 2006) and up to 70% overlap for alien Bombus terrestris and native *Bombus* species in Japan (Matsumura et al. 2004), indicating high potential for competition. However, it still remains controversial whether competition actually occurs and impacts native pollinator population viability (Stout and Morales 2009). Whereas several studies show no support for negative effects of domesticated alien pollinators (Steffan-Dewenter and Tscharntke 2000; Roubik and Wolda 2001), others report impacts on reproductive success and body size (Thomson 2006; Goulson and Sparrow 2009). Alien pollinators can also have negative effects through genetic dilution, for instance, sub-species of managed honey bees and several bumblebees can interbreed with endemic populations, thereby eroding genetic diversity of native populations or even leading to the extinction of local sub-species (Franck et al. 1998). There is good evidence that translocated alien bees can increase the risk of pathogen spread (Stout and Morales 2009), including further spread of the ubiquitous *Varroa* mite into new areas such as Hawaii. Infection of colonies by multiple pathogens, and the resultant interactions between pathogens and other environmental stressors, is proposed as one of the reasons for the recently observed honeybee colony collapse disorder (Cox-Foster et al. 2007; Anderson and East 2008; Watanabe 2008) a phenomenon which the authors expect new studies to support. Climate change can affect the spread and virulence of pests and pathogens (Le Conte and Navajas 2008; Schweiger et al. 2008), whereas other factors such as land-use change, pesticide load, or decreased resource availability might increase bee susceptibility to pests and pathogens or vice versa. Although little is known about the potential for interand intra-specific transfer of pathogens in bee communities, there is evidence that the extent and role of host shifts and shared pathogens has been underestimated (Woolhouseet al. (2005). This is particularly true for honey bee viruses, including the widespread deformed wing virus (Ribière et al. 2008)), which is able to replicate within its mite vector (Ongus et al. 2004). Honey bee viruses can invade multiple host species (Eyer et al. 2009) and are thus likely to infect non-Apis wild bees and wild bee viruses may be able to infect honey bees. Indeed, preliminary data suggest that the virulence of deformed wing virus might be higher in bumblebees than in its original host, honey bees (Genersch et al. 2006). Nonnative domestic bees can also act as dispersal vectors for parasites and associated diseases, leading to the infection of congenerics (e.g. Varroa mites in Apis, *Nosema* spp. in Bombus and Ascosphaera apis fungus in Megachile Goulson 2003). Whereas the introduction of pest species (e.g. small hive beetle, Aethina tumida) and various pathogenic viruses have been shown to pose significant threats to feral and managed honey bees (Neumann and Elzen 2004), their effects on wild native pollinators remain unknown. There is, however, evidence suggesting a host shift of A. tumida in the USA to commercial bumblebee colonies (Spiewok and Neumann 2006).

17.5.6 Major Threat from Apis mellifera

Many importations of *Apis mellifera* in south and south-east Asia have proved disastrous for beekeeping with *Apis cerana*. When kept sympatrically, *Apis cerana* and *Apis mellifera* colonies frequently robbed each other (Koeniger 1982). Another major problem is the transfer of parasites from one species to another. A parasite mite of brood and adults, *Varroa destructor* co-exist with *Apis cerana* and causes no serious damage to this native bee species. In several countries of Asia, where both these species are kept together, the parasite has infested *Apis mellifera* colonies and became a serious pest to this unadapted host, now killing thousands of colonies every year. It is now well documented that through importations of *Apis mellifera*, *Apis cerana* populations in its native habitat are facing serious risk of extinction. On the other hand, also native *Apis cerana* populations are threatened by pests and parasites of exotic western honey bee *Apis mellifera* for which *Apis cerana* is lacking resistance. For example, there are several reports in the literature that Thai Sac Brood

Virus Disease, European Foul Brood and possibly Acarine Disease jumped in to *Apis cerana* and other Asian bee species from *Apis mellifera* in Nepal, India and other Asian countries killing large number of native bee colonies every year (Saville 2000). Due to these afflictions, populations of *Apis cerana* colonies practically reduced to the level of extinction but through natural selections within two decades, normal population of this bee species stand restored from 10% of surviving colonies (Abrol 2009). These risk factors may vary between different habitat types, landscapes and bio-geographical region. The relative importance of these factors and in particular their combined effects on *Apis cerana* genetic diversity loss are unknown.

Large scale importations and multiplications of exotic *Apis mellifera* in to developing countries of south and south-east Asia for better economic returns in terms of higher honey production has also become a myth. This bee species is now so seriously infested with parasitic mites, European Foul Brood, hornets/wasps/birds, wax moths that beekeeping with this exotic species require intensive treatment with chemicals to control these afflictions which are very expensive and making this enterprise economically unviable. The intensity and the need for chemical treatment of *A. mellifera* colonies for mite, diseases and pest control reveal that beekeepers in developing country of south and south-east Asia with large uneducated, ignorant populations in isolated areas are using chemical prescriptions indiscriminately and thus affecting the quality of honey. Partap et al. (2000) in the field study reported that worker bees of *A. mellifera* carried significantly heavier pollen loads from both peach and plum flowers than those of *A. cerana* worker bees. However, studies conducted on the pollination of strawberry showed that *A. cerana* collected heavier pollen loads during morning and noon hours showing time and crop specificity. But the introduced species, *A. mellifera* completely replaced domesticated native *A. cerana* bees as indicated by the absence of worker bees during early, mid and late hours under Chitwan condition. In addition, beekeepers are keeping *A. mellifera* and slowly replacing the native honeybee *A. cerana*, and thus a decline of *A. cerana* bees has been recorded in the country.

17.5.7 Pesticide Poisoning of Honeybees

Beekeeping and pesticides both have become essential inputs of modern agricultural management technology. By ignoring either of two, global food production would be seriously impaired. Since the advent of synthetic pesticides several decades ago, the beekeeping industry, both in the developed and developing countries, have been incurring heavy losses. In developed countries, large scale monoculture cultivation of crops and a high degree of mechanization had greatly amplified the problem of honeybee poisoning by pesticides. However, in recent years, education and public relations have achieved much in reducing bee losses due to pesticide poisoning in the developed world.

In developing countries, all species of honeybee still face very risk because agricultural practices often include insecticide application carried out in ignorance of indifference to the indispensability of bees. In all the developing countries of south and south-east Asia, a large area of land is being brought under the cultivation of high yielding exotic cultivars of crops and along with them their pests have also become introduced either through human error, accidentally or lack of proper quantitative facilities. For the control of these pests, a large number of biocides are coming into use. Because of the lack of information, farmers in the region use blanket application without caring, as to what and how much to use and when. Unlike developed countries, there is also lack of legislation to prohibit the use of pesticides to the extent that kill bees. Both the misuse and excessive use of pesticides disturb the natural ecosystem and produce serious environmental problems adding costs in four ways to the people: (i) health related expenses, (ii) environmental pollution, (iii) yield loss due to non-target pesticide application resulting in pesticide induced pest resurgence and destruction of natural enemies and (iv) financial burden both to poor farmers and the country as a whole. Pesticide problem on pollinators is severe in the developed country like USA (loss of about 320 million US$/year) and is equally important for other countries as well.

Integrated pest management technologies for protection of honeybees from harmful effects of broad-spectrum biocides are lacking. Such over reliance on chemical methods is adversely affecting environmental health including health hazards to human beings and decline in other non-target animal populations. Amongst the latter, honeybees because of their social behavior, run the highest risk of pesticide poisoning.

In many parts of the world, pesticides are used to control insect pests on a large scale, but pollinators (as well as the natural predators of the pests) are usually more susceptible to the pesticide than the target insects. Widespread use of pesticides in many parts of the world has reduced the overall numbers of pollinators (Pimentel et al. 1992) and this, particularly in the case of rare insect pollinators and/or rare plants, can have a devastating impact on pollination systems (Nabhan and Buchmann 1997a). there is also concern that sublethal doses of pesticides may disrupt the pollinating behaviour of all types of bees and render them more susceptible to diseases and parasites (Allen-Wardell et al. 1998).

17.5.8 Diseases and Enemies

There are frequent reports of *Apis cerana* colonies being affected by *Nosema*, virus cluster and sac brood diseases in the Hindu Kush Himalayan region. Recently, the European foul brood disease has badly affected *Apis cerana* colonies in Kathmandu valley of Nepal.

Amongst the mites, *Acarapis woodi*, *Varroa jacobsonii*, *Neocyphalaeps*, *Tropiolaelaps* sp and *Pymotes naferi* have been reported on *Apis cerana*. Amongst these, Acarine disease poses a serious problem (Verma 1987).

Amongst the predators, five different species of wasps pose a serious threat to beekeeping industry in this region. However, because of its shimmering and evasive behavior, *Apis cerana* can resist the attacks of wasps better than *Apis mellifera*. Two species of wax moths, *Gallaria mellonella* and *Archoria grisella* are serious pests in *Apis cerana* colonies as this native species of honeybee do not collect propolis to guard against the attack of moths.

In recent years, Thai sac brood virus disease has been reported from all countries where *Apis cerana* is found. In early eighties, the incidence and severity of this disease increased at such an alarming rate that more than 95% of colonies infected in different countries were killed by this disease (Rana et al. 1987). This resulted in great economic loss to beekeeping with *Apis cerana* in Asia not only in terms of honey and beeswax production but also through adversely affected pollination services. The problem was particularly severe in the temperate region of the country where disease was more widespread than in tropical and sub-tropical region.

The presence of Thai sac brood virus in the diseased colonies of *Apis cerana* in northern India was confirmed by conducting electron microscopic and serological studies (Rana et al. 1987).

Different control measures recommended earlier to control the spread of sac brood disease in *Apis mellifera* were unsuccessful in *Apis cerana* (Rana et al. 1987). However, about 5% of colonies in the affected areas were resistant and escaped the attack of this disease. Detailed investigations on such colonies indicate that some mechanism of resistance to the sac brood virus disease exists in *Apis cerana*. In *Nature*, this disease has a 5 years cycle, and after this period, about 5% of the surviving colonies start multiplying in a normal way and normal population is then restored.

Due to the incidence to Thai sac brood virus disease in *Apis cerana* in recent years, the beekeepers in the region had no choice but to adopt beekeeping with *Apis mellifera* which is not only free from this disease but is also giving higher economic returns to the farmers. Consequently, *Apis cerana* has been completely abandoned by the farmers in the region and it has now become endangered/threatened species of mere academic interest to the researchers in conservation biology.

Nepal did not know any serious bee disease until 1980, when the serious outbreak of the sacbrood disease caused by the Thai sacbrood virus, occurred first along the eastern border areas. The disease spread so fast that within 4 years it covered the entire length of the country, and reached to peak in western border areas within 3 years. During the time, almost 90% of the colonies lost (Kafle 1992; Shrestha and Shrestha 2000). By 1984, the disease started to subside and the bees started to regain normal condition again from the eastern border. The Asian mite, *Varroa jacobsoni* is associated with *A. cerana* and *A. dorsata* bees but causes no serious problem to them, but it is fatal to *A. mellifera* colonies. *A. mellifera* colonies may collapse in the near future unless timely precautionary measures taken. Farmers' training to beekeeping in modern hives, regular supervision and seasonal management seem necessary to establish good apiaries free of disease and pests.

Global populations of European honeybees have suffered for many years from a range of diseases such as European and American foulbroods, with parasites causing additional problems in recent years. The honeybee tracheal mite (*Acarapis woodi*) was discovered in the 1920s and slowly spread throughout the world, reaching the USA in the 1980s. Today it is found in all countries except Australia, New Zealand, Scandinavia and Canada. The mites infect the tracheal walls of young adult bees and shorten their lives, reducing honey production and pollination efficacy (Morse 1978). the *Varroa* mite (*Varroa jacobsoni*), a more serious pest of honeybees, is cosmopolitan throughout the world except a few isolated countries such as Australia. In 1987 it was detected in Florida and within a short period had spread across most of the USA. The mite feeds externally on bee larvae, pupae and adults and, if left unchecked, will kill most bee colonies in 7 months to 3 years (Ritter 1981).

17.5.9 Human Predations

Beekeeping in Asian region is marked by a long history of honey hunting methods that killed most of the bees, destroyed the brood and left no honey stores behind in the nest for consumption by bees during dearth periods. Such harmful exploitation by man resulted either in the loss of bee colonies or development of undesirable traits like absconding or swarming colonies have the tendency to return to the same nesting site each year, they are thus subjected to further harmful exploitation as these locations are well known to people. The net result of such human predation is both temporal and spatial decline in bee populations in its native habitat (Bishop 1992).

Honey hunting of *A. dorsata* and *A. laboriosa* honeybees is one of the most destructive method responsible for reduction in the number of colonies (Thapa 2006). As a result of habitat destruction and honey hunting, the wild honeybees, *A. dorsata* and *A. laboriosa* have been declining (Pokhrel 2006).

17.5.10 Global Warming and Climate Change

Global warming is caused by something known as the green house effect, brought about by the ability of the atmosphere to be selective in its response to different types of radiation. CO_2 (56%), CH_4 (14%), CFCs (23%) and N_2O (7%) are main green house gases of which, CO_2 accounts more than 50% for global warming. Atmospheric temperature increased by 1.5–5.50°C by the year 2030, causing loss of 10–15% arable productive costal land due to melting of polar ice caps and raise of sea level and CO_2 concentration increased from 290 ppm 100 year ago to 350 ppm today and likely to go up 440–500 ppm by 2100. European scientists have warned that a long-term 2°C or more increase in the average global temperature could threaten Latin America water supplies, reduced food yield in Asia and rise in extreme weather condition in the Caribbean. Global warming alters precarious habitats or eliminates food supplies. Based on the sample of 1,103 land plants and animals, it has been estimated that 15–37% would eventually become extinct as a result of climate change expected by 2050. Similarly, Californian scientists analysing 9,787 living and 129 extinct bird species, reported that tenth of all bird species could be extinct by 2100 and by then another 15% could be on the brick of extinction. The vulture population of India has crashed down by 95% in the last decade. These birds keep down insect populations, spread seeds, and pollinate flowering plants and scavenge on carrions. More intense and erratic rainfall events are expected to be a feature of climatic change. The fate of agriculture of Nepal lies on rainfall, early rainfall in April, May in the hills and mountain to sow the seed of corn with some rainfall in June and heavy rainfall in July for rainy season crops. If this does not happen then entire hills become famine stricken area. Similarly, agriculture in terai area starts with early rainfall in July and heavy but discontinuous rainfall up to the end of September (some time up to December). First rain helps paddy *Plantation* and second rain helps wheat *Plantation*. If one failed the second crop is also likely to be failure unless artificial pumping ground water or irrigation water provided. Climatic changes have been realized for past few years. Hills are getting more landslides and glacial lakes out burst and more of cloud burst brought in scattered rain. Terai is experiencing heavy rain in some area and drought condition in other areas. It appears that country's modulation capacity to absorb heavy flood and increase low flow has now changed because of environment degradation which directly influence habitat and its biotic flora and fauna.

Most evidence for climate change impacts on pollinators comes from butterflies, though studies on other pollinators remain scant. Recent climate change has already affected butterfly distributions (Hickling et al. 2006), and future changes, which are predicted to be greater in extent than recent historical changes, are likely to have even more severe impacts (Settele et al. 2008). These patterns are consistent with the few studies on bees; (Williams et al. 2007) found a relationship between climatic niche and declines in British bumblebees, whereas Dormann et al. (2008) projected general declines in future bee species richness in Europe. Such impacts of climate change occur at all organisational levels from the individual level (e.g. changing the temporal activity of bees Stone and Willmer 1989), through population genetics (e.g. *Evolutionary* change in butterflies (Thomas et al. 2001)), species level shifts (e.g. changes in phenology Hegland et al. 2009), bumblebee declines due to narrower climatic niches (Williams et al. 2007), or local or regional extinction of butterfly species (Parmesan et al. 1999; Thomas et al. 2001), to the community level (e.g. changing composition and functioning of pollinator communities (Memmott et al. 2007)). In addition to such direct impacts, indirect effects, when climate change affects interacting species, might be equally important but is poorly studied. Climate change-induced mismatches in temporal (Hegland et al. 2009a, b) and spatial co-occurrence (Schweiger et al. 2008), and morphological and physiological interdependencies of differently responding animal-pollinated plants and pollinators can potentially disrupt their interactions (Memmott et al. 2007).

17.5.11 Population Vulnerability Analysis (PVA)

According to Gilpin and Soule (1986), loss of genetic diversity of species leading to its extinction is a systems phenomenon involving the interaction of processes and states. It is to be based on three interacting fields i.e. Population Phenotype (PP), Environment (E) and Population Structure and Fitness (PSF). When such model is applied in relation to loss of genetic diversity in *Apis cerana*, the first field (PP) includes behavioral and genetic components such as frequent swarming and robbing, production of large number of laying workers, inbreeding depression and drift inbreeding. A second field, the environment (E) is the context. It includes all abiotic and biotic factors that influence the population. In case of *Apis cerana*, the loss of habitat quantity and quality as a result of rapid agricultural transformation and deforestation in the region and pesticide hazards due to their indiscriminate use are important abiotic components. The biotic components include introduction of exotic *Apis mellifera*, epidemic of sac brood virus disease and human predations as a result of traditional honey hunting methods. Population Phenotype (PP) and Environment (E) together determine the third field, the Population Structure and Fitness (PSF). This is the field in which dynamic consequences of interactions of PP and E are manifested in terms of patch distribution, population fragmentation, demographic randomness, reduced effective population size, growth rate and distribution leading to stochastic and deterministic extinction. The decay in one component can exacerbate not only itself but also the behavior of other components (Gilpin and Soule 1986).

17.5.12 Other Factors

Two other factors whose impact on pollinators is not so clear are Africanised bees and the role of genetically engineered crops. Long term studies in South America have shown that the invasion of the aggressive and adaptable Africanised bees into native ecosystems has undoubtedly caused the loss of some native species of bees, but their impact on overall pollination systems is still under review (Roubik 2000), given that they have negative effects in some regions but neutral and occasionally positive effects in others. Genetic engineering and “the rapid development of transgenic crops raises additional causes for concern among specialists on bees” (Dias et al. 1999). The practice of incorporating the insecticidal *Bacillus thuringiensis* (Bt) gene into crops has raised concerns about the effect of pollen from these plants on pollinators, but so far the evidence is scant. Some studies have suggested GM pollen from a number of crops reduces the survival rate of caterpillars such as the Monarch or Wanderer Butterfly (*Danaus plexippus*), as well as European Honeybees (Conner et al. 2003).

17.5.13 Consequences of Decline

1. Less frequent flower visitation, abrupt or gradual decrease of seed and fruit production.
2. Beekeeping sector in danger in several areas in Europe.
3. Self-compatible flower plants can suffer from inbreeding.
4. Pistil senescence.

17.5.14 Colony Collapse Disorder (CCD)

Colony Collapse Disorder (CCD) has been described as a major cause of decline of honeybee colonies. It is described as a multifactorial syndrome which has been leading to low number of adult bees in the hives which still held food supplies and immature bees (brood). The following symptoms were reported:

1. Complete absence of adult bees in colonies, with no or little build up of dead bees in the colonies.
2. Presence of capped brood.
3. Presence of food stores, both honey and bee bread.
4. In collapsing colonies:
5. Insufficient of workforce, mostly consisting in young adults bees.
6. The queen is present.
7. The cluster is reluctant to consume provided feed, such as sugar syrup and protein supplement.

17.5.14.1 CCD Causes

According to Frazier et al. (2007), the causes of CCD are not yet known. The potential causes investigated by "The CCD working group" are, but are not limited to:

1. **Chemical residue/contamination** in the wax, food stores and bees. Due to the *Evolution* of resistances to chemicals of mites and other pathogens, beekeepers may be increasing dose rates or trying cocktails of chemicals exposing commercial honey bees to levels of chemical residue that are inimical to worker longevity.
2. **Pathogens** in the bees and brood. For example, European Foul Brood (caused by *Mellisococcus pluton*), and American Foul Brood (caused by *Paenibacillus larvae*) on larvae and pupae,
3. **Parasite load** in the bees and brood. For example, *Varroa destructor* on adult bees.
4. **Nutritional fitness** of the adult bees
5. **Level of stress** in adult bees as indicated by stress induced proteins
6. **Lack of genetic diversity** and lineage of bees making them more vulnerable to the development of epidemics, Examples of topics that The CCD working group is not currently investigating:
7. **Agricultural insecticides**. American agricultural systems are dependent on the use of pesticides. Where insecticides are used, honey bee losses are common, and where bees are required for pollination, careful management is required to minimize bee losses.
8. **Changed agricultural practise**. Due to reduced honey yields nation-wide, beekeepers seek alternative income beyond honey production (for example colonies for almond pollination, crop that is totally dependant on bee pollination).

Anecdotal evidence suggests that CCD is more common in businesses in which bees are trucked large distances and rented for pollination.

9. **GMO crops**. Some GMO crops, specifically Bt Corn have been suggested as a potential cause of CCD. While this possibility has not been ruled out, the weight of evidence reported here argues strongly that the current use of Bt crops is not associated with CCD (Dively 2007), CCD symptoms do not fit what would be expected in Bt affected organisms and there is no strong evidence that GM crops cause acute toxicity to honey bees. For this reason GMO crops are not a "top" priority at the moment. According to Dively (2007).
10. **Radiation** transmitted by cell towers: The distribution of both affected and non-affected CCD apiaries does not make this a likely cause. Also cell phone service is not available in some areas where affected commercial apiaries are located in the west. For this reason, it is currently not a top priority.
11. **Cool brood**. If the brood is incubated a little outside the ±0.5°C of 34.5°C range (nest temperature maintained by bees), the resulting adults are normal physically, but show deficiencies in learning and memory (Tautz et al. 2003; Jones et al. 2005). If colonies were unable to maintain optimal brood nest temperatures, CCD-like symptoms might be apparent. The working group on CCD is now concentrating on three different hypotheses:
    (a) Reemerging pathogens responsible for CCD. It has become clear in recent years that many pathogens have the ability to impair the immune defences of their hosts.
    (b) Stresses working together to weaken bee colonies and allowing stress-pathogens to cause final collapse. For example stresses are encountered by bee colonies that are part of migratory operations. As a result of the migratory process, multiple stressors impact in these operations can cause significant losses of honey bee colonies.
    (c) Environmental chemicals causing the immuno-suppression of bees and triggering CCD.

Amongst other, the neonicotinoids, a class of pesticides that have been extensively adopted for pest management. Although highly effective in controlling insect pests; these chemicals are known to be highly toxic to honey bees and other pollinators.

17.5.15 Agriculture Practices

Improper use of pesticides, herbicides and insecticides, for example coating seeds with regular or systemic insecticide (such as Imidacloprid), which is absorbed by the root and migrates through every part of the plant including pollen and nectar, poses a potential threat for pollinators such as honeybees and other insects. A study by (Bonmatin et al. 1994): revealed that pesticides, including the ones mentioned above, cause bees to lose their sense of direction. This is the goal for insects harmful to the crops, but should be avoided for useful pollinators. In fact other studies revealed the high toxicity of Imidacloprid and associated inert ingredients for cats, fish, rats, rabbits, birds and earthworms (Cox 2001).

The replacement of natural plant communities by monoculture, is also a factor since most monoculture are not capable of sustaining pollinator populations: wheat and corn do not provide nectar or pollen needs for any bee species (Cane and Tepedino 2001). Adding to this, insecticides are applied not only on agricultural fields but also in backyards, recreational areas, forests and mosquito-ridden marshes and swamps. The broad-spectrum insecticides that are commonly used are often as toxic to beneficial insects as they are to the target species (Johansen and Mayer 1990).

Whether managed or wild, pollinators need protection from excessive exposure to pesticides and other chemicals that can poison them or impair their reproduction. These chemicals can also eliminate nectar sources for pollinators, destroy larval host plants for moths and butterflies, and deplete nesting materials for bees (Nabhan and Buchmann 1997a). On the other hand, it may be that plant losses from chronic herbicide use are, in fact, driving losses of pollinator species, and not vice versa (Cane and Tepedino 2001).

17.6 The Decline of Other Bee Species

In natural systems, particularly biodiversity hotspots such as tropical rainforests, the decline in pollinator numbers has a more significant effect because their services are essential to maintain that diversity. The more plant species that are present in a habitat, the less is the access for each species to the pool of pollinators. As each pollinator declines and the ‘pollination limitation’ increases, the risk of extinction for any plant species also increases (Vamosi et al. 2006). Pollination limitation, involving reproductive shortfall or failure of seed set, is thought to be in the range of 50–60% in rare plant species or plants found in fragmented habitats (Allen-Wardell et al. 1998), and some research suggests more than 60% of plant species studied are pollination limited (Burd 1994). Forests have the added burden of habitat loss due to agricultural encroachment, habitat fragmentation, and the invasion of Africanised bees (Roubik 2000).

Aside from biodiversity hotspots, there are a number of other natural ecosystems particularly susceptible to the effects of pollinator decline. In tropical communities dominated by large tree species, such as figs, where each fig species is dependent on one or two species of fig wasps for pollination, and where 80% of the vertebrate species rely on the fruit as the basis of their diet, loss of a few pollinator species can be catastrophic to the entire ecosystem. This is also the case on islands, where pollinator guilds are often depauperate even without human interference, and a number of plant species may rely on a single pollinator (Allen-Wardell et al. 1998).

One particularly important area for pollinators is the interface between agricultural lands and natural ecosystems. When managed pollinators such as European honeybees are not capable of pollinating a crop to full capacity, other bee species from surrounding areas may be able to complete the task (Kremen and Ricketts 2000). However, the impact of pesticides and other human-generated activities may extend for some distance into natural ecosystems, affecting both the crops and native plant species.

17.6.1 Multiple Drivers and Pressures

The drivers described above act simultaneously and could act synergistically on pollinator communities (Tylianakis et al. 2008). Based on theoretical considerations and supported by evidence from a broad range of organisms, including pollinators such as butterflies, Didham et al. (2007) conclude that non additive effects of multiple drivers and pressures can be particularly important. However, most studies to date addressing effects of multiple drivers have been relatively limited in scope. The potential for interacting effects requires that multiple drivers be simultaneously considered if we are to understand how pollinators and animal-pollinated plants will respond to global change (Tylianakis et al. 2008; Memmott et al. 2007; Schweiger et al. 2008). One of the few insights into the interacting effects of multiple pressures is for domesticated honey bees.

17.6.2 The Pollination Crisis

The risk of relying on a single pollinator is becoming clear, and global organizations are recognizing the need for a diversity of pollinators, particularly native species. Many of these species need to be managed if they are to fulfill their potential as pollinators of agricultural and horticultural crops, because “although the most important causes of pollination disruption are shared among regions of the world, their consequences vary widely in complex, idiosyncratic ways” (Kremen and Ricketts 2000). As much as anything, the pollination crisis may be an economic crisis; Southwick and Southwick (1992) estimated the then economic loss due to declines in European honeybee populations to be US$ 5.7 billion per year worldwide.

The potential loss of pollinators, particularly specialist pollinators such as orchid wasps, has serious consequences for not only individual plant species but, potentially, entire plant guilds and ecosystems; “the loss of specialised pollinators will strongly select for self-compatibility, self-pollination, and reduced genetic variability in plants, resulting in a possible reduction in their *Evolution*ary adaptability to environmental change” (Allen-Wardell et al. 1998). These effects may then cause further ripples through natural and managed ecosystems; in Canadian blueberry fields, a reduction in available pollinators due to the overuse of pesticides affected a great range of organisms including invertebrates, birds, bears and even humans (Kevan 1977).

In the last two decades there have been a number of examples of local or widespread failure of crops directly attributable to the pollinator decline, including failure of pumpkins, cherries, alfalfa, blueberries, cashews and Brazil nuts (Allen-Wardell et al. 1998). There may also be a reduction in crop quality due to lack of pollinators (e.g. fewer seeds fertilized in fruit and therefore smaller fruit) and, additionally, crop failures attributed to other factors, such as poor weather, may be exacerbated by lack of pollinators.

The International Convention on Biological Diversity specifically cites pollination as a key ecosystem function that is threatened globally. Its aims are to address the lack of taxonomic information on pollinators, and promote the conservation and the restoration and sustainable use of pollinator diversity in agricultural and related ecosystems. The Sao Paulo Declaration on Pollinators (1999), based on the available global evidence at the time, reported that "the numbers of native bees are dwindling, some species seriously so" (Dias et al. 1999). One practical way to redress the problem is to begin the search for alternative pollinators now. "For some years several species of wild bees have been managed for the pollination of crops, and the management of additional species for glasshouse crops has developed rapidly during the past few years" (Dias et al. 1999).

17.6.3 Impacts of Pollinator Declines

Since agricultural activities were first recorded, there have been shortages of pollinators. Today it seems that pollination systems in many areas of agriculture are threatened by the inadequacy or lack of sustainable managed, indigenous, or imported pollinators. Pollinator shortages can adversely affect crop production and commodity markets. It is widely believed that pollination is in such serious jeopardy from the viewpoints of agricultural productivity and food security (Kevan and Imperatriz-Fonseca 2002) that the Convention on Biological Diversity and the Food and Agricultural Organization of the United Nations have recently (1998–2000) taken on leading roles internationally in this area.

The Food and Agriculture Organization (FAO) of the U.N. (Williams 1996) estimates that of the slightly more than 100 crop species that provide 90% of food supplies for 146 countries, 71 are bee-pollinated (mainly by wild bees), and several others are pollinated by thrips, wasps, flies, beetles, moths and other insects. In Europe alone, 84% of the 264 crop species are animal-pollinated and 4,000 vegetable species have their life assured thanks to the pollination of the bees (Ingram et al. 1996). Pollinators are essential for the reproduction of many wild flowers and crops: for one out of every three bites eaten, one can thank a bee, butterfly, bat, bird or other pollinator (Free 1993). As Simon Potts (University of Reading) says: "The economic value of pollination worldwide is thought to be between £30 and 70 billion each year" [i.e. 45–100 billions €]. Any loss in biodiversity is a matter of public concern, but losses of pollinating insects may be particularly troublesome because of the potential effects on plant reproduction and hence on food supply security.

Many agricultural crops and natural plant populations are dependent on pollination and often on the services provided by wild, unmanaged, pollinator communities (Cane and Tepedino 2001).

Several researches have highlighted the different factors leading to pollinators decline (Biesmeijer et al. 2006) such as modern agricultural practices and use of pesticides, habitat fragmentation, climate change, also to a lower extent lack of floral diversity, competition from non-native species, diseases, predators and parasites.

North America where about a third of honey bees disappeared in several months. In the UK and the Netherlands, a 70% drop of wild flowers that require insect pollination has been recorded as well as a shift in pollinator community composition since the 1980s. In UK (Thomas et al. 2004) 71% of butterfly species have decreased and 3.4% became extinct over the past 20 years, illustrating the greatest net loss compared to native vascular plants (28% decrease in 40 years) and birds (54% decrease in 20 years) of the same area in the UK. Most species of non-migratory butterflies that reach the northern margins of their geographic ranges in Britain have declined over the last 30 years (as they have elsewhere in northern Europe Warren et al. 2001). In North America, also a significant decline in commercially managed honeybee colonies has occurred with honey bee colonies down by 50% in the past 50 years.

17.6.4 The Impact of Declining Pollinator Populations on Agriculture

It is recognized that agricultural production, agro-ecosystem diversity and biodiversity are threatened by declining populations of pollinators. Many pollinator population densities are being reduced below levels at which they can sustain pollination services in agroecosystems, natural ecosystems, and for the maintenance of wild plant reproductive capacity. The major contributors to this decline in pollinator populations are, *inter alia*, habitat loss and fragmentation, land management practices, agricultural and industrial chemicals, parasites and diseases, and the introduction of alien species. Ecological dangers of pollinator decline include the loss of essential ecosystem services (particularly agro-ecosystem services) and functions that pollinators provide. Ecosystem services in their turn have their own value ñ biophysical, but also economic. For example, for the entire biosphere, the value of ecological services (most of which outside the market) was estimated to be in the range of US$ 16–54 trillion per year, with an average of US$ 33 trillion per year (Costanza et al. 1997). Services that are provided by native pollinators (non-honeybee species) are estimated to be worth US$ 4.1 billion a year to United States agriculture alone (Prescott-Allen and Prescott-Allen 1990). The value of the annual global contribution of pollinators to the major pollinator-dependant crops is estimated to exceed US$ 54 billion (Kenmore and Krell 1998). In the Canadian prairies, the value of pollinators to the alfalfa seed industry has been placed at about CAD six million per year (Kevan and Phillips 2001).

Examples from Asia (e.g. northern Pakistan, parts of China) show linkages between declining natural insect populations and decreasing crop yields – as a result, people have begun to *manage the crop-associated biodiversity* (i.e. pollinators) in order to maintain their crop yields and quality. For example, farmers in Himachal Pradesh (in northwestern India) are using honeybees to pollinate their apples (Partap 2003). Due to declining pollinator populations and changing cultivation practices, an increasing number of farmers around the world are now paying for pollination services and are importing and raising non-native pollinators to ensure crop production. In many developing countries, however, external pollination services are not available and rural communities have to live with reduced quantity, quality, and diversity of foods. In fruit orchards in Western China, the decline of useful insect populations has led farmers to pollinating by hand, acting as human bees. Despite a general recognition of the impact of declining pollinator populations on ecosystem functioning, and despite the examples of the ecological and economic impacts as well as examples of where this is occurring, bottlenecks and constraints hinder the conservation and management of pollinators in sustainable agriculture. An example of a globally recognized bottleneck is the lack of taxonomic information, which hampers progress that could be made in identifying and analysing firstly pollinator populations important to agriculture, and their behaviour patterns, but also best management practices. Best management practices are not readily available or known in all areas of the world, and especially not to all peoples. Indeed, a lack of awareness of pollinator issues from the farmer to the extension worker to the policy maker ñ is also a set-back for the promotion of issues related to the conservation and management of pollinators within the context of sustainable agriculture. Recognition of these bottlenecks and constraints as well as a need for action contributed to the international arena is response to the conservation and management of pollinators, in agricultural and non systems.

17.6.5 Threats to Pollination Systems

The collapse of pollinator mutualisms has been identified as one potential consequence of anthropogenic land use change (Kearns and Inouye 1997; Allen-Wardell et al. 1998; Kearns et al. 1998; Wilcock and Neiland 2002). Declines in pollinators have been reported from most continents (Kearns et al. 1998; Kevan and Phillips 2001). Land clearance, fragmentation, agricultural practices, herbicides, pesticides and the introduction of exotic plant and pollinator species (Table 17.3) have all been implicated in a serious decline in pollinators that has been referred to as a "pollination crisis" (Buchmann and Nabhan 1996). Loss of or interruption to pollinator services may have several outcomes. The most obvious result is a loss or reduction in seed set, however, impacts may also extend to reduced offspring vigour as a result of self pollination, decreasing heterozygosity, and in the increased expression of deleterious traits, resulting from inbreeding (Kearns and Inouye 1997). Ultimately, loss of seeds, fruits or plants will affect animals that rely on these resources.

Table 17.3 Summary of threats to pollination systems

Threat	Effect	Impacts
Fragmentation	Reduced population size • Isolation • Hostile matrix • Alteration of visitor behaviour	1. Increased genetic drift, in-breeding depression, increased threat of extinction, reduced pollen dispersal, reduced fitness (Rathcke and Jules 1993; Kearns et al. 1998). 2. Increased reproductive success (Cunningham 2000). 3. Temporary reduction in pollinator activity (Becker et al. 1991). 4. Genetic erosion of small populations (Cane and Tepedino 2001; Ghazoul et al. 1998, Oostermeijer et al. 1998). 5. No reduction of reproductive success, substantial between and within-site variability (Costin et al. 2001). 6. Effect of isolation tied to pollinator mobility (Law 2001). 7. High genetic differentiation among geographically close patches (Dutech et al. 2002). 8. Pollen clogging by generalist pollinators (Kunin 1997; Groom 2001).
Agricultural practices	• Land clearing • Pesticide spraying • Herbicide spraying • Extensive monocultures • Grazing • Resource depletion	Pesticides reduce pollinator numbers (Batra 1995). 1. Poisoning of pollinators resulting in death, behavioural changes and reduced mobility (Johansen 1977). 2. Contamination of pollen and honey (Kearns et al. 1998). 3. Herbicides reduce availability of nectar plants, remove nesting sites, destroy larval food sources for pollinators (Kevan 1975a, b; Kearns et al. 1998; Richards 2001). 4. Grazing changes nesting sites, decreasing water availability, and replacement of native grass species with introduced pasture grasses (Kearns and Inouye 1997).

(continued)

Table 17.3 (continued)

Threat	Effect	Impacts
Invasive species	• Displacement of pollinators by feral competitors • Displacement of native plants	1. Feral honeybees compete for pollen normally available to native pollinators, altering pollen dispersal patterns through foraging that differs from native pollinators, and depleting nectar supplies to nectar feeding pollinators (England et al. 2001). 2. Introduced bees implicated in successful spread of exotic plant species where native animal species are not suitable pollinators (Stout et al. 2002).

Like most tropical landscapes, the Wet Tropics have been subjected to processes of fragmentation over the last 100 years or so. Plant species ‘marooned’ in these fragments may or may not be part of viable populations – and it may take much longer than 100 years before this becomes evident. Pollination and the subsequent reproductive performance of plants in fragments becomes a crucial issue. Understanding the changes that will occur to pollination processes and outcomes in fragments is an essential first step in managing these changes and attempting to ensure the long-term future of our forests. That having been said, there is almost no data available on this topic. The study by Law and Lean (1999) on *Sygygium cormiflorum* did demonstrate that visits by vertebrates to the flowers were skewed in favour of bats over birds in fragmented situations.

17.7 International Conventions/Relevant Policy Measures/Recommendations

17.7.1 What Should be Done Now?

17.7.1.1 Educate the Public on the Importance of Pollinators

As stated previously, humans rely totally on pollination for survival and “the management and protection of wild pollinators is an issue of paramount importance to our food supply system” (Allen-Wardell et al. 1998). The European Pollinator Initiative and the Sao Paulo Declaration on Pollinator Decline both raise the need for increased public awareness of the importance of pollinators, particularly bees, and both emphasise the value in targeting the world’s education systems (Dias et al. 1999). The landmark paper on the global pollination crisis, co-authored by 22 pollination ecologists, scientists and resource managers, and endorsed by 13 universities and international organisations, “identified the need for…a better focus at primary, secondary and higher education levels on how pollination services benefit society” (Allen-Wardell et al. 1998).

17.7.1.2 Raise Awareness of the Pollination Crisis

Pollination ecologists and environmental scientists around the world are well aware of the pollination crisis and “an increasing number of organisations are beginning to promote the restoration of ecological functions such as pollination” (Kremen and Ricketts 2000) to the rest of the community. Time is short, as “populations of many native plants and their pollinators are being diminished and lost due to habitat fragmentation, degradation and loss” (Allen-Wardell et al. 1998) at an increasingly rapid rate, and “loss of pollinators from a biotic community may not be easily reversible. We do not know…how to remedy the loss of native pollinators, or even if such remedies are possible” (Allen-Wardell et al. 1998). The global organisations currently tackling the pollination crisis emphasise the need to raise awareness, and the European Pollinator Initiative plan of action aims to:

1. Educate land managers, farmers and conservationists;
2. Train the next generation of researchers and taxonomists; and
3. Support national plans for the conservation of bees and increase the awareness of governments, industry and the public.

There are a range of options to remediate the pollination crisis but, “as with many conservation issues, the final challenge will be to gather sufficient public support to implement [pollination crisis] solutions” (Kremen and Ricketts 2000).

17.7.1.3 Undertake Research on Alternative Pollinators

One of the biggest hurdles in overcoming the pollination crisis is lack of knowledge, as “there have been few comprehensive studies of pollination webs” (Corbet 2000) and a serious threat to conserving pollination systems is the paucity of verifiable scientific data on pollinator abundance or effect (Roubik 2000). The European Pollinator Initiative identifies the need to “develop alternate species of pollinator for management” as a key element, and the International Pollinator Initiative highlights the need to “assess breeding techniques of native pollinators” before serious work can begin (Dias et al. 1999).

Management of a range of bee species is required to maintain the world’s pollination systems, particularly in agricultural areas, but management is unlikely until more is known about their taxonomy, ecology and biology. Over most of the world, even in managed agricultural areas, the pollination ecology (i.e. which species are undertaking what proportion of the pollination) is very poorly known. In natural ecosystems our knowledge is significantly poorer still. Without properly understanding the current situation it is difficult to determine remedies. Other important questions which require answers to assess and rectify the situation include:

1. Which local bee species are suitable as pollinators in each region of the globe?
2. How effective are they as pollinators and how do they compare with pollination services provided by European honeybees?
3. Can their services be improved through management and what management techniques are necessary?
4. Can local species be translocated to other areas and still have the same pollination efficacy without further disrupting the local ecosystems?
5. Over what area do the bees forage and therefore what is their pollination radius?
6. Do the bees require roosting and/or nesting sites and can these be provided by the agriculturalist, or do they require natural areas to be set aside?
7. If supplemental feeding of colonies is required, over what area do they need to forage and how is this affected by habitat fragmentation
8. What impact will local predators and parasites have on the bees and what impact will an artificially elevated bee population have on local food webs?

The most basic requirement to answer these questions is information on the biology of each species. Social bees require different management strategies to solitary bees; nesting and foraging sites differ markedly between species; their survival rate and longevity is in part dependent on the habitat, including agricultural habitats; and the way each species harvests nectar and the efficacy of pollen transfer is also dependent on their biology and social system (Klein et al. 2002). Research is required at all levels and efforts must be made wherever possible to invest in the development or domestication of (non-*Apis*) alternative pollinators that can be employed when the services provided by managed honey bees are inadequate to ensure high fruit set (Allen-Wardell et al. 1998). Wherever preliminary studies have been undertaken around the world, the situation has been found to be more complex than at first glance (Klein et al. 2002), and the situation is particularly important in Australia, where “groups of native bees that have special importance for pollination systems need to be identified and cross-checks with possible conservation threats need to be made” (Schwarz and Hogendoorn 1999).

17.7.1.4 Larval Stage Conservation

Important invertebrate pollinators have discrete larval stages whose mobility and habitat requirements are dramatically different from those of the winged adult. Conservation initiatives have sometimes been slow to consider the needs of different life-cycle stages. For example, many conservation-minded researchers advocate planting nectar plants for butterflies, but then fail to foster their larval host plants (Cane and Tepedino 2001).

17.7.1.5 Alternative Agricultural

Alternative agricultural techniques can provide non-toxic methods of weed and insect control that incorporate use of habitat set-asides for beneficial insect populations and require the use of fewer toxins. Gardeners and farmers can rely on alternative non-toxic methods to control pests and weeds. More widespread practice of such methods has the potential to reduce wildlife exposure to insecticides, herbicides and fungicides (Corbet 1995). Farmers that set aside land to support wild pollinators could be rewarded for such a practice. Unploughed farmland set aside for several years can produce vegetation that supports considerable insect diversity and benefits nearby crops by providing pollinators and other beneficial insects. Large-scale protection and management of habitat networks are required to minimize habitat-related declines and to maximize the ability of species to track the distribution of suitable climate. A major objective will be to identify, test and document good agricultural practices for pollinator conservation and management, through an "ecosystem approach". Farmers might be encouraged to protect "corridors" that connect natural habitats, or uncultivated areas within and around cultivated ones.

17.7.2 Level of Knowledge/Awareness

Studies reveal that level of knowledge about biodiversity conservation; pollination and pollinators in farmers are inadequate. Majority of farmers are not aware of biodiversity conservation and natural pollinators or managed pollination of crops.

17.7.3 National Policy on Pollinators

It is clear that insects including honeybees are unquestionably the main pollinating agents for many crop plants. Their role in pollinating vast array of flowering plants and maintaining biological diversity is beyond the imagination of poor farmers, politicians, policy makers and even scientists are in dilemma. Beekeeping is known for honey production as well as pollination services to crops, but the later has received no attention in research and development activities in the country. Beekeeping important service of pollination has not only been underplayed by the planners, government authorities and also the agriculturists have ignored altogether.

17.7.4 Conservation and Utilization of Pollinators

Honeybees show preference to more attractive floral rewards neglecting the less attractive ones (Free 1984). When two or more species of bees compete for the same floral sources, the stronger and more competitive species displace the weaker one from the resources and geographic areas affecting crop pollination. Presence of *Apis mellifera* L has displaced and reduced the number of *Apis cerana* Fab. honeybees from the resources (Neupane 2001; Mishra 1997). It has become increasingly clear that the pollination needs of a crop species varies greatly with the locality and cultivar concerned, so ideally pollination investigations are necessary in each general locality where crop is grown. Plant species are now grown for food, or other uses, in many parts of the world far from where they originated, and sometimes in absence of their natural pollinators. In such circumstances, careful consideration should be given to import natural pollinators with the introduced plant species. In addition, increased need for hybrid seed production has often posed several pollinating problems and indeed the breeders of insect pollinated crops should always ensure that the quality and quantity of pollen and nectar produced will attract sufficient pollinators even when competitive sources are nearby. Pollinator's distribution is not systematic; some areas overcrowded with bees and others having practically none. Proper placement of the pollinators and even their attraction to pollinating crops is necessary for good result for ensuring effective pollination. If placed properly, honeybees worked equally well in all directions and were evenly spread in flowers (Ingram et al. 1996).

For several decades, bee researchers and beekeepers have tried to conserve pollinating insects like honeybees providing nesting sites and good forage, and protecting them from pesticides. Managed pollination of crops that has been largely neglected part of agriculture requires due attention to increase productivity and quality. In this regard, little work has been done on the number of bee visits per flower, or the effect of cross-visitation between cultivars in relation to fruit set on crop cultivars either dependent upon or benefited by bee pollination.

Some recommendations have been made, without support or data, on colonies per hectare and suggested placement. There is no indication given as to the relative bee population per unit of flowers and also no relation is shown between colonies per hectare and bees per flower. Studies on the foraging preference and effect of foraging competition of different honeybee species to crop pollination should find priority in future research for different ecological regions.

In the developed countries, insect pollination has increased considerably during the past few decades and arrangements for insect pollination are now part of standard management practices when growing many crops. For example, in the USA alone, over million honeybee colonies are rented annually for pollination services.

With hybrid seed production, it is likely that demands for pollination will become greater still in the near future. In the developing countries, pollination by honeybees and other pollinators is completely neglected by everyone- policy makers, naturalists, researchers, extension workers and farmers. Rather it is just opposite that farmers are complaining loss of crops due to bees and other pollinators considering them as crop pests. As far as conservationist is concerned most emphasis have given to large mammals, birds, and reptiles, and almost nil to insect pollinators. Biodiversity can not be isolated from pollinators' diversity, and therefore, there is a need to address pollinators and their conservation issues in existing acts and regulations to take care of pollinator issue. Community members as users of local resources should be aware about importance of wild bee conservation for environment improvement, and benefit sharing.

At the present day, there is now a general increased environmental awareness for sensible habitat management that may help pollinators likely to increase. Discovering potential pollinators, devising management techniques, and increasing their population for commercial exploitation requires immediate attention. Research studies are needed in this direction to conserve honeybees and other natural pollinators, exploit their potentiality in crop pollination and allow them to develop in the pollution free environment.

17.7.5 The International Response

The Convention on Biological Diversity (CBD) and its programme of work on agricultural biological diversity has focused of the conservation o pollinators. CBD (decision III/11) in its third meeting of the Conference of the Parties (COP) recognized the importance of agricultural biodiversity and decided to establish a multi-year programme of activities on agricultural biological diversity. This also involved calling for priority attention to components of biological diversity responsible for the maintenance of ecosystem services important for the sustainability of agriculture, including pollinators. COP Decision III/11 also encouraged interested parties and international organizations to conduct case studies on pollinators, including consideration of the monitoring of the loss of pollinators worldwide; the identification of the specific causes of pollinator decline; the estimation of the economic cost associated with reduced pollination of crops; the identification and promotion of best practices and technologies for more sustainable agriculture; and the identification and encouragement of the adoption of conservation practices to maintain pollinators or to promote their re-establishment. Subsequent declarations at Sau Paulo Brazil and Kenya endorsed the Programme of Work on Agricultural Biodiversity (decision COP V/5) with the objective to promote the positive effects and mitigate the negative impacts of agricultural systems and practices on biological diversity in agro-ecosystems and their interface with other ecosystems; to promote the conservation and sustainable use of genetic resources of actual and potential value for food and agriculture; and to promote the fair and equitable sharing of benefits arising out of the use of genetic resources. The objectives of the International Initiative for the Conservation and Sustainable Use of pollinators (IPI) are to promote co-ordinated action world-wide to monitor pollinator decline, its causes and its impact on pollination services, address the lack of taxonomic information on pollinators; assess the economic value of pollination and the economic impact of the decline of pollination services; and to promote the conservation and the restoration and sustainable use of pollinator diversity agriculture and related ecosystems.

A number of other activities and initiatives have been developed, and are being implemented, to respond to the issues related to the conservation and sustainable use of pollinators. Just a few examples of such initiatives include the African Pollinator Initiative, The Brazilian Pollinator Initiative, the European Pollinator Initiative and the North American Pollinator Protection Campaign are other examples. The International Centre for Integrated Mountain Development (ICIMOD) and India is also undertaking extensive work in the area of pollination in the Hindu-Kush Himalaya region.

17.8 Conclusions

Growing evidence points to substantial losses of pollinators in many regions of the globe, with the strongest evidence coming from Europe and North America. Further studies on other continents are needed to map the ubiquity of the phenomenon. The integration of existing national and local monitoring schemes and the establishment of a global programme could yield important data to help direct policy decisions regarding pollinators. Threats to pollinators are diverse, and might interact; the current challenge is to better quantify the relative importance of a range of drivers and in particular their synergistic effects. With continued pressure from known drivers such as habitat loss and pathogens, coupled with the clear ecological and economic risks associated with pollinator loss, there is a continued need to improve our understanding of the *Nature*, causes and consequences of declines in pollinator services at local, national, continental and global scales. Given the weight of evidence of pollinator loss and associated risks, investment in developing mitigation options such as agri-environment schemes, protected area networks and alternative managed pollinators is essential to ensure sustainable pollination services in a changing world.

A concerted effort, from the global community that deals with issues related to environment and agriculture, to undertake its activities by taking into account pollinator considerations would assist in the implementation of the IPI. In this regard, COP decision V/5 invites relevant leading organizations to collaborate in supporting actions in Parties and countries subject to pollinator decline. In addition, increasing awareness and understanding of the role and value of pollinator conservation and sustainable use should lead to the development and implementation of local, national, regional and international policies, programmes and projects that integrate pollinators considerations, hence contributing to sustainable agriculture.

Anthropogenic activities may be detrimental to some species but beneficial to others, with sometimes subtle and counter intuitive causal linkages. It is essential to recognize that pollination is not a free service, and that investment and stewardship are required to protect and sustain it. Economic assessments of agricultural productivity should account for the “cost” of sustaining wild and managed pollinator populations. There is a need for well-documented cases of specific pollinator declines notwithstanding, rapid extrapolation from our current knowledge to imply worldwide pollinator and crop production crises might be inappropriate and premature, much uncertainty remains regarding pollinator-pollination declines. As Albert Einstein put it bluntly, “No bees, no food for mankind. The bee is the basis for life on this earth.”

References

Abrol DP (2009) Bees and beekeeping in India, 2nd edn. Kalyani Publishers, Ludhiana, 720 pp

Aguilar R et al (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol Lett 9:968–980

Aizen M, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr Biol 19:915–918

Aizen M, Garibaldi L, Cunningham S, Klein A (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. Curr Biol 18:1572–1575

Allen MF, Ball BV (1996) The incidence and world distribution of honey bee viruses. Bee World 77:141–162

Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, Cox PA, Dalton V, Feinsinger P, Ingram M, Inouye D, Jones CE, Kennedy K, Kevan P, Koopowitz H, Medelllin R, Medellin-Morales S, Nabhan GP, Pavlik B, Tepedino V, Torchio P, Walker S (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conserv Biol 12(1):8–17

Allsopp MH, de Lange WJ, Veldtman R (2008) Valuing insect pollination services with cost of replacement. PLoS One 3:e3128

Amos. ca. 760 B.C., Amos 7: 14. In: The holy bible containing the old and new testaments translated out of the original tongues and with former translations diligently compared and revised by his majesty's special command [King James' version]. Eyre and Spottiswoode, London

Anderson D, East IJ (2008) The latest buzz about colony collapse disorder. Science 319:724–725

Aristotle. ca. 350 B.C. *Historia animalium.* Republished in 1910. In: The works of Aristotle translated into English (trans: D'Arcy Wentworth Thompson), vol IV. Oxford University Press, London

Ashman TL et al (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology 85:2408–2421

Aston D (2010) Honey bee winter loss survey for England, 2007–8. J Apic Res 49(1):111–112

Bailey L (2002) The Isle of wight disease. Central Association of Bee-Keepers, Poole, 11 pp

Bailey L, Ball BV (1991) Honey bee pathology. Academic, London, 193 pp

Banda HJ, Paxton RJ (1991) Pollination of greenhouse tomatoes by bees. Acta Hort 288:194–198

Barnett EA, Charlton AJ, Fletcher MR (2007) Incidents of bee poisoning with pesticides in the United Kingdom, 1994–2003. Pest Manag Sci 63:1051–1057

Bascompte J et al (2003) The nested assembly of plant animal mutualistic networks. Proc Natl Acad Sci USA 100:9383–9387

Bascompte J et al (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431–433

Batra SWT (1995) Bees and pollination in our changing environment. Apidologie 26:361–370

Becker P, Moure JS, Peralta FJA (1991) More about euglossine bees in Amazonian forest fragments. Biotropica 23(4b):586–591

Belaoussoff S, Kevan PG (1998) Toward an ecological approach for the assessment of ecosystem health. Ecosyst Heal 4:4–8

Belt T (1876) Bees and clover. Nature (London) 13:26

Berthoud H, Imdorf A, Haueter M, Radloff S, Neumann P (2010) Virus infections and winter losses of honey bee colonies (*Apis mellifera*). J Apic Res 49(1):60–65

Biesmeijer JC et al (2006) Parallel declines in pollinators and insect pollinated plants in Britain and the Netherlands. Science 313:351–354

Bishop M (1992) Strategies for beekeeping development in Nepal. In: *Honeybees in Mountain Agriculture*. (ed.) L.R.Verma, Oxford and IBH Publishing Co., New Delhi

Bohart GE (1957) Pollination of alfalfa and red clover. Ann Rev Entomol 2:355–380

Bohart GE (1972) Management of habitats for wild bees. Proc Tall Timbers Conf Ecol Anim Control Habitat Manag 3:253–266

Bond WJ (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philos. Trans. R. Soc. Lond. B, 344:83–90

Bonmatin JM, Marchand PA, Charvet R, Colin ME (1994) Fate of systemic insecticides in fields (Imidacloprid and Fipronil) and risks for pollinators, in first European conference of apidology, Udine 19–23 Sept 2004

Brittain CA et al (2010) Impacts of a pesticide on pollinator species richness at different spatial scales. Basic Appl Ecol 11:106–115

Brodschneider R, Moosbeckhofer R, Crailsheim K (2010) Surveys as a tool to record winter losses of honey bee colonies: a two year case study in Austria and South Tyrol. J Apic Res 49(1):23–30

Brosi BJ et al (2008) The effects of forest fragmentation on bee communities in tropical countryside. J Appl Ecol 45:773–783

Brown MJF, Paxton RJ (2009) The conservation of bees: a global perspective. Apidologie 40:410–416

Buchmann SE (1983) Buzz pollination in angiosperms. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp 73–113

Buchmann SE, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington, DC

Burd M (1994) Bateman principle and reproduction – the role of pollen limitation in fruit and seed set. Bot Rev 60:83–139

Cane JH, Tepedino VJ (2001) Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. Conserv Ecol 5(1): 1. [online] URL: www.consecol.org/vol5/iss1/art1

Cane JH et al (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecol Appl 16:632–644

Cardoso da Silva JM, Tabarelli M (2000) Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404:72–74

Carré G et al (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. Agric Ecosyst Environ 133:40–47

Carreck NL, Ball BV, Martin SJ (2010a) The epidemiology of cloudy wing virus infections in honey bee colonies in the UK. J Apic Res 49(1):66–71

Carreck NL, Ball BV, Martin SJ (2010b) Honey bee colony collapse and changes in viral prevalence associated with *Varroa destructor*. J Apic Res 49(1):93–94

Carvell C et al (2006) Declines in forage availability for bumblebees at a national scale. Biol Conserv 132:481–489

Charriere J-D, Neumann P (2010) Surveys to estimate colony losses in Switzerland. J Apic Res 49(1):132–133

Chauzat M-P, Carpentier P, Madec F, Bougeard S, Cougoule N, Drajnudel P, Clément M-C, Aubert M, Faucon J-P (2010a) The role of infectious agents and parasites in the health of honey bee colonies in France. J Apic Res 49(1):30–39

Chauzat M-P, Martel A-C, Blanchard P, Clément M-C, Schurr F, Lair C, Ribière M, Wallner K, Rosenkranz P, Faucon J-P (2010b) A case report of a honey bee colony poisoning incident in France. J Apic Res 49(1):113–115

Chauzat M-P, Martel A-C, Zeggane S, Drajnudel P, Schurr F, Clément M-C, Ribière-Chabert M, Aubert M, Faucon J-P (2010c) A case control study and a survey on mortalities of honey bee colonies (*Apis mellifera*) in France during the winter of 2005–6. J Apic Res 49(1):40–51

Choi SY (1984) Brief report on the status of Korean beekeeping. In: Proceedings of the Expert Consultion Beekeep. *Apis mellifera*. Tropical Sub-tropical Asia. FAO, Rome, pp 170–190

Condit IJ (1920) Caprifigs and caprification. Calif Agric Exp Stat Bull 319:341–375

Condit IJ, Swingle WT (1947) The fig. Chronica Botanica, Waltham

Conner AJ, Glare TR, Nap J (2003) The release of genetically modified crops into the environment. Part II. Overview of ecological risk assessment. Plant J 33:19–46

Corbet SA (1995) Insects, plants and succession: advantages of long-term set-aside. Agric Ecosyst Environ 53:201–217

Corbet SA (2000) Conserving compartments in pollination webs. Conserv Biol 14(5):1229–1231

Costanza R, D'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Rifkin RG, Sutton O, van den Belt M (1997) The value of the world's ecosystem and natural capital. Nature (London) 387:253–260

Costin BJ, Morgan JW, Young AG (2001) Reproductive success does not decline in fragmented populations of *Leucochrysum albicans* subsp. *albicans* var. *tricolor* (Asteraceae). Biol Conserv 98(3):273–284

Cox C (2001) Imidacloprid, insecticide factsheet. *J Pestic Reform*, vol 21(1). http://www.pesticide.org/imidacloprid.pdf

Cox PA, Elmquist T, Pierson E, Rainey WE (1991) Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. Conserv Biol 5:448–454

Cox-Foster DL et al (2007) A metagenomic survey of microbes in honey bee colony collapse disorder. Science 318:283–287

Crailsheim K, Brodschneider R, Neumann P (2009) The COLOSS puzzle: filling in the gaps. In: Proceedings of the 4th COLOSS conference, 3–4 Mar 2009. Zagreb, pp 46–47

Crane E (1992) Beekeeping in mountain life-support systems. In: Verma LR (ed) Honeybees in mountain agriculture. Proceedings of international expert meeting on beekeeping development in the Hindu Kush-Himalayan Region, Kathmandu, Nepal, 21–23 June 1989. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, pp 17–27

Cunningham SA (2000) Depressed pollination in habitat fragments causes low fruit set. Proc R Soc Lond Series B 267:1149–1152

Currie RW, Pernal SF, Guzman-Novoa E (2010) Honey bee colony losses in Canada. J Apic Res 49(1):104–106. doi:DOI: 10.3896/IBRA.1.49.1.18

Dahle B (2010) The role of *Varroa destructor* for honey bee colony losses in Norway. J Apic Res 49(1):124–125

Desneux N, Decourtye A, Delpuech JM (2007) The sublethal effects of pesticides on beneficial arthropods. Annu Rev Entomol 52:81–106

Dias BSF, Raw A, Imperatri-Fonseca VL (1999) International pollinators initiative: the Sao Paulo declaration on pollinators. Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees. Brazilian Ministry of the Environment, Brazil, 79 pp

Didham RK et al (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–496

Dively GP (2007) Summary of research on the non-target effect of BT corn pollen on honeybees. http://www.ento.psu.edu/MAAREC/CCDPpt/NontargeteffectsofBt.pdf

Dormann CF et al (2008) Prediction uncertainty of environmental change effects on temperate European biodiversity. Ecol Lett 11:235–244

Dunning JW (1886) The importation of humble bees into New Zealand. Trans R Entomol Soc Lond 6:32–34

Dutech C, Seiter J, Petronelli P, Joly HI, Jarne P (2002) Evidence of low gene flow in a neotropical clustered tree species in two rainforest stands of French Guiana. Mol Ecol 11:725–738

Eisen G (1891) The first introduction of *Blastophaga psenes* into California. Insect Life 4:128–129

Ellis JD, Munn PA (2005) The worldwide health status of honey bees. Bee World 86(88):101

Ellis JD, Evans JD, Pettis JS (2010) Colony losses, managed colony population decline and colony collapse disorder in the United States. J Apic Res 49(1):134–136

England PR, Beynon F, Ayre DJ, Whelan RJ (2001) Molecular genetic assessment of mating-system variation in a naturally bird-pollinated shrub: contributions from birds and introduced honeybees. Conserv Biol 15(6):1645–1655

Eyer M et al (2009) Small hive beetle, *Aethina tumida*, as a potential biological vector of honeybee viruses. Apidologie 40:419–428

FAO (1993) Harvesting *nature*'s diversity. FAO, Rome

Fontaine C et al (2006) Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. PLoS Biol 4:e1. doi:10.1371/journal.pbio.0040001

Fortuna MA, Bascompte J (2006) Habitat loss and the structure of plant–animal mutualistic networks. Ecol Lett 9:278–283

Franck P et al (1998) The origin of west European subspecies of honeybees (*Apis mellifera*): new insights from microsatellite and mitochondrial data. Evolution 52:1119–1134

Fraser JG (1935) The golden bough, 3rd edn. Macmillan, New York

Frazier M, vanEngelsdor D, Caro D (2007) Collapse Disorder Affecting Honey Bee (*Apis mellifera*) colonies Edited by the CCD working group at www.agr.state.il.us/programs/bees/CCD.pdf Penn State University

Free JB (1984) Beekeeping and pollination in developing countries. In: Second international conference on apiculture in tropical countries. Indian Agricultural Research Institute, New Delhi, pp 475–488

Free JB (1993) Insect pollination of crops, 2nd edn. Academic, London

Fries I (2009) Nosema ceranae in European honey bees (*Apis mellifera*). J Invertebr Pathol 103 Suppl 1:S 73–79

Gabriel D, Tscharntke T (2007) Insect pollinated plants benefit from organic farming. Agric Ecosyst Environ 118:43–48

Gajger IT, Tomljanović Z, Petrinec Z (2010) Monitoring health status of Croatian honey bee colonies and possible reasons for winter losses. J Apic Res 49(1):107–108

Galil J (1967) Sycomore wasps from ancient Egyptian tombs. Israel J Entomol 2:1–9

Galil J (1968) An ancient technique for ripening sycomore fruit in east-mediterranean countries. Econ Bot 22:178–190

Galil J, Eisikowitch D (1968) On the pollination ecology of *Ficus sycomorus* in East Africa. Ecology 49:259–269

Galil J, Eisikowitch D (1969a) Further studies on the pollination ecology of *Ficus sycomorus* L. (Hymenoptera, Chalcidoidea, Agaonidae). Tijdschrift voor Entomol 112:1–13

Galil J, Eisikowitch D (1969b) Note on pollen transport, pollination and protection of ovaries in *Ficus sycomorus*. New Phytol 68:1243–1244

Galil J, Eisikowitch D (1974) Further studies on the pollination ecology of *Ficus sycomorus.* II. Pocket filling and emptying by *Ceratosolen arabicus* Mayr. New Phytol 73:515–528

Gallai N et al (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol Econ 68:810–821

Garibaldi LA et al (2009) Pollinator shortage and global crop yield – looking at the whole spectrum of pollinator dependency. Commun Integr Biol 2:37–39

Genersch E et al (2006) Detection of deformed wing virus, a honey bee viral pathogen, in bumble bees (*Bombus terrestris* and *Bombus pascuorum*) with wing deformities. J Invertebr Pathol 91:61–63

Ghazoul J (2005a) Buzziness as usual? Questioning the global pollination crisis. Trends Ecol Evol 20:367–373

Ghazoul J (2005b) Response to Steffan-Dewenter et al.: questioning the global pollination crisis. Trends Ecol Evol 20:652–653

Ghazoul J, Liston KA, Bowles TJB (1998) Disturbance-induced density dependent seed set in *Shorea siamensis* (Diperocarpaceae), a tropical forest tree. J Ecol 86:462–473

Gilpin M, Soulé M (1986) Minimum viable populations: processes of species extinction (Chapter 2, pp. 19–34). In: Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc, Sunderland, 585 pp

Goor A (1965) The history of the fig in the Holy Land from ancient times to the present. Econ Bot 19:124–135

Goulson D (2003) Effects of introduced bees on native ecosystems. Annu Rev Ecol Syst 34:1–26

Goulson D, Sparrow K (2009) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. J Insect Conserv 13:177–181

Goulson D et al (2008) Decline and conservation of bumble bees. Annu Rev Entomol 53:191–208

Gray A, Peterson M, Teale A (2010) An update on recent colony losses in Scotland from a sample survey covering during 2006–2008. J Apic Res 49(1):129–131

Groom MJ (2001) Consequences of subpopulation isolation for pollination, herbivory, and population growth in *Clarkia concinna concinna* (Onagraceae). Biol Conserv 100:55–61

Gutierrez D (2009) Honey bee collapse strikes Japan, up to fifty percent of honey bees gone. *Natural News*, 28 Apr 2009. www.naturalnews.com/026151_Japan_honeybees_honey.html

Haddad N, Bataeneh A, Albaba I, Obeid D, Abdulrahman S (2009) Status of colony losses in the Middle East. In: Proceedings of the 41st Apimondia congress, Montpellier, p 36

Harz M, Müller F, Rademacher E (2010) Organic acids: acute toxicity on *Apis mellifera* and recovery in the haemolymph. J Apic Res 49(1):95–96

Hatjina F, Bouga M, Karatasou A, Kontothanasi A, Charistos L, Emmanouil C, Emmanouil N, Maistros A-D (2010) Data on honey bee losses in Greece: a preliminary note. J Apic Res 49(1):116–118. doi:DOI:10.3896/IBRA.1.49.1.23

Hegland SJ, Totland Ø (2008) Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? Oikos 117:883–891

Hegland SJ et al (2009) How does climate warming affect plant– pollinator interactions? Ecol Lett 12:184–195

Hendrickx F et al (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. J Appl Ecol 44:340–351

Henslow G (1892) Egyptian figs. Nature (London) 47:102

Henslow G (1902) The sycomore fig. J R Hort Soc Lond 27:128–131

Herodotus 485–425 B.C. *Historiae.* Republished. In: Wordsworth classics of world literature (trans: Rawlinson G). Ware

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) *The distributions of a wide range of taxonomic groups are expanding polewards*. Global Change Biol 12:450–455

Hobbs GA (1967) Domestication of alfalfa leaf-cutter bees. Canada Department of Agriculture Publication Number 1313, Ottawa, Ontario

Hoehn P et al (2008) Functional group diversity of bee pollinators increases crop yield. Proc R Soc Lond B Biol Sci 275:2283–2291

Holzschuh A et al (2008) Agricultural landscapes with organic crops support higher pollinator diversity. Oikos 117:354–361

Hopkins I (1914) History of the bumblebee in New Zealand – its introduction and results. New Zealand Department of Agriculture, Industry and Commerce Bulletin Number 46 (new series), Christchurch

Ingram M, Nabhan G, Stephen Buchmann (1996) Global pesticide campaigner, vol 6, number 4, Dec 1996

Ismail A, Ibrahim AG (1986) The potential for ceratopogonid midges as insect pollinators of cocoa in Malaysia. In: Hussein MY, Ibrahim AG (eds) Biological control in the tropics. Universiti Pertanian Malaysia, Serdang, pp 471–484

Ivanova EN, Petrov PP (2010) Regional differences in honey bee winter losses in Bulgaria during the period 2006–9. J Apic Res 49(1):102–103

Jaffée R (2010) Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses. Conserv Biol 24:583–593

Janzen DH (1974) The de-flowering of Central America. Nat Hist 83:48–53

Johansen CA (1977) Pesticides and pollinators. Ann Rev Entomol 22:177–192

Johansen CA, Mayer DF (1990) Pollinator protection: a bee and pesticide handbook. Wicwas Press, Cheshire

Jones J, Helliwell P, Beekman M, Maleszka RJ, Oldroyd BP (2005) The effects of rearing temperature on developmental stability and learning and memory in the honey bee, *Apis mellifera*. J Comp Physiol A 191:1121–1129

Kafle GP (1992) Salient features of beekeeping in Nepal. In: Verma LR (ed) Honeybees in the mountain agriculture. Oxford and IBH Pub. Co. Pvt. Ltd, New Delhi, pp 155–162

Karise R (2007) Foraging behaviour and physiology of bees: impact of insecticides. Ph.D. thesis, Estonian University of Life Sciences, Tartu, pp 1–123

Kearns CA, Inouye DW (1997) Pollinators, flowering plants, and conservation biology. BioScience 47:297–307

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant–pollinator interactions. Annu Rev Ecol Syst 29:83–112

Keimer L (1928) An ancient Egyptian knife in modern Egypt. Anc Egypt 1928:65–66

Kenmore P, Krell R (1998) Global perspectives on pollination in agriculture and agroecosystem management. International workshop on the conservation and sustainable use of pollinators in agriculture, with emphasis on bees. Oct 7–9, Sao Paulo

Kerr EA, Kribs W (1955) Electric vibrator as an aid in greenhouse tomato production. Queensland J Agric Science 2:157–169

Kevan PG (1974) Pollination, pesticides, and environmental quality. BioScience 24:198–199

Kevan PG (1975a) Pollination and environmental conservation. Environ Conserv 2:293–298

Kevan PG (1975b) Forest application of the insecticide Fenitrothion and its effects on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in southern New Brunswick, Canada. Biol Conserv 7:301–309

Kevan PG (1977) Blueberry crops in Nova Scotia and New Brunswick – pesticides and crop reductions. Can J Agric Econ 25:61–64

Kevan PG (1997) Honeybees for better apples and much higher yields: study shows pollination services pay dividends. Can Fruitgrow 14:16

Kevan PG (1999) Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agric Ecosyst Environ 74:373–393

Kevan PG, LaBerge WE (1979) Demise and recovery of native pollinator populations through pesticide use and some economic implications. In: Proceedings of the fourth international symposium on pollination, Maryland agricultural experiment station special miscellaneous publication number 1, College Park, pp 489–508

Kevan PG, Oppermann EB (1980) Blueberry production in New Brunswick, Nova Scotia and Maine: reply to Wood et al. Can J Agric Econ 28:81–84

Kevan PG, Phillips TP (2001) The economic impacts of pollinator declines: an approach to assessing the consequences. Conserv Ecol 5(1)

Kevan PG, Plowright RC (1995) Impact of pesticides on forest pollination. In: Armstrong JA, Ives WGH (eds) Forest insect pests in Canada. Natural Resources Canada/Canadian Forest Service, Science and Sustainable Development Directorate, Ottawa, pp 607–618

Kevan PG, Hussein NY, Hussey N, Wahid MB (1986) Modelling the use of *Elaeidobius kamerunicus* for pollination of oil palm. Planter (Malaysia) 62:89–99

Kevan PG, Straver WA, Offer M, Laverty TM (1991) Pollination of greenhouse tomatoes by bumblebees in Ontario. Proc Entomol Soc Ontario 122:15–19

Kevan PG, Greco CF, Belaoussoff S (1997) Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths. J Appl Ecol 34:1122–1136

Kleijn D, Raemakers I (2008) A retrospective analysis of pollen host plant use by stable and declining bumblebee species. Ecology 89:1811–1823

Klein A-M, Steffan-Dewenter I, Buchori D, Tscharntke T (2002) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conserv Biol 16(4):1003–1014

Klein A-M, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc R Soc B 274:303–313

Knuth P (1909) Handbook of flower pollination: based upon Hermann Müller's work 'The fertilization of flowers by insects', vol III, Observations on flower pollination made in Europe and the arctic regions on species belonging to the natural orders Goodenovieae to Cycadeae. Oxford University Press, London

Koeniger N (1982) Interactions among the four species of the genus' *Apis*. In: Breed MD, Michcner CD, Evans E (eds) The biology of social insects. Westview Press, Boulder, pp 59–64

Kraus B, Page RE (1995) Effect of Varroa jacobsoni (Mesostigmata: Varroidae) on feral *Apis mellifera* (Hymenoptera: Apidae) in California. Environ Entomol 24:1473–1480

Kremen C, Ricketts T (2000) Global perspectives on pollination disruptions. Conserv Biol 14(5):1226–1228

Kremen C et al (2002) Crop pollination from native bees at risk from agricultural intensification. Proc Natl Acad Sci USA 99:16812–16816

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, Packer L, Potts SG, Roulston T, Steffan-Dewenter I, Vazquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein A-M, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol Lett 10:299–314

Kunin WE (1997) Population biology and rarity: on the complex density dependence in ninsect-plant interactions. In: Kunin WE, Gaston KJ (eds) The biology of rarity. Chapman and Hall, London, pp 150–173

Lambdon PW et al (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. Preslia 80:101–149

Larsen TH et al (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecol Lett 8:538–547

Lavergne S et al (2006) Fingerprints of environmental change on the rare Mediterranean flora: a 115-year study. Glob Change Biol 12:1466–1478

Law BS (2001) The diet of the common blossom bat (*Syconycteris australis*) in upland tropical rainforest and the importance of riparian areas. Wildl Res 28:619–626

Law BS, Lean M (1999) Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforests. Biol Conserv 91:201–212

Le Conte Y, Navajas M (2008) Climate change: impact on honey bee populations and diseases. Rev Sci Tech Off Int Epizoot 27:499–510

Lindsley DL, Zimm GG (1992) The genome of *Drosophila melanogaster*. Academic, San Diego, 1133 pp

Loper GM (1995) A documented loss of feral bees due to mite infestations in Southern Arizona. Am Bee J 135:823–824

Losey JE, Vaughan M (2006) The economic value of ecological services provided by Insects. BioScience 56:311–323

MacKenzie KE, Winston ML (1984) Diversity and abundance of native bee pollinators of berry crops and natural vegetation in the Lower Fraser Valley, British Columbia. Can Entomol 116:965–974

Maori E, Lavi S, Mozes-Koch R, Gantman Y, Peretz Y, Edelbaum O, Tanne E, Sela I (2007) Isolation and characterization of Israeli acute paralysis virus, a dicistrovirus affecting honey bees in Israel: evidence for diversity due to intra- and inter -species recombination. J Gen Virol 88:3428–3438

Margoliouth DS (1905) Mohammed and the rise of Islam, 3rd edn. Putnam, New York

Martin SJ, Medina LM (2004) Africanized honey bees have unique tolerance to Varroa mites. Trends Parasitol 20:112–114

Martin SJ, Ball BV, Carreck NL (2010) Prevalence and persistence of deformed wing virus (DWV) in untreated or acaricidetreated *Varroa destructor* infested honey bee (*Apis mellifera*) colonies. J Apic Res 49(1):72–79

Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH, (eds) (1996) The conservation of bees. Linnean society symposium series number 18. Academic, London

Matsumura C et al (2004) Invasion status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in Southern Hokkaido. Japan Glob Environ Res 8:51–66

Maués MM (2002) Reproductive phenology and pollination of the Brazil nut tree (*Bertholletia excelsa* Humb. & Bonpl. Lecythidaceae) in eastern Amazonia. In: Kevan PG, Imperatriz-Fonseca VL (eds). Pollinating bees: the conservation link between agriculture and nature. Brasília, Ministry of Environment, Secretariat for Biodiversity and Forests, pp 245–254

Mbaya JKS, Kevan PG (1995) Applied pollination in Africa. In: Roubik DW (ed). Pollination of cultivated plants in the tropics. FAO, Food and Agriculture Service Bulletin Number 118, Rome, pp 57–62

McGregor SE (1976) Insect pollination of cultivated crop plants. U.S. Department of Agriculture Handbook Number 496, Washington, DC

Medrzycki P, Sgolastra F, Bortolotti L, Bogo G, Tosi S, Padovani E, Porrini C, Sabatini AG (2010) Influence of brood rearing temperature on honey bee development and susceptibility to poisoning by pesticides. J Apic Res 49(1):52–59

Meeuse BJD (1981) The story of pollination. Ronald Press, New York

Meixner MD, Costa C, Kryger P, Hatjina F, Bouga M, Ivanova E, Büchler R (2010) Conserving diversity and vitality for honey bee breeding. J Apic Res 49(1):85–92

Memmott J et al (2004) Tolerance of pollination networks to species extinctions. Proc R Soc Lond B Biol Sci 271:2605–2611

Memmott J et al (2007) Global warming and the disruption of plant – pollinator interactions. Ecol Lett 10:710–717

Mishra RC (ed) (1997) Perspective in Indian apiculture. Agro Botanica, India

Morandin LA (2000) Bumble bee (Bombus impatiens) pollination of greenhouse tomatoes. Thesis, University of Western Ontario, London

Morandin LA et al (2005) Lethal and sub-lethal effects of spinosad on bumble bees (Bombus impatiens Cresson). Pest Manag Sci 61:619–626

Moritz RFA et al (2007) The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees. J Insect Conserv 11:391–397

Morse RA (ed) (1978) Honey bee pests, predators and diseases. Cornell University Press, Ithaca, 430 pp

Morse RA, Calderone NW (2000) The value of honey bees as pollinators of U.S. crops in 2000. Bee Cult 128:2–15

Mutinelli F, Costa C, Lodesani M, Baggio A, Medrzycki P, Formato G, Porrini C (2010) Honey bee colony losses in Italy. J Apic Res 49(1):119–120

Nabhan GP, Buchmann SL (1997a) Pollination services: Biodiversity's direct link to world food stability. In: Daly G (ed) Ecosystem services. Island Press, Washington, DC, pp 133–150

Nabhan GP, Buchmann SE (1997b) Services provided by pollinators. In: Daily GC (ed) Nature's services: societal dependence on natural ecosystems. Island Press, Washington, DC, pp 133–150

National Research Council (US) (2007) Committee on the Status of Pollinators in North America. National Academies Press, 2007 - Science - 307 pages

Natural Research Council (2006) Status of pollinators in North America. National Academic Press, Washington, DC

Neumann P, Carreck C (2010) Honey bee colony losses: a global perspective. J Apic Res 49:1–6

Neumann P, Elzen PJ (2004) The biology of the small hive beetle (Aethina tumida, Coleoptera: Nitidulidae): gaps in our knowledge of an invasive species. Apidologie 35:229–247

Neupane KR (2001) Foraging preference of honeybee species to selected horticultural crops. M. Sc. Thesis submitted to IAAS, Rampur, Chitwan, Nepal

Nguyen BK, Van Der Zee R, Vejsnæs F, Le Conte Y, Ritter W (2010) COLOSS working group 1: monitoring and diagnosis. J Apic Res 49(1):97–99

Oldroyd BP (2007) What's killing American honey bees? PLoS Biol 5(6):e168. doi:10.1371/journal.pbio.0050168

Olmstead A, Woolen DB (1987) Bee pollination and productivity growth: the case of alfalfa. Am J Agric Econ 69:56–63

Ongus JR et al (2004) Complete sequence of a picorna-like virus of the genus *Iflavirus* replicating in the mite *Varroa destructor*. J Gen Virol 85:3747–3755

Oostermeijer JGB, Luijten SH, Krenova ZV, Debn Mijls HCM (1998) Relationship between population and habitat characteristics and reproduction of the rare *Gentiana pneumonanthe* L. Conservation Biology 12(5):1042–1053

Parmesan C et al (1999) Pole ward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583

Partap U (2003) Improving agricultural productivity and livelihoods through pollination: some issues and challenges. In: Waliyar F, Collette L, Kenmore PE. Beyond the gene Horizon: sustaining agricultural productivity and enhancing livelihoods through optimization of crop and crop-associated biodiversity with emphasis on semi-arid tropical agroecosystems. Proceedings of a workshop, 23–25 Sept 2002. ICRISAT/FAO, Patancheru

Partap U, Shukla AN, Verma LR (2000) Pollination of peach and plum by *Apis cerana*. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Partap U (eds). Asian bees and beekeeping in Asia: progress of research and development. Proceedings of the fourth AAA international conference. Oxford and IBH Publishing Co. Pvt. Ltd, Kathmandu, pp 171–173, 23–28 Mar 1998

Paxton RJ (2010) Does infection by *Nosema ceranae* cause “colony collapse disorder” in honey bees (*Apis mellifera*)? J Apic Res 49(1):80–84. doi:DOI: 10.3896/IBRA.1.49.1.11

Peck O, Bolton JL (1946) Alfalfa seed production in northern Saskatchewan as affected by bees, with a report on the means of increasing the populations of native bees. Sci Agric 26:338–418

Pimentel D, Stachow U, Takacs DA, Brubaker HW, Dumas AR, Meaney JJ, O’Neil J, Onsi DE, Corzilius DB (1992) Conserving biological diversity in agricultural/forestry systems. BioScience 42:354–362

Pokhrel S (2006) Status and management of domesticated and wild honeybees (*Apis* spp.) in Chitwan, Nepal. Ph.D. dissertation, TU. Institute of Agriculture and Animal Sciences, Rampur, 243 pp

Potts SG, Roberts SPM, Dean R, Marris G, Brown MA, Jones HR, Neumann P, Settele J (2010a) Declines of managed honey bees and beekeepers in Europe. J Apic Res 49(1):15–22

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010b) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25(6):345–353

Prescott-Allen R, Prescott-Allen C (1990) How many plants feed the world? Conserv Biol 4:365–374

Rana BS, Garg ID, Paul Khurana SM, Verma LR, Agrawal HO (1987) Thai sacbrood virus of honeybees (*Apis cerana indica* F) in the North West Himalayas. Indian J Virol 2:127–131

Rasmont P, Mersch P (1988) Première estimation de la derive faunique chez les bourdons de la Belgique (Hymenoptera, Apidae). Ann Soc R Zool Belg 118:141–147

Rathcke BJ, Jules ES (1993) Habitat fragmentation and plant–pollinator interaction. Curr Sci 65:273–277

Reasoner PW (1891) The condition of tropical and semi-tropical fruits. U.S. Department of Agriculture, Division of Pomology, Bulletin number 1, Washington, DC

Rennie J, White PB, Harvey EJ (1921) Isle of wight disease in hive bees. Trans R Soc Edinburgh 52:737–779

Ribière M et al (2008) Natural history and geographical distribution of honey bee viruses. In: Aubert MFA (ed) Virology and the honey bee. European Commission, Bruxelles, pp 15–84

Richards AJ (2001) Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? Ann Bot (Lond) 88:165–172

Ricketts TH et al (2008) Landscape effects on crop pollination services: are there general patterns? Ecol Lett 11:499–515

Ritter W (1981) Varroa disease of the honeybee *Apis mellifera*. Bee World 62:141–153

Roberts SPM, Potts SG (2010) The status of European non-Apis bees. J Apic Res 49(1):137–138

Robertson AW, Kelly D, Ladley JJ, Sparrow AD (1999) Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). Conserv Biol 13:499–508

Rortais A et al (2005) Modes of honeybees exposure to systemic insecticides: estimated amounts of contaminated pollen and nectar consumed by different categories of bees. Apidologie 36:71–83

Roubik DW (ed) (1995) Pollination of cultivated plants in the tropics. FAO, Food and Agriculture Service Bulletin Number 118, Rome

Roubik DW (2000) Pollination system stability in Tropical America. Conserv Biol 14(5):1235–1236

Roubik DW, Wolda H (2001) Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. Popul Ecol 43:53–62

Sakai T (1992) *Apis cerana* beekeeping in Japan. In: Verma LR (ed) Honeybees in mountain agriculture. Oxford/IBH Publishing Co, New Delhi

Sammataro D et al (2000) Parasitic mites of honey bees: life history, implications, and impact. Annu Rev Entomol 45:519–548

Santrac V, Granato A, Mutinelli F (2010) Detection of *Nosema ceranae* in *Apis mellifera* from Bosnia and Herzegovina. J Apic Res 49(1):100–101

Saville, Naomi M (2000) Farmer-participatory extension in Jumla, Western Nepal. In: Matsuka M (ed) Asian bees and beekeeping: progress of research and development. Oxford/IBH, New Delhi, pp 230–236

Schwarz MP, Hogendoorn K (1999) Biodiversity and conservation of Australian native bees. In: Ponder W, Lunney D (eds) The other 99%: the conservation and biodiversity of invertebrates, Transactions of the Royal Zoological Society of New South Wales, Sydney, pp 388–393

Schweiger O et al (2008) Climate change can cause spatial mismatch of trophic interacting species. Ecology 89:3472–3479

Scott-Dupree CD, Winston ML (1987) Wild bee diversity and abundance in orchard and uncultivated habitats in the Okanagan Valley, British Columbia. Can Entomol 119:735–745

Settele J et al (2008) Climatic risk atlas of European butterflies. BioRisk 1:1–710. doi:10.3897/biorisk.1

Shrestha JB, Shrestha KK (2000) Beekeeping in Nepal: Problems and Potentials. In: Matsuka, M., L. R. Verma, S. Wongsiri, K. K. Shrestha, and U. Partap (eds.) *Asian bees and beekeeping, progress of research and development: Proceedings of Fourth Asian Apicultural Association International Conference Kathmandu, Nepal, March 23–28, 1998*. New Delhi, Oxford and IBH

Siebert JW (1980) Beekeeping, pollination and externalities in California agriculture. Am J Agric Econ 62:165–171

Soroker V, Hetzroni A, Yacobson B, Voet H, Slabezki S, Efrat H, Chejanovsky N (2009) Colony losses in Israel: incidence of viral infection and beehive populations. In: Proceedings of the 41st Apimondia congress, Mointpellier, p 38

Southwick EE, Southwick L Jr (1992) Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. J Econ Entomol 85:621–633

Spiewok S, Neumann P (2006) Infestation of commercial bumblebee (*Bombus impatiens*) field colonies by small hive beetles (*Aethina tumida*). Ecol Entomol 31:623–628

Steffan-Dewenter I et al (2006) Bee diversity and plant–pollinator interactions in fragmented landscapes. In: Waser NM, Ollerton J (eds) Specialization and generalization in plant–pollinator interactions. University of Chicago Press, Chicago, pp 387–410

Steffan-Dewenter I, Tscharntke T (2000) Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122:288–296

Steffan-Dewenter I, Westphal C (2008) The interplay of pollinator diversity, pollination services and landscape change. J Appl Ecol 45:737–741

Steffan-Dewenter I et al (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421–1432

Steffan-Dewenter I, Potts SG, Packer L (2005) Pollinator diversity and crop pollination services are at risk. Trends Ecol Evol 20:651–652

Stephen WP (1955) Alfalfa pollination in Manitoba. J Econ Entomol 48:543–548

Stone GN, Willmer PG (1989) Warm-up rates and body temperatures in bees – the importance of body size, thermal regime and phylogeny. J Exp Biol 147:303–328

Stout J, Morales CL (2009) Ecological impacts of invasive alien species on bees. Apidologie 40:388–409

Stout JC, Kells AR, Goulson D (2002) Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. Biological Conservation 106:425–434

Sutton SL, Collins NM (1991) Insects and tropical forest conservation. In: Collins NM, Thomas JA (eds) The conservation of insects and their habitats. Academic, London, pp 405–422

Syed RA (1979) Studies on oil palm pollination. Bull Entomol Res 69:213–224

Syed RA, Law IH, Corley RHV (1982) Insect pollination of oil palm: introduction, establishment and pollinating efficiency of *Elaeidobius kamerunicus* in Malaysia. Planter (Malaysia) 58:547–561

Tautz J, Maier S, Groh C, Rossler W, Brockmann A (2003) Behavioral performance in adult honey bees is influenced by the temperature experienced during their larval development. Proc Nat Acad Sci USA 100:7343–7347

Thapa RB (2006) Honeybees and other insect pollinators of cultivated plants: a review. J Inst Agric Anim Sci 27:1–23

Theophrastus. 372–287 B.C. *Peri phyton historia.* Republished in 1961. In: Inquiring into plants (trans: Hart A). Heinemann, London

Thomas CD et al (2001) Ecological and evolutionary processes at expanding range margins. Nature 411:577–581

Thomas JA, Telfer MG et al (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303(5665):1879–1881

Thompson HM, Hunt LV (1999) Extrapolating from honeybees to bumblebees in pesticide risk assessment. Ecotoxicology 8:147–166

Thomson DM (2006) Detecting the effects of introduced species: a case study of competition between Apis and Bombus. Oikos 114:407–418

Topolska G, Gajda A, Pohorecka K, Bober A, Kasprzak S, Skubida M, Semkiw P (2010) Winter colony losses in Poland. J Apic Res 49(1):126–128. doi:10.3896/IBRA.1.49.1.27

Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol Evol 21:208–216

Tscharntke T, Klein A-M, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol Lett 8:857–874

Tylianakis JM et al (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Tylor EB (1889) Fertilization of date palm in ancient Assyria. Academy (London) 35:396

UNEP (1993) Global biodiversity. UNEP, Nairobi

Vamosi JC, Knight TM, Steets JA, Mazer SJ, Burd M, Ashman T-L (2006) Pollination decays in biodiversity hotspots. Proc Natl Acad Sci USA 103(4):956–961

Van Der Zee R (2010) Colony losses in the Netherlands. J Apic Res 49(1):121–123

vanEngelsdorp D et al (2008) A survey of honey bee colony losses in the U.S., Fall 2007 to Spring 2008. PLoS ONE 3:e4071. doi:DOI:10.1371/ journal.pone.0004071

Vanengelsdorp D, Meixner MD (2009) A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. *J Invertebr Pathol* (in press). DOI 10.1016/j.jip.2009.06.011

vanEngelsdorp D, Underwood R, Caron D, Hayes J Jr (2007) An estimate of managed colony losses in the winter of 2006–2007: a report commissioned by the apiary inspectors of America. Am Bee J 147:599–603

Vanengelsdorp D, Evans JD, Saegerman C, Mullin C, Haubruge E, Nguyen BK, Frazier M, Frazier J, Coxfoster D, Chen Y, Underwood RM, Tarpy DR, Pettis JS (2009) Colony collapse disorder: a descriptive study. PloS ONE 4:e6481

Vanengelsdorp D, Hayes J Jr, Underwood RM, Pettis JS (2010) A survey of honey bee colony losses in the US, fall 2008 to spring 2009. J Apic Res 49(1):7–14

vanEnglesdorp D, Meixner M (2010) A historical review of managed honey bee populations in Europe and the United States and factors that may affect them. J Invertebr Pathol 103:S80–S95

Vejsnæs F, Kryger P (2010) Factors involved in the recent increase in colony losses in Denmark. J Apic Res 49(1):109–110

Verma LR (1987) Pollination ecology of apple orchids by hymenopterous insects in Matiama Narkanda temperate zone. Final report. Ministry of Environment and Forests, Govt. of India, p 118

Verma LR (1990) Beekeeping in integrated mountain development. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi

Verma LR (ed) (1992b) Honeybees in mountain agriculture. Oxford and IBH Publishing Company, New Delhi (Keywords: beekeeping, environmental effects)

Verma LR (1992a) Declining genetic diversity of *Api cerana* in Hindu-Kush Himalayan region. In: Asian apiculture. Connor LJ et al. (ed) pp 81–88

Verma S (1993) Biodiversity in Asian honey bees: cytological perspectives. In: Connor LJ, Rinderer TE, Sylvester HA, Wongsiri S (eds) Asian apiculture. Wicwas Press, Cheshire, pp 89–93, Keywords: genetics, honey, reproduction

Warren MS, Hill JK et al (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414(6859):65–69

Watanabe ME (2008) Colony collapse disorder: many suspects, no smoking gun. Bioscience 58:384–388

Westphal C et al (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecol Lett 6:961–965

Wilcock C, Neiland R (2002) Pollination failure in plants: why it happens and when it matters. Trends Plant Sci 7(6):270–277

Williams IH (1996) Aspects of bee diversity and crop pollination in the European Union. In: Metheson A (ed) The conservation of bees. Academic, London, pp 63–80

Williams PH et al (2007) Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? Biol Conserv 138:493–505

Williams PH, Osborne JL (2009) Bumblebee vulnerability and conservation world-wide. Apidologie 40:367–387

Wilson EO (1999) The diversity of life, new editionth edn. W.W. Norton and Company, Inc., New York

Winder JA (1977) Some organic substrates which serve as insect breeding sites in Bahian cocoa *Planta*tions. Rev Braz Biol 37:351–356

Winfree R, Kremen C (2009) Are ecosystem services stabilized by differences among species? A test using crop pollination. Proc R Soc Lond B Biol Sci 276:229–237

Winfree R et al (2007) Effect of human disturbance on bee communities in a forested ecosystem. Conserv Biol 21:213–223

Winfree R et al (2009) A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076

Woolhouse MEJ et al (2005) Emerging pathogens: the epidemiology and *Evolution* of species jumps. Trends Ecol Evol 20:238–244

Young AM (1982) Effect of shade cover and availability of midge breeding sites on pollinating midge populations and fruit set in two cacao farms. J Appl Ecol 19:149–155

Zhen-Ming J, Guanhang Y, Shuangxiu H, Shikui L, Zaijin R (1992) The advancement of apicultural science and technology in China. In: Verma LR (ed) Honeybees in mountain agriculture. Oxford and IBH Publishing Co Pty Ltd, New Delhi, pp 133–147

Chapter 18
The Problem of Diseases in Bees

Abstract Problem of diseases is a serious concern both in domesticated and wild soiltary bees. When disease strikes a hive of bees, it can devastate the colony and spread to the entire beekeeping operation. All bees are susceptible to diseases, and when they are domesticated, their population densities increase to suit human needs, making them more susceptible. Decline in their population has threatened the food security on global scale through deficit of pollinators. Most attempts at disease control have centered on drug treatments leading to resistance in disease causing pathogens and problem of residues in hive products. This chapter discusses how disease control strategies could be improved by breeding bees for disease resistance and better hygienic behaviour allowing researchers to identify that time and place in the management system for which the pathogen is most vulnerable, followed by targeting treatments to that stage.

18.1 Introduction

The total area of cultivated land worldwide has increased 466% since 1700 (Mayer and Turner 1992). With the green revolution in 1960s, intensification of agriculture resulted in large yield increases (Griggs 1993), yield increases have continued with more recent developments in high yielding crops, GM crops, mechanization and chemical application. About one billion people – one-fifth of the world's human population – are now undernourished because of chronic instabilities in food production and distribution. Recent surveys document that more than 30 genera of animals – consisting of hundreds of species of floral visitors – are required to pollinate the 100 or so crops that feed the world (Prescott-Allen and Prescott-Allen 1990; Buchmann and Nabhan 1996). Only 15% of these crops are serviced by domestic honey bees, while at least 80% are pollinated by wild bees and other wildlife. Honey bees, economically the most important pollinators of crops worldwide, are in decline. For instance, the number of commercial bee colonies in united states has plummeted from 5.9 million colonies in the late 1940s, to 4.3 million in 1985, and to 2.7 million

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in 1995 (USDA-ARS 1991). The loss of one quarter of all managed honey bee colonies since 1990 signals one of the most severe declines in any agricultural input. This demise has been brought on by the spread of diseases and parasitic mites. This unfortunate trend continues, despite the economic value of honeybees to agriculture (Southwick and Southwick 1992). Similar trend exists in other parts of the world.

The recent dramatic losses of honey bee colonies around the world have focused public attention on the health status of the honey bee *Apis mellifera* L. (Currie et al. 2010; Neumann and Carreck 2010) but the study of bee health dates as far back as fourth century B.C. when Aristotle (384–322 B.C.) described a bee disease which "is indicated in a lassitude on the part of the bees and in malodorousness of the hive" (Historia animalium IX.40.626b). Written records of treatments of bee diseases through chemical means are almost as ancient; Virgil (70–19 B.C.) recommends a number of treatments for honey bees "weakened with wretched disease" ranging from burning fragrant resin to pounded oak-apples with dry rose petals or dried grapes with thyme (Georgics IV verses 251–280). Today, there are over 30 identified pests and pathogens of honey bees worldwide (Morse and Flottum 1997; Ellis and Munn 2005) and thousands of studies of assessing the efficacy of various chemotherapeutic treatments.

Originating in Africa (Whitfield et al. 2006), honey bees were exported by man all over the world and with few exceptions their pests and pathogens have accompanied them (Ellis and Munn 2005; vanEngelsdorp and Meixner 2010). Honey bees have become increasingly important for crop pollination (Klein et al. 2007) and approximately 80% of all insect pollination is attributed to honey bees (Pimentel et al. 1997). The crops requiring managed pollinators such as honey bees have increased while stocks of honey bees have declined during recent years (Aizen et al. 2008).

Several different agents of disease, some newly discovered, have been causing increasing concern in recent years in many parts of the world. Some new parasites like *Varroa destructor* Anderson and Truemann hitherto unknown has been discovered which has threatened the very existence of beekeeping industry and crop pollination across the globe. The recent discovery of *Varroa destructor* and ability of their genotypes to reproduce both on the drone and worker broods of *A. mellifera* has led to their spread out of Asia, and resulted in heavy losses of *A. mellifera* colonies throughout the world. These mites have killed tens of thousands of honey bee colonies in different parts of the world in recent years. Of the two genotypes, the Korea genotype is the most widespread and common. It is found on *A. mellifera* in the UK, Europe, the Middle East, Africa, Asia, Canada, North and South America and New Zealand. The Japan/Thailand genotype has only been reported on *A. mellifera* from Japan, Thailand and the America.

Over and above its direct economic value to humans, pollination by bees provides essential maintenance of the structure and function of a wide range of natural communities which are at risk of collapse. A new strain of *Nosema* disease *Nosema ceranae* (microsporidian protozoan) that causes, a disease of the eastern honey bee, *Apis cerana* has been identified associated with "spring dwindling," disappearing disease, autumn collapse, "bee depopulation syndrome" or "Colony Collapse Disorder (CCD)" in *A. mellifera*. Apparently this pathogen has jumped host from *Apis cerana* to *Apis mellifera* in the last 10 years and is spreading rapidly. *Nosema* *ceranae* has a pathology that is different from *Nosema apis*. The causative agent for *Nosema* is *Nosema apis*, which rarely causes major losses in infected colonies. However, high mortality rate demonstrates that *N. ceranae* is highly pathogenic to *Apis mellifera*. Bees die within 8 days after exposure to *N. ceranae* which is faster than bees exposed to *N. apis*. Some new viruses and bacteria have been discovered.

18.2 Problem of Diseases in Honeybees

Research in agriculture mostly focuses on development of new technologies rather than on environmental impacts. Pollinators primarily bees are essential to agriculture, providing significant yield benefit in over 66% crop species. Currently dramatic losses of managed honeybees with suspected worldwide losses of wild pollinators are focusing research on an impending still poorly documented pollination crisis. Pollination is a necessary ecosystem service that is being threatened by conversion of natural land to agriculture and pesticide use (Allen-Wardell et al. 1998). Pollination is essential for production of many crops, but the interaction between wild pollinators and modern agricultural practices has not been well studied. Many biologists feel that we may be facing pollination crisis in which both wild and managed pollinators are disappearing at alarming rates due to habitat fragmentation, disease, intensive monoculture and pesticide use resulting in serious threat to biodiversity and agricultural stability.

Bees of the *Apis* genus are distributed throughout the world in highly diverse climates (Fig. 18.1). The *Apis mellifera* species, whose distribution range extends to sub-Saharan Africa, northern Europe and Central Asia, is found in a wide variety of environments, including the oases of the African desert, the Alps, the fringes of the tundra and the mists of the United Kingdom. Its ecotypes have adapted remarkably well to their biotopes. The other honey bee species of the *Apis* genus are distributed around Asia, particularly tropical south-east Asia (Ruttner 1988). A change in climatic conditions is bound to have an impact on the survival of these ecotypes or of honey bee species that are closely associated with their environment. Migration and changes in their life cycle and behaviour could help them to survive in new biotopes. As the honey bee's genetic variability will be crucial to its adaptation, we would do well to ensure that we preserve this genetic variability. Honey bees will also need to adapt to a whole array of predators, parasites and pathogens surrounding them. Not only will the relationships between hosts and parasites change, honey bees will have to cope with new stresses arising from trade-facilitated transfers of pathogens among honey bee species. In such a context, climate change could create new opportunities for establishing honey bees in undreamt-of regions or habitats.

The honey bee: an economically valuable species the long-term survival of farming worldwide relies in part on insect pollinators. In monetary terms, they contribute an estimated US$ 117 billion per year (Costanza et al. 1997); around 35% of agricultural crops depend directly on pollinators (Klein et al. 2007) and 84% of cultivated plant species are involved with the activity of these insects (Williams 1996). The European honey bee, *Apis mellifera*, is the most economically valuable pollinator

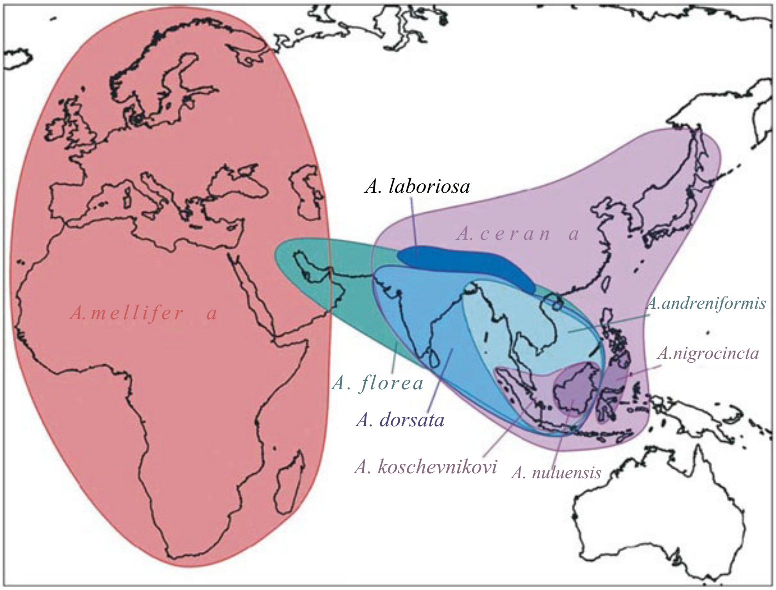

Fig. 18.1 Distribution of species of the *Apis* genus (amended in accordance with Franck et al. 2000)

of agricultural crops worldwide (Johnson 2007). Honey bees are also crucial for maintaining biodiversity because they pollinate numerous plant species that require an obligatory pollinator for fertilisation (Allen-Wardell et al. 1998; Michener 2000).

Ten honey bee species of the *Apis* genus have so far been identified (Arias and Sheppard 2006). The distribution of these species is highly uneven. *Apis mellifera*, which originates from Africa, has followed two waves of colonisation in Eurasia (Whitfield et al. 2006) and has been exported to other continents. The nine other species have remained in the areas where they originated, in Asia, which is the most likely birthplace of the *Apis* genus.

18.2.1 Bee Diseases and Parasites

Numerous predators, parasites (mites) and pathogens (protozoa, bacteria and viruses) prey upon the honey bee which include:

18.2.1.1 Mites

The honey bee tracheal mite, *Acarapis woodi*, is a parasite of *Apis mellifera* and *Apis cerana*. It lodges itself in the trachea of worker bees, where it breeds, and eventually suffocates them (Sammataro et al. 2000). Although it was a pest in the twentieth century, the tracheal mite is now no longer a major problem for world apiculture. *Tropilaelaps* spp. is a parasitic mite of *Apis dorsata* honey bees in tropical Asia. The introduction of *Apis mellifera* into the distribution range of *Apis dorsata* has provided the *Tropilaelaps* mite with a new host. A recent study based on molecular markers has identified at least four *Tropilaelaps* species in Asia, although *T. clareae* is the only one that is parasitic to *Apis mellifera* (Anderson and Morgan 2007). In this region of the world, *Apis mellifera* is also prey to another parasitic mite, *Varroa destructor*, with the two species engaged in fierce competition for parasitism. *Tropilaelaps* are brood parasites, feeding on the haemolymph of the bee brood and breeding there. A proliferation of these parasites can kill honey bee colonies and encourage the emergence of other pathogens.

The mite is so reliant on brood that it dies after more than 7 days without it. The *Varroa* mite, *Varroa destructor*, is a pest that destroys colonies of *Apis mellifera* worldwide, with the exception of Australia where it is not yet present. Scientists tend to attribute honey bee mortality largely to the *Varroa* mite. Originally a parasite of the Asian honey bee, *Apis cerana*, it was transferred to the European honey bee, *Apis mellifera*, in the mid-twentieth century by exchanges of genetic material among many countries (Oldroyd 1999). Left untreated, colonies infested with the *Varroa* parasite die after 2–3 years. It is impossible to eradicate this parasitic infection.

Varroa mites help to diminish the honey bee's immune response and encourage the development of viral infections (Gregory et al. 2005). They are also active vectors in the transmission of viruses and bacteria (Yang and Cox-Foster 2005; 2007). The problems with *Varroa* parasite control are typical of those encountered in curbing any insect pest population. *Varroa* are becoming resistant to the acaricides used by beekeepers to control them (Milani 1999). The recent discovery in several parts of the world (notably the United States of America [USA] (Harbo and Harris 2005)) and Europe (Le Conte et al. 2007) of honey bee colonies able to tolerate heavy infestations of *Varroa destructor* opens the door to lasting solutions for controlling the parasite. The biological basis of this tolerance has begun to be unravelled using innovative genomic methods that suggest that honey bee tolerance of *Varroa* is determined more by behaviour than by immunological factors (Navajas et al. 2010).

18.2.1.2 Protozoa

Nosema apis is a microsporidian that attacks the midgut wall of adult honey bees. The disease can develop with no visible symptoms or manifest itself as a weakening of the colony, possibly ending in death. Colony infestation is latent. The disease tends to emerge mainly in early spring following long, wet winters: during winter, honey bees are prevented from going outside and drop their excrement inside the hive, forming a source of contagion for other bees. After this, the disease spreads rapidly. Even though *Nosema apis* exhibits signs common with other diseases, the disease can be identified by certain signs observable when inspecting the colony and in the laboratory (Jean-Prost and Le Conte 2005).

Nosema cerana is another microsporidian species that resembles *Nosema apis* (Fries et al. 1996). It is a parasite of *Apis cerana* and has been transferred to *Apis mellifera* by exchanges of genetic material. It was recently identified in Europe (Fries et al. 1996; Higes et al. 2006). Since then, it has been found the world over. *Nosema cerana* does not cause the same signs in honey bees as *Nosema apis*. Only molecular techniques can differentiate between the two microsporidians (Higes et al. 2006). This parasite is considered to be responsible for sharply dwindling honey bee populations in Spain (Higes et al. 2006).

18.2.1.3 Bacteria

The bacteria pathogenic to honey bees attack the brood. American foulbrood, a disease that has been known since ancient times, is caused by *Bacillus larvae*. This serious, highly contagious disease occurs across the globe (Jean-Prost and Le Conte 2005). European foulbrood is caused by *Melissicoccus pluton*, in association with other bacteria. It tends to gain a foothold in weakened colonies in spring and at first is benign. A supply of pollen from outside the nest is usually all colonies need to overcome the disease, although heavy losses have been reported in the past (Jean-Prost and Le Conte 2005). At present, only antibiotics are effective in treating these protozoa and foulbroods, but they are no longer authorized because of the hazard of residues in honey.

18.2.1.4 Viruses

Eighteen different viruses have been identified in honey bees of the *Apis* genus. Some of these viruses are highly anecdotal, while others are latent and can be extremely prolific among the bees in our hives without causing any noticeable signs (Tentcheva et al. 2004). For reasons as yet unknown, these viruses can become highly pathogenic to honey bees, causing trembling and paralysis that are observable at the colony entrance. This is the case with chronic paralysis virus (CPV) and acute paralysis virus (APV). It is not yet known how these viruses act to kill bees. No treatment exists to control such viruses, which can weaken or kill the colony. These pathologies can be stemmed by a supply of quality pollen from foraging bees. *Varroa* weakens the bee's immune system and encourages viral growth (Chen et al. 2006).

18.3 Diseases and Parasites: Changes in Disease Profiles and Incidence

Some known pathogens are distributed worldwide. They include: *Varroa destructor* in the case of *Apis mellifera* and *Apis cerana*; bacteria that cause American and European foulbrood; *Nosema apis* and *N. cerana*; and numerous viruses affecting

Apis mellifera. These pathogens tend to have different haplotypes of varying virulence. Climate change can encourage the transfer of these haplotypes to honey bee populations. Other pathogens or haplotypes have more limited distribution ranges, such as *Tropilaelaps*, which to date has been found only in Asia (Sammataro et al. 2000). Climate change will lead to movements of honey bees of different species and races, bringing them into contact with pathogens with which they have never co-evolved, as has occurred with *Varroa destructor* and *Apis mellifera*. In the space of a few decades last century, two extremely homogeneous haplotypes of this honey bee parasite were sufficient to invade virtually the entire *Apis mellifera* distribution range (Solignac et al. 2005). History therefore shows that such encounters can be catastrophic and that honey bees will need human assistance to survive. Honey bee movements may be spontaneous and linked to changes in geographical distribution, or the result of exchanges of bees among beekeepers. There could be changes in the geographical distribution of diseases whose expression depends on climatic factors. This has happened with chalkbrood disease, which is caused by the fungus *Ascosphera apis*, which develops mainly in a humid environment.

18.4 How Will the Pathogen/Bee Interaction Evolve?

Recent results from a metagenomic study by American researchers on honey bee populations suffering from colony collapse disorder are highly instructive in this respect (Cox-Foster et al. 2007). They have shown that honey bee colonies are infested by numerous pathogens, including imported ones. There is therefore a high likelihood that as yet unidentified pathogens exist on certain honey bee species or races. Pathogen species infesting different honey bee races or species can be brought into contact with new hosts. The recent discovery of *Nosema cerana* (Higes et al. 2006) and the Israeli acute paralysis virus (Cox-Foster et al. 2007) among *Apis mellifera* is a potent example of the role humans can play in movements of honey bee populations. Climate change could modify the interactions among these different pathogens. *Tropilaelaps* is an interesting case in point. The *Tropilaelaps* mite does not yet infest *Apis mellifera* because this honey bee's development cycle includes a period without brood, on which the mite is utterly reliant for its survival (Sammataro et al. 2000). However, if climate change induces warmer winters, *Apis mellifera* would have to adapt towards a continual brood cycle, which would render it a potential host for *Tropilaelaps*.

18.5 Consequences for Bee Health and Socioeconomic Impact

Honey bees will require human protection, if only because of their importance for agricultural production and markets. It seems clear that bees will come into contact with new pathogens. The high mortality rate and colony collapses that we are currently seeing demonstrate the fragility of honey bee populations worldwide. As has been the case with the *Varroa* threat to *Apis mellifera*, our honey bees will need to be aided with medicines and appropriate control methods to prevent them from becoming extinct.

18.6 Climate Change Can Facilitate the Emergence of New Invasive Species

Numerous examples have revealed the fragility of the host–parasite balance and shown that even slight climate changes impact on the establishment of invasive species that are currently at the fringes of the honey bees' distribution range. The situation of honey bees can also evolve when predators colonise new areas. A stark example is that of the bee-eater, a magnificent bird that feeds on *Hymenoptera* and bees. The bee-eater originated in the Mediterranean region but has extended its distribution range, causing only minimal harm to beekeepers so far. In France it is now found north of the Loire. A second example is an apiary pest, the small hive beetle (*Aethina tumida*), which originated in South Africa and develops on the weakest honey bee colonies. The parasite was imported into the USA, probably on citrus fruit on which the beetle can also develop. It has compounded the problems of American beekeepers, especially in hot and humid regions. The cold climate has halted the beetle's northward progression. Climate change will promote the extension of its distribution range. Measures have been taken to prevent this insect pest from being imported into Europe, where it is considered a potential hazard.

18.7 Recent Cases of Mortality

The consensus among researchers is that a combination of factors is responsible for this honey bee mortality. Pesticides kill many colonies every year. New pathogens have been added to the already long list of honey bee diseases. However, researchers agree that the bees' environment and stress, both of which are influenced by climate change, have been decisive factors in this heavy mortality (Oldroyd 2007; Pettis et al. 2007). There appear to be strong interactions between diseases, pesticides, environment and climate. Climate change has an action on each of these factors. To understand the effect of climate change on the *Evolution* of honey bee populations, each of these factors will need to be taken into account.

18.8 Pollinators and Biodiversity

Our recent analyses of global inventories of biodiversity indicate that more than 100,000 different animal species – and perhaps as many as 200,000 – play roles in pollinating the 250,000 kinds of wild flowering plants on this planet. In addition to countless bees, wasps, moths, butterflies, flies, beetles, and other invertebrates, perhaps 1500 species of vertebrates serve as pollinators. Hummingbirds are the best known vertebrate pollinators in the Americas, but perching birds, flying foxes, fruit bats, possums, lemurs, rodents, and even a gecko function as effective pollinators elsewhere in the world. The ultimate reproductive consequences of pollinator scarcity on wild plants is not appreciated and remains understudied (Burd 1994; Nabhan and Fleming 1993). The few existing studies indicate that many species of wild plants may be suffering decreased reproductive success as a result of low visitation rates by pollinators. In Iowa, where only 200 acres of unplowed prairie remain intact, low seed yields in prairie wildflowers has been linked to lack of adequate visitation rates by pollinators (Hendrix 1994). Rare cacti in U.S. national parks and adjacent to heavily sprayed cotton fields showed high levels of floral abortion due to paucity of pollinating moths (Suzan et al. 1994). In urban Tokyo, a primrose almost completely failed to set seed due to local disturbance of its bumblebee pollinator (Washitani et al. 1994). In a 17-year study in French Guiana, a shift in native pollinator populations to a fauna dominated by Africanized bees caused a 40% drop in seed set of tropical legumes (Roubik 1995).

18.9 Threats to Wild Pollinators

Alternative pollinators often play important economic roles. The ground-nesting alkali bee, for example, a more effective pollinator of alfalfa than is the honey bee (O'Toole 1993). A diversity of wild pollinators are important in tropical agricultural crops (Roubik 1995). Complete inventories of the effective pollinators of cultivated crops and other valuable plants are urgently needed. Globally, over 180 species of birds and mammals in 100 genera of vertebrate pollinators are already listed as endangered, and untold invertebrates are at risk as well (Buchmann and Nabhan 1996). Because some wild pollinators need undisturbed habitat for nesting, roosting and foraging, they are very susceptible to habitat degradation and fragmentation (Buchmann and Nabhan 1996). In Costa Rica wild bee diversity in degraded forest land dropped from 70 to 37 species in 14 years (Buchmann and Nabhan 1996). While the exact mechanism responsible for population declines is uncertain, one strong possibility is that habitat fragments do not provide the diversity of resources needed by pollinators. For example, they may require plants that flower sequentially, providing food sources throughout the season, or may require alternative nectar and pollen sources. Lepidopteran pollinators require host plants for their larvae, and bees require nesting resources. Elimination of these resources can lead to declines in pollinator populations (Buchmann and Nabhan 1996). Aculeate Hymenoptera is now probably the most rapidly declining group of insects in Europe and other countries across the globe (Day 1991; O'Toole 1993), and there is a growing focus on habitat management in order to conserve wild bees and wasps in several countries of the world. Thus, a national mapping scheme of wild bee populations has been initiated which include Germany (Schwenninger 1999; Westrich 1996), The Netherlands (Peeters et al. 1999), Sweden (Svensson et al. 1990), and Britain (Kloet and Hincks 1978). In the German area Baden-Württemberg, 57% of the listed 429 bee species are endangered or close to extinction (Westrich 1989), and in Britain, 11.1% of the bee species are considered either vulnerable, endangered or extinct (O'Toole 1994).

Another threat to wild pollinators is exposure to pesticides and other toxins than can poison them or impair their reproduction. For example, aerial spraying for coniferous forest pests in Canada in the mid-1970s reduced populations of native bees to the extent that blueberry yields were reduced for a period of 4 years (Kevan and Plowright 1995). Field studies in the deserts of the southwest U.S. have found that pollinators remaining in small fragments of natural habitat are particularly susceptible to pesticide spraying on adjacent croplands (Suzan et al. 1994). Herbicides can eliminate nectar sources for pollinators, larval host plants for moths and butterflies, and deplete nesting materials for bees (Buchmann and Nabhan 1996). Certain pollinators, such as bats, hummingbirds, moths and butterflies migrate seasonally over long and short distances between mountain ranges, regions, or countries. Their migratory routes are often well-defined nectar corridors where the sequence of flowering over a season offers the pollinators sufficient energy to sustain their journey. Many of these nectar corridors are no longer fully intact; however, land conversion has eliminated some floral resources over 20–60 mile segments, in some cases longer than what energy-depleted pollinators can fly in 1 day (Nabhan and Fleming 1993).

18.9.1 Diseases and Enemies of Wild Pollinators

18.9.1.1 Bumblebees

Bumble bees carry a lot of parasites and diseases. Ecto-parasitic mites like *Parasitus fucorum*, *Kuzinia laevis*, *Scutacarus acarorum*, *Glycyphagus domesticus* and *Hypoaspis* are often found in colonies in *Nature*. In a commercial rearing unit these mites disappear. The endo-parasitic mite *Locustacarus buchneri* can ruin a commercial rearing unit. In *Nature* parasitic flies like *Senotainia tricuspus* and *Brachycoma devia* can impede colony founding by preventing the queen from ovipositioning. The nematode *Sphaerularia bombi* infects hibernating queens. The nematode prevents the development of the corpora allata of the queen which consequently inhibits ovary development. Infected queens hibernate but do not found a colony. Unicellular parasites like *Nosema bombi*, *Apicystis bombi* and *Crithidia bombi* all have a variable though negative impact on colony development.

Probably more bumblebees are killed by parasites than by predators. This may be because the bumblebee females are armed with a sting, but it is also due to the protection given by their warning colouration. Some crab spiders ambush bumblebees at flowers, and a few species of bird can remove the sting before eating the bumblebee, e.g. bee-eaters, spotted flycatchers and shrikes. Other predators are small mammals, badgers, foxes, and minks, and in the U.S. skunks and bears all break open and destroy nests to eat the larvae, bees and food stores, but there are no vertebrate predators that specialise in bumblebees. In the U.S. there are wasps called beewolves in the genus *Philanthus*, these wasps specialise in hunting bumblebees. The bumblebee is caught while feeding and is paralysed with a sting, it is taken back to the nest and enclosed with a wasp egg in a cell, there are usually about five bumblebees in each cell. Cuckoo bumblebees, *Psithyrus* spp. Cuckoo females enter the bumblebee nest and lay their eggs, the bumblebee workers then rear these eggs as if they were their own sisters. Wax moth, *Aphomia sociella*. The adult moth enters the bumblebee nest and lays her eggs, at first the caterpillars feed on nest debris, but as the grow they switch to feeding on the wax food cells, food stores and even larvae. Normally this destroys the nest. The moth leaves the nest to overwinter as a pupa in a sheltered spot. Invasion of the nest by the north American wax moth *Vitula edmandsii* does not always lead to the destruction of the nest as it does not feed on the larvae. *Brachycoma devia* is a fly that look a little like the common house fly. The female enters the bumblebee nest and lays larvae (this fly does not lay eggs) among the bumblebee larvae. The fly larvae attach themselves to a bumblebee larvae and wait. Once the bumblebee larva has spun its cocoon the fly larvae start feeding on it and suck it dry. When they are fully grown they leave the bumblebee cocoon and pupates in the bumblebee nest. Conopid flies. The female fly waits on flowers till a bumblebee comes to feed, then she jumps on the bee and quickly pierces the bees body and lays her egg inside it. The egg hatches inside the bee and feeds off its abdominal contents till it more or less fills the entire abdomen. The bumblebee dies and the fly larva pupates inside the husk of the dead bumblebee body emerging as an adult fly next summer. *Sphaerularia bombi* a nematode (tiny worm). This parasite is only found in queens and affect her behaviour. The bumblebee queen is infected by an adult female worm while the queen hibernates. In the spring when the queen emerges from hibernation the worm begins to grow, then it turns its whole reproductive system inside out. The uterus grows and grows till it is between 1 and 2 cm long, while the rest of the worm is only a thin thing of a few millimetres. In a normal queen a hormone would be released and her ovaries would start to develop stimulating her to start building a nest, but somehow this does not happen in an infected queen. Meanwhile the worm releases up to 100,000 eggs into the blood of the queen, these eggs hatch and develop, moving into the gut and reproductive system. During this time the queen feeds only for herself, she makes no attempt to find a nest site, and her ovaries do not develop. Often she returns to her hibernation site, here the worm larvae are discharged with faeces into the soil. The mature worms mate, and wait for another queen to use the site to hibernate. Various species will invade bumblebee nests if they find them and eat stores, eggs and grubs, this often destroys the colony. Certain hoverfiles, e.g. *Volucella bombylans*. The adult female fly enters the bumblebee nest and lays her eggs. The fly eggs hatch and the larvae feed on nest debris, doing no apparent harm. The fly overwinters as a pupa in the empty bumblebee nest. This hoverfly is also a bumblebee mimic, it even buzzes if handled. Certain mites, e.g. *Parasitus fucorum*. These mites are often seen attached to the thorax of bumblebees. They scavenge on nest debris, then attach themselves to young queens and hibernate with them. These mites often have even smaller mites living on them! Certain beetles, e.g. *Antherophagus* spp. These feed on nest debris and use adult bumblebees for dispersal.

Life Cycle

Parasite of bumblebees which typically overwinter in underground burrows. Parasitized bumblebee queens make numerous unsuccessful attempts to dig burrows in June. Each time they alight and attempt to dig, hundreds of third stage larvae are discharged or exit through the anal opening of the bumblebee. These larvae molt during July and into August developing through the fourth larval stage to adults. During this same period infected bees die from the infestation. The adult nematodes mate and the impregnated females become the infective stage. In autumn and fall when healthy queens are seeking hibernation sites, they are attacked by the infective female nematodes. Infective females penetrate the queens during hibernation. Normally only one female is found per bumblebee queen although as high as 74 have been recorded. When the queen emerges in the spring the nematode is a mature female and may already be producing eggs. By June the parasite is matured and third stage larvae are evident in the insect's hemocoel, midgut, and hindgut. A fascinating feature of this nematode is the ability to completely evert the reproductive system which then proceeds to enlarge independently of the original female body. The prolapsed uterus may be from 6 to 30 times the length of the original female and 300 times the volume. Two molts within the egg have been observed. Males and workers which do not hibernate, are never parasitized.

18.9.1.2 Leaf Cutter Bees

The leafcutter bee is attacked by numerous insects, and considerable attention must be given to maintenance of a pest-free population if an increase in bee populations is to be realized (Waters 1971; Parker and Potter 1974). Table 18.1 lists the common insects associated with leafcutter bee nests in some parts of the United States. Probably the most important type of parasite–predator control is the maintenance of clean bee stocks by excluding pest populations through changing nesting media yearly or by utilizing emergence traps. Most pest species can be controlled during incubation or emergence through the use of sprays or traps. Currently, chalk brood, a disease associated with bee larvae, is increasing. In some Western States, the incidence of this disease has increased to as high as 80% of the overwintered bee larvae. However, little is known of the causal organism and its taxonomic status. We still do not know whether the organism is the cause or merely a symptom of these bee losses. Until these questions are adequately researched, control measures cannot be devised. However, it been shown that growers who use clean nesting media have less chalk brood than those who reuse infested nesting media. Kapil and Jain (1980) reported 10 parasites parasitizing five species of Megachild bees and a small carpenter bee *Pithitis smaragdula* (Table 18.2). They included Bombilid one spp. Chalcid two species chrysidids two species, cuckoo bees one species and tachinids two species. The Chalcid wasp *Monodontomerus obscurus* Westwood, Hymenoptera: Torymidae; an Eurytomid

Table 18.1 Characteristics of nest associates of the alfalfa leafcutter bee

	Native +; introduced 0	Predators +; parasites 0; scavengers –	Important +; minor 0	Control measures
Moths				
Plodia interpunctella	0	+0	0	Light traps
Vitula edmandsae	+	+0	0	Light traps
Wasps				
Sapyga pumila	+	0	+	Emergence traps
Monodontomerus obscurus	0	0	+	Emergence sprays
Monodontomerus montivaga	+	0	+	Emergence
Pteromalus megachilids	0	0	+	Emergence
Tetrastichus megachilids	+	0	+0	Emergence sprays, traps
Melittobia chalybii	+	0	0	Destroy
Dibrachys masculipennis	0	0	0	Destroy
Leucospis affinis	+	0	0	Nesting media
Vespula spp.	+	±	0	Traps
Formica spp.	+	±	0	Barrier
Bees				
Coelioxys funeraria	+	0	0	Early emergence?
Coelioxys gilensis	+	0	0	(?)
Coelioxis	+	0	0	(?)
Stelis sp.	+	0	0	(?)
Dipera flies				
Anthrax irroratus	+	0	0	Emergence
Beetles				
Nemognatha lutea	+	+	0	Eliminate host plants
Trichodes ornatus	+	+	+	Traps
Ptinus californicus	+	–	0	Sprays, loose cell
Trogoderma glabra	+	+–	0	Cold treatment, traps
Trogoderma variabile	+	–	0	Baits
Tribolium castaneum	+	–	0	Santitation
T. audox, *T. brevicornis*	+	–	0	Santitation
Oryzaephilus surinamensis	0	–	0	Santitation
Cryptolestes ferrugineus	0	–	0	Santitation
Tenebroides maurtanicus	0	–	0	Sanitation
Earwigs				
Forficula auricularia	0	±	0	Barriers

have been found parasitizing all the five species of megachild bees, whereas others have been species specific. Three species of cuckoo bees – *Coelioxys minutes* (Hymenoptera: Megachilidae) associated with *Megachile nana*, *C. fuscipennis* with *Megachile flavipes* and *Megachile femorata* and *C. decipiens* with *M. cephalotes*. There is only one bombilid species – Argyramoeba distigma (Diptera: Bombilidae) associated with all the megachilid bees. Chrysidids include two species – a large sized *Chrysis fuscipennis* (Hymenoptera: Chrysididae) attacking mainly the individuals in mud cells of *M. flavipes*, *M. femorata* and *M. lanata*. The other species *C. tricantha* parasitizes the cells of *M. nana* and *P. smaragdula*. The two species of tachinids – *Caiusa indica* and *C. testacea* (Diptera: Calliphoridae) are parasites of *M. nana.*

18.9.1.3 Alkali Bees

Numerous diseases, pests, and other enemies inflict damage on alkali bees. They include ambush bugs, bee flies, chalcids, clerid beetles, conopid flies, cuckoo bees, meloid beetles, robber flies, tiger beetles, velvet ants, and wasps. Crab spiders are also a problem, but mites, although present, are of little consequence. Vertebrate enemies include birds that feed on the adults and mice and skunks, which usually feed on the larvae. Bacterial and fungal diseases may suddenly strike and seriously diminish the population of a bee bed. Trampling of the nesting sites by livestock, traffic by vehicles, unwise use of pesticides, and flooding during the active bee season can also reduce populations or destroy the site.

18.9.1.4 Alfalfa Leafcutter Bees

The tiny parasitic wasp (*Sapyga pumila* Cresson) first mentioned by Torchio (1963) as a potential threat was verified by Torchio (1970) as causing a high percentage (6.9–65.3%) of the cells to be parasitized. Torchio (1972) recommended trapping for satisfactory control of this wasp. Some degree of control has been devised for the other insect enemies. Birds can be screened away from the nests with chicken wire, and rodent control measures can protect the bees and their nesting materials from mice. Insecticides sprayed over alfalfa field can be a serious problem. Alfalfa leaf material used in the nest can be toxic if treated with persistent insecticides even before the blooms appear or the bees emerge. Confining the bees for protection from pesticides is a poor solution but moving the bee boards at night to a cool dark place for a day or two may be feasible.

18.10 Chalkbrood Control in Alfalfa Leafcutting Bee

Chalkbrood (*Ascosphaera* spp.) is a fungal disease of not only honey bee larvae but other important commercial pollinators such as the alfalfa leafcutting bee *Megachile rotundata* F. and the blue orchard bee *Osmia lignaria propinqua* Cresson (Gilliam and Vandenberg 1997). Found worldwide, chalkbrood disease is rarely lethal to honey bee colonies but can reduce colony foraging capacity up to 49% (Heath 1982b, c) impacting both pollination efficacy and honey production. Although a wide range of chemicals have been evaluated for the control of chalkbrood, none has been successfully adopted for use (Aronstein and Murray 2010). Widespread acceptance of a chemical for the treatment of chalkbrood requires that it must be effective, easy to use, and economical (Hale and Menapace 1980). Moreover, it must not compromise the safety and quality of the honey produced for human consumption. Contamination of honey by the residues of drugs used in the treatment of honey bee diseases is an important public safety issue and can affect the import and export of hive products between countries (McKee 2003; Martel et al. 2006). Interest in the study and use of natural compounds as an alternative to antibiotics to control honey bee diseases has increased in recent years especially as concerns over antibiotic resistance grow (Davis and Ward 2003).

Chalkbrood disease of leafcutting bees was first identified in American bee populations in the early 1970s. It spread rapidly through wild and domestic leafcutting bee populations throughout the northwest United States, and within several years caused population losses as high as 60% in some states. Chalkbrood is now found at economically damaging levels in all major American alfalfa seed-growing areas where leafcutting bees are used for pollination. From 1982 to 1984, chalkbrood disease was identified at low levels in Alberta, Saskatchewan and Manitoba. Since then it has become well established in southern Alberta, causing losses of up to 28%. For unknown reasons it has not reached similar proportions in Saskatchewan or Manitoba. Chalkbrood, a fungal disease of bees, is caused by species of the genus *Ascosphaera*. Different species of *Ascosphaera* affect honey bees, leafcutting bees, and other solitary bees. The species which affects the alfalfa leafcutting bee is *Ascosphaera aggregata.*

18.10.1 Life Cycle

Chalkbrood causes the death of leafcutting bee larvae. The dormant stage of chalkbrood is a spore which survives for many years under Canadian conditions. When an adult female leafcutting bee emerges from her cell, if she chews through a cocoon containing a chalkbrood cadaver she becomes dusted with spores, which stick to her body hairs. These spores then become mixed into the pollen balls which she prepares prior to laying her eggs. The young leafcutting larva eats the pollen ball and ingests chalkbrood spores. Once in the larval gut, the spores germinate and the fungus grows, moving through the gut wall into the body cavity. Eventually the larval tissues are broken down and the larva dies. Death generally occurs in the final larval instar before pupation, so dead larvae are usually fullsized. Once the larva is dead the fungus may begin to form spores in spore cysts between larval skin layers (Fig. 18.2). When mature, these spore cysts are easily shattered allowing spore dispersal. The fungus may not form spores, and these nonsporulating cadavers are not infective. Also, the fungus may only partially sporulate.

Table 18.2 Megachild bees bee species and their parasites (Kapil and Jain 1980)

Megachild bees	
Bee species	Parasite
Megachile haryanensis Rahman (ex. *Megachile nana* Bingh)	Cuckoo bees – *Coelioxys minutus* (Hymenoptera: Megachilidae), *Argyramoeba distigma* (Diptera: Bombilidae), *C. tricantha*, *Caiusa indica*, *C. testacea* (Diptera: Calliphoridae)
Chalicodoma rubripes (Morawitz) (ex. *Megachile flavipes* Spinola)	*C. fuscipennis*, Argyramoeba distigma (Diptera: Bombilidae)
Megachile femorata Smith	*C. fuscipennis*, Argyramoeba distigma (Diptera: Bombilidae)
Chalicodoma lanata F. (ex. *M. lanata* Lepel)	*Caiusa indica* and *C. testacea* (Diptera: Calliphoridae)
Chalicodoma cephalotes Smith (ex. *Megachile cephalotes* Smith)	*C. decipien*, Argyramoeba distigma (Diptera: Bombilidae)
Pithitis smaragdula F.	*C. tricantha* (Hymenoptera: Chrysididae)

18.10.2 Symptoms

Figure 18.2 illustrates a sporulating cadaver. Spore cysts under the skin give the larva a black, grey or dark tan appearance (Figure la), often with a honeycomb-like surface. The dry larval skin takes on a metallic sheen. Spore cysts are shiny black and oblong, and are packed closely together under the larval skin. In cross-section, body tissues are dry and are surrounded by a ring of oblong spore cysts between the skin layers. Figure 18.2 illustrates a nonsporulating cadaver. The cadaver is a tan colour, and the dry skin imparts a metallic sheen to its surface. The cross-section shows dry larval tissues surrounded by a ring of slightly darker tissue.

18.10.3 Prevention and Control of Chalkbrood Disease

18.10.3.1 Purchase of Bees and Equipment

The most common way of spreading chalkbrood is in cocoons and used nesting equipment. Ensure that chalkbrood is absent before buying leafcutting bee cocoons. Do not buy bees from regions known to have chalkbrood. Before buying used leafcutting bee nests or other equipment, determine that chalkbrood has not been found in the beekeeping operation. Clean and sterilize all used equipment and nests before using them, and preferably before moving them to your farm. Keep newly purchased bees and equipment separate from the existing operation. Sample their offspring separately to determine disease status before incorporating them into the main operation. Chalkbrood spores are known to occur in used wood nesting material it is therefore advisible not to use used nesting equipment including bee boards.

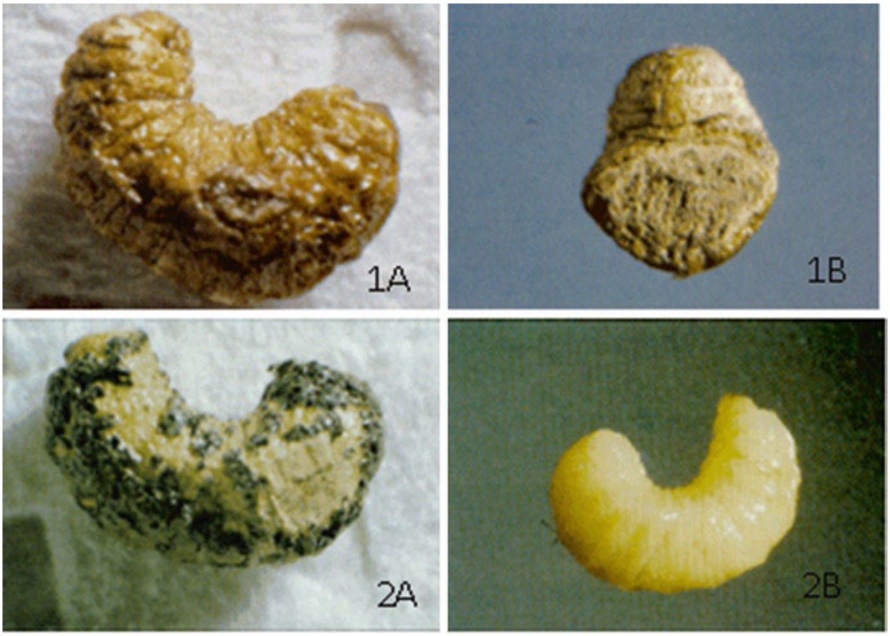

Fig. 18.2 Classical sporulating chalkbrood cadaver (*Ascosphaera aggregata*) (*1A*) side view (*1B*) cross section. Classical nonsporulating chalkbrood cadaver (*Ascosphaera aggregata*) (*2A*) side view (*2B*) cross section

18.10.3.2 Loose Cell Management

Use of loose cell management is the best option where the cocoons are removed from nests each year, stored and incubated as individual cocoons, rather than in tunnels. This principle is essential for control of diseases, molds and parasites, since it allows sterilization of nesting material and treatment of cocoons. Remove cocoons from nesting material each year. Do not purchase solid block-type nesting material unless you can remove the cocoons from it. Cocoon groups can be broken into individual cocoons to prevent adults from chewing through other cocoons when emerging. Use a "cell-breaking" apparatus, BUT take care that the apparatus is adjusted properly and is not crushing cocoons. Tumble the cocoons to remove debris, and burn the debris. Sterilize the nesting material prior to use. Surface sterilize the cocoons prior to incubation.

18.10.3.3 Treatment of Nesting Material

Bleach Treatment of Nesting Material

Treat nesting material in the spring. Dip nests in a 3–5% solution of bleach for 3–5 min. Bleach, or sodium hypochlorite, is available in a 5% solution from grocery stores (e.g. Javex) or in a 12% solution from agricultural chemical suppliers. Use the following formula to determine the quantity of 12% bleach required to make up the amount and the percentage desired.

$$\frac{\begin{array}{c}\text{Volume} \times \text{Percent of dilute solution}\\ \text{dilute solution desired}\end{array}}{12} = \text{Volume of 12\% liquid bleach required}$$

$$\frac{\text{e.g. 200 gallon tank} \times 5\%}{12} = \text{83.3 gallons 12\% of liquid bleach required}$$

Calcium hypochlorite may also be used. It is available as a powder containing 65% chlorine. It tends to leave a calcium sludge in the tank unless well mixed, and may leave a chalky residue on nest surfaces. Use the following formula to determine how much calcium hypochlorite to use:

$$\frac{\begin{array}{c}\text{Volume (ga)} \times 10 \times \text{Percent of dilute}\\ \text{solution dilute solution desired}\end{array}}{65} = \text{Weight (lb) of 65\% dry bleach required}$$

$$\frac{\text{e.g. 200 gallon tank} \times 10 \times 5\%}{65} = \text{154 lb of 65\% dry bleach required}$$

Add a surfactant at the rate of 0.1% to both of these solutions to ensure wetting of all surfaces. Bleach solutions lose strength with time, with exposure to air, and when mixed with organic material such as leaf pieces. Test the solution every few hours using a bleach test kit. Test in the morning if the solution is used for more than 1 day. Add bleach as required. Stack dipped nests in staggered fashion, holes down, or take them directly to the field shelters to dry. Allow several days for polystyrene and styrofoam nests to dry and 2 weeks for wood nests to dry before bees are released. Bleach is extremely corrosive and harmful to skin, eyes and lungs. READ THE LABEL! Make sure that you are wearing eye protection, protective clothing and a respirator with a chlorine filter while using bleach. Do not tuck pant legs into boots. Remove bleach-soaked clothing. If bleach contacts eyes, rinse for 15 min with water and seek medical attention. If bleach is swallowed, do not induce vomiting; drink as much water as possible to dilute the bleach, and seek medical attention. Dispose of used bleach solution by spreading it over an area where soil sterilization will not be a concern, and where there is no possibility of contamination of water bodies or septic systems.

18.10.3.4 Heat Treatment of Wood Nesting Material

Exposure to temperatures of 93°C (200°F) for 12 h will kill chalkbrood spores. A kiln or oven must be designed to heat equipment evenly, to avoid hot and cold spots. Use circulating fans, and stack nests to facilitate air circulation during heating. Set up the kiln in a separate shed to minimize the potential for fire damage to other buildings and equipment. The length of time nests are treated will depend on the time required to reach a temperature of 93°C.

18.10.3.5 Paraformaldehyde Fumigation of Nesting Material

Paraformaldehyde is a white crystalline substance which gives off formaldehyde gas when heated. Paraformaldehyde fumigation of nest material is very effective for control of chalkbrood and other molds. Extreme caution must be taken when handling and using paraformaldehyde. Adequate ventilation following its use is essential. Under no circumstances should paraformaldehyde be exposed to an open flame. READ THE LABEL! To fumigate with paraformaldehyde, place the nesting material in cross-stacked piles in the fumigation chamber. Problems can occur with persistent formaldehyde vapour after fumigating, so treat nesting material in a room or building set aside for this purpose only. The building or the room to be used for fumigation must have an air exhaust system with air intake capability rated to the capacity of the exhaust system. In addition, you must be able to seal and lock the room or building. Condition the nesting material in the chamber for 48 h at 20–25°C with a relative humidity of 60–70%. Use circulation fans to ensure even humidity and temperature throughout the chamber. Fumigate with paraformaldehyde at a rate of 20 g of product per cubic metre of fumigation chamber (1.1 lb of product per 1000 cubic feet). Place the product in one or more electric frying pans attached to electric timers. Paraformaldehyde prills should be loaded to a depth no higher than the sides of each frying pan. Use gloves, eye protection, and a dust mask or respirator. Set the timer to heat the paraformaldehyde for 4 h at the maximum heat setting, then seal and lock the chamber. Do not re-enter the chamber once fumigation has begun.

After a 24 h period, begin continuous ventilation of the chamber by exhausting air. Ensure an adequate incoming flow of fresh air. Ventilate for 48–72 h. If you can still smell an odour of formaldehyde, or your eyes sting, ventilate for an additional 24–48 h. Enter the chamber only after completion of adequate ventilation. Use a full-face NIOSH approved respirator with formaldehyde or acid gas cartridge. Also, wear coveralls and gloves. Place nesting material directly into the field for aeration prior to bee release.

18.10.3.6 Surface Sterilization of Bee Cocoons

Both bleach treatment and paraformaldehyde fumigation can be used to surface sterilize bee cocoons, killing chalkbrood and other mold spores. Adult bees will emerge from incubation trays carrying fewer spores.

18.10.3.7 Bleach Treatment of Cocoons

Treat the cocoons just prior to incubation. Use the same dip tank as you use for nests. Use liquid bleach rather than dry bleach to make up the solution, otherwise the cocoons will become coated with a chalky residue. Construct mesh cages of similar dimensions to your nests. Fill them with cocoons and dip the cocoons for

3 min in a 3% bleach solution. Air dry cocoons thoroughly, away from heat and direct sunlight! Then place them in incubation trays and begin incubation.

18.10.3.8 Paraformaldehyde Fumigation of Cocoons

Because problems may occur with persistence of paraformaldehyde vapour, treatment of cocoons should be undertaken in a facility set aside for paraformaldehyde fumigation and not used for other purposes. If you plan to fumigate your leafcutting bee cocoons, you first must ensure that your incubator is equipped with a hooded exhaust fan in the 1600–2200 maximum cubic feet per minute (cfm) range. Air intake capability must be adequate for the exhaust capacity. A two-speed or variable speed exhaust fan will allow you to adjust your air exhaust rate. You will need air circulation fans within the incubator. You may also need to upgrade your heating capacity to maintain the incubation temperature of 30°C with continuous air exhaust during incubation. Without this equipment you should not proceed with fumigation of your cocoons. Fumigate cocoons just prior to incubation. Place the cocoons in incubation trays in the fumigation chamber. Condition the cocoons for 48 h at 20–25°C with a relative humidity of 60–70%. Fumigate with paraformaldehyde at a rate of 1.1 lb/1000 ft^3 of fumigation chamber (20 $\mathrm{g/m}^3$). Place the product in one or more electric frying pans attached to electric timers. Handle paraformaldehyde prills with caution and do not load prills to a depth higher than the sides of the frying pan. Wear gloves, eye protection and a dust mask or respirator.

Set the frying pan to its maximum heat setting, set the timer to provide power for 4 h, then seal and lock the chamber. After 24 h, actively ventilate for 48–72 h. Following ventilation, transfer incubation trays to the incubator. Use a full-face NIOSH-approved respirator with formaldehyde or acid gas cartridge, and wear coveralls and gloves.

Begin incubation at 30°C. Traces of formaldehyde gas will be released from cells and trays, requiring continuous ventilation. Leave the exhaust fans running at a high enough rate that you cannot detect formaldehyde in the incubator. On day 7 place dichlorvos strips in the incubator to control parasites. Turn the air exhaust system off for the parasite control period. On day 13 remove the dichlorvos strips, and turn the exhaust system on to remove both the dichlorvos and the formaldehyde gas which has accumulated. After ventilating for 24–48 h, turn the exhaust fan down and run it as required, to remove any traces of formaldehyde gas.

18.10.3.9 Field Practices

1. **Do not share equipment, incubator or bees.** Sharing is a good way to import disease problems. If you must, first ensure that chalkbrood is not present in any of the operations involved.
2. **Do not dump old cocoons in the field.** If chalkbrood cadavers are present in the old cocoons the adult leafcutter bees will come into contact with them, and will be exposed to chalkbrood spores. Collect and burn the old cocoons.

3. **Keep field shelters clean and free of debris.** Spray the shelter interiors with a 3–5% bleach solution applied with a back pack sprayer, to help control chalkbrood and mold spores. Wear protective clothing and a respirator. Allow time for the shelters to dry before releasing bees.
4. **Disinfect cell removers, tumblers and cell breakers each year.** Use a 3–5% bleach solution and a back pack sprayer. Rinse the equipment with water, dry thoroughly, and spray with a light oil to help prevent corrosion. Alternately, fumigate the bee handling equipment with paraformaldehyde, following the directions given above for fumigation of cocoons and nesting equipment.
5. **Keep nests from each field as separate lots during stripping and sampling.** If chalkbrood shows up it may be limited to one or more lots, allowing you to sell the affected lots and keep the clean lots.

18.11 The Alkali Bee

Alkali bees are attacked by a number of insects and animals. Among the more common are the bombyliid (*Heterostylum robustum*), a sarcophagid fly (*Euphytomina nomivora*), and conopid flies (*Zondion obliquefasciatum*). Generally, high populations of these flies indicate the bed is not adequately populated with bees, since well-populated sites provide good defense by limiting oviposition by the flies. Some fly control has been obtained by traps or sprays. A recent nest predator found in some areas is the black blister beetle (*Meloe nigra*). This beetle is easily controlled, since the flightless females must crawl from the site to deposit their eggs. Various methods are used to discourage vertebrate predators such as birds and skunks. Federal laws now protect most animals, so growers must seek information at the local level before using control measures. Heavy rain also can contribute to the destruction of bee cells by creating a favorable environment for soil pathogens to develop and destroy the pollen. No effective control measures have been developed to protect bees from infrequent drenching by summer rains.

18.12 Problems in the Management of Bee Diseases

Chemotherapy is adversely effecting beekeeping industry through development of resistance and the problem of residues in honey and pollen (Bogdanov et al. 1998). The development of resistance in honey bee pests and diseases means that conventional drug treatments are becoming less effective (Lodesani and Cecilia 2005). The chemical residues in bee products are a serious problem for beekeepers. Bees are often bred for behavioral traits which are not in harmony with their natural survival strategies. As a consequence, they function less efficiently under nutritional stress conditions and their immune system can be compromised by toxic elements in the environments. In many cases when the beekeepers see their livelihoods threatened by disease in the bee colonies they used drugs as a first option – if they can afford them and they are locally available. In the short term this option is often the most convenient economically and usually does not require in-depth knowledge of the biology of the pest. The main diseases that affect honey bees worldwide and for which chemical treatments are used are the bacterial infections American (AFB) and European (EFB) foulbrood, and the parasitic mite, *Varroa destructor.* However, due to the development of resistant strains of AFB and *Varroa* and the problem of residues (antibiotics in honey and acaricides in wax), the limits of chemotherapy have become evident.

Generally, a treatment with a given chemical removes nearly all the non-resistant individuals at first, but leaves the resistant individuals alive. If the number of survivors containing the genes for resistance is high enough, then resistance in the population will develop more quickly when the chemical treatments is used. The only effect that we can have on this process is to speed it up or to slow it down. If every new generation of the pest is exposed to the pesticide, then resistance will develop at a faster rate. For this reason, timing and dosage of any pesticides application is important in the development of resistance and abuse, under use or misuse of chemotherapeutic substances must be avoided.

18.12.1 Resistance to Acaricides

Although effective acaricides to control *Varroa destructor* are available, the mite has a damaging effect on beekeeping with most *Apis mellifera* subspecies. Mite infestation constitutes a continuous risk, which may lead to weakness or loss of colonies as soon as failure of the employed treatment occurs. Resistance to acaricides is a serious problem in chemotherapy for *V. destructor* and can cause disastrous colony losses if control of the mite relies on ineffective treatments (Lodesani et al. 1995).

18.12.2 Fluvalinate Resistance

The phenomenon of fluvalinate resistant mites was first reported in Italy (Lodesani et al. 1995) where, in the first half of the 1990s, it caused the loss of a considerable number of colonies (Astuti et al. 1995). Cases of fluvalinate resistant mites have been observed in France (Faucon et al. 1995) in Switzerland (Fluri 1995). In Finland (Korpela 1999), in the UK (Thompson et al. 2002), and in other Western European countries. Similar reports of the phenomenon have come from Argentina, the USA (Baxter et al. 1998) and Israel (Mozes-Koch et al. 2000).

Concerning the situation in European countries, the temporal spread of mite resistance suggests that it has arisen only once or twice and that the major cause for the rapid spread of resistant mites is the movement of bee colonies by beekeepers (Martin 2004). Two different mechanisms of resistant been suggested for fluvalinate: one concerns the increase in the levels of detoxification enzymes, such as mono-oxygenases (Mozes-Koch et al. 2000) in mite populations in Europe and

Israel (monoxygenases are the enzymes that make fluvalinate almost harmless to the bee); the other concerns a reduced target-site (sodium channel) sensitivity to pyrethroids in the nervous system (knockdown resistance: a mechanism reported for many insect pests) as was found in the Florida and Michigan mite populations (Wang et al. 2002). These studies suggest that pyrethroid resistance has arisen twice.

In the "Italian" fluvalinate-resistant mite strain, cross-resistance between fluvalinate and two closely related pyrethroids-flumethrin and acrinathrin – was found (Milani 1995). The presence of cross-resistance is not unexpected due to the similarity in the molecules of the active ingredient. Thus, these pyrethroids cannot be used as alternatives to fluvalinate where Apistan (tau-fluvalinate) fails in controlling Varroa (Elzen et al. 1999). Mites resistant to fluvalinate do not show an increased tolerance to coumaphos, but it is not known whether resistance to coumaphos increases tolerance to fluvalinate. Similarly, the mite *V. destructor* has developed resistance against other acaricides such as coumaphos and amitraz.

18.12.3 Coumaphos

Some *V. destructor* populations are resistant to coumaphos, a widely used organophosphate acaricide. The first reports concerning a modest but significant increase in the mites tolerance to coumaphos in some areas of northern Italy date back to 1997(Dalla et al. 1997). In 1991, populations of *V. destructor* with a LC_{50} increased by about 20-times were detected in northern Italy. Later, bee losses due to failure in the control of the mite with coumaphos were observed in other regions (Spreafico et al. 2001). More recently, coumaphos resistant populations were also reported in Switzerland (Martin 2004) and in the USA (Pettis 2004) only a few years after the commercialization of a gradual-release coumaphos-based anti-varroa treatment product.

18.12.4 Amitraz Resistance

In Croatia lack of efficacy of treatments with amitraz (Dujin et al. 1991) was reported and it seems that the most likely explanation is the presence of resistant mites. More recently, inefficacy in the field of an amitraz-based product has been observed in France and in the some states in the USA. In laboratory assays, mites from the USA (Martin 2004) showed an increased tolerance to amitraz (Elzen et al. 1999).

18.12.5 Resistance Management

The only way to halt the development of resistance to a certain product is by interrupting its use in the control strategy, and possibly that of all related compounds, for a certain period of time.

18.12.6 AFB

In the control of AFB, alternative to chemically synthesized antibiotics do exist and are viable. In countries in which the use of antibiotics is the only strategy against infective brood diseases by the honey bee colony, there is an urgent need to identify new control approaches. In a long-term strategy, sanitary practices and common sense are the best tools beekeepers can use to prevent the spread of AFB. Recognizing disease symptoms in honey bee colonies is an essential part of good beekeeping management. Early detection allows for prompt remedial action and helps in preventing serious diseases outbreaks and economic losses. Regular inspection of the brood combs, being thoroughly familiar with visual detection of brood diseases, reducing the exchange of hive equipment between hives and apiaries, replacing 20% of all brood frames each year, burning all the colonies with evident disease symptoms (or shaking bees onto foundations if the disease is limited to a few brood cells) are the most recommended practices to drastically reduce AFB incidence in apiaries.

18.12.7 Alternative Treatments Strategies

Many botanical compounds have been evaluated as control agents against AFB. One in vitro assay demonstrated the antimicrobial activity of linoleic acid (Carpana et al. 2005; Evans 2004; Faucon et al. 1995; Feldlaufer et al. 1993) and citrus seed extract and, to a lesser degree, that of the essential oils from *Cinnamomun zeylanicum*, *Alaysia triphylla* (lemon verbena), *Cymbopogon citrates* (lemongrass) and *Eugenia caryophyllata* (Eugenia). In field tests, combining treatment of infected hives with linoleic acid with brood elimination led to a significant reduction disease reoccurrence.

18.13 Management of Diseases

18.13.1 Breeding Queens for Disease Resistance

The internal environment of a honeybee colony (characterised by constant warm temperatures, high humidity and extensive contact between individuals) is highly conducive to the spread of parasites and pathogens (Milne 1983). Honeybees are attacked by various brood and adult bee diseases which are caused by viruses, bacteria and fungi. They include bacterial diseases such as American foul brood caused by *Bacillus larvae* and European foul brood by *Paenobacillus plutonius.* Chalkbrood disease is caused by *Ascosphaera apis* and stonebrood by *Aspergillus flavus.* Thai sac brood and sac brood are viral diseases. Nosema, Amoeba, bee paralysis, septicemia are the adult bee diseases. Besides, ectoparasitic mites such as *Varroa jacobsoni*, *Tropilaelaps clareae* and endoparasitic mite such as *Acarapis woodi* are the serious enemies of honeybees. Chalkbrood, a highly infectious disease that affects honeybee brood, is caused by ingestion of the heterothallic fungus *Ascosphaera api*s. The disease is characterized by the presence of mummified larvae (Gilliam et al. 1978; Mehr et al. 1976). While the disease is most apparent in summer, *A. apis* spores can survive throughout the year in honey, in stored pollen and in the gut of adult bees. These spores are highly resilient and may remain infectious for 15–38 years (Gilliam 1990). Frequent food and water sharing among nestmates contributes to the infectious *Nature* of the disease. However, chalkbrood is also stress related and certain predisposing physiological and environmental conditions are required for the development of infection (Gilliam 1978; Heath 1982a). Further, it is clear that some stocks are far less affected by *A. apis* than others (Gilliam 1986).

A more sustainable approach could be to focus efforts on breeding bees resistant to the disease, so as to reduce or eliminate the need for antibiotics (Abrol 1993). Direct resistance toward P.I. larvae by honey bee larvae was observed and selected for by Rothenbubhler and colleagues decades ago. While mechanisms of this resistance remain unclear, there is recent evidence that such resistance is both heritable and variable in bee populations. On a more practical level, the most important mechanism of resistant to AFB is hygienic behaviour in adult bees towards infected larvae. The methodology to test this characteristic (using liquid nitrogen or a freezer) is well described and easy to apply in the field. It would benefit the beekeeping industry to have hygienic lines of bees commercially available: the frequency of this trait would increase in the general bee population, increasing the chances that a queen could encounter drones that carry the trait and, finally, reduce the incidence of the disease, avoiding the antibiotic treatments.

Resistance to chalkbrood does occur in some colonies, and resistant bees can be selectively bred (Gilliam et al. 1983). Good nest cleaning – or “hygienic” behaviour, in which bees uncap and remove dead and diseased brood – inhibits the survival of the fungus *A. apis* (Gilliam et al. 1983; Spivak and Gilliam 1998a, b), and is correlated with resistance to chalkbrood (Gilliam et al. 1988; Milne 1983; Palacio et al. 2000).

Although other mechanisms have been demonstrated, hygienic behaviour remains the primary mechanism of resistance to chalkbrood and other brood diseases, such as American foulbrood (Gilliam et al. 1988; Spivak and Gilliam 1993, 1998a; Woodrow and Holst 1942). Shah (2000) reported that magnitude of hygienic behaviour was significantly correlated with the amount of TSBV killed larvae indicating that hygienic behaviour confers some resistance to TSBV in *A. cerana*. Interestingly, different colonies in the same apiary exhibited different levels of susceptibilities to infection thereby suggesting that resistance to TSBV not only depends upon hygienic behaviour but is a complex phenomenon involving other mechanisms as well.

Hygienic behavior is a mechanism of resistance to at least 2 diseases of honeybees: American foulbrood, caused by the bacterium *Paenibacillus larvae* (Woodrow and Holst 1942; Rothenbuhler 1964a, b); and chalkbrood caused by the fungus *Ascosphaera apis* (Massen ex Claussen) Olive and Spiltoir (Gilliam et al. 1983, 1988; Spivak and Downey 1998; Spivak and Reuter 1998). Hygienic behavior also is one mechanism of defense against the parasitic mite *Varroa jacobsoni* Oudemans (Spivak and Downey 1998). Hygienic behavior may also be a defense against

HBTM as well as other diseases. The original host of the varroa mite, *Apis cerana*, is known to remove mite infested pupae from the hive, and in doing so interrupts the mite's life cycle. *Apis cerana* is the original host of *Varroa jacobsoni*; Behavioural and physiological adaptations of *Apis cerana* keep infestations low (Peng et al. 1987). They effectively remove mites from bodies by self-grooming and perform grooming dance to attract other bees to remove mites. They bite, puncture and drop the mites outside the hive. Furthermore, they are equally effective in removing mites from the brood cells. *Apis mellifera* on the other hand has a limited capacity to detect and recognise mites. Grooming behaviour is also infrequent. This hygienic behavior is also seen in other species of honeybees. In European honeybees (*Apis mellifera*), *A. mellifera carnica* and *A. m. ligustica* are two examples of colonies that have shown a high level of hygienic behavior. Colonies of *A. m. ligustica* Spinola specifically bred for hygienic behavior removed significantly more infested pupae than non-hygienic colonies (Milne 1985; Spivak 1996; Spivak and Downey 1998).

Breeding honeybees for resistance to *Varroa* (*Varroa destructor*) has been a goal since Varroa began to move into the worldwide population of honeybees. At times this goal seems unreachable. However, we now know that resistance to *Varroa* does exist in honeybees. And it seems to exist in more than one form. The aim is to produce honeybees that are genetically resistant to Varroa, and we may define mite resistance in honeybees as a slower growth or a decline of the mite population in a colony.

18.14 Conclusions

Honeybees have evolved elaborate and diverse defence mechanisms to protect their brood, adults and food against a broad range of pests ranging from viruses to vertebrates. One such mechanism is the hygienic behaviour. Dead or parasitized brood are removed from their cells by hygienic workers who detect, uncap and remove them providing protection against brood diseases and tolerance to ectoparasitic mites *Varroa jacobsoni*. The resistance trait could readily be increased through a breeding programme using a field assay (freeze killed brood). The selected queens could be reared from each of these colonies by grafting worker larvae, which could be tested and re tested for their hygienic behaviour.

References

Abrol DP (1993) Honeybee – virus infection and immunity. Korean J Apic 8(2):116–118

Aizen MA, Garibaldi LA, Cunningham SA, Klein AM (2008) Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. Curr Biol 18:1572–1575

Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, Cox PA, Dalton V, Feinsinger P, Ingram M, Inouye D, Jones CE, Kennedy K, Kevan P, Koopowitz H, Medellin R, Medellin-Morales S, Nabhan GP, Pavlik B, Tepedino V, Torchio P, Walker S (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conserv Biol 12(1):8–17

Anderson DL, Morgan MJ (2007) Genetic and morphological variation of bee-parasitic *Tropilaelaps* mites (*Acari: Laelapidae*): new and re-defined species. Exp Appl Acarol 43(1):1–24

Arias MC, Sheppard WS (2006) Corrigendum to: phylogenetic relationships of honey bees (Hymenoptera: Apinae: Apini) inferred from nuclear and mitochondrial DNA sequence data (*Molec Phylogenet Evol* 2005 37(1):25–35). *Molec Phylogenet Evol* 40(1):315–315

Aristotle (384–350 B.C.) (1910) *Historia animalium*. Oxford University Press, Oxford

Aronstein KA, Murray KD (2010) Chalkbrood disease in honey bees. J Invertebr Pathol 103: S20–S29

Astuti M, Spreafico M, Colomobo M (1995) Indagine sullefficacia degli interventi di controllo di *Varroa jacobsoni* attuati nel 1993 in Lombardia. La selezione veterinaria 11:935–944

Baxter J, Eischen F, Pettis J, WilsonW T, Shimanuki H (1998) Detection of fluvalinate resistant varroamites in US honey bees. Am Bee J 138:291

Bogdanov S, Kilchenmann V, Imdorf A (1998) Acaricide residues in some bee products. J Apic Res 37(2):57–67

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington, DC

Burd M (1994) Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. Bot Rev 60:81–109

Carpana E, Ferroo A, Torresani A, Cassnelli C (2005) Valutazione di alcune sostanze naturali nella proflassi della peste Americana. Apoidea 2(1):15–21

Chen YP, Evans J, Feldlaufer M (2006) Horizontal and vertical transmission of viruses in the honeybee *Apis mellifera*. J Invertebr Pathol 92(3):152–159

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387(6630):253–260

Cox-Foster DL, Conlan S, Holmes EC, Palacios G, Evans JD, Moran NA, Quan PL, Briese T, Hornig M, Geiser DM, Martinson V, van Engelsdorp D, Kalkstein AL, Drysdale A, Hui J, Zhai JH, Cui LW, Hutchison SK, Simons JF, Egholm M, Pettis JS, Lipkin WI (2007) A metagenomic survey of microbes in honey bee colony collapse disorder. Science 318(5848):283–287

Currie RW, Pernal SF, Guzmán-Novoa E (2010) Honey bee colony losses in Canada. J Apic Res 49:104–106

Dalla VG, Lodesani M, Milani M (1997) Sviluppo di resistentza at fosforganici in *Varroa jacobsoni*. L'Ape nostra amica 1:610

Davis C, Ward W (2003) Control of chalkbrood disease with natural products. Publ. No. 03/107, Rural Industries Research and Development Corporation, Kingston ACT, Australia

Day MC (1991) Towards the conservation of aculeate Hymenoptera in Europe, Nature and Environment Series, No. 51, Council of Europe

Dujin T, Jovanovic V, Suvakov D, Milkovic Z (1991) Effect of using amitraz preparations for several years on the development of resistant strains of *Varroa jacobsoni*. Veterinarski Glasnik 45(11–12):851–855, 28

Ellis JD, Munn PA (2005) The worldwide health status of honey bees. Bee World 86:88–101

Elzen PJ, Baxter JR, Spivak M, Wilson WT (1999) Amitraz resistance in varroa: new discovery in North America. Am Bee J 139(5):362

Evans JD (2004) Transcriptional immune responses by honeybees larvae during invasion by the bacterial pathogen, *Paenibacillus larvae*. J Invertebr Pathol 85:105–111

Faucon JP, Drajnudel P, Fleche C (1995) Decrease in Apistan efficacy used against varroosis in the honey bee (*Apis mellifera*). Apidologie 26(4):291–296

Feldlaufer MF, Knox DA, Lusby WR, Shimanuki H (1993) Antimicrobial activity of fatty acids against *Bacillus larvae*, the causative agent of American foulbrood disease. Apidologie 24:95–101

Fluri P (1995) Tessin: efficacite de l' Apistan et du Bayvarol en regression. J Suisse Apic 6:198–199

Franck P, Garnery L, Solignac M, Cornuet JM (2000) Molecular confirmation of a fourth lineage in from the Near East. Apidologie 31(2):167–180

Fries I, Feng F, da Silva A, Slemenda SB, Pieniazek NJ (1996) *Nosema ceranae* n. sp. (Microspora, Nosematidae), morphological and molecular characterization of a microsporidian parasite of the Asian honey bee *Apis cerana* (Hymenoptera, Apidae). Eur J Protistol 32(3):356–365

Gilliam M (1978) Fungi. In: Morse RA (ed.) Honey bee pests, predators, and diseases. Comstock Pub. Associates a division of Cornell University Press, Ithaca, pp 78–101

Gilliam M (1986) Infectivity and Survival of the Chalkbrood Pathogen, *Ascosphaera*-Apis, in colonies of Honey-Bees, Apis-Mellifera. Apidologie 17(2):93–99

Gilliam M (1990) Chalkbrood disease of honey bees, *Apis mellifera*, caused by the fungus, *Ascosphaera api*s: a review of past and current research. In: 5th International colloquium on invertebrate pathology and microbial control, Adelaide, Australia, pp 398–402

Gilliam M, Vandenberg JD (1997) Fungi. In: Morse RA, Flottum K (eds.) Honey bee pests, predators and diseases, 3rd edn. A.I. Root Company, Medina, pp 81–110

Gilliam M, Taber S III, Bray Rose J (1978) Chalkbrood disease of honey bees, *Apis mellifera* L.: a progress report. Apidologie 9(1):75–89

Gilliam M, Taber S III, Richardson GV (1983) Hygienic behavior of honey bees in relation to chalkbrood disease. Apidologie 14(1):29–39

Gilliam M, Taber S III, Lorenz BJ, Prest DB (1988) Factors affecting development of chalkbrood disease in colonies of honey bees, *Apis mellifera*, fed pollen contaminate *Ascosphaera api*s. J Invertebr Pathol 52:314–325

Gregory PG, Evans JD, Rinderer T, de Guzman L (2005) Conditional immune-gene suppression of honeybees parasitized by *Varroa* mites. J Insect Sci 5(7):1–5

Griggs D (1993) The world food problem. Blackwell Publishers, Oxford

Hale PJ, Menapace DM (1980) Effect of time and temperature on the viability of *Ascosphaera apis*. J Invert Pathol 36:429–430

Harbo JR, Harris JW (2005) Suppressed mite reproduction explained by the behaviour of adult bees. J Apicult Res 44(1):21–23

Heath LAF (1982a) Development of chalk brood in a honeybee colony: a review. Bee World 63: 119–135

Heath LAF (1982b) Development of chalk brood in a honey bee colony: a review. Bee World 63:119–130

Heath LAF (1982c) Chalk brood pathogens: a review. Bee World 63:130–135

Hendrix SD (1994) Effects of population size on fertilization, seed production, and seed predation in two prairie legumes. North Am Prairie Conf Proc 13:115–119

Higes M, Martin R, Meana A (2006) *Nosema ceranae*, a new microsporidian parasite in honeybees in Europe. J Invertebr Pathol 92(2):93–95

Jean-Prost P, Le Conte Y (2005) Apiculture. Connaître l'abeille – conduire le rucher. Lavoisier, Paris, 698 pp

Johnson R (2007) Recent honey bee colony declines. Congressional Research Service Report for Congress. Available at: www.fas.org/sgp/crs/misc/RL33938.pdf (Accessed on 7 May 2008)

Kapil RP, Jain KL (1980) Biology and utilization of insect pollinators for crop production. Final technical report PL-480 Project, Haryana Agricultural University, Hisar, India, p 12

Kevan PG, Plowright RC (1995) Impact of pesticides on forest pollination. In: Armstrong JA, Ives WGH (eds) Forest insect pests in Canada. Natural Resources Canada, Canadian Forest Service, Science and Sustainable Development Directorate, Ottawa, pp 607–618

Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc Roy Soc Lond B Biol Sci 274(1608):303–313

Kloet GS, Hincks WD (eds.) (1978) A check list of British insects. In: Handbooks for the identification of British Insects, Second edition. Part 4. Hymcnoptera. Royal Entomological Society of London

Korpela S (1999) Resistance towards Apistan in Varroa mites detected in Finland – a challenge for beekeepers. Mehilainen 16:42–46

Le Conte Y, de Vaublanc G, Crauser D, Jeanne F, Rousselle J-C, Bécard J-M (2007) Honey bee colonies that have survived *Varroa destructor*. Apidologie 38:1–7

Lodesani M, Cecilia C (2005) Limits of chemotherapy in beekeeping: development o resistance and the problem of residues. Bee World 86:102–109

Lodesani M, Olombo M, Spreafico M (1995) Ineffectiveness of Apistan treatment against the mite *Varroa jacobsoni* Oud. in several districts of Lombardy (Italy). Apidologie 26:67–72

Martel AC, Zegganea S, Drajnudela P, Faucona JP, Auber M (2006) Tetracycline residues in honey after hive treatment. Food Addit Contam A 23:265–273

Martin SJ (2004) Acaricide (pyrethroid) resistance in *Varroa destructor*. Bee World 85:67–72

Mayer WB, Turner BLI (1992) Human population growth and global land use/cover change. Ann Rev Ecol Syst 23:39–61

McKee B (2003) Prevention of residues in honey: a future perspective. Apiacta 38:173–177

Mehr Z, Menapace DM, Wilson WT, Sackett RR (1976) Studies on the initiation and spread of chalkbrood within an apiary. Am Bee J 116(6):266–268

Michener C (2000) The bees of the world. Johns Hopkins University Press, Baltimore

Milani N (1995) The resistance of *Varroa jacobsoni* Oud. to pyrethroids: a laboratory assay. Apidologie 26:415–429

Milani N (1999) The resistance of *Varroa jacobsoni Oud.* to acaricides. Apidologie 30:229–234

Milne CPJ (1983) Honey bee (Hymenotpera: Apidae) hygienic behavior and resistance to chalkbrood. Ann Entomol Soc Am 76:384–387

Milne CPJ (1985) Estimates of the heritabilities of and genetic correlation between two components of honey bee (Hymenoptera: Apidae) hygienic behaviour: uncapping and removing. Ann Entomol Soc Am 78(6):841–844, 26

Morse RA, Flottum K (eds) (1997) Honey bee pests, predators and diseases, 3rd edn. A.I. Root Company, Medina

Mozes-Koch R, Slabezki Y, Efrat H, Kalev H, Kamer Y, Yakobson BA, Dag A (2000) First detection in Israel of fluvalinate resistance in the varroa mite using bioassay and biochemical methods. Exp Appl Acarol 24:35–43

Nabhan GP, Fleming T (1993) The conservation of mutualism. Conserv Biol 7:457–462

Navajas M, Migeon A, Alaux C, Cros-Arteil S, Martin-Magniette MM, Robinson GE, Evans JD, Crauser D, Neumann P, Carreck C (2010) Honey bee colony losses: a global perspective. J Apic Res 49:1–6

Neumann P, Carreck C (2010) Honey bee colony losses: a global perspective. J Apic Res 49:1–6

Oldroyd BP (1999) Co-evolution while you wait: *Varroa jacobsoni*, a new parasite of western honeybees. Trends Ecol Evol 14(8):312–315

Oldroyd BP (2007) What's killing American honey bees? PLoS Biol 5(6):e168. doi:10.1371/journal.pbio.0050168

O'Toole C (1993) Diversity of native bees and agro ecosystems. In: LaSalle J, Gauld ID (eds) Hymenoptera and biodiversity. CAB International, Wallingford, pp 169–196

O'Toole C (1994) Who cares for solitary bees? In: Forage for bees in an agricultural landscape, (ed A. Metheson), pp 47–56. International Bee Research Association, Cardiff, UK

Palacio MA, Figini EE, Ruffinengo SR, Rodriguez EM, del Hoyo ML, Bedascarrasbure EL (2000) Changes in a population of *Apis mellifera* L. selected for hygienic behaviour and its relation to brood disease tolerance. Apidologie 31:471–47

Parker FD, Potter HW (1974) Methods of transferring and establishing the alkali bee. Environ Entomol 3(5):739–743

Peeters TMJ, Raemakers IP, Smit J (1999) Voorlopige atlas van de Nederlandse bijen (Apidae). European Invertebrate Survey- Nederland, Leiden press, Leiden

Peng CYS, Fang YZ, Xu SY, Ge LS (1987) The resistance mechanism of the Asian honey bee *Apis cerana* Fabr. to an ectoparasitic mite, *Varroa jacobsoni* Oudemans. J Invertebr Pathol 49:54–60

Pettis JS (2004) A scientific note on *Varroa destructor* resistance to coumaphos in the United States. Apidologie 35:91–92

Pettis J, Vanengelsdorp D, Cox-Foster D (2007) Colony collapse disorder working group pathogen sub-group progress report. Am Bee J 147(7):595–597

Pimentel D, Wilson C, McCullum C, Huang R, Dwen P, Flack J, Tran Q, Saltman T, Cliff B (1997) Economic and environmental benefits of biodiversity. Bioscience 47:747–757

Prescott-Allen R, Prescott-Allen C (1990) How many plants feed the world. Conserv Biol 4: 365–374

Rothenbuhler WC (1964a) Behavior genetics of nest cleaning in honey bees I. Responses of four inbred lines to disease-killed brood. Anim Behav 12:578–583

Rothenbuhler WC (1964b) Behavior genetics of nest cleaning in honey bees IV. Response of F1 and backcross generations to disease-killed brood. Am Zool 4:111–112

Roubik DW (1995) Pollination of cultivated plants in the tropics, Rome, FAO, Agricultural Services Bulletin Number 118

Ruttner F (1988) Biogeography and taxonomy of honeybees. Springer, New York

Sammataro D, Gerson U, Needham G (2000) Parasitic mites of honey bees: life history, implications, and impact. Annu Rev Entomol 45:519–548

Schwenninger HR (1999) Die Wildbienen Stuttgarts Verbreitung, Gefährdung und Schutz (*Schriftenreihe des Amtes für Umweltschutz, 5, Landeshauptstadt Stuttgart Umweltschutz- und Ordnungsreferat, Amt für Umweltschutz, Abteilung Umweltplanung, ökologische Grundlagen und Naturschutz*)

Shah TA (2000) Hygenic behaviour in relation to thai sac brood virus disease in *Apis cerana*. Indian Bee J 62(1–2):35–40

Solignac M, Cornuet JM, Vautrin D, Le Conte Y, Anderson D, Evans J, Cros-Arteil S, Navajas M (2005) The invasive Korea and Japan types of *Varroa destructor*, ectoparasitic mites of the Western honeybee (*Apis mellifera*), are two partly isolated clones. Proc Roy Soc Lond B Biol Sci 272(1561):411–419

Southwick EE, Southwick L Jr (1992) Estimating the economic value of honeybees (Hymenoptera: Apidae) as agricultural pollinators in the United States. J Econ Entomol 85(3):621–633

Spivak M (1996) Honeybee hygienic behaviour and defense against *Varroa jacobsoni*. Apidologie 27:245–260

Spivak M, Downey D (1998) Field assays for hygienic behavior in honey bees (Apidae: Hymenoptera). J Econ Entomol 91:64–70

Spivak M, Gilliam M (1993) Facultative expression of hygienic behaviour of honey bees in relation to disease resistance. J Apic Res 32(3/4):147–157

Spivak M, Gilliam M (1998a) Hygienic behaviour of honey bees and its application for control of brood diseases and varroa–Part II. Studies on hygienic behaviour since the Rothenbuhler era. Bee World 79(4):169–186

Spivak M, Gilliam M (1998b) Hygienic behaviour of honey bees and its application for control of brood diseases and varroa. Part I. Hygienic behaviour and resistance to American foulbrood. Bee World 79(3):124–134

Spivak M, Reuter GS (1998) Honey bee hygienic behavior. Am Bee J 138(4):283–286

Spreafico M, Eordegh FR, Bernardinelli I, Colombo M (2001) First detection of strains of Varroa destructor resistant to coumaphos. Apidologie 32:49–55

Suzan H, Nabhan GP, Patten DT (1994) Nurse plant and floral biology of a rare night-blooming cereus, *Peniocereus striatus* (Brandegee) Buxbaum. Conserv Biol 8:461–470

Svensson BG, Erlandsson S, Janzon L-Å (1990) Catalogus Insectorum Suecidae: Hymenoptera, Apoidea: 2. Andrenidae and Halictidae. Entomologisk Tidskrift 111:47–52

Tentcheva D, Gauthier L, Zappulla N, Dainat B, Cousserans F, Colin ME, Bergoin M, Tentcheva D, Gauthier L, Zappulla N, Dainat B, Cousserans F, Colin ME, Bergoin M (2004) Prevalence and seasonal variations of six bee viruses in *Apis mellifera* L. and *Varroa destructor* mite populations in France. Appl Environ Microbiol 70(12):7185–7191

Thompson M, Brown MA, Ball RF, Bew MH (2002) First report of *Varroa destructor resistance to pyrethroids in the U.K.* Apidologie 33:537–546

Torchio PE (1963) A chalcid was parasite of the alfalfa leaf-cutting bee. Utah Agr Expt Sta Farm Home Sci 24:70–71

Torchio PE (1970) The biology of sapyga pumila cresson and its importance as a parasite of the alfalfa leafcutter bee megachile rotundata (Fabricius). In the indispensable pollinators, ark. Agr Ext Serv Misc Pub 127:84–88

Torchio P (1972) *Sapyga pumila* Cresson, a parasite of *Megachile rotundata* (Hymenoptera: Sapygidae, Megachilidae) II. Methods for control. Melanderia 10:23–30

USDA-ARS (1991) Pollination workshop proceedings. Unpublished, Denver, CO

vanEngelsdorp D, Meixner MD (2010) A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. J Invertebr Pathol 103:S80–S95

Virgil (70-19 B.C.) (2002) Georgics IV (as translated by A.S. Kline). http://www.poetryintranslation.com/PITBR/Latin/VirgilGeorgicsIV.htm

Wang R, Liu Z, Dong K, Elzen PJ, Pettis J, Huang ZY (2002) Association of novel mutation in a sodium channel gene with fluvalinate resistance in the mite *Varroa destructor*. J Apic Res 40:17–25

Washitani I, Osawa R, Namai H, Niwa M (1994) Patterns of female fertility in heterostylous *Primula sieboldii* under severe pollinator limitation. J Ecol 82:571–579

Waters ND (1971) Insect enemies of the alfalfa leaf-cutter bee and their control. p 4. University of Idaho current information series 163

Westrich P (1989) Die Wildbienen Baden-Württembergs. Allgemeiner Teil: Lebensräume, Verhalten, Ökologie und Schutz, Verlag Eugen Ulmer, Stuttgart, Germany

Westrich P (1996) Habitat requirements of central European bees and the problems of partial habitats. In: Matheson A et al (eds) The conservation of bees. Academic, London/San Diego, pp 1–16

Whitfield CW, Behura SK, Berlocher SH, Clark AG, Johnston JS, Sheppard WS, Smith DR, Suarez AV, Weaver D, Tsutsui ND (2006) Thrice out of Africa: ancient and recent expansions of the honey bee, *Apis mellifera*. Science 314:642–645

Williams IH (1996) Aspects of bee diversity and crop pollination in the European Union. In: Matheson A, Buchmann SL, Toole CO', Westrich P, Williams IH (eds) The conservation of bees. Linnean society symposium series No. 18. Academic, London, pp 63–80

Woodrow AW, Holst EC (1942) The mechanism of colony resistance to American foulbrood. J Econ Entomol 35(3):327–330

Yang X, Cox-Foster DL (2005) Impact of an ectoparasite on the immunity and pathology of an invertebrate: evidence for host immunosuppression and viral amplification. Proc Natl Acad Sci USA 102(21):7470–7475

Yang X, Cox-Foster D (2007) Effects of parasitization by *Varroa destructor* on survivorship and physiological traits of *Apis mellifera* in correlation with viral incidence and microbial challenge. Parasitology 134:405–412

Chapter 19
Consequences of Introduced Honeybees Upon Native Bee Communities

Abstract Biological invasions represent both an increasingly important applied problem and a tool for gaining insight into the structure of ecological communities. Although competitive interactions between invasive and native species are considered among the most important mechanisms driving invasion dynamics, such interactions are in general poorly understood. The European honey bee (*Apis mellifera*) is a widespread and economically important invader that now has a near-global distribution long suspected to competitively suppress many native bee species. Besides, various bumblebees (*Bombus* sp.), the alfalfa leafcutter bee *Megachile rotundata*, and various other solitary species have been introduced to countries far beyond their home range. Possible negative consequences of these introductions include: competition with native pollinators for floral resources; competition for nest sites; co-introduction of natural enemies, particularly pathogens that may infect native organisms; pollination of exotic weeds; and disruption of pollination of native plants. Interspecific competition for a limited resource can result in the reduction of survival, growth and/or reproduction in one of the species involved. As the impact of honey bees on native bees depends on the resource quality and quantity, it is recommended to assess the habitat quality in relation to its fauna by experts before any introduction of bee hives to deduce the number of hives, which can be introduced with a minimum impact. Thomson (*Ecology* 85:458–470, 2004) reported that *Bombus occidentalis* colonies exposed to competition with Apis experienced increased nectar scarcity and responded by reallocating foragers from pollen to nectar collection, resulting in lowered rates of larval production. These results provide evidence that Apis competitively suppresses a native social bee known to be an important pollinator, with the potential for cascading effects on native plant communities. Likewise introduction of *Apis mellifera* eliminated *Apis cerana japonica* in China and Japan and *Apis cerana indica* in Indian subcontinent including India, Pakistan, Nepal, Bangladesh and other neighbouring countries. How Apis influences native communities is of particular interest in light of both growing concerns over declines of many native pollinator species and uncertainty about the implications of disease-driven Apis declines and the spread of Africanized Apis strains.

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Negative impacts of exotic bees need to be carefully assessed before further introductions are carried out.

19.1 Introduction

The devastating impacts that some exotic organisms have wreaked on native ecosystems surely ought to have taught us a lesson as to the perils of allowing release of alien species. The introduction of Nile perch to Lake Victoria, and of cane toads, prickly pear, rabbits, foxes, and cats among numerous others to Australia, are perhaps some of the best known examples, but they constitute only the tip of the iceberg. Australia alone had 24 introduced mammal species, 26 birds, 6 reptiles, 1 amphibian, 31 fish, more than 200 known invertebrates, and no less than 2,700 non-native plants at the last count (Alexander 1996; reviewed in Low 1999). A strong case can be made that exotic species represent the biggest threat to global biodiversity after habitat loss (Pimm et al. 1995; Low 1999). Whereas the threat posed by exotic species is now widely appreciated, exotic bees appear to have received disproportionately little attention. Bees are widely perceived to be beneficial, for their role in the pollination of crops and wildflowers and, in the case of the honeybee *Apis mellifera* (L.) (Apidae), for the production of honey. Because of these economic benefits there is reluctance to regard bees as potentially damaging to the environment. As long ago as 1872, Darwin stated that honeybees in Australia were "rapidly exterminating the small, stingless native bee." In fact the bee he refers to, presumably *Trigona carbonaria* Sm., is still abundant. However, almost no research was carried out upon the impact of honeybees until the 1980s, by which time they had long since become established on every continent except Antarctica.

In this chapter the information is reviewed on the extent to which the bees have been artificially distributed around the globe. Three bee species, the honeybee *A. mellifera*, the bumblebee *Bombus terrestris* (L.) (Apidae), and the alfalfa leafcutter bee *Megachile rotundata* (Fabr.), are of particular concern because their range has been considerably expanded owing to both deliberate and accidental releases. I examine the potential consequences of this range expansion.

The possible undesirable effects of exotic bees include:

1. Competition with native flower visitors for floral resources;
2. Competition with native organisms for nest sites;
3. Transmission of parasites or pathogens to native organisms;
4. Changes in seed set of native plants (either increases or decreases);
5. Pollination of exotic weeds.

I examine evidence for each of these processes in turn. Reviewing studies to date serves to highlight the substantial gaps in our knowledge. I suggest further experimental approaches that may provide less equivocal answers as to the threat posed by these exotic organisms.

19.2 Distribution and Abundance of Introduced Bees

The honeybee is thought to be native to Africa, western Asia, and southeast Europe (Michener 1974), although its association with man is so ancient that it is hard to be certain of its origins. It has certainly been domesticated for at least 4,000 years (Crane 1990), and has been introduced to almost every country in the world. It is now among the most widespread and abundant insects on earth. The European strain of the honeybee appears to be adapted to temperate and Mediterranean climates, and flourishing feral populations occur throughout much of Asia, North America, the southern half of South America, and Australia. Major events in this range expansion include its introduction to North America in about 1620 (Buchmann and Nabhan 1996), to Australia in 1826 (Doull 1973), and to New Zealand in 1839 (Hopkins 1911). The African race, *A. mellifera scutellata* Lepeletier, is associated with tropical forests and savannas, and has spread throughout the neotropics and into North America following its introduction to Brazil in 1957.

More recently, bumblebees (*Bombus* spp.), a group whose natural range is largely confined to the temperate northern hemisphere, have been introduced to various countries to enhance crop pollination. New Zealand has four established *Bombus* species native to the U.K., *B. hortorum* (L.), *B. terrestris, B. subterraneus* (L.), and *B. ruderatus* (F.), following introductions in 1885 and 1906 intended to improve pollination of red clover, *Trifolium repens* (Hopkins 1914). *B. hortorum* and *B. subterraneus* have restricted distributions within New Zealand, whereas *B. terrestris* and *B. ruderatus* have become ubiquitous (Macfarlane and Gurr 1995). *B. terrestris* spread into Israel in the 1960s (Dafni and Shmida 1996), perhaps as a result of the presence of introduced weeds. This species has also become established in the wild in Japan following escapes from commercial colonies used for pollination in glass houses (Dafni 1998). Most recently, *B. terrestris* arrived in Hobart, Tasmania, in 1992, perhaps accidentally transported in cargo, and has since spread out to occupy a substantial portion of the island (Buttermore 1997; Stout and Goulson 2000; Hingston et al. 2002). *B. ruderatus* was introduced to Chile in 1982 and 1983 for pollination of red clover (Arretz and Macfarlane 1986), and by 1994 had spread to Argentina (Abrahamovich et al. 2001).

The only other group of bees to have been deliberately redistributed around the globe in substantial numbers are the Megachilidae. Perhaps because of the importance of alfalfa as a crop in the United States, a plant which is not adequately pollinated by honeybees, this country has shown particular enthusiasm for introducing exotic pollinators. The most widespread is *M. rotundata*, a native of Eurasia that appeared in North America in the 1930s, and which is now widely used commercially for pollination of alfalfa (Bohart 1972). A range of other species have been imported to pollinate various crops, including *Osmia cornuta* Latr. from Spain for pollination of almonds (Torchio 1987), *Osmia cornifrons* (Radoszkowski) from Japan for pollination of fruit trees (Batra 1979), *Osmia coerulescens* (L.) from Europe for pollination of red clover (Parker 1981), and *Megachile apicalis* Spinola from Europe for pollination of alfalfa (Cooper 1984; Stephen 1987). Furthermore, species have been moved within the United States and established in regions far from their home ranges; *Osmia ribifloris biedermannii* Michener from the west coast has been released in Maine to pollinate blueberries (Stubbs et al. 1994). At least three exotic Megachilidae are now established in California, *M. apicalis*, *M. rotundata*, and *M. concinna* (Smith) (Frankie et al. 1998), and *M. rotundata* even occurs in the Everglades National Park, Florida (Pascarella et al. 1999). New introductions continue to occur; for example *M. sculpturalis* Smith, a native of China and Japan was recently recorded in North Carolina (Mangum and Brooks 1997).

The fate of some deliberate introductions is not known. For example *Chalicodoma nigripes* from Egypt and *Pithitis smaragulda* F. from India were introduced to the United States in the 1970s for pollination of alfalfa, but to my knowledge it is not known if these species became established (Daly et al. 1971; Parker et al. 1976). One megachilid, *M. rotunda* was introduced to New Zealand in 1971 for pollination of alfalfa and flourished (Donovan 1975). Recently this species also became established in southern Australia (Woodward 1996). One final bee that has expanded its range with the deliberate help of man is the alkali bee, *Nomia melanderi* (Cockerell) (Halictidae). This native of North America was introduced to New Zealand in 1971 for pollination of alfalfa and has become established at restricted sites (Donovan 1975, 1979). A summary of the distribution of exotic bee species is given in Table 19.1.

Bees are a large group (about 20,000 species are known), but little is known about basic aspects of the ecology of most species. For the majority we have only a rudimentary knowledge of their natural distribution. It is almost certain that other species have been transported by man to new locations, but that these events have gone unrecorded.

Both *B. terrestris* and *A. mellifera* are social species, with colonies attaining sizes of up to 500 and 50,000 individuals, respectively. In their natural range, nest density estimates for *A. mellifera* vary from 0.5 to >70 nests/km^2 in Europe (Visscher and Seeley 1982; Oldroyd et al. 1995) and 4.2 nests/km^2 in Botswana (McNally and Schneider 1996). Where honeybees have been introduced, estimates include 50–150 nests/km^2 in southern Australia (Oldroyd et al. 1997) and 6–100 nests/km^2 for Africanized bees in the neotropics (Roubik 1983, 1988; Otis 1991). Densities are no doubt greatly influenced by variation in habitat quality and availability of nest sites. Given the large numbers of workers per nest, even the lowest estimates indicate substantial densities of foragers. No information is available on densities of nests of *B. terrestris*, either within their natural range or where they are introduced, because they are notoriously hard to locate.

In general both honeybees and *B. terrestris* appear to maintain higher population densities than semisocial and solitary species across a broad range of habitats and geographic regions (South Australia, Pyke and Balzer 1985; California, Dobson 1993; Brazil, Wilms et al. 1997; New Zealand, Donovan 1980; Israel, Dafni 1998). It is often impossible to determine how large the equilibrium feral population of honeybees would be because wild populations are supplemented by swarms from commercial hives, and foragers observed in the field are likely to originate from both managed and wild colonies. Little information is available on populations of

Table 19.1 The distribution and origins of known exotic bee species

Species	Family	Introduced range	Origin	References
Apis mellifera	Apidae	North and South America, Eastern Asia, Australia, and New Zealand	Eastern Europe, Western Asia, Africa	Hopkins (1911), Doull (1973) and Buchmann and Nabhan (1996)
Apis mellifera	Apidae	India	Italy	Atwal (1962)
Bombus terrestris	Apidae	Israel, Japan, New Zealand, Tasmania, Europe	Europe	Hopkins (1914), Dafni and Shmida (1996), Buttermore (1997), Dafni (1998) and Stout and Goulson (2000)
Bombus ruderatus	Apidae	New Zealand, Chile, Argentina	Europe	Hopkins (1914) and Arretz and Macfarlane (1986)
Bombus hortorum	Apidae	New Zealand, Iceland	Europe	Hopkins (1914) and Prys-Jones et al. (1981)
Bombus lucorum	Apidae	Iceland	Europe	Prys-Jones et al. (1981)
Bombus subterraneus	Apidae	New Zealand	Europe	Hopkins (1914b)
Megachile rotundata	Megachilidae	North America, Australia, New Zealand	Eurasia	Bohart (1972), Donovan (1975), Woodward (1996), Frankie et al. (1998) and Pascarella et al. (1999)
Megachile apicalis	Megachilidae	United States	Europe	Cooper (1984) and Stephen (1987)
Megachile concinna	Megachilidae	California	Europe	Frankie et al. (1998)
Megachile sculpturalis	Megachilidae	North Carolina	China, Japan	Mangum and Brooks (1997)
Osmia coerulescens	Megachilidae	United States	Europe	Parker (1981)
Osmia cornifrons	Megachilidae	United States	Japan	Batra (1979)
Osmia cornuta	Megachilidae	United States	Europe	Torchio (1987)
Osmia ribifloris biedermannii	Megachilidae	Maine Southwestern	United States	Stubbs et al. (1994)
Pithitis smaragulda	Megachilidae	United States	India	Daly et al. (1971)
Chalicodoma nigripes	Megachilidae	United States (establishment unknown)	Egypt	Parker et al. (1976)
Nomia melanderi	Halictidae	New Zealand	North America	Donovan (1975, 1979)

the introduced Megachilidae, but one study suggests that these solitary species do not attain high densities in Australia (Woodward 1996).

Because introduced bees are widespread, any deleterious effects of their presence are now occurring on a large scale. The abundance of honeybees and bumblebees makes such effects more probable. Some researchers have concluded that competition with native organisms is inevitable (Roubik 1978; Roubik and Buchmann 1984; Sugden et al. 1996) in the temperate climates where they naturally occur. Thus, in terms of the time of year at which they are active, they overlap with almost all other flower visitors with which they co-occur.

19.3 Competitions with Native Organisms for Floral Resources

Demonstration of niche overlap does not prove that competition is occurring. In fact it is notoriously difficult to provide unambiguous evidence of competition, particularly in mobile organisms. Because of this there is no clear agreement as to whether non-native bees have had a significant negative impact upon native pollinator populations (compare Robertson et al. 1989; Buchmann and Nabhan 1996; Sugden et al. 1996 with Butz Huryn 1997).

The majority of studies to date have been carried out in the neotropics, stimulated by the arrival of Africanized honeybees, and in Australia, where awareness of the possible impacts of introduced species is unusually high. Australia also has a large native bee fauna of over 1,500 species (Cardale 1993) that is arguably the most distinctive in the world (Michener 1965). Most work has focused on the effects of honeybees.

19.4 Effects on Foraging Behavior

Each honeybee nest harvests 10–60 kg/year of pollen and also requires 20–150 kg/year of honey (Stanley and Liskens 1974; Roubik et al. 1984; Buchmann 1996). Crude extrapolation from the range of nest densities that have been recorded suggests that honeybees may gather 5–9,000 kg pollen and 10–22,500 kg honey km^2/year. In New Zealand, 8,000 tons of honey is harvested from about 227,000 commercial hives every year (this does not take into account honey used by the bees themselves, or that gathered by feral colonies) (Donovan 1980). I am unaware of any estimates of the total amounts of pollen or nectar available in natural habitats over a year, and it no doubt varies enormously, but common sense suggests that honeybees must use a substantial proportion of the available floral resources.

Honeybees commonly deter other bee species from foraging on the richest sources of forage (Wratt 1968; Eickwort and Ginsberg 1980; Roubik 1978, 1980, 1996a, b; Wilms and Wiechers 1997; Gross 2001) (although in one instance the converse had been reported, Menke 1954). Native organisms are often displaced to less profitable forage (Holmes 1964; Schaffer et al. 1979, 1983; Ginsberg 1983). In Panama, the presence of Africanized honeybees effectively eliminated foraging peaks of Meliponine bees because these native species were prevented from visiting their preferred sources of forage; as a result, the rate at which pollen was accrued in the nest was lower (Roubik et al. 1986). Displacement of native organisms has been attributed to the larger size of honeybee when compared to the majority of bee species (Roubik 1980), but is not necessarily size related. For example, the presence of honeybees has been found to deter foraging by hummingbirds (Schaffer et al. 1983). Similarly, in a year when honeybees were naturally scarce, native bumblebees in Colorado were found to expand their diet breadth to include flowers usually visited mainly by honeybees (Pleasants 1981).

Hingston and McQuillan (1999) examined interactions between bumblebees and native bees in Tasmania and concluded that native bees were deterred from foraging by the presence of bumblebees, perhaps because bumblebees depressed availability of floral resources. Honeybees have been shown to depress availability of nectar and pollen (Paton 1990, 1996; Wills et al. 1990; Horskins and Turner 1999), which may explain why other flower visitors then choose to forage elsewhere. Most authors concur that honeybees are not particularly aggressive to other insects while foraging, so that impacts on other species occur primarily through exploitative competition (Schaffer et al. 1979, 1983; Thorp 1987; Roubik 1991). However, honeybees have been found to displace smaller species from flowers by physical disturbance (Gross and Mackay 1998). Honeybees do attack nests of other honey-storing species to steal the honey, a behavior that may have contributed to the decline of *Apis cerana* in Japan (Sakagami 1959).

Both honeybees and bumblebees begin foraging earlier in the morning than many native bee species (Corbet et al. 1993; Dafni and Shmida 1996; Horskins and Turner 1999). Honeybees are able to achieve this owing to their large size (compared to most bees) and also owing to heat retention within their large nests (Roubik 1989a, b). Bumblebees are able to begin foraging earlier still because of their great size and densely hairy body. It has been argued that depletion of nectar before native bees begin to forage may result in a significant asymmetry in competition in favor of these introduced species (Matthews 1984; Hopper 1987; Anderson 1989; Dafni and Shmida 1996; Schwarz and Hurst 1997).

Asymmetries in competition may also occur because of the ability of honeybees and bumblebees to communicate the availability and/or location of valuable food sources with nest mates, so improving foraging efficiency (von Frisch 1967; Dornhaus and Chittka 1999) (the majority of bee species are solitary, and each individual must discover the best places to forage by trial and error). Thus social species are collectively able to locate new resources more quickly, which again may enable them to gather the bulk of the resources before solitary species arrive (Roubik 1980, 1981; Schwarz and Hurst 1997).

Honeybees and bumblebees appear to be unusual in the distances over which they are capable of foraging. Honeybees are known to forage over 10 km from their nest, on occasion up to 20 km (Seeley 1985; Schwarz and Hurst 1997), and *B. terrestris* up to at least 4 km (Goulson and Stout 2001). Little is known of the foraging range of most other bee species, but those estimates that are available suggest that they are generally lower. For example *Melipona fasciata* travels up to 2.4 km (Roubik and Aluja 1983) and Trigonini over 1 km (Roubik et al. 1986). Solitary bee species are generally thought to travel only a few hundred meters at most (Schwarz and Hurst 1997).

Managed honeybee hives have further advantages over wild bee species; they are often given supplementary feeds when floral resources are scarce, and they are moved to track changing patterns of floral abundance. In this way populations of honeybees may be elevated far above those that could naturally persist in particular habitats.

Asymmetries in competition may not be stable, because the relative competitive abilities of bee species are likely to vary during the day according to temperature and resource availability, and are likely to vary spatially according to the types of flowers available (Corbet et al. 1995). The main exotic bees are large compared to most of the native species with which they might compete; *B. terrestris* weighs 109–315 mg (Prys-Jones 1982), and *A. mellifera* workers 98 § 2.8 mg (Corbet et al. 1995). They also have longer tongues than many native species, particularly in Australia where most native species are short tongued (Armstrong 1979). Large bees are at a competitive advantage in cool conditions because of their ability to maintain a body temperature considerably higher than the ambient air temperature.

They can thus forage earlier and later in the day than most smaller bees, and during cooler weather. Bees with longer tongues can also extract nectar from deeper flowers. However, large bees are not always at an advantage. The energetic cost of foraging is approximately proportional to weight (Heinrich 1979). Thus large bees burn energy faster. As nectar resources decline, the marginal rate of return will be reached more quickly by large bees. Also, long tongues are inefficient at handling shallow flowers. Thus large bees are likely to be at a competitive advantage early in the day and during cool weather, and they will be favored by the presence of deep flowers that provide them with a resource that other bees cannot access. But small bees with short tongues can forage profitably on shallow flowers even when rewards per flower are below the minimum threshold for large bees. Although in general honeybees and bumblebees are able to forage at cooler temperatures than native bees, there may be exceptions. The Australian native *Exoneura xanthoclypeata* is adapted for foraging in cool conditions (Tierney 1994). It has been argued that this species is specialized for foraging on (naturally) uncontested resources early in the day, and that this species may be particularly susceptible to competition with exotic bees that forage at the same time (Schwarz and Hurst 1997).

The outcome of interactions between exotic and native flower visitors depends upon whether floral resources are limiting. Resource availability is likely to vary greatly during the year as different plant species come into flower (Carpenter 1978). When an abundant or large plant flowers, it may provide a nectar flush. Competition is unlikely to occur during such periods (Tepedino and Stanton 1981). Overall, it seems probable that depression of resources by introduced bees is likely to have negative effects on native bee species, at least at some times of the year. To determine whether these effects are largely trivial (such as forcing native bees to modify their foraging preferences) or profound (resulting in competitive exclusion), population-level studies are necessary.

19.5 Evidence for Population-Level Changes

The only way to test unequivocally whether floral resources are limiting is to conduct experiments in which the abundance of the introduced bee species is artificially manipulated, and the population size of native species is then monitored. If populations are significantly higher in the absence of the introduced bee, then competition is occurring. Such experiments have proved to be exceedingly hard to accomplish. Excluding bees from an area is difficult. Within- and between-season variation is likely to be large, so such experiments need to be well replicated, with replicates situated many kilometers apart, and conducted over several years. No such study has been carried out.

An alternative approach, which is far easier but provides more equivocal data, is to correlate patterns of diversity of native bees with abundance of exotic bees, without manipulating their distribution. Aizen and Feinsinger (1994) found that fragmentation of forests in Argentina resulted in a decline in native flower visitors and an increase in honeybee populations. Similarly, Kato et al. (1999) studied oceanic islands in the northwest Pacific, and found that indigenous bees were rare or absent on islands where honeybees were numerous. On Mt Carmel in Israel, Dafni and Shmida (1996) reported declines in abundance of medium- and large-sized native bees (and also of honeybees) following arrival of *B. terrestris* in 1978. Conversely, Goulson et al. (2002) found no evidence for reduced abundance or diversity of native Tasmanian bees in areas colonized by *B. terrestris*, but did find that native bee abundance was considerably higher in the few sites where honeybees were absent. However, such studies can be criticized on the grounds that the relationship between exotic bee abundance and declining native bee populations (if found) need not be causative (Butz Huryn 1997). Increasing honeybee populations are often associated with increased environmental disturbance by man, which may explain declines in native bees.

Some researchers have attempted to manipulate numbers of introduced bees, either enhancing populations in experimental plots by placing hives within them, or conversely by remove hives from experimental plots in areas where hives have traditionally been placed. Areas without hives usually still have some honeybees, since there are likely to be some feral nests, and also because honeybees can forage over great distances. Replicates of the treatment without hives need to be sited many kilometers from replicates with hives to ensure that bees do not travel between the two, so many studies have been carried out without replication (e.g., Sugden and Pyke 1991). Despite these limitations, some interesting results have been obtained. Wenner and Thorp (1994) found that removal of feral nests and hives from part of Santa Cruz Island in California resulted in marked increases in numbers of native bees and other flower-visiting insects. Addition of honeybee hives caused the

Australian nectivorous bird *Phylidonyris novaehollandiae* to expand its home foraging range and to avoid parts of inflorescences favored by honeybees (Paton 1993), but a comparison of areas with and without hives found no difference in the density of this bird species (Paton 1995). Roubik (1978) found a decrease in abundance of native insects when he placed hives of the Africanized honeybee in forests in French Guiana. However, Roubik (1982a, 1983) found no consistent detrimental effects on brood size, honey, and pollen stores in nests of two Meliponine bee species in Panama when Africanized honeybee hives were placed nearby for 30 days.

Monitoring of numbers of native bee species using light traps over many years since the arrival of Africanized bee has not revealed any clear declines in abundance (Wolda and Roubik 1986; Roubik 1991; Roubik and Wolda 2001). Roubik (1996a, b) describes the introduction of Africanized honeybees to the neotropics as a vast experiment, but it is an experiment without replicates or controls, so interpreting the results is difficult. Sugden and Pyke (1991) and Schwarz et al. (1991, 1992a, b) failed to find clear evidence for a link between abundance of honeybees and reproductive success of anthophorid bees belonging to the genus *Exoneura* in Australia in experiments in which they greatly enhanced honeybee numbers at experimental sites.

However, the native species that they studied are themselves polylectic (Schwarz and Hurst 1997). As such they are the species least likely to be affected by competition. The majority of bee species are more specialized; in a review of data for 960 solitary bee species, Schemske (1983) found that 64% gathered pollen from only one plant family, often only one genus. For example, some Australian halictine bees have only been recorded on flowers of *Wahlenbergia* sp. (Michener 1965). Very little is known about such species, and no studies have been carried out to determine whether they are adversely affected by exotic bees (Schwarz and Hurst 1997). Also, the Australian studies of Sugden and Pyke (1991) and Schwarz et al. (1991, 1992a,b) were carried out in flower-rich heathlands; floral resources are more likely to be limiting in arid regions of Australia (Schwarz and Hurst 1997), and these areas often contain the highest native bee diversity (Michener 1979; O'Toole and Raw 1991). The *Exoneura* species studied in Australia had coexisted with honeybees for 180 years, so it is not surprising that they are not greatly affected by competition with this species. If there are species that are excluded by competition with exotic bees, honeybees in particular, there is no point looking for them in places where these bees are abundant. Unfortunately this leaves rather few places where they might occur. Overall, there is no indisputable evidence that introduced bees have had a substantial impact via competition with native species. Given the difficulties involved in carrying out rigorous manipulative experiments, this should not be interpreted as the absence of competition. The abundance of exotic bees, the high levels of niche overlap, and evidence of resource depression and displacement of native pollinators, all point to the likelihood that competition is occurring. But we do not know whether such competition results (or resulted) in competitive exclusion. The best way to test for such competition is to carry out replicated experiments in which exotic bee numbers are manipulated and native pollinator numbers and reproductive success monitored over long periods. Ideally, such studies should target native species that are not generalists, and areas where floral resources are not abundant.

19.6 Competition for Nest Sites

Honeybees nest in cavities, usually in old trees, and there is clear potential for competition. Many other organisms, including bees, mammals, and birds use such cavities for shelter or for nesting. In managed woodland, old trees with cavities are often in short supply. Hence it seems likely that honeybees may compete with native organisms for these sites, but rigorous studies are scarce. Both Oldroyd et al. (1994) and Moller and Tilley (1989) found that nesting holes were not in limiting supply in particular forests in Victoria and New Zealand, respectively. However, both studies were confined to small geographic areas, and it is hard to draw any general conclusions without further work. *B. terrestris* generally nests in existing cavities below ground, often using abandoned rodent holes (Donovan and Wier 1978), and spaces beneath man-made structures such as garden sheds (personal observation). To my knowledge there have been no studies to determine whether such sites are used by native organisms in any of the countries to which this species has been introduced, although Donovan (1980) considered it unlikely that bumblebees compete with native bee species for nest sites in New Zealand. Megachilidae nest in small cavities in wood. Donovan (1980) reported that nests sites used by *M. rotundata* overlap with those used by native bees belonging to the Hylaeinae, and also with mason wasps and spiders in New Zealand. However, it is not known whether availability of sites is limiting. Barthell and Thorp (1995) found that introduced *M. apicalis* in California aggressively usurp native species from nests sites, and concluded that competition was likely. However, subsequent work suggested that differences in habitat preferences between native and introduced species, and an abundance of nest sites may mean that competition is weak or absent (Barthell et al. 1998). Nothing is known of niche overlap in nesting requirements between introduced Megachilidae and native species elsewhere in North America or in Australia.

19.7 Transmission of Parasites or Pathogens to Native Organisms

A great deal is known about the pathogens and parasites of honeybees, and to a lesser extent bumblebees and leafcutter bees, since these species are of economic importance. Bees and their nests support a diverse microflora including pathogenic, commensal and mutualistic organisms (Gilliam and Taber 1991; Goerzen 1991; Gilliam 1997). Many pathogens are likely to have been transported to new regions with their hosts, particularly where introductions were made many years ago when awareness of bee natural enemies was low. Thus for example the honeybee diseases chalkbrood, caused by the fungus *Ascosphaera apis*, foulbrood, caused by the bacteria *Paenibacillus larvae*, the microsporidian *Nosema apis*, and the mite *Varroa destructor* now occur throughout much of the world. Hive beetles, *Aethina tumida*, were recently transported from Africa to North America, where they are proving to be serious pests of commercial honeybee colonies (Evans et al. 2000). Similarly, bumblebees in

New Zealand are host to a parasitic nematode and three mite species, all of which are thought to have come from the U.K. with the original introduction of bees (Donovan 1980). During more recent deliberate introductions of exotic bees, such as that of *N. melanderi* to New Zealand, care has been taken to eliminate pathogens or parasites before bees were released (Donovan 1979). However, parasites are easily overlooked. Queens of *Bombus ignitus* are currently sent from their native Japan to the Netherlands, where they are induced to found colonies. The colonies are then returned to Japan for commercial purposes. Goka et al. (2001) recently discovered that the returned colonies are infested with a European race of the tracheal mite *Locustacarus buchneri*. It is hard to exaggerate our ignorance of the natural enemies of most bee species, particularly their pathogens. We do not know what species infect them, or what the host ranges of these pathogens are. Very little is known of the susceptibility of native organisms to the parasites and pathogens that have been introduced with exotic bees. In a survey of natural enemies of native and introduced bees in New Zealand, Donovan (1980) concluded that no enemies of introduced bees were attacking native bees, but that the converse was true. A chalcidoid parasite of native bees was found to attack *M. rotundata* and, rarely, *B. terrestris*. One fungus, *Bettsia alvei*, which is a pathogen of honeybee hives elsewhere in the world was recorded infecting a native bee in New Zealand, but it is not known whether the fungus is also native to New Zealand. Indeed the natural geographic range of bee pathogens is almost wholly unknown. Some bee pathogens have a broad host range; for example, chalkbrood (*A. apis*), is also known to infect *A. cerana* (Gilliam et al. 1993) and the distantly related *Xylocopa californica* (Gilliam et al. 1994). The related chalkbrood fungus *Ascosphaera aggregata* is commonly found infecting *M. rotundata*; in Canada, where *M. rotundata* is an exotic species, this fungus infects the native bees *Megachile pugnata* Say (Goerzen et al. 1992) and *M. relativa* Cresson (Goerzen et al. 1990).

It seems likely that these few recorded instances of exotic bee pathogens infecting native species are just the tip of the iceberg, since so few studies have been carried out. As to whether these pathogens have had, or are having, a significant impact on native species, we do not know; if the introduction of a new pathogen were to lead to an epizootic in native insects, it would almost certainly go unnoticed. In other better known organisms, exotic pathogens have had disastrous impacts; for example the introduction of several crayfish species from North America has led to elimination of the native species *Astacus astacus* and *Austropotamobius pallipes* from large portions of Europe. The native species have little resistance to the exotic fungal pathogen *Aphanomyces astaci* that is carried by the introduced crayfish (Butler and Stein 1985). Studies of the incidence and identity of pathogen and parasite infestations of wild populations of native bees are urgently needed.

19.8 Effects on Pollination of Native Flora

Recently, concerns have been expressed that exotic bees may reduce pollination of native plants, or alter the population structure of these plants by mediating different patterns of pollen transfer to native pollinators (Butz Huryn 1997; Gross and Mackay 1998).

Efficient pollination requires a match between the morphology of the flower and that of the pollinator (reviews in Ramsey 1988; Burd 1994). If there is a mismatch, then floral rewards may be gathered without efficient transfer of pollen, a process known as floral parasitism (McDade and Kinsman 1980). Specialized obligate relationship between plants and pollinators do exist (reviewed in Goulson 1999) but are the exception (Waser et al. 1996). Most flowers are visited by a range of pollinator species, each of which will provide a different quality of pollinator service. The efficiency of honeybees as pollinators of native plants in Australia and North America was reviewed by Butz Huryn (1997). She concluded that honeybees provide an effective pollination service to the majority of the flower species that they visit, although they do act as floral parasites when visiting a small number of plant species such as *Grevillea X gaudichaudii* in Australia (Taylor and Whelan 1988) and *Impatiens capensis* and *Vaccinium ashei* in North America (Wilson and Thomson 1991; Cane and Payne 1988). Similar results have been found for honeybees visiting Jamaican flora (Percival 1974). That honeybees are effective pollinators of many plants, even ones with which they did not coevolve is not surprising. After all, they have been used for centuries to pollinate a broad range of crops. Thus pollination of the native Australian *Banksia ornata* was increased by the presence of honeybee hives (Paton 1995), and honeybees have proved to be as effective as native bees in pollinating wild cashews, *Anacardium occidentale* in South America (Freitas and Paxton 1998). However, their presence may result in reduced seed set of some native plants. Roubik (1996a, b) reported declining seed set in the neotropical plant *Mimosa pudica* when honeybees were the dominant visitors, compared to sites where native bees were the more abundant, while Aizen and Feinsinger (1994) found reduced pollination of a range of Argentinian plant species in areas where forests were fragmented and honeybees more abundant. Gross and Mackay (1998) demonstrated that honeybees were poor pollinators of the Australian native *Melastoma affine*, so that when honeybees were the last visitors to a flower, seed set was reduced. As Roubik (1996a, b) points out, if native pollinators are lost (be it through competition with exotic bees, habitat loss, or use of pesticides) then we cannot expect honeybees to provide an adequate replacement pollination service for all wild plants and crops.

No studies have yet been reported of the effects of exotic bumblebees on the seed set of native plants. *B. terrestris* has the potential to disrupt pollinator services in a different way. This bee species is known to rob flowers. When the structure of the flower renders the nectaries inaccessible, *B. terrestris* (and some other bee species) may use their powerful mandibles to bite through the base of the corolla (Inouye 1983). In this way they act as floral parasites, removing nectar without effecting pollination. In Tasmania they rob some bird-pollinated plants in this way (personal observation). The effects of this behavior are hard to predict. Robbers have been found to reduce the amount of reward available, resulting in decreased visitation rates by pollinators (McDade and Kinsman 1980) and a reduction in seed set (Roubik 1982b; Roubik et al. 1985; Irwin and Brody 1999). Robbing can damage floral tissues preventing seed production (Galen 1983). However, nectar robbing may have little influence on plant fecundity if nectar robbers also collect pollen and in doing so effect pollination, or if other pollinators are present (Newton and Hill 1983;

Arizmendi et al. 1995; Morris 1996; Stout et al. 2000). Some plants may actually benefit from the activity of nectar robbers by forcing legitimate foragers to make more long-distance flights hence increasing genetic variability through outcrossing (Zimmerman and Cook 1985).

A second possible detrimental effect of exotic bees is that they may alter the population structure by affecting a different pattern of pollen transport to native pollinators. In South Australia, Paton (1990, 1993) found that honeybees extracted more nectar and pollen from a range of flower species than did birds, the primary native pollinators. However, honeybees moved between plants far less than did birds, and so were less effective in cross-pollinating, resulting in decreased seed set. Several other studies have reported that interplant movement by honeybees is lower than that of other visitors (McGregor et al. 1959; Heinrich and Raven 1972, Silander and Primack 1978). Of course other pollinators often also move small distances, and it has been argued that honeybees are not unusual in this respect (Butz Huryn 1997). However, this is not true. Workers of social bees are unusual in that they are not constrained in their foraging behavior by the need to find mates, locate oviposition sites or guard a territory. In contrast, for example, butterflies intersperse visits to flowers with long patrolling flights in which they search for mates or oviposition sites (Goulson et al. 1997). Thus honeybees, bumblebees, and other social bees do tend to engage in fewer long flights than other species (Schmitt 1980; Waser 1982). The most obvious possible effect of exotic social bees in this respect is increased self-pollination, which could result in reduced seed set if the plant is self-infertile. Reduced interpatch pollen movement could result in reproductive fragmentation of plant populations. There are at present no data available on the impact of exotic bees on the genetic structure of plant populations. Clearly it is not possible to generalize as to the effects that exotic bees will have on seed set of native flowers. For some species they will provide effective pollination, for others they will not. Where native pollinators have declined for other reasons, for example as a result of habitat loss and fragmentation, exotic bees may provide a valuable replacement pollinator service for native flowers. Where exotic bees are floral parasites, the effect will depend on whether rates of parasitism are sufficient to deter native pollinators. Any change in seed set (including increases) of plant species within a community could lead to long-term ecological change, but such effects would be exceedingly hard to detect among the much larger environmental changes that are currently taking place.

19.9 Pollination of Exotic Weeds

As we have seen, both honeybees and bumblebees visit a broad range of flowers. They also appear to prefer to visit exotic flowers (Telleria 1993; Thorp et al. 1994). For example, in Ontario, 75% of pollen collected by honeybees was from introduced plants (Stimec et al. 1997). In New Zealand, *B. terrestris* has been recorded visiting 400 exotic plant species but only 19 native species (Macfarlane 1976). The three other introduced *Bombus* species also visit mainly introduced plants (Donovan 1980). In the highlands of New Zealand, honeybees rely almost exclusively on introduced plants for pollen during most of the season (Pearson and Braiden 1990). Introduced *Megachile rotunda* appear to feed exclusively on introduced plants in Australia (Woodward 1996).

Do visits by exotic bees improve seed set of weeds? In general, rather little is known of the pollination biology of non-native plants, and it is unclear whether inadequate pollination is commonly a limiting factor (Richardson et al. 2000). By virtue of their abundance and foraging preferences, exotic bees often make up a very large proportion of insect visits to weeds. For example in a site dominated by European weeds in Tasmania, honeybees and bumblebees were the major flower visitors and comprised 98% of all insect visits to creeping thistle, *Cirsium arvense*. In North America, honeybees increase seed set of the yellow star thistle, *Centaurea solstitialis* (Barthell et al. 2001) and are the main pollinators of two important weeds, purple loosestrife, *Lythrum salicaria* (Mal et al. 1992) and *Raphanus sativus* (Stanton 1987). Donovan (1980) reports that bumblebees are major pollinators of introduced weeds in New Zealand. It thus seems obvious and inevitable that exotic bees will prove to be important pollinators of various weeds (Sugden et al. 1996).

Remarkably, this view has been challenged. It is hard to agree with the conclusions of Butz Huryn and Moller (1995) that “Although honey bees may be important pollinators of some weeds, they probably do not contribute substantially to weed problems.” Butz Huryn (1997) argues that most weeds do not rely on insect pollination, either because they are anemophilous, self-pollinating, apomictic, or primarily reproduce vegetatively. This is undoubtedly true of some weed species.

For example of the 33 worst environmental weeds in New Zealand (Williams and Timmins 1990), nine fall into one of these categories (Butz Huryn and Moller 1995). However, 16 require pollination and are visited by honeybees, and one is pollinated more or less exclusively by them (the barberry shrub, *Berberis darwinii*). Eight more are listed as having unknown pollination mechanisms (Butz Huryn and Moller 1995). This group includes the tree lupin, *Lupinus arboreus*, and broom, *Cytisus scoparius*, which are self-incompatible and rely on pollination by bumblebees (Stout et al. 2002a, b; Stout 2000). It also includes gorse, *Ulex europeaus*, which is thought to depend on honeybee pollination, and in which seed set is greatly reduced by a lack of pollinators in the Chatham Islands where honeybees and bumblebees are absent (McFarlane et al. 1992). Thus at least four major weeds in New Zealand are pollinated primarily by exotic bees. *L. arboreus* is currently a minor weed in Tasmania. However, seed set in areas recently colonized by *B. terrestris* has increased dramatically, and it is likely that *L. arboreus* may become as problematic in Tasmania as it is in New Zealand now that it has an effective pollinator (Stout et al. 2002a, b). Its zygomorphic flowers have to be forced apart to expose the stamens and stigma; only a large, powerful bee is able to do this, and no such bees are native to Tasmania. *L. arboreus* is only one of many weeds in Tasmania, New Zealand, and southern Australia that originated in the temperate northern hemisphere and are coadapted for pollination by bumblebees.

Demonstrating that exotic bees increase seed set of weeds is not sufficient in itself to conclusively show that the action of the bees will increase the weed population (Butz Huryn 1997). No long-term studies of weed population dynamics in relation to the presence or absence of exotic bees have been carried out. Because most weed species are short-lived and dependent on high reproductive rates, it seems probable that seed production is a crucial factor in determining their abundance. Key factor analysis of the life history could reveal whether seed set is directly related to population size.

At present, Australia alone has 2,700 exotic weed species, and the costs of control and loss of yields due to these weeds costs an estimated AU$3 billion per year (Common Wealth of Australia 1997). The environmental costs are less easy to quantify but are certainly large. Most of these weed species are at present of trivial importance. The recent arrival of the bumblebee may awake some of these "sleeper" weeds, particularly if they are adapted for bumblebee pollination. Positive feedback between abundance of weeds and abundance of bumblebees is probable, since an increase in weed populations will encourage more bumblebees, and vice versa. If even one new major weed occurs in Australia due to the presence of bumblebees, the economic and environmental costs could be substantial.

19.10 Loss of Genetic Diversity: Causes and Consequences

Despite its economic usefulness, biodiversity of Asian hive bee *Apis cerana* is suffering precipitous decline and is threatened with extinction in its entire native habitat. For example, in Japan, beekeeping with this native bee species has been completely replaced by European honeybee, *Apis mellifera* and only a few beekeepers and research institutes are raising *Apis cerana* colonies (Sakai 1992). In China, out of more than 8.5 million colonies of bees kept in modern hive, 70% are exotic *Apis mellifera* (Zhen-Ming et al. 1992). Similarly, in South Korea, only 16% beekeeping is with native *Apis cerana* and remaining has been replaced by exotic *Apis mellifera* (Choi 1984).

In Hindu Kush Himalayan range, beekeeping with *Apis cerana* is being replaced by *Apis mellifera* at such a fast rate that populations of native *Apis cerana* is declining to a level that is no longer viable. These countries include Afghanistan, Bhutan, Myanmar, Nepal, India, Bangladesh and Pakistan (Verma 1994). Eva Crane during a visit of some mountain areas of north-west Frontier province of Pakistan in 1989 concluded that *Apis cerana* populations may soon become an endangered species (Crane 1992). Thus, the existing centuries old and long established craft of beekeeping with *Apis cerana* has now almost got destroyed in its entire native habitat. *Apis cerana* remains till now a forgotten and completely ignored species. Therefore, from biodiversity conservation point of view, it will be disastrous to leave this important genetic resource at its own and definitely require research and development interventions for its conservation and sustainable uses both in natural and agricultural eco-systems.

19.11 Causes and Consequences of Declining *Apis cerana* Diversity

In seeking ways to conserve genetic diversity of *Apis cerana*, it is necessary to have a clear understanding of the major threats which this bee species is facing in its own native habitat. Like any other threatened biological resources, decline in *Apis cerana* population is also being threatened by human mismanagement, misguided scientific and economic policies and faulty institutions. Major threats include the following:

19.11.1 Major Threat from Apis mellifera

Many importations of *Apis mellifera* in south and south-east Asia have proved disastrous for beekeeping with *Apis cerana*. When kept sympatrically, *Apis cerana* and *Apis mellifera* colonies frequently robbed each other (Koeniger 1982). Another major problem is the transfer of parasites from one species to another. A parasite mite of brood and adults, *Varroa destructor* co-exist with *Apis cerana* and causes no serious damage to this native bee species. In several countries of Asia, where both these species are kept together, the parasite has infested *Apis mellifera* colonies and became a serious pest to this unadapted host, now killing thousands of colonies every year. It is now well documented that through importations of *Apis mellifera*, *Apis cerana* populations in its native habitat are facing serious risk of extinction.

On the other hand, also native *Apis cerana* populations are threatened by pests and parasites of exotic western honey bee *Apis mellifera* for which *Apis cerana* is lacking resistance. For example, there are several reports in the literature that Thai Sac Brood Virus Disease, European Foul Brood and possibly Acarine Disease jumped in to *Apis cerana* and other Asian bee species from *Apis mellifera* in Nepal, India and other Asian countries killing large number of native bee colonies every year (Saville and Naomi 2000; Allen et al. 1990). Abrol (2009) reported three viral diseases affecting *Apis cerana* namely, Thai Sac Brood Virus, Kashmir Bee Virus and *Apis* Iridescent Virus and all these virus diseases probably spread from *Apis mellifera.*

Due to these afflictions, populations of *Apis cerana* colonies practically reduced to the level of extinction but through natural selections within two decades, normal population of this bee species stand restored from 10% of surviving colonies (Reddy 1999; Ge et al. 2000; Ahmad and Partap 2000). These risk factors may vary between different habitat types, landscapes and bio-geographical region. The relative importance of these factors and in particular their combined effects on *Apis cerana* genetic diversity loss are unknown.

Large scale importations and multiplications of exotic *Apis mellifera* in to developing countries of south and south-east Asia for better economic returns in terms of higher honey production has also become a myth. This bee species is now so seriously infested with parasitic mites, European Foul Brood, hornets/wasps/birds, wax moths that beekeeping with this exotic species require intensive treatment with chemicals to control these afflictions which are very expensive and making this enterprise economically unviable. The intensity and the need for chemical treatment of *A. mellifera* colonies for mite, diseases and pest control reveal that beekeepers in developing country of south and south-east Asia with large uneducated, ignorant populations in isolated areas are using chemical prescriptions indiscriminately and thus affecting the quality of honey (Abrol 2009).

19.11.2 Exotic Pollinators

The accidental or deliberate importation of pollinators into new geographic regions has lately become a concern to some environmentalists. The widespread European honey bee and bumble bees imported into some regions (Dunning 1886) may be displacing native bees or other pollinators of the native flora, or they may provide unsatisfactory pollination of these plants (Pyke and Balzer 1983; Vogel and Westerkamp 1991; Westerkamp 1991; Wilson and Thomson 1991; Thomson and Thomson 1992; Kato 1993; Paton 1993). *Bombus terrestris* L. is now widely distributed for pollination of crops and is another potential competitor (Donovan 1990; Semmens et al. 1993; Semmens 1996; Kato 1993). Although several species of solitary bees have been distributed to new regions for pollinating crops, they are less likely to displace native bees than is the ubiquitous European honey bee, due to their greater host-specificity, climatic limitations, shorter foraging ranges, specific conditions for nesting, and brief adult life (Donovan 1990). The principles that apply to the importation and establishment of exotic pollinators resemble those of classical biological control (Batra 1982), in which beneficial organisms are sought near the center of origin of the problem-causing organism in a similar climate, observed and tested for lack of harm to other beneficial or rare organisms, imported into quarantine where their parasites can be eliminated, tested with hosts again, in confinement and then released for a specific purpose into their new environments. Considerable effort has gone into identifying the most efficient pollinators of several Eurasian crops that may be worthy of importation into North America, South America, Australia and New Zealand where native pollinators are not well adapted to pollinate these crops (Parker et al. 1987). Conversely, American pollinators of sunflowers, cotton, passion fruit, squashes and gourds, avocado, tomato, chili, blueberries and cranberries have been studied in areas where these crops are believed to have originated, the goal being to introduce their pollinating bees into areas where the crops are now grown without their most efficient pollinators (Parker et al. 1987).

Large human populations can currently only be maintained by agriculture, which must alter native environments. Humans, like all organisms, may be expected to increase in population (absent natural enemies), until all available resources are fully exploited, either directly (as in agriculture), or indirectly, for example, when biota and other natural resources have been assessed and then reserved for possible future value (in economic terms, internalized). The impact of humans is large, complex, and irreversible (Vitousek 1994). One way to provide for more habitat in which to conserve native bees and other biodiversity, as well as nonrenewable resources, would be to improve the yields on existing crop lands. This can be accomplished, in part, by introducing the most efficient pollinators for these crops.

The large bumblebee, *Bombus terrestris* (L.), is naturally distributed in Europe and adjacent territories, including England, most of Scotland, the north coast of Africa, southern Scandinavia, major Mediterranean Islands, and some Atlantic Islands (Madeira and the Canary Islands) (Estoup et al. 1996; Chittka et al. 2004; Velthuis and van Doorn 2006). Since *B. terrestris* became commercially available as a valuable pollinator of greenhouse crops in the late 1980s, this species has been shipped throughout the world in vast numbers (Goka et al. 2001; Hingston et al. 2002). The invasive potential of *B. terrestris* has been suggested by its successful naturalization in New Zealand (Donovan and Wier 1978; Donovan 1980; MacFarlane and Gurr 1995; Goulson and Hanley 2004), Israel (Dafni and Shmida 1996; Dafni 1998), Chile (Ruz and Herrera 2001) Japan, *B. terrestris* has been used for pollination of greenhouse crops, particularly tomatoes (*Solanum lycopersicum* L.), since 1991 (Ono 1998). Importation of *B. terrestris* colonies has been increasing annually, and approximately 70,000 colonies were used in 2004 (Kunitake and Goka 2006). Since the introduction of *B. terrestris* to Japan in 1991, researchers have warned about the strong potential impacts on native bumblebee species and mutualistic pollination systems (Kato 1993; Washitani and Morimoto 1993; Washitani et al. 1997). Unfortunately, the warnings are becoming real. In 1996 a naturally occurring nest, which was the first evidence of naturalization of *B. terrestris* in Japan, was found in Monbetsu in the Hidaka region of Hokkaido, northern Japan, close to the agricultural area where *B. terrestris* was mass introduced (Washitani 1998). Since then, increasing numbers of *B. terrestris* queens emerging from hibernation have been recorded around the area, and this species had become dominant in the bumblebee fauna by 2003 (Matsumura et al. 2004). Monitoring in the Hidaka region revealed that *B. terrestris* foraged on the flowers of approximately 100 species, of which 40 were native, suggesting potential competition for floral resource with native bumblebees (Matsumura et al. 2004). Mass infestation of *B. terrestris* queens was observed in 2003 in the Iburi region of Hokkaido, about 10 km away from a large source of bumblebees introduced for greenhouse tomato cultivation (Yokoyama et al. 2004). The *B. terrestris* observed in the Iburi region appear to be naturalized and this species could have adverse effects on native flower-visiting insects through competition, either for floral resources (nectar and pollen) or for nest sites. Inoue et al. (2007) reported that there were considerable niche overlaps in flower resource use between introduced *B. terrestris* and native *B. hypocrita sapporoensis*/*B. pseudobaicalensis*. They suggested that competition for nest sites rather than flower resources is the major ecological mechanism for displacement of native bees. The large reduction of *B. hypocrita sapporoensis* queen indicates that *B. terrestris* may cause local extinction of native bumblebees. Control of established *B. terrestris* populations and prevention of further range expansion are urgently needed.

19.12 Impact of Importations on Native Bees

There have always been efforts to acquire races of bees which could serve as good honey producers, pollinators with better qualitative and quantitative characters. This has necessitated importing good bee stocks from one country to another. There are instances where these imports made by observing proper quarantine measures had contributed substantially to the economy but unwanted races of honeybees have caused serious concern for beekeeping and public health. Importation of honeybees and other pollinators that are not indigenous to any country may endanger local honeybees and other pollinators. The inherent problems of accidental entry of parasites, pests and diseases and undesirable *Apis spp* to non existent areas, thereby threatening the existence of honeybees and other local pollinators have been reviewed by Gatoria et al. (2000) and Abrol (2001). The competition between existing honeybees and exotic species may lead to the elimination of indigenous species e.g. introduction of *Apis mellifera* eliminated *Apis cerana japonica* in Japan and the fate of *Apis cerana indica* in India is not different. Therefore there is a need of legislative measures to control the entry of pests and diseases.

19.12.1 Import of Pollinators

Import of *Megachile rotundata* F. in Bulgaria from France and Canada proved to be effective pollinator of Lucerne (Dochkova 1984). Similarly, Aballay et al. (1986) reported the successful establishment of *Bombus ruderatus* (F.) imported from Newzealand into Chile for pollination of red clover (*Trifolium pretense* L.). Following the success of some earlier introduction of bumble bees for pollination of red clover in Newzealand, two bees *Megachile rotundata* and *Nomia melanderi* Cockerell were introduced as pollinators of Lucerne (Donovan 1990). Richards and Krunic (1990) imported *M. rotundata* bees from Canada for pollination of alfalfa (*Medicago sativa* L.) in Yugoslavia which also proved worthwhile. Kevan and Laverty (1990) cautioned in Canada that parasitic mite like *Varroa jacobsoni* Oudemans can survive on imported pollinators or on non honeybee insects that may come in contact with infested honeybees visiting these flowers in their native country. Hence, the import of pollinators is made through strict quarantine procedures after ensuring them free from such parasites.

19.12.2 Import of Honeybee Packages, Queen Bees and Spread of Enemies and Diseases

In order to reduce the risk of introduction of *V. jacobsoni* the import of honeybees from USA into Canada was prohibited in 1987 (Switzer 1993). During 1988, Canada closed the border ‘against import of queen bees from USA to prevent and slow down the introduction of *Acarapis woodi Rennie* and *V. jacobsoni.* The act was widely supported by Canadian beekeepers as it resulted in the annual saving of three million dollars on account of miticidal treatment (Winston 1994). During 1992, *V. jacobsoni* was detected in feral colonies of Asian honeybees (*Apis cerana* F.) on Dauan island adjacent to Papua New Guinea (Australian territory). The island was immediately declared as infested zone and adjacent areas as surveillance zones, monitored by Australian quarantine and inspection service (AQUIS). Schrader and Reid (1986) stated that it was because of strict quarantine rules that ensured the absence of American foulbrood, *Braula* and parasitic mites in New Zealand.

Deodikar (1971) attributed the first reported acarine disease (*Acarapis woodi*) in 1950s in India to the importation of *Apis mellifera* and suggested that quarantine law should be made applicable to bees also. Kshirsagar et al. (1981) suggested the need of setting up of a quarantine procedure an offshore island in order to prevent the entry of honeybee diseases and enemies into the country. Routine monitoring in Georgia (USA) detected *A. woodi* in April, 1985. The infested apiary was destroyed and quarantine of all apiaries within 3.2 km imposed (Hall et al. 1987) there were no reports of occurrence of *A. woodi* in Finland until 1991. During summer of 1991 many queen bees were imported from USA with proper health certificates when attendant workers of 9 queen from a batch of 300 queens were examined, 17 out of 52 bees were found to be infested with *A. woodi* (Korpela and Fakhimzadeh 1991), thus putting a question mark even on the validity of health certificates. Whitten (1979) discussed the establishment of rigorous quarantine procedures in Australia to minimize the risk of the introduction of exotic diseases and parasitic mites.

About one quarter of a million mated queens were shipped to western Canada each year from United States (Jay and Dixon 1982). However 0.5–18.00% of imported queens were infected with *Nosema apis Zanders*. Later on reports of occurrence of *Nosema apis and* amoeba (*Malphihamoeba mellificae* Prell) were reported by Liu et al. (1987). Liu (1991) reported the isolation of three Australian strains of Kashmir bee virus from bees in different parts of the Australia and cautioned the import of bees as the infected bees carry the virus in inactive phase for long.

Bacterial diseases like American foul brood (Singh 1961) from U.P. India and European foul brood in Maharashtra (Diwan 1971) from *Apis cerana* have been reported but thereafter neither in *Apis cerana* nor in *A. mellifera* bacterial diseases were found till 2000. Recently, European foul brood has been detected (Abrol and Ball 2006) which could be consequence of illegal trafficking of the queen bees into India from across the border, thereby necessitating strict quarantine in India. The European wasp *Vespula germanica* is native to Europe, North Africa and temperate Asia. It first reached Tasmania in 1959, where it soon became well established. However, it was not until 1977 that the European wasp was first recorded on the mainland in Melbourne Australia in 1977 and it is now a pest in South Eastern Australia and in the south of Western Australia. It has also spread to New Zealand, South Africa and Chile (Akre and MacDonald 1986).

19.12.3 Africanized/Killer Bees

Accidental release of Africanized honeybees (AHB), *Apis mellifera scutellata* (*Apis mellifera adansonii* Laterille) in Brazil during 1957 is one of the most debated problem. Because of its defensiveness and aggressive temperament, it has created a serious public nuisance and has been designated as a killer bee. Stibick (1984) advocated very hard steps ranging from destruction of swarms to aerial spraying of insecticides. The AHB has spread throughout the south and central America and at present is heading northwards from southern U.S. replacing European honeybee races in many countries (Cobey 1999).

19.12.4 Cape Bee Problem

Allsopp and Creewe (1953) reported the invasion of AHB (*A. mellifera scutellata*) colonies by the cape bees (*A. mellifera capensis* Escholtz) and their usurpation of *scutellata queens.* This phenomenon was later on dubbed as ‘cape bee problem’. The invasion of AHB colonies by cape bees resulted in dwindling and dying of 50,000–1,00,000 bee colonies since 1991 from Transvaal and north cape region of Africa (Allsopp 1993). During 1993, legislation was set up under agricultural pest act 1983(Act No. 36) to prevent movement of cape bees into zone of AHB (Transvaal region). All cape bee colonies already in the region in that were eradicated under this act.

Roubik (2009) found that the exotic Africanized honey bees did not produce a negative effect on native bees, including species that were solitary or highly eusocial. Major differences over time were found in honey bee abundance on flowers near habitat experiencing the greatest degree of disturbance, compared to deep forest areas. At the population level, there was no sudden decline in bees after AHB arrival, and relatively steady or sinusoidal population dynamics. However, the native bees shifted their foraging time or floral species. A principal conclusion is that such competition is silent, in floristically rich habitats, because bees compensate behaviorally for competition. Other factors limit their populations. Leigh et al. (2009) reported that colonies, like human civilizations, respond to increased competition with both increased specialization and generalization. It was interesting to find that Africanized honey bees seldom or never skirmish with or show any aggression toward other foragers on flowers. (Roubik 1978, 1980, 1982a, b, 1983, 1988, 1989a, b, 1990, 1991, 1996a, b). The European honey bees, compared to Africanized honey bee colonies in the same apiaries, displayed a quantitative overlap in pollen species harvest of only 55%. They also are best regarded as distinct races of *A. mellifera* (Francoy et al. 2008). More important, the European honey bees chose to specialize, i.e., focus a major effort in forage collection, on considerably fewer species than the AHB. The European bees under direct competition for food with AHB were 33% more specialized, and their pollen use included 33% more species. evidently, the European bees were both more generalized and specialized than before the pressure of competition from a clearly more dominant (and abundant) honey bee was upon them. The total estimated pollen species used by *A. mellifera* included about 20% of the 860 local vascular plant flora. Curiously, one species of nectarless tree (*Cecropia peltata*) was the dominant pollen type used by both races of *A. mellifera* during experiments, whereas it was barely present in the pre-AHB period.

19.13 Conclusions

Both *A. mellifera* and *B. terrestris* are now abundant over large areas where they naturally did not occur. They are both polylectic, and thus use resources utilized by a broad range of native species. Various Megachilidae have been introduced to North America and one species to Australia and New Zealand, but very little is known about their impacts.

It seems almost certain that abundant and widespread exotic organisms that single-handedly utilize a large proportion of the available floral resources do impact on local flower-visiting fauna. Consider, for example, the Tasmania native bee community. One hundred and eighty years ago this presumably consisted of a large number of small, solitary and subsocial species. Over 100 species are known to be present today, and many more probably exist. Nowadays, by far the most abundant flower-visiting insects at almost every site is the honeybee, often out numbering all other flower-visiting insects by a factor of 10 or more (Goulson et al. 2002). In the southeast, the second most abundant flower visitor is usually the bumblebee, *B. terrestris*. The majority of floral resources are gathered by these bees, often during the morning before native bees have become active. It is hard to conceive how the introduction of these exotic species and their associated pathogens could not have substantially altered the diversity and abundance of native bees. Unfortunately we will never know what the abundance and diversity of the Tasmanian bee fauna were like before the introduction of the honeybee. Of course the same applies to most other regions such as North America where the honeybee has now been established for nearly 400 years. It is quite possible that some, perhaps many, native bee species were driven to extinction by the introduction of this numerically dominant species or by exotic pathogens that arrived with it. Even were it practical or considered desirable to eradicate honeybees from certain areas, it would be too late for such species.

Similarly, the introduction of exotic bees must increase seed set and hence weediness of some exotic plants, particularly when, as in the case of the bumblebee in Australia, many of the weeds were introduced from the same geographic region and are co-adapted with the introduced bee. It must be remembered that introduced bees provide substantial benefits to man in terms of pollination of crops, and in the case of the honeybee, in providing honey. These quantifiable benefits should be weighed against the likely costs. In areas where weeds pollinated by exotic bees are a serious threat, and/or where native communities of flora and fauna are particularly valued, it may be that the benefits provided by these species are outweighed by the costs. Clearly further research, particularly rigorous manipulative experiments, are needed to determine how much introduced bees contribute to weed problems and whether they do substantially impact upon native pollinator communities. The cautionary principle argues that in the meantime we should at the very least prevent further deliberate release of exotic bee species (such as of bumblebees in mainland Australia, and speculative introductions of various solitary bee species in the United States). Unlike many of the other impacts that man has on the environment, introduction of exotic species is usually irreversible. It would also seem sensible to avoid placing honeybee hives within environmentally sensitive areas where possible, particularly areas where the native flora is threatened by invasion with weed species.

References

Aballay FE, Ruiz M, Maraboli A, Arretz VP (1986) Analysis of the establishment in Chile of *Bombus ruderatus* (F.) introduced for red clover (Trifolium pratense L.) pollination. Invest Agric 9(1):31–36

Abrahamovich AH, Telleria MC, Dıaz NB (2001) *Bombus* species and their associated flora in Argentina. Bee World 82:76–87

Abrol DP (2001) Import – export policy of honey bees and other pollinators. Indian Bee J 63(3&4): 55–58

Abrol DP (2009) Bees and beekeeping in India, 2nd edn. Kalyani Publishers Ludhiana, India, 719pp

Abrol DP, Ball BV (2006) New record of European foul brood (EFB) – a bacterial disease of honeybee *Apis mellifera* L. in Jammu, India. J Res SKUAST-J 5(2):256–260

Ahmad F, Partap U (2000) Indigenous honeybee of the Himalayas: a community based approach to conserving biodiversity and increasing farm productivity. Six Monthly Progress Report (Jan-June 2000). ICIMOD, Kathmandu, Nepal

Aizen MA, Feinsinger P (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. Ecology 75:330–351

Akre RD, MacDonald JF (1986) Biology, economic importance and control of yellow jackets. In: Vinson, S.B. (ed). Economic Impact and Control of Social Insects. Praeger, New York

Alexander N (ed) (1996) Australia: state of the environment 1996. Melbourne, CSIRO, 78pp

Allen MF, Ball BV, Underwood BA (1990) An isolation of *Melissococcus pluton* from *Apis laboriosa*. J Invertebr Pathol 55:439–440

Allsopp MH (1993) Summarized overview of the *Capensis* problem. S Afr Bee J 65:127–136

Anderson JME (1989) Honeybees in natural ecosystems. In: Noble JC, Bradstock RA (eds) Mediterranean landscapes in Australia: Mallee ecosystems and their management. CSIRO, East Melbourne, pp 300–304

Arizmendi MC, Dominguez CA, Dirzo R (1995) The role of an avian nectar robber and of hummingbird pollinators in the reproduction of two plant species. Funct Ecol 10:119–127

Armstrong JA (1979) Biotic pollination mechanisms in the Australian flora – a review. NZ J Bot 17:467–508

Arretz PV, Macfarlane RP (1986) The introduction of *Bombus ruderatus* to Chile for red clover pollination. Bee World 67:15–22

Barthell JF, Thorp RW (1995) Nest usurpation among females of an introduced leaf-cutter bee, *Megachile apicalis*. Southwest Entomol 20:117–124

Barthell JF, Frankie GW, Thorp RW (1998) Invader effects in a community of cavity nesting megachilid bees (Hymenoptera: Megachilidae). Environ Entomol 27:240–247

Barthell JF, Randall JM, Thorp RW, Wenner AM (2001) Promotion of seed set in yellow star thistle by honey bees: evidence of an invasive mutualism. Ecol Appl 11:1870–1883

Batra SWT (1979) *Osmia cornifrons* and *Pithitis smaragulda*, two Asian bees introduced into the United States for crop pollination. In: MC Dewey (ed) Proceedings of IV international symposium pollination, College Park, University of Maryland Agricultural Experiment Station Special Miscellaneous Publication I, pp 79–83

Batra SWT (1982) Biological control in agroecosystems. Science 25:134–139

Bohart GE (1972) Management of wild bees for the pollination of crops. Annu Rev Entomol 17:287–312

Buchmann SL (1996) Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. See Matheson et al. 1996, pp 125–142

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island, Washington, DC

Burd M (1994) Bateman’s principle and plant reproduction: the role of pollen limitation in fruit and seed set. Bot Rev 60:83–139

Butler MJ, Stein RA (1985) An analysis of the mechanisms governing species replacements in crayfish. Oecologia 66:168–177

Buttermore RE (1997) Observations of successful *Bombus terrestris* (L.) (Hymenoptera: Apidae) colonies in southern Tasmania. Aust J Entomol 36:251–254

Butz Huryn VM (1997) Ecological impacts of introduced honey bees. Q Rev Biol 72:275–297

Butz Huryn VM, Moller H (1995) An assessment of the contribution of honeybees (*Apis mellifera*) to weed reproduction in New Zealand protected natural areas. NZ J Ecol 19: 111–122

Cane JH, Payne JA (1988) Foraging ecology of the bee *Habropoda laboriosa* (Hymenoptera: Anthophoridae), an oligolege of blueberries (Ericaceae: *Vaccimium*) in the southeastern United States. Ann Entomol Soc Am 81:419–427

Cardale JC (1993) Hymenoptera: Apoidea. In: Houston WWK, Maynard GV (eds) Zoological catalogue of Australia, vol 10. Australian Government Publishing Service, Canberra

Carpenter FL (1978) A spectrum of nectar-eater communities. Am Zool 18:809–819

Chittka L, Ings TC, Raine NE (2004) Chance and adaptation in the *Evolution* of island bumblebee behaviour. Popul Ecol 46:243–251

Choi SY (1984) Brief report on the status of Korean Beekeeping. Proceedings of the Expert Consultation (ed) FAG, pp 170–190

Cobey S (1999) The new world Carniolan closed population breeding project. In: Proceeding of 36th Apimondia Congress Vancouver, Canada, Apimondia Publication House, Bucharest, pp 26–27

Common Wealth of Australia (1997) The national weeds strategy. Commonwealth of Australia, Canberra

Cooper KW (1984) Discovery of the first resident population of the European bee, *Megachile apicalis*, in the United States (Hymenoptera: Megachilidae). Entomol News 95:225–226

Corbet SA, Fussell M, Ake R, Fraser A, Gunson C et al (1993) Temperature and the pollinating activity of social bees. Ecol Entomol 18:17–30

Corbet SA, Saville NM, Fussell M, Prys-Jones OE, Unwin DM (1995) The competition box: a graphical aid to forecasting pollinator performance. J Appl Ecol 32:707–719

Crane E (1990) Bees and beekeeping: science, practice, and world resources. Cornell University Press, Comstock/Ithaca

Crane E (1992) The past and present status of beekeeping with stingless bees. Bee World 73:29–42

Dafni A (1998) The threat of *Bombus terrestris* spread. Bee World 79:113–114

Dafni A, Shmida A (1996) The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt. Carmel, Israel. In: Matheson A (ed) The conservation of bees. The Linnean Society of London and The International Bee Research Association, London, pp 183–200

Daly HV, Bohart GE, Thorp RW (1971) Introduction of small carpenter bees in California for pollination. I. Release of Pithitis smaragulda. J Econ Entomol 64:1145–1150

Deodikar GB (1971) Code of conduct for conservation of bees and beekeeping. Indian Bee J 33(1/2):14–22

Diwan VV (1971) Occurrence of a new bacterial disease of Indian honeybees Apisindica F., Curr. Science 40:196–197

Dobson HEM (1993) Bee fauna associated with shrubs in 2 California chaparral communities. Pan-Pac Entomol 69:77–94

Dochkova B (1984) [Studies on the economic importance of *Megachile rotunda* (Hymenoptera, Megachilidae)]. Rastenievudni Nauki 21:116–121

Donovan BJ (1975) Introduction of new bee species for pollinating lucerne. Proc NZ Grasslands Assoc 36:123–128

Donovan BJ (1979) Importation, establishment and propagation of the alkali bee *Nomia melanderi* Cockerell (Hymenoptera: Halictidae) in New Zealand. In: Proceedings of 4th International Symposium on Pollination, Maryland Agricultural Experiment Station Special Miscellaneous Publication, Maryland, 1:257–268

Donovan BJ (1980) Interactions between native and introduced bees in New Zealand. NZ J Ecol 3:104–116

Donovan BJ (1990) Selection and importation of new pollinators to New Zealand. NZ Entomol 13:26–32

Donovan BJ, Wier SS (1978) Development of hives for field population increase, and studies on the life cycles of the four species of introduced bumble bees in New Zealand. NZ J Agric Res 21:733–756

Dornhaus A, Chittka L (1999) Insect behaviour: evolutionary origins of bee dances. Nature 401:38

Doull K (1973) Bees and their role in pollination. Aust Plants 7:223–236

Dunning JW (1886) The importation of humble bees into New Zealand. Trans R Entomol Soc London 6:32–34

Eickwort GC, Ginsberg HS (1980) Foraging and mating behaviour in Apoidea. Annu Rev Entomol 25:421–426

Estoup A, Solignac M, Cornuet JM, Goudet J, Scholl A (1996) Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. Mol Ecol 5:19–31

Evans JD, Pettis JS, Shimanuki H (2000) Mitochondrial DNA relationships in an emergent pest of honey bees: *Aethina tumida* (Coleoptera: Nitidulidae) from the United States and Africa. Ann Entomol Soc Am 93:415–420

Francoy TM, Wittmann D, Drauschke S, Müller S, Steinhage V et al (2008) Identification of Africanized honey bees through wing morphometrics: two fast and efficient procedures. Apidologie 39(5):488–494

Frankie GW, Thorp RW, Newstrom-Lloyd LE, Rizzardi MA, Barthell JF et al (1998) Monitoring solitary bees in modified wildland habitats: implications for bee ecology and conservation. Environ Entomol 27:1137–1148

Freitas BM, Paxton RJ (1998) A comparison of two pollinators: the introduced honey bee *Apis mellifera* and an indigenous bee *Centris tarsata* on cashew *Anacardium occidentale* in its native range of NE Brazil. J Appl Ecol 35:109–121

Galen C (1983) The effects of nectar thieving ants on seedset in floral scent morphs of *Polemonium viscosum*. Oikos 41:245–249

Gatoria GS, Chhunneja PK, Singh D (2000) Import of pollinator, package bees, quieen bees and associated problems. Indian Bee J 62:1–9

Ge F, Xye YB, Nie QS (2000) Natural recovery of Chinese bee populations of Changbai Mountains. In: Matsuka (ed) Asian bees and beekeeping. Oxford and IBH Publishing Co. Ltd, New Delhi, pp. 26

Gilliam M (1997) Identification and roles of non-pathogenic microflora associated with honey bees. FEMS Microbiol Lett 155:1–10

Gilliam M, Taber S (1991) Diseases, pests, and normal microflora of honeybees, *Apis mellifera*, from feral colonies. J Invertebr Pathol 58:286–289

Gilliam M, Lorenz BJ, Prest DB, Camazine S (1993) *Ascosphaera apis* from *Apis cerana* from South Korea. J Invertebr Pathol 61:111–112

Gilliam M, Lorenz BJ, Buchmann SL (1994) *Ascosphaera apis*, the chalkbrood pathogen of the honeybee, *Apis mellifera*, from larvae of a carpenter-bee, *Xylocopa californica arizonensis*. J Invertebr Pathol 63:307–309

Ginsberg HS (1983) Foraging ecology of bees in an old field. Ecology 64:165–175

Goerzen DW (1991) Microflora associated with the alfalfa leafcutting bee, *Megachile rotundata* (Fab) (Hymenoptera, Megachilidae) in Saskatchewan, Canada. Apidologie 22:553–561

Goerzen DW, Erlandson MA, Bissett J (1990) Occurrence of chalkbrood caused by *Ascosphaera aggregata* Skou in a native leafcutting bee, *Megachile relativa* Cresson (Hymenoptera, Megachilidae), in Saskatchewan. Can Entomol 122:1269–1270

Goerzen DW, Dumouchel L, Bissett J (1992) Occurrence of chalkbrood caused by *Ascosphaera aggregata* Skou in a native leafcutting bee, *Megachile pugnata* Say (Hymenoptera, Megachilidae), in Saskatchewan. Can Entomol 124:557–558

Goka K, Okabe K, Yoneda M, Niwa S (2001) Bumblebee commercialization will cause worldwide migration of parasitic mites. Mol Ecol 10:2095–2099

Goulson D (1999) Foraging strategies for gathering nectar and pollen in insects. Perspect Plant Ecol Evol Syst 2:185–209

Goulson D, Hanley ME (2004) Distribution and forage use of exotic bumblebees in South Island, New Zealand. NZ J Ecol 28:225–232

Goulson D, Stout JC (2001) Homing ability of bumblebees; evidence for a large foraging range? Apidologie 32:105–112

Goulson D, Ollerton J, Sluman C (1997) Foraging strategies in the small skipper butterfly, *Thymelicus flavus*; when to switch? Anim Behav 53:1009–1016

Goulson D, Stout JC, Kells AR (2002) Do alien bumblebees compete with native flower visiting insects in Tasmania? J Insect Conserv 6:179–189

Gross CL (2001) The effect of introduced honeybees on native bee visitation and fruit-set in *Dillwynia juniperina* (Fabaceae) in a fragmented ecosystem. Biol Conserv 102:89–95

Gross CL, Mackay D (1998) Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). Biol Conserv 86:169–178

Hall DR, Cork A, Lester A (1987) Identification and role of female pheromone. J Chem Ecol 13:1575–1589

Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge

Heinrich B, Raven PH (1972) Energetics and pollination ecology. Science 176:597–602

Hingston AB, McQuillan PB (1999) Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). Aust J Zool 47:59–65

Hingston AB, Marsden-Smedley J, Driscoll DA, Corbett S, Fenton J, Anderson R, Plowman C, Mowling F, Jenkin M, Matsui K, Bonham KJ, Ilowski M, McQuillin PB, Yaxley B, Reid T, Storey D, Poole L, Mallick SA, Fitzgerald N, Kirkpatrick LB, Febey J, Harwood AG, Michaels KF, Russell MJ, Black PG, Emmerson L, Visoiu M, Morgan J, Breen S, Gates S, Bantich MN, Desmarchelier JM (2002) Extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). Aust Ecol 27:162–172

Holmes FO (1964) The distribution of honey bees and bumblebees on nectar secreting plants. *Am Bee J* January:12–13

Hopkins I (1911) Australasian bee manual. Gordon and Gotch, Wellington, 173pp

Hopkins I (1914) History of the bumblebee in New Zealand: its introduction and results. NZ Dept Agric Ind Commer 46:1–29

Hopper SD (1987) Impact of honeybees on Western Australia's nectarivorous fauna. In: Blyth J (ed) Beekeeping and land management. Western Australia CALM, Albany, pp 59–71

Horskins K, Turner VB (1999) Resource use and foraging patterns of honeybees, *Apis mellifera*, and native insects on flowers of *Eucalyptus costata*. Aust J Ecol 24:221–227

Inoue MN, Yokoyama J, Washitani I (2007) Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). J Insect Conserv 10

Inouye DW (1983) The ecology of nectar robbing. In: Elias TS, Bentley B (eds) The biology of nectarines. Columbia University Press, New York, pp 152–173

Irwin RE, Brody AK (1999) Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). Ecology 80:1703–1712

Jay SC, Dixon D (1982) Nosema disease in package honeybees, queens and attendant workers shipped to western Canada. J Apic Res 21(4):216–221

Kato M (1993) Impacts of the introduction of *Bombus terrestris* colonies upon pollination mutualism in Japan. Honeybee Sci 14:110–114 (in Japanese)

Kato M, Shibata A, Yasui T, Nagamasu H (1999) Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara) Islands. Res Popul Ecol 2: 217–228

Kevan PG, Laverty TM (1990) A brief survey and caution about importing alternative pollinators into Canada. Varroa can survive outside the hive and away from honey bees. Can Beekeep 15:176–177

Koeniger N (1982) Interactions among the four species of *Apis*. In: Breed MD (ed) Biology of socialinsects. Westview Press, Boulder

Korpela S, Fakhimzadeh K (1991) Tracheal mites in Finland. Am Bee J 131(9):587–588

Kshirsagar KK, Chauhan RM, Singh YK (1981) Occurrence of sac brood disease in *Apis cerana Fab*. Indian Bee J 43(2):44

Kunitake Y, Goka K (2006) Environmental risk assessment and management decisions for introduced insects – legal controls on *Bombus terrestris* by Invasive Alien Species Act. Jpn J Plant Protect 60:196–197 (in Japanese)

Leigh EG Jr, Vermeij GJ, Wikelski M (2009) What do human economies, large islands and forest fragments reveal about the factors limiting ecosystem evolution? J Evol Biol 22(1):1–12

Liu TP (1991) Virus-like particles in the tracheal mite *Acarapis woodi* (Rennie). Apidologie 22:213–219

Liu TP, Nelson DL, Collins MM (1987) Amoeba- and nosema-infected queen honeybees and worker attendants shipped in mailing cages to western Canada. J Apic Res 26:56–58

Low T (1999) Feral future. Penguin, Ringwood

Macfarlane RP (1976) Bees and pollination. In: Ferro DN (ed) New Zealand insect pests. Lincoln University Collage of Agriculture, New Zealand, pp 221–229

MacFarlane RP, Gurr L (1995) Distribution of bumble bees in New Zealand. NZ Entomol 18:29–36

Mal TK, Lovett-Doust J, Lovett-Doust L, Mulligan GA (1992) The biology of Canadian weeds. 100. *Lythrum salicaria*. Can J Plant Sci 72:1305–1330

Mangum WA, Brooks RW (1997) First records of *Megachile* (*Callomegachile*) *sculpturalis* Smith (Hymenoptera: Megachilidae) in the continental United States. J Kans Entomol Soc 70:140–142

Matsumura C, Yokoyama J, Washitani I (2004) Invasion status and potential impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in southern Hokkaido, Japan. Global Environ Res 8:51–66

Matthews E (1984) To bee or not? Bees in National Parks – the introduced honeybee in conservation parks in South Australia. Magazine of South Australian National Parks Association, Adelaide, pp 9–14

McDade LA, Kinsman S (1980) The impact of floral parasitism in two neotropical hummingbird-pollinated plant species. Evolution 34:944–958

McFarlane RP, Grundell JM, Dugdale JS (1992) Gorse on the Chatham islands: seed formation, arthropod associates and control. In: Proceedings of the 45th New Zealand plant protection conference, pp 251–255

McGregor SE, Alcorn EB, Kuitz EB Jr, Butler GD Jr (1959) Bee visitors to Saguaro flowers. J Econ Entomol 52:1002–1004

McNally LC, Schneider SS (1996) Spatial distribution and nesting biology of colonies of the African honey bee *Apis mellifera scutellata* (Hymenoptera: Apidae) in Botswana. Afr Environ Entomol 25:643–652

Menke HF (1954) Insect pollination in relation to alfalfa seed production in Washington. Wash Agric Exp Stn Bull 555:1–24

Michener CD (1965) A classification of the bees of the Australian and South Pacific regions. Bull Am Mus Nat Hist 130:1–324

Michener CD (1974) The social behavior of the bees: a comparative study, 2nd edn. Harvard University Press, Cambridge, 404 pp

Michener CD (1979) Biogeography of bees. Ann Mo Bot Gard 66:277–347

Moller H, Tilley JAV (1989) Beech honeydew: seasonal variation and use by wasps, honey bees and other insects. NZ J Zool 16:289–302

Morris WF (1996) Mutualism denied? Nectar-robbing bumble bees do not reduce female or male success of bluebells. Ecology 77:1451–1462

Newton SD, Hill GD (1983) Robbing of field bean flowers by the short-tongued bumble bee *Bombus terrestris* L. J Apicult Res 22:124–129

O'Toole C, Raw A (1991) Bees of the world. Blandford, London

Oldroyd BP, Lawler SH, Crozier RH (1994) Do feral honey-bees (*Apis mellifera*) and regent parrots (*Polytelis anthopeplus*) compete for nest sites. Aust J Ecol 19:444–450

Oldroyd BP, Smolenski A, Lawler S, Estoup A, Crozier R (1995) Colony aggregations in *Apis mellifera* L. Apidologie 26:119–130

Oldroyd BP, Thexton EG, Lawler SH, Crozier RH (1997) Population demography of Australian feral bees (*Apis mellifera*). Oecologia 111:381–387

Ono M (1998) Why is now the bumblebees? Nat Insects 33:2–3 (in Japanese)

Otis GW (1991) Population biology of the Africanized honey bee. See Spivak et al 1991, pp 213–234

Parker FD (1981) A candidate for red clover, *Osmia coerulescens* L. J Apicult Res 20:62–65

Parker FD, Torchio PF, Nye WP, Pedersen M (1976) Utilization of additional species and populations of leafcutter bees for alfalfa pollination. J Apicult Res 15:89–92

Parker FD, Batra SWT, Tepedino VJ (1987) New pollinators for our crops. Agric Zool Rev 2:279–304

Pascarella JB, Waddington KD, Neal PR (1999) The bee fauna (Hymenoptera: Apoidea) of Everglades National Park, Florida and adjacent areas: distribution, phenology, and biogeography. J Kans Entomol Soc 72:32–45

Paton DC (1990) Budgets for the use of floral resources in mallee heath. In: Noble JC, Joss PJ, Jones GK (eds) The Mallee lands: a conservation perspective. CSIRO, Melbourne, pp 189–193

Paton DC (1993) Honeybees in the Australian environment: does *Apis mellifera* disrupt or benefit the native biota? Bioscience 43:95–103

Paton DC (1995) Impact of honeybees on the flora and fauna of Banksia heathlands in Ngarkat Conservation Park. SASTA J 95:3–11

Paton DC (1996) Overview of feral and managed honeybees in Australia: distribution, abundance, extent of interactions with native biota, evidence of impacts and future research. Australian Nature. Conservation Agency, Canberra

Pearson WD, Braiden V (1990) Seasonal pollen collection by honeybees from grass shrub highlands in Canterbury, New Zealand. J Apicult Res 29:206–213

Percival M (1974) Floral ecology of coastal scrub in Southeast Jamaica. Biotropica 6:104–129

Pimm SL, Russell GJ, Gittleman JL, Brookes TM (1995) The future of biodiversity. Science 269:347–350

Pleasants JM (1981) Bumblebee response to variation in nectar availability. Ecology 62:1648–1661

Prys-Jones OE (1982) Ecological studies of foraging and life history in bumblebees. PhD thesis, University of Cambridge, UK

Prys-Jones OE, Ólafsson E, Kristja'nsson K (1981) The Icelandic bumble bee fauna (Bombus Latr., Apidae) and its distributional ecology. J Apicult Res 20:189–197

Pyke GH, Balzer L (1983) The effects of the introduced honeybee (*Apis mellifera*) on Australian native bees. Hawkesbury Agricultural College, Richmond, pp 18–22

Pyke GH, Balzer L (1985) The effects of the introduced honey-bee on Australian native bees. In: NSW national parks wildland Service Occasional Paper No. 7

Ramsey MW (1988) Differences in pollinator effectiveness of birds and insects visiting *Banksia menziesii* (Protaceae). Oecologia 76:119–124

Reddy MS (1999) Revival of beekeeping in Karnataka. Beekeep Dev 52:14–15

Richards KW, Krunic MD (1990) Introduction of alfalfa leafcutter bees to pollinate alfalfa in Yugoslavia. Entomologist 109(3):130–135

Richardson DM, Allsop N, D'Antonio CM, Milton SJ, Rejmanek M (2000) Plant invasions – the role of mutualisms. Biol Rev Cambr Philos Soc 75:65–93

Robertson P, Bennett AF, Lumsden LF, Silveira CE, Johnson PG, et al (1989) Fauna of the Mallee study area north-western Victoria. In: National parks wildland division technical Report Series, No. 87. Department of Conservation Forests, Lands, Victoria, pp 41–42

Roubik DW (1978) Competitive interactions between neotropical pollinators an Africanized honeybees. Science 201:1030–1032

Roubik DW (1980) Foraging behavior of commercial Africanized honeybees and stingless bees. Ecology 61:8336–8345

Roubik DW (1981) Comparative foraging behaviour of *Apis mellifera* and *Trigona corvine* (Hymenoptera: Apidae) on *Baltimorarecta* (Compositae). Rev Biol Trop 29:177–184

Roubik DW (1982a) Ecological impact of Africanized honeybees on native neotropical pollinators. In: Jaisson P (ed) Social insects of the tropics. Universit´e Paris-Nord, Paris, pp 233–247

Roubik DW (1982b) The ecological impact of nectar robbing bees and pollinating hummingbirds on a tropical shrub. Ecology 63:354–360

Roubik DW (1983) Experimental community studies: time-series tests of competition between African and neotropical bees. Ecology 64:971–978

Roubik DW (1988) An overview of Africanized honey-bee populations: reproduction, diet and competition. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman C (eds) Africanized honey bees and bee mites. Westview, Boulder, pp 45–54

Roubik DW (1989a) Ecology and natural history of tropical bees. Cambridge University Press, New York, p 514

Roubik DW (1989b) Ecology and natural history of tropical bees. Cambridge University Press, Cambridge, UK

Roubik DW (1990) Niche preemption in tropical bee communities: a comparison of neotropical and Malesian faunas. In: Sakagami SF, Ohgushi R, Roubik DW (eds) Natural history of social wasps and bees in equatorial Sumatra. Hokkaido University Press, Sapporo, pp 245–257

Roubik DW (1991) Aspects of Africanized honey bee ecology in tropical America. In: Spivak M, Breed MD, Fletcher DJC (eds) The African honey bee. Westview Press, Boulder, pp 147–158

Roubik DW (1996a) Measuring the meaning of honey bees. In: Matheson A, Buchmann SL, O'toole C, Westrich P, Williams IH (eds) The conservation of bees. Academic Press, Ltd, London, pp 163–172

Roubik DW (1996b) African honey bees as exotic pollinators in French Guiana. See Matheson et al 1996, pp 173–182

Roubik DW (2009) Ecological impact on native bees by the invasive africanized honey bee. Acta Biol Colomb 14(2):23–29

Roubik DW, Aluja M (1983) Flight ranges of *Melipona* and *Trigona* in tropical forests. J Kans Entomol Soc 56:217–222

Roubik DW, Buchmann SL (1984) Nectar selection by *Melipona* and *Apis mellifera* (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. Oecologia 61:1–10

Roubik DW, Wolda H (2001) Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. Popul Ecol 43:53–62

Roubik DW, Schmalzel RJ, Moreno JE (1984) Estudio apibotanico de Panam´a: cosecha y fuentes de polen y nectar usados por *Apis mellifera* y sus patrones estacionales y anuales. In: Bol. T´ec. No. 24. Org. Int. Reg. Sanidad Agropecuaria Mex., Centro Am. Panama, 73 pp

Roubik DW, Holbrook NM, Parrav G (1985) Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). Oecologia 66:161–167

Roubik DW, Moreno JE, Vergara C, Wittman D (1986) Sporadic food competition with the African honey bee: projected impact on neotropical social species. J Trop Ecol 2:97–111

Ruz L, Herrera R (2001) Preliminary observations on foraging activities of *Bombus dahlbomii* and *Bombus terrestris* (Hym: Apidae) on native and non-native vegetation in Chile. Acta Horticulturae 561:165–169

Sakagami SF (1959) Some interspecific relations between Japanese and European honeybees. J Anim Ecol 28:51–68

Sakai T (1992) *Apis cerana* beekeeping in Japan. In: Verma LR (ed) Honeybees in mountain agriculture. Oxford/IBH Publishing Co, New Delhi

Saville, Naomi M (2000) Farmer-participatory extension in Jumla, Western Nepal. In: Matsuka M (ed) Asian bees and beekeeping: progress of research and development. Oxford/IBH, New Delhi, pp 230–236

Schaffer WM, Jensen DB, Hobbs DE, Gurevitch J, Todd JR, Valentine SM (1979) Competition, foraging energetics, and the cost of sociality in three species of bees. Ecology 60:976–987

Schaffer WM, Zeh DW, Buchmann SL, Kleinhans S, Valentine Schaffer M, Antrim J (1983) Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 64:564–577

Schemske DW (1983) Limits to specialization and co*Evolution* in plant-animal mutualisms. In: Nitecki MH (ed) CoEvolution. University of Chicago Press, Chicago, pp 67–109

Schmitt D (1980) Pollinator foraging behaviour and gene dispersal in *Senecio* (Compositae). Evolution 34:934–943

Schrader M, Reid M (1986) Control of honey bee diseases and pests in New Zealand. Am Bee J 126(11):742–745

Schwarz MP, Hurst PS (1997) Effects of introduced honey bees on Australia's native bee fauna. Vic Nat 114:7–12

Schwarz MP, Gross CL, Kukuk PF (1991) Assessment of competition between honeybees and native bees. Progress Report World Wildland Fund, Australian Project P158, July 1991

Schwarz MP, Gross CL, Kukuk PF (1992a) Assessment of competition between honeybees and native bees. Progress Report World Wildland Fund, Australian Project P158, Jan 1992

Schwarz MP, Gross CL, Kukuk PF(1992b) Assessment of competition between honeybees and native bees. Progress Report World Wildland Fund, Australian Project P158, July 1992

Seeley TD (1985) The information-center strategy of honeybee foraging. Fortschritte der Zoologie 31:75–90

Semmens TD (1996) Flower visitation by the bumble bee *Bombus terrestris* (L) (Hymenoptera: Apidae) in Tasmania. Aust Entomol 23:33–35

Semmens TD, Turner E, Buttermore R (1993) Bombus terrestris (L) (Hymenoptera: Apidae) now established in Tasmania. J Aust Entomol Soc 32:346

Silander J, Primack R (1978) Pollination intensity and seed set in the evening primrose (Oenothera fruticosa). Am Midl Nat 100(1):213–216

Singh S (1961) Appearance of American foul brood disease in Indian honey bee (*Apis cerana indica* Fabr.). Indian Bee J 23(7/9):46–50

Stanley RG, Liskens HF (1974) Pollen: biology, biochemistry, management. Springer Verlag, Berlin

Stanton ML (1987) Reproductive biology of petal color variants in wild populations of *Raphanus sativus* II: Factors limiting seed production. Am J Bot 74:188–196

Stephen WP (1987) *Megachile* (*Eutricharea*) *apicalis*, an introduced bee with potential as a domesticable alfalfa pollinator. J Kans Entomol Soc 60:583–584

Stibick JNL (1984) Animal and plant health inspection service strategy and the African honey bee. Bull Entomol Soc Am 30:22–26

Stimec J, ScottDupree CD, McAndrews JH (1997) Honey bee, *Apis mellifera*, pollen foraging in southern Ontario. Can Field-Nat 111:454–456

Stout JC (2000) Does size matter? Bumblebee behaviour and the pollination of *Cytisus scoparius* L. (Fabaceae). Apidologie 31:129–139

Stout JC, Goulson D (2000) Bumble bees in Tasmania: their distribution and potential impact on Australian flora and fauna. Bee World 81:80–86

Stout JC, Allen JA, Goulson D (2000) Nectar robbing, forager efficiency and seed set: bumblebees foraging on the self incompatible plant *Linaria vulgaris* Mill. (Scrophulariaceae). Acta Oecol 21:277–283

Stout JC, Kells AR, Goulson D (2002a) Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania? Biol Conserv 106:425–434

Stout JC, Kells AR, Goulson D (2002b) Pollination of a sleeper weed, *Lupinus arboreaus*, by introduced bumblebees in Tasmania. Biol Conserv 106:425–34

Stubbs CS, Drummond FA, Osgood EA (1994) *Osmia ribifloris biedermannii* and *Megachile rotundata* (Hymenoptera: Megachilidae) introduced into the lowbush blueberry agroecosystem in Maine. J Kans Entomol Soc 67:173–185

Sugden EA, Pyke GH (1991) Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. Aust J Ecol 16:171–181

Sugden EA, Thorp RW, Buchmann SL (1996) Honey bee native bee competition: focal point for environmental change and apicultural response in Australia. Bee World 77:26–44

Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. Evol Ecol 7:533–555

Taylor G, Whelan RJ (1988) Can honeybees pollinate *Grevillea*? Aust Zool 24:193–196

Telleria MC (1993) Flowering and pollen collection by the honeybee (*Apis mellifera* L. var *ligustica*) in the Pampas region of Argentina. Apidologie 24:109–120

Tepedino VJ, Stanton NL (1981) Diversity and competition in bee-plant communities on short-grass prairie. Oikos 36:35–44

Thomson JD, Thomson BA (1992) Pollen presentation and viability schedules in animal pollinated plants: consequences for reproductive success. In: Wyatt R (ed) Ecology and *evolution* of plant reproduction: new approaches. Chapman and Hall, New York, pp 1–24

Thorp RW (1987) World overview of the interactions between honeybees and other flora and fauna. In: Blyth JD (ed) Beekeeping and land management. Department of Conservation of Land Management, Como, pp 40–47

Thorp RW, Wenner AM, Barthell JF (1994) Flowers visited by honeybees and native bees on Santa Cruz Island. See Halvorson and Maender 1994, pp 351–365

Tierney SM (1994) Life cycle and social organization of two native bees in the subgenus *Brevineura*. Unpublished BSc (Hons) thesis, Flinders University South Australia

Torchio PF (1987) Use of non-honey bee species as pollinators of crops. Proc Entomol Soc Ont 118:111–124

Velthuis HHW, van Doorn A (2006) A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. Apidologie 37: 421–451

Verma LR (1994) Honeybee pollination strategies for sustainable agriculture and conservation of biodiversity in Hindu Kush-Himalayan Region. In: Proceedings of regional conference. Environment and Biodiversity, Kathmandu, Nepal, 1994, pp 157–162

Visscher PK, Seeley TD (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology 63:1790–1801

Vitousek PM (1994) Beyond global warming: ecology and global change. Ecology 75:1861–1876

Vogel S, Westerkamp C (1991) Pollination: an integrating factor of biocenoses. In: Seitz A, Loeschoke V (eds) Species conservation: a population-biological approach. Birkhäuser Verlag, Basel

von Frisch K (1967) The dance language and orientation of bees. Harvard University Press, Cambridge

Waser NM (1982) A comparison of distances flown by different visitors to flowers of the same species. Oecologia 55:251–257

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043–1060

Washitani I (1998) Conservation-ecological issues of the recent invasion of *Bombus terrestris* into Japan. Jpn J Ecol 48:73–78 (in Japanese)

Washitani I, Morimoto N (1993) Alien plants and animals naturalized in Japan. Hoikusya, Tokyo (in Japanese)

Washitani I, Suzuki K, Kato M, Ono M (1997) A field guide to bumblebees. Bun-ichi-sogo shuppan, Tokyo (in Japanese)

Wenner AM, Thorp RW (1994) Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. See Halvorson and Maender 1994, pp 513–522

Westerkamp C (1991) Honeybees are poor pollinators – 2 why? PI Syst Evol 177:71–75

Whitten M (1979) Genetics of the honey bee in Australia. Rockefeller Foundation, New York, USA

Williams PA, Timmins SM. 1990. Weeds in New Zealand protected natural areas: a review for the Department of Conservation. Science Research Series No. 14, Department of Conservation, Wellington, 114 pp

Wills RT, Lyons MN, Bell DT (1990) The European honey bee in Western Australian kwongan: foraging preferences and some implications for management. Proc Ecol Soc Aust 16:167–176

Wilms W, Wiechers B (1997) Floral resource partitioning between native *Melipona* bees and the introduced Africanized honey bee in the Brazilian Atlantic rain forest. Apidologie 28:339–355

Wilms W, Wendel L, Zillikens A, Blochtein B, Engels W (1997) Bees and other insects recorded on flowering trees in a subtropical Araucaria forest in southern Brazil. Stud Neotrop Fauna Environ 32:220–226

Wilson P, Thomson JD (1991) Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. Ecology 72:1503–1507

Winston ML (1994) The Africanized "Killer" bee: biology and public health. Invited review, Q. Rev. Medicine 87:263–267

Wolda H, Roubik DW (1986) Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. Ecology 67:426–433

Woodward DR (1996) Monitoring for impact of the introduced leafcutting bee, *Megachile rotundata* (F) (Hymenoptera: Megachilidae), near release sites in South Australia. Aust J Entomol 35:187–191

Wratt EC (1968) The pollinating activities of bumble bees and honey bees in relation to temperature, competing forage plants, and competition from other foragers. J Apicult Res 7(61):66

Yokoyama J, Matsumura C, Nakajima M, Sugiura N, Matsumoto M, Kato M, Suzuki K, Washitani I (2004) Evaluation of present status on naturalization of introduced bumblebee, *Bombus terrestris*, and development of extermination procedure against the species for conservation of native bumblebee species (2). Ann Rep Pro Natura Fund 13:47–54 (in Japanese)

Zhen-Ming J, Guanhang Y, Shuangxiu H, Shikui L, Zaijin R (1992) The advancement of apicultural science and technology in China. In: Verma LR (ed) Honeybees in mountain agriculture. Oxford/IBH Publishing Co Pvt Ltd, New Delhi, pp 133–147

Zimmerman M, Cook S (1985) Pollinator foraging, experimental nectar-robbing and plant fitness in *Impatiens capensis*. Am Midl Nat 113:84–91

Chapter 20
Genetically Modified Plants and Bees

Abstract Genetically modified crops which have opened new avenues of species alteration has been accompanied by concerns of their adverse effects on nontarget organisms such as bees. GM crops are commercially modified for pest and or herbicide resistance. Transgenes such as BT may be expressed in pollen and in the plant parts and secretions collected by bees. Available information suggests that crops transformed with genes coding for Bt proteins donot harm bees. Similarly, herbicide resistant crops are not likely to pose direct toxicity to bees yet greater weed control in herbicide resistant crops may be responsible foe lower bee abundance in these crops than the non transformed ones. However, reduced use of pesticides with insect resistant GM crops and reduced tillage that is possible with herbicide resistant crops could be beneficial to bee populations compared to conventional agriculture. Evidently risk of GM crops should be assessed on a case by case basis in relation to feasible alternatives.

20.1 Introduction

Genetic engineering of crop plants has opened a new era of species alteration what was not possible with traditional plant breeding or mutagenesis. As a consequence entire community of life has become a source of new genes for crops (Chrispeels and Sadava 2003). Accompanying the creation of novel crop varieties is the potential for environmental impact, beneficial or harmful. Commercialization of genetically modified crops is not without adverse effects on nontarget organisms. Bees are nontarget organisms that have intrinsic environmental value and that also directly benefits crop production through their role as pollinators, making the question of how GM crops affect bees an economic as well as a conservation issue. Genetic modification does not refer to one or even a few type of alterations of plants, but rather to a process that is used to insert novel genes that that can be as widely different

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from each other as they may be from the environmental impacts they cause. Evidently, there is no simple answer to the question of potential harm to bees or other organisms from GM crops.

Crops have systematically been improved through plant breeding for over 150 years programs for tolerance to pests and abiotic stresses resulting in improved productivity, processing and nutritional characteristics (Beversdorf 1993). Although world hunger may be more related to food distribution and unequal assess than to insufficient food production per se (Matson et al. 1997) further agricultural expansion, cultivar improvement and intensification are inevitable (Tilman et al. 2001) with the world's population expected to grow from 6.5 billion at present to over 9 billion by 2050 (U.S. Census Bureau 2008). Despite controversy, cultivation of GM crops is an integral present and future component of agricultural development.

The DNA of all organisms is fundamentally identical, so that genes and parts of genes can be exchanged. In the 1970s the first recombinant organisms were created and by the mid-1980s field trials had begun with GM crop plants. By the year 2004, 17 countries around the world were growing at least one transgenic crop. The leaders in GM crop production by area grown (millions of ha: percent of total) are the United States (47.6; 59%), Argentina (16.2; 20%), Canada (5.4; 6%), Brazil (5.4; 6%) and China (3.7; 5%). The rate of commercialization of GM crops has considerably increased since 1996. Twenty-nine percent of corn, cotton soybean and canola are now genetically modified globally. Herbicide tolerance has been the dominant trait introduced into crop species (97.2% of GM acreage), followed by insect resistance (19% of GM acreage; James 2005).

Genetically modified, "transgenic" plants (GM plants) carry genetic information derived from other organisms (bacteria, plants or animals), or have been modified by genetic engineering to provide them with new properties. Genetically modified (GM) plants manifest new traits via the production (expression) of novel proteins encoded by inserted transgenes (DNA). Many insect resistant crops carry genetic information originally derived from the soil bacterium *Bacillus thuringiensis.* This gene enables the bacteria or the GM plant to produce a protein with insecticidal activity. Therefore, the crop plant can protect itself against insect pests. There are numerous variants of the gene, encoding different proteins active in a highly specific manner against defined groups of insects. For example, cotton modified to contain a Bt (*Bacillus thuringiensis*) gene and expressing Bt insecticidal protein in its leaves and buds will be protected from caterpillar attack. Both the transgene DNA and the novel protein in such plants could be considered "GM material". Cry3B is one of these proteins with activity against beetles.

Bees and plants are inseparable and depend upon each other for their survival and perpetuation of race. Bees collect pollen and nectar from plants as food for their colonies. They may also collect honeydew (plant sap that has been ingested and then excreted by sucking insects such as aphids) for food and plant resin to make propolis with which to seal up cracks in the hive. With GM plants, there is a possibility that transgene DNA and/or novel proteins may be present in the plant parts and secretions collected by bees. Unfortunately new technologies often are adopted before environmental impact are reasonably well understood. Neglecting environmental impacts of agriculture threatens to disrupt ecosystem services such as pollination, possibly reducing or eliminating any yield benefit from agricultural intensification and expansion. Two fundamental questions regarding genetically modified crops and bees are (1) whether GM crops have an impact on bees and bee populations either negatively or positively, and if so (2) whether the GM crops have an impact on bees, will this affect crop pollination and yield (Brødsgaard et al. 2001). Since ees are primary agents for cross pollination of several crops travelling considerable distances and potentially causing crossing of GM and non-GM crops. A hive may contain up to 50,000 bees and individual bees may visit up to 100 flowers on each trip out. Hive products intended for human consumption and derived from the plant parts collected by bees include honey (from nectar or honeydew, and containing traces of pollen), pollen and propolis. Honey can be contaminated by GM pollen, leading to potential economic losses for beekeepers. Evidently, there is a need to analyse whether Cry3B proteins have negative effects on honeybees. Other products, such as pure royal jelly, bee venom and beeswax, are secretions from the bees themselves and would not be expected to contain any plant matter.

In this chapter an attempt has been made to explore the impact or lack of impact of GM plants on bees and the crop pollination, and also suggest research that should be done to mitigate the negative effects of genetically modified crops on bees.

20.2 GM Material in Plant Parts Collected by Bees

For the purposes of this discussion, "GM material" is defined as either transgene DNA or novel proteins encoded by transgenes. (This is also the definition used in the Australian and New Zealand Food Authority (ANZFA) regulations concerning food labelling in relation to GM.) Plant parts collected by bees are pollen, nectar, resin or honeydew (sap that has passed through the digestive system of a sap-sucking insect). In GM plants, transgene DNA may occur in any plant tissue which normally carries DNA, but the novel protein which it encodes will not necessarily be expressed in every tissue, since this process is directed by the promoter (switch) on the gene in question. There are many different promoters available to genetic engineers. Some switch on transgene expression in all parts of the plant, while others switch it off in all but one tissue (e.g. a root-specific promoter). Potential for GM material to be collected by bees.

20.2.1 Pollen

Since pollen is a plant tissue composed of cells capable of protein synthesis, it is reasonable to expect to find transgene DNA in pollen grains and also novel protein, if the transgene's promoter permits it. Table 20.1 presents currently available data on novel protein expression levels in pollen from GM plants. Compared to leaves,

Table 20.1 Expression of novel proteins in pollen of GM plants

Plant	Novel protein encoded by transgene	Promoter	Expression level of novel protein in pollen	Expression level as% of total soluble protein (estimated)[a]	References
Maize	Bt toxin	Maize pollen specific and PEP[b] (leafspecific) promoters	260–418 ng/mg (of total soluble protein)	0.026–0.0418	Kozeil et al. (1993)
Cotton	Bt toxin	Cry 1Ac CaMV 35S[c]	0.6 µg per g fresh weight	0.00024	Greenplate (1997)
Oilseed rape	Oryzacystatin I	CaMV 35S[c]	Nil	0	Bonadé Bottino et al. (1998)
Oilseed rape	Bowman-Birk trypsin inhibitor	CaMV 35S[c]	Nil	0	Jouanin et al. (1998)
Oilseed rape	nptII (kanamycin resistance)	NOS	1.61 ng/mg of total protein	0.000161	Anon A (1998)
Cotton	Bt toxin	Cry1Ac CaMV 35S[c]	11 ng/g fresh weight	0.0000044	Anon V (2001)

[a] Values expressed as a proportion of fresh pollen weight in the original reference have been converted using the assumption that fresh pollen is 25% protein

[b] Phosphoenolpyruvate

[c] Cauliflower mosaic virus 35S promoter

which are about 2% protein, pollen has a high protein content, estimated to be between 8% and 40% (Herbert 1992), and for this reason transgenes may be expected to express novel proteins at reasonable levels in pollen. However, one of the most commonly-used promoters in GM plants, cauliflower mosaic virus (CaMV) 35S promoter, does not drive pollen expression particularly well. For example, in leaves, this promoter can drive expression of novel proteins such as protease inhibitors up to about 0.4% of total protein, but the same protein will be undetectable in the pollen of the those plants (Bonadé Bottino et al. 1998). The highest recorded level of a novel protein expressed in pollen via the CaMV 35S promoter is 0.6 μg per g pollen (fresh weight) for a Bt toxin in cotton (Greenplate 1997). This is equivalent to 0.00024% w:w of total soluble protein, assuming the pollen is 25% protein (Table 20.1).

Higher levels of novel proteins may occur in pollen if the transgene includes a pollen specific promoter such as that derived from maize (Kozeil et al. 1993). Expression levels as high as 0.0418% w:w of total soluble protein have been recorded for a Bt toxin with this promoter in maize pollen (Kozeil et al. 1993; Table 20.1). This type of GM Bt-maize (referred to as an event 176 hybrid) was used as the source of insecticidal pollen in the much-publicised early monarch butterfly studies of Losey et al. (1999) and Jesse and Obrycki (2000). Subsequent studies compared the effects of event 176 pollen with that of other Bt-maize hybrids in which the gene was controlled by the CaMV 35S promoter (referred to as MON810 or Bt11 hybrids). Pollen from the latter hybrids had negligible effects on monarch larvae (Stanley-Horn et al. 2001; Hellmich et al. 2001). The registration of maize hybrids derived from event 176 will terminate in the United States in 2001 (Stanley-Horn et al. 2001). New biotechnological developments aimed at eliminating the problems associated with transgene DNA and expression of novel proteins in pollen are discussed in Sect. 20.4. The motivation for these developments centres mainly on concerns about gene flow to other plants and allergens in pollen, rather than for bees and bee products.

In summary, it is possible that GM material could occur in pollen harvested for human use from hives placed where bees may forage from GM crops. The actual concentration will depend on how much GM pollen is taken relative to pollen from other plants and how much transgene DNA or novel protein the GM plant produces in its pollen. Similarly, pollen containing GM material could also be present in honey harvested from bees foraging on GM crops.

20.2.2 Nectar

Nectar is a plant secretion, rather than a tissue, and has no cellular content. As such, transgene DNA is not likely to occur in nectar and there are no records of any RNA or DNA in nectar. Most nectars are also free of protein, being composed principally of sugars and sometimes free amino acids (Baker and Baker 1973, 1977). There are exceptions to this however. Recently, tobacco plants have been found to secrete a limited array of proteins to a concentration of about 0.024% protein of total nectar (Carter et al. 1999). Leek nectar has also been shown to contain two proteins, a lectin and an alliinase, comprising about 0.022% of the nectar (Peumans et al. 1997). Both of these proteins were inactivated or degraded when leek nectar was made into honey by bees, presumably by the action of enzymes in the bee's honey stomach. Incidentally, these authors also found two new proteins in the honey that had no equivalents in leek nectar and concluded that these must have come from the bees themselves (e.g. enzymes secreted by the honey stomach). Consequently, it is theoretically possible that some GM plants could secrete novel proteins with their nectar, although their concentrations are likely to be very low. Consequently, bees could gather such nectar, but the honey they make from it may not necessarily contain the nectar proteins in active form. Presumably because of nectar's low protein content, there has been only one record of an examination of nectar from a GM plant. Jouanin et al. (1998) noted that Bowman-Birk soybean trypsin inhibitor (BBI) could not be detected in the nectar (or pollen) of transgenic oilseed rape plants containing the BBI gene under the control of CaMV 35S promoter.

20.2.3 Plant Resins and Gums

There are no records of DNA or RNA being detected in plant gums or resins. Proteins, however, have been recorded from some of these plant secretions. For example, gum arabic (from *Acacia* species) is 2–4% protein (Menzies et al. 1996) and proteins have been recorded from pea root mucilage and rye root exudate (Knee et al. 2001; Siciliano et al. 1998). There are no references to the presence of either DNA or RNA in propolis. The composition of propolis varies from sample to sample due to the variety of plant resins and gums utilised by the bees and the collection techniques used by beekeepers to obtain propolis from the hive. One report describes a propolis with a protein content of about 2.5% (Tuha and Simuth 1991). Novel proteins from GM plants may conceivably find their way into the gums, exudates and resins that bees collect to make propolis, but there is, as yet, no published evidence to support this idea.

20.2.4 Plant Sap and Honeydew

Honeydew is excreted by sap-sucking insects such as aphids. As well as the sugars that predominate, phloem sap also contains free amino acids, small peptides and sometimes proteins (Salvucci et al. 1998). For example, phloem exudates from squash, cucumber and castor oil plant have been shown to contain proteins, some of which appear to be important in the transport of plant viruses (Christeller et al. 1998; Kruger et al. 2001; Schobert et al. 2000; Owens et al. 2001). Similarly plant mRNA (messenger RNA) is known to circulate in plants (translocate) via the phloem

(Oparka and Santa-Cruz 2000). Thus, phloem sap from GM plants could conceivably contain both transgene mRNA and novel proteins. There are no published studies describing the fate of plant RNA after digestion by plant-sucking insects and no records of RNA or DNA in the honeydew they excrete. However, a DNA-tracking study has shown that squash leaf curl virus can pass intact through the guts and into the honeydew of whiteflies (Rosell et al. 1999). It is commonly thought that sucking insects lack digestive proteases and utilise only the free amino acids in sap for their nitrogen needs (e.g. Rahbé et al. 1995; Sandström and Moran 2001). From this it might be concluded that sap proteins would pass into honeydew intact. However, when whiteflies were fed with labelled cotton leaf proteins, these were digested and excreted only as amino acids in the resultant honeydew (Salvucci et al. 1998). Thus it remains debatable whether or not novel proteins from transgenic plants could find their way into honeydew and if they would persist in honey made from it.

20.3 Records of GM Material in Bee Products

Currently two methods may be used to determine the GM status of foods. With the polymerase chain reaction (PCR) test for transgene DNA, a "primer" (consisting of a piece of DNA with a sequence that could only occur in the transgene) is added to a sample of the food to be tested. If the primer matches any DNA in the sample, then the PCR will cause this DNA to be "amplified". The amplified DNA can then be stained and visualised to give an indication that the sample contains some transgene DNA. With quantitative PCR, the concentration of transgene DNA in the sample may also be estimated. Theoretically this method is very sensitive and can detect even one or two pieces of transgene DNA in a sample. In practice, its sensitivity will depend on the *Nature* of the food being tested and the transgene DNA sequence that is being sought. For example, a study of GM soyabeans and maize (Lin et al. 2000) showed that PCR using a CaMV 35S primer had a detection limit of 0.1% w:w of GM soyabeans, but with a nos (nopaline synthase) primer the test had a limit of 1%. With a CDPK-cry (maize calcium-dependent protein kinase promoter with Bt toxin) primer, PCR had a detection limit of 0.1% w:w for GM maize and with a cry1Ab (Bt toxin) primer the limit was 2%. The second detection method uses enzyme-linked immunosorbent assay (ELISA) to detect novel proteins in food. With this method, an antibody to the novel protein in question is prepared and linked to an enzyme which catalyses a reaction resulting in a coloured end-product. The enzyme-linked antibody is added to the food sample and, if the novel protein is present, it links to the protein and cannot be washed away. The colour reagents are then added and the intensity of the coloured end-product gives a measure of the concentration of the novel protein in the food.

Pollen represents the most likely source of transgene DNA and novel proteins in bee products. It is also commonly present in the most widely-consumed bee product, honey. Because of this, the only attempts to measure GM material in bee products have focussed on honey and its pollen "contaminant". There are no records of attempts to detect GM material in honey from honeydew, pollen intended as human food or propolis. Most New Zealand honeys (including clover honey) contain between 20,000 and 100,000 pollen grains per 10 g (Moar 1985). This is considered the "normal range", but some honeys have pollen concentrations above or below this range. Molan (1998) states that concentrations as low as 500 grains and as high as 5 million per 10 g are possible. In the United Kingdom, shop-bought honeys were found to contain between 20,000 and 80,000 grains per 10 g (Anon 1998). Eady et al. (1995) found 100,000 pollen grains per ml in a commercial honey derived from garden flowers (in the UK). If we assume that an "average" pollen grain weighs 0.03 μg (Stanley and Linskens 1974), then these figures translate as follows:

500 grains per 10 g is equivalent to 0.00015% w:w pollen in honey
20,000 grains per 10 g is equivalent to 0.006% w:w pollen in honey
80,000 grains per 10 g is equivalent to 0.024% w:w pollen in honey
100,000 grains per 10 g is equivalent to 0.03% w:w pollen in honey
100,000 grains per ml is equivalent to 0.3% w:v pollen in honey
5 million grains per 10 g is equivalent to 1.5% w:w pollen in honey.

The stability of transgene DNA and novel proteins in GM pollen stored in honey has been assessed using pollen from modified tobacco and *Arabidopsis* plants with marker genes on pollen specific promoters (Eady et al. 1995). A PCR test showed that transgene DNA remained "relatively intact" even after 7 weeks in a commercial honey sample. Similarly, novel protein was detected unchanged after 6 weeks in honey. The authors pointed out that the experimental system they used represented a "worst-case scenario" for the presence of GM material in honey and that "the concentration of a given, potentially toxic pollen-borne protein is expected to be very low in natural honey made from nearby transgenic plants". However, they also pointed out that even vanishingly small quantities of some proteins may cause allergic reactions.

There are only two published studies of attempts to measure GM material in natural honey made by bees foraging near GM plants. The first was carried out by the UK Ministry of Agriculture, Fisheries and Food (now the Department for Environment, Food and Rural Affairs) (Anon 1998a, b). In this study a sample of honey was taken from a "hive close to a transgenic oilseed rape field", pollen extracted from it and ELISA used to quantify the amount of npt II protein (which confers kanamycin resistance) present. Two readings from the single sample gave a mean of 1.61 ng per mg (0.00016% w:w) of total protein in the pollen sample. A control sample of nontransgenic oilseed rape honey was not included. Pollen samples taken from two GM tobacco plants containing the same transgene construct (nptII and nos promoter) gave mean readings of 35.1 pg and 1.39 ng of nptII protein per mg of total protein (3.51 × 10–6% and 0.000139%, respectively). This report also stated that DNA could be extracted from a number of commercially available honey samples and from honey derived from transgenic oilseed rape (presumably the same sample used in the protein analysis), but the details of this part of the study are not given in the report.

The second study was commissioned by Friends of the Earth in the UK (Anon B 2000; Anon C 2000), who were concerned that pollen from unidentified GM-oilseed rape field research sites could occur in honey without beekeepers' knowledge. They purchased 11 jars of locally produced honey and honey comb from retail outlets in an area of England where GM herbicide-tolerant oilseed rape crops had been trialed. Each sample was checked for oilseed rape pollen content and nine of the samples found to contain significant quantities (actual amounts and detection limits not stated) of this pollen. Sub-samples were taken from these honeys and sent to the Austrian Federal Environmental Agency Laboratory. PCR was used to determine whether any of the samples contained DNA sequences corresponding to the herbicide-tolerance gene (bar or pat gene) and the nos gene promoter or terminator used in such GM oilseed rape plants. Two of the nine samples gave positive results for the pat gene and the nos promoter, suggesting that pollen from GM oilseed rape had found its way into honey. Unfortunately, Friends of the Earth could not afford to have a quantitative analysis conducted which would have shown how much GM pollen might be in the honey (Anon B 2000). The apparent lack of appropriate controls in this study (honey from a region where only non-GM oilseed rape was grown) is also unfortunate. The bar, pat and nos genes are all derived originally from common bacteria (*Streptomyces* and *Agrobacterium*) (Wehrmann et al. 1996), suggesting that they may commonly contaminate natural products such as honey. Bar, pat or nos DNA from these bacteria would also give positive results with the PCR tests conducted. While it may be argued that this is unlikely, inclusion of suitable controls would have removed all doubt from this study. The results of this honey study have subsequently been used by Friends of the Earth and UK beekeepers to call for a halt to field research on GM plants, particularly a series of "farm-scale" trials of GM herbicide-tolerant crops which commenced in the UK in 1999. Diamand (1999) gives further details of this campaign.

20.3.1 GM Plants Occurring in Hive Products

The relevance of this to the production and marketing of bee products will depend on the tolerance limits for GM material in food. GM plants are now being grown commercially in 13 different countries. In 2000, the estimated global area planted with these crops was 44.2 million hectares (James 2000). Ninety-nine percent of these crops were grown in the USA, Canada, Argentina and China. Herbicide-tolerant soybean was the most common GM crop, occupying 59% of the global area, followed by Bt corn (maize), herbicide-tolerant canola (oilseed rape), herbicide-tolerant corn, herbicide-tolerant cotton, Bt/herbicide-tolerant cotton, Bt cotton and Bt/herbicide-tolerant corn. In addition to these commercially available varieties, many other plants can now be genetically modified. Field trials are under way overseas for field crops (e.g. wheat, rice, barley, tobacco), flowers (e.g. roses, carnations), trees (e.g. poplar, spruce, sweet gum), oil crops (e.g. sunflower, peanut), grasses, sugar crops (beet and cane), fruits (e.g. apple, cranberry, grape, melon,

Table 20.2 Crops which could be genetically modified and their relevance to honey bees

Crops for which GM varieties might become available	Role of honey bees in relation to crop	Potential hive products from crop
White clover	Very important nectar source and pollen source to a lesser extent; bees required for seed production	Honey; pollen
Maize	Bees may collect pollen if no other forage available	
Potato	Bees may visit, but flowers have no nectar, little pollen	
Vegetable brassicas	Good source of nectar and pollen (to a lesser extent); bees required for seed production when crop not self fertile	Honey; pollen
Cotton	Source of pollen and nectar	Honey; pollen
Apples	Source of pollen and nectar (to a lesser extent); bees required for adequate pollination	Pollen; propolis?
Eucalyptus	Ornamental species are good source of nectar and pollen (to a lesser extent)	Honey; pollen; propolis?

strawberry) and vegetables (e.g. tomato, potato, broccoli, carrot, eggplant, lettuce, pea). Of the commercial crops, white clover is the most important for honey production. Trees grown for shelter (e.g. willow, hawthorn) and for fruit (e.g. apple, pear) and field crops (e.g. *brassicas*, sunflowers) can also be useful sources of forage for bees. Bees are also used to pollinate crops for fruit, vegetable and seed production. There have also been reports of bees visiting plants such as corn, grasses and potatoes in the absence of better sources of forage and of the occurrence of traces of pine pollen in honey. Since pollen is a plant tissue composed of cells capable of protein synthesis, it is reasonable to expect to find transgene DNA in pollen grains and also novel protein, if the transgene's promoter permits it. Table 20.1 presents currently available data on novel protein expression levels in pollen from GM plants. Thus, if modified, some of these plants might represent sources of GM materials that could be collected by bees. Compared to leaves, which are about 2% protein, pollen has a high protein content, estimated to be between 8% and 40%, and for this reason transgenes may be expected to express novel proteins at reasonable levels in pollen. Crops which could be genetically modified and their relevance to honey bees are listed in Table 20.2.

20.4 Is GM Honey Safe?

Honey contains pollen grains from plants that bees have visited, and can therefore be contaminated by GM pollen. It is not known what effect honey containing GM pollen could have on people consuming it. For example, the novel proteins produced by GM crops can also be present in their pollen are already cases of people who are allergic to honey, and this has been linked to pollen in the honey. Genetic engineering is imprecise and unpredictable. Genes are inserted from organisms which have never been eaten as food, and so new proteins are introduced into the human and animal food chains. There is concern that these could cause allergic reactions or other health effects.

There are between 20,000 and 80,000 pollen grains in a portion (10 g) of honey. This means that honey containing GM pollen could pose a potential health risk. The researchers who studied this problem concluded that if GM pollen contained novel toxins or proteins it “could pose problems, not only to man who consumes honey as a food, but also to bee populations which rely on pollen as the sole source of protein”.

It has been found that bees can pass proteins from nectar unchanged into honey. If GM crops produce novel proteins or toxins in the nectar as well, this may further threaten the safety of honey produced from GM crops. GM plants may also contain genes which provide resistance to commonly used antibiotics such as ampicillin. There is concern that these could be passed on to the bacteria that live in humans and animals. DNA from pollen has been found to be able to survive in honey for 7 weeks. It may be that this could be a route for such gene transfer. In spite of the risks, there has been almost no safety testing of GM pollen, either for humans or for bees. Even the food safety tests of GM crops have been limited to short-term tests on animals.

20.5 Bees and Gene Pollution

Honey bees commonly forage up to 2 km from the hive, but oilseed rape fields are such an attractive source of nectar that bees may travel at least 5 km to get to them. When the oilseed rape was in flower, it made up 70% of the pollen that the bees carried back to the hive. One bee returning to the hive had 60,000 oilseed rape pollen grains stuck to its body. As the bees brush past each other in the hive any GM pollen is spread throughout the colony and taken out again by other bees. Not only are bee hives near to GM oilseed rape fields likely to become contaminated with GM pollen, but the bees may spread GM pollen to non-GM crops several miles away. It is likely that in the future farmers will be growing oilseed rape for the “GM-free” market. In such cases, contamination of the crop could cause financial loss to the farmer. At the moment it is unclear who would be held liable for this, and whether the beekeeper might be held responsible as well as the farmer who grows the GM crop.

20.6 Impact on Beekeepers

As it stands, GM crops pose a serious threat to beekeepers and honey production. Honey contaminated with GM pollen will either have to be disposed of safely or sold as a GM product. Either of these options is likely to cause financial harm to beekeepers.

20.6.1 Impact on Wild Bees

Wild bees are vital for the survival of many of our wild plants, as well as being important for crops. Some species of wild plants are dependent on wild bees for their pollination and survival. Several species of bumblebees and solitary bees are also important pollinators for food crops. The decline of bumblebees and solitary bee populations has been linked to modern intensive farming. The widespread use of herbicides and the increased intensity of farming has removed the habitats that wild bees make nests in, and reduced the numbers of wild plants which they use for food. The widespread use of GM herbicide-tolerant crops is likely to threaten further wild bee populations.

It is clear that growing GM crops pose a serious threat to beekeepers and honey production. Issues around food safety, liability, the cost to beekeepers and the threat to wild bee populations have yet to be resolved. Vital questions need to be answered and there needs to be a full public debate on the acceptable uses of genetic engineering.

20.7 Bt Insect Protection of Crops and Honey Bees

Genetically modified crops are being blamed for the declining number of bees? Though scientists from France have allegedly determined that *Baccillus Thuringiensis*, a bacteria normally found in the soil, and which has been widely used to develop various genetically modified crops, is behind deaths of honey bees (Amos 2009). However, there findings have not been supported by many researchers. There is strong evidence that the production of specific insecticidal proteins from the soil bacterium *Bacillus thuringiensis* (Bt) in crops to control targeted caterpillar pests and beetles does not pose a risk to honeybees.

There is extensive information on the lack of non-target effects to diverse groups of beneficial insects including honey bees and other pollinators from Bt microbial preparations that contain Bt proteins. Bt proteins are ideal for use in organic production and in Bt crops because they bind specifically to receptors on the mid-gut of sensitive caterpillar pests and have no deleterious effect on beneficial/non-target insects under the conditions of use, including predators and parasitoids of targeted caterpillar pests and honeybees. Extensive studies on honeybee safety assessments on all insect-protected crops, including Bt corn and Bt cotton have shown that the Bt proteins in these crops have no adverse effect on the honeybee. Specific studies involving Cry1Ab provide strong evidence of the safety of MON 810 Bt corn to the honeybee (similar studies have been conducted with other Bt proteins in genetically modified crops). The EPA concluded that based on the weight of evidence there are no unreasonable adverse effects of the Cry1Ab protein expressed in MON 810 Bt corn to non-target wildlife or beneficial invertebrates.

There is extensive information on the lack of non-target effects to diverse groups of beneficial insects including honey bees and other pollinators from Bt microbial preparations that contain Bt proteins. The Bt proteins produced in Bt corn and Bt cotton are present in microbial products used in agricultural systems to control targeted pests. Bt proteins are extremely selective and are toxic only to specific pests. A generalized mode of action for Bt proteins includes ingestion of the protein crystals by insects, solubilization of the crystals in the insect midgut and proteolytic processing of the released Bt protein by enzymes, and binding of the partially digested "activated" protein to specific high-affinity receptors on the surface of the midgut epithelium of target insects. Bt proteins are ideal for use in organic production and in Bt crops because they bind specifically to receptors on the mid-gut of sensitive caterpillar pests and have no deleterious effect on beneficial/non-target insects.

20.8 Safety Assessment of Bt Crops

EPA evaluated studies of potential effects on a wide variety of non-target organisms that might be exposed to the Bt protein, e.g., birds, fish, honeybees, ladybugs, parasitic wasps, lacewings, springtails, aquatic invertebrates and earthworms. Such non-target organisms are important to a healthy ecosystem, especially the predatory, parasitic, and pollinating insects. These risk assessments demonstrated that Bt proteins expressed in Bt crops do not exhibit detrimental effects to non-target organisms in populations exposed to the levels of Bt proteins produced in plant tissues. To illustrate how the different Bt proteins produced in Bt crops are evaluated for safety to the honeybee, two representative studies are described below for the Cry1Ab protein produced in MON 810 Bt corn. These studies with Cry1Ab protein were conducted with the trypsin-resistant core because this is the insecticidally-active portion of the Cry1Ab protein. Specific studies designed to assess the potential for adverse effects to developing larval and adult honeybees are described below.

20.8.1 Honeybee Larva

The primary route of exposure for honey bee larvae to the Cry1Ab protein is ingestion of pollen collected by foraging adults from genetically modified plants. Therefore, honey bee larvae were exposed to Cry1Ab protein in their natural diet by including a maximum hazard dose (20 ppm in distilled water mixed with honey) in developing brood cells. This maximum nominal concentration of 20 ppm was approximately 100 times greater than the maximum expected Cry1Ab protein level in MON 810 pollen. In addition to this treatment group, a negative control group was treated with distilled water. Another control group was treated with heat-attenuated (inactivated) Cry1Ab protein (20 ppm), and one set of larvae received no treatment (untreated control). At least 50 bees (1–4 days old) were in each replicate, and there were three replicates for each group. The treatments were administered to each larval cell through an electronic micro-applicator, which delivered 5 µl (?L) of the test diet.

There were no statistically significant ($P > 0.05$) differences in honeybee larval survival to adult emergence among the four treatment groups. The mean adult survival rates after emergence ranged from 91.7% to 96.0% across all groups, including the controls and Cry1Ab-treated groups. This study demonstrates that honeybee larvae were not adversely affected after being exposed to Cry1Ab protein at a concentration of 20 ppm in their diet.

20.8.2 Adult Honeybee

Adult bees reared in bee hives were immobilized using CO_2. The test diet was prepared by mixing the appropriate amount of the insecticidally-active Cry1Ab protein with a honey–water (50–50) syrup to a concentration of 20 ppm (µg protein/g diet; ppm). The negative control group was fed the same diet with the exception that no Cry1Ab protein was added to the honey–water mixture. A second control group was fed heat-attenuated (inactivated) Cry1Ab protein at the same concentration (20 ppm) as the treatment group. A fourth test system was an empty cage to measure the amount of diet loss due to evaporation. All diets were presented to the bees in a 6 ml shell vial inserted through a cork in the holding cage lid. Three replicates of four test groups of at least 40 adult honeybees were selected and placed in each holding cage. Two observations were made the first day and were made daily for the duration of the 9-day study. At the time of the daily observation, the test diets were replaced with free.

Adult honeybees exposed to the Cry1Ab protein in a honey–water solution for 9 days at a concentration of 20 ppm showed no signs of treatment-related mortality or toxicity. At the end of the testing period, the mortality percentage was calculated for each group. Mortality in the treatment and the negative control groups was 16.20% and 22.28%, respectively. The heat-attenuated control group mortality was 32.59%. Mortality showed a sharp increase in all three groups from days 6 through 9. At the termination of the test, the highest mortality was observed in the group that was fed the heat-attenuated Cry1Ab protein diet, while the lowest mortality was observed in the group that was fed the Cry1Ab protein diet. The mortalities in the treatment group are not considered to be treatment-related because the two control groups showed a higher percentage of mortality over the same time interval. There was no significant statistical difference ($P > 0.05$) in mortality patterns between any of the groups.

The studies concluded that based on the weight of evidence there are no unreasonable adverse effects of the Cry1Ab protein expressed in MON 810 Bt corn to non-target wildlife or beneficial invertebrates. They reported no measurable deleterious effects were observed in submitted studies of the Cry1Ab protein administered to honey bee larvae, honey bee adults, parasitic wasps, Ladybird beetles, green lacewings, Collembola (springtails), and Daphnia.

Arpaia (1996) found that the development of the larvae, the pupal weight and the number of bees in the Bt-exposed colonies were not affected. The conclusion of these experiments was that for honeybees no negative effects of GM crops producing the Cry3A protein are to be expected. Very similar experiments have also been conducted for numerous other Bt proteins, for example for Cry1Ab produced in MON810 maize plants (Babendreier et al. 2005). In no instance, negative effects of Bt proteins on the health of honeybees have been published (Malone et al. 1999; Malone and Pham-Delègue 2001, 2002; Keil et al. 2002; Malone 2004; O'Callaghan et al. 2005; Sanvido et al. 2006). Also other aspects of the honeybee's development were investigated. Several scientists looked at possible effects of Bt protein on the hypopharyngeal glands of worker bees, where protein rich food for the brood is produced. Neither for Cry1Ba (Malone et al. 2004) nor for Cry1Ab (Babendreier et al. 2005, 2006), detrimental effects of the purified insecticidal proteins were observed.

Honeybee's flight activity likewise was unaffected by Cry1Ba (Malone et al. 2001). In one case, a possible effect of Cry1Ab on the foraging activity was reported. However, this single experiment was carried out in winter, without direct comparison to untreated bees, and has not been repeated since, so that it is difficult to derive firm conclusions from this observation (Ramirez-Romero et al. 2005). Even the gut flora of honeybees, which is important to their health, was tested for its sensitivity against Cry1Ba; no effect was observed (Babendreier et al. 2007). Taken together, no evidence for risks to honey bee's health from Bt proteins used in GM crops has been reported in the scientific literature so far.

20.9 Potential Impacts of GM Plants on Bee Health

Although not directly related to the presence of GM material in bee products, there may be impacts of GM plants on bee health that could affect on the bees' ability to produce honey, pollen and propolis. There is a growing body of published research on the impacts of GM plants and novel proteins on bee health (Table 20.3). This research has recently been reviewed (Malone and Pham-Delègue 2001, 2002; Pham-Delègue et al. 2002). These reviews are summarized below. GM plants may have direct or indirect effects on bees. Direct effects are those that arise when a bee ingests a novel protein expressed by a GM plant. Indirect effects may arise if the process of introducing the transgene into the plant results in inadvertent changes to plant phenotype affecting its attractiveness or nutritive value to bees.

20.10 Direct Effects of Novel Proteins on Bees

Potentially, the ingestion of a novel protein expressed in pollen or perhaps occurring in nectar, resin or honeydew from a GM plant may affect bee behaviour, development or survival, or it may have no effect. As pointed out above pollen represents

Table 20.3 Effects of novel proteins and GM plants on bees (Malone and Pham-Delègue 2001)

Novel protein or GM Plant	Type of experiment	Results
Bt toxins (lepidopteran active)	Larval survival	Not toxic
	Adult survival (in lab and in colony)	Not toxic
	Adult food consumption	No effect
	Adult flight activity (protein fed to colony)	No effect
Bt toxins (coleopteran active)	Larval survival	Not toxic
	Larval survival, pupal weight (protein fed to colony)	No effects
Bt-corn (lepidopteranactive)	Larval development, adult survival, foraging frequency (in field)	No effects
Serine protease inhibitors	Adult survival (in lab and in colony)	High concentrations reduce survival by a few days; low concentrations have no effect
	Adult digestive proteases	Inhibition of some proteases
	Adult flight activity (protein fed to colony)	Flight activity begins a few days earlier (when fed a high concentration)
	Olfactory learning response	One inhibitor offered in sugar reward reduced ability to learn; others did no
	Larval survival	High concentrations reduce survival
Cysteine protease Inhibitors	Adult survival	No effect
Cysteine protease inhibitor-expressing oilseed rape	Foraging behaviour	No effect
Chitinase	Adult survival	No effect
	Olfactory learning Response	No effect
	Foraging behaviour (sugar feeder with chitinase added)	No effect
Chitinase-expressing oilseed rape	Foraging behaviour	No effect
β-1,3 glucanase	Adult survival	No effect
	Olfactory learning Response	No effect
	Foraging behaviour (sugar feeder with β-1,3 glucanase added)	No effect
Biotin-binding protein (avidin)	Adult survival	No effect
	Adult food consumption	No effect
	Larval development and Survival	No effect
Herbicide (glufosinate) resistant oilseed rape (patgene)	Larval and adult survival, foraging behaviour (in colony)	No effect

the most likely vehicle for the expression of novel proteins. Adult bees consume significant quantities of pollen during their first week after emergence and they have received the most research attention to date. Bee larvae also ingest pollen, especially during the later instars, but their food is composed in large part of glandular secretions from nurse adult bees.

Many experiments have been conducted in which bees are fed with purified novel proteins at concentrations estimated to approximate or to exceed likely pollen expression levels. Novel proteins with insecticidal properties aimed at making GM plants pest resistant have been the most thoroughly tested. There have also been trials conducted with small colonies of bees and potted flowering GM plants in glasshouses or under mesh in the field. Tests have assessed food consumption by adult bees, adult bee survival, olfactory learning and foraging behaviour in adult bees, larval bee development and survival. Results to date are briefly summarised in Table 20.3.

20.11 Indirect Effects of GM Plants on Bees

Indirect effects of transgenic plants on bees may occur when genetic modification results in an unexpected change in the plant's phenotype. Insertional mutagenesis is one such change. In this case, the random positioning of the transgene in the plant's genome interferes with a gene or suite of genes needed for a "normal" phenotype. For example, an insertional mutagenesis event that resulted in plants without flowers would have a definite negative impact on bees. Less obvious changes, such as alterations in nectar quality or volume would be harder, but not impossible, to detect. Effects due to insertional mutagenesis will vary among different lines of plants derived from separate transformation events and can easily be eliminated by line selection. Pleiotropic effects represent a second type of inadvertent phenotypic change. In this case, it is not the position of the transgene, but its product, which interferes unexpectedly with a biochemical pathway in the plant to create a phenotypic change. Such changes would occur in all lines of the transgenic plant and could not be remedied by line selection. Nectar analyses of GM oilseed rape plants have suggested that some modification events may lead to phenotypic changes that could influence bee behaviour (Pham-Delègue et al. 2002). One line of GM oilseed rape expressing a chitinase produced more nectar of higher sugar concentration than the corresponding control line, as did one herbicide-resistant line compared with its control.

20.12 Bumblebees and Purified Bt Protein

Since bumblebees play an important ecological role, their sensitivity against Bt protein was analysed as well – like that of honeybees and many other non-target-organisms. When bumblebees took up purified Cry1Ac protein with their food, no effect on feeding behaviour, weight, colony size, amount of brood or the sex ratio of the progeny was observed (Morandin and Winston 2003).

20.13 Honeybees and Bt Maize

In their natural environment, honeybees collect nectar and pollen as food for themselves and for the brood. Maize fields are not very attractive sources for food when alternatives exist. In Europe, insect resistant Bt maize with the construct MON810 (protein Cry1Ab) is the only GM crop being grown in significant amounts. Research has shown that nectar contains only small amounts of protein, and therefore practically is free from Bt protein (Malone and Pham-Delègue 2001). The main route by which honeybees in Europe can come into contact with Bt protein therefore is feeding on pollen of Bt maize. How much of it do honeybees actually take up? For an assessment, it is important to know how much maize pollen honeybees collect, and feed to the larvae. To investigate this, honeybee colonies were kept in large tents with maize plants, without access to alternative food plants. The gut content of the larvae was analysed microscopically. It turned out that the larvae devour only small numbers of maize pollen grains – sufficient for less than 5% of their protein need (Babendreier et al. 2004, 2006). Their exposure towards the Bt protein contained in pollen from insect resistant maize therefore is rather limited.

Direct feeding of honeybee larvae with pollen from the GM maize varieties Bt11 (Cry1Ab) or TC1507 (Cry1F), which are not yet approved for planting in Europe, demonstrated no effects of this treatment on the mortality of larvae or pupae, or the pupal weight (Hanley et al. 2003). Also feeding honeybees over 10 days with pollen from MON810 maize (Cry1Ab) did not affect their survival or the development of their hypopharyngeal gland (Babendreier et al. 2005, 2006), or their gut flora (Babendreier et al. 2007). Direct contact to flowers of Bt maize plants had no influence on honeybee mortality (Bailey et al. 2005).

Taken together, direct uptake of Bt maize pollen by honeybees or their brood does not appear to have negative effects on them, which also has been shown in numerous other studies and review articles (Keil et al. 2002; Malone 2004; Malone et al. 2004; O'Callaghan et al. 2005; Sanvido et al. 2006).

20.14 Honeybees and Herbicide Tolerant Oilseed Rape

Currently, no GM oilseed rape is planted commercially in Europe. In the US and Canada, on the other hand, it's use is widespread, with approx. 4.8 million hectares of herbicide tolerant (HT) oilseed rape being grown. These plants are insensitive against certain broadband herbicides, and enable the farmer to control weeds more efficiently, with less labour. Since nectar and pollen from oilseed rape are an important food source for them, possible effects of these plants on honeybees were examined.

In nectar and pollen of different GM oilseed rape varieties, the protein encoded by the transgene could not be detected (Pham-Delègue et al. 2002). In general, the likelihood of honeybee's exposure to these substances appears to be rather low. During filed trials in Canada, colonies were put up next to large fields with conventional or herbicide tolerant GM oilseed rape. Honeybees collected comparable amounts of pollen from both varieties. No influence of diet on larval survival or pupal weight was observed. Also the number of bees returning to the colony after foraging did not differ (Huang et al. 2004). Behavioural studies demonstrated that bees do not discriminate between transgenic and conventional oilseed rape, and do not prefer one over the other (Pierre et al. 2003).

Since herbicide tolerant oilseed rape permits later, but more efficient weed control, in general fewer flowering weeds are found in fields with HT oilseed rape at the end of the growing season. These fields therefore are less attractive for bees specialising on weeds than conventional or organic oilseed rape fields, which show a higher biodiversity also among weeds (Haughton et al. 2003, 2005; Bohan et al. 2005; Morandin and Winston 2005). However, in summertime after flowering the attractiveness of oilseed rape fields for bees is rather low. It is unlikely that the observed differences between fields with HT oilseed rape and conventional varieties will have an effect on the bee's population in general, since they can select their food sources within a large area. Already at the field margins, only small differences in the number of bees were observed (Roy et al. 2003).

20.15 Honeybees and Other Transgenic Plants

Also several other GM crops that are not grown commercially in Europe at present were analysed for possible effects on bees. For herbicide tolerant beet, similar observations as for HT oilseed rape were made during farm scale evaluations: because of smaller numbers of weeds, the number of bees on these fields also tended to be lower. Opposite observations were made in fields of HT maize. Here, more bees were found, because efficient weed control early in the growing season allowed for an increased biodiversity later in the summer (Haughton et al. 2003). The observed effects on the number of bees within the fields did not extend to the field margins, where numbers were comparable (Roy et al. 2003).

Studies of other GM crops, like insect resistant Bt cotton, can be found in the literature. Also here, no negative influence of approved transgenic plants on bees was reported (Liu et al. 1997, 2000, 2005, 2009; Velkov et al. 2005).

20.16 Transgenic Plants and Honeybee Colony Collapse Disorder CCD

In the spring of 2007, beekeepers in the US reported a novel kind of bee colony die-off. Numerous colonies left their hives and disappeared without a trace. In several European countries, like Germany and Switzerland, similar observations were made. This phenomenon, termed "colony collapse disorder CCD" in the US, has also been referred to as "Honeybee AIDS" in some popular media. Its causes are unknown so far, despite intense efforts to elucidate the underlying mechanisms.

Since already 40% of US maize fields are planted with genetically modified, insect resistant Bt-varieties, there was some speculation about a possible link between growing GM crops and the occurrence of colony collapse disorder. An observation from the German University of Jena, made in the framework a biosafety research programme with transgenic Bt-maize, was cited as hint for such a connection. For healthy honeybees, no evidence for acute or chronic toxic effects of Bt maize was reported. However, in one experiment, the bees were unwittingly infested by parasites (microsporidia), so that the trial had to be aborted due to strong negative effects on the bee's health and survival. For these infested honeybees, feeding on Bt maize pollen appeared to accelerate their decline further. This single observation could not be repeated or confirmed in further experiments. Several points argue against a direct connection between the cultivation of GM crops and the colony collapse disorder. Already in the past, before GM crops were used in agriculture, honeybee colony die-offs were observed regularly. Today, there is a lack of geographic correlation between GM crop plantings and regions where colony collapse is observed. CCD is observed in many US states where few GM crops are grown, in contrast several stronghold states of US biotech agriculture do not report CCD. In addition, colony die-offs in Europe are observed in regions where no GM crops are grown, such as in Switzerland. GM crops therefore are unlikely to be the cause for CCD; experts rather suggest the exposure to chemicals, pathogens or other stress factors or the lack of genetic diversity among the honeybees.

20.17 Gene Transfer in the Honeybee Gut

In the year 2000, several media reported about research results from the German University of Jena, suggesting a possible gene transfer from herbicide tolerant GM oilseed rape to bacteria in the gut of honeybees. It was assumed that micro-organisms from the gut flora had taken up a gene from the GM plants, thereby becoming resistant against the herbicide themselves.

To follow up on the possibility of gene transfer, scientists analyzed to which extent pollen from GM oilseed rape is collected by honeybees, mason bees and bumblebees. All species indeed collect and eat the transgenic pollen, providing a direct contact to the bee's gut bacteria (Sick et al. 2004). Forty percent of these micro-organisms turned out to be herbicide-resistant. A more detailed molecular genetic analysis revealed, that none of these micro-organisms had taken up the transgene from the GM oilseed rape, but that this herbicide resistance had been present naturally in micro-organisms from the bee gut (Mohr and Tebbe 2007).

In brief, so far, no evidence for direct or indirect damages to bees by currently approved GM crops has been reported in the scientific literature. This is the result of numerous experiments in the laboratory or the field, in some of which the exposure towards GM crops or their products possible under natural conditions has been strongly exaggerated. Changing agricultural practices, like they are possible e. g. with herbicide tolerant crops, can result in changes to the number and seasonal composition of weeds within the fields – which is also the case for conventional agricultural practices, and not a direct result of the genetic modification. For mobile insects like bees, which have a large natural habitat far exceeding single fields, no negative consequences of such changes are to be expected.

Strategies to minimise inclusion of GM material in bee products include:

Separating GM and non-GM crops (effectiveness will depend on bee flight distances)
Screening GM crops with bee-proof mesh (not practical except on a very small scale)
Using bee attractants such as a sugar syrup spray on non-GM crops
Using bee repellents such as some pesticides on GM crops
Using GM plants where the transgene is not expressed in pollen, or the transgene
Occurs only in chloroplasts, or where pollen or flower formation is blocked
Removing pollen grains from honey by filtering after harvest.
Separation of flowering GM crops and hives

One method for ensuring that bee products derived from GM and non-GM plants are kept separate would be to plant the different crops far enough apart to ensure that bees from a single hive could not visit both. This physical separation of the hive from the undesired flower source is the rationale used in the production of organic honey. Hives must be placed at least 3, 5 or 7 km (depending on the standard used) from nonorganically grown crops. However, these organic rules recognise that, with this method, some contamination is inevitable and so maximum pesticide tolerance limits are set. It has been suggested that similar limits will need to be set for GM material in organic products (Moyes and Dale 1999; Christey and Woodfield 2001), but it appears that a "zero-tolerance" policy is in place thus far. The required distance for GM/non-GM crop separation would depend on the maximum distance that a bee will travel to forage on that crop and it may vary depending on the relative attractiveness of the crop compared to other flowering plants in the same area. Information on bee foraging distances is summarised below. Temporal separation of GM and non-GM crops (taking advantage of different flowering times) may also provide a possible means of separation. Beekeepers have extensive experience in ensuring that their bees preferentially visit a particular plant in flower, since they must do this to produce unifloral honeys. This usually involves siting hives where the desired plant predominates at the appropriate time to capture its "nectar flow". While these methods are adequate for producing honeys of sufficient floral purity to satisfy consumer demand, they do not allow for the exclusion of pollen from a range of plants from the honey. To be called unifloral, a honey must have at least 45% of its total pollen content from the nominal plant species (Molan 1998). Thus pollen from other plants commonly occurs in "unifloral" honeys. Concurrent foraging visits to other flowering plants account for only some of this pollen. Contamination may also occur when honey is extracted by crushing combs or using a loosening device (as with thixotropic honeys), since this can release stored pollen from nearby cells in the comb. Re-using comb from which honey was extracted during the previous season can also lead to contamination with "old" pollen.

20.18 Bee Foraging Distances

According to Winston (1987), most honey bees in agricultural areas forage within a few hundred metres of their hives, although significant populations have been found at 3.7 km. In forested regions, they forage at a median radius of 1.7 km from the hive and most can be found within 6 km. He points out that bees can be recruited to feeding stations up to 10 km from a hive if there are no competing food sources. Williams (2001) confirms this 10 km maximum flight distance. According to Gary (1992), bees have a strong tendency to forage at the nearest source for each floral species in an area. He also mentions “distant flight” behaviour in agricultural areas where attractive crops are planted in widely dispersed fields, such that significant bee populations may be found at least 6.5 km from an apiary. Gary notes that bees in a desert will fly up to 13.7 km to a food source if there are no other food sources closer to the hive. This is the maximum bee foraging distance mentioned in the literature. Moyes and Dale (1999) note mean foraging distances of 1.66 km and 557 m for bees foraging on flowering carrots and onions, respectively, and maximum distances for these crops on 6.17 and 4.25 km. Ramsay et al. (1999) notes bees flying 5 km to reach an oilseed rape field. In New Zealand, a 5 km distance is generally recognised as being the minimum when shifting hives to ensure that they will not return to their old hive site (Matheson 1997). Friends of the Earth recently commissioned a study of pollen dispersal by honey bees from a herbicide-tolerant GM oilseed rape farm-scale field trial site (Emberlin and Brooks 2001). Pollen traps were placed on six hives, two at each of three apiary sites, up to 4.5 km from the flowering GM oilseed rape crop. There were apparently no other flowering crops in the vicinity. Forty samples of pollen were taken from the traps and examined for oilseed rape pollen pellets (identified by colour and shape). Of these, six samples (presumably one from each hive) with numerous oilseed rape pollen grains were selected and sent for DNA analysis to the Austrian Federal Environment Agency Laboratory. PCR tests for the nos terminator and bar gene (see Sect. 20.2.2 above) gave positive results for each of the six pollen samples, suggesting that even bees from the furthest hive had gathered pollen from the trial site. Once again, there was no analysis of control samples of oilseed rape pollen collected from non-GM crops, so that the possibility of microbial contamination giving positive readings for nos or bar DNA cannot be discounted. The literature thus suggests that a distance of more than 13.7 km from hive to GM crop would give a 100% guarantee that bees would not forage on the crop. However, this figure is derived from an experiment with bees in a desert with no other sources of forage, which is not a realistic agricultural situation. A better approach perhaps would be to define realistic foraging distances for different cropping situations and to assign probabilities that a least one copy of transgene DNA will occur in a pollen or honey sample as a function of distance. This approach supposes a zero tolerance limit for such DNA in these bee products. A less stringent limit would produce a different set of probability values.

20.19 Accidental Inclusion of Wind-Borne Pollen in Bee Products

A second possible source of GM pollen in hives and bee products could be that from GM crops which produce significant quantities of wind-borne pollen, e.g. ryegrass or pine. The discovery of a tiny amount of pine pollen in a sample of New Zealand clover honey (Moar 1985) suggests that such an occurrence may not be completely improbable. However, there are no published data on how close a honey-producing hive would have to be to a pine *Plantation* or ryegrass pasture for such pollen to occur in the honey or pollen harvested from that hive.

20.20 Feasibility of the Crop/Bee Separation Approach

Making sure that bees are sufficiently distant from any GM crop site to prevent visits to the crop or accidental occurrence of pollen from that crop in hives during any honey-making season could ensure that no or minimal GM pollen is accidentally introduced into the honey made that season. This would require careful, planned deployment of GM crops, especially clover or oilseed rape. Excellent communication between land-users and beekeepers would also be required. Since such communication is already an important factor in the success of beekeeping businesses, this should be achievable. However, some beekeepers have reported that they have been deterred from shifting to organic honey production by increased complications in dealing with landowners (Bourn et al. 1999), even without a consideration of the possibility of GM crops.

The carry-over from year to year of pollen in frames of empty comb and perhaps other hive equipment may mean that an equipment labelling and "quarantine" system, similar to that already employed in New Zealand for American foulbrood control (Goodwin and Van Eaton 1999), would need to be implemented to segregate "GM" and "non-GM" hives.

The stringency of the techniques that will need to be used will, of course, be dictated by the tolerance limits for unintentional presence of GM material in bee products set by the countries where the honey will be sold.

20.21 Screening the Crop to Exclude Bees

Screening a crop with bee-proof mesh would be practical only for small-scale field trial plots. It may be feasible for commercial crops of extremely valuable GM plants, for example those grown to produce very valuable proteins for extraction and purification ("biopharming"), where the areas planted may be relatively small.

20.22 Bee Management Techniques to Direct Bees to Visit Particular Crops

A number of bee management techniques have been developed to enhance bee visits to particular crops, usually in order to increase pollination and/or fruit set. The most obvious method is to simply place hives near the crop and away from other flowering plants. This method's usefulness in relation to the presence of GM material in bee products has been covered in Sect. 20.22.1. Most of the other methods are based on the application of a bee attractant to the crop. They are summarised below.

A number of chemicals have also been identified as bee repellents. Some are insecticides and their bee-repellent qualities have been noted as a side-effect, whereas others have been used deliberately to keep bees away from potentially harmful insecticides or poisons intended for control of pests. These are summarized below. Both strategies could be of use where there some GM material can be tolerated, e.g. for honey which at present does not require a GM label in New Zealand, Australian, EU, North American and Asian markets. They would not be suitable for situations where there is "zero tolerance" for GM material in bee products.

20.22.1 Bee Attractants and Other Methods to Maximise Foraging on a Crop

Spraying crops with sugar syrup in order to increase bee visits, pollination and fruit set has produced mixed results. Goodwin (1997) reviewed this use of sugar syrup and concluded that it was an unreliable method but potentially useful if further research could improve reliability. A number of commercial products based on sugar syrup (e.g. Beeline, Bee-Q and BeeLure) are sold for spraying on crops to improve pollination. These also have mixed success and there are many reports of their failure to increase bee visits or seed set (e.g. Burgett and Fisher 1979; Belletti and Zani 1981; Rajotte and Fell 1982; Margalith et al. 1984; Singh and Sinha 1997; Ambrose et al. 1995). Other commercial products for this purpose are based bee pheromones (e.g. BeeHere, Bee Scent and QMP). Success has been reported with their use on raspberries (Neira et al. 1997), strawberries (Butts 1991), cranberry (MacKenzie and Averill 1992), apple, cherry, pear and plum (Mayer et al. 1989). However, failure has been reported with some crops, such as apricots (McLaren et al. 1992), kiwifruit (Tsirakoglou et al. 1997), watermelon and cucumber (Ambrose et al. 1995).

A second use of sugar syrup is to feed syrup scented with the flowers of the target crops to bees, with a view to recruiting more bees to forage on the crop. Goodwin (1997) also reviewed this technique. He reported that it had mixed success and had received little attention over the last 30 years.

A third approach to improving crop pollination is to increase the number of pollen gatherers in a colony by feeding unscented sugar syrup within the hive

(Goodwin 1997). Increases in pollen collection using this method have been reported for a number of crop plants, although actual improvements in their pollination have not been assessed. Syrup feeding may also increase pollen collection from plants other than the target crop, so this method may have limited use in directing bees to forage only on a particular crop within their flight range. Finally, breeding crops with increased levels of honey bee attractive floral volatiles (e.g. linalool) has been suggested as a method for increasing bee visits to crops such as alfalfa (Henning et al. 1992).

20.22.2 Bee Repellents and Other Methods to Prevent Bee Visits to a Crop

Trap crops (non-GM borders grown around a GM crop) are used to minimise pollen flow via insects and wind from a GM crop. These take advantage of the fact that pollen dispersal has a highly leptokurtic distribution (i.e. pollen levels decrease dramatically within metres of the crop and then remain at very low levels over a far greater distance) (Williams 2001). While this may help to reduce concerns about cross-pollination, its impact on GM pollen presence in bee products is not known. Williams (2001) also suggests that planting a surrounding trap crop of preferred bee forage may have potential as a means of reducing bee visits to a GM crop. Pollen traps fitted to hives have been tried, but found to be unreliable, as a means of reducing the amounts of insecticide-treated pollen entering a hive from sprayed crops nearby (Erickson et al. 1997). Such traps may be of some use as a means of excluding GM pollen, but this has not yet been investigated. A number of chemicals have been identified as honey bee repellents. Atkins et al. (1975) reported 42% and 69% bee repellence from flowering crops sprayed with ethyl hexanediol and decylamine, respectively.

Some pesticides appear to have bee repellent properties. For example, some pyrethroid insecticides have been shown to repel bees and this is thought to explain why this chemical causes less mortality in the field than would be expected from laboratory-based toxicity tests (Rieth and Levin 1987, 1988; De Wael and van Laere 1989). Fries (1985) noted that cypermethrin reduced oilseed rape pollen collection by honey bees. Orthene sprayed on pre-flowering raspberries resulted in a failure of pollination by honey bees. The fungicide captan, although not toxic to honey bees, repels them if applied to flowering plants (van Praagh and von der Ohe 1982). Other compounds have been tested for their ability to repel bees, but not other insects, from insecticides or other poisons sprayed on crops or used in baits. The honeybee pheromone 2-heptanone was tested for this purpose but was found to be impractical and not sufficiently reliable (Rieth 1986). Goodwin and Houten (1991) had better success with blackstrap molasses added to 1080/jam baits used to kill possums. They identified oxalic acid as the bee-repellent component of the molasses. However, the use of oxalic acid on flowering crops has not been tested and the possibility of phytotoxicity has not been discounted (M. Goodwin, pers. comm.).

20.23 Biotechnological Solutions

There are a number of biotechnological approaches which may help to reduce GM material in bee products. Most are being developed in order to minimise crosspollination (and thus gene flow from GM crops) and some are aimed at improving crop yield or reducing pollen allergenicity problems by eliminating flowering. Promoters that direct transgene expression to tissues other than pollen or the nectaries could be used to minimise the presence of novel proteins in pollen and nectar. For example, leaf- or root-specific promoters are being developed (e.g. Santamaria et al. 2001; Imura et al. 2001), especially for transgenes encoding insecticidal proteins, so that the proteins occur where pest insects feed and not where beneficial insects such as bees do. However, with this method the transgene will still be present in pollen and will thus continue to represent a potential source of GM material for bee products. The following discussion will focus on methods which may eliminate transgene DNA from pollen.

20.23.1 Modification of Chloroplast DNA

Commercially available GM plants have been modified via the insertion of a transgene into the plant's nuclear genome, so that every plant cell with a nucleus will contain the new DNA. However, chloroplasts, like some other organelles, contain their own DNA, separate from that contained within the nucleus. This is known as the chloroplast genome. It is possible to insert a transgene into the chloroplast genome so that only plant tissues composed of chloroplast-containing cells will carry the transgene and have the ability to express the novel protein it encodes (e.g. Daniell et al. 1998). Since the leaves, shoots and stems of plants are often the desired sites for expression of new traits (e.g. pest or disease resistance or altered nutritional properties), this method has potential for conferring such traits while avoiding the difficulties that the transgene's presence in pollen may pose (e.g. Lutz et al. 2001; De Gray et al. 2001).

In most flowering plants the chloroplast genome is absent from pollen. Because of this, chloroplast DNA sequences are used to study maternal inheritance in many plants (e.g. Balfourier et al. 2000). However, the conifers are a well-known exception to this and chloroplast genome sequences have been used for paternity analysis in *Pinus radiata* in New Zealand (Kent and Richardson 1997). Paternal transmission of chloroplasts is also known in carrots (Moyes and Dale 1999), and on some occasions in some other angiosperms, e.g. runner beans, peas, potatoes, meadow grass (Moyes and Dale 1999), tobacco, lucerne (Stewart and Prakash 1998; Daniell et al. 1998) and pelargonium (James et al. 2001). Thus the effectiveness of this method for eliminating GM material from the pollen of GM plants will depend on the plant concerned. Flowering GM crop species visited by honey bees may be suitable candidates for this method. Scott and Wilkinson (1999) studied rates of maternal inheritance of chloroplast DNA in oilseed rape and concluded that there will be no or negligible pollen-mediated chloroplast-transgene dispersal from this crop. McKinnon et al. (2001) drew a similar conclusion from a study of eucalyptus.

20.23.2 GM Plants Without Pollen

Male sterility is used in conventional hybrid plant breeding to control pollination and many crops have natural male sterility systems that can be exploited (Christey and Woodfield 2001). It can also be introduced into crop plants via genetic modification. Several different strategies are being investigated, but one of the best known is the barnase/barstar system. With this, a bacterial gene encoding a cytotoxic enzyme, barnase (*Bacillus amyloliquefaciens* RNase) is placed on a tapetum- or pollen-specific promoter so that it is expressed only in the anthers during pollen grain formation. Because it is cytotoxic, barnase disrupts this process so that the plants produce either no pollen, deformed or inviable pollen. Plants can also be modified to carry another gene from the same bacterium called barstar. This encodes a protein which inactivates barnase and blocks its cytotoxic effect. If the barstar gene is driven by an inducible promoter (i.e. one that works only when triggered by the application of a particular chemical), then it becomes possible to switch pollen production back on when desired by spraying with the inducing chemical. A number of GM male-sterile crop plants have now been successfully developed (but apparently not yet commercialised) with the barnase system, e.g. oilseed mustard (Arun et al. 2001), cabbage (Zhu et al. 2001), alfalfa (Rosellini et al. 2001), tobacco (Li et al. 1997), wheat (de Block et al. 1997), soyabean (Guo and Lin 1997), poplar (Li et al. 2000) and rice (Zhang et al. 1998). Obviously male-sterile GM plants completely lacking pollen would not be a source of GM material for honey bees. However, it is not certain whether deformed or inviable pollen would be rejected by foraging honey bees. Bees are known to exhibit preferences among pollen types when presented with a choice, apparently choosing on the basis of odour and physical configuration of the pollen grains (Winston 1987).

20.23.3 GM Plants Without Flowers

GM techniques may also be used to retard or prevent flowering, thus preventing undesirable gene flow from pollen dispersal. There may also be benefits in eliminating flowering from some crops in order to encourage vegetative growth (e.g. forage plant production) and to reduce the production of allergenic pollen (e.g. ryegrass). There are very obvious detrimental implications for honey bees in having non-flowering plants, especially with crops that are important for honey production, such as clover. The loss of flowers even from species that are chiefly windpollinated, such as maize, could impact negatively on honey bees that may rely on these plants as a supplementary pollen source. However, if the demand for GM-free bee products is sufficiently high, then the option of non-flowering GM plants may become attractive. One strategy to prevent flower formation uses the barnase (cytotoxic) gene attached to genes that are expressed only in inflorescences, such as a MADS gene (Lemmetyinen et al. 2001). There are no reports of the impacts of such plants on honey bees or bee products.

20.23.4 Post-harvest Honey Treatments

If GM pollen could be removed from honey after harvest, the likelihood of GM material (DNA or protein) occurrence would be greatly reduced or eliminated. Honey is generally filtered after harvest to remove wax and debris before packaging (comb honey is an obvious exception to this). It is sometimes stated that the filtering of commercial honey reduces the level of pollen to 0.1% or less (Anon 2001). This figure accords with most of the reports quantifying pollen content of honey (see Sect. 20.2), but not all. For example, Eady et al. (1995) reported 100,000 grains per ml in a UK commercial honey (equivalent to about 0.3%) and Moar (1985) gave a maximum pollen concentration of 5 million grains per 10 g of honey (about 1.5%). In New Zealand, a relatively coarse nylon fabric filter is usually used to filter honey (Matheson 1997) and this is unlikely to remove all pollen grains, although more sophisticated filtration units that use mesh filters may remove significant quantities of pollen (Bryant 1987). High pressure filters using a series of paper filters, sometimes with diatomaceous earth added, are available and used in the United States (Tew 1992). Molan (1998) reported that honey that has been filtered with diatomaceous earth has no pollen left in it.

20.24 Market Reaction to Honey from Countries Where GM Crops Are Grown

New Zealand beekeepers have expressed concern about the loss of markets for bee products should GM crops be grown in New Zealand and at the Royal Commission on Genetic Modification they called for a moratorium on field releases of GM plants (Anon 2001a, b). Food labelling laws and food standards define acceptable levels of GM material in honey and other bee products intended as food. These levels vary between 1% and 5% from country to country and the organic market apparently requires a complete absence of GM material (see Sect. 20.3 for details). Bee products able to comply with these standards should have full access to these markets.

However, consumers will be influenced not only by the legal label but also by other factors that affect their perceptions of a product, such as the country of origin. For example, customers may not be entirely satisfied by the GM food labels in their country and may choose to buy produce from countries known not to grow GM crops. It is not certain how important consumer perceptions of the "GM status" of the country of origin will be in the marketing of bee products, but the experiences of honey producers from countries where GM crops are grown may be instructive.

20.24.1 Market Reaction to Honey from Canada

GM herbicide-tolerant canola (oilseed rape) has been grown extensively for many years in Canada and at present at least 70% of Canada's canola is GM (H. Clay, pers. comm.). Canola represents a very significant nectar source for Canadian honey producers. In 1999 Canadian honey met some market resistance in Germany because of unconfirmed reports of traces of GM material in a honey sample. Canadian producers could not guarantee that their export product was free of GM canola pollen, even though the Canadian Honey Council pointed out that filtering removed all but 0.1% (w:w) pollen from honey. In their 1998/1999 report on the Canadian Honey Situation and Trends, Agriculture and Agri-Food Canada reported that "issues over GMO were a concern for many honey producers who were exporting to certain markets" (Parent and Pearen 1999). This event was extensively reported and is still quoted in popular articles on GM foods (e.g. Anon 2001; Munro 2002). Agriculture and Agri-Food Canada's most recent advice to Canadian farmers wishing to export to the European Union notes that many Canadian GM varieties of canola are not registered in the EU and so Canadian canola seed cannot be accepted there unless it can be guaranteed GM-free. These guidelines mention Germany as an export destination for honey but do not mention any requirement for GM labelling. Heather Clay, of the Canadian Honey Council, states that there was "a temporary drop in sales of Canadian honey to Germany, but the market has since recovered" and that "the large exporters report that it is business as usual in Europe" (H. Clay, pers. comm., 3 June 2002).

20.24.2 Market Reaction to Honey from Argentina, the United States and Australia

Argentina is one of the world's biggest exporters of honey (70,363 tonnes in 1997) (Parent and Pearen 1999; Anon 1998). It is also one of the top growers of GM crops, although these are principally soybeans and maize and not honey-yielding plants (James 2000). Perhaps for this reason there have been no reports of difficulties with exports of honey from Argentina, even to Germany which is its largest export market (Anon 1998a, b). In the United States honey is produced primarily for the domestic market; in 1997 it exported only 3,296 tonnes of honey (in comparison, Canada exported 7,407 tonnes in the same year, mostly to the United States and Germany)

(Anon 1998a, b). Germany, Japan and Yemen are its major markets and there have been no reports of difficulties with these in connection with the GM crops grown extensively in the United States, which include the honey-producing plants, canola and cotton. GM cotton grown in Australia (150,000 ha planted in 2000; James 2000) has apparently not yet posed problems for Australian honey producers. GM canola has not yet been released commercially in Australia. Interestingly, the state government of New South Wales, a key canola-producing region, has recently announced plans to introduce legislation which will rule out the establishment of GM-free planting zones.

20.25 Potential Impacts of GM Plants on Bee Health

Although not directly related to the presence of GM material in bee products, there may be impacts of GM plants on bee health that could affect on the bees' ability to produce honey, pollen and propolis. There is a growing body of published research on the impacts of GM plants and novel proteins on bee health. This research has recently been reviewed (Malone and Pham-Delègue 2001, 2002; Pham-Delègue et al. 2002). GM plants may have direct or indirect effects on bees. Direct effects are those that arise when a bee ingests a novel protein expressed by a GM plant. Indirect effects may arise if the process of introducing the transgene into the plant results in inadvertent changes to plant phenotype affecting its attractiveness or nutritive value to bees.

20.26 GMO Crops and Malnutrition of Bees

Genetically Modified Organisms (GMO) and "Terminator Seeds" are matter of concern for declining bees (Amos 2009). The genetic modification of the plant leads to the concurrent genetic modification of the flower pollen. When the flower pollen becomes genetically modified or sterile, the bees will potentially go malnourished and die of illness due to the lack of nutrients and the interruption of the digestive capacity of what they feed on through the summer and over the winter hibernation process. It is certain that the digestive shutdown is due to hard material in the digestive tract that compromises the immune system. It has been found that the bees that are ingesting GMO pollen are having severe digestive problems. Stone like contents were found in poorly laying queens which when ground and mounted, some unidentified floating objects (UFO's) were observed. There were fragments of pollen grains husks in all samples examined. The inability of the bees to pass matter digestively seems to be quite similar to the present-day problems in the human digestive system. Evidently, the proof is obvious that one of the major reasons of the bees' decline is by the ingestion of GMO proteins. The Economic impact of the bee colony collapse would mean inflation, scarcity of agricultural commodities, and ultimately the collapse of agriculture. The Environmental Impact of scarcity and increased demand for resources will beyond doubt have severe repercussions for our long-term food security. The bio-diversity of the bees causes positive economic and ecological externalities. The negative externalities have yet to be fully grasped or understood.

The economic impact that the scarcity of bees will potentially have on our society as a whole is very worrisome. In the end, only our children will fully realize; that it was greed that destroyed our beautiful blue planet.

20.26.1 Direct Effects of Novel Proteins on Bees

Potentially, the ingestion of a novel protein expressed in pollen or perhaps occurring in nectar, resin or honeydew from a GM plant may affect bee behaviour, development or survival, or it may have no effect. As pointed out above (Sect. 20.2), pollen represents the most likely vehicle for the expression of novel proteins. Adult bees consume significant quantities of pollen during their first week after emergence and they have received the most research attention to date. Bee larvae also ingest pollen, especially during the later instars, but their food is composed in large part of glandular secretions from nurse adult bees.

Many experiments have been conducted in which bees are fed with purified novel proteins at concentrations estimated to approximate or to exceed likely pollen expression levels. Novel proteins with insecticidal properties aimed at making GM plants pest resistant have been the most thoroughly tested. There have also been trials conducted with small colonies of bees and potted flowering GM plants in glasshouses or under mesh in the field. Tests have assessed food consumption by adult bees, adult bee survival, olfactory learning and foraging behaviour in adult bees, larval bee development and survival. Results to date are briefly summarised in Table 20.3.

20.26.2 Indirect Effects of GM Plants on Bees

Indirect effects of transgenic plants on bees may occur when genetic modification results in an unexpected change in the plant's phenotype. Insertional mutagenesis is one such change. In this case, the random positioning of the transgene in the plant's genome interferes with a gene or suite of genes needed for a "normal" phenotype. For example, an insertional mutagenesis event that resulted in plants without flowers would have a definite negative impact on bees. Less obvious changes, such as alterations in nectar quality or volume would be harder, but not impossible, to detect.

Effects due to insertional mutagenesis will vary among different lines of plants derived from separate transformation events and can easily be eliminated by line selection. Pleiotropic effects represent a second type of inadvertent phenotypic change. In this case, it is not the position of the transgene, but its product, which interferes unexpectedly with a biochemical pathway in the plant to create a phenotypic change. Such changes would occur in all lines of the transgenic plant and could not be remedied by line selection.

Nectar analyses of GM oilseed rape plants have suggested that some modification events may lead to phenotypic changes that could influence bee behaviour (Pham-Delègue et al. 2002). One line of GM oilseed rape expressing a chitinase produced more nectar of higher sugar concentration than the corresponding control line, as did one herbicide-resistant line compared with its control.

20.26.3 Contamination of Crops

According to "Planet Ark." (2003), UK researchers have found that bees carrying GM rapeseed pollen had contaminated conventional plants more than 26 km (16 miles) away and that if farmers grew GM rapeseed for one season, "impurities could stay in the soil for up to 16 years if not rigorously controlled". They further explain that bees carrying GM spread it around to all the other plants making natural plants genetically modified plants. If this continues it will be hard to know what is natural and what is unnatural and there shall be no choice to pick between GMOs and natural because of all blending together. This is a serious issue which needs to be taken seriously. Another fact is that GMOs are bad for the environment because of cross pollination. Cross pollination is a negative effect of GMOs because it doesn't give the consumers a choice between GMOs or natural. Evidently, the GMOs are not to be used until further testing.

20.27 Conclusions

There are a number of research teams continuing to investigate the effects of GM plants on honey bees. Current research aims to determine whether feeding young adult bees with a Bt toxin, a protease inhibitor or a biotin-binding protein affects their ability to develop hypopharyngeal glands. In France, the effects of Bt-corn on bee larvae are being determined and an assay of bee defensive behaviour (stinging) is being developed. In Denmark, the effects of protease inhibitors on bee larvae are being assessed. In Canada, the effects of Bt-sweetcorn pollen on bees are being determined and work on impacts of GM plants on bumblebees and wild bees is planned. In New Zealand and overseas, many molecular biologists developing GM plants are moving their emphasis away from "input traits", such as herbicide tolerance, insect resistance, disease resistance or drought tolerance, and towards "output traits", such as altered nutritional qualities, improved processing traits, altered flowering and plant form and the production of valuable proteins in GM plants ("biopharming") (Christey and Woodfield 2001). The potential effects of these new traits on bees will need to be tested. For example, altering the nutritional qualities of plants could well affect the attractiveness of pollen to honey bees, since lipid profiles have been shown to be important in determining the phagostimulatory and antibacterial properties of some pollens (Singh et al. 1999; Manning 2001).

References

Ambrose JT, Schultheis HR, Bambara SB, Mangum W (1995) An evaluation of selected commercial bee attractants in the pollination of cucumbers and watermelons. Am Bee J 135(4):267–272

Amos B (2009) Death of the bees: GMO crops and the decline of bee colonies in North America. http://www.globalresearch.ca/index.php?context=vaandaid=8436 7 von 7 29.03.2009 21:59

Anon A (1998) MAFF Project No. 2B 067. Honey from genetically modified plants: integrity of DNA, and entry of GM-derived proteins into the food chain via honey. Laboratory of the Government Chemist, London

Anon B (2000) GM contamination of honey. Available at http://www.greenpeace.se/np/s/NPS_pdf/Contaminationofhoney.pdf

Anon C (2000) Press release: GM trials threaten UK honey. Available at http://www.foe.co.uk/pubsinfo/infoteam/pressrel/2000/20000516185312.html

Anon R (2001a) Report of the royal commission on genetic modification. Available at http://www.gmcommission.govt.nz/RCGM/index.html

Anon V (2001b) Bt plant-incorporated protectants. Biopesticides registration action document, United States Environmental Protection Agency, 29 Sept 2001. Available at http://www.epa.gov/oppbppd1/biopesticides/otherdocs/bt_brad/Bt_BRAD_II.pdf

Arpaia S (1996) Ecological impacts of Bt-transgenic plants: assessing possible effects of CryIIIB on honeybee (*Apis mellifera* L.) colonies. J Genet Breed 50:315–319

Arun J, Panchali B, Arumugam N, Vibha G, Burma PK, Deepak P, Jagannath A, Bandyopadhyay P, Gupta V, Pental D (2001) The use of a spacre DNA fragment insulates the tissue-specific expression of a cytotoxic gene (barnase) and allows high-frequency generation of transgenic male sterile lines in *Brassica juncea* L. Mol Breed 8(1):11–23

Atkins EL, Macdonald RL, Greywood-Hale EA (1975) Repellent additives to reduce pesticide hazards to honey bees: field tests. Environ Entomol 4(2):207–210

Babendreier D, Kalberer N, Romeis J, Fluri P, Bigler F (2004) Pollen consumption in honey bee larvae: a step forward in the risk assessment of transgenic plants. Apidologie 35:293–300

Babendreier D, Kalberer NM, Romeis J, Fluri P, Mulligan E, Bigler F (2005) Influence of Bt-transgenic pollen, Bt-toxin and protease inhibitor (SBTI) ingestion on development of the hypopharyngeal glands in honeybees. Apidologie 36:585–594

Babendreier D, Romeis J, Bigler F, Fluri P (2006) Neue erkenntnisse zu möglichen auswirkungen von transgenem bt-mais auf bienen. Forschungsanstalt agroscope liebefeld-posieux alp, Schweiz

Babendreier D, Joller D, Romeis J, Bigler F, Widmer F (2007) Bacterial community structures in honeybee intestines and their response to two insecticidal proteins. FEMS Microbiol Ecol 59:600–610

Bailey J, Scott-Dupree C, Harris R, Tolman J, Harris B (2005) Contact and oral toxicity to honey bees (*Apis mellifera*) of agents registered for use for sweet corn insect control in Ontario, Canada. Apidologie 36:623–633

Baker HG, Baker I (1973) Amino acids in nectar and their evolutionary significance. Nature 241:543–545

Baker HG, Baker I (1977) Intraspecific constancy of floral nectar amino acid complements. Bot Gaz 138:183–191

Balfourier F, Imbert C, Charmet G (2000) Evidence for phylogeographic structure in *Lolium* species related to the spread of agriculture in Europe. A cpDNA study. Theor Appl Genet 101(1–2):131–138

Belletti A, Zani A (1981) A bee attractant for carrots grown for seed. Sementi Elette 27(5):23–27

Beversdorf WD (1993) Traditional crop breeding practice: an historical review to serve as a baseline for assessing the role of modern biotechnology. Paris Organisation for Economic Co-operation and Development, Paris

Bohan DA, Boffey CWH, Brooks DR, Clark SJ, Dewar AM, Firbank LG, Haughton AJ, Hawes C, Heard MS, May MJ, Osborne JL, Perry JN, Rothery P, Roy DB, Scott RJ, Squire GR, Woiwod IP, Champion GT (2005) Effects on weed and invertebrate abundance and diversity of herbicide management in genetically modified herbicide-tolerant winter-sown oilseed rape. Proc R Soc Biol sci 272:463–474

Bonadé Bottino M, Girard C, Le Métayer M, Picard-Nizou AL, Sandoz G, Lerin J, Pham-Delègue MH, Jouanin L (1998) Effects of transgenic oilseed rape expressing proteinase inhibitors on pest and beneficial insects. In: Proceedings of the international symposium on Brassicas. *Acta Hort* 459, pp 235–239

Bourn D, Newton B, Campbell H (1999) Strategies for ‘Greening’ the New Zealand honey industry. An evaluation of the development of organic and other standards. In: Studies of rural sustainability research report no. 8. Department of Anthropology, University of Otago, Dunedin

Brødsgaard et al. (2001) Environmental risk assessment of transgenic plants using honey bee larvae. Abstracts of the XXXVII international apicultural congress 28 Oct–1 Nov 2001, Durban, South Africa. Apimondia 2001. Produced by Document Transformation Technologies

Bryant T (1987) Honey filtration unit. N Z Beekeeper 196:25–26

Burgett M, Fisher GC (1979) An evaluation of Beeline as a pollinator attractant on red clover. Am Bee J 119(5):356–357

Butts KM (1991) Bee attractants: improving strawberry quality? *Citrus and Vegetable Magazine*, 55(3,12):16–17

Carter C, Graham RA, Thornburg RW (1999) Nectarin I is a novel, soluble germin-like protein expressed in the nectar of *Nicotiana* sp. Plant Mol Biol 41:207–216

Chrispeels MJ, Sadava DE (2003) Plants, genes and crop biotechnology, 2nd edn. Jones & Bartlett, Boston

Christeller JT, Farley PC, Ramsay RJ, Sullivan PA, Laing WA (1998) Purification, characterization and cloning of an aspartic proteinase inhibitor from squash phloem exudate. Eur J Biochem 254(1):160–167

Christey M, Woodfield D (2001) Coexistence of genetically modified and nongenetically modified crops. Report prepared for the Ministry for the Environment. Crop and Food Research Confidential Report No. 427

Daniell H, Datta R, Varma S, Gray S, Lee SB (1998) Containment of herbicide resistance through genetic engineering of the chloroplast genome. Nat Biotechnol 16(4):345–348

De Block M, Debrouwer D, Moens T (1997) The development of a nuclear male sterility system in wheat. Expression of the barnase gene under the control of tapetum specific promoters. Theor Appl Genet 95(1–2):125–131

De Gray G, Rajasekaran K, Smith F, Sanford J, Daniell H (2001) Expression of an antimicrobial peptide via the chloroplast genome to control phytopathogenic bacteria and fungi. Plant Physiol 127:852–862

De Wael L, van Laere O (1989) Toxicity and the repellent activity of synthetic pyrethroids towards the honeybee (*Apis mellifera* L.). In: Proceedings of the XXXIst international congress of apiculture, Warsaw, Poland, 19–25 Aug 1987. Published by Bucharest, Apimondia Publishing House, Romania, pp 209–216

Diamand E (1999) Briefing. Bees, honey and genetically modified crops. Available at http://www.foe.co.uk/resource/briefings/bees_honey_gm_crops.html

Eady C, Twell D, Lindsey K (1995) Pollen viability and transgene expression following storage in honey. Transgenic Res 4:226–231

Emberlin J, Brooks S (2001) Pollen movement from a genetically modified oilseed rape crop. Available on request from info@foe.co.uk

Erickson EH, Erickson BH, Flottum PK, Wyman JA, Wedberg JL, Page RE (1997) Effects of selected insecticide formulations, phased application and colony management strategies on honey bee mortality in processing sweetcorn. J Apic Res 36(1):3–13

Fries I (1985) Honeybees and cypermethrin/deltamethrin in fields of flowering seed rape. Vaxtskyddsrapporter 32:169–178

Gary NE (1992) Activities and behavior of honey bees. In: Graham JM (ed) The hive and the honey bee, vol 8. Dadant and Sons, Hamilton, pp 269–372

Goodwin RM (1997) Feeding sugar syrup to honey bee colonies to improve pollination: a review. Bee World 78(2):56–62

Goodwin RM, Houten T (1991) Poisoning of honey bees (*Apis mellifera*) by sodium flouroacetate (1080) in baits. N Z J Zool 18(1):45–51

Goodwin M, Van Eaton C (1999) Elimination of American foulbrood without the use of drugs. A practical manual for beekeepers. National Beekeepers Association of New Zealand, Inc, Wellington

Greenplate J (1997) Response to reports of early damage in 1996 commercial Bt transgenic cotton (Bollgard™) plantings. Soc Invert Pathol Newsl 29:15–18

Guo ZB, Lin JX (1997) Genetic engineering of male sterile and fertility restorer in soybean. Soybean Genet Newsl 24:50

Hanley AV, Huang ZY, Pett WL (2003) Effects of dietary transgenic Bt corn pollen on larvae of *Apis mellifera* and *Galleria mellonella*. J Apic Res 42:77–81

Haughton AJ, Champion GT, Hawes C, Heard MS, Brooks DR, Bohan DA, Clark SJ, Dewar AM, Firbank LG, Osborne JL, Perry JN, Rothery P, Roy DB, Scot RJ, Woiwod IP, Birchall C, Skellern MP, Walker JH, Baker P, El B, Dewar AJG, Garner BH, Haylock LA, Horne SL, Mason NS, Sands RJN, Walker MJ (2003) Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods. Philos Trans R Soc London Ser B Biol Sci 358:1863–1877

Haughton AJ, Hawes C, Heard MS, May MJ, Osborne JL, Perry JN, Rothery P, Roy DB, Scott RJ, Squire GR, Woiwod IP, Champion GT (2005) Effects on weed and invertebrate abundance and diversity of herbicide management in genetically modified herbicide-tolerant winter-sown oilseed rape. Proc R Soc B Biol Sci 272:463–474

Hellmich RL, Siegried BD, Sears MK, Stanley-Horn DE, Daniels MJ, Mattila HR, Spencer T, Bidne KG, Lewis LC (2001) Monarch larvae sensitivity to *Bacillus thuringiensis* purified proteins and pollen. Proc Nat Acad Sci USA 98(21):11925–11930

Henning JA, Peng YS, Montague MA, Teuber LR (1992) Honey bee (Hymenoptera: Apidae) behavioral response to primary alfalfa (Rosales: Fabaceae) floral volatiles. J Econ Entomol Entomol Soc Am 85(1):233–239

Herbert EW Jr (1992) Honey bee nutrition. In: Graham JM (ed) The hive and the honey bee. Dadant and Sons, Hamilton

Huang ZY, Hanley AV, Pett WL, Langenberger M, Duan JJ (2004) Field and semifield evaluation of impacts of transgenic canola pollen on survival and development of worker honey bees. J Econ Entomol 97:1517–1523

Imura Y, Seki H, Toyoda K, Ichinose Y, Shiraishi T, Yamada T (2001) Contrary operations of Box-I element of pea phenylalanine ammonia-lyase gene 1 promoter for organ-specific expression. Plant Physiol Biochem 39(5):355–362

James C (2000) ISAAA Briefs No. 21 – 2000 preview. Global status of commercialised transgenic crops: 2000. Available at http://www.isaaa.org/publications/briefs/Brief_21.htm

James C (2005) Global status of commercialized biotech/GM crops: 2005, ISAAA Brief No. 34. International Service for the Acquisition of Agri-biotech Applications, Ithaca

James CM, Barrett JA, Russell SJ, Gibby M (2001) A rapid PCR based method to establish the potential for paternal inheritance of chloroplasts in *Pelargonium*. Plant Mol Biol Rep 19(2):163–167

Jesse LCH, Obrycki JJ (2000) Field deposition of Bt transgenic corn pollen: lethal effects on the monarch butterfly. *Oecologia*. Available at athene.em.springer.de

Jouanin L, Girard C, Bonadé-Bottino M, Le Metayer M, Picard Nizou A, Lerin J, Pham-Delègue M (1998) Impact of oilseed rape expressing proteinase inhibitors on coleopteran pests and honeybees. Cahiers Agric 7:531–536

Keil S, Romeis J, Fluri P, Bigler F (2002) Sind honigbienen durch den einsatz von insektenresistenten transgenen pflanzen einem risiko ausgesetzt? Forschungsanstalt agroscope liebefeld posieux alp, schweizerisches zentrum für bienenforschung

Kent J, Richardson TE (1997) Fluorescently labelled, multiplexed chloroplast microsatellites for high throughput paternity analysis in *Pinus radiata*. N Z J For Sci 27(3):305–312

Knee EM, Gong FC, Gao MS, Teplitski M, Jones AR, Foxworthy A, Mort AJ, Bauer WD (2001) Root mucilage from pea and its utilization by rhizosphere bacteria as a sole carbon source. Mol Plant Microbe Interact 14(6):775–784

Kozeil MG, Beland GL, Bowman C, Carozzi NB, Crenshaw R, Crossland L, Dawson J, Desai N, Hill M, Kadwell S, Launis K, Lewis K, Maddox D, McPherson K, Meghji MR, Merlin E, Rhodes R, Warren G, Wright M, Evola SV (1993) Field performance of elite transgenic maize plants expressing an insecticidal protein derived from *Bacillus thuringiensis*. Biotechnology 11:194–200

Kruger C, Hell R, Stephan UW (2001) A metal-binding LEA protein trafficks micronutrients in the phloem of *Ricinus communis* L. Plant nutrition: food security and sustainability of agro ecosystems through basic and applied research. In: Horst WJ, Schenk MK, Burkert A, Claassen N, Flessa H, Frommer WB, Goldbach H Olfs HW, Romheld V et al. (eds) Fourteenth international plant nutrition colloquium, Hannover, Germany. Kluwer Academic Publishers, Dordrecht, Netherlands, pp 194–195

Lemmetyinen J, Pennanen T, Lannenpaa M, Sopanen T (2001) Prevention of flower formation in dicotyledons. Mol Breed 7(4):341–350

Li SG, Liu YL, Zhu F, Luo YY (1997) Genetically-engineered male sterile tobacco plants and their sensitivity to temperature. Acta Bot Sin 39(3):231–235

Li L, Qi LW, Han YF, Wang YC, Li WB (2000) A study on the introduction of male sterility of antiinsect transgenic *Populus nigra* by the TA29-Barnase gene. Sci Silvae Sin 36(1):28–32

Lin HY, Chiueh LC, Shih YC (2000) Detection of genetically modified soybeans and maize by the polymerase chain reaction method. J Food Drug Anal 8(3):200–207

Liu JH, Selinger LB, Cheng KJ et al (1997) Plant seed oil-bodies as an immobilization matrix for a recombinant xylanase from the rumen fungus Neocallimastix patriciarum. Molecular Breeding 3:463–470

Liu JH, Ishitani M, Halfter U, Kim CS, Zhu JK (2000) Arabidopsis thaliana SOS2gene encodes a protein kinase that is required for salt tolerance. Proc. Natl. Acad. Sci USA 97:3730–3734

Liu B, Xu CG, Yan FM, Gong RZ (2005) The impacts of the pollen of insect-resistant transgenic cotton on honeybees. Biodivers Conserv 14:3487–3496

Liu B, Shu C, Xue K, Zhou KX, Li XG, Liu DD, Zheng YP, Xu CR (2009) The oral toxicity of the transgenic Bt+CpTI cotton pollen to honey bees (*Apis mellifera*). Ecotoxicol Environ Safe 72:1163–1169

Losey JE, Rayor LS, Carter ME (1999) Transgenic pollen harms monarch larvae. Nature 399:214

Lutz KA, Knapp JE, Maliga P (2001) Expression of bar in the plastid genome confers herbicide resistance. Plant Physiol 125:1585–1590

MacKenzie KE, Averill AL (1992) A new honey bee attractant, the queen mandibular pheromone. Cranberries 56:13–14

Malone LA (2004) Potential effects of GM crops on honey bee health. Bee World 85:29–36

Malone LA, Pham-Delègue MH (2001) Effects of transgene products on honey bees (*Apis mellifera*) and bumblebees (*Bombus* sp.). Apidologie 32:287–304

Malone LA, Pham-Delègue MH (2002) Using proteins to assess the potential impacts of genetically modified plants on honey bees. In: Devillers J, Pham-Delègue MH (eds) Honey bees: estimating the environmental impact of chemicals, vol 14. Taylor & Francis, London, pp 290–311

Malone LA, Burgess EPJ, Stefanovic D (1999) Effects of a bacillus thuringiensis toxin, two bacillus thuringiensis biopesticide formulations, and a soybean trypsin inhibitor on honey bee (*Apis mellifera* l.) Survival and food consumption. Apidologie 30(6):465–473

Malone LA, Burgess EPJ, Gatehouse HS, Voisey CR, Tregidga EL, Philip BA (2001) Effects of ingestion of a *Bacillus thuringiensis* toxin and a trypsin inhibitor on honey bee flight activity and longevity. Apidologie 32:57–68

Malone LA, Todd JH, Burgess EPJ, Christeller JT (2004) Development of hypopharyngeal glands in adult honey bees fed with a Bt toxin, a biotin-binding protein and a protease inhibitor. Apidologie 35:655–664

Manning R (2001) Fatty acids in pollen: a review of their importance for honey bees. Bee World 82(2):60–75

Margalith R, Lensky Y, Rabinowitch HD, Rapp R (1984) An evaluation of Beeline as a honeybee attractant to cucumbers and its effect on hybrid seed production. J Apic Res 23(1):50–54

Matheson A (1997) Practical beekeeping in New Zealand. GP Publications, Wellington

Matson PA, Parton WJ, Power AG, Swift MJ (1997) Agriculture intensification and ecosystem properties. Science 277:504–509

Mayer DF, Britt RL, Lunden JD (1989) Evaluation of Bee Scent as a honey bee attractant. Am Bee J 129(1):41–42

McKinnon GE, Vaillancourt RE, Tilyard PA, Potts BM (2001) Maternal inheritance of the chloroplast genome in *Eucalyptus globulus* and interspecific hybrids. Genome 44(5):831–835

McLaren GF, Fraser JA, Grant JE (1992) Pollination of apricots. Orchardist N Z 65(8,20): 22–23

Menzies AR, Osman ME, Malik AA, Baldwin TC (1996) A comparison of the physicochemical and immunological properties of the plant gum exudates of *Acacia Senegal* (gum arabic) and *Acacia seyal* (gum tahla). Food Addit Contam 13(8):991–999

Moar NT (1985) Pollen analysis of New Zealand honey. N Z J Agric Res 28:39–70

Mohr KI, Tebbe CC (2007) Field study results on the probability and risk of a horizontal gene transfer from transgenic herbicide-resistant oilseed rape pollen to gut bacteria of bees. Appl Microbiol Biotechnol 75(3):573–582, 2. 2. 2007

Molan P (1998) The limitations of the methods of identifying the floral source of honeys. Bee World 79(2):59–68

Morandin LA, Winston ML (2003) Effects of novel pesticides on bumble bee (Hymenoptera: Apidae) colony health and foraging ability. Environ Entomol 32(3):555–563

Morandin LA, Winston ML (2005) Wild bee abundance and seed production in conventional, organic, and genetically modified canola. Ecol Appl 15(3):871–881

Moyes CL, Dale PJ (1999) MAFF Research Project OF0157. Organic farming and gene transfer from genetically modified crops. Available at http://www.gmissues.org/orgreport.htm

Munro M (2002) Genetic threats blowin' in the wind: scientists warm modified crops are 'escaping and going rogues' (June 7 *National Post*). Available on request from WansbroughD@maf.govt.nz

Neira MC, Lobos NS, Riveros MG, Carrillo RL, Pessot RZ, Mundaca NB (1997) Insect fauna associated with flowers of raspberries (*Rubus idaeus* L., cv Meeker) and evaluation of the pollination activity of *Apis mellifera* L. under the influence of a pheromonal attractant. Rev Chilena Entomol 24:37–44

O'Callaghan M, Glare TR, Burgess EPJ, Malone LA (2005) Effects of plants genetically modified for insect resistance on nontarget organisms. Annu Rev Entomol 50:271–292

Oparka KJ, Santa-Cruz S (2000) The great escape: phloem transport and unloading of macromolecules. Annu Rev Plant Physiol Plant Mol Biol 51:323–347

Owens RA, Blackburn M, Ding B (2001) Possible involvement of the phloem lectin in long-distance viroid movement. Mol Plant Microbe Interact 14(7):905–909

Parent G, Pearen D (1999) 1998/99 Canadian honey situation and trends. Available at http://www.agr.gc.ca/misb/hort/honey.html

Peumans WJ, Smeets K, van Nerum K, van Leuven F, van Damme EJM (1997) Lectin and alliinase are the predominant proteins in nectar from leek (*Allium porrum* L.) flowers. Planta 201:298–302

Pham-Delègue MH, Jouanin L, Sandoz JC (2002) Direct and indirect effects of genetically modified plants on the honey bee. In: Devillers J, Pham-Delègue MH (eds) Honey bees: estimating the environmental impact of chemicals, vol 15. Taylor & Francis, London, pp 312–326, *ca* 118(3): 313–319

Pierre J, Marsault D, Genecque E, Renard M, Champolivier J, Pham-Delègue MH (2003) Effects of herbicide-tolerant transgenic oilseed rape genotypes on honey bees and other pollinating insects under field conditions. Entomol Exp Appl 108:159–168

Planet Ark. Canadian Growers Warn UK Farmers of GMO Crop Risks. 4 Nov 2003. 15 Mar 2009. http://www.planetark.com/dailynewsstory.cfm/newsid/22745/story.htm

Porlingis J (1997) Techniques to increase the attractiveness of kiwi flowers to honey bees. In: Tsirakoglou V, Thrasyvoulou A, Hatjina F, Sfakiotakis E (ed) Proceedings of the third international symposium on Kiwifruit, Thessaloniki, Greece, 19–22 Sept 1995. *Acta Hort* 444:439–443

Rahbé Y, Sauvion N, Febvay G, Peumans WJ, Gatehouse AMR (1995) Toxicity of lectins and processing of ingested proteins in the pea aphid *Acrythosiphon pisum*. Entomol Exp Appl 76:143–155

Rajotte EG, Fell RD (1982) A commercial bee attractant ineffective in enhancing apple pollination. Hortscience 17(2):230–231

Ramirez-Romero R, Josette C, Pham-Delègue MH (2005) Effects of Cry1Ab protoxin, deltamethrin and imidacloprid on the foraging activity and the learning performances of the honeybee *Apis mellifera*, a comparative approach. Apidologie 36:601–611

Ramirez-Romero R, Desneux N, Decourtye A, Chaffiol A, Pham-Delègue MH (2008) Does Cry1Ab protein affect learning performance of the honey bee *Apis mellifera* L. (Hymenoptera, Apidae)? Ecotoxicol Environ Safe 70:327–333

Ramsay G, Thompson CE, Neilson S, Mackay GR (1999) Honey bees as vectors of GM oilseed rape pollen. In: Lutman PJW (ed) Gene flow and agriculture: relevance for transgenic crops. BCPC symposium proceedings no. 72, BCPC, London, pp 209–214

Rieth JP (1986) The repellent effect of pyrethroid insecticides on honey bees. PhD dissertation, University of Arizona, USA. X + 100 pp

Rieth JP, Levin MD (1987) The pyrethroid insecticide hazard to honey bees. Am Bee J 127(11):789–790

Rieth JP, Levin MD (1988) The repellent effect of two pyrethroid insecticides on the honey bee. Physiol Entomol 13(2):213–218

Rosell RC, Torres JI, Brown JK (1999) Tracing the geminivirus-whitefly transmission pathway by polymerase chain reaction in whitefly extracts, saliva, haemolymph, and honeydew. Phytopathology 89(3):239–246

Rosellini D, Pezzotti M, Veronesi F (2001) Characterization of transgenic male sterility in alfalfa. Euphytica 118(3):313–319

Roy DB, Bohan DA, Haughton AJ, Hill MO, Jl O, Clark SJ, Perry JN, Rothery P, Scott RJ, Brooks DR, Champion GT, Hawes C, Heard MS, Firbank LG (2003) Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the farm scale evaluations of genetically modified herbicide-tolerant crops. Philos Trans R Soc London Ser B Biol Sci 358(1439):1879–1898

Salvucci ME, Rosell RC, Brown JK (1998) Uptake and metabolism of leaf proteins by the silverleaf whitefly. Arch Insect Biochem Physiol 39:155–165

Sandström JP, Moran NA (2001) Amino acid budgets in three aphid species using the same host plant. Physiol Entomol 26:202–211

Santamaria M, Thomson CJ, Read ND, Loake GJ (2001) The promoter of a basic PR1-like gene, AtPRB1, from *Arabidopsis* establishes an organ-specific expression pattern and responsiveness to ethylene and methyl jasmonate. Plant Mol Biol 47(5):641–652

Sanvido O, Stark M, Romeis J, Bigler F (2006) Ecological impacts of genetically modified crops. Experiences from ten years of experimental field research and commercial cultivation. Art-schriftenreihe nr. 01, agroscope reckenholz-tänikon research station art, switzerland

Schobert C, Gottschalk M, Kovar DR, Staiger CJ, Yoo BC, Lucas WJ (2000) Characterization of *Ricinus communis* phloem profilin, RcPRO1. Plant Mol Biol 42(5):719–730

Scott SE, Wilkinson MJ (1999) Low probability of chloroplast movement from oilseed rape (*Brassica napus*) into wild *Brassica rapa*. Nat Biotechnol 17(4):390–393

Siciliano SD, Goldie H, Germida JJ (1998) Enzymatic activity in root exudates of Dahurian wild rye (*Elymus dauricus*) that degrades 2-cholorbenzoic acid. J Agric Food Chem 46(1):5–7

Sick M, Kuhne S, Hommel B (2004) Transgenic rape pollen in larval food of bees – component of a model study on the probability of horizontal plant-to-bacteria gene transfer. [original title: transgener rapspollen in der bienennahrung – teil einer modelluntersuchung zur wahrscheinlichkeit des horizontalen gentransfers von pflanzen auf bakterien]. Mitteilungen Deutschen Gesellschaft Allgemeine Angew Entomol 14:423–426

Singh PB, Sinha SN (1997) Effect of Bee-Q on honeybee visit and seed yield of hybrid sunflower. Seed Res 24(2):151–153

Singh S, Saini K, Jain KL (1999) Quantitative comparison of lipids in some pollens and their phagostimulatory effects in honey bees. J Apic Res 38(1–2):87–92

Stanley RG, Linskens HF (1974) Pollen, biology biochemistry management. Springer, Berlin, Heidelberg, New York

Stanley-Horn DE, Dively GP, Hellmich RL, Mattila HR, Sears MK, Rose R, Jesse LCH, Losey JE, Obrycki JJ, Lewis L (2001) Assessing the impact of Cry1Ab-expressing corn pollen on monarch butterfly larvae in field studies. Proc Nat Acad Sci USA 98(21):11931–11936

Stewart CN Jr, Prakash CS (1998) Chloroplast-transgenic plants are not a gene flow panacea. Nat Biotechnol 16(5):401

Tew JE (1992) Honey and wax – a consideration of production, processing and packaging techniques. In: Graham JM (ed) The hive and the honey bee, vol 15. Dadant and Sons, Hamilton, pp 657–704

Tilman D, Fargione J, Wolff B et al (2001) Forecasting agriculturally driven global environmental change. Science 292:281–284

Tuha M, Simuth J (1991) Some properties of water-soluble proteins of propolis. Farm Obz 60(12):539–542

U.S. Census Bureau's (2008) Statistical Abstract – Looking at America's. The Flowing Data Book. Data http://flowingdata.com/2008/05/21/us-census-bureaus-2008-statistical-abstract-looking-at-americas-data/

Van Praagh JP, von der Ohe W (1982) The possibility of masking the repellent effect of plant protection compounds not dangerous to bees. Gartenbauwissenschaft 47(3):114–115

Velkov VV, Medvinsky AB, Sokolov MS, Marchenko AI (2005) Will transgenic plants adversely affect the environment? J Biosci 30:515–548

Wehrmann A, van Vliet A, Opsomer C, Botterman J, Schulz A (1996) The similarities of bar and pat gene products make them equally applicable for plant engineers. Nat Biotechnol 14(10):1274–1278

Williams IH (2001) Bee-mediated pollen and gene flow from GM plants. In: Benedek P, Richards KW (eds) Proceedings 8th pollination symposium. *Acta Hort* 561:25–33

Winston ML (1987) The biology of the honey bee. Harvard University Press, Cambridge

Zhang XG, Liu RL, Kang LY, Zhu YG, Tian P (1998) Construction of expression vectors of male sterility and its fertility restoration in rice (*Oryza sativa* L.). Acta Agron Sin 24(5):629–634

Zhu YY, Gong J, Wu XG, Yang HJ, Shen GZ, Wang XQ, Yin LQ, Lu GH, Wang JA, Wan XS (2001) Preliminary study on flower characteristics and segregation of male sterility of transgenic plants with TA29-Barnase in cabbage (*Brassica oleracea* var. capitata). Acta Agr Shanghai 17(1):79–82

Chapter 21
Management of Pollinators for Crop Plants and Wildlife

Abstract Pollinating animals are critically important to the maintenance of virtually all terrestrial ecosystems, yet the population status of most pollinating species often goes unnoticed. Butterflies, moths, bats, birds, bees, beetles, flies, ants, and wasps assist almost all flowering plants in their reproduction, helping them to develop the seeds, foliage, nuts, and fruits that ensure the survival of innumerable wildlife and human populations worldwide. Sadly, many pollinator populations are declining precipitously around the world. Several pollinators are in the list of endangered species. Management efforts to restore healthy populations of an endangered flowering plant must also consider the animal pollinators that may assist in its reproduction. Likewise, endangered and threatened species of pollinators may have coevolved with a distinct species of flowering host plant.

21.1 Introduction

Pollination as a biotic process has both commercial and ecological value. In the context of agriculture, pollination provides a wide range of benefits to a broad diversity of commodities across the entire world. In some cases, production of the commodity itself results directly from the act of pollination (for example, fruit production). In other cases, although pollination does not result in production of the commodity itself, the process contributes to crop propagation (for example, production of seeds used to grow a root crop such as carrots) or quality (for example, size of tomatoes has been linked to repeated pollination). There are indirect benefits as well, through food-chain relationships. Alfalfa seed, a bee-pollinated crop with an annual value of $109 million (direct effect), is used to produce hay for livestock forage that is valued at $4.6 billion per year (indirect effect) (Morse and Calderone 2000).

Countless wild flowers are considered of little overall economic significance, but in addition to their beauty they prevent erosion of the soil, and provide seeds, nuts,

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and fruit for wildlife. For example, Knott (1950) stated that ten of the most heavily used species of non cultivated plants providing food for quail and pheasant were found in the following plant families: Amaranthaceae, Gramineae, Leguminosae, Polygonaceae, and Rosaceae. The first two families are basically anemophilous, but the others are entomophilous. Manning (1943) and Yeager (1937) also listed numerous forest plants dependent upon or benefited by insect pollination for production of fruits, nuts, or seeds – a goodly percentage of which make up the diets of squirrels, bears, and raccoons (Knott 1950). Hassan (1972) reported that parasitic hymenoptera utilize pollen and nectar of wild flowers. He stated that the populations of these insects are highest in crops near these food sources, and he inferred that an ample supply of nectar and pollen increased their longevity and productiveness. Equally significant is another often overlooked part that wild flowers play in the ecological relationship of an area. Their nectar and pollen provide the continual supply of vital food needed by insect pollinators. In turn, the insects serve as pollinating agents for numerous species of these plants, and contribute to their survival and genetic prosperity.

Some vertebrates also operate as pollinators of ecologically and economically important plants. Tropical trees of the family Bombacaceae, which includes species used for timber, silk cotton, balsa wood, and other products, rely primarily on bats for pollination (Bawa 1990; Watson and Dallwitz 1992). Many columnar cacti and agaves, which are important sources of alcoholic beverages (tequila, mescal) and other products (sisal fibers), also depend on bats and birds for pollination (Arizaga and Ezcurra 2002; Arizaga et al. 2002; Fleming et al. 2001a,b; Grant and Grant 1979; Rocha et al. 2005; Valiente-Banuet et al. 1996; but see also Slauson 2000, 2001). Globally, pollinators are fundamentally important for the production of roughly 30% of the human diet and most fibers (cotton and flax), edible oils, alcoholic beverages, nutraceuticals, and medicines created from plants (Buchmann and Nabhan 1996; McGregor 1976; Roubik 1995).

Estimating the value of pollinators and pollination in natural ecosystems and predicting the consequences of their losses are considerably more challenging than estimating their economic value in agriculture. Such estimates are complicated by both the number of species involved (globally, more than 400,000) and the relative paucity of information available for most of those species.

In this chapter an attempt has been made to focus on key issues related to adaptive management of pollinators and ecosystems. It deals with conservation measures, rehabilitation of landscapes, targeted research programmes and finally animal husbandry. These form part of a total reiterative management cycle of assessment, policy and planning, implementation, capacity building, mainstreaming and monitoring and review. The expanding awareness, understanding and value of the multiple goods and services provided by pollinators can help make forest and agriculture more sustainable and improve productivity in agroecosystems. The technologies that promote the positive and mitigate the negative impacts of humans on pollinator diversity need to be identified and conveyed to the agricultural and forestry communities.

Pollinator-friendly agriculture and natural ecosystem management requires

1. Identification of interactions between pollinators and plants that support effective pollinator functioning.

2. Conservation of natural areas needed to optimise pollinator services.
3. Development of active pollination management technology, such as megachileculture (raising leafcutter bees), bombiculture (rearing bumblebees) and meliponiculture (managing stingless bees).
4. Development of plant lists for nectar and pollen (food plants) for various regions, including larval host plants for butterflies and moths.

21.2 Conservation Measures

Agroecosystems and wild lands may be losing the pollinator communities that are critical to their productivity. There are well-documented losses of pollinators (Buchmann and Nabhan 1996). It is evident that there are losses of vertebrate pollinators but it is also suspected that invertebrate pollinators are being lost. Loss of native pollinators can result from habitat loss, a shortage of bare ground for nesting caused by alien plants, and the insidious effects of invasive alien pollinators. The strategies aimed at conservation of pollinators require assessment of pollinators, capacity building and mainstreaming conservation and pollination services.

21.2.1 Assessment of Pollinators and Pollination Services

Assessing both pollinator declines and pollen deposition deficits, which may result in diminished seed and fruit sets, is one of the principal priorities identified by international pollination experts, and is therefore one of the elements in the IPI Plan of Action. Such an assessment is needed to provide a comprehensive analysis of the status and trends of pollinator diversity and distribution and to provide information useful for enhancing pollinator conservation and sustainable use.

Assessing pollinator status and trends is complicated. Scientific data on the status of pollinators and the state of pollination services are inadequate. Observations suggest that a decline in pollinator abundance is occurring, but often these observations are considered anecdotal. Documenting a decline reliably can help identify specific areas of concern. Measurement and assessment of pollination services therefore need to be properly planned and designed to produce verifiable results.

To accurately assess the extent of pollinator declines, standardized methodologies should be applied globally. There are several approaches to measuring the current status of pollinators, identifying trends in pollinator diversity and abundance, and assessing the adequacy of pollination services. There are also several methodologies for documenting pollinator occurrence across time and/or across environmental gradients, directly and/or indirectly. Pilot methods exist to collect information for assessing the monetary value of pollination services for commercial crops, but more collaborative studies between agricultural economists, natural resource and environmental economists, agronomists and pollination biologists should be fostered. Accurate assessment depends on the correct taxonomic identification of pollinators and the plants they visit and on basic scientific and technical information on pollinators and pollinator–plant relationships. Taxonomic capacity is currently insufficient and building it must form a priority pillar in pollinator conservation. The Global Taxonomic Initiative under the CBD provides a forum for addressing this problem.

21.2.1.1 Assessing the State of Pollination Services

Though answering particular questions may require specific protocols, a core methodology that would permit comparison of results globally is needed. Tools for assessing pollination services should therefore ideally be simple, standardized and applicable in a variety of habitats worldwide and universally used by researchers assessing pollination.

Protocols for Monitoring and Assessment

A recent review of bee studies (Williams et al. 2001) found existing approaches to be of limited use in differentiating between natural population fluctuations and human-induced changes, and recommended approaches that would optimise our ability to detect change. Evidently, standardized protocols for monitoring pollinators are an immediate need. Protocols and sampling methodologies e.g. netting at flowers in standardized grids and use of colorful plastic pan traps filled with soapy water for repeatable, multi-year sampling of native bees have been developed (Cane et al. 2000).

Monitoring Pollination Services Through Time (Direct Monitoring)

The IPI, the World Conservation Union and many other bodies recognize the critical importance of global monitoring systems for understanding the status and sustainability of pollinating animals worldwide. Detection of human-induced changes in plant–pollinator mutualisms presumes knowledge of the natural fluctuations in the abundance of both pollinators and flowers, against which human-induced changes can be assessed. Such baseline knowledge for monitoring programmes is scarce. The natural abundance of many invertebrates, including pollinators, varies greatly between seasons (Cane et al. 2005; Williams et al. 2001; Kearns 2001; Roubik 2001), complicating and delaying efforts to detect trends. Hilton and Miller (2003) demonstrated the importance of long-term surveys and stressed the need to broaden them. (Monitoring for vertebrate pollinators may be easier than for invertebrates, because their population densities normally vary less between seasons.) Policy and management decisions, however, need to be made quickly and should be based on the best available information. Therefore monitoring needs to be undertaken in anticipation of policy/management needs.

Monitoring Pollinator Services Over Space (Indirect Monitoring) and Across Disturbance Regimes in the Landscape

Bees are generally very sensitive to insecticides. Efforts to control plant pests can have severe unintended consequences for pollination. The impact of insecticide application on pollination services and the resulting crop yields depends on the kind of pesticide, dosage, formulation and timing of application. Herbicides are not usually directly toxic to bees and other pollinators, but can have important impacts through eliminating larval host plants (weeds) for Lepidoptera or reducing nectar and pollen for bees. Malathion is very toxic, especially in its micro-encapsulated form where it mimics and travels like pollen grains, and is collected by bees (Johansen and Mayer 1990).

Taxonomy

Accurate genus and species identifications are essential for understanding pollination (Cane 2001). Identifications of principal pollinators are severely hampered by a shortage, in all countries, of taxonomists (O'Toole 1993) and a dearth of modern identification keys catalogues, automated identification technology and revisionary studies. (Revisions are comparative studies of all the species in a group and include identification tools. They prevent duplicate naming of the same species and facilitate species identifications.) The taxonomic impediment is greater for invertebrate animals than for vertebrates because of their greater diversity. O'Toole (1993) discusses the need for taxonomic research in the bees. Michener (2000), a recent comprehensive revision of the genera and subgenera of bees of the world, is an excellent reference for this large and important group of pollinators, summarising the state of knowledge on bee systematics. It provides a common taxonomic framework worldwide and a platform for catalogues and species level revisions needed for conservation-related studies of bees. Similar references are needed for other insect pollinator groups.

Faunal Studies

Properly designed faunal studies are needed that include comprehensive sampling of pollinator communities, provide detailed information on spatial and temporal pollinator distribution and abundance, and elucidate plant–pollinator relationships. Communities of pollinators are dynamic in time and space, with some being active as adults for only a few days or weeks. Although numerous faunal surveys have been conducted, few have used standardised or statistically comparable methodologies and thus may be of limited value for long-term monitoring (Michener 1979; Williams et al. 2001). Exceptions are long-term studies of orchid bees (euglossini) in Panamanian tropical forests (Roubik 2001) censused at chemical baits, and nocturnal tropical bees at light traps on Barro Colorado Island (Roubik and Wolda 2001; Wolda 1992). For most areas of the world there simply are no baseline data for pollinator populations, or studies conducted over enough years to reveal true declines.

Ecosystem Faunal Surveys

Faunal surveys of representative habitats in major ecosystems of the world should be conducted. They should be designed to supply regional pollinator patterns of abundance and diversity; baseline data for long-term monitoring; material of known species and new species for taxonomic studies; plant relationships and basic information for selecting crop pollinators; and details on species abundance through time and across space. Data should be collected and recorded in a way that enables retrieval by other researchers.

Pollinator–Plant Relationships

Asymmetry in plant–pollinator relationships appears to be typical (Vázquez and Aizen 2004). Seldom do pollinator species visit a single plant species. Similarly, few plant species are visited by just one pollinator. The predominant pollinator may change between seasons and between sites. Further, pollinators differ in their efficacy. Sometimes the most abundant flower visitor provides fewer pollination services than a less common visitor. Therefore the whole pollinator guild for each plant species, and similarly the whole plant guild for the pollinators, needs to be understood for the conservation and sustainable use of biological diversity, including agricultural biodiversity. Causes of knowledge gaps in pollinator–plant relationships are insufficient sampling intervals across the entire flowering season, poor coverage of different habitats and geographical areas and inadequate survey durations. Faunal and plant–pollinator studies are concentrated in a few regions, while there is little knowledge about major parts of the world.

Pollinator Life Histories and Nesting Habits

Knowledge of pollinator life history is often essential for conserving pollinators and managing pollination. Basic information needs for bee conservation include nesting sites, substrate (dead wood, stems, soil, etc.), building materials (mud, leaves, resin, fibre) and food plants. Some specialist pollinators have very short active seasons and these may be finely timed to coincide with their host plants' flowering time. Generally, bees that nest in hollow sticks or bore holes in wood are easier to manage. For many bats, access to caves with appropriate characteristics, such as cave entrances, ceiling height and internal topography, is limited.

Some of recommendations for assessment of pollinators and pollination services include

Assessing the state of pollination services

1. Develop protocols for monitoring and assessment. Existing initiatives need to be refined and tested. Their use in Long Term Ecological Research sites and biosphere reserves for the development of long-term baseline data should be considered.

2. Improve knowledge of the specific resource needs of key pollinators to enable better management of the habitat characteristics that help maintain their populations. Studies on fragments, as reserves, may generate data and practical insights of critical importance for pollinator conservation.

Assessing the economic value of pollinators

1. Undertake rigorous assessments of agricultural crop pollinators – how much production depends on pollinators, which ones are self-compatible, and what are the relative contributions of different pollinators.
2. Research ways to increase production through improved pollinator management of varieties of crops that benefit from pollination. This can be used to ascertain the added value due to pollination.

Assessing capacity, resource and research needs

1. Produce electronic catalogues, hosted on internet servers, and regularly update. Use interchangeable, standardized formats designed for electronic dissemination. Build onto existing global and regional checklists of pollinator species and expand these to include all pollinator taxa and all geographic regions.
2. Develop semi- and fully automated specimen identifications systems and make software available to researchers.
3. Conduct pollinator censuses, at regular intervals, lasting at least 4 years, and standardise sampling.
4. Conduct formal surveys of representative habitats in major ecosystems of the world. They should be designed to supply regional pollinator patterns of abundance and diversity; baseline data for long-term monitoring; material of known species and new species for taxonomic studies; plant relationships and
5. Undertake further observation and targeted research into a deeper understanding of pollinator–plant relationships.

21.3 Capacity Building in Conservation and Management of Pollination Services

Capacity building for conservation and management of pollination services must cover a wide range, from formal education at all levels, to the informal building of capacity amongst farmers, land managers, policy makers and other target groups, including the public as a whole. A particular emphasis is needed on building capacity in taxonomy and pollinator identification, since this is one of the major impediments to pollinator conservation.

21.3.1 Formal Education

Migratory pollinators have the potential to capture the interest and imagination of schoolchildren across borders, and have been featured in several cross-border school programs. For instance, at the secondary level in the Ghanaian curriculum, there is good coverage, including highlighting the characteristics of plants that depend on different types of pollination systems. At university level, however, the coverage is actually much less. In several other countries where similar stocktaking assessments have been carried out, the general impression is that there is a lost opportunity to feature pollination biology as a subject in secondary school curriculum. At the university level, courses in pollination biology are available, but not common. Courses that address pollination are offered, for instance, in India and Brazil, but not in many other developing countries. Globally, pollinator conservation has rarely been integrated into courses on conservation biology, and pollination is not generally taught as part of agricultural sciences.

21.3.2 Informal Education Short Courses

In the last 5 years, there have been several short courses on bee identification and pollination that have been developed. Among these have been: USA: The Bee Course (since 1999 in Portal, Arizona, with four to five international participants each year) two Africa: The African Bee Course (in 2003 in Ghana and Kenya and again in 2006 and 2008 in Kenya) Argentina: "Ecologia de la Polinizacion" course at Universidad Nacional del Comahue, Argentina, in 2005.

21.3.3 Farmer and Extension Training

The actions that will need to be taken to conserve and manage pollinators are not completely known; to a large extent, capacity must be built in an adaptive way, as knowledge is being gathered. Conserving a natural service cannot be done by simple prescriptions; land managers will need to work with the challenges of their local ecology and develop management systems tailored to a specific site. Those people most knowledgeable about pollination of a particular crop may be on another continent; therefore long-distance means of sharing information to build capacity needs to be developed. The Food and Agriculture Organization of the United Nations is working with partners to develop modules on pollination for Farmer Field Schools. In the United States, researchers have worked together with non-governmental organizations to bring the outcomes of crop pollination research to farmers, natural resource specialists working with farmers, and natural area managers. They have produced a publication, "Farming for Bees. Guidelines for Providing Native Bee Habitat on Farms", that promotes a three-step approach to pollinator conservation on farms, and other outreach material on management of wild pollinators (for details see chapter).

21.4 Mainstreaming Conservation and Management of Pollination Services

Inspite of pivotal role of pollination services to food production and ecosystem regeneration, has rarely been a matter of concern to policymakers, to address in explicit policies to conserve and more effectively manage pollination services. Strategic ways are needed to mainstream pollination concerns into the relevant sectors and promote "pro-pollinator" actions. In addition to governmental policy, the role of citizen bodies in promoting pollination services is essential. This chapter discusses the developments in both.

21.4.1 Intergovernmental Initiatives

In recognition of a looming pollination crisis, there has been a mobilization of effort on several levels to address pollination management and conservation. On a global level, the international community has identified the importance of pollinators. Decision II/11 of the United Nations Convention on Biological Diversity (CBD) established the Programme of Work on Agricultural Biodiversity and called for priority attention to be given to components of biological diversity responsible for the maintenance of ecosystem services important for the sustainability of agriculture, including pollinators. In October 1998, the Workshop on the Conservation and Sustainable Use of Pollinators in Agriculture, with an Emphasis on Bees, was held in Saõ Paulo, Brazil. The outcome of this workshop was the São Paulo Declaration on Pollinators, which was submitted by the Government of Brazil to the CBD's fifth meeting of its Subsidiary Body for Scientific, Technical and Technological Advice (SBSTA 5).

Considering the urgent need to address the issue of the worldwide decline in pollinator diversity, the Conference of the Parties to the Convention Biological Diversity established an International Initiative for the Conservation and Sustainable Use of Pollinators (also known as the International Pollinators Initiative-IPI) in 2000 (COP decision V/5, section II) and requested the development of a plan of action. The CBD Executive Secretary was requested to "invite the Food and Agriculture Organization of the United Nations to facilitate and co-ordinate the Initiative in close co-operation with other relevant organizations." In November 2000, FAO organized a meeting with the participation of key experts to discuss how to elaborate the International Pollinators Initiative. Subsequently, a plan of action was prepared by FAO and the CBD Secretariat. The aim of the International Initiative for the Conservation and Sustainable Use of Pollinators (IPI) is to promote coordinated action worldwide to: Monitor pollinator decline, its causes and its impact on pollination services; Address the lack of taxonomic information on pollinators; Assess the economic value of pollination and the economic impact of the decline of pollination services; and Promote the conservation, restoration and sustainable use of pollinator diversity in agriculture and related ecosystems.

21.4.2 Government Policy

The principal national sectors in which pollination merits consideration include environment and agriculture. Every country that is party to the Convention on Biological Diversity has committed themselves to develop a National Biodiversity Strategy and Action Plan (NBSAP); a number of countries have included consideration of pollination in their NBSAP. For example, in Pakistan's NBSAP, pollinators are specifically mentioned: "Biodiversity provides free of charge services worth hundreds of billions of rupees every year that are crucial to the well-being of Pakistan's society. These services include clean water, pure air, pollination, soil formation and protection, crop pest control, and the provision of foods, fuel, fibres and drugs. As elsewhere, these services are not widely recognised, nor are they properly valued in economic, or even social terms. Reduction in biodiversity (including local extinction of species) affects these ecosystem services. The sustainability of ecosystems depends to a large extent on the buffering capacity provided by having a rich and healthy diversity of genes, species and habitats. In that respect, biological diversity is like economic diversity in a city; it is essential for long term survival and a sound investment in the future." South Africa's National Biodiversity Strategy and Action Plan recognizes the dependence of production sectors such as cultivation and Plantation forestry on ecosystem services, including pollination.

In the UK, the National Biodiversity Action Plan1 includes three types of specific action plans, for species, habitats and local planning. In addition, there are several other data and information products which include :

1. Biodiversity Action Reporting System (BARS): a web-based information system that hosts and supports the planning, monitoring and reporting requirements of national and local Biodiversity Action Plans, and provides data for the reporting rounds.
2. Habitat Management on the web Habitat Management on the Web: a search engine designed to provide information about how best to manage non-marine habitats in the UK for biodiversity and conservation.
3. Species account pages" Species account pages: the provision of collated information about UK BAP priority species, including why they are a priority, how they are protected and actions required.

Countries that are Parties to the Convention on Biological Diversity (CBD) have agreed to develop mechanisms for sharing biodiversity data with the public both on a national and on an international basis, through a clearinghouse mechanism. Through the clearinghouse mechanism, the CBD has fostered more efficient biodiversity information management in a number of countries. Pollination trends and news have been featured in the United States biodiversity information management portal, and in IABIN (Inter-American Biodiversity Information Network). IABIN was established in 1996 to provide the networking information infrastructure (such as standards and protocols) and biodiversity information content required by the countries of the Americas to improve decision-making, particularly for issues at the interface of human development and biodiversity conservation. To date, 191 countries have become parties to the Convention.

21.4.3 Protected Areas

Pollinators have rarely figured in the design of protected areas, but that is changing. In Mexico, where bats are critical to the vegetation structure of over a vast areas of land and to the economic activities of pulque and tequila producers, concern over their status has prompted the government to amend Mexico's Federal Law of Wildlife to encompass all caves and crevices as protected areas6. The European community has identified and protected 431 Prime Butterfly Areas in 37 sites7; in Serbia a Natura 2000 site (seriously threatened habitats protected by EU legislation) was protected because it serves as hoverfly habitat. It has been noted that for insect pollinators the design of protected areas will require special considerations8. There are multiple considerations with respect to pollinator conservation: forage plants, very specific nesting habitats such as soft banks for ground-nesting bees, and the fact that bees, for instance of medium body size, can regularly fly up to 2 km between nest sites and forage patches. But provided that reserve selection, design, and management can address the foraging and nesting needs of bees, networks of even small reserves could hold hope for sustaining considerable pollinator diversity and the ecological services pollinators provide.

21.4.4 Biodiversity Regulations

More than a decade and a half after the adoption of the Convention on Biological Diversity (CBD), many countries are in the process of mainstreaming their commitments into national-level biodiversity regulations. While many of these are in draft form, they offer some strong tools for putting pollinator conservation into policy. For example, where the biological diversity is not in a protected area, Kenya's Environmental Management and Coordination Act provides for the Minister of Environment and Natural Resources "to declare any area of land…to be a protected natural environment for the purpose of promoting and preserving specific ecological processes, natural environment systems, natural beauty or the preservation of biological diversity in general." In developing the guidelines and regulations to support this Act, a multi-stakeholder biodiversity taskforce first defined "specific ecological processes" to include soil erosion control, watershed services, soil fertility maintenance, microclimate regulation, pollination services, and wildlife migrations. Secondly, they recognized that the Ministry does not have sufficient eyes and ears to identify all such sites of environmental significance that might merit gazettement as a protected natural environment. Thus, provision has been made in the biodiversity regulations, for: "other lead agencies, District Environmental Committees, Provincial Environmental Committees, local communities and other members of civil society (to) propose sites for consideration as Environmentally Significant Areas." Through such measures, a community of coffee farmers, for example, could ask for the protection of a small forest or riparian zone that provides alternative forage and nesting sites to coffee pollinators.

21.4.5 Red Lists

Red Lists are national lists developed using the World Conservation Union (IUCN) criteria to identify levels of threats to species. For threatened pollinators, they can be very effective tools for guiding policy and local activities to prevent species loss. In Europe there are red lists including bees for: Spain, Switzerland, Germany, Great Britain, Lithuania, Latvia, Netherlands, Norway, Poland, Finland and Slovenia. These lists on average contain about a quarter of the total number of bee species in the country and may be up to half (e.g. Germany and Netherlands). The current Brazilian national and regional red lists include 130 terrestrial invertebrate species, of which 42% are butterflies. The red list for North America includes 58 bees and 59 butterflies and moths. Many other countries include hoverflies and butterflies in their national red lists.

21.4.6 National Pollinator Initiatives

Brazil's national pollinator initiative, the Brazilian Pollinator Initiative (BPI) has a unique governmental structure, and has been active on many fronts. Brazil has formulated an Understanding for Technical Cooperation between its Environment and Agriculture ministries regarding research on biodiversity and forests, including pollinator conservation and management. A national committee of the Brazilian Pollinators Initiative is charged with a number of tasks; amongst these, they have undertaken an inventory of pollination demands of each region of the country for crops with pollination management needs, an exercise that will guide the initiative to focus on priority crops10. In 2004, the BPI supported a resolution that was adopted in Brazil to regulate the protection and use of native bees, including stingless bee breeding11. The resolution sought to rectify the fact that under previous policy, the rearing and management of an introduced bee (the honeybee) was legal, while sustainable use of an important natural resource in Brazil, stingless bees, was not legally recognized. The resolution noted the following factors: (1) the native bees, in any development phase, and living in natural environments outside captivity, are considered part of the wild Brazilian fauna; (2) these bees, their nests, shelters and natural breeding sites belong to the people and they are subject to collective use by the terms of the Federal Constitution; (3) the value of meliponiculture (beekeeping with stingless bees) to the local and regional economy and the importance of pollination by wild bees to the ecosystem stability and to agriculture sustainability; and (4) Brazil has been a major international proponent of the International Pollinators Initiative and its efforts to conserve and sustainably manage pollinators.

21.4.7 Agriculture

In the agricultural sector, pollination has often been overlooked in rural development strategies and is not included as a technological input in most agricultural development packages. High value agriculture is promoted by many governments, and agricultural development institutions offer packages of practices for different types of crops, but most overlook the importance of managing pollination to achieve a sustainable yield. Introducing substantive changes in agricultural development will first require changes in agricultural research and development investment policies, such that the research agenda recognizes pollination as an important aspect of crop productivity and seeks to identify optimal ways to use and conserve pollinators. Changing grower behaviour based on research findings is also another challenge that the policy environment can impact. The importance of a supportive enabling environment for pollination services in agriculture is highlighted in the case study contribution on blueberries in Maine, USA. A multi-year research project aimed at securing pollination services for lowbush blueberries was funded by the state in Maine in response to a recognized crisis: crosspollination of lowbush blueberry by bees is essential for obtaining good fruit set and yield12, yet native wild bees have been heavily impacted by pesticide use and habitat loss. Growers have turned to renting honey bee colonies, yet parasites, diseases, the threat of Africanized honeybees, and low profit margins have jeopardized the supply of honey bees and contributed to a substantial increase in the rental price per colony. The research documented proven techniques of conserving native bees at the same time as reducing costs for honeybee rentals. But despite the fact that the authors of the study produced and disseminated educational publications, presented many grower talks, and conducted demonstration trials on native bee conservation, very few growers have actually adopted the recommendations for the conservation of native bees. The authors conclude that, "we have come to believe that specific local, state, or national incentives, such as tax credits or other mechanisms, are necessary to motivate growers to implement conservation practices."

21.4.7.1 Pollination and Crop Production

China has officially recognized pollination as an agricultural input, along with other conventional inputs such as fertilizers and pesticides13. But the degree to which pollination can contribute to sustainable crop yields has not been addressed in agricultural policies in most countries.

21.4.7.2 Pollination and Regulation of Agricultural Chemicals

More than 30 years ago, Rachel Carson wrote the book "Silent Spring", outlining the detrimental effects of pesticides on the environment. Ms. Carson warned the world not just about "Silent Springs" but also about "fruitless falls" – in which there is no pollination and subsequently no fruit, due to pesticide poisonings of pollinators14. In many countries, there have been efforts to protect honeybees from poisoning by agricultural chemicals, but toxicity to other wild pollinators is rarely considered in agricultural regulations or included in label warnings.

21.4.7.3 Pollination and Land Stewardship Programs

In Europe, agri-environmental schemes have been developed to reduce the use of agricultural chemicals and nutrients and to encourage farmers to carry out environmentally beneficial activities on their land15. The aim is to enhance biological diversity across a range of plant and animal groups, including pollinators. The cost to the farmer in supplying these environmental services is compensated through payments. Examples of the types of land management activities carried out include:

Reversion of intensively used land to biologically diverse but unprofitable extensive land uses.
Reduction in the use of nutrients.
Reduction or cessation of use of pesticides (e.g. organic farming).
Creation of *Nature* zones taken out of production.
Continuation of traditional environmental land management in zones liable to neglect.

Maintenance of landscape features which are no longer agriculturally viable. In the United Kingdom, a number of other land stewardship schemes exist, and new ones are under development that will specifically encourage pollinator-friendly options such as16: Buffer strips. Sown field margins provide forage (nectar and pollen) and nesting resources for pollinators as well as buffering boundary habitats against agrochemical sprays. Sown grasslands. Including pollen and nectar flowers in grassland mixes can increase the diversity, abundance and availability of forage resources. hedgerow management. Careful management of hedges can create and protect habitats suitable for pollinators. Permanent grasslands. Establishing grasslands with very low inputs provides long-term habitats for pollinators.

21.4.7.4 Partnerships to Promote Pollinators

In many regions and countries of the world, civil society groupings have formed around the issue of pollinator declines, conservation and sustainable management. In countries as diverse as Colombia, Kenya and Ghana, national pollinator initiatives have been established and lead by civil society17. Often these are organized by national wild bees specialists, addressing scientific issues such as taxonomic identifications, pollinator distributions, community ecology of wild bees and plant–bee interactions. In Kenya, and in Ghana, representatives of the private sector have joined national pollinator initiatives. Additionally, in a number of regions around the world, pollinator initiatives have been formed, and are building regional capacity in assessment and advocacy for pollinator conservation and use.

The North American Pollinator Protection Campaign (NAPC) brings together experts in academia, research, government agencies, agriculture, private industry, environmental groups and interested individuals from Mexico, Canada, and the United States18. This public-private collaboration has made considerable progress in advancing the pollinator conservation agenda in the minds of the public and decision makers. NAPC's specific goals are to: Strengthen the network of organizations working to conserve and protect pollinator populations.

Raise awareness and educate about pollinators' contribution to agriculture, ecosystem health, and a healthy and affordable food supply. Promote open dialogue about pollinator conservation among individuals, institutions, and groups. Encourage collaborative partnerships and actions to multiply success in pollinator protection programs.

Promote conservation, protection, and restoration of pollinator habitats. Document and support scientific, economic, and policy research, spanning a wide range of disciplines, concerning pollinators and pollinator habitat. NAPC works through a set of committees, including Conservation, Education, Special Partnerships, and Policies and Practices, that are action oriented: committees are asked to identify their target audiences, the specific behaviors that need to be encouraged with this audience, ways to measure the outcomes of these behaviors, and the benefits and barriers to those behaviors. Amongst the means they have used to advocate for more positive outcomes for pollinators are included information bulletins for target audiences, encouraging research and analysis by proposing a US National Academy of Sciences survey of the status of pollinators in North America, the sponsorship of a "Pollinator Protection Award" to corporate members of the Wildlife Habitat Council that show exceptional pollinator friendly practices, and through advocacy for international, national and regional policies and practices that require or encourage the protection of pollinators or their habitats. The NAPC *Nature*'s Partners curriculum offers a range of inquiry-based activities suitable for classrooms and gardens. Amongst their present successes in mainstreaming pollination, they are working with the conservationists of the state of Montana to design incentives for farmers, ranchers and landowners who invest in the health of pollinators by planting native and pollinator friendly plants in buffer zones. The hope is to develop this program as a case study to implement in states or regions.

The African Pollinator Initiative (API) is an Africa-wide group of people interested in and committed to protecting, understanding and promoting the essential process of pollination for sustaining livelihoods and conserving biological diversity in Africa. It was established during the first African Pollinator Initiative workshop held in Kenya in 2002, and has produced a plan of action, a special issue of the International Journal of Tropical Insect Science, featuring pollination research findings in Africa, and an initial stocktaking report of "Crops, Browse and Pollinators in Africa"19. The API Plan of Action is organized around four components: Public Education and Awareness, Placing Pollination in the Mainstream, Conservation and Restoration, and Capacity Building.

The European Pollinator Initiative (EPI) was formed in response to growing evidence and concern over local declines of pollinators and loss of pollination services in Europe, and a sense that the problem is more widespread20. Although many scientists, governments and NGO's are working to conserve, manage and promote pollinators and the services they provide, there has been relatively little interaction between these groups at the continental level. Research and information exchange has been fragmented and in some cases has overlapped, and it was recognized that the full potential for conserving and sustainably managing pollinators for maximum societal benefit in Europe was far from being met. As a response, EPI has developed the following approaches:

An interim steering committee has been established to guide the initial development of the EPI.

Europe has been partitioned into 16 regions and each has a representative who is responsible for coordinating local activities. These representatives are informing potentially interested parties in their region and also feeding back information on local issues and concerns relating to pollination.

In the short-term a centralized expertise database is being constructed. Longer term activities are covered by the EPI "Plan of Action". EPI's Plan of Action is organised around the four elements of the International Pollinator Initiative:

1. Assessment – Quantifying the loss of pollinators in Europe and the risks associated with the loss of pollination services. These assessment objectives are already being pursued through the ALARM project21 and national activities in other countries including Italy and Ireland.
2. Adaptive management – Identifying the best management practices and technologies to overcome declines in pollinators and the services they provide.
3. Capacity Building – Build and strengthen alliances and expertise in Europe to increase the benefits from pollination.
4. Mainstreaming – Supporting national plans for the conservation and sustainable use of pollinators, and increasing the awareness of governments, industry and the public. Amongst other civil society organizations supporting pollinator conservation is the International Bee Research Association (IBRA), a not-for-profit organization with a worldwide membership that was established in 194922. IBRA aims to increase awareness of the vital role of bees in the environment and encourages the use of bees as wealth creators. It is a global network with a wealth of expertise and an extensive knowledge base that promotes the study and conservation of all bees and their value as bio-indicators.

Evidently, mainstreaming pollinator conservation and sustainable use into public policy requires the efforts of a diverse set of actors, from government agencies, intergovernmental organizations and civil society. Initiatives and efforts have been initiated on several levels. However, concrete and explicit policy approaches to conserve and better manage pollination services have not been well articulated in most countries or regions. Approaches at the local level in developing pro-pollinator policy are also needed, since this is the level at which most actions need to take place. The conservation of pollinators should be better integrated into regional, national and local policy for the environment, agriculture, and development sectors. Exchange of information on different policy approaches to conserve and better manage pollination services should be encouraged. Local level measures to encourage pollinator-friendly land management decisions merit better identification.

Some of the causes for decline of pollinators and suggestions for their rebuild up are elucidated in case studies conducted in different parts of the world which include;

21.4.7.5 Habitat Loss in Asia

The International Centre for Integrated Mountain Development (ICIMOD) has carried out research on pollination and associated productivity of mountain crops over the past decade. The project has identified loss of habitat and the associated decrease in food and nesting sites for pollinators, resulting from the expansion of farming into forests and grassland areas, as a major cause of decreased mountain crop productivity. As a result of their findings, the project is making efforts towards conservation of pollinators through raising awareness among farmers and policy makers (Partap and Partap 2002; Ahmad et al. 2002).

21.4.7.6 Indicator Species in Brazil

Central and South American native bee populations are declining in several disturbed habitats, including fragmented natural ecosystems. Lima-Verde and Freitas (2002) identified *Melipona quinquefasciata* as an indicator of stingless bee habitat loss. They mapped its distribution in fragmented ecosystems on the northeastern Brazilian plateaus. Knowledge about the bee species and its habitat now enables conservation measures to prevent this stingless bee species from going extinct. These measures include reducing firewood gathering and agricultural expansion, which destroy the ecosystem needed for ground-nesting bees and their floral host plants.

21.4.7.7 Persistence in a Farming System

Marlin and LaBerge (2001) demonstrated that although land uses and land cover in Macoupin County, Illinois (US) have changed during the past two centuries, the bee community in the early 1970s resembled that found at the turn of the century. The diversity persisted probably because diverse habitats within the heterogeneously used agricultural matrix contained the variety of host plants and nesting sites required by the bees. Advice given for land management was maintenance of diversity in land use, including the retention of natural areas, hedgerows etc.

Loss of pollinators can also result from the spread of disease, or invasive alien species.

21.4.7.8 Quarantine Measures

New Zealand has strict quarantine measures to prevent the introduction of undesirable organisms. The movement of hive bees between North and South Island is strictly prohibited to halt the spread of *Varroa* mites. Although the honey bee is exotic to New Zealand, it is an important agricultural pollinator.

21.4.7.9 Invasive Bumblebees Around the World

Recent concern about invasive alien pollinators has focused on planned introductions of *Bombus terrestris*, a European bumblebee widely used for pollinating greenhouse crops, such as tomatoes, in other areas. Colonies have been exported to Japan, Israel and Chile (*Bombus ruderatus* in this example), and have subsequently naturalised in these regions. In Israel, feral *Bombus terrestris* colonies are a significant ecological threat, with populations of several native bees, including native *Apis mellifera*, showing significant declines (Dafni 1998). Bumblebees forage widely (5 km from nests), are more efficient at exploiting limited nectar resources, and cause significant reduction in seed production of their nectar plants. The result of this lowered reproductive output of indigenous flora is reduced post-fire regeneration (Dafni and Shmida 1996). More recently *Bombus terrestris* has been deliberately introduced into Mexico, and accidentally introduced into Tasmania, which poses a threat to Australia. If it becomes established in North America, it is plausible that it will expand to include the range of closely related native *Bombus*. Possible negative outcomes include introduction of diseases (e.g. *Nosema* and *Crithidia*), parasites and competition for floral resources with native bumblebees (Imhoof and Schmid-Hempel, 1998). For example, in Tasmania, *Bombus terrestris* has invaded most of the island (Hingston et al. 2002) and is associated with increases in seed production in weeds (Stout et al. 2002). To avoid the introduction of a species that can become invasive, efforts are under way in Colombia to breed native *Bombus* species for greenhouse pollination.

The importation of exotic species should be a last resort. First try to manage indigenous species and never import species that are known to become invasive. Before any exotic species are imported ensure that appropriate risk analysis and cost/benefit studies are undertaken, as in the case of oil palm pollinators (Martins et al. 2003).

21.4.7.10 Rehabilitation of Landscapes

Loss of habitat through land use changes, e.g. due to conversion of natural areas to agriculture, mining or urban development, has been identified as the principal cause of pollinator decline. Farmers can be encouraged to restore some of their farmland to forest or grasslands, road planners can ensure roadsides and infrastructure servitudes are reseeded with pollinator-friendly plant species, and urban planners can be encouraged to consider native floral diversity in parks.

21.4.7.11 Maximize Floral Diversity

Sakagami and Fukuda (1973) sampled two sites in Japan, one in the city's Botanical Garden and the other on the University of Hokkaido campus. The nine-hectare Botanical Garden contained a mixture of natural and exotic plant species.

The University site was 150 ha and contained primarily native vegetation. Both were isolated from continuous tracts of natural vegetation by the city. Despite its smaller size, the Botanical Garden yielded one-third more native bee species, perhaps a response to increased floral diversity.

Abundance and diversity of pollinators can improve pollination (Steffan-Dewenter et al. 2003). Because crops generally have limited flowering periods, maximising the floral diversity in the ecosystem will help maintain the abundance and diversity of pollinators for adequate pollination of crops – and wild plants. The assemblage of flowering plants that will maintain pollinators should include those with a variety of floral structures and long, overlapping blooming periods. Modern hybrids should be introduced with caution because they often have inadequate pollen and/or nectar since plant breeders do not select for these.

Increased productivity and sustainable land use should be sufficient incentive for sustaining pollinator species and numbers, but government incentives should encourage this process. Although not necessarily targeting pollination per se, such incentives are increasingly becoming part of national policies. The use of pesticides or other agrochemicals may cause pollinator declines. Here rehabilitation strategies should focus on using other methods of pest control, such as biological control and integrated pest management. Farmer knowledge can be increased through educational organisations such as farmer field schools, agricultural extension agents and agricultural colleges. Pollinator restoration and the management of native pollinators are in their infancy. It may be necessary to reintroduce native pollinators. This is not easy, and procedures for doing so are largely unexplored.

21.4.7.12 Agri-Environmental Schemes

There is a need to encourage farmers to carry out environmentally beneficial activities on their land and to enhance biological diversity, including pollinators. The cost to the farmer of supplying these environmental services is compensated through payments. The types of land management activities encouraged include

1. Conversion of intensively used land to biologically diverse, yet commercially profitable, lands.
2. Reduction in the use of synthetic fertilisers.
3. Reduction or cessation of pesticide use (organic farming and no-till agriculture).
4. Creation of *Nature* zones not used for production. Planting of wildflower mixes or use of blooming cover crops that can later be ploughed under as green manure.
5. Continuation of traditional land management in areas likely to be neglected.
6. Maintenance of landscape features that are no longer used for agriculture.

The EU applies agri-environmental measures that support farming practices specifically designed to help protect the environment and maintain the countryside. Farmers commit themselves, for a five-year minimum period, to adopt environmentally-friendly farming techniques that go beyond the usual good agricultural practice. In return they receive payments that compensate for additional costs and loss of income that arise as a result of altered farming practices. Examples of commitments covered by national/regional agri-environmental schemes are

1. Extending environmentally favourable farming.
2. Management of low-intensity pasture systems.
3. Integrated farm management and organic agriculture.
4. Preservation of landscape and historical features such as hedgerows, ditches and woods.
5. Conservation of high-value habitats and their associated biodiversity.

Agri-environment measures have become the principal instrument for achieving environmental objectives within the Common Agricultural Policy. In 2003, 15 EU member states were participating in the EU Agri-Environmental Schemes, including 900,000 farms encompassing 27 million hectares, or 20% of EU farmland (http://europa.eu.int/comm/agriculture/envir/index_en.htm#measures).

21.4.7.13 Conversion of Crop Lands in Asia

In a few mountain areas of China since 1999 the government has initiated programmes encouraging the conversion of croplands by farmers to forests and grasslands. Such programmes may help restore pollinator populations and improve natural ecosystems.

21.4.7.14 Cacao in Tropical America

Diminished biodiversity in agroforestry cropping systems has reduced effective pollination of cacao (*Theobroma cacao*) in Central and South America (especially Costa Rica and Brazil). Overly fastidious management (“cleanliness”) of *Planta*tions included the removal of rotting vegetation, the substrate in which the pollinating midges undergo larval development (Winder and Silva 1972), and yield reductions ensued. Purposeful replacement of appropriate plant materials such as palm trunks (Ismail and Ibrahim 1986) will restore adequate pollination by fly pollinators – various midges.

21.4.7.15 Soursop in Brazil

Soursop (*Annona muricata*) is a tropical fruit crop pollinated by beetles that use its flowers for food, protection and finding mates (Webber 1996). In Brazil, the number of pollinating beetles in commercial orchards is usually inadequate and growers need to hand-pollinate flowers to ensure adequate fruit set and reduce malformation in fruit. Currently, the highest quality fruits result from the labour intensive and costly practice of hand-pollination. The shortage of pollinators is due to ploughing and herbicide use, which eliminate the short grass in orchards, the roots of which are the only source of food for the pollinator's larvae. Stopping the use of herbicides and ploughing, and introducing mowing to control the grass, increased and maintained pollinator numbers to satisfactory levels (Aguiar et al. 2000).

21.4.7.16 Butterfly Adult and Larvae Plants

Vegetation for butterflies and moths must include nectar plants and foliage planted for their larvae. No caterpillars feeding on foliage results in no adult butterflies and moths later in the season. The concept of "partial habitats" (Westrich 1996; Tepedino 1979) is broadly applicable to insect pollinators. Immature stages of invertebrate pollinators are difficult to locate and impractical to sample, but their requirements must be understood and met when classifying habitat diversity, mapping habitat fragments, evaluating habitat change or restoring degraded lands.

21.4.7.17 Reversal of Pollinator Depletion

Because many pollinators are highly mobile, in areas where they have been depleted their losses are usually reversible in carefully planned rehabilitation programmes. This is easier when they are adjacent to natural habitats with intact pollinator populations. Restoration of vegetation must include the correct nectar and pollen host plants for the pollinators under consideration. Nesting materials, which may include *inter alia* plant resins, leaves, mud, sand and dead trees (containing beetle burrows) may have to be provided. In healthy natural ecosystems and diverse, low intensity, agroecosystems pollination is usually considered to be a "free service" – the cost of this "free" service being the maintenance of a diverse ecosystem. Where pollination services are inadequate, pollination management may be required. There are a number of potential approaches, and targeted research may be needed to identify the correct one. These approaches are discussed in Matheson (1994).

21.5 Targeted Research Programmes

Targeted research is research designed to address specific concerns. For pollinator biodiversity conservation, it should address issues such as the diversity of pollinators in an ecosystem, their nest and host plant requirements, and their roles as pollinators.

21.5.1 Apple Pollination in India

In the Himachal Pradesh Province, in the Indian Himalayas, apple productivity declined continuously for several years because of inadequate pollination. Farmers now use honey bees (*Apis mellifera* or *Apis cerana*) to pollinate the apples.

Some farmers keep their own honey bees, while others rent them from the Department of Horticulture or from private beekeepers. At present only Himachal Pradesh, in the entire Hindu Kush–Himalayan region, has a well-organised pollination system. This large-scale use of honey bees has led to a new vocation. The success of this enterprise resulted from targeted research into apple pollination by honey bees.

21.5.2 Managing Indigenous Pollinators

Australian government agencies have a long history of investigating the use of honey bees for pollinating crops. Recently, the use of native stingless bees (*Trigona* spp.) for macadamia and cucurbits, and the blue-banded bee, *Amegilla* spp., for pollinating tomatoes in glasshouses, has been instigated. The latter is likely to overcome the need to introduce exotic bumblebees into Australia.

21.5.3 Passion Fruit in Brazil

Passion fruit (*Passiflora edulis*) growers, especially on smaller farms in Ceará, Brazil, hand-pollinate their crops because the only efficient pollinator of its large flowers, the carpenter bee (*Xylocopa* spp.), is rare in commercial orchards. Because the family work force is needed for other farm activities, many farmers have discontinued passion fruit production. Researchers at the Federal University of Ceará (Freitas and Oliveira-Filho 2001) have developed efficient nesting boxes for large carpenter bees, and this has increased yield by 92.3% and made hand-pollination unnecessary. Similar technology has been developed in Mardan, Malaysia (Roubik 1995).

21.5.4 Alfalfa Fields in North America

Although alfalfa is not native to North America, it is pollinated by a wide array of bees, especially solitary, leaf-cutting bees (*Megachile* spp.), of which the alfalfa leafcutting bee is a non-native cultivated species. Many leafcutting bees make their nests in tunnels left by wood-boring insects. In the 1940s, in parts of western Canada, farmers cleared land to join together parcels of small fields for alfalfa seed production. This practice reduced brush and wood piles, and the edge: area ratio of the fields. As a result, nesting habitat for native pollinators was diminished and alfalfa growing in the centre of large fields remained unpollinated. Seed yields overall per acre declined. In Manitoba, Stephen (1955) recorded yields of 1,000 kg/ha from small fields, but only 15 kg/ha from large fields. The pioneering work of Bohart (1972) and Hobbs (1967) gave rise to the multimillion-dollar industry of "megachileculture", whose huge economic benefits are described by Olmstead and

Woolen (1987). Today, the problem of alfalfa seed production is largely solved by management of domesticated alfalfa leafcutting bees (*Megachile rotundata*).

21.5.5 Reducing Pesticide Use in Canada

The adverse effects of some pesticides on pollinators are well understood (Johansen and Mayer 1990). The effects of the organophosphorus pesticide fenitrothion on blueberry pollinators in New Brunswick, Canada, were a massive demise of the pollinators and an annual harvest loss of about 75% in the blueberry crop in the affected regions (Kevan 1975a, b, 1977; Kevan and LaBerge 1979; Kevan and Oppermann 1980; Kevan and Plowright 1995; Kevan and Baker 1999). This resulted in research into "bee-safer" insecticides, and blueberry lands received a buffer where only these insecticides could be used.

In assessing the impact of agro-chemicals on pollinators, the type, timing and methods of application of the pesticides should be considered. When applying any pesticide, or other agrochemical, strict adherence to safety (operator and pollinator) guidelines should be followed. Often less toxic alternative insecticides could be used. Honey bee colonies can be covered to keep foragers in their nests during spraying, or spraying can be done at night.

21.5.6 Promoting Pollinator Husbandry

Pollinator husbandry is the use of technology for keeping pollinators, mostly through the provision of nests and nesting material. The practices should include adequate nectar, pollen and/or larval host plants, and ensuring that nesting sites and nest-making materials are available. Flowering plants in the vicinity should be diverse, and have long and overlapping blooming periods. Care should be taken to avoid the use of toxic agrochemicals.

21.5.7 Indigenous Honey Bees in Asia

ICIMOD has an ongoing programme promoting the use of indigenous honey bees for pollination in India, Nepal and Pakistan. It includes training for farmers in managing honey bees for crop pollination.

21.5.8 Honey Bees in Australia

A key objective of the Australian Government's Rural Industries Research and Development Corporation is to improve the productivity and profitability of the

Australian beekeeping industry. While they do not directly train and educate apiarists, they provide key research results from targeted research and husbandry information via their web site (www.rirdc.gov.au/programs/hb.html). Their publications provide information on disease management and nutrition for bees. The mission statement of the Australian Honey Bee Industry Council is "To maximize the efficient use of industry resources and funds to ensure the long-term economic viability, security and prosperity of the Australian honey bee industry" (www.zeta.org.au/~anbrc/index.html).

21.5.9 Native Bees in Australia

Australian native bee ecology and husbandry received little attention until the advent of the Australian Native Bee Research Centre, a privately funded NGO. This organisation shares information on blue-banded bees (*Amegilla* spp.) and stingless bees (*Trigona* species) (www.zeta.org.au/~anbrc/index.html), among others.

21.5.10 Eastern Honey Bee for Pollination

The Asian hive bee (*Apis cerana*), a cavity nesting species in the genus Apis, contains seven species (Engel 1999). This Asian honey bee has been managed for centuries in Japan and China for honey and wax production. It pollinates *Cymbidium* orchids and has recently been managed for the pollination of other crops (Kevan 1995).

Summary of recommendations for adaptive management of pollinators for crop plants and wildlife.

21.5.11 Conservation Measures

Avoid importation of exotic pollinators. First try to manage indigenous species. Never import species that are known to become invasive and, before importing, ensure that appropriate risk analysis and cost/benefit studies are done. Maximise diversity and abundance of pollinators to improve pollination, including floral diversity in the ecosystem. The flowering plants that will maintain pollinators should include those with different floral structures and long, overlapping blooming periods. Modern hybrids often have inadequate pollen and/or nectar.

21.5.12 Rehabilitation of Landscapes

Reverse pollinator depletion through carefully planned programmes. This is more successful in areas adjacent to natural habitats with intact pollinator populations. Vegetation must include the correct nectar and pollen plants and nesting materials.

21.6 Targeted Research Programmes

The type, timing and methods of application of the pesticides are all-important for pollinator conservation. When applying any pesticide, or other agrochemical, follow safely guidelines. Often, less toxic alternative insecticides could be used.

21.7 Promoting Pollinator Husbandry

Pollinator husbandry programmes can improve pollination and create employment.

References

Aguiar JR, Bueno DM, Freitas BM, Soares AA (2000) Tecido nutritivo em flores de gravioleira. *Annona muricata L.* Rev Ciência Agronômica 31:51–55

Ahmad F, Partap U, Joshi SR, Gurung MB (2002) Why the HKH region needs the Himalayan honeybee *Apis cerana*. Briefing paper, January 2002. ICIMOD, Kathmandu, Nepal

Arizaga S, Ezcurra E (2002) Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette. Am J Bot 89:632–641

Arizaga S, Ezcurra E, Peters E, de Arellano FR, Vega E (2002) Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. I. Floral biology and pollination mechanisms. Am J Bot 87:1004–1010

Bawa KS (1990) Plant–pollinator interactions in tropical rain forests. Annu Rev Ecol Syst 21:399–422

Bohart GE (1972) Management of wild bees for the pollination of crops. Annu Rev Entomol 17:287–312

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island Press, Washington

Cane JH (2001) Habitat fragmentation and native bees: a premature verdict? Conserv Ecol 5(1):3. www.consecol.org/vol5/iss1/art3

Cane JH, Minckley RL, Kervin L (2000) Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. J Kans Entomol Soc 73:225–231

Cane JH, Minckley RL, Kervin L, Roulston TH (2005) Temporally persistent patterns of incidence and abundance in a pollinator guild at annual and decadal scales: the bees of *Larrea tridentata*. Biol J Linn Soc 85:319–329

Dafni A (1998) The threat of *Bombus terrestris* spread. Bee World 79:113–114

Dafni A, Shmida A (1996) The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt Carmel, Israel. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) The conservation of bees. Academic Press, New York, pp 183–200

Engel MS (1999) The taxonomy of recent and fossil honey bees (Hymenoptera: Apidae: Apis). Journal of Hymenoptera Research 8:165–196

Fleming TH, Sahley CT, Holland JN, Nason JD, Hamrick JL (2001a) Sonoran desert columnar cacti and the *evolution* of generalized pollination systems. Ecol Monogr 71:511–530

Fleming TH, Tibbitts T, Petryszyn Y, Dalton V (2001b) Current status of pollinating bats in the southwestern United States. In: O'Shea T, Bogan M (eds) Monitoring bat populations in the United States. U.S. Geological Survey, Fort Collins

Freitas BM, Oliveira-Filho JH (2001) Criação racional de mamangavas para polinização em áreas agrícolas. BNB, Fortaleza

Grant V, Grant KA (1979) The pollination spectrum in the southwestern american cactus flora. Plant Systemat Evol 133:29–37

Hassan E (1972) The importance of wild flowers and bush growth as a source of food for adult parasitic hymenoptera. In: 14th International congress in entomology (Abstracts), Canberra, Australia, Aug 22–30, p 214

Hilton Jr. B, Miller MW (2003) Annual survival and recruitment in a Ruby-throated Hummingbird population, excluding the effect of transient individuals. Condor 105:54–62

Hingston AB, Marsden-Smedley J, Driscoll DA et al (2002) Extent of invasion of Tasmanian native vegetation by the exotic bumblebee Bombus terrestris (Apoidea: Apidae). Aust Ecol 27(2):162–172

Hobbs GA (1967) Obtaining and protecting red-clover pollinating species of *Bombus* (Hymenoptera: Apidae). Can Entomol 99:943–951

Imhoof B, Schmid-Hempel P (1998) Single-clone and mixed-clone infections versus host environment in *Crithidia bombi* infecting bumblebees. Parasitology 117(4):331–336

Ismail A, Ibrahim AG (1986) The potential for ceratopogonid midges as insect pollinators of cocoa in Malaysia. In: Hussein MY, Ibrahim AG (eds) Biological control in the tropics. Universiti Pertanian Malaysia, Serdang, pp 471–484

Johansen CA, Mayer DF (1990) Pollinator Protection. A Bee and Pesticide Handbook. Wicwas Press, Cheshire, CT, USA, 212 pp

Kearns CA (2001) North American dipteran pollinators: assessing their value and conservation status. Conserv Ecol 5(1):5. www.consecol.org/vol5/iss1/art5

Kevan PG (1975a) Forest application of the insecticide Fenitrothion and its effect on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in southern New Brunswick, Canada. Biol Conserv 7:301–309

Kevan PG (1975b) Pollination and environmental conservation. Environ Conserv 2:222–227

Kevan PG (1977) Blueberry crops in Nova Scotia and New Brunswick – pesticide and crop reductions. Can J Agric Econ 25:61–64

Kevan PG (1995) Integrating science and development to successful apiculture. In: Kevan PG (ed) The Asiatic hive bee: apiculture, biology, and role in sustainable development in tropical and subtropical Asia. Enviroquest, Cambridge, pp 251–255

Kevan PG, Baker HG (1999) Insects on flowers. In: Huffaker CB, Gutierrez AP (eds) Ecological entomology, 2nd edn. Wiley and Sons, New York, pp 553–584

Kevan PG, LaBerge WE (1979) Demise and recovery of native pollinator populations through pesticide use and some economic implications. In: DM Caron (ed) Proceedings IV international symposium on pollination (Maryland Agricultural Experimental Station Special Miscellaneous Publication) No. 1, pp 489–508

Kevan PG, Oppermann EB (1980) Blueberry production in New Brunswick, Nova Scotia, and Maine. Can J Agric Econ 28:81–84

Kevan PG, Plowright RC (1995) Impact of pesticides on forest pollination. In: Armstrong JA, Ives WGH (eds) Forest insect pests in Canada. Natural Resources Canada, Ottawa, pp 607–618

Knott MP (1950) Wildlife and its dependence on seed production. In Iowa State Apiarist Rpt, 1949, pp 139–140

Lima-Verde LW, Freitas BM (2002) Occurrence and biogeographic aspects of *Melipona quinquefasciata* in NE Brazil (Hymenoptera, Apidae). Braz J Biol 62(3):479–486, Pollinators and pollination: a resource book for policy and practice

Manning LE (1943) Your shade trees: all that flowers does not fruit. Am Forests 49(10):492–493

Marlin JC, LaBerge WE (2001) The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. Conserv Ecol 5(1):9. www.consecol.org/vol5/iss1/art9/

Martins D, Gemmill B, Eardley C (eds) (2003) Plan of action of the African pollinator initiative. African Pollinator Initiative, Nairobi

Matheson A (1994) The impact of Varroa infestation on beekeeping. In: Matheson A (ed) New perspective on Varroa, IBRA, Cardiff, UK, pp 27–31

McGregor SE (1976) Insect pollination of cultivated crop plants. US Department of Agriculture, Agricultural Handbook No. 496. US Govt. Printing Office, Washington

Michener CD (1979) Biogeography of the bees. Ann Mo Bot Gard 66:277–347

Michener CD (2000) The bees of the world. Johns Hopkins University Press, Baltimore/London

Morse RA, Calderone NW (2000) The value of honey bees as pollinators of US crops in 2000. Bee Culture Magazine, Mar

Olmstead A, Woolen DB (1987) Bee pollination and productivity growth: the case of alfalfa. Am J Agri Econ 69:56–63

O'Toole C (1993) Diversity of native bees and agroecosystems. In: LaSalle J, Gauld D (eds) Hymenoptera and biodiversity. CAB International, Wallingford, pp 169–196

Partap U, Partap T (2002) Warning signals from the apple valleys of the HKH: Productivity concerns and pollination problems. ICIMOD, Kathmandu, p 124

Rocha M, Valera A, Eguiarte LE (2005) Reproductive ecology of five sympatric *Agave littaea* (Agavaceae) species in Central Mexico. Am J Bot 92:330–1341

Roubik DW (1995) Pollination of cultivated plants in the tropics. FAO Agric Serv Bull 118:1–196

Roubik DW (2001) Ups and downs in pollinator populations: when is there a decline? Conserv Ecol 5(1):2. www.consecol.org/vol5/iss1/art2

Roubik DW, Wolda H (2001) Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. Popul Ecol 43:53–62, Pollinators and pollination: a resource book for policy and practice

Sakagami SF, Fukuda H (1973) Wild bee survey at the campus of Hokkaido University. J Fac Sci Hokkaido Univ Ser VI, Zool 19:190–250

Slauson LA (2000) Pollination biology of two chiropterophilous agaves in Arizona. Am J Bot 87:825–836

Slauson LA (2001) Insights on the pollination biology of *Agave* (Agavaceae). Haseltonia 8:10–23

Steffan-Dewenter I, Klein AM, Gaebele VAT, Tscharntke T (2003) Bee diversity and plant–pollinator interactions in fragmented landscapes. In: Waser NM, Ollerton J (eds) Specialization and generalization in plant–pollinator interactions. Chicago Press, Chicago

Stephen WP (1955) Alfalfa pollination in Manitoba. J Econ Entomol 48:543–548

Stout JC, Kells AR, Goulson D (2002) Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. Biol Conserv 106:425–434

Tepedino VJ (1979) The importance of bees and other insect pollinators in maintaining floral species composition. Great Basin Nat Mem 3:139–150

Valiente-Banuet A, Arizmendi MC, Rojas-Martínez A, Domínguez-Canseco L (1996) Ecological relationships between columnar cacti and nectar feeding bats in Mexico. J Trop Ecol 12:103–119

Vázquez DP, Aizen MA (2004) Asymmetric specialization: a pervasive feature of plant-pollinator interactions. Ecology 85:1251–1257

Watson L, MJ Dallwitz (1992) The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: June 2, 2006. http://delta

Webber AC (1996) Biologia floral, polinização e aspectos fenológicos de algumas Annonaceae na Amazônia Central. PhD thesis. INPA/FUA, Manaus

Westrich P (1996) Habitat requirements of central European bees and the problems of partial habitats. In: Matheson A, Buchmann SL, O'Toole C, Westrich P, Williams IH (eds) The conservation of bees. Academic Press, New York, pp 1–16

Williams NM, Minckley RL, Silveira FA (2001) Variation in native bee faunas and its implications for detecting community changes. Conserv Ecol 5(1):7. www.consecol.org/vol5/iss1/art7

Winder JA, Silva P (1972) Cacao pollination: microdiptera of cacao *Planta*tions and some of their breeding places. Bull Entomol Res 61:651–655

Wolda H (1992) Trends in abundance of tropical forest insects. Oecologia 89:47–52, Pollinators and pollination: a resource book for policy and practice

Yeager AF (1937) Pollination studies with North Dakota fruits. Amer Soc Hort Sci Proc 35:12–13

Chapter 22

The Role of Pollination in Improving Food Security and Livelihoods

Abstract The focus of agriculture is slowly shifting from traditional cereal crops to high-value cash crops farming such as fruits and vegetables. This transformation from subsistence systems to commercial agriculture poses new challenges for improving and maintaining productivity and quality. Among these challenges are crop failures due to inadequate pollination. This is caused by several factors, the most important of which include the lack of adequate number of pollinators as a result of decline in pollinator populations and diversity due to several factors such as decline in wilderness and loss of habitat, land use changes, monoculture-dominated agriculture and excessive and indiscriminate use of agricultural chemicals and pesticides. Consequently, the need for ensuring pollination particularly through conserving pollinators and incorporating managed crop pollination has increased and will increase further. This calls for a more intensive focus on the issue from the perspective of policy, research, development and extension. Policy reorientation, improving institutional capabilities and human resources development are the key areas needing attention.

22.1 Introduction

Crop-associated biodiversity (CAB) refers to biodiversity that supports the functioning of ecosystem services necessary for agriculture, as well as contributing to the maintenance of ecosystem health and resilience. CAB is an intrinsic and important part of agricultural ecosystems, and includes components such as pollinators. Pollinators contribute to the maintenance of biodiversity, and ensure the survival of plant species including plants that provide food security to innumerable rural households. Pollination is an essential ecosystem service that enables plant reproduction and food production for humans and animals (fruits and seeds – also impacting on the quality and yield) that depend, to a large extent, on the symbiosis between species, i.e., the pollinated and the pollinator. The reduction and/or loss of either will affect the survival of both.

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Pollinator diversity is directly dependent on plant diversity and vice-versa – no other natural phenomenon illustrates more vividly the principle that conservation measures must be directed at ecological processes, and not just individual species. Indeed, pollination, a fundamental step for plant reproduction, is an ecological service that cannot be taken for granted. Plants are the primary producers in terrestrial ecosystems and direct providers of many ecosystem services such as carbon sequestration, prevention of soil erosion, nitrogen fixation, maintenance of water tables, greenhouse gas absorption, and food and habitat providers for most other terrestrial and many aquatic life forms. Pollinators, through facilitating plant reproduction, thus play a crucial role in the maintenance of ecosystem services (Batra 1985, 1997). Pollination requires pollinating agents which themselves require resources for nesting, feeding and reproduction in the form of vegetation, prey, and certain habitat conditions, as well as the application of pollinator-friendly land-use management practices to ensuring their survival.

22.2 The Pollinators

Over 75% of the major world crops and 80% of all flowering plant species rely on animal pollinators (Nabhan and Buchmann 1997; Kevan et al. 2002). Of the hundred or so animal-pollinated crops which make up most of the world's food supply, 15% are pollinated by domestic bees, while at least 80% are pollinated by wild bee species and other wildlife (Prescott-Allen and Prescott-Allen 1990; Ingram et al. 1996). Diversity among species, including agricultural crops, depends on animal pollination. Thus, pollinators are essential for diet diversity, biodiversity, and the maintenance of natural resources.

The principle pollinators are bees. Approximately 73% of the world's cultivated crops, such as cashews, squash, mangoes, cocoa, cranberries and blueberries, are pollinated by some variety of bees, 19% by flies, 6.5% by bats, 5% by wasps, 5% by beetles, 4% by birds, and 4% by butterflies and moths (Freitas et al. 2004). Of the hundred principal crops that make up most of the world's food supply, only 15% are pollinated by domestic bees (mostly honey bees, bumble bees and alfalfa leafcutter bees), while at least 80% are pollinated by wild bees and other wildlife (as there are an estimated 25,000 bee species, the total number of pollinators probably exceeds 40,000 species).

The 25,000 different species of bees differ significantly in size and habit requirements, and diverge accordingly in the plants they visit and pollinate. Though bees form the most important group of pollinators, other animals, such as bats, birds, butterflies, moths, flies and beetles also play key roles in pollination. Both the diversity of wild plants and the variability of food crops depend on this diversity.

Pollination is a complicated process with some being generalists and others being species-specific. Likewise, many different pollinators visit some plants, while other plants have species-specific pollinator requirements. Given this complexity, managing pollination as an ecosystem service requires a comprehensive understanding of the pollination process and the application of that knowledge in the design and implementation of intricate management practices. In most cases, there is limited knowledge about the exact relations between individual plant species and their pollinators.

22.3 The Issues: The Impact of Declining Pollinator Populations on Agriculture

It is recognized that agricultural production, agro-ecosystem diversity and biodiversity are threatened by declining populations of pollinators. Many pollinator population densities are being reduced below levels at which they can sustain pollination services in agroecosystems, natural ecosystems, and for the maintenance of wild plant reproductive capacity. The major contributors to this decline in pollinator populations are, *inter alia*, habitat loss and fragmentation, land management practices, agricultural and industrial chemicals, parasites and diseases, and the introduction of alien species. Ecological dangers of pollinator decline include the loss of essential ecosystem services (particularly agro-ecosystem services) and functions that pollinators provide. Ecosystem services in their turn have their own value – biophysical, but also economic. For example, for the entire biosphere, the value of ecological services (most of which outside the market) was estimated to be in the range of US$ 16–54 trillion per year, with an average of US$ 33 trillion per year (Costanza et al. 1987). Services that are provided by native pollinators (non-honeybee species) are estimated to be worth US$ 4.1 billion a year to United States agriculture alone (Prescott-Allen and Prescott-Allen 1990). The value of the annual global contribution of pollinators to the major pollinator-dependant crops is estimated to exceed US$ 54 billion (Kenmore and Krell 1998). In the Canadian prairies, the value of pollinators to the alfalfa seed industry has been placed at about CAD six million per year (Kevan and Phillips 2001).

Examples from Asia (e.g. northern Pakistan, parts of China) show linkages between declining natural insect populations and decreasing crop yields – as a result, people have begun to *manage the crop-associated biodiversity* (i.e. pollinators) in order to maintain their crop yields and quality. For example, farmers in Himachal Pradesh (in northwestern India) are using honeybees to pollinate their apples (Partap 2003). Due to declining pollinator populations and changing cultivation practices, an increasing number of farmers around the world are now paying for pollination services and are importing and raising non-native pollinators to ensure crop production. In many developing countries, however, external pollination services are not available and rural communities have to live with reduced quantity, quality, and diversity of foods. In fruit orchards in Western China, the decline of useful insect populations has led farmers to pollinating by hand, acting as human bees (Partap 2003). Despite a general recognition of the impact of declining pollinator populations on ecosystem functioning, and despite the examples of the ecological and economic impacts as well as examples of where this is occurring, bottlenecks and constraints hinder the conservation and management of pollinators in sustainable agriculture. An example of a globally recognized bottleneck is the lack of taxonomic information, which hampers progress that could be made in identifying and analysing firstly pollinator populations important to agriculture, and their behaviour patterns, but also best management practices. Best management practices are not readily available or known in all areas of the world, and especially not to all peoples. Indeed, a lack of awareness of pollinator issues – from the farmer to the extension worker to the policy maker – is also a set-back for the promotion of issues related to the conservation and management of pollinators within the context of sustainable agriculture. Recognition of these bottlenecks and constraints as well as a need for action contributed to the international arena's response to the conservation and management of pollinators, in agricultural systems (and non).

The importance of pollination in improving food security and livelihoods through enhancing agricultural productivity is well known. An attempt has been made to analyze such issues as the decline in pollinator populations and its impact on agricultural productivity and implications on pollination management, and challenges to integrate pollination as a necessary input in agricultural policies and plans in the light of available information on pollination. This paper also emphasizes the need to conserve pollinator diversity to ensure pollination and at the same time it tries to present an alternative perception to beekeeping and that is "to promote" beekeeping primarily for crop pollination with honey and other bee products as by products". This new approach combines the two benefits well but institutional reorientation in the context of policies, research and extension might be necessary.

22.3.1 Case Study: Cash Crops Farming in the Himalayan Region

Agriculture is the basis of the livelihood of over 80% of the rural population in most of the countries of the world. However, more than 90% of the farmers in the hill and mountain areas are marginal or small land-holding families, cultivating less than one hectare of land each (Koirala and Thapa 1997; Partap 1999). Most agricultural land in the mountain areas is not only marginal in terms of potential productivity, but its quality also appears to be deteriorating as indicated by declining soil fertility and crop productivity. As a result, many mountain families face food shortages of varying degrees that contribute to the chain reaction process of poverty–resource degradation–scarcity–poverty (Jodha and Shrestha 1993). Therefore, it is necessary to explore all possible ways of increasing the sustainable productivity and carrying capacity of the farming systems in the mountains in order to improve the livelihoods of marginal mountain households (Partap 1998a, b, 1999).

This, however, cannot be done by emphasizing the cultivation of cereal crops alone. If the poor mountain farmers are going to compete favourably in the modern world, they must be given options and alternatives that are not already captured by the competition. Development efforts tend to focus on exploring farming approaches

Table 22.1 Cash crop farming in the Himalayan region

Cash crops	Province, country	Area (000 ha)	Annual production (000 ton)
Apple	Indian Himalayas	227.61	1320.49
	Nepal	4.97	30.46
	Bhutan	2.03	13.00
	Chinese Himalayas[a]	82.86	208.22
	Pakistan[b]	49.46	637.97
Citrus	Bhutan[c]	8.00	77.00
	Nepal[d]	1.20	6.00
	Northwest Indian Himalayas[e]	39.80	100.00
	Chinese Himalayas[a]	0.20	0.80
	Pakistan		
Other fruit crops	Bhutan	0.13	–
	Chinese Himalayas (Sichuan, Yunnan)[a]	61.60	354.20
	Indian Himalayas[f]	530.00	1,595.00
	Pakistan[g]	39.10	386.20
Vegetable crops	Bhutan[c]	6.00	22.30
	Chinese Himalayas[f]	14.50	26.30
	Indian Himalayas[f]	318.10	1,354.40
	Nepal[f]	140.00	741.60
	Pakistan[f]	282.90	1,418.80
Oilseed crops	Chinese Himalayas (Sichuan, Yunnan)[a]	1,172.60	1,756.30
Other crops (chilli, ginger, pulses, oilseeds, tea, cardamom, cotton, potato, tomato, etc.)	Bhutan	105.60	125.40
	Chinese Himalayas (Sichuan, Yunnan)[a]	2,276.30	16,688.20
	Himachal Pradesh, India	–	–
	Uttaranchal, India[g]	19.00	392.00
	Balochistan, Pakistan[g]	5.00	765.00
	NWFP, Pakistan[g]	9.20	90.50

Sources

[a] Agricultural Statistics of China, 1997; and Agricultural Census of Tibet, 1997

[b] Agricultural Statistics of Pakistan. Ministry of Food, Agriculture and Livestock, Economic Wing, Islamabad Government of Pakistan, 1998–1999; and Khan 2004

[c] Policy and Planning Division, Ministry of Agriculture, Royal Government of Bhutan, 1999

[d] Agricultural Statistics of Nepal (1998/1999), Department of Agriculture, HMG, Nepal

[e] National Horticulture Board, New Delhi, India 1998, Department of Horticulture, Himachal Pradesh 1998

[f] Partap and Partap 1997

[g] Tulachan 2001

to increase the productivity and carrying capacity of farms (Partap and Partap 1997; Partap 1999). Cash crops farming – fruit and vegetable crops suitable to specific agro-climatic conditions – is one comparative advantage that can be exploited by these farmers. For example, in uplands of the Himalayan region, off-season vegetables and fruits provide the comparative advantage to the farmers. As a result the focus of mountain agriculture is shifting from traditional cereal crops farming to high value cash crops and the cultivation of such crops as apples, almonds, pear, peaches, plums and cherries and off-season vegetables, both for local and export markets is increasing (Table 22.1).

22.4 The Role of Pollination in Improving Food Security and Livelihoods

For a farmer, the most desired goal in agriculture is to get the maximum possible crop yields and better quality fruit and seeds under given inputs and ecological settings. It is particularly important to get a premium price for the produce when farmers are engaged in cash crop farming. There are two well known methods for improving crop productivity. The first method is making use of agronomic inputs, including plant husbandry techniques such as the use of good quality seeds and planting material, and practices to improve yields, for example, providing good irrigation, organic manure and inorganic fertilizers and pesticides. The second method includes the use of biotechnological techniques, such as manipulating rate of photosynthesis and biological nitrogen fixation, etc. These conventional techniques ensure healthy growth of crop plants, but work up to a limit. At some stage crop productivity becomes stagnant or declines with additional inputs for the known agronomic potentials of crop will have been harnessed (Partap and Partap 1997).

The third and relatively less known method of enhancing crop productivity is through managing pollination of crops using friendly insects, which in the process of searching for food perform this useful service to farmers (Partap and Partap 1997). Pollination is an ecological process based on the principle of mutual interactions or inter-relationships (known as proto-cooperation) between the pollinated (plant) and the pollinator. Pollinators visit the flowers of the plants to obtain their food (i.e. nectar and pollen) and in return pollinate them. In many cases it is the result of the intricate relationship between plants and its pollinators and the reduction or loss of either affects the survival of both. In recent years the Convention on Biological Diversity (CBD) has recognized pollination as a key driver in the maintenance of biodiversity and ecosystem function.

The pollination process involves the transfer of pollen from the male part of the flower called “anthers” to the female part called “stigma” of the same flower (self-pollination) or another flower of the same or another plant of the same species (cross- pollination). Pollination is vital for completing the life cycle of plants and ensuring production of fruit and seed whether agricultural crops or natural vegetation/flora. This ecological process is an essential prerequisite for fertilization and fruit/seed set. If there is no pollination, there will be no fertilization, no fruits or seeds will be formed and farmers will harvest no crop. Pollination is therefore the most crucial process in the life cycle of the plants and is essential for crop production and biodiversity conservation and helps enhance farm income and rural livelihoods. Figure 22.1 shows the relationship of pollination to improved livelihoods through enhancing agricultural productivity and biodiversity conservation.

Many cash crops are actually self-sterile and require cross-pollination to produce seeds and fruit (McGregor 1976; Free 1993). But it is not only self-sterile varieties that benefit from cross-pollination, but self-fertile varieties also produce more and better quality seeds and fruits if they are cross-pollinated (Free 1993). Logically, the increase in the cultivation of cross-pollinated cash crops will also increase the need

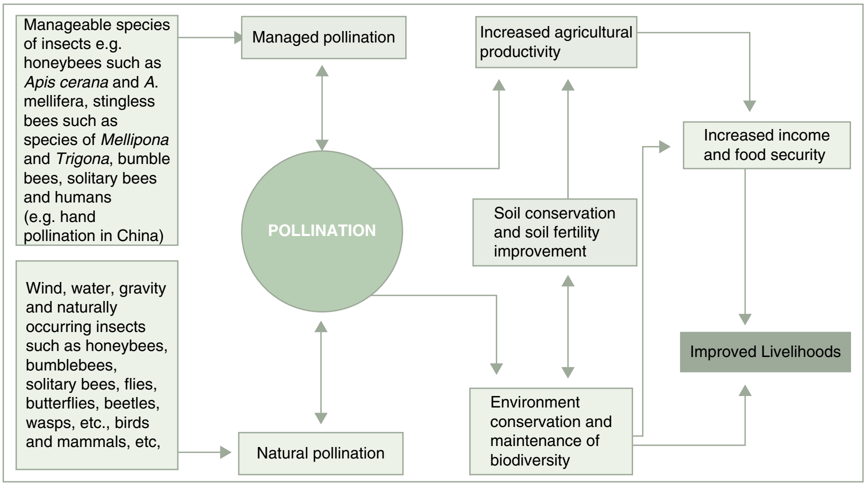

Fig. 22.1 Contribution of pollination to agricultural productivity and improving rural livelihood

for managed pollination. Equally interesting is the adoption of apiculture as a new enterprise by many people. Promoting use of beekeeping for pollination of cash crops will be of benefit to both the beekeeper who will receive money for the pollination services of his honeybees and harvest honey and to the farmer whose income will be increased through boosting crop productivity as a result of pollination services of bees. This will help ensure food security and enhance the livelihoods of both the farmers and the beekeepers (Fig. 22.1). This system of hiring and renting honeybee colonies for apple pollination is being practiced in Himachal Pradesh in northwest Indian Himalayas. In Maoxian county in the Hengduan Mountains a somewhat similar but rather unsustainable system of apple pollination is prevalent. Here, farmers hire "human pollinators" for pollinating apple and pear trees by hand.

22.5 Inadequate Pollination as a Factor Affecting Crop Productivity

The ongoing transformation from subsistence to cash crop farming poses new challenges for maintaining crop productivity and quality. There are signs that across the HKH region the overall productivity of many mountain crops is going down. Possibly the worst affected crops are the cash crops like fruit, particularly apples, and off-season vegetables that are the hope of the region in terms of providing farmers with cash income and underpinning development efforts. This reduction in productivity is taking place despite extensive efforts at extension and information to support improvements in a range of management practices, and strong support for the introduction of successful commercial varieties. The studies revealed that among the several factors affecting mountain crop productivity pollination plays an important role. Evidence of this emerging pollination problem has been documented in a series of field studies carried out by ICIMOD across the Himalayan region (Partap 1998a, b; Partap and Partap 2000; Partap et al. 2000, 2001). These studies investigated the state of inadequate pollination, its cause factors and its impact on crop productivity.

22.6 Pollinator Diversity and Its Role in Enhancing Crop Productivity

Pollinators provide an essential ecosystem service that contributes to the maintenance of biodiversity and ensures the survival of plant species including crop plants. Two types of pollinators occur in *Nature*. These include abiotic pollinators such as wind, water and gravity, and biotic pollinators such as insects, birds and various mammals. It has been estimated that over three quarters of the world's crops and over 80% of all flowering plants depend on animal pollinators, especially bees (Kenmore and Krell 1998). Globally the annual contribution of pollinators to the agricultural crops has been estimated at about US$ 54 billion (Kenmore and Krell 1998).

Insects are the most commonly occurring pollinators of many agricultural and horticultural crops. Different kinds of insect pollinators such as bees, flies, beetles, butterflies, moths and wasps are important pollinators of many crops. Among insects, bees are more effective pollinators than other insects because, unlike other insects, they are social and collect nectar and pollen not only to satisfy their own needs but to feed their young; their body hairs help transfer pollen from one flower to another; they show flower constancy and move from one flower to another of the same species; and many species can be reared and managed for pollination.

Over 25,000 species of bees are found in the world. These include honeybees, bumble bees, stingless bees and solitary bees. Bees are the most effective pollinators of crops and natural flora and are reported to pollinate over 70% of the world's cultivated crops. It has also been reported that about 15% of the 100 principal crops are pollinated by domestic bees (i.e. manageable species e.g. hive-kept species of honeybees, bumble bees, alfalfa bees, etc.), while at least 80% are pollinated by the wild bees (Kenmore and Krell 1998). These non-honeybee pollinators are estimated to provide the pollination services worth US$ 4.1 billion per year to the US agriculture (Prescott-Allen and Prescott-Allen 1990).

22.7 The Issue of Declining Pollinator Populations

In recent years there is a world-wide decline in pollinator populations and diversity. The factors causing this decline could be the decline in the habitat, with the accompanying decrease in their food (nectar and pollen) supplies as a result of decline in pristine areas, land use changes, increase in monoculture-dominated agriculture, and negative impacts of modern agricultural interventions, e.g. use of chemical fertilizers and pesticides (Verma and Partap 1993; Partap and Partap 1997, 2002). Earlier, farmers used to grow a variety of crops, which bloomed during different months of the year and provided food and shelter for a number of natural insect pollinators and hence the pollination problem never existed. Monocropping also requires pesticide use to control various pests and diseases. Thus, it not only reduced the diversity of food sources of pollinator but also led to the killing of many pollinators due to pesticides. The insecticides have contributed to the extermination of both the diversity and abundance of pollinating insects. Changes in climate might also be affecting insect numbers (Partap and Partap 2002).

22.7.1 Impact of Decline in Pollinator Population and Diversity

The decline in pollinator population and diversity presents a serious threat to agricultural production and conservation and maintenance of biodiversity in many parts of the world. One indicator of the decline in natural insect pollinators is decreasing crop yields and quality despite necessary agronomic inputs. Examples can be found in Himachal Pradesh in northwest India, northern Pakistan and parts of China where despite all agronomic inputs, production and quality of fruit crops, such as apples, almonds, cherries and pears, is declining. Extreme negative impact of declining pollinator populations can be seen in other areas, for example in northern Pakistan where both farmers and institutions have failed to understand the importance of managed pollination. Disappointed with the very low yields and quality of apples as a result of poor pollination several farmers in Azad Jammu and Kashmir of Pakistan have chopped off their apple trees (Partap 2001).

One implication of the decline in the pollinator populations as well as diversity is that it has created the need for managed pollination in order to maintain crop yields and quality. In fact, farmers engaged in cash crops' farming in those areas where pollinator populations have declined are forced to manage pollination of their crops through different ways. For example, farmers in Himachal Pradesh in northwest India are using honeybees for pollination of their apples, while those in Maoxian county in Hengduan Mountains of China are pollinating their crops, e.g. apples and pears, through hand pollination using human beings as pollinators (beekeepers do not rent their honeybee colonies for pollination of these crops because farmers make excessive use of pesticides even during flowering season). Hand pollination is an interesting method of pollinating crops and provides employment and income generating opportunities to many people during apple flowering season. But at the same time it is an expensive, time-consuming and highly unsustainable proposition of crop pollination owing to the increased labour scarcity and costs. Moreover, a large part of farmers' income is used in managing pollination of their crops.

22.8 The Importance of Pollinator Management for Cash Crop Pollination in the Himalayas

As explained earlier in this paper the populations of these pollinators are declining in several intensively cultivated areas. Thus, the need to conserve, promote and diversify pollinator resources is pressing in several countries of the developing world. This calls for initiating research and extension activities in this direction and developing strategies to promote conservation and sustainable use of pollinators. This will require much wider understanding of the multiple services provided by the pollinator diversity and the factors that influence them, including farmers, in order to secure sustained pollinator services in agricultural ecosystems. This calls for initiating efforts at awareness, research and extension level. Certain measures suggested for increasing the number of insect pollinators include habitat conservation, discouraging over-use of pesticides, promoting integrated pest management (IPM), awareness raising, formulating policies to include managed crop pollination as an input in agricultural development packages and strengthening R and D systems.

Many species of bumblebees (*Bombus* spp.) and solitary bees like *Amegilla*, *Andrena*, *Anthophora*, *Ceratina*, *Halictus*, *Lasioglossum* (*Evylaeus*), *Megachile*, *Nomia*, *Osmia*, *Pithis*, and *Xylocopa* can be reared on a large scale and managed for crop pollination. In fact in many developed countries various insect pollinators, including some species of bumblebees and solitary bees, are being reared and managed commercially for pollination of various crops, particularly those that are less or uneffectively pollinated by honeybees. Bumblebees, for example, are used for the pollination of potatoes, tomatoes, strawberries and other crops grown in glasshouses, alkali bees and leaf cutter bees for the pollination of alfalfa, horn-faced bees for apples, almonds and other fruit trees, and other species of solitary bees for pollination of cotton, mustards, lucerne and berseem. In Japan the solitary bee *Osmia cornifrons* Rad. is being reared and managed on a large scale to pollinate about one-third of all apple crops (Batra 1995; Sekita 2001).

There is good potential for the managed use of non-*Apis* pollinators in the developing countries. There are thousands of hectares of land under crops that need cross-pollination. In cold and arid areas, for example Balochistan (Pakistan), Mustang (Nepal) and Lahul (Himachal Pradesh), where stationary beekeeping cannot be practised because of the prevailing cold and dry climatic conditions and lack of forage during the larger part of the year, conserving and managing non-honeybees for pollination can be a good option. Their conservation can be ensured simply by avoiding use of pesticides during the period when crops and other plants are blooming. This could be of great help in saving these pollinators from the hazardous effects of pesticides because the period of adult life of these insects coincides with the flowering of crops.

Even though both the need and the potential exist, the practice of rearing and managing natural pollinators for crop pollination is practically absent in the developing countries. The reason is that most institutions do not have the mandate and necessary expertise in this field. Thus, development and use of these insects in this part of world will take a long time. Major research and extension efforts will be needed before such insects can be reared and managed for pollination of crops in the region. However, efforts towards the conservation of these non-*Apis* pollinators can be initiated. The first step in this direction could be to save them from the harmful impacts of pesticides. For this, there is need to raise awareness about the harmful effects of agricultural chemicals and pesticides on these invaluable pollinators. There is also need to train farmers and extension workers to make safe use of carefully selected, less toxic pesticides outside the blooming period of crops.

22.9 Managed Pollination as a Solution to Address the Immediate Problem of Cash Crop Pollination

Promoting conservation and management of naturally occurring insect pollinators is very important for sustaining agricultural productivity in the long run. Efforts – both at research and extension level-must be continued to identify, assess and develop techniques/methodology to rear and manage them for enhancing crop pollination. But as already explained the population of these bees are declining and there is a lack of scientific manpower and institutional infrastructure to rear and promote them in the countries of the Himalayan region. Moreover, the problem of pollination has already started in several areas. Therefore, promoting managed pollination is essential to address this immediate problem of inadequate pollination in several cash crops, for example, apples and pears. Our findings revealed two different cases of managed pollination of apple crops in the Himalayan region; one in Himachal Pradesh a small province in north-western Indian Himalayas where farmers are using manageable species of honeybees (*Apis cerana* and *Apis mellifera*) for pollination of their apple crop, and another in Maoxian valley located in the northwest of Sichuan Province of China where farmers employ “human bees” to pollinate their apples by hand (hand pollination). The details of these case studies are given in the following text.

22.10 Honeybees as the Most Efficient and Manageable Pollinators

As explained, many varieties of these cash crops are partially or completely self-incompatible and cannot produce fruit or seed without cross-pollination of their flowers. Moreover, it is not only self-incompatible varieties that benefit from cross-pollination, but self-fertile varieties also produce better quality fruit and seeds if they are cross pollinated (Free 1993). While other agronomic inputs, such as the use of manure, fertilizers, pesticides and irrigation are important, without cross-pollination desired crop yield and quality of harvest cannot be achieved.

Honeybees are the most widely known of all the bees because they provide honey, beeswax and other products and beekeeping is a prevailing tradition among mountain farming communities. They are the most efficient pollinators of cultivated crops because their body parts are especially modified to pick up pollen grains, they have body hair, have potential for long working hours, show flower constancy, and adaptability to different climates (Free 1964, 1966; McGregor 1976). Research has shown that pollination by honeybees increases fruit set, enhances fruit quality and reduces fruit drop in apple (Dulta and Verma 1987). Among different species of honeybees, the hive-kept species (*Apis cerana* and *Apis mellifera*) are of special value because they can be managed for pollination and moved to fields/orchards where and when necessary for pollination. Pollination using honeybees is the most cost-effective method for pollinating apple and other fruit crops. Use of beekeeping is, therefore, the most promising method of cash crop pollination in the Himalayan region.

In fact, the main significance of honeybees and beekeeping is pollination, whereas hive products are of secondary value. It has been estimated that the benefit of using honeybees for enhancing crop yields through cross-pollination is much higher than their role as produces of honey and beeswax. Various estimates have been made to prove the economic value of honeybees in agriculture in developed countries. Recent estimates by Morse and Calderone (2000) show that the value of honeybee pollination to crop production in the US is US$ 14.6 billion. Similar estimates have been made for other countries. For example the value of honeybee pollination has been estimated at CAN$ 1.2 billion in Canadian agriculture (Winston and Scott 1984), US$ 3 billion in EEC (Williams 1992), and US$ 2.3 billion in New Zealand (Matheson and Schrader 1987). Cadoret (1992) estimated that the direct contribution of honeybee pollination to increase farm production in 20 Mediterranean countries was US$ 5.2 billion per year – 3.2 billion in developing countries and two billion in other countries.

22.10.1 Experimental Research on the Impact of Honeybee Pollination on Crop Productivity in the Himalayan Region

Honeybees are reported to play a vital role in enhancing the productivity levels of different crops such as fruit and nuts, vegetables, pulses, oilseeds and forage crops. A number of studies have been done to show the impact of honeybee pollination on different cash crops. However, the role of honeybees is not very well understood in the countries of the Himalayan region. Most of the research work has been done in developed countries of the world where honeybees are being used for the pollination of various crops. However, the limited research carried out in the countries of the Himalayan region has proved that bee pollination increases the yield and quality of various crops (Table 22.2).

Table 22.2 Impact of honeybee (*Apis cerana*) pollination on fruit productivity

Crop	Increase in fruit set (%)	Increase in fruit weight (%)	Increase in fruit size (length, diameter) (%)	References
Apple	10	33	15, 10	Verma and Dulta (1986)
Peach	22	44	29, 23	Partap et al. (2000)
Plum	13	39	11, 14	Partap et al. (2000)
Citrus	24	35	9, 35 also, premature fruit drop decreased by 46%, increased juice by 68% and sugar contents in juice by 39%	Partap (2000a)
Strawberry	112	48	Misshapen fruits decreased by 50%	Partap (2000b)

Table 22.3 Impact of honeybee (*Apis cerana*) pollination on vegetable seed production

Crop	Increase in pod setting (%)	Increase in seed setting (%)	Increase in seed weight (%)
Cabbage	28	35	40
Cauliflower	24	34	37
Radish	23	24	34
Broad leaf mustard	11	14	17
Lettuce	12	21	9

Sources: Partap and Verma (1992, 1994); Verma and Partap (1993, 1994)

These experiments showed that bee pollination increased yield and fruit quality in apple (Dulta and Verma 1987; Gupta et al. 1993), peach, plum, citrus, kiwi (Gupta et al. 2000) and strawberry (Partap 2000a, b; Partap et al. 2000). Bee pollination did not only increase the fruit set but also reduced fruit drop in apple, peach, plum and citrus (Dulta and Verma 1987; Partap 2000a, b; Partap et al. 2000). Reports have also indicated an increase in fruit juice and sugar content in citrus fruits (Partap 2000a, b). In strawberry, bee pollination reportedly reduces the percentage of misshapen fruits (Partap 2000a, b).

Studies have shown that honeybee pollination enhanced seed production and quality of seed in various vegetable crops such as cabbage, cauliflower, radish, broad leaf mustard and lettuce (Partap and Verma 1992, 1994; Verma and Partap 1993, 1994). These results confirm the usefulness of bee pollination and its role in increasing crop productivity and improving the quality of fruits and seeds (Table 22.3).

Scientific evidence confirms that bee pollination also improves the yield and quality of other vegetable crops such as asparagus, carrots, onion, turnips and several other crops (Deodikar and Suryanarayana 1977). Recent experiments carried out in different parts of the northeast Himalayan region show that honeybee pollination does not only increase fruit set in rapeseed and sunflower but also increases the oil contents in these oilseed crops (Singh et al. 2000).

The quality of pollination is determined by the number of colonies per unit area, strength of bee colonies, placement of colonies in the field, time of placement of bee colonies, and the weather conditions. Experiences from pilot experiments have shown that the best results are achieved by placing strong bee colonies, having large amount of unsealed brood, free of diseases, at the time of 5–10% flowering in the crop (Free 1993; Verma and Partap 1993).

22.10.2 The Significance of Honeybee Diversity for Pollination

The Himalayan region is one of the richest in honeybee species' diversity in the world. There are five species of honeybees: three wild species that cannot be kept in hives – the giant honeybee (*Apis dorsata*), the little bee (*Apis florea*), and the rock bee (*Apis laboriosa*) – and two hive-bee species, the Asian hive bee (*Apis cerana*), and the introduced bee (*Apis mellifera*). All honeybees are good crop pollinators, but because the wild species cannot be kept in man-made hives they cannot be transported to the sites where bees are needed for crop pollination. The honeybee species' diversity in the Himalayan region holds much potential for wider use in managing crop pollination in ways suited to the conditions in specific areas. In particular, the native hive honeybee *Apis cerana* offers clear advantages as a pollinator in remote and higher altitude area (Partap and Partap 1997, 2002; Partap et al. 2001). Partap and Partap (2002) suggested an area-based approach to use the existing honeybees' diversity for pollination.

22.10.3 Managed Pollination Through Using Honeybees for Apple Pollination in the Himalayan Region: A Case Study from Himachal Pradesh, India

In the developed countries like the US, Canada, Europe and Japan honeybees are used as one of the inputs in agriculture. These countries are for long using honeybees for pollination of crops such as apples, almonds, pears, plums, cucumbers, melons, watermelons, and a number of berries. But the Himalayan region lags far behind in making use of honeybees for crop pollination. Even though plenty of scientific evidence is now available to prove that honeybees increase the productivity of various cash crops, still the practice of using honeybees for crop pollination does not exists in the Himalayan region. While in the US first colonies of honeybee, *Apis mellifera* were rented for pollination of pears in Virginia in 1895 (Waite 1895) and for apple pollination in 1909 in New Jersey (Morse and Calderone 2000), in the Himalayan region (in Himachal Pradesh) first colonies of honeybees were rented for apple pollination only recently in 1996.

A recent survey carried out by the author in apple farming areas of Bhutan, China, India, Nepal and Pakistan revealed that it is only in Himachal Pradesh in northwestern Indian Himalayas where honeybees are being used for apple pollination (Partap 1998b). Here, some farmers keep their own honeybee colonies while others rent them from the Department of Horticulture or from the private beekeepers. The fees for renting bee colonies either *Apis cerana* or *A. mellifera* is Indian rupees 800 (US$ 16) per colony for 2 weeks. This includes Rs 500 (US$ 10) as refundable security deposit and Rs. 300 (US$ 6) per colony per 2 weeks of rent. *Apis mellifera* is the main bee species made available to farmers from government institution and private beekeepers for pollination purpose.

At present, Himachal Pradesh is the only place in the whole of the HKH region where a well-organized system has been established for hiring and renting honeybee colonies. A number of pollination entrepreneurs (beekeepers who rent honeybee colonies for crop pollination) have now started up in the state to complement the official services. The findings also revealed that in addition to increasing the number of insect pollinators by renting colonies of honeybees, some farmers are trying to save the populations of existing pollinators by making judicious use of carefully selected, less toxic pesticides and spraying outside the flowering period of apple. Even though beekeeping is a common tradition throughout the Himalayan region, yet renting honeybees for crop pollination is not much known in other countries. In Pakistan, Bhutan and Nepal farmers are not aware of the importance of pollination and the existing pollination crises in their orchards. Thus, any kinds of management efforts are also absent.

22.11 Hand-Pollination (Using Humans as Pollinators): A Case Study from Maoxian Valley, China

Among other countries of the Himalayan region, it is in China where farmers have understood the value of managed pollination. There is a serious problem of apple and pear pollination in Maoxian county of China because pollinators have been killed by the overuse of pesticides and beekeepers do not rent their honeybees for pollination for the same reason. But unlike Himachal Pradesh, farmers pollinate their apples by hand. Hand-pollination is a common practice of managing pollination in apple crop in this valley where every family member – men, women and children are engaged in pollination of apple flowers making it a community effort (Partap and Partap 2000). Here people do the work that can otherwise be done more efficiently by honeybees and other insect pollinators. They pollinate large areas of apples and pears by hand to make sure that each flower is properly pollinated (Partap and Partap 2000). Therefore, hand-pollination has been promoted by the local government and is now a common practice of managing pollination in apple crop in this valley.

Various cooperation mechanisms among farmers have also evolved for sharing labour and skills. Farmers having larger orchards generally employ labourers for this purpose. Even though beekeeping is common in the area, the practice of renting honeybee colonies for pollination is surprisingly absent. Two reasons were assigned for it; one, it was not promoted in the first place; and second, beekeepers are hesitant to rent their bee colonies because of excessive use of pesticide sprays on apples.

Hand pollination is a laborious and time-consuming method of crop pollination. Even though it is the most reliable method of ensuring apple pollination today, it will not be sustainable as a long-term solution, largely because of increasing labour scarcity and costs. Therefore, in areas where agriculture is diversifying to new cash crops there is a need to raise awareness among people and local research and extension systems about not only the significance of managing pollination but also for using bee pollinators as an alternative to the prevalent practice of pollination by hand. The risk of pesticides can be minimized through judicious use, as well as by adopting practices like integrated pest management practices (Partap et al. 2001; Partap and Partap 2002).

22.12 Challenges in Managed Crop Pollination

As reported in the earlier sections of this paper, insect pollinators including manageable species of honeybees, stingless bees, bumblebees and solitary bees can play an important role in pollination and in areas like N. America, Europe, and Japan they are used extensively to ensure pollination of fruit and vegetable crops. However, although both the need and the potential exist in the developing countries, the practice of managed pollination is practically absent. Forget about rearing and using species of bumblebees and solitary bees; here there is even no practice of using hive bees such as *Apis cerana* and *Apis mellifera* and stingless bees even though beekeeping is a tradition throughout the developing countries (Crane 1992). Development and use of insects other than hive bees in this part of world will take a long time and need major research and extension efforts before such insects can be reared and managed for pollination of crops in the region.

This section discusses the issues and challenges in ensuring crop pollination through using manageable species as well as promoting conservation and sustainable use of natural pollinators as a sustainable solution to enhance agricultural productivity. Figure 22.2 presents the challenges to integrate pollination with farming systems and enhancing rural livelihoods through promoting managed pollination and conserving pollinator populations. The main constraints to promoting managed pollination by using honeybees and other pollinators are lack of awareness and understanding among farmers, extension workers, planners and policy-makers about the importance of pollinators and pollination, lack of integrating pollination in agricultural development packages, scarcity of managed colonies of honeybees, and lack of knowledge about conservation, rearing and use of pollinators and their pollination behaviour.

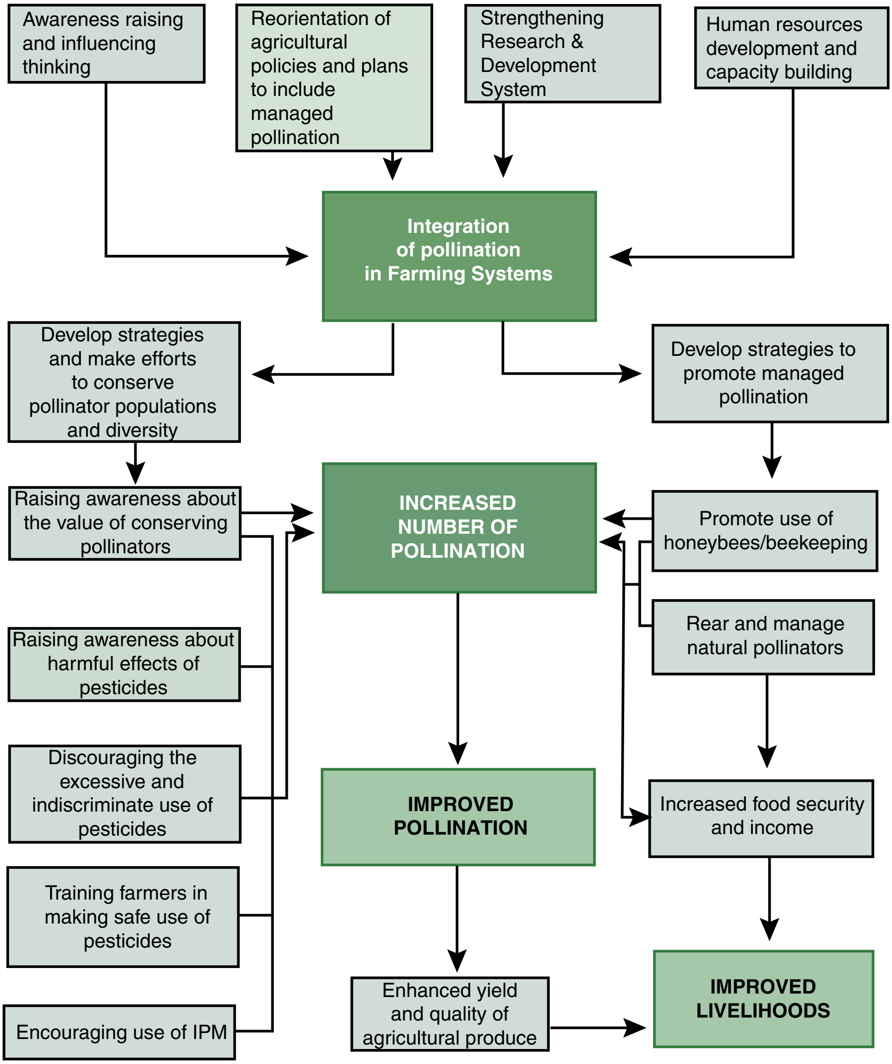

Fig. 22.2 Awareness raising, reorientation of agricultural development policies to include pollination as an input, institutional strengthening R and D institutions, human resources development and capacity building are necessary to integrate pollination in farming systems and enhance agricultural productivity and livelihoods of rural people

22.13 Awareness Raising

Lack of awareness at all levels – be it farmers, extension workers, and professionals at policy and planning level – is one of the main problems in promoting managed pollination. With a few exceptions of farmers in those areas where there is a pollination problem, people are not aware of the value of honeybees (including other pollinators) for agricultural production. This is both because beekeeping has always been promoted exclusively as an enterprise for honey production and because cash crops' farming is a new activity in many developing countries, and there is no indigenous knowledge on the need for managed crop pollination for enhancing cash crop production. Raising awareness at all levels about the importance of managed crop pollination through beekeeping and other pollinators is the first step as part of development efforts.

22.14 Including Pollination as a Technological Input to Agricultural Development Packages

Pollination has been overlooked in agricultural development strategies and is not included as a technological input in agricultural development packages. High value agriculture is being promoted in several areas and extension institutions offer packages of practices for each type of crop, but the importance of managing pollination to achieve higher yields has been overlooked. Thus farmers have no way of knowing how essential it can be. This weakness in the agricultural extension system needs to be addressed.

Since pollination is essential for the production of fruits and seeds, it should be included in agricultural development packages by promoting beekeeping for crop pollination as a "double benefit approach". Thus the most important step in promoting the wider use of honeybees for crop pollination is to include beekeeping as part of agricultural development efforts. Including managed crop pollination in agricultural development packages will also help develop strategies to conserve, promote and use other pollinators.

22.15 Influencing Thinking About Bees and Beekeeping

Traditional thinking is that beekeeping is for honey production, its role in crop pollination is rarely considered. Today, most government agencies are only engaged in promoting beekeeping for honey production. The move towards introduction of *Apis mellifera* to increase honey production is an example of this. Thus there is need to change the general "mindset" about honeybees and beekeeping, and to raise awareness about the importance of managed crop pollination.

22.16 Strengthening Research and Development Institutions

Managed crop pollination is a relatively new area. There are few institutions with explicit mandates or expertise for research and extension in this area. Most institutions are working only with beekeeping and promoting it as a cottage industry to increase family income through the sale of honey. Promoting the value of honeybees as reliable pollinators of agricultural crops will require special efforts to strengthen research and extension systems. This is necessary in order to underline applied research in key areas of managed crop pollination. Issues such as decline of pollinator populations and the need to conserve them need to be addressed by the institutions.

22.17 Human Resources Development and Capacity Building

Lack of knowledge among farmers about the pollination behaviour of honeybees is another constraint hindering the use of honeybees for crop pollination. Even those farmers, who do know that they can use honeybees to increase apple pollination and yield, don't always know how to use the bees. Though linked with the institutional strengthening, it requires more focus to build the capacities of individual farmers, development workers and farmer-led organizations that are the agents of change. There is need to train farmers and beekeepers in managing honeybees for crop pollination. There is also need to develop human resources and build their capacities to initiate activities in the area of conserving, rearing and using pollinators to improve pollination and thus agricultural productivity.

22.18 Crop Pollination Investment Prospects

The inputs of pollinators in agriculture husbandry and biodiversity conservation have not been recognized by policy makers, planners, development workers and farmers. There is no conceptual clarity and recognition of the value of pollinators. There is also need for a change in thinking about the value of honeybees as crop pollinators at all levels: policy, planning, research, beekeeping and farming. The initial thrust of the pollination programme should be to raise awareness about the significance of managing pollination through honeybees and generate knowledge and information to facilitate the formulation of strategies to ensure the wider use of beekeeping for pollination. Honeybees should be seen as crop pollinators first, and as honey producers second. Changes in research and development investment policies may be needed to encourage this. It is also necessary to evolve strategies to promote investment in research and development that will enhance the use of honeybees and other pollinators for pollination. This means developing area-based approaches, making full use of the existing diversity of pollinators including honeybees.

22.19 Gender Concerns in Pollinator Management and Managed Pollination

Women play an important role in agriculture and food production in several developing countries. They are the dominant labour force in agriculture and make a crucial contribution through engaging themselves in all agricultural activities from preparation of the soil to post-harvest operations. Development of rural women and encouraging their full participation as equal partners in the social and economic mainstream is one of the greatest challenges being faced by several developing countries today.

Pollinator management and managed pollination have direct impact on improving women's lives in terms of increasing the economic/food security and reducing their drudgery. Information on the role and significance of women and how their livelihood is affected by failure of pollination and better management of crop pollination is presented here to make a case why future strategies relating to managing pollination should give due attention to gender roles and capacity building.

Let us first analyze how women are affected by managed pollination. As reported, the most visible impact of crop pollination failure is seen in cash crops. Cash crops have played a major role in improving food security and livelihoods of farmers in hills and mountains. Increased productivity through managed pollination has direct implications for women's lives in terms of increasing their economic security. Better pollination leads to increased agricultural production resulting in increased family income leading to enhanced food security and livelihoods. This also ensures better health, nutrition and education for women. On the other hand declining crop yields through lack of adequate pollination increases drudgery as the women have to work extra hard to achieve food security. Therefore, involvement of women in managed pollination should be encouraged.

Our studies also show that women are key to successful management of pollinators (Partap 1998a, b; Partap and Partap 2000, 2002). In Himachal Pradesh, where honeybees are being used for pollination of fruit crops, women farmers manage colonies for use in their own orchards as well as for renting (Partap 1998a, b; Partap and Partap 2002). There are numerous local women farmers' associations in Himachal Pradesh, known as *Mahila Mandals*, which are actively engaged in beekeeping for renting bee colonies for pollination. These hill women farmers are being encouraged to raise honeybees and rent them for apple pollination. As a result a number of women beekeepers' groups are coming up. This has not only increased the income of these "women-headed pollination entrepreneurs" through renting bee colonies for pollination but also through sale of honey. In Hengduan mountains of China women are the backbone of the hand pollination process of fruit trees. Thus, it is necessary to evolve strategies for improving the skills of women in this field.

It is necessary to encourage women's involvement in management of pollinators and pollination in other countries also by creating a conducive environment through extension and demonstration activities, empowering them through training, research, and involving them in projects at national and international levels. While designing training programmes and formulating policies on pollination and conservation and sustainable use of pollinators special consideration should be given to the training of women and building their capacities. For example, women can be encouraged to take up beekeeping for pollination as an income generating activity. Programmes to provide training and support to such pollination entrepreneurs headed by the women can be launched. Such programmes may include capacity building, training and transfer of knowledge and appropriate technology. This will also help in bringing them into the mainstream of development.

22.20 Beekeeping Helps to Create Sustainable Livelihood

Beekeeping, however, is crucially important for agricultural well-being; it represents and symbolizes the natural biological interdependence that comes from insects, pollination and production of seed. Useful small-scale efforts to encourage beekeeping interventions can be found throughout the world, helping people to strengthen livelihoods and ensuring maintenance of habitat and biodiversity. Strengthening livelihoods means helping people to become less vulnerable to poverty. This is achieved by helping them to gain greater access to a range of assets such as beekeeping, and supporting their capacity to build these assets into successful livelihood activities. People who have limited cash or financial savings often have other assets or strengths – as opposed to needs – that can be mobilized. Chambers and Conway (1992) developed what is now the accepted definition of a livelihood:

> A livelihood comprises the capabilities, assets and activities required for a means of living. A livelihood is sustainable when it can cope with and recover from stresses and shocks and maintain or enhance its capabilities and assets both now and in the future, while not undermining the natural resource base.

22.20.1 Beekeeping Assets

Individual livelihoods depend on access to many types of assets which fall into five categories: natural, human, physical, social and financial. To understand this, think about your own livelihood and all the diverse assets you depend upon: your skills, access to transport, equipment, telecommunications and the social networks you have been born into or have created yourself. No individual category of capital assets, such as finance, is sufficient on its own to create a livelihood. Beekeeping is a useful means of strengthening livelihoods because it uses and creates a range of assets. Successful beekeeping draws upon small categories of capital assets, although financial capital is not essential for getting started in productive beekeeping.

22.20.2 Natural Capital Assets

Beekeeping livelihoods are built upon natural resource stocks: bees, flowering plants and water. Bees collect gums and resins from plants and use plants and trees as habitat for nesting. Bees are a natural resource, and freely available in the wild. Where bees have not been poisoned, damaged or harmed, they will collect wherever they are able, provided the natural conditions include available flowering plants. Wild or cultivated areas, wasteland and even areas where there may be land mines all have value for beekeeping. Beekeeping is possible in arid areas and places where crops or other enterprises have failed; the roots of nectar-bearing trees may still be able to reach the water table far below the surface. This makes beekeeping feasible in marginal conditions, which is important for people who need to restore their livelihoods or create new ones. Beekeeping fits in well alongside many other livelihood endeavours because it uses the same natural resources as, for example, forestry, agriculture and conservation activities. Beekeeping provides an excellent bonus in addition to other crops rather than instead of them, because only bees are capable of harvesting nectar and pollen. There is no competition with other insects or animals for these resources that otherwise would be inaccessible to people. Beekeeping ensures the continuation of natural assets through pollination of wild and cultivated plants. Flowering plants and bees are interdependent: one cannot exist without the other. As bees visit flowers, they collect food and their pollination activities ensure future generations of food plants, available for future generations of bees and for people too.

22.20.2.1 Types of Capital Assets Needed for Beekeeping

Natural: bees, a place to keep them, water, sunshine, biodiversity and environmental resources;
Human: skills, knowledge, good health and strength, and marketing expertise;
Physical: tools, equipment, transport, roads, clean water, energy and buildings;
Social: help from families, friends and networks, membership of groups and access to a wider society, market information and research findings;
Financial: cash, savings and access to credit or grants. for people too. It is a perfect self sustaining activity. Pollination is difficult to quantify, but if it could be measured it would be the most economically significant value of beekeeping. By definition, a livelihood should enhance capabilities "while not undermining the natural resource base" (Chambers and Conway 1992). Beekeeping goes beyond this, because it actually helps to sustain the natural resource base. Throughout the world, beekeeping has traditionally been part of village agriculture. Now, as farming practices change, it is essential to ensure that beekeeping is retained and encouraged in order to provide continued populations of pollinating insects.

Human Assets

Many societies have considerable traditional knowledge and skills concerning bees, honey and related products. The products of beekeeping are often used by women: the important *tej* (honey wine) industry in Ethiopia, for example, is run by that is possible for people living in the most difficult circumstances, perhaps isolated by war or sanctions. This is because bees are almost always available in the wild and equipment can be made from whatever materials are at hand.

Beekeeping Outcomes

Beekeeping produces a number of quite different outcomes.

- Pollination of flowering plants, both wild and cultivated, is vital for continued life on earth. However, this essential process is difficult to quantify.
- People everywhere like honey, the best-known beekeeping product. Honey is a traditional medicine or food in most societies. Whether sold fresh at village level or in sophisticated packaging, honey generates income and can create livelihoods for several sectors within a society.
- Beeswax is a valuable product of beekeeping, and much of the world's supply comes from developing countries.
- Beekeeping products such as pollen, propolis and royal jelly can be harvested and marketed, although special techniques and equipment are needed for some of these products.
- Beekeepers and other community members can create assets by using honey, beeswax and other products to make secondary products such as candles, skin ointments and beer. Elsewhere in Africa, women brew and sell honey beer. These are the types of human assets or skills needed to create livelihoods within a society. Beekeeping projects have sometimes ignored existing knowledge or implied that it was wrong or out of date, which is worse. The best beekeeping projects recognize existing skills and build on them for greater income generation and to ensure sustainability.

Physical Assets

Successful beekeeping enterprises require production equipment and infrastructure such as transport, water, energy, roads, communication systems and buildings. There are many ways to manage bees and obtain crops of honey, beeswax or other products. In sustainable beekeeping projects, all equipment must be made and mended locally which, in turn, contributes to the livelihoods of other local people. Beekeeping can add to the livelihoods of many different sectors within a society including village and urban traders, carpenters who make hives and stands, tailors who make veils, clothing and gloves and those who make and sell tools and containers.

Social Assets

Social resources such as networks and producer and marketing associations have great significance for beekeeping development. Local associations provide the means for beekeepers to advance their craft, lobby for the protection of bees, organize collective processing for honey and wax, and gain access to markets. Access to networks at a wider level through non-governmental organizations (NGOs) such as Apimondia and Bees *for* Development helps beekeepers to make national and international contacts, find sources of training, markets and new research results, and improve their understanding of the industry.

Financial Assets

Although significant financial assets are not essential to initiate beekeeping activities at subsistence level, they are essential for development of beekeeping enterprises. Successful marketing depends on adequate supplies of containers for processing and packaging. Credit is necessary for beekeeping associations to run collection centres and for traders to buy honey and beeswax. A good beekeeping project will utilize available assets; it will not depend on imported resources or equipment, such as the beeswax foundation used in frame hives. There are situations all over the world where beekeeping can be especially valuable because it remains an activity. Secondary product brings a far better return for the producer than selling the raw commodity. This work strengthens people's livelihoods.

- Products of beekeeping are used for apitherapy in many societies.
- Honey, beeswax and products made from them, such as candles, wine and food items, have cultural value in many societies and may be used in rituals for births, marriages, funerals and religious, celebrations.
- Beekeepers are generally respected for their craft. Bees and beekeeping have a wholesome reputation. Images of bees are used as symbols of hard work and industry, often by banks and financial institutions. These outcomes are real and they strengthen people's livelihoods, even though some of them cannot be fully quantified. Beekeeping helps people to become less vulnerable, strengthens their ability to plan for the future and reduces the danger that they will slip into poverty in a time of crisis, for example, if a family member becomes ill.

22.21 Beekeeping and Ancillary Industries in Improving Food Security and Livelihoods

In addition to the benefits obtained from pollination which help improving livelihood, the direct benefits of beekeeping can be obtained through ancillary industries which depend upon beekeeping. An ancillary unit is defined as a unit which produces parts, components, sub-assemblies, and tooling for supply against known or anticipated demand of one or more large units manufacturing/assembling complete product and which is not a subsidiary to or controlled by any large unit in regard to the negotiation of contracts for supply of its goods to any large unit. This shall not, however, preclude an ancillary unit from entering into an agreement with a large unit giving it the first option to take formers output.

22.21.1 Industries Necessary for Apiculture

22.21.1.1 Supply Industries

There are a number of specialist industries which operate solely (or predominantly) to supply requisites to the beekeeping industry. While not quantified as a part of the beekeeping industry, their existence is certainly a part of the indirect economic impact generated by the industry. This "supply" sector includes:

(i) **Beehive manufacturers** – while only small in number, companies manufacturing hives for the industry tend to specialize in this activity.
(ii) **Extractor/uncapping machinery** – any company skilled in the production of stainless steel equipment for the food industry would be capable of manufacturing the machinery required to "uncap" combs, and extract honey.
(iii) **Packers' equipment** – bottles and bottling equipment are required by packers. In addition, drum manufacturers provide the special galvanized drum, made with side bung that is not generally available from other sources for producers and packers. A gradual change to plastic drums is taking place, with intermediate bulk containers, of pallet size being used which hold more honey than do the traditional drums.
(iv) **Heat source** – every honey producer requires a steam or hot water boiler to generate steam, and hot water, for processing honey and wax. While not requiring a specialized manufacturing activity, the beekeeping industry generates a demand for such equipment.
(v) **Transport/handling equipment** – all commercial beekeepers must purchase trucks and utilities for transporting and servicing hives. Many also own front end loaders for loading hives, on pallets, and loading drums or use other forms of mechanisation.
(vi) **Other equipment** – beekeepers also have a need for other equipment such as electric generators and mobile extracting units. While the first two items (as for heat sources) do not require a specialized manufacturing activity, expenditure by the beekeeping industry can provide an important source of demand.
(vii) **Quality assurance** – beekeepers and packers are increasingly introducing quality assured premises and equipment for handling honey, as a food product for human consumption. Again, this is not necessarily a specialised activity unique to the industry, but represents an additional demand for existing services.

It is clear that a considerable amount of other economic activity is generated as a result of the activities of the honey bee industry.

22.21.2 Industries Dependent on Apiculture

Major products of beekeeping are: honey, beeswax. In addition, specialized segments of the industry concentrate beekeeping activities towards the production of: queen bees, package bees – the provision of specialist paid honey bee pollination services for horticultural and agricultural industries. Queen bees and package bees are sold to other beekeepers both within the and overseas. Honey and beeswax are still produced by queen and package bee producers, but these products are not the prime goal of their beekeeping activities. Other minor products from the industry include: – pollen, royal jelly, propolis, bee venom. The economic dimensions of the industry, and the direct and indirect impacts that beekeeping are as given below.

22.21.2.1 Industry by Sector

The overall apiary industry should be considered in terms of a number of sectors, as follows:

Honey

Honey is the prime output of commercial beekeepers, and is produced by bees from plant nectar. The major producers are Russia, China, USA, Mexico, Argentina, Canada, Brazil and Australia. The major exporters are China, Mexico and Argentina, but the highest colony yields are recorded in Australia and Canada which have a favourable environment as well as highly developed colony management. The major consumers and importers are the industrialized countries led by Germany, Japan, USA and UK. The increased consumption over the last few years can be attributed to the general increase in living standards and a higher interest in natural and health products. Western Europe as a whole imported approximately 140,000 tonnes which is about 55% of consumption. The average EU per capita consumption of 600 g per year varies widely amongst individual nations, from Greece with 300 g per capita to Germany with 1,800 g per capita.

In general, light-coloured honeys bring the highest price and dark ones are most frequently used for industrial production. Mild flavoured honeys are preferred, but characteristically flavoured honeys bring top prices in some countries. Large honey packers usually prefer honeys with a low tendency to crystallize. Some unifloral honeys such as Hungarian Black Locust honey bring twice the price of regular, multifloral honey. Small shipments into Switzerland of unifloral honeys such as lavender honey, in most cases already bottled, bring much higher prices. Local prices in most developing countries are higher than the international market prices and prices in neighbouring countries with less honey production or favourable exchange rates may sometimes be quite attractive.

Expansion of markets with honey-containing products should be considered on a national level or for across-the-border trade. Consumer education and of course, spending power will probably be the most important factors influencing the possibility of expanding local markets or for increased product diversity. The examples given in this chapter might serve as ideas for possible modification and adaptation to individual circumstances.

Beeswax

Beeswax is a substance secreted by the worker bees. It is recovered by beekeepers primarily from honey comb cappings, and also from cull combs and wax pieces. Beeswax is used in certain pharmaceutical and cosmetic preparations, as a base for polishes and some ointments, for candles – and for comb foundation for beekeeping. It has the highest melting point of natural waxes, and can be sold in either the raw or refined form. Commercial beeswax is generally refined for sale by a manufacturer of apiary products.

The cosmetics and pharmaceutical industries have no complete substitute for beeswax. At least small quantities will always be needed to maintain quality and specific characteristics. Like honey prices, prices for beeswax may vary considerably from place to place.

Markets and prices for products made from beeswax vary widely from country to country. In these industries, beeswax forms only a minuscule part both of the manufacturing process and of the final product. It is used in candle making, skin creams, grafting wax for horticulture, polishes and varnishes, paste furniture polish, liquid furniture polish, spray polish, floor polish, shoe polish, cream type. Cravons, leather preserves, waterproofing textiles and paper, paint, wood preservative, swarm lure, veterinary wound cream, adhesive lotions.

Live Bees

The production of queen bees, and of entire colonies of bees, is the main diversification available to beekeepers. The queen bee industry is dependent on the existence of a profitable honey industry and on an export market to buy queens at a period when little or no sales. For example, in Australia the demand for queen bees is estimated at around 155,670 per annum – at an average price of $ 9 per queen, this represents a farm-gate value of around $ 1.5 million. This is a conservative figure because export sales – estimated by industry sources to be $ 0.75 million – are not recorded separately and have not been added. Live bee exports is a potential growth area for the beekeeping industry, as further markets develop.

Package bees and nucleus colonies are other forms of live bee production, and are sold both within the country and overseas. Again, data on total value of production for this sector of the industry is not available, and has been estimated on the basis of known production. The total value of this sector has been assumed to be

$ 2.25 million, which is almost certainly an under-estimate, but which has been used as a conservative minimum. In India where great potential of beekeeping exists marketing for live bees can be much more.

Other Products

In addition to honey and wax, active beehives are also a source of other products. These include:

Royal jelly – a milky white smooth jelly secreted by nurse bees, used to feed developing queen larvae and young worker bee larvae. The production of royal jelly is a very specialized procedure, and flora conditions must be ideal before production can be considered. Royal jelly is used as tablets, or mixed into creams and shampoos. Royal jelly can be sold in its fresh state, unprocessed except for being frozen or cooled, mixed with other products, or freeze-dried for further use in other preparations. The fresh production and sale can be handled by enterprises of all sizes since no special technology is required. In its unprocessed form it can also be included directly in many food and dietary supplements as well as medicine-like products or cosmetics. For larger industrial scale use, royal jelly is preferred in its freeze-dried form, because of easier handling and storing. Freeze-dried royal jelly can be included in the same products as the fresh form. The production of freeze-dried royal jelly requires an investment of at least US$ 10,000 for a freeze-dryer, sufficient production volume and an accessible market for the raw material or its value added products. Products containing royal jelly should be specially marked or packaged in order to distinguish them from similar products without it.

As Dietary Supplement

Royal jelly belongs to a group of products generically described as “dietary supplements”. These are products which are consumed not for their caloric content nor for pleasure, but to supplement the normal diet with substances in which it might be lacking.

As Ingredient in Food Products

A mixture of royal jelly in honey (1–3% royal jelly) is probably the most common way in which royal jelly is used as a food ingredient. Among the advantages of this product are that no special technology is required and the honey masks any visible changes in the royal jelly. The final product is pleasant-tasting and it provides the beneficial effects of both products.

As Ingredient in Medicine-Like Products

In medicine-like formulations royal jelly is generally included for its stimulatory effects. However, it is also used to solve specific health problems. A variety of formulations are available, often containing ingredients otherwise used to alleviate particular afflictions, or as medicine.

As Ingredient in Cosmetics

Except in Asia, probably the largest use of royal jelly is in cosmetics. Royal jelly is included in many dermatological preparations, but mostly in those used for skin refreshing, and skin regeneration or rejuvenation. It is also used in creams or ointments for healing burns and other wounds.

Others

The only other known uses for royal jelly are in animal nutrition. In particular, royal jelly has occasionally been used (fresh or freeze-dried) to stimulate race horses. For experimental purposes it is also used as a food for rearing mites and insects.

Royal Jelly Collection

Royal jelly is produced by stimulating colonies to produce queen bees outside the conditions in which they would naturally do so (swarming and queen replacement). It requires very little investment but is only possible with movable comb hives.

Propolis: A by-product of the bee hive. It originates as a gum secretion gathered by bees from a variety of plants, and can vary in colour depending on the plant species of origin. Propolis has remarkable therapeutic qualities, and is much sought after in some countries for the treatment of a range of human ailments, and for cosmetic purposes. It is used by honey bees as an antiseptic to varnish the interior of honey comb cells used by the hive to rear young brood, to seal cracks in the hive from the winter chill, and for general hive cleanliness purposes. The market for raw material and secondary products containing propolis will probably continue to grow as they find more acceptance in medicinal uses and as more cosmetic manufacturers realize their benefits and marketing value.

Bee venom: Collected by stimulating bees with a mild electric current. The venom is processed, and used in the preparation of pharmaceutical materials. It can be used to detect hypersensitivity or allergic reaction to bee stings. Bee venom is a highly specialized product with only very few buyers. The market volume is relatively small too, although there are no comprehensive surveys. The main venom producer is the USA which has produced only about 3 kg of dry venom during the last 30 years (Mraz 1982) but there is a large producer in Brazil and more or less significant amounts are produced in many other countries. Prices in 1990 varied greatly between US$ 100 and US$ 200 per gram of dry venom (Schmidt and Buchmann 1992). Prepared for injections or sold in smaller quantities, prices can be much higher. However, the beekeeper often does not get this price. The prevailing prices in European and Asian markets are generally slightly lower.

Pollen: Pollen can also be harvested by beekeepers, at a rate of around 7–10 kg per hive per year. Pollen is used by bee colonies as a source of protein, but harvesting pollen by the beekeeper requires detailed knowledge of resources, hive management, species flowering variations and timing, and hive response to different honeys and pollens. Pollen is collected via specialized traps fitted to the hives, and must be processed rapidly after collection (usually via freezing or drying) to avoid excessive moisture absorption and fermentation. Many beekeepers harvest pollen to feed back to their hives during periods of natural pollen deficiency. Dried pollen prices in the USA range from US$ 5 to 13 per kg wholesale and US$ 11 30 per kg retail. Encapsulated pollen or pollen tablets sell vials of 50–100 units and retail at prices of up to US$ 900 per kg, at least in Italy and the bulk pollen consumer market seems to be growing in industrialized countries, but pollen tablets are still a common feature of health food stores and command an excessively high price. Encapsulation and extraction of pollen lend themselves easily to small scale manufacturing and result in safer consumer products.

Most of the buyers and large scale sellers of pollen are also honey traders. Crane (1990) however, reports that a lot of commercial pollen is not bee collected, but machine-collected from certain wind pollinated plants which release very large quantities of dry pollen. At least in industrialized countries and those with increasing numbers of health conscious consumers, pollen consumption is likely to increase further. On the other hand, there seems to be a wide market for reasonably priced, encapsulated pollen and tablets.

Paid Pollination Services

Some beekeepers receive payment for placing hives in close proximity to flowering crops, according to contractual arrangements with farmers. For example, rates for pollination services in inland Australia varied between $ 25 and $ 35 per hive in 1996, with variations between crops. It has been estimated that at least $ 2.9 million is received by the industry in this way, based on total payments received for pollination services in Tasmania (Gifford 1989) and multiplied up to an Australian figure by numbers of hives.

Similar concept is picking up throughout the world including India. In Himachal Pradesh, India this practice has already started and is likely to be followed in other states as the awareness about pollination benefits is realized by the farming community.

Evidently**,** to ensure the country's self-sufficiency in foodstuffs, to receive foreign currency from excess production, the stabilization of rural populations by complementary activities of both a financially rewarding and environmental *Nature*, and there is no doubt that beekeeping fits perfectly within this framework and hence, efforts are required to popularize and increase beekeeping still an enormous potential waiting to be tapped.

22.22 Conclusions

Like soil, water and nutrients, pollination is also a limiting factor in crop productivity. The declining agricultural productivity can be attributed to a number of factors, but pollination plays a crucial role. We may make use of plant husbandry techniques, such as the use of better quality seed and planting material and provide all agronomic inputs including, good irrigation, use of organic and inorganic fertilizers and biocides, but if there is no pollination, no fruit or seed will be formed.

The pollination problem is relatively new and needs due attention at this early stage. Since pollinator scarcity is the main factor responsible for inadequate pollination, solutions to this lie in increasing the number of pollinators. This can be done by conserving populations of natural insect pollinators by promoting integrated pest management and making judicious use of chemical fertilizers and pesticides, however, the most practical and preferred solution to increase the number of pollinators would be by promoting manageable species of honeybees for pollination. There is need to formulate policies that include pollination as an integrated input to agricultural production technologies. Other challenges include strengthening research and extension institutions and human resources development. The ancillary industries play an important role in improving livelihood and food security.

In conclusion, it is apparent that both traditional beekeeping and the environmental and culturally appropriate enhancements that have been introduced have minimal negative ecological impact. Beekeeping has an important role to play in addressing issues of rural poverty, in building rural self reliance and in diversifying income sources in order to better enable communities to cope with the periods of climatic and economic uncertainty (Gooneratne and Mbilnyi 1992). Moreover, beekeeping can enhance the position and income of women. Beekeeping relies on indigenous skills and interests, uses locally available resources and has a positive effect on other forms of farming through the increased pollination of cultivated crops. External and donar agencies through appropriate technology and carefully targeted support can clearly help to ensure community and ecological sustainability. As a source of food and income or through the vital role that it plays in plant pollination, an as an indicator of environmental health, beekeeping is an important component of community based natural resource use and management.

References

Batra SWT (1985) Bees and pollination in our changing environment. Apidologie 26:361–370

Batra SWT (1995) Solitary bees for blueberry pollination. In: Proceedings of the 7th southeastern blueberry conference, Savannah, pp 69–72

Batra SWT (1997) Solitary bees for orchard pollination. Pennsylvania Fruit News, Apr 1997

Cadoret JP (1992) Doorway doses help defeat honeybees' vampire enemy. Ceres FAO Rev 24:8–9

Chambers R, Conway GR (1992) Sustainable rural livelihoods: practical concepts for the 21st century. Discussion paper 269. Institute of Development Studies, Brighton, UK

Costanza R, Sklar FH, Day JW (1987) Using the Coastal Ecological Landscape Spatial Simulation (CELSS) Model for Wetland Management. Coastal Zone '87. Proceeding of the 5th Symposium on Coastal and Ocean Management 4:3879–3890

Crane E (1990) Bees and beekeeping: science, practice and world resources. Cornell University Press, New York

Crane E (1992) The past and present status of beekeeping with stingless bees. Bee World 73:29–42

Deodikar GB, Suryanarayana MC (1977) Pollination in the services of increasing farm production in India. In: Nair PKK (ed) Advances in pollen spore research. Today and Tomorrow Printers and Publishers, New Delhi, pp 60–82

Dulta PC, Verma LR (1987) Role of insect pollinators on yield and quality of apple fruit. Indian J Hort 44:274–279

Free JB (1964) The behaviour of honeybees on sunflowers (*Helianthus annus* L.). J Appl Ecol 1:19–27

Free JB (1966) The pollinating efficiency of honeybee visits to apple flowers. J Hort Sci 41:91–94

Free JB (1993) Insect pollination of crops, 2nd edn. Academic Press, London

Freitas BM, Otávio J, Pereira P, Fortaleza CE (eds) (2004) Solitary bees conservation, rearing and management for pollination. A contribution to the International Workshop on Solitary Bees and Their Role in Pollination, held in Beberibe, Ceará, Brazil, in April 2004, 282 p

Gifford D (1989) Tasmanian Pollination Industry. Paper presented at Seminar organised by Department of Primary Industry, Tasmania, and Tasmanian Beekeepers' Association. Hobart and Deloraine (Tasmania), 19 and 20 September, 1989

Gooneratne W, Mbilnyi M (eds) (1992) Reviving local self-reliance: people's responses to economic crisis in eastern and southern Africa. United Nations centre for Regional Development, Nagoya

Gupta JK, Goyal NP, Sharma JP, Gautam DR (1993) The effect of placement of varying numbers of *Apis mellifera* colonies on the fruit set in apple orchards having different proportions of pollinisers. In: Veeresh GK, Uma Shankar R, Ganeshaiah KN (eds) Proceedings of the international symposium on pollination in the tropics. International Union for Studies on Social Insects, Bangalore

Gupta JK, Rana BS, Sharma HK (2000) Pollination of kiwifruit in Himachal Pradesh. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Uma Partap (eds) Asian bees and beekeeping: progress of research and development. Proceedings of the fourth international conference, Kathmandu. Oxford and IBH Publishing Company Private Limited, New Delhi, 274pp, 23–28 Mar 1998

Ingram M, Nabhan GC, Buchmann SL (1996) Impending pollination crisis threatens biodiversity and agriculture. Tropinet 7:1–10

Jodha NS, Shrestha S (1993) Sustainable and more productive mountain agriculture: problems and prospects. In: Mountain environment and development – part 3 (thematic papers). ICIMOD, Kathmandu, pp 1–65

Kenmore P, Krell R (1998) Global perspectives on pollination in agriculture and agroecosystem management. International workshop on the conservation and sustainable use of pollinators in agriculture, with emphasis on bees, Sao Paulo, Brazil, 7–9 Oct 1998

Kevan PG, Phillips TP (2001) The economic impacts of pollinator declines: an approach to assessing the consequences. Conserv Ecol 5(1):8

Kevan PG, Imperatriz-Fonseca V, Frankie GW, O'Toole C, Jones R, Vergara CH (eds) (2002) Pollinating bees: the conservation link between agriculture and nature. In: Proceedings of the workshop on the conservation and sustainable use of pollinators in agriculture, with emphasis on bees. S. Paulo, in Oct 1998. Secretariat for Biodiversity and Forests, Ministry of the Environment, Government of Brazil, Brasilia, 313 pp

Khan MR (2004) The role of honey bees *Apis mellifera* L. (Hymenoptera: Apidae) in pollination of apple. Pakistan Journal of Biological Sciences 7(3):359–362

Koirala GP, Thapa GB (1997) Food security challenges: where does Nepal stand? HMG/N, MOA/Winrock International, Kathmandu, 41 p

Matheson AG, Schrader M (1987) The Value of Honey Bees to New Zealand's Primary Production. Nelson, New Zealand: Ministry of Agriculture and Fisheries

McGregor SE (1976) Insect pollination of cultivated crop plants. United States Department of Agriculture (USDA), Washington DC

Morse RA, Calderone NW (2000) The value of honey bees as pollinators of US crops in 2000. Electronic Document Downloaded from the Internet Page. http://bee.airoot.com/beeculture/pollination2000

Mraz C (1982) Bee venom for arthritis - an update. Amer Bee J 122:121–123

Nabhan GP, Buchmann SL (1997) Pollination services: biodiversity's direct link to world food stability. In: Daily GC (ed) Nature's services: societal dependence on natural ecosystems. Island Press, Washington DC, pp 133–150

Partap T (1998a) Agricultural sustainability challenges in upland areas of semi arid and humid Asia. In: Proceedings of the study meeting on sloping land agriculture and natural resources management. Asian Productivity Organisation, Tokyo, pp 39–84

Partap U (1998b) Successful pollination of apples in Himachal Pradesh. Beekeeping Dev 48:6–7

Partap T (1999) Sustainable land management in marginal mountain areas of the Himalayan region. Mountain Res Dev 19:251–260

Partap U (2000a) Foraging behaviour of *Apis cerana* on citrus (*Citrus sinensis* var. Red Junar) and its impact on fruit production. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Uma Partap (eds) Asian bees and beekeeping: progress of research and development. Proceedings of the fourth AAA international conference, Kathmandu. Oxford and IBH Publishing Company Private Limited, New Delhi, 274pp, 23–28 Mar 1998

Partap U (2000b) Pollination of strawberry by the Asian hive bee, *Apis cerana* F. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK,Uma Partap (eds) Asian bees and beekeeping in Asia: progress of research and development. Proceedings of the fourth AAA international conference, Kathmandu. Oxford and IBH Publishing Company Private Limited, New Delhi, 274pp, 23–28 Mar 1998

Partap U (2001) Warning signals from the Apple Valleys. Video Film, 31 minutes and 7 seconds, VHS Format, ICIMOD, Kathmandu

Partap U (2003) Improving agricultural productivity and livelihoods through pollination: some issues and challenges. In: Waliyar F, Collette L, Kenmore PE(eds) Beyond the gene horizon: sustaining agricultural productivity and enhancing livelihoods through optimization of crop and crop-associated biodiversity with emphasis on semi-arid tropical agroecosystems. Proceedings of a workshop, ICRISAT/FAO, Patancheru, India, 23–25 Sept 2002

Partap U, Partap T (1997) Managed crop pollination: the missing dimension of mountain agricultural productivity. Mountain Farming Systems' Discussion Paper Series No. MFS 97/1, ICIMOD, Kathmandu

Partap U, Partap T (2000) Pollination of apples in China. Beekeeping Dev 54:6–7

Partap U, Partap T (2002) Warning signals from Apple Valleys of the HKH region: productivity concerns and pollination problems. ICIMOD, Kathmandu, pp 106

Partap U, Verma LR (1992) Floral biology and foraging behaviour of *Apis cerana* on lettuce crop and its impact on seed production. Progr Hort 24:42–47

Partap U, Verma LR (1994) Pollination of radish by *Apis cerana*. J Apic Res 33:237–241

Partap U, Shukla AN, Verma LR (2000). Impact of *Apis cerana* pollination on fruit quality and yield in peach and plum in the Kathmandu valley of Nepal. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Uma Partap (eds) Asian bees and beekeeping: progress of research and development. Proceedings of the fourth AAA international conference, Kathmandu. Oxford and IBH Publishing Company Private Limited, New Delhi, 274pp, 23–28 Mar 1998

Partap U, Partap T, Yonghua H (2001) Pollination failure in apple crop and farmers' management strategies. Acta Hort 561:225–230

Prescott-Allen R, Prescott-Allen C (1990) How many crops plants feed the world? Conserv Biol 4:365–374

Schmidt JO, Buchmann SL (1992) The hive and the honey bee. In: Graham JM (ed) Dadant and Sons: Hamilton, IL. 1324 p

Sekita N (2001) Managing *Osmia cornifrons* to pollinate apples in Aomori prefecture, Japan. Acta Hort 561:303–308

Singh MP, Singh KI, Devi CS (2000) Role of *Apis cerana* pollination on yield and quality of rapeseed and sunflower crops. In: Matsuka M, Verma LR, Wongsiri S, Shrestha KK, Uma Partap (eds) Asian bees and beekeeping in Asia: progress of research and development. Proceedings of the fourth AAA international conference, Kathmandu. Oxford and IBH Publishing Company Private Limited, New Delhi, 274pp, 23–28 Mar 1998

Tulachan PM (2001) State of mountain agriculture in the Hindu Kush-Himalayas: a regional comparative analysis. Kathmandu, ICIMOD, 2001. 70 p

Verma LR, Dulta PC (1986) Foraging behaviour of honeybee *Apis cerana* and *A. mellifera* in pollinating apple flowers. J Apic Res 25:197–201

Verma LR, Partap U (1993) The Asian hive bee, *Apis cerana*, as a pollinator in vegetable seed production. ICIMOD, Kathmandu, 52 pp

Verma LR, Partap U (1994) Foraging behaviour of *Apis cerana* on cabbage and cauliflower and its impact on seed production. J Apic Res 33:231–236

Waite MB (1895) The pollination of pear flowers. U.S. Department of Agriculture, Vegetable Pathology Bulletin 5, 86 pp

Williams IH (1992) Apiculture for agriculture. British Beekeepers' Association, Spring Convention. Stone Leigh, pp 14–18

Winston ML, Scott CD (1984) The value of bee pollination to Canadian agriculture. Can Beekeep 11:134

Chapter 23
Capacity Building and Awareness for Pollinators

Abstract This chapter discusses the capacity building for conservation and management of pollination services and covers a wide range, from formal education at all levels, to the informal building ofcapacity amongst farmers, land managers, policy makers and other target groups, including the public as a whole. A particular emphasis has been laid on building capacity in taxonomy and pollinator identification, since this is one of the major impediments to pollinator conservation.

23.1 Introduction

While considering criticality of food production and human livelihood, pollination is a keystone process in both human-managed and natural terrestrial ecosystems. Especially, in agro-ecosystems, pollinators are essential for orchard, horticultural and forage production, as well as the production of seed for many root and fibre crops. More than 75% of the major world crops and 80% of all flowering plant species rely on animal pollinators. Of the hundred or so animal-pollinated crops which make up most of the world's food supply, 15% are pollinated by domestic bees, while at least 80% are pollinated by wild bee species and other wildlife Diversity among species, including agricultural crops, depends on animal pollination. Thus, pollinators are essential for 'diet diversity', biodiversity, and the maintenance of natural resources. Unfortunately, pollination as a factor in food production and security is little understood and appreciated, in part because it has been provided by *Nature* at no explicit cost to human communities.

This ignorance has resulted in considerable decline in pollinator populations across the world. The pollination biologists now widely accept that pollinators have declined in numbers resulting in decreased seed and fruit set in the plants that they service. With the threat of increased impacts on pollination services a consensus seems to be arrived that to identify, in multiple agro-ecosystems and ecologies, the practices that will prevent the loss of pollination services provided by indigenous pollinators. This would however require capacity building of different stakeholder

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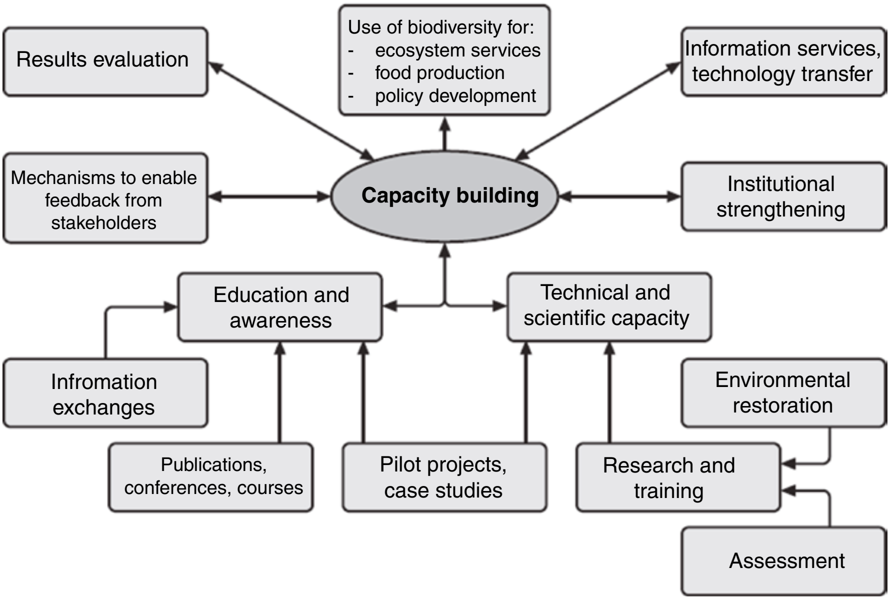

Fig. 23.1 Diagrammatic illustration of the pivotal role of capacity building in pollinator biodiversity conservation (Diagram by V. Fonseca)

groups spanning from researchers to the farmers. This would enable them in understanding the highly diversified ecology of pollinators and pollinator dependent crops.

Capacity building includes building human knowledge, skills and institutional capabilities, and it all begins with awareness. Human capacity building involves both formal and informal education, and scientific and technical training. Institutional capacity building involves developing networks and infrastructure and providing literature on how pollination as an ecosystem service contributes to ecological and economic well-being. Capacity building for conservation and management of pollination services must cover a wide range, from formal education at all levels, to the informal building of capacity amongst farmers, land managers, policy makers and other target groups, including the public as a whole. A particular emphasis is needed on building capacity in taxonomy and pollinator identification, since this is one of the major impediments to pollinator conservation (Fig. 23.1).

23.2 Pollinator and Pollination Awareness

In 1996, two independent events greatly stimulated awareness of the importance of conserving pollinator diversity: the Forgotten Pollinators Campaign, and the COP decision III/11 of the CBD, which established the multi-year Programme of Work on Agricultural Biodiversity, and placed pollination in its initial list of thematic areas. Subsequently, in 1998, an international workshop in Saõ Paulo, Brazil, was held, resulting in the Saõ Paulo Declaration on Pollinators. This Declaration was considered by the CBD's scientific body (the Subsidiary Body on Scientific, Technical and Technological Advice, known as SBSTTA, in recommendation V/9), and subsequently the International Pollinators Initiative (IPI) was established by parties to the CBD (Decision V/5) (as explained in the Introduction). An element of the Plan of Action of the IPI is to raise public awareness about the value of pollinator diversity and the multiple goods and services pollinators provide. Awareness is needed to help citizens and policy makers recognise the economic and ecological value of pollinating animals, and the potential impacts of the loss of pollinator-related ecosystem services and functions.

23.3 Capacity Building in Conservation and Management of Pollination Services

Biological diversity responsible for the maintenance of ecosystem services important for the functioning sustainability of agriculture.

1. Development of a Knowledge Base
2. Assess the economic value of pollinators
3. Extension and promotion of pollinator-friendly Best Management Practices
4. Capacity building and awareness raising (Plate 5)
5. Promote awareness about the value of pollinator diversity and the multiple goods and services it provides for sustainable productivity
6. Promote enhanced capabilities to manage pollinator diversity at local level
7. Monitor pollinator decline, its causes and its impact on pollination services
8. Assess the economic value of pollination and the economic impact of the decline of pollination services, and

Plate 5 Capacity building for pollinator awareness

9. Promote the conservation and the restoration and sustainable use of pollinator diversity in agriculture and related ecosystems. Local knowledge of management of pollinator diversity
10. To strengthen capacities of farmers, indigenous and local communities, and their organizations and other stakeholders, to manage pollinator diversity so as to increase its benefits, and to promote awareness and responsible action

Seven countries Brazil, Ghana, India, Kenya, Nepal, Pakistan, South Africa, spanning a range of agro-ecosystems, socio-economic conditions and ecologies, have recognized that pollination services provided by biodiversity need to be actively managed and conserved, to avoid the risk of being lost. All have some existing commitment to building capacity and enabling environments for conserving and managing wild pollinators; Brazil along with several African partners has taken a lead in establishing a global initiative on pollinator conservation. Seven countries have worked together to identify activities that can address the threats to pollinators, and which will expand global understanding, capacity and awareness of the conservation and sustainable use of pollinators for agriculture.

Some pollinators such as bees also provide food and additional income for rural families, in the form of honey and other by-products – thus, declining pollinator populations impact on the sustainable livelihoods of rural families. A decline in pollinator populations also affects plant biodiversity. Native pollinator species may decrease when their nesting habitats are destroyed, when they find less wild flowering plants to forage on throughout their life cycle, and when they are impacted by injudicious use of pesticides.

In Asia, the domesticated honeybee, *Apis mellifera* (and its several Asian relatives) have been utilized to provide managed pollination systems, but for many crops, honeybees are either not effective or are optimal pollinators. The process of securing effective pollinators to service agricultural fields is not always easy, and there is a renewed interest in ensuring pollination services through practices that support wild pollinators (Fig. 23.2). In response to these realizations, during the development of the National Agricultural Biodiversity Programme (NABP) – as part of the NABP thematic area of crop-associated biodiversity – the issue of conducting activities related to the conservation and sustainable use of pollinators was given priority. Government priorities for the activities on pollinators focused on fruits and vegetables building capacity was also seen as a priority. Knowledge on integration of pollination by bees is illustrated in Fig. 23.2.

23.3.1 Following Strategy for Capacity Building Implementation is Proposed

Build local capacities at different levels for:

1. Design and implementation of interventions to mitigate threats on pollinator populations.

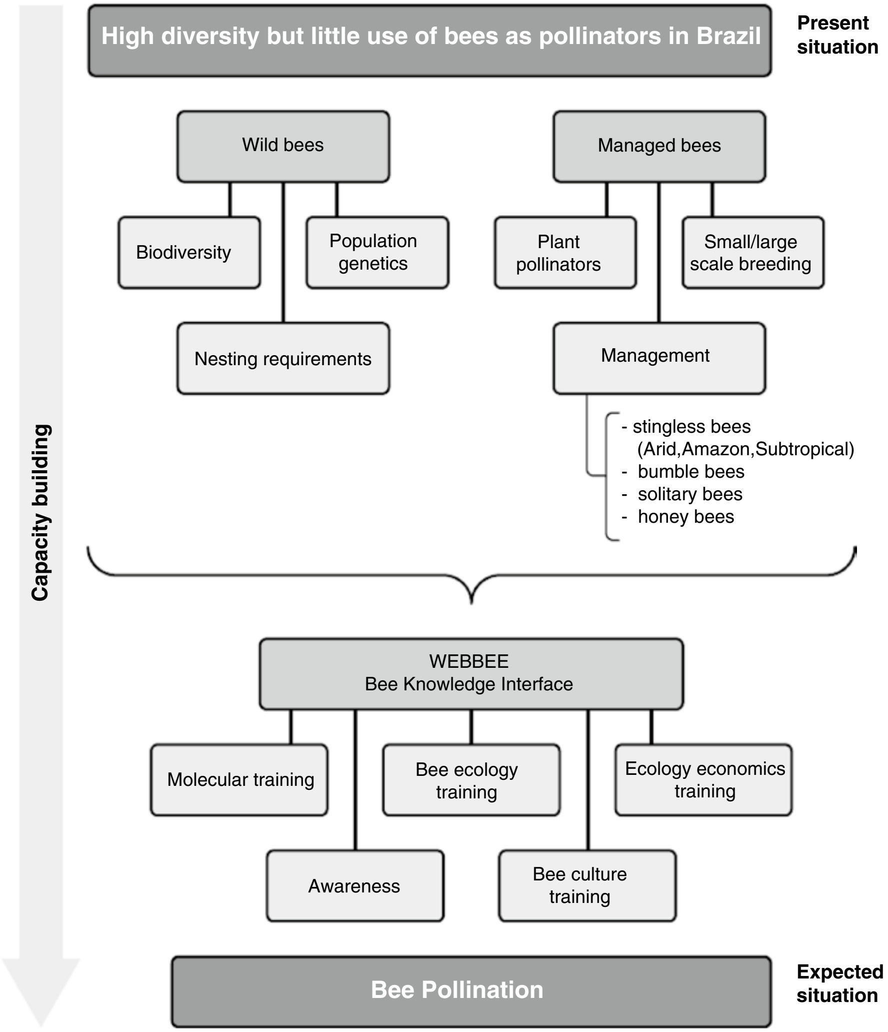

Fig. 23.2 Knowledge integration of pollination by bees (Diagram by V. Fonseca 2004)

2. Establish and promote sustainable pollinator management practices in participatory manner.
3. Enhance public awareness on the role and value of pollination services in ecological conservation and sustainable development in the region.

23.3.1.1 Grass Root Level

Capacity building should begin at this level to give theoretical as well as practical insight into different types of pollinating insects and their gainful utilization in crop production. Likely beneficiaries include farming community, orchidists/progressive beekeepers, and unemployed youth. It is envisaged to build capacity through organization of short duration courses/farmers field schools to harness income generating potential of pollinators, especially Bee Keeping. Also, during the course/farmers field school participants will be exposed to basic understanding of pollinators/pollination and its importance, particularly for sustainability of agricultural and horticultural crops.

23.3.1.2 Education Level

Capacity building programmes are envisaged for School and College-Undergraduate; and University-Postgraduate and Research level. Participants will be provided with easy to grasp reading material (preferably regional languages). Considering the need for improving understanding on pollinators/and pollination at university/research level short term courses for selected PG/research students of the region be organised.

23.3.1.3 Multipliers Level

Capacity building is proposed as one among most important aspects of the project. Relevant NGOs, Community Groups (like beekeepers association, fruit growers association, women welfare groups, etc.); teachers and extension workers will form the target group. In view of their continuous interaction with grass root, educational and planner/manager level stakeholders, it is proposed to build the capacity at this level to develop a strong team of Trainers. Identified Zonal partners in consultation with other relevant experts will impart training. Training modules will include: (i) Exposure to the subject; (ii) importance of the subject; (iii) basics of pollinator identification; (iv) methods of data collection and compilation; (v) development communication skills and scientific reporting. Also, the participants will be exposed to the basics of group management so as to act as effective trainers.

23.3.1.4 Planner and Managerial

Level awareness generation is proposed to be achieved through development of policy briefs; information broachers and audio visual aids. Also it is proposed to organize 1 day awareness programmes. The target group includes – planning level officers in relevant departments (i.e. agriculture, horticulture, forestry, environment, etc.), officers of rural development departments; field managers (i.e. project directors, farm managers, PA managers, etc.); watershed management officers; school college principals, etc. Intension is to stress upon the policy makers/mangers about the importance of pollination as an essential ecosystem service.

23.4 Mainstreaming

Many countries are now developing biodiversity strategies and action plans in the context of the Convention on Biological Diversity, and many also have a number of other policies, strategies and plans related to agriculture, the environment and national development. Decision V/5 of the Conference of Parties to the Convention on Biological Diversity seeks to promote the mainstreaming of agricultural biodiversity considerations into national strategies and action plans; to mainstream the action plans for components of agricultural biodiversity in sectoral development plans concerned with food, agriculture, forestry and fisheries, and to promote synergy and avoid duplication between the plans for the various components. Pollinator conservation and sustainable use is an important aspect of agricultural biodiversity and should be integrated into this mainstreaming process. In addition, this requires reliable and accessible information, but many countries do not have well developed information, communication or early-warning systems or the capacity to respond to identified threats.

23.4.1 Activities

Integrate considerations of pollinator diversity, and related dimensions of agricultural biodiversity, including host plant diversity, at species, ecosystem and landscape levels, consistent with the ecosystem approach, into biodiversity strategies and action plans, and into planning processes in the agricultural sector. Support the development or adaptation of relevant systems of information, early warning and communication to enable effective assessment of the state of pollinator diversity and threats to it, in support of national strategies and action plans, and of appropriate response mechanisms.

Strengthen national institutions to support taxonomy of bees and other pollinators, through, *inter alia*:

(a) Assessing national taxonomic needs (this would contribute to activity 1.3);
(b) Maintaining continuity of taxonomic and reference collections of bees;
(c) Recognition of centres of excellence in bee taxonomy and establishment of centres of excellence as appropriate;
(d) Repatriation of data through capacity-building and benefit-sharing.

Include considerations of pollinator diversity, and related dimensions of agricultural biodiversity, including host plant diversity, at species, ecosystem and landscape levels, consistent with the ecosystem approach, in formal educational programmes at all levels. Integrate pollination issues as a component of sustainable management into agricultural, biological and environmental science courses and curricula and in primary and secondary schools by using local examples and relevant examples from other regions. Promote applied research on pollination in agricultural ecosystems through training of post-graduates.

23.4.2 Ways and Means

1. Activities would be implemented primarily at national level through enhanced communication, coordination mechanisms and planning processes that involve all stakeholder groups, facilitated by international organizations, and by funding mechanisms.
2. Additional resources may be needed for national capacity-building.
3. The taxonomic elements would also be promoted through the Global Taxonomy Initiative.

23.4.3 Timing of Expected Outputs

Capacity-building aims to strengthen the capacities of farmers, indigenous and local communities, and their organizations and other stakeholders, to manage pollinator diversity so as to increase its benefits, and to promote awareness and responsible action.

The management of pollinator diversity involves many stakeholders and often implies transfers of costs and benefits between stakeholder groups. It is therefore essential that mechanisms be developed not only to consult stakeholder groups, but also to facilitate their genuine participation in decision-making and in the sharing of benefits. Farmer groups, and other producer organizations, can be instrumental in furthering the interests of farmers in optimizing sustainable, diversified, production systems and consequently in promoting responsible actions concerning the conservation and sustainable use of pollinator diversity.

One major area which needs addressing is the capacity of countries to address the Taxonomic Impediment, which derives from serious shortfalls in investment in training, research and collections management. It seriously limits our capability to assess and monitor pollinator decline globally, in order to conserve pollinator diversity and to manage it sustainably. The global Taxonomic Impediment is costly, especially when expressed in terms of those research initiatives in pollination and conservation ecology which are wholly dependent on access to sound bee taxonomy and are rendered wholly non-viable in its absence. There is also a global Taxonomic Deficit, that is, the unacceptably high numbers of bee genera for which identification keys are not available.

The activities required include:

1. Promote awareness about the value of pollinator diversity and the multiple goods and services it provides for sustainable productivity, amongst producer organizations, agricultural cooperatives and enterprises, and consumers, with a view to promoting responsible practices.
2. Identify and promote possible improvements in the policy environment, including benefit-sharing arrangements and incentive measures, to support local-level management of pollinators and related dimensions of biodiversity in agricultural

ecosystems. This could include consideration of how existing or new certification schemes might contribute to the conservation and sustainable use of pollinator diversity.

3. Promote enhanced capabilities to manage pollinator diversity at local level by promoting partnerships among and between farmers, researchers, extension workers and food processors, inter alia, through the establishment of local-level forums for farmers, and other stakeholders to evolve genuine partnerships, including training and education programmes.
4. Build taxonomic capacity to carry out inventories of the pollinator diversity and distribution in order to optimise their management, through, inter alia the training of taxonomists and parataxonomists of bees and other pollinators.
5. Develop tools and mechanisms for the international and regional exchange of information for the conservation, restoration and sustainable use of pollinators. This may include:
    (a) Establishing an inventory of existing pollination and pollinators experts to serve as a pool for consultations in technology transfer, and establish an international advisory group on pollinator conservation.
    (b) Disseminating information on pollination in agricultural environments through databases, websites, and networks. This may include the establishment of an international information network on pollinator conservation and promotion of networks of farmers and farmers' organizations at regional level for exchange of information and experiences.
    (c) Developing and updating global and national lists of threatened pollinator species, and produce multilingual manuals on pollinator conservation and restoration for farmers.

23.5 Capacity Building Has Been Successful in Exploiting Pollinators as Illustrated in Following Few Examples

23.5.1 Agave and Tequila

Tequila is produced from agave, a bat-pollinated plant. Scientists have helped increase awareness of the importance of pollination to the tequila industry – hoping that such awareness will lead to improved management. Agaves are New World plants that typically die after sexual reproduction. They are very important plants for local and national economies. Leaf fibre is widely used for utility ropes, rugs, textiles, and many other domestic and industrial uses. When the plant starts to produce the blooming stalk, the centre of the plant increases its sugar content, and many cultural groups use this resource; in Mexico agaves have been used to produce alcoholic beverages, such as tequila and mezcal, for at least 700 years (Ramírez and López 1985). In Mexico about 55,000 ha are cultivated with agave (Valenzuela 2003).

To make tequila, the flowering stalk is cut off, thus preventing flowering and thwarting pollination. Agaves can also reproduce asexually, through vegetative bulbils that grow at the base of the main flower stalks after the plants have flowered, and only in the absence of pollinators. The presence of bulbils therefore indicates pollinator scarcity. Human-induced vegetative reproduction, poor varietal selection and a government requirement for a single commercial variety have resulted in little genetic variation in the agave used for tequila (Gil Vega et al. 2001) and fibre (Colunga et al. 1999). The current varieties have suffered from infections from the fungus *Fusarium* and a root rot bacteria, *Erwinia carotovora*, which together have killed over 30% of the plants. The resultant shortage has increased the price of tequila. The limited genetic diversity of the agaves may have played a role in their susceptibility to infection. Sexual reproduction, via pollinators, is needed to increase the genetic diversity of commercially used agave plants. This may prove to be very important for the tequila industry, and points to the need for increased awareness and increased collaboration to address the maintenance of the genetic diversity of an important economic commodity.

Several international networks for coordinating regional pollinator biodiversity conservation awareness and activities have been formed in response to the establishment of the IPI. These include the North American Pollinator Protection Campaign (NAPPC), the African Pollinator Initiative (API) and the European Pollinator Initiative (EPI). The following actions are suggested to help promote global awareness of pollinators and pollination and build capacity in pollinator conservation and restoration efforts:

1. Disseminate high-quality and easy-to-understand information about pollinators and their conservation to a wide variety of audiences and users through a variety of media such as books, magazines, newspapers, pamphlets, electronic media, television and radio. (Children's books about pollinating animals can help inspire the next generation and influence future policies.)
2. Establish educational outreach and training programmes, including programmes for indigenous communities. This is being done for stingless bees in Central and South America (Imperatriz-Fonseca 2004).
3. Define criteria and use indicators to evaluate the status of, and threats to, agricultural production from potential, or actual, pollinator losses.
4. Create and disseminate manuals for farmers, translated into their native languages, on pollinator conservation and restoration practices.
5. Approach International Standards Organisations for certification of 'pollination friendly' products, for example 'bee smart' labels. Bees (honey bees and bumblebees) have already been used to good advantage on produce packaging in several countries.
6. Ensure that pesticide labels address important pollinator safety issues to be observed during application and post-application.
7. Develop business incentives (and remove disincentives) for pollinator conservation, as has been done in the EU Agri-Environmental Schemes.
8. Encourage national or international entertainment and scientific celebrities to lend their voices to pollinator conservation.

23.5.2 The Forgotten Pollinators Campaign and Book

In 1994S. Buchmann and G. Nabhan founded and directed the Forgotten Pollinators Campaign, which ran until 1999, from the Arizona-Sonora Desert Museum (ASDM) in Tucson, US. An integral part of this highly effective tri-national campaign (US, Canada and Mexico) was on-site educational exhibits about Sonoran Desert pollinators (bees, birds, bats, butterflies, flies, moths and wasps). Individual pollinator gardens were created, and they continue to inspire and educate people on pollination. The Campaign hosted symposia and workshops, published newsletters and academic books, and set up a website. The Forgotten Pollinators Campaign helped stimulate the Migratory Pollinators Campaign, which examined pollinator issues in the US/ Mexico border area, as well as the North American Pollinator Protection Campaign (NAPPC) and the book *The Forgotten Pollinators* (Buchmann and Nabhan 1996).

23.5.3 Education and Training

Widespread awareness about pollinator declines is relatively recent. Pollinator conservation has become a dynamic and engaging new area for research and development. There are, however, very few institutions in developing and developed countries with explicit mandates, and expertise, in research and extension in this area of biological endeavour. Most scientific and government institutions work solely with honey bees, promoting honey bee husbandry as a cottage industry to increase family income through the sale of honey, beeswax and other honey bee products. While research on conserving pollinators and their food plants exists, it is generally limited to a few interested individual scientists and is not institutionally mandated or adequately funded. Research and funding for long-term ecological studies and pollinator identification are especially under-appreciated and relatively poorly funded. Promoting pollinator conservation and sustainable use for fruit and vegetable seed crops production, and for overall biodiversity maintenance, requires special efforts to strengthen research, training and extension systems.

Insufficient knowledge among farmers and pest control operators about the importance of pollinators and pollination processes hinders the conservation and sustainable use of natural pollinators. Addressing this constraint requires building capacity through informational networks among farmers, extension workers, development agencies and researchers. Beekeepers need to manage honey bees for crop pollination as well as honey production. The types of training needed include

1. Introductory courses in pollination and pollinators for agriculture in primary and secondary school programmes, using an ecosystem approach.
2. Introductory courses in pollinator identification, biology and conservation, using an ecosystem approach, in agricultural colleges.
3. Hands-on training for farmers and extension workers in the conservation and sustainable use of pollinators in agricultural landscapes.

4. Technical skills in determining the economic value of pollinators and the detrimental effects of pesticide use on pollinators. The outcome should focus on improving the economic and social benefits through increasing yield and improving produce quality and management practices.
5. Teaching the causes and effects of insufficient pollinator biodiversity on seed and fruit production, and the importance of maintaining refuges for beneficial organisms, which also help maintain water tables and reduce soil erosion. Many threatened animals depend on fruit or seeds as their main energy source, including fruit-eating seed-dispersing bats and birds.

In addition, institutional infrastructure must be created for regional and national identification centres (along with new tools for identification), and for training parataxonomists. The global taxonomic impediment is exacerbated by an aging guild of taxonomists, few new ones entering the field and a backlog of undetermined pollinator vouchers in museums.

23.5.4 Training in Pollinator Identification

Scientific cooperation among the various pollinator initiatives, campaigns and organisations can help improve the transfer of scientific knowledge and training in taxonomy, management techniques and standard sampling methodologies and protocols for rapid assessment. Strengthening scientific institutions, through scientific publications, seminars, conferences, courses, workshops, catalogues, evaluation guidelines, mechanisms for stakeholder feedback, and information exchange through personal, institutional and electronic networks, is also valuable for building capacity.

One way to build taxonomic capacity may be through training parataxonomists, whose work includes

1. Collecting specimens, especially for monitoring and faunistic studies.
2. Preparing specimens: curation, mounting, labelling, identification and databasing.
3. Sorting into taxonomic groups (subfamily, tribe, and genus).
4. Photographing, such as creating electronic types from primary types.
5. Maintaining collections (e.g. fumigation against museum pests).

It has been suggested that taxonomists and taxonomic service-providing institutions should provide training for parataxonomists in accordance with a generally agreed curriculum, and certification on a national or regional basis, either as individual training or in training courses. Parataxonomists should be eligible for academic upgrading in their profession after a satisfactory period of activity (Dias et al. 1999).

23.5.5 Parataxonomists in Costa Rica

The training of parataxonomists in developing countries was pioneered by INBIO (Instituto Nacional de Biodiversidad) in Costa Rica. This was an innovative government sponsored programme. It was one of the first organisations to train and use technicians as parataxonomists working alongside mentor taxonomists. As a result, in its 15-year history, INBIO staff have documented and discovered over 2,000 species of plants and animals native to Costa Rica (www.inbio.ac.cr/es/default2.html).99

Traditionally taxonomists have provided free-of-charge identification services for invertebrates because of the large number of species and because they are difficult to separate. This is not ideal. Pollination biologists, ecologists, extension officers and farmers need to be able to identify pollinators. It is important for pollination ecologists and conservation biologists to include funding for identification services in their grant proposals. Through the intelligent deployment of parataxonomists, interactive keys, automated pattern recognition and genetic barcodes, easy identification services can be accomplished, leaving time for taxonomists to describe species, undertake generic revisions and analyse phylogeny (the *Evolution*ary relatedness between species).

Many taxonomic resources needed by entomologists working in developing countries are located in museums in the developed world and inaccessible to scientists in their countries of origin. This information needs to be shared (images of types and specimen databases will contribute). The Global Biodiversity Information Facility (GBIF) (www.gbif.org) is concerned with developing specimen databases for all collections and has made calls for proposals for seed money. Pollinators have been listed as a priority.

23.5.6 Overcoming the Taxonomic Impediment in Mexico

The Programa Cooperativo sobre la Apifauna Mexicana (PCAM) is a partnership between bee taxonomists from several institutes in the US and Mexico. This programme has produced one major, highly illustrated work, which facilitates the identification of all bees from North and Central America to genera (Michener et al. 1994). Databases have been created giving distributional and taxonomic information for the species. Thousands of bee specimens collected during five PCAM expeditions in northern Mexico have been deposited in the SNOW museum at the University of Kansas, Lawrence, US. An ongoing specimen-level databasing effort (at the University of Kansas) has captured this PCAM bee information, but the database is not yet online or accessible to the public. The original PCAM bee data (coordinated by D. Yanega at the University of California, Riverside) can be found online (www.inhs.uiuc.edu/cbd/collections/insect/mexicanbees.html).

23.5.7 Sharing Information in Africa

The African Pollinator Initiative (API) has as one of its objectives the sharing of information and expertise between bee taxonomists, pollination researchers, farmers, conservationists and policy makers. In Kenya, the pollinators for several crops and their alternate forage resources were documented. Eggplant blossoms, for example, are buzz-pollinated (i.e. anthers must be sonicated to release pollen) by large carpenter bees (*Xylocopa caffra*) and nomiine bees (*Nomia* sp.). A colourful educational poster on this has been created, printed and distributed to local farmers.

23.5.8 Using Communication Technology in Brazil

Communication technology can benefit capacity building through enabling the pollinator biodiversity conservation initiatives, including the International Pollinator Initiative (IPI) and several regional initiatives, to achieve their goals, and to permit cooperation between groups. For this purpose Brazil has developed Webbee (www.webbee.org.br/bpi/bees_rural_development.htm), which provides information, case studies and recommendations.

23.6 Conclusions

There is a paucity of attention to pollination services, at all levels of formal and informal education. Nonetheless, a number of initiatives have developed innovative approaches and curriculum material, which can be used as a basis for scaling-up the building of capacity to manage pollination services. There is a need to implement capacity building initiatives within countries, including through extension services, local government, educational and civil-society organizations, including farmer/producer and consumer organizations, and mechanisms emphasizing farmer-farmer exchange. There are opportunities for cooperation with the food processing industry in terms of supplying pesticide-free or low-residue products from agricultural systems that maintain pollinator diversity. Pilot projects for this element might be generated under the Initiative. Funding is likely to be on a project or programme basis. Catalytic support may need to be provided through national, regional and global programmes, organizations, facilities and funding mechanisms, in particular to support capacity-building, exchange and feedback of policy and market information, and of lessons learned from this and programme element between local organizations and policy makers, nationally, regionally and globally. The taxonomic elements would also be promoted through the Global Taxonomy Initiative.

References

Buchmann SL, Nabhan GP (1996) The forgotten pollinators. Island Press/Shearwater Books, San Francisco

Colunga P, Coello-Coello J, Eguiarte LE, Piñero D (1999) Isozymatic variation and phylogenetic relationship between heneqúen (*Agave fourcroydes*) and its wild ancestor *A. angustifolia* (Agavaceae). Am J Bot 86:115–123

Dias BSF, Raw A and Imperatriz-Fonseca VL (1999) International Pollinators Initiative: The São Paulo Declaration on Pollinators – Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees. Brazilian Ministry of the Environment – MMA, University of São Paulo USP and Brazilian Corporation for Agricultural Research – EMBRAPA (www.mma.gov.br/port/sbf/chm/doc/pollinas.pdf).

Gil Vega K, Gonzalez Chavira M, Martinez de la Vega O, Simpson J, Vandermark G (2001) Analysis of genetic diversity in *Agave tequilana* var. *azul* using RAPD markers. Euphytica 119:335–341

Imperatriz-Fonseca VL (2004) How to get stingless bees nests in *Nature*? RAPS Case study contribution, available at: http://www.fao.org/ag/AGP/AGPS/C-CAB/Caselist.htm

Michener CD, McGinley RJ, Danforth BN (1994) The bee genera of north and central America. Smithsonian Institution Press, Washington, DC

Ramírez M P and López A (1985) Investigación sobre la utilización de fibra de agave en el estado de Oaxaca. Plan de Desarrollo Agroindustrial del Agave en el Estado de Oaxaca. Instituto Tecnológico de Oaxaca, Oaxaca, Mexico. Unpublished technical report

Valenzuela-Zapata AG (2003) El Agave Tequilero. Cultivo e Industria de México, 3e. Mundi-Prensa México, Río Pánuco, 141 Co., Cuauhtémoc, 06500, México, DF, México

Index

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