

Tropical Fruits and Frugivores

The Search for Strong Interactors

Edited by
J. Lawrence Dew and
Jean Philippe Boubli



Springer

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Edited by

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Preface

This book documents interactions between plants and animals that biologists consider particularly important for conserving the habitats that they study. Here we undertake a cross-continental comparison of the relationships between tropical plants and the frugivorous animal communities that depend on them. The chapters in this book originate from a symposium that brought together more than 30 biologists from around the world to share and compare their research on these interactions. The symposium was funded by the National Science Foundation, the Wildlife Conservation Society, and the Institute for the Conservation of Tropical Environments. It was held in Panama City, Panama, at a conference entitled “Tropical Forests, Past, Present, and Future” hosted by the Association for Tropical Biology and the Smithsonian Tropical Research Institute. The editors would like to thank everyone who helped bring the project to fruition.

CHAPTER 1.

INTRODUCTION: FRUGIVORY, PHENOLOGY, AND RAINFOREST CONSERVATION

J. LAWRENCE DEW

Species diversity on Earth is highest in the tropics, and if we are to protect as much of this diversity as possible from human-caused extinction then conserving the tropical rainforests is a top priority (Myers, 1984). In tropical rainforests much of the primary production is passed on to the second trophic level in the form of fruit pulp. Up to 90% of tropical forest tree species produce fleshy, nutritious fruits that are crucial food resources for large portions of the animal community (Frankie et al. 1974, Gentry, 1983). Some researchers have found that the resources produced by a few key taxa, such as the fruits of fig trees, sustain the bulk of tropical vertebrate communities during seasonal periods of low food availability (Peres, 2000; Terborgh, 1983, 1986). Likewise, particular frugivorous animals are known to serve as vital “mobile links” upon which many of these plants depend to disperse their seeds (Gilbert, 1980; Howe, 1983). The potential conservation applications of this phenomenon are great (Chapman, 1995; Simberloff, 1998).

Temporal patterns of the abundance and distribution of fruits and other plant resources help determine the biomass and diversity of consumers that can be sustained by the plant community. The chapters that follow examine these relationships in each major region of the tropics. The aims of this book are, first, to compare the varying phenological rhythms of different tropical forests; second, to identify key plant taxa that sustain tropical forest frugivores in different regions; third, to identify animals which are of particular significance to these plant communities; and finally, to examine the relevance of these interactions to conservation.

The first of these explorations takes place in Panama, where Katharine Milton and her coauthors examine vertebrate responses to seasonal variation in fruit availability. They demonstrate the complexity of accurately documenting these

patterns even in the best-studied tropical forests. In the following chapter Pablo Stevenson scrutinizes the issue of keystone resources in a Colombian forest. He finds that the search for such resources in Amazonia is not as clear-cut as it once might have seemed.

Tropical forests differ greatly in plant composition, with different sets of plants producing fleshy animal-dispersed fruits. One step towards understanding patterns of consumer abundance and diversity is to understand what governs the floristic composition of tropical forests (Phillips et al., 1994). Chapter 4 by Jean Philippe Boubli examines these relationships in a comparison of two forests within Amazonia that have different animal and plant assemblages.

The authors in this book clearly demonstrate the value of collecting long-term datasets on fruiting phenology. An excellent example of this is found in Chapter 5, by Colin Chapman and his colleagues. Their analysis of phenology at a Ugandan site shows that the tropical rainforests are not immune to the effects of global environmental change. In Chapter 6 An Bollen and her coauthors compare two forests in Madagascar, examining the potential evolutionary importance of frugivores on fruit traits. Patricia Wright and colleagues in Chapter 7 then turn the tables and illustrate the evolutionary effects of strong community-wide fruiting seasonality on a unique frugivore coterie.

The final section of the book explores the patterns of Australasia. In Chapter 8 T. Ganesh and Priya Davidar examine the phenological patterns of a wet forest in southern India. Tim O'Brien and Margaret Kinnaird then compare two forests in Indonesia that show remarkable ecological differences despite close proximity. In chapters 10 and 11 Andrew Mack and Debra Wright search for keystone seed dispersers in New Guinea. David Westcott completes the tour in Chapter 12 by documenting interactions in a community of plants and frugivores in tropical Australia.

Our panel of experts revealed crucial roles played by some seed-dispersing frugivores and their food plants. Several new examples of possible keystone species were documented. Other studies found hyperdiverse systems like rainforests to be difficult places to find tightly coevolved fruit-frugivore relationships. One clear pattern that emerges from these papers is that tropical forests, whether they have one or two annual wet and dry seasons, or if they are ever-wet with aseasonal rainfall, all show regular, annual, community-wide fluctuations in fruit availability. Yet, the ecological importance of superannual variation in resource abundance was found by several authors to have been overlooked by scientists so far. Also underemphasized have been key plants that fruit during annual community-wide seasons of fruit abundance, providing important caloric resources that allow some animals to accumulate fat reserves. Several authors articulate clear and novel conservation implications of these ecological interactions, particularly in light of current rates of habitat fragmentation and global change.

Power et al. (1996) wrote, "Identifying keystone species is difficult--but essential to understanding how loss of species will affect ecosystems." By bringing together researchers to compare their study sites and address these issues, we have attempted to help focus the search. The scientists in this volume identify numerous tropical

taxa that are important to ecosystem structure and function in biomass, productivity, and/or functional role (Odum, 1971, Bond, 2001). These researchers reexamine the terms “strong interactors,” “keystone resources,” and “keystone mutualists,” describing promising directions for future research, and emphasizing the utility of these species interactions to conservation. As scientists and conservationists, we hope that this work will serve as an impetus for action in the tropics.

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CHAPTER 2.

DO FRUGIVORE POPULATION FLUCTUATIONS REFLECT FRUIT PRODUCTION? EVIDENCE FROM PANAMA

KATHARINE MILTON, JACALYN GIACALONE, S. JOSEPH WRIGHT,
GRETCHEN STOCKMAYER

Abstract

To conserve tropical mammals, it is important to understand factors affecting the range of population fluctuations that normally occur over both the short and long term. Annual shifts in the population size of many species may be tied, at least in part, to phenological production patterns of plants, which in turn are often affected by climatic events. To examine the influence of annual fruit crop size on population dynamics of frugivorous mammals, we compared estimates of fruit production and the relative abundance of four frugivorous mammal species (agoutis, squirrels, capuchin monkeys, howler monkeys) for 15 years on Barro Colorado Island, Republic of Panama. Species differed in the magnitude of population fluctuation. Howler monkey population estimates showed little annual fluctuation and no significant relationship to fruit production. In contrast, population estimates for agoutis, squirrels and capuchin monkeys showed interannual fluctuations, at times dramatic, but these were not always concordant nor did they necessarily appear to relate to fruit production estimates, either within years or with a one- or two-year lag. Fruit production data suggest that, on average, in any given year only 20 to 30% of the mid-to-late rainy season species producing fruits important to frugivores will have an unusually good year; other species will have an average to sub-standard year. The next year, 20 to 30% of the other important fruit species in this temporal cohort will have an unusually good year—though one cannot predict in advance which species they will be. This oscillating production pattern makes it difficult to predict, except in extreme years, how the frugivore community or individual species will be affected by fruit availability. To draw conclusions on this topic, more detailed data are required on annual fruit production patterns of a representative sample of individuals of important fruit species as well as data on reproductive and other relevant traits of each mammal species. The possibility remains that many mammal populations may be affected more immediately by top-down factors such as predators, parasites or disease rather than by bottom-up factors such as fruit availability. As population parameters for each mammal species are likely influenced by a continuously varying combination of factors, barring effects of rare environmental events, the particular set of factors affecting the population dynamics of one frugivorous species in any given year may not necessarily impact similarly in that year on other frugivorous species at that same site.

Key words: Fruit production, population dynamics, tropical forests, Panama, mammals, monkeys, agoutis, squirrels, El Niño Southern Oscillation (ENSO)

INTRODUCTION

Tropical forests and their animal populations were once regarded as stable and unchanging (Karr & Freemark, 1983; Wikelski et al., 2000). Extensive research has shown, however, that tropical forests experience a wide range of climatic and other environmental fluctuations both within and between annual cycles, calling into question the hypothesized stability of their vertebrate populations (Foster, 1982a,b; Foster & Terborgh, 1998; Swaine et al., 1987; Whitmore, 1991; Wolda, 1983). It has been suggested that climatic fluctuations, particularly the timing and amount of rainfall received in a given region, may influence phenological production patterns, affecting fruit set (Alvin, 1960; Foster, 1982a,b; Matthews, 1963; Milton, 1982; Wright et al., 1999). In turn, the availability of edible fruits is hypothesized to play a critical role in the population dynamics of many frugivorous mammals inhabiting tropical forests (Foster, 1982a; Glanz et al., 1982; Leigh, 1999; Smythe et al., 1982; Van Schaik et al., 1993; Wright et al., 1999). It seems reasonable to assume that for any given site in years when fruit abundance is low many frugivore populations might decline due to a lack of suitable food. And in years when fruit abundance is high one might predict a corresponding increase in frugivore reproduction, survivorship, and total numbers.

Available evidence, however, suggests that the actual situation is neither as clear nor as linear and predictable as such assumptions imply. For example, it has been proposed that many tropical forest communities are characterized by the presence of *keystone* fruit resources (Gautier-Hion & Michaloud, 1989; Gilbert, 1980; Peres, 1994; Terborgh, 1983)—that is, resources available to a large component of the frugivore community during periods of forest-wide fruit scarcity which serve to buffer them until new crops of more preferred fruit species appear. In this scenario, keystone resources tide resident frugivores over during periods of forest-wide fruit scarcity, averting population declines. However, other data indicate that many frugivore species have specific “fallback” foods that can be relied on until better fruiting conditions prevail (Bodmer, 1990; Conklin-Brittain et al., 1998; Fragoso, 1998; Furuichi et al., 2001; Glanz et al., 1982; Milton, 1980; Smythe et al., 1982; Terborgh, 1987). How does the concept of community-wide keystone resources relate to observations of species-specific fallback foods?

Then there are long-standing demographic concepts such as density dependent mechanisms which imply that many animal populations have behavioral or other mechanisms (e.g., predators, parasites) that help maintain population size below levels at which food scarcity generally might pose a problem (Getz, 1996; Herre, 1993; Milton, 1982; but see Den Boer & Reddingius, 1996). Observations suggest that some frugivore populations oscillate notably in size over relatively short time periods whereas populations of other species appear stable for many generations (Giacalone-Madden et al., 1990; Milton, 1996). How can all of these concepts—keystone resources, fall back foods, density dependent mechanisms and so on—be reconciled with such disparate demographic observations?

Understanding factors which influence the population dynamics of tropical frugivores is clearly a problem of no small magnitude. It is also a problem of considerable current interest to ecologists and conservation biologists. Tropical moist forests are responsible for almost 32% of terrestrial net primary productivity and are a major resource of global importance (Leith & Whittaker, 1975). Seed dispersal by resident frugivores is believed to play a critical role in the continued maintenance of the high plant species diversity characteristic of tropical forests (Corlett, 2002; Dirzo & Miranda, 1991; Jordano & Godoy, 2002; Wright & Duber, 2001). Because of intensive habitat destruction and hunting pressures in many tropical regions, the opportunity to compile long-term data sets on plant-animal interactions over large expanses of undisturbed tropical forest may be running out. Yet a better understanding of such relationships is essential if we wish to make predictive statements about the causal factors which relate to natural shifts in frugivore densities and abundances at particular sites and the effects of such shifts on forest structure and composition (Andresen, 1994; Asquith et al., 1997, 1999; Dirzo & Miranda, 1991; 1999; Wright & Duber, 2001). The ability to accurately estimate the range of population fluctuations that normally occur over the short and long term also seems necessary for informed conservation decisions, which need to take into account the influence of reserve size and resource availability on the population dynamics of resident frugivores.

METHODS

In this paper, we compare 15 years of data (1987- 2001) on ripe fruit production with data on population censuses for four frugivorous mammal species living on Barro Colorado Island (BCI), Panama. Detailed descriptions of the history, flora and fauna of BCI are available in the literature (Foster & Brokaw, 1982; Leigh et al., 1982).

Study Site

To briefly review, BCI is a 1600 ha nature preserve, established in 1914. The entire island is densely covered in mature forest and old secondary growth (Foster & Brokaw, 1982; Milton, 1980). As BCI is a nature preserve, there is minimal interference in its ecology. Most animal species found on the island are the descendants of populations naturally occurring in the area prior to creation of the Panama Canal. Annual rainfall and fruit production patterns are presented later in the text.

Study Subjects

The four mammal species selected for examination were agoutis (*Dasyprocta punctata*), squirrels (*Sciurus granatensis*), capuchin monkeys (*Cebus capucinus*), and howler monkeys (*Alouatta palliata*). These four species are heavily dependent

on fruits in the diet (>40% of the annual diet from fruit in all cases) but differ in important ways in their life history strategies and uses of particular kinds of fruits.

Agoutis, which on BCI associate in pairs, are strictly terrestrial, relying on fallen fruits, often dropped by one of the other focal species in this study. They have specialized incisors that make it possible to feed on the large, hard seeds from genera such as *Dipteryx* (Fabaceae), *Astrocaryum* (Palmae), *Attalea* (Palmae), and *Socratea* (Palmae). Many such seeds are buried for storage, thus providing backup food supplies to help carry animals through shortages of fresh fruits (Smythe et al., 1982). Agoutis also feed heavily on a great variety of other fruits and flowers. They are relatively rapid breeders, since an adult female in good condition may breed up to three times per year, giving birth to one or two offspring each time. Mortality, hypothesized to relate to food shortages (Smythe et al., 1982), appears to affect immature individuals first, since adults defend territories and food caches.

Red-tailed squirrels, which are solitary, make use of the same hard seeds as agoutis, and may utilize stored supplies for many months after the fruits actually fall. Their diet is composed largely (ca. 99%) of plant material, mainly fruits, seeds, and some flowers (Giacalone-Madden et al., 1990; Glanz et al., 1982). In comparison with agoutis and monkeys, BCI squirrels have an extended season for use of these critical resources because they are arboreal, and can feed on seeds in trees before the pulp of the fruit is fully ripened. Squirrels often store seeds in tree cavities, out of reach of agoutis, and seeds comprise 50-90% or more of the diet, depending on time of year.

Squirrels on BCI may breed twice a year and produce litters with a mean size of just under two. Adult females, which may live for 8-9 years, defend territories (Giacalone, unpub.). Some data suggest a link between annual patterns of fruit abundance and the population dynamics of BCI squirrels. In times of poor fruit supply, for example, squirrels have been observed to drastically decrease breeding activity (Giacalone-Madden et al., 1990; Glanz et al., 1982). Squirrels rarely breed in the period August to December, a time of relatively low fruit availability on BCI (Foster, 1982; Milton, 1980, 1990, 1996; Wright et al., 1999) and usually begin breeding when *Dipteryx panamensis* fruits (considered an important dietary resource) begin to ripen in late December (Glanz et al., 1982).

White-faced monkeys (or capuchins) on BCI live in relatively closed social units averaging 8 individuals and composed of adults of both sexes and their immature offspring (Oppenheimer, 1982; Rowell & Mitchell, 1991). Capuchins rely heavily on small "bird fruits" in the diet as well as the soft parts of larger fruits. However, they cannot make use of seeds from some of the very hard fruits used by agoutis and squirrels, nor do they store seeds for later use. Capuchins are also seasonally dependent on invertebrates (10-40% of the diet, depending on time of year) and smaller vertebrates in the diet and these are consumed opportunistically on a daily basis along with ripe fruits (Oppenheimer, 1982; Rowell & Mitchell 1991). Capuchins usually produce one offspring every other year, but females are not reproductively active until their fourth or fifth year (Oppenheimer, 1982).

Howler monkeys on BCI live in relatively closed social units averaging 19 individuals and composed of adults of both sexes and their immature offspring

Howler monkeys have no access to hard-shelled seeds, but feed heavily on softer ripe fruits whenever possible as well as portions of many immature fruits. Fruit-eating makes up $42.1 \pm 26.3\%$ of annual feeding time (Milton, 1980, mean \pm 1 SD, $n = 9$ monthly values, covering all seasons). Howler monkeys, also rely heavily on leaves in the diet ($48.2 \pm 26.3\%$). Unlike the other three species in our sample, howler monkeys can live for weeks on diets composed largely or entirely of leaves (Milton, 1980). Female howlers typically give birth to a single offspring every 17-20 months and births can take place at any time of year (Milton, 1982).

The following analysis examines annual census data on these four mammal species to determine how successfully population declines or increases might be predicted based on annual fruit production data. Though we have an unusual wealth of comparative material on fruit production patterns, life histories, feeding records, and long-term censuses, our results emphasize nothing so much as the fact that much remains to be discovered about plant-animal interactions in tropical forests and how best to study them.

Data Sets: Rainfall and Fruitfall

Rainfall Patterns

As rainfall is believed to affect patterns of fruit production in tropical forests, we first examine rainfall data. BCI is characterized by an annual average of 2633 ± 462 mm of rainfall per year (mean + 1 SD derived from 73 years of rainfall data, 1929-2001, provided by the Environmental Science Program, BCI). During the 15-year study period, rainfall showed considerable interannual variation (Fig. 1) and there were two El Niño Southern Oscillation (ENSO) years, 1992 and 1997.

The rainy season typically begins each year in mid-April and continues through November into December (Fig. 2). There is an approximately three-month-long dry season from January through March, when mean monthly rainfall averages 45 mm.

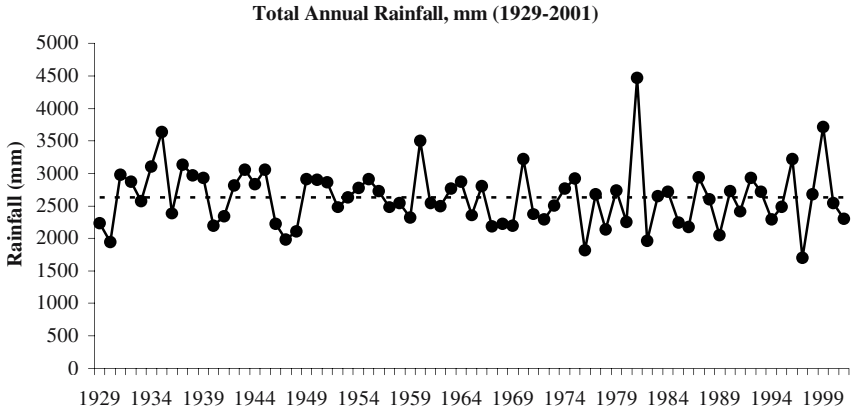


Figure 1. Total annual rainfall data for Barro Colorado Island (BCI) over a 73-yr period, 1929-2001. Annual average rainfall = 2633 ± 462 mm of rainfall. Dashed line at 2,633mm is the mean value for period 1929-2001.

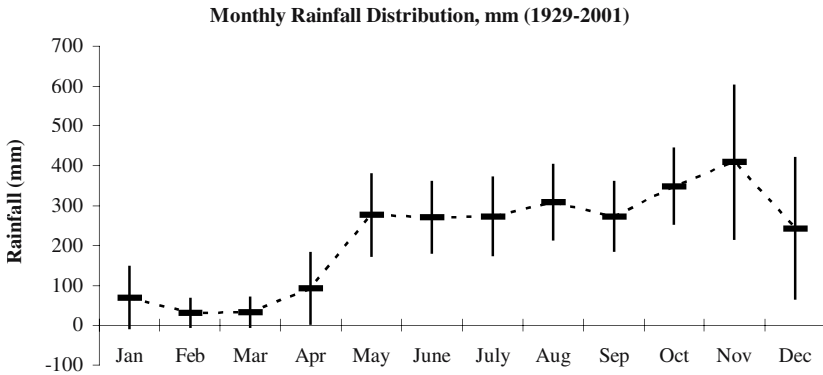


Figure 2. Average monthly rainfall in mm for BCI over a 73-yr period, 1929-2001. The solid lines and error bars represent mean monthly rainfall \pm one standard deviation.

Annual Fruit Production Patterns

Dry mass fruit production is considered perhaps the single best index of fruit availability for frugivores and granivores (Wright et al., 1999). This paper includes analysis of data collected from two sets of fruit traps. One data set is based on fruit dry mass, while the other relies on counts of seeds expressed as "seed equivalents."

Figure 3 shows summed monthly fruit dry mass production on BCI as determined weekly for 59 litter traps over 15-yr (1987-2001). Traps were randomly located in an area of older forest in the southwest section of the island known as Poachers' Peninsula (see Wright et al., 1999 for details of data collection). Monthly fruit production is more or less the inverse of monthly rainfall—in months when rainfall is low, fruitfall into traps is high, in months when rainfall is high, fruitfall into traps is low (Fig. 3). No bimodal annual pattern is detectable in fruit production or even oscillating peaks and valleys. Rather, dry mass fruit production typically rises to its annual peak around February of each year and stays elevated into April when, with one slight upward permutation in July, it gradually declines over the rest of the year (Fig. 3). Fruitfall typically reaches its annual low point during the two wettest months of the year, October and November.

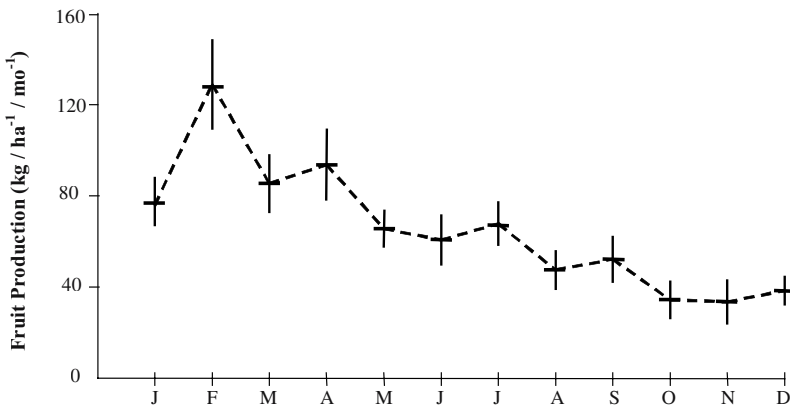


Figure 3. Monthly dry mass fruit production summed over all species for BCI over a 15-yr period. The solid lines and error bars represent mean productivity ± 1 SD (calculated from 1 Jan. 1987-31 Dec. 2001). Data derive from 59 fruit traps; see text for details of data collection.

The second data set uses data on "seed equivalents" derived from counts of fruits, seeds and other fruit parts falling into 200 litter traps placed in old growth

forest on the central plateau of the island (details of fruit trap placement and fruit collection are found in Wright et al., 1999). "Seed equivalents" for each species are expressed as the sum of seeds plus mature fruits of a species multiplied by the average seed-to-fruit ratio for each species. Seed equivalents could be divided by the seed-to-fruit ratio to estimate "fruit equivalents" or the number of fruits represented. We use seed equivalents as a relative index of fruit production throughout this paper because traps capture many more seeds than fruits.

The number of traps containing seeds or fruits of a species each week provides a measure of how widespread fruit production by that species was. The average number of fruit species per fruit trap per week provides a measure of how many species were maturing fruit and is useful for monthly and seasonal comparisons. Intact fruits falling into traps were also divided into two categories, mature or immature fruits, providing an additional data set on whole fruits in traps by species and their stage of maturation.

Subsample of Fruits Used by Focal Mammal Species

Seeds in traps come from all fruit types produced in the BCI forest and many of these species are not eaten by mammals. From all species in traps, we selected 60 species known to produce fruits of importance in the diet of one or more of our focal mammal species and examined annual fruit production patterns for these 60 species. For inclusion in analyses a species had to have at least one weekly sample in the 15-yr period with more than 50 seeds and more than five traps containing fruit of that species. Only 39 of the 60 species met these requirements. Unless otherwise noted, all production estimates discussed below derive from these 39 edible fruit species.¹

RESULTS

Patterns and Correlations

Fruit Production and Rainfall

When relative annual mature fruit production is compared with relative annual rainfall over the 15-yr study period (Fig. 4), no clear pattern emerges. No correlation was found between rainfall and mature fruit production either within years (Pearson correlation coefficient, $r=0.041$) or when annual rainfall was lagged back one ($r=0.461$) or two years ($r=-0.308$) relative to the year of fruit production.

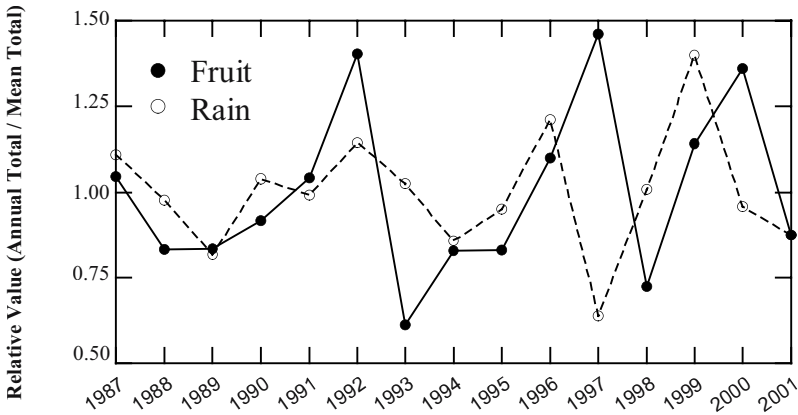


Figure 4. Relative annual rainfall expressed against relative annual fruit production over a 15-yr period on BCI. The dashed line represents rainfall while the solid line represents dry mass fruit production. Data derive from 200 fruit traps, see text for details of data collection.

Fruit Production for 39 Edible Species

Summed annual production data for the 39 edible species (Fig. 5a) as well as number of traps with fruits (Fig. 5b) showed interannual fluctuation. Annual fluctuations are best appreciated by viewing data on individual species. Fig. 6a and b shows annual fruit production patterns for *Quararibea asterolepis* (Bombacaceae) and *Coccoloba parimensis* (Polygonaceae), respectively, over the 15 yrs of the study. Such annual fluctuation was highly characteristic of most other species in this sample as well.

The pattern of monthly fruit production for the 39 edible species (Fig. 7a) is very similar to that shown in Fig. 3 for monthly fruit dry mass production for all species but the single broad peak for the 39 species, April and May, comes slightly later in the year than that for fruit production as a whole (Feb-April). The number of traps with fruit of one or more of the 39 species (Fig. 7b), in contrast, shows a peak in Aug-Oct. This August-October peak is largely attributable to *Trichilia tuberculata* (Meliaceae) and *Quararibea asterolepis*, which are the first and fifth most common canopy tree species in old growth forest on BCI. These very abundant species ripen fruit between August and October and seeds from these species reach most traps. Other fruit species in the diets of our four frugivore species are notably less abundant or produce far fewer seeds.

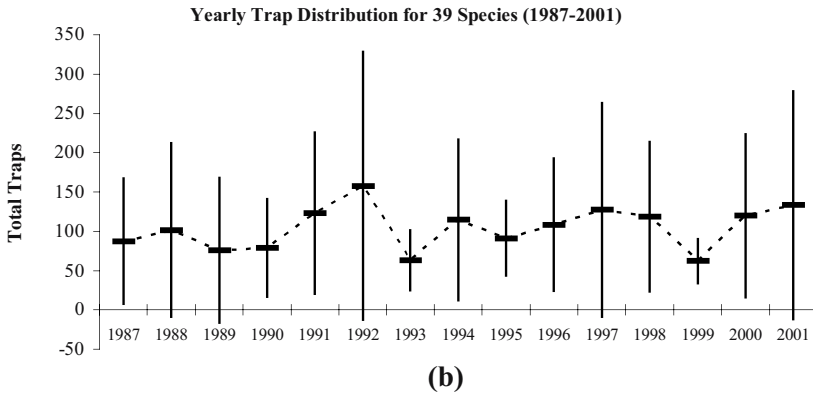
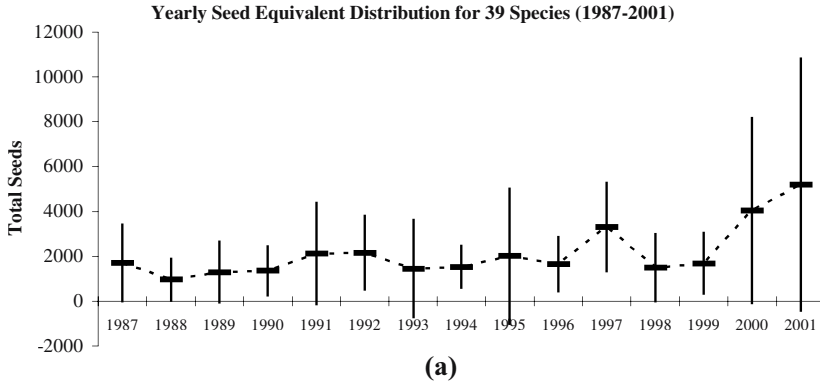
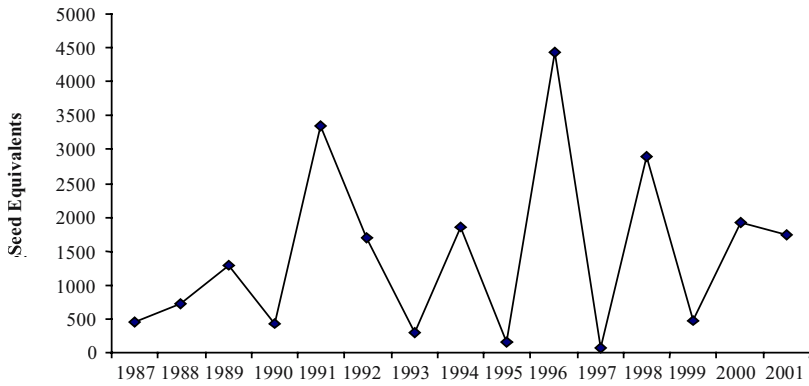
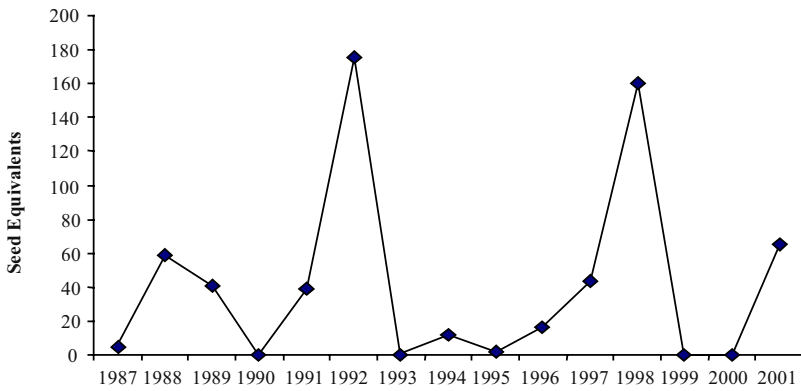


Figure 5. a) Summed annual fruit production (seed equivalent) data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. b) Summed annual fruit trap data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. For both figures, the solid lines and error bars represent mean values \pm one standard deviation.



(a)



(b)

Figure 6. Annual fruit production data for a) *Quararibea asterolepis* and b) *Coccoloba paraensis* over a 15-yr period.

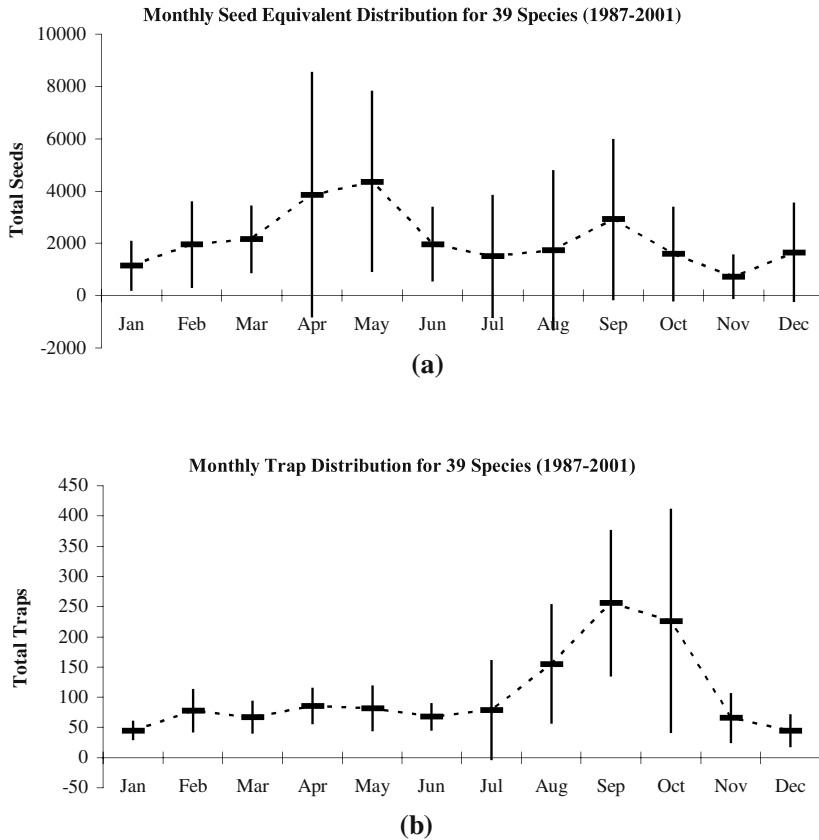


Figure 7. a) Summed monthly fruit production (seed equivalent) data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. b) Summed monthly fruit trap data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation.

Species-specific Production Patterns

Each year, the seasonal timing of fruit production by a given species typically showed high predictability while the amount of fruit produced did not. Three examples help illustrate this point. *Spondias mombin* (Anacardiaceae) is a species whose fruits are eaten by a wide range of frugivores on BCI. The population-wide

timing of annual fruit production by *S. mombin* is highly predictable (Fig. 8a). Ripe fruits invariably become available to frugivores in September—occasionally appearing as early as July-August and extend through September into October. Fruit was produced by *S. mombin* in all 15 years of the sample (Fig. 8b).

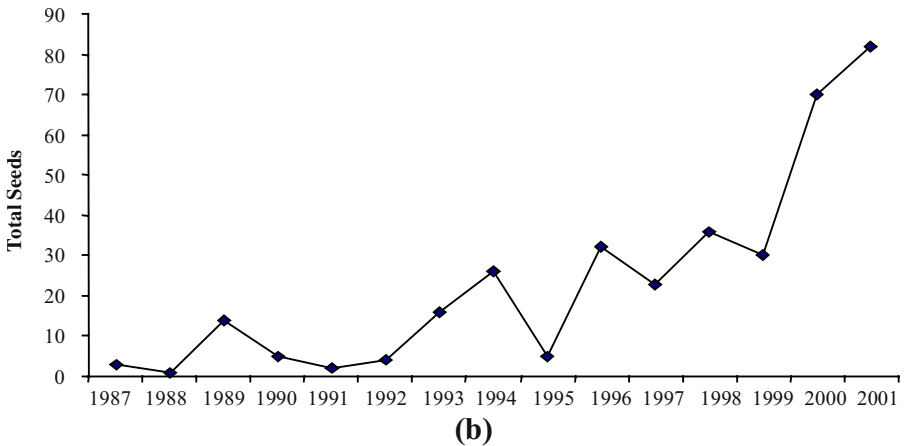
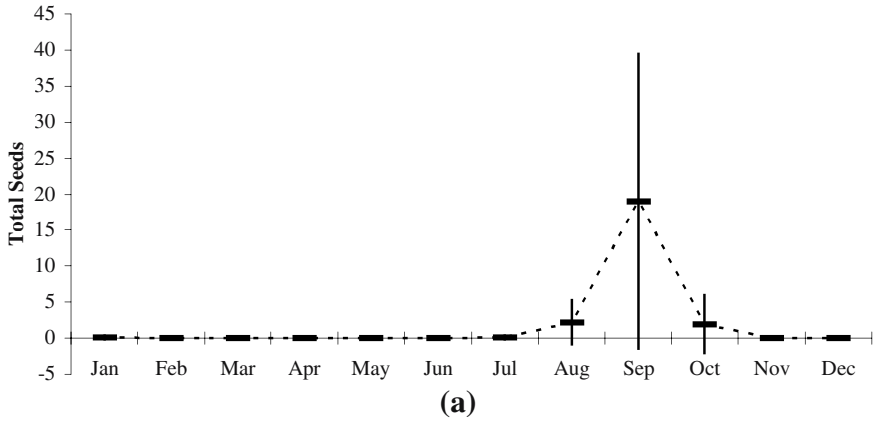


Figure 8. a) Pattern of monthly ripe fruit production by *Spondias mombin* on BCI over a 15-yr period. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production by *Spondias mombin* on BCI over a 15-yr period.

This element of predictability vanishes when considering the amount of fruit produced by *S. mombin* in different years (Fig. 8b, range 1-82 seed equivalents, depending on year). Likewise, in some years, more traps contained *S. mombin* fruits

(range 1 to 14 traps) than in other years. No temporal autocorrelation was evident for annual fruit crop size --a year of low fruit production by *S. mombin* might be followed by one to several years of higher, lower or similar fruit production (Fig. 8b).

Dipteryx panamensis, a critical early dry season resource for many BCI frugivores, presents a very similar picture (Fig. 9a, b). The annual timing of ripe fruit production is highly predictable, beginning in Nov-Dec, peaking in Jan-Feb and ending in March.

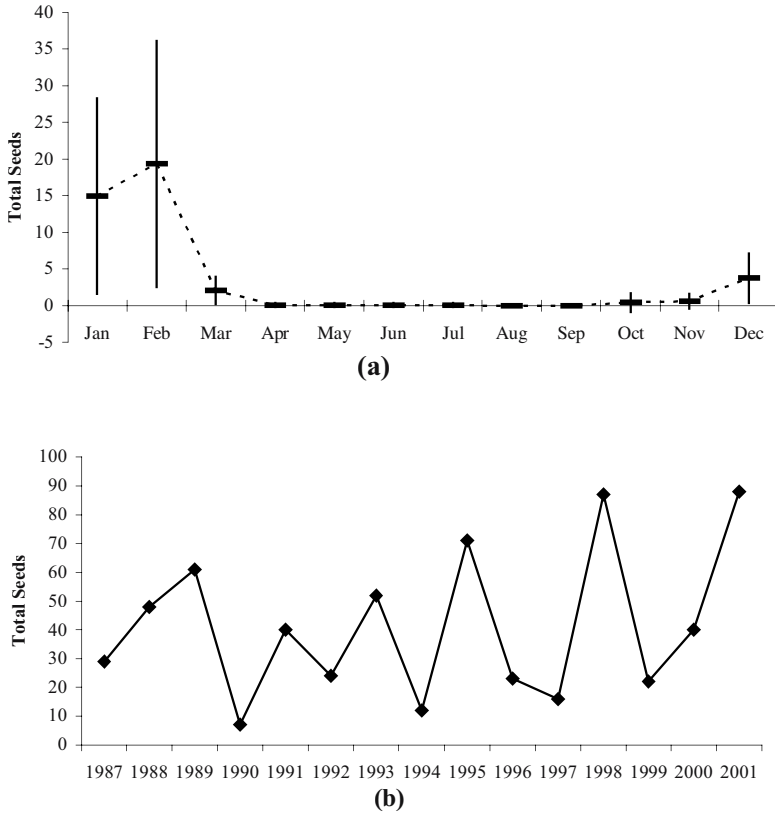


Figure 9. a) Pattern of monthly ripe fruit production for *Dipteryx panamensis* on BCI over a 15-yr period. The solid line and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production for *Dipteryx panamensis* over a 15-yr period.

Fruit was produced by *D. panamensis* in all 15 sample years. But the amount of fruit produced per year was highly variable (range 7 to 88 seed equivalents depending on year) as were the number of traps with fruit (range 6 to 51 traps). A

see-saw effect was noted between most pairs of years but the time series autocorrelation with a one-year lag was not quite significant ($r=0.51$, $p=0.053$) (Fig. 9b).

A final species, *Brosimum alicastrum* (Moraceae), also an important fruit resource, produces ripe fruit most heavily in May – July each year (Fig. 10 a, b). Fruit was produced by *B. alicastrum* in all 15 years of the sample. However, the amount of fruit produced varied notably between years (76-1406 seed equivalents, depending on year) as did the number of traps with fruit (range 19-75 traps). In some years, ripe fruit from *B. alicastrum* was available to frugivores over a period of two or more months, whereas in other years, fruit production by this species was noted for only two or three weeks.

Based on these patterns, which seem representative of the majority of species in our sample, we conclude that a BCI frugivore can rely confidently on some fruit from most of these species at predictable times each year, excepting species from genera such as *Ficus* (Moraceae), which generally show intraspecific asynchrony in phenology and can produce fruit in any month of the year (e.g., Milton, 1991). How much fruit a given species will produce and how long this fruit will be available in any given year, however, seem highly unpredictable.

Mammal Census Results

Howler Monkeys

To compile data, KM walked the BCI trail system, usually over a period of 7-10 days per sample month, and counted all members of any howler troop encountered, noting down the sex of each adult animal and assigning immature animals to juvenile or infant classes. All areas of the island were covered in censuses. Further descriptions of this census protocol can be found in Milton 1982 and 1996. In some years howler troops were censused in several different months whereas in other years only a single monthly census was taken. Because of this variability, annual data were smoothed for analysis using a LOWESS smoother.

One might assume that many new howler troops were formed over the 15-yr sample period. However, several island-wide estimates of the total number of howler troops (~ 60 troops) on BCI did not indicate that new troops were being formed to any detectable degree (Milton, 1982, 1996 and unpublished data). Rather, the island appears to be well saturated with howler monkeys, each troop and its descendents occupying the same basic home range generation after generation. For this reason, mean troop size for a given year can be used as an indication of howler population size for that year.

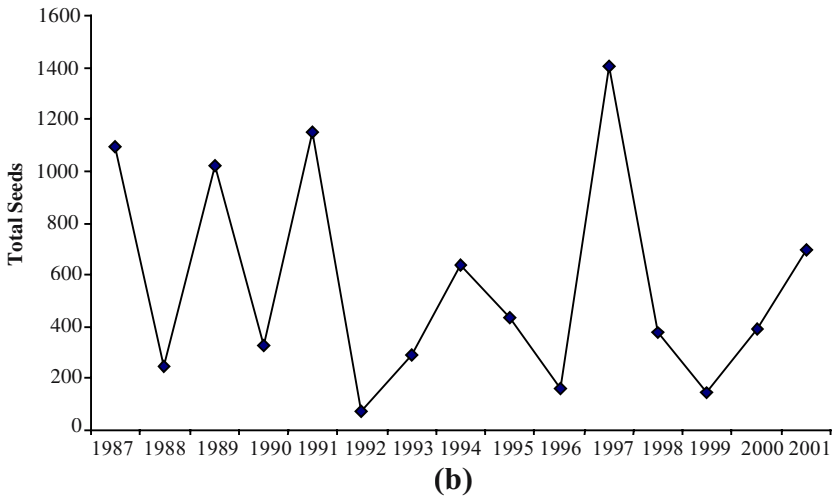
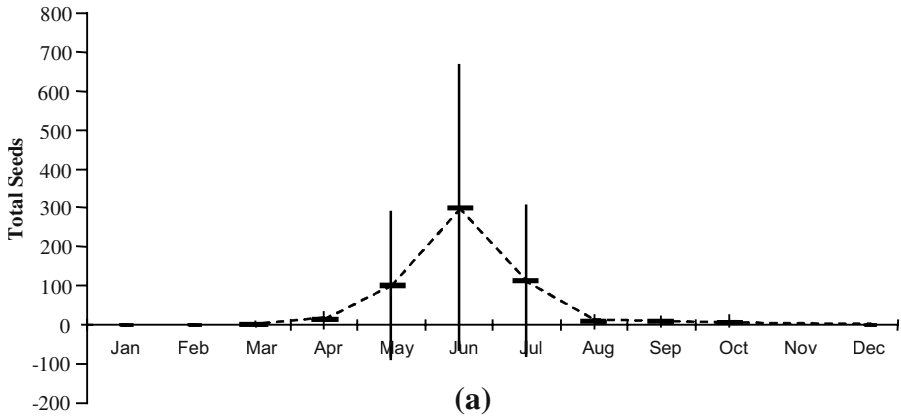


Figure 10. a) Pattern of monthly ripe fruit production by *Brosimum alicastrum* over a 15-yr period. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production for *Brosimum alicastrum* over a 15-yr period.

No significant difference in mean annual troop size for howlers was detected over the 15-yr period (ANOVA, $F = 1.63$, $P > F = 0.07$, $df = 14, 244$). This result is not what one would predict if variability in annual fruit production showed a direct

relationship to howler population size. KM has long contended that howler troop size on BCI tends to decline as the rainy season progresses and census data suggest such a trend. In addition, significantly more howler monkeys are found dead between July-December than January-June (Mann-Whitney U-test; $Z = 3.323$, $P, \leq 0.009$, $n = 43$ months Jan-June, 48 months Jul-Dec). This is a persistent annual pattern (Milton, 1982, 1990, 1996).

However, troop counts for the 15-yr sample did not support the assumption of significantly smaller troop size in howlers in the rainy half of the year. No significant seasonal difference in mean troop size could be found for howler monkeys in the first relative to the second half of the year regardless of the test employed (t-test, Mann-Whitney U-test and an ANOVA were run on these data). Results were the same whether all 15 years of data were analyzed or only those eight years for which there were troop counts in both seasons of that year.

We then examined monthly means for troop size for the 15-yr sample (Fig. 11). Mean troop size in January and in June differed significantly from all other months (Wilcoxon rank sum test: January, $Z = -2.19$, $n = 257$, $P > Z = 0.03$; June, $Z = -2.36$, $n = 259$, $P > Z = 0.02$; the same results were obtained for both months using a t-test). Testing for differences between mean number of individuals in each age class by month showed significantly more adult monkeys present in troops in January and June (Jan: Mann-Whitney U, $Z = -2.17$, $n = 259$, $P > Z = 0.03$; June, Mann-Whitney U, $Z = -2.70$, $n = 259$, $P > Z = 0.01$). Significantly more infants were also present in troops in January (Mann-Whitney U, $Z = -2.05$, $n = 259$, $P > Z = 0.04$) and June ($Z = -1.76$, $n = 259$, $P > Z = 0.08$). Results suggest two intra-annual population cycles for howlers per year, a peak and a trough followed by a peak and a trough. Neither January nor June stand out on BCI in terms of monthly fruit production or amount of rainfall received.

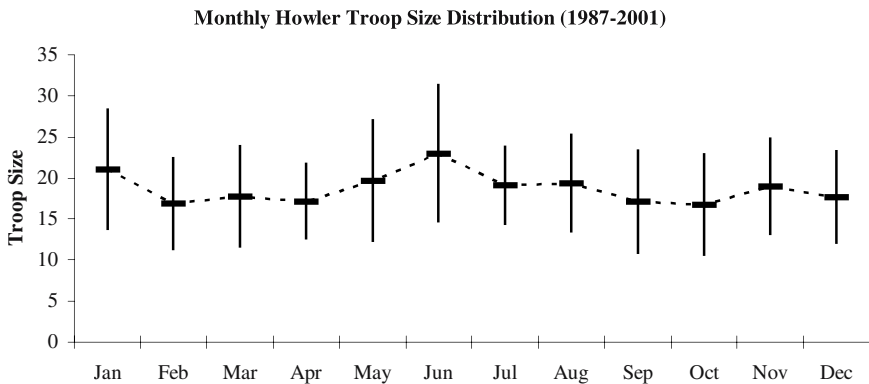


Figure 11. Monthly howler troop size distribution 1987-2001. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation.

Squirrels, Agoutis, Capuchin Monkeys

The other focal mammal species, squirrels, agoutis and capuchin monkeys, were censused annually in December-January by J. Giacalone and G. Willis. Censuses were conducted in the morning, largely between 7 and 10 am by an observer who walked along the island trail system at a speed of approximately 1 km/h, noting down the species, height above ground, distance from the trail and initial detection distance from the observer of all animals encountered, along with the time and location of the encounter. Each annual census included over 100 km and covered all trail segments on BCI at least once. Data presented here represent the number of sightings of individuals of each species for each sample year adjusted by the number of km of trail walked in that year; these results can be used to estimate population size for each species for each sample year. For analysis, all estimates were assigned to the December year of that census. We present only 14 yrs of data for the three species (1987–2000) as the 2001–2002 census data were not available for analysis.

Each species showed notable interannual variation in estimated numbers; extreme estimates for a particular species differed by more than 100% (Fig. 12). The direction of change for one species did not necessarily track the direction of change for the other species (Fig. 12). This lack of concordance is not what one would predict if variability in annual fruit production showed a direct relationship to frugivore population estimates.

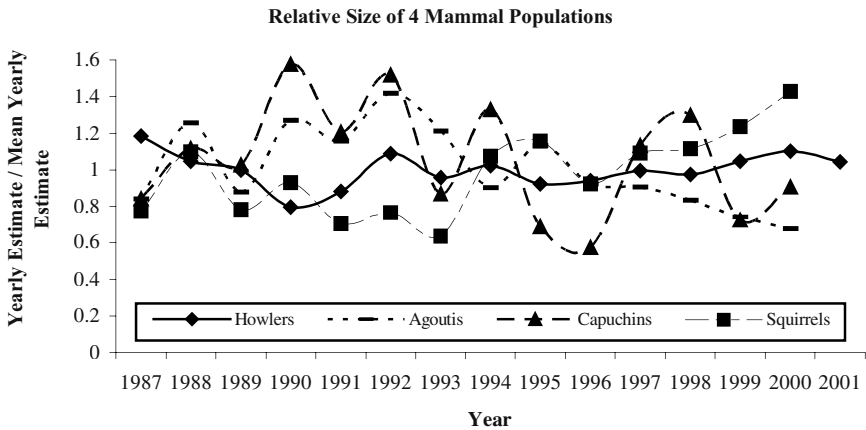


Figure 12. Relative annual size of each of the 4 frugivore populations (15 yrs for howler monkeys; 14 yrs for the other three species).

Squirrels and agoutis have specialized dentition to exploit hard-shelled seeds and for this reason might be viewed as members of a guild. As such, their populations might be expected to track together in response to the relative availability of such seeds. As shown in Fig. 12, the agouti and squirrel populations on BCI might show

concordance for two or three years but then one species increases in numbers and the other declines. This pattern suggests that absolute fruit abundance does not explain population fluctuations for the two species. Perhaps, for example, each species relies on a somewhat different set of primary fruit species, including those producing hard-shelled seeds.

To investigate this possibility, we tested for significant correlations between annual population estimates for each of the four mammal species and annual fruit production estimates for each of the 39 edible fruit species. We used a t-test to evaluate the significance of Pearson product-moment correlation coefficients. This is justified if the distribution of the two variables is bivariate normal. While it is difficult to verify a bivariate normal distribution with the number of data points we have, examination of the data did not find strong evidence that the normality assumption was inappropriate.

Squirrel numbers showed a significant positive within-year correlation (≤ 0.05 level of significance) with fruit production (seed equivalent) data for six fruit species, capuchin numbers with four, agouti numbers with two and howler numbers with one. Given feeding records for each species on BCI, most such correlations appeared plausible.

Time-lag Effects

We then tested for a one- or two-year lag effect between fruit production and population size of each mammal species (i.e., one year lag = abundance of a fruit species in year A relative to abundance of a given frugivore species in year A + 1; two-year lag = abundance of a fruit species in year A relative to abundance of a given frugivore in year A + 2). Squirrel population estimates showed a significant correlation at a one year lag in relation to fruit production for four fruit species and a significant correlation at a two year lag for eight species; capuchin population estimates showed a significant correlation at a one-year lag with zero species and a significant correlation at a 2-yr lag with two species; agouti population estimates showed a significant correlation at a 1-yr lag with three fruit species and a significant correlation at a two year lag with zero species; howler monkeys showed no correlations with any fruit species at a one year lag and a significant correlation at a 2-yr lag for two species.

Our 39 fruit species contained various species placed in the same genera. From these, we selected 10 genera (the 10 most speciose or best represented in seed equivalent data) and summed total production data for each genus for each sample year. We used these estimates to test for correlations with annual population size for each mammal species (looking within years and with a one-year or two-year lag). Squirrels showed three significant correlations – all within-year, with the genera *Miconia* (Melastomataceae), *Spondias* and *Doliocarpus* (Dilleniaceae). Capuchins showed one significant correlation, a within-year correlation with fruits of the genus *Coccoloba*. Agoutis showed one significant correlation, within-year, with fruits of the genus *Chrysophyllum* (Sapotaceae). Howlers showed no correlation with any

genus within years or at a one- or two-year lag. Given the dietary habits of each mammal species, most such correlations appeared plausible.

Because of the large number of tests employed, some of the significant results are likely spurious. To control for this, we re-evaluated the significance of each correlation using a sequential Bonferroni technique. This more rigorous test produced just one significant correlation between the abundance of any of the four mammal populations at any of the three time lags (0, 1, and 2 years) and considered several indices of fruit production (total immature fruit, total mature fruit, total number of fruit species in traps, the 39 important fruit species as a group, each of the 39 fruit species separately, each of the 10 important fruit genera separately). The single significant correlation was between squirrels and *Spondias mombin* at a one-year lag.

Yet, when we compare population patterns for a given mammal species against patterns for some highly preferred fruit species, results, at times, seemed suggestive in spite of the lack of significant correlation indicated by the Bonferroni technique. In Fig. 13, for example, we show annual estimates for capuchin numbers and fruit production by *Doliocarpus major* over a 15 yr period. The two patterns seem to track fairly well. All of the tests we employed measured linear associations between variables. The relationship between the population estimates of a given frugivore species and estimates of the abundance of a given fruit species may, however, not be linear. As we have only 15 data points for three of the four mammal species, we are limited in our ability to do more with data at present.

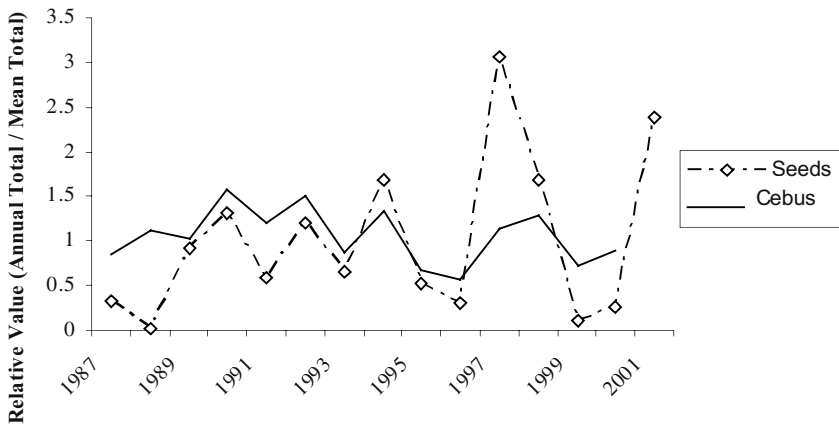


Figure 13. Relative annual estimates for population size of *Cebus capucinus* and total mature fruit production by *Doliocarpus major* over a 15-yr period.

We also noted that some fruit species long regarded as tightly associated with the reproductive biology of one or more of our focal mammal species, for example,

Dipteryx, *Astrocaryum*, *Gustavia* (Lecythidaceae) and *Attalea* for squirrels (Glanz et al., 1982), showed no correlation with population estimates for that species using either the Pearson product-moment correlation coefficient or the Bonferroni technique. However, judging from sample size, of these four species only *Dipteryx* was well represented in trap data. Ripe fruits of these four species are either large relative to most fruits on BCI or, in the case of the palm species, generally occur on only one infructescence in one area of the tree at any given time. The size and placement patterns of traps may not have accurately sampled production in these four important fruit species. Very small-seeded fruits such as those of *Ficus*, a genus of strong dietary importance to howlers, may likewise not be accurately reflected in trap data as seeds are minute, variable in number and difficult to identify as to species.

Basically, with data in hand, of the four mammal species, it appears that squirrels, with by far the smallest body size, show the highest number of suggestive links with particular fruit species. We predict that squirrel population dynamics will be found to be more closely tied to a wider range of fruit species than is the case for our other three mammal species, followed by capuchins and agoutis, who have almost identical body size and finally by the considerably larger-bodied howler monkeys. Howler monkey population dynamics do not appear closely tied to any fruit species, perhaps because, unlike the other three species, howler monkeys can also depend on leaves as food.

Effects of Unusual Years

Though our data failed to show any simple direct correlation between annual fruit production and frugivore numbers on BCI, other researchers have detected such an association under specific conditions. In 1982, Foster suggested that excessive rain out of season might be highly disruptive to the forest frugivore community in terms of fruit set. A weak dry season (unusually short and wet) was hypothesized to lead to fruit failure in the rainy season of that year, causing island-wide famine and unusually high frugivore mortality (Foster, 1982).

In 1999, Wright and his associates refined Foster's observations and presented a 2-yr cycle model related to El Niño years. This model predicted that a warm sunny El Niño year, immediately followed by a year with "a mild dry season" (which they defined quantitatively and which was unusually short and wet) would result in fruit failure by many species that same year, extending into the early months of the subsequent year. Such fruit failure during the mid-to-late rainy season and subsequent early dry season, was predicted to lead to island-wide famine, causing unusually high mortality in frugivorous mammals (Wright et al., 1999).

Only one El Niño year (1992) followed by the requisite "mild dry season" year (1993) occurred in our 15-yr sample. Wright et al. (1999) speculated that frugivore populations may have increased in size during the 1992 El Niño year when community-wide fruit production was unusually high (Fig. 4). Indeed, our data show that all four of the frugivores studied here increased in abundance between

December 1991 and December 1992 (Fig. 12). After the mild dry season of 1993, also as predicted by the model, many tree species on BCI produced fruit crops well below mean size and some species failed to set fruit (Wright et al., 1999). Cadaver recovery showed that two mammal species, collared peccaries and white-tailed deer, suffered significantly higher than average mortality in late 1993 (Wright et al., 1999). Census data compiled by Wright et al. (1999) indicated some other mammal species (e.g., coatis; Gompper, 1996) also declined in numbers between December 1992 and December 1993, apparently due to famine caused by fruit shortage. All four of our focal mammal species, using three independent estimates, showed a decline in numbers in 1993.

Typical Years

We then compared the full 15 years of data on mammal densities and fruit production with information for 1992-1993 to see if these two unusual years might provide insight into factors affecting population fluctuations in other years. Though population size for all of our focal species declined in 1993, only the squirrel population seemed unusually low and squirrel population size was also depressed in 1991 and 1992 (Fig. 12). Squirrel numbers did recover slightly in 1992, the El Niño year, only to sink to their lowest level in 1993. However, it was not unusual for our focal mammal species to show concurrent population declines or increases. Three out of four of our focal species also fell below their relative means in 1987, 1989, and 1996 while all four species were elevated above their relative means in 1988 and three out of four were elevated in 1994 and 1997 (Fig. 12). In general, the overall pattern for these species (howlers to a less dramatic extent) over the 15-yr period was one of constant oscillation.

The 1997 El Niño year (the only other El Niño year in our 15-yr data set) produced the highest peak in overall fruit abundance on BCI in the 15-yr sample (Fig. 4). Similar to 1992, three out of four of our focal mammal species showed an increase in population size in 1997. The following year, 1998, did not have a "mild dry season" and therefore did not meet conditions of the Wright et al. (1999) model. In 1998, two of our four species increased and two declined in population size relative to their population size in 1997. However, only agouti population size was below its relative mean in 1998 and it was also below the mean in the El Niño year, 1997, and in 1999 and 2000.

Data on annual fruit production (each of the 15 years expressed in relation to the 15-yr mean) showed that 1993 and 1998 were the two lowest years in overall fruit production on BCI in the 15-yr sample. Both years followed warm, sunny El Niño years (1992 and 1997) with overall high fruit production (Fig. 4). Of particular interest, however, in terms of the El Niño famine model are species producing edible ripe fruit crops in the mid-to-late rainy season. As noted, the late rainy season is the time of year when overall fruit production on BCI declines to its lowest level (Fig. 3), and when overall mammal mortality is highest (Milton, 1982, 1990, 1996; Wright et al., 1996).

In their 1999 paper, Wright et al. presented a figure of the 25 fruit species on BCI showing “greatest mean dry mass fruit production” between 10 August of one year and 7 February of the following year (this evaluation based on 10 1/2 years of data on dry mass fruit production from 59 fruit traps, 18 November 1985-30 June 1996). Only fourteen of these 25 species produce fruit of known importance to mammalian frugivores on BCI. The other 11 species: (1) produce wind-dispersed fruits, (2) were not known to KM and JG and likely are not important foods for mammalian frugivores on BCI or (3) also produce fruit during other months. Following predictions of the Wright et al. model, 13 of these 14 edible species showed fruit production depressed below the mean, often well below the mean between 10 August 1993-7 February 1994 (Wright et al., 1999).

However, examination of seed equivalent data for 8 of these 14 species over our 15-yr sample suggests that it is not uncommon for a number of important species to show low fruit production in the same year (Fig. 14). Only one of these 8 species, *Trichilea tuberculata*, actually had its single worst year of fruit production in 1993 (the year following the 1992 El Niño yr); *Hyeronima laxiflora* (Euphorbiaceae) had its single worst year in 1992, an el Niño year; *Quararibea asterolepis* had its single worst year in 1997, another el Niño year; *Dipteryx panamensis* had its single worst year in 1990, *Spondias mombin* in 1991 and so on (Fig. 14). The fruit production patterns presented in Figure 14 suggest that it would be difficult to predict the strength of annual fruit production for these species as there is considerable interannual variability.

What Can Be Predicted?

Using these species as an example, what can be predicted about annual fruit production from the 15 years of seed equivalent data? If any pattern is apparent in Figure 14, it is one indicating that, in any given year, the probability is high that only 20 to 30% of the important mid rainy to early dry season species will have an unusually good year in terms of fruit production; other species will have an average to sub-standard year (Fig. 14). The next year, 20 to 30% of the *other* species in this temporal cohort can be predicted to have an unusually good year though one cannot predict in advance exactly which species these will be. This oscillating production pattern makes it difficult to predict, except in extreme circumstances, how the frugivore community or particular frugivore species will be affected by fruit availability in any given year.

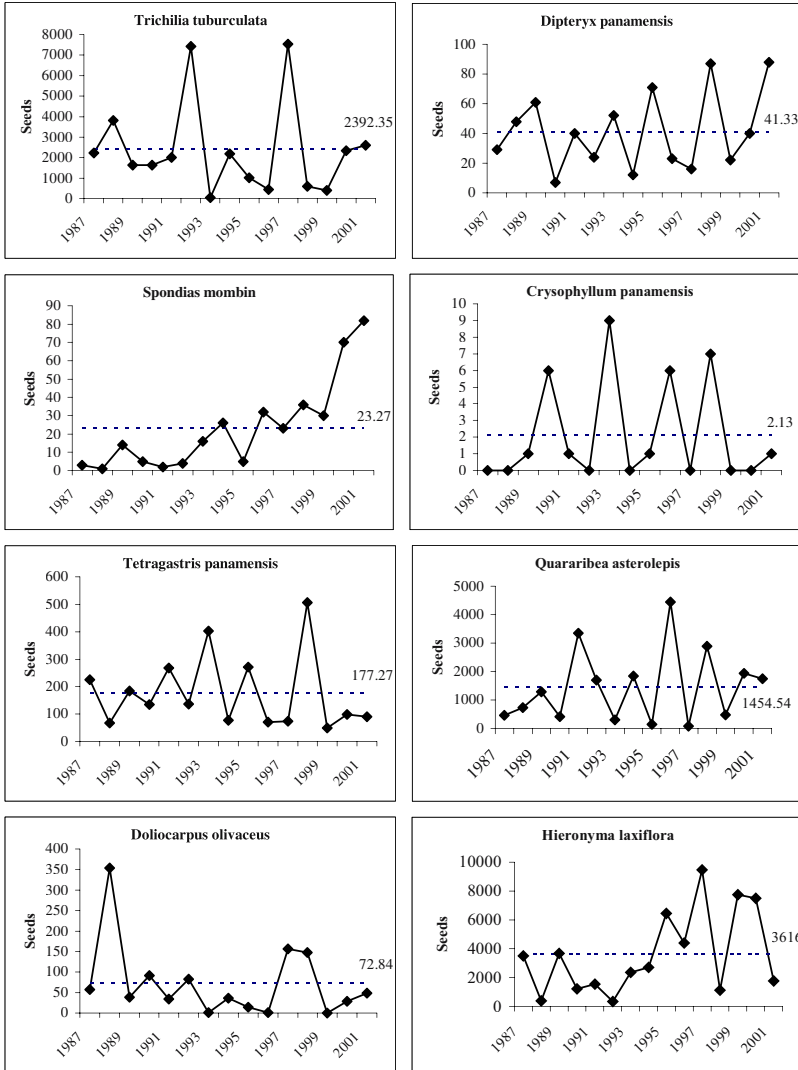


Figure 14. Annual total fruit production (as estimated from seed equivalents) for 8 tree species fruiting in the mid-to-late rainy season on BCI. For each species, the solid line graphs the annual total. The dashed line graphs the mean value for the 15-yr period. All species are important mid-to-late rainy season food species for many mammals on BCI, including one or more focal mammal species.

DISCUSSION

It is a simple matter to state our major conclusion: namely that, though strong relationships likely exist between animal numbers and fruit production patterns on some level, with data in hand we can find no clear evidence to support this assumption except in extreme years. Our data suggest that the frugivore community can depend on at least some ripe fruit from most edible species at predictable times each year but in any given year, data also suggest that only a small subset of such species will show high productivity; other species will generally show average to low productivity. This pattern appears to be relatively constant and largely unpredictable in terms of which particular species will have an unusually good fruit crop in any given year (except to say that it generally will *not* be species or individuals which produced an unusually good crop in the preceding year). This fruiting pattern likely reflects the interplay of the particular top down and bottom up factors impinging on tree species (or individual trees) at any given time. It is possible that animal numbers are affected more by predators, parasites or disease than by fruit availability or by a complex and constantly oscillating combination of top-down and bottom-up factors (Milton, 1986). However, the lack of correlation we noted for animal numbers and fruit production patterns may also reflect, at least in part, limitations inherent in our sampling methods and data. A brief discussion of some of these perceived limitations may prove helpful for those interested in carrying out similar long-term studies.

Fruit Trap Data

The trap data utilized for this analysis were not compiled to study factors affecting the population dynamics of frugivorous mammals. Rather, these data were compiled to monitor interannual variation in seed set for the more abundant tree and liana species on BCI and to provide input for demographic studies of plants (Harms et al., 2000; Hubbell et al., 1999). The study design of randomly located seed traps provides large overall sample sizes and reliable estimates of production by the plant community as a whole. Randomly located traps also provide reliable production estimates for abundant plant species and those producing copious numbers of small seeds.

However, randomly located traps are far less reliable for rare plant species and for plant species that produce smaller numbers of large seeds or fruits produced in few large infructescences. Many tree species in areas of older forest on BCI can be regarded as rare (Milton, 1980) and various of the important food species for one or more of our focal mammal species produce small numbers of large seeds or seeds in clusters. The use of random fruit traps for general collection needs to be combined with traps that focus on a number of individuals of particular fruit species important in the diet of particular mammal species. This approach might provide data more

useful for examination of fruit-mammal relationships though this method could overlook the possible importance of many secondary food species.

Mammal Census Data

The accuracy of mammal census protocols deserves further study. Different census techniques need to be modified and calibrated such that they reliably produce similar results. For example, JG's strip census method and KM's troop count census method at times showed little annual concordance in terms of howler monkey numbers (Fig. 15). Techniques are required that produce estimates in basic agreement.

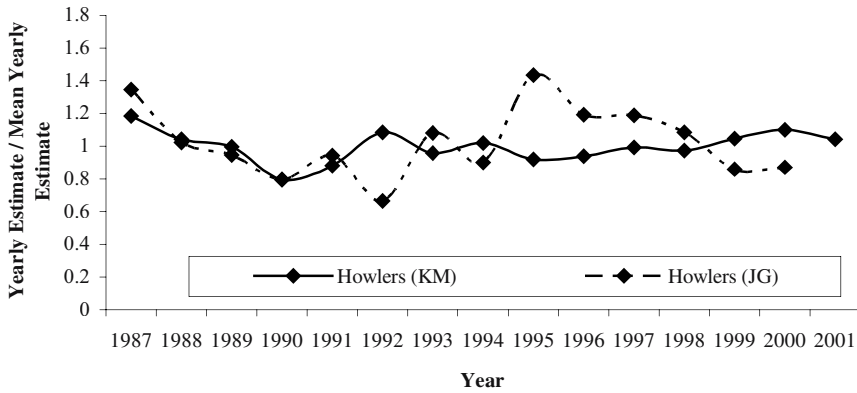


Figure 15. A comparison of results of annual howler monkey population estimates derived by using a strip censusing method (JG) or an individual troop count method (KM). See text for details of each sampling technique.

Standard mammal strip census methods are used widely now in tropical forests but our data suggest that such methods may work well only for certain species. Solitary or paired species such as squirrels or agoutis are likely to be accurately counted. Social species such as capuchin monkeys, however, which live in closed social units but which tend to forage spread out over a wide area, may be greatly under- or over-estimated. Social species such as spider monkeys, which live at relatively low densities, have a fission-fusion pattern of social organization and range over a large area pose special censusing difficulties.

Integration of Fruit and Mammal Data

Another area deserving study is how to relate fruit production data to animal population data most meaningfully. Annual troop and/or population composition data, reproductive data and other relevant information for each mammal species need to be integrated in a biologically meaningful manner with fruit production data. Island-wide famines are rare events but some mammals of most species on BCI die every year, particularly during the mid-to-late rainy season (Foster, 1982; Milton, 1982, 1990, 1996; Wright et al., 1996, 1999). In some years, not necessarily a year following an El Niño year, animals from one or more species may die in far higher numbers than in other years. For example, in 1989, significantly more howler monkeys were found dead in the BCI forest than in any other year in KM's 28 years of work on BCI (Milton, 1993). Howler mortality in 1989 showed no correlation with island-wide fruit production estimates for 1989, 1988 or 1990 (Milton, 1993).

Looking at an earlier data set, we also noted that from January 1981 through January 1982, the BCI squirrel population suffered its greatest decline in 20 years. The *Dipteryx* crop, which is extremely important to squirrels on BCI, failed in January 1981 and *Gustavia*, another critical fruit species for squirrels (Glanz et al., 1982), also failed later that same year at what would have been the height of the squirrel breeding season (Giacalone-Madden et al., 1990). However, no El Niño year occurred immediately prior to these events and the very pronounced El Niño of 1982 did not appear to have a widespread impact on BCI mammal populations. It seems that particular fruit species of key dietary importance to particular mammal species may need to be monitored in relation to one another rather than--or in addition to-- broader sampling of the floral and faunal communities before we will begin to better understand the complexities of this ecosystem. Too, though fruit production may be an important factor affecting population size for many mammal species, data from this and other sites suggest that population fluctuations of some species can also be influenced by predator and parasite pressures (Gadgil & Prasad, 1984; Milton, 1993, 1996).

Tropical forests, which comprise the most complicated ecosystem on earth, are not proving amenable to facile analysis, even at sites as well studied as BCI. Eventually, however, as we continue to refine and improve our questions and methods of data collection, we are confident that the population dynamics of particular mammal species and their relationships, if any, to the production patterns of particular plant species will be better understood.

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NOTE

1) In this paper we adopted three conventions that differ from earlier treatment of the same fruit production data by Wright et al. (1999). Our goal was to evaluate possible relationships between annual mature fruit production by particular plant species and population fluctuations of particular frugivore species. In contrast, Wright et al. (1999) sought to evaluate the consequences of a sustained period of very low community-level fruit production for a range of frugivore species. In terms of differences in our analytical treatments, first, for data series that are the sum of seed equivalents, we weight each seed found in frugivore diets equally regardless of the fruit species. Wright et al. (1999) considered all plant species with fruits or seeds in traps (not just species known to be in frugivore diets) and weighted all fruit species equally rather than weighting individual seeds equally. However, as most analyses presented in this paper deal with data series that are sums of seed equivalents for individual fruit species only, they are not affected by this difference in treatment. Second, we report untransformed values of fruit production. Wright et al. (1999) reported logarithms of annual fruit production because untransformed values are strongly skewed (unpublished analyses of J. Wright). This is of minor concern in our paper because we are interested in *relative* levels of production. Third, we associated fruit production with the calendar year or month mature fruits were captured in traps. Wright et al. (1999) associated annual fruit production with the meteorological year of the appropriate flowering event. This difference explains discrepancies in the timing of fruit production reported here and by Wright et al. (1999).

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CHAPTER 3.

POTENTIAL KEYSTONE PLANT SPECIES FOR THE FRUGIVORE COMMUNITY AT TINIGUA PARK, COLOMBIA

PABLO STEVENSON

Abstract

Different practical problems restrict the possibility of rigorously testing the role of plants as keystone species in tropical forests, and therefore we do not yet know the impacts that could result from their removal. Currently, the criteria used to suggest keystone plant species in tropical forests include an assessment of their importance in supporting frugivore communities during periods of fruit scarcity, their reliability during these periods, their abundance, and the number of species that feed on their fruits. However, even for resources that match these criteria it has been shown that the density of these plant species is not necessarily correlated with the abundance of frugivores, so their relevance is still an open question. In this study I use information on feeding behavior and phenological data collected over three years in Tinigua National Park, Colombia, to identify potential plant keystone resources for the fruit-eating animals. Among 29 plant species that produced fruit or were consumed in periods of fruit scarcity, I found virtually no case of a species that could maintain a large proportion of the frugivore community. Plant species previously suggested playing keystone roles, such as palms and figs, were included in the list. But palms did not support a very large coterie of frugivores and figs were reliable only at the genus level. The fact that only 3 of the 29 species suggested to play keystone roles at Tinigua were present in a recent review of the potential keystone resources in Neotropical forests (Peres, 2000), suggests that species playing important roles in one community may be unimportant in other localities. I conclude that postulating keystone resources in tropical forests might lead to strategies to protect local animal guilds, but it is difficult to find species that could support the majority of frugivores in complex communities and it is naïve to generalize about their roles across localities. I suggest that the bulk of frugivores in Tinigua (i.e. primates) may use fat reserves accumulated during periods of fruit abundance to survive the lean period, and therefore keystone resources might not be restricted to particular seasons.

Key words: Frugivory, keystone resources, phenology, primates, tropical forests

INTRODUCTION

The concept of keystone resources has changed through time, so several definitions have been used for keystone species in different efforts to identify them. The keystone species term was used for the first time to describe a predator that controlled a rocky intertidal community (Paine, 1969). The most common definitions of keystone species or resources are based on the occurrence of drastic changes at the community level caused by their removal (Mills et al., 1993). Authors disagree in how dramatic the change has to be to merit keystone status for the species: the term has been used for species whose removal causes changes in the density of only a few other species (Fincke et al., 1997), up to the complete loss of integrity of the community (Power et al., 1985; Terborgh et al., 2001). Therefore, the definition of keystone species has changed to make the concept useful for conservation purposes. A common feature of the earliest works trying to identify keystone species was that they proposed organisms (species or guilds) whose removal was expected to result in the disappearance of at least half of the assemblage under study (Mills et al., 1993). Although any definition based on a particular percentage may be greatly affected by the size of the assemblage under consideration, the protection of a keystone species may benefit the stability and integrity of a community more than the conservation of other species without such strong interactions. This is the potential use of keystone species in conservation biology.

Mills et al. (1993) suggested using community importance values that measure interaction strength to quantitatively infer keystone species. These values could be calculated for each species as the percentage of other species lost from the community following its removal. Keystone species might be useful for conservation programs only if there are large asymmetries in the community importance values among the species of that particular community. The methodology for calculating these values should be based on the results of perturbation experiments, in which one species is removed, and the responses of other species are measured over appropriate time scales and compared to controls. However, when the interest is maintaining biodiversity (i.e. in tropical forests), it would be difficult and unethical to monitor long-term effects of removal of one species. In this case, pulse experiments (similar to Bender et al., 1984) looking at short term effects on fitness components (e.g. growth rates) might be an option. A common alternative method is a comparative approach, in which a community that has lost one species (usually by human intervention) is compared to a similar community with the complete original set of species. Two main problems occur in this kind of analysis. First is the difficulty of having appropriate replicates, because spatial heterogeneity may obscure the impact of species removal, and a related problem is that without knowledge of the natural variation in the study communities and without controls, it is difficult to ascertain whether the changes observed in the altered community are caused by the removal.

A recent consensus definition states that “a keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance” (Power & Mills, 1995). This definition is also based on the presence of strong interactions, but it incorporates the restriction of dominance within the community. According to this view, dominant elements in the community should be distinguished from keystone species even though both groups participate in strong interactions. Although this distinction seems ecologically appropriate, the purpose should not only be preserving keystone species without considering dominants. In fact, the dominance criterion was not part of the original formulation of keystone plant resources (Howe, 1977; Terborgh, 1986).

Gilbert (1980) used the term “mobile links” to refer to animals that play crucial roles in the persistence of various plant species, which in turn may produce the primary food to sustain the community. Gilbert discussed two groups including pollinators and seed dispersers. There are also examples in tropical rain forest ecology literature of several plant resources such as figs and palm species which have been postulated to be keystone species because they produce fruits during periods of fruit scarcity. Terborgh (1986) reached this conclusion based on an analysis of the energy provided by the fruits in the plant community of Cocha Cashu, Peru. Based on previous studies of fruit availability and frugivore abundance (Janson, 1984; Janson & Emmons, 1990), Terborgh showed that in periods of fruit scarcity the energy provided by the plant community is below the amount required to support the resident guild of frugivores. Patterns of fruiting seasonality seem to be common in many Neotropical forests (van Schaik et al., 1993; van Schaik & Pfannes, 2002), as is the consistent use of a few plant sources by frugivores during periods of fruit shortage (Peres, 2000).

If resources such as figs and palms are supporting the community of frugivores, then one would expect to find higher frugivore biomass in places where these resources are more abundant. However, a recent study suggested the abundance of the proposed plant keystone resources such as palms and figs is not correlated with the biomass of primates (Stevenson, 2001), which constitute one of the most important frugivore groups in the New World (Terborgh & van Schaik, 1987). These findings run contrary to expectations if the plants are really keystone resources for the frugivore community. However, methodological issues complicate the picture because it is difficult to quantify fig abundance. For example, the basal area and the density of figs in plots including plants larger than 10 cm DBH. may under represent fig abundance, because some fig species are hemi-epiphytes with only thin roots reaching the ground. Therefore, it is not clear if the postulated keystone role of these resources really exists, and in any case it appears risky to take conservation actions based on the abundance of these apparently critical resources.

The main objectives of this paper are: 1) to describe the patterns of fruit production in the lowland tropical forest of Tinigua National Park, Colombia; 2) to present a list of the potential keystone plant species that produce fruit during periods of general scarcity; 3) to compare these resources with the food items ingested by a variety of frugivores in this community; 4) to evaluate using the available evidence (in the absence of experimental studies) the potential role of these species as

keystone resources, and 5) to discuss the potential value of plant keystone resources to community dynamics and conservation programs.

METHODS

Site description

The study site is located in a tropical lowland forest on the Eastern border of Tinigua National Park (201,875 ha), west of La Macarena mountains, Departamento del Meta, Colombia (2° 40' north and 74° 10' west, 350-400 m over sea level). The study site, Centro de Investigaciones Ecológicas La Macarena (CIEM), consists of three research stations on the West margin of Río Duda. Rainfall is seasonal in the region, with a 2-3 month dry period occurring between December and March (Stevenson, 2002). Average annual precipitation at Paujil Station during the study periods (March 1990-February 1991, August 1996-July 1997, and January-December 2000) was 2782 mm. I estimated fruit abundance using a combination of phenological transects and fruit morphological information, using a new methodology to assess fruit production from phenological and morphological data (Stevenson, 2002). For the first two study years when I did not estimate individual fruit crops, I used the average crop size in the final year for each species, unless differences between years were evident. In the former cases I used the maximum or minimum crop estimates from just one year. I defined periods of fruit shortage as those when the production was less than one third of the maximum production during the year cycle. This proportion is similar to the one found by Terborgh in his original analysis of keystone plant resources (1986).

I extracted production data from the months of fruit scarcity (usually between September and January in our study site), to suggest keystone resources. All species producing ripe fruit at those shortage periods were ranked according to their production during lean periods.

Frugivore Consumption

The most complete data on frugivore feeding behavior during the study period was collected on woolly monkeys (*Lagothrix lagothricha*), which were continuously studied during those three years. I described the fruit diet of the woolly monkeys at Tinigua following more than 2000 h of focal observations (Stevenson, 2002), when the number of minutes spent feeding on different plant species was measured. A separate database included information on other primate species (Stevenson, 2000, Link pers. comm.). In these cases the sample time was shorter, but for all species dietary information was collected during at least one complete season of fruit scarcity.

I gathered information on feeding behavior of the general frugivore community from observations of focal trees with ripe fruits from 75 plant species that were observed during periods of high frugivore activity (6:10-10:00), for a total of more than 3400 h.

RESULTS

I have found a consistent pattern of fruit production in the study area for all the years when phenological information has been recorded (Figs. 1 a, b, and c). There is generally a unimodal distribution of ripe fleshy fruits across the year. The period of fruit scarcity occurs at the end of the rainy season. An increase in fruit availability starts during the dry season and reaches a maximum at the end of the dry season or the beginning of the rainy season (between March and May). Finally, fruit production drops at the middle of the rainy season and very few species produce ripe fruits during periods of fruit scarcity (usually between September and January); therefore, those species in fruit during those months could be postulated to play keystone roles in the community.

It is evident, however, that there is variability in the species that produce ripe fruits during periods of fruit scarcity (Table 1). Except for three relatively common species, two palms *Oenocarpus bataua* and *Iriartea deltoidea*, and one tree, *Gustavia hexapetala*, none of the other species was among the most important plants producing ripe fruits during lean periods for all three study years.

In general, high fruit production during scarcity periods was not a good predictor of the species that were consumed by frugivores during those periods. For example, correlation coefficients between production and fruit consumption by woolly monkeys in fruit scarcity periods for all study years was always low (1990: $r^2=0.04$, $F=3.0$, $p=0.09$, $n=80$ species; 1996: $r^2=0.09$, $F=10.0$, $p=0.002$, $n=102$; 2000: $r^2=0.03$, $F=2.3$, $p=0.13$, $n=86$). Two reasons may explain the lack of correlation. First, there was high incidence of consumption of unripe fruits during periods of fruit scarcity (see below), and the monkeys did not ingest some of the fruits available during scarcity periods. For example, after more than 2000 h of observation, I have not observed the woolly monkeys ingesting fruits of *Oenocarpus bataua*, in spite of its abundance and high energy content. Dew (2001) found the same to be true at another Amazonian site in Ecuador. Probably this rejection is due to high tannin contents in the pulp of the fruit (Stevenson et al., 2000).

Based on the fruit consumption by the woolly monkeys during periods of fruit scarcity a set of potential keystone plants is presented in Table 2. Again there is variability in the importance of different fruiting plant species in the diet of woolly monkeys during scarcity periods. Except for *Gustavia hexapetala*, which was actually the most consumed species in the overall diet in all three years, none of the remaining fruit species was important in all study years. This variability could be related to several factors, such as: 1) fortuitous production of species with unpredictable fruiting patterns (i.e. *Ficus* spp.). 2) Small changes in the timing of production of the species (i.e. *Inga alba* producing fruits in January instead of February or *Spondias venulosa* and *Henriettella fissanthera* delaying production

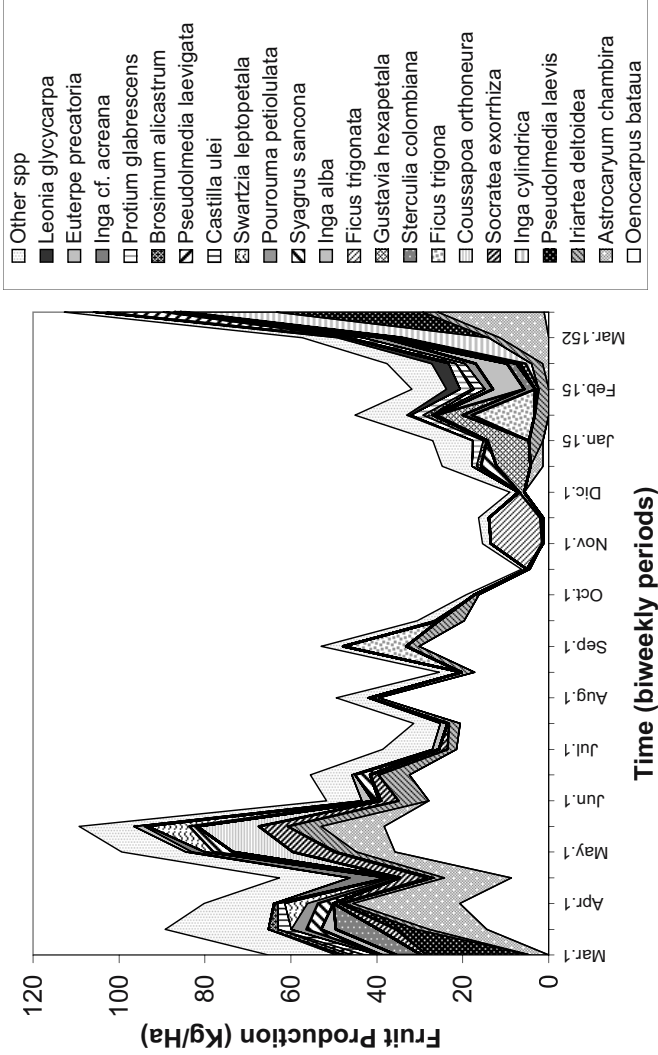


Figure 1a. Temporal variation in the production of ripe, fleshy fruits in Tinigua National Park over an annual cycle: 1990. The production of the main species are shown in different patterns, and the upper line indicates the overall pattern of production. Fruit production was estimated according to a new methodology (Stevenson 2002), and crop size was not measured but inferred from other years (See text for methodological details).

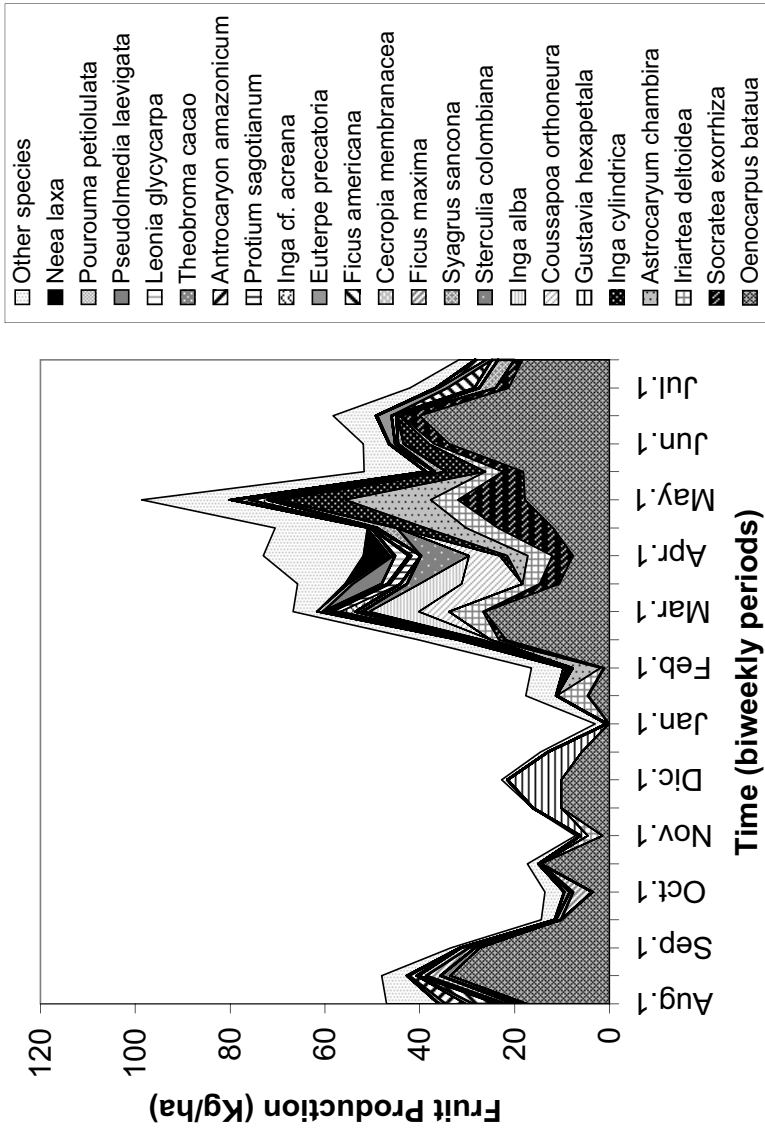


Figure 1b. Temporal variation in the production of ripe fleshy fruits in Tinigua National Park over an annual cycle: 1996. The production of the main species are shown in different patterns, and the upper line indicates the overall pattern of production.

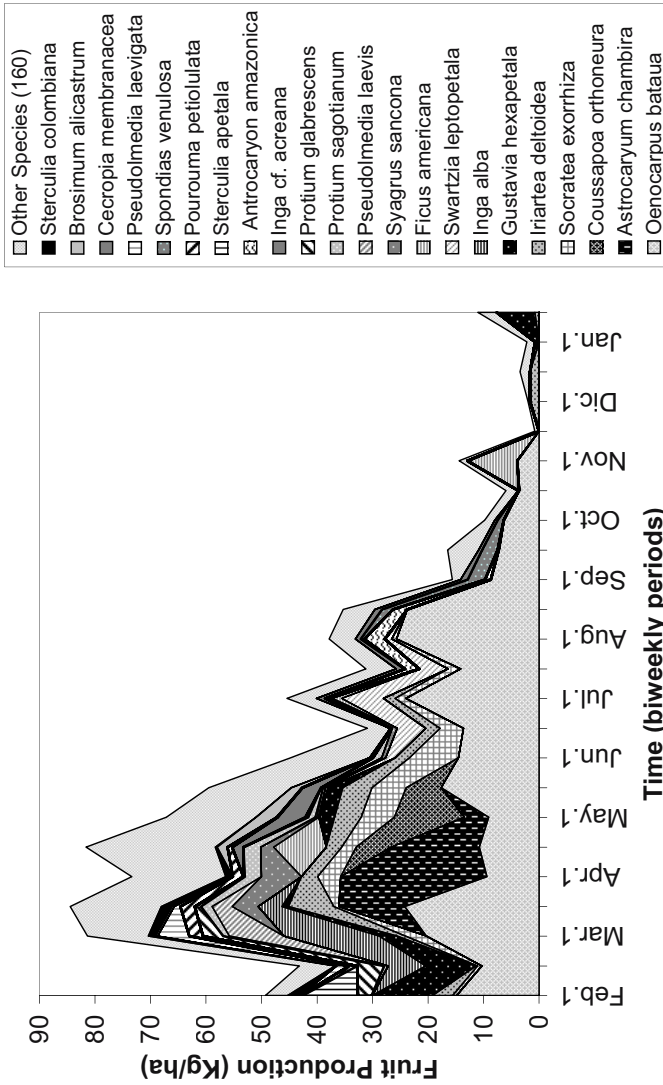


Figure 1c. Temporal variation in the production of ripe fleshy fruits in Tinigua National Park over an annual cycle:2000. The production of the main species are shown in different patterns, and the upper line indicates the overall pattern of production.

Table 1. Potential keystone plant species producing fruit in periods of fruit scarcity during three different years at Tinigua Park. Estimates of fruit production are in kg/ha.

<i>Species (1990)</i>	<i>Prod.</i>	<i>Species (1996)</i>	<i>Prod.</i>	<i>Species (2000)</i>	<i>Prod.</i>
<i>Oenocarpus bataua</i>	87.2	<i>Oenocarpus bataua</i>	60.3	<i>Oenocarpus bataua</i>	29.7
<i>Ficus trigonata</i>	23.8	<i>Gustavia hexapetala</i>	26.5	<i>Ficus americana</i>	8.9
<i>Gustavia hexapetala</i>	22.4	<i>Iriartea deltoidea</i>	9.5	<i>Gustavia hexapetala</i>	7.5
<i>Ficus trigona</i>	14.7	<i>Ficus maxima</i>	4.0	<i>Spondias venulosa</i>	6.9
<i>Iriartea deltoidea</i>	14.1	<i>Ficus pertusa</i>	3.2	<i>Cecropia membranacea</i>	5.4
<i>Bursera inversa</i>	6.6	<i>Cecropia membranacea</i>	2.5	<i>Iriartea deltoidea</i>	4.0
<i>Sterculia apetala</i>	5.2	<i>Cecropia engleriana</i>	1.5	<i>Henriettella fissanthera</i>	2.8
<i>Ficus andicola</i>	4.6	<i>Ficus obtusifolia</i>	1.5	<i>Apeiba aspera</i>	2.7
<i>Spondias venulosa</i>	4.6	<i>Pourouma bicolor</i>	1.5	<i>Ficus sphenophylla</i>	1.9
<i>Protium glabrescens</i>	4.6	<i>Euterpe precatoria</i>	1.4	<i>Protium robustum</i>	1.4
<i>Genus (1990)</i>		<i>Genus (1996)</i>		<i>Genus (2000)</i>	
<i>Oenocarpus</i>	87.2	<i>Oenocarpus</i>	60.3	<i>Oenocarpus</i>	29.7
<i>Ficus</i>	43.1	<i>Gustavia</i>	26.6	<i>Ficus</i>	11.8
<i>Gustavia</i>	22.5	<i>Ficus</i>	10.8	<i>Gustavia</i>	7.5
<i>Iriartea</i>	14.1	<i>Iriartea</i>	9.5	<i>Spondias</i>	7.1
<i>Bursera</i>	6.6	<i>Cecropia</i>	8.1	<i>Cecropia</i>	5.4
<i>Sterculia</i>	5.2	<i>Virola</i>	2.1	<i>Iriartea</i>	4.0
<i>Protium</i>	5.1	<i>Pourouma</i>	1.7	<i>Apeiba</i>	2.9
<i>Spondias</i>	4.6	<i>Apeiba</i>	1.6	<i>Henriettella</i>	2.8
<i>Syagrus</i>	3.6	<i>Euterpe</i>	1.4	<i>Protium</i>	1.9
<i>Virola</i>	3.5	<i>Protium</i>	1.3	<i>Virola</i>	1.7

until September). 3) Changes in fruit production patterns (i.e. poor fruit production in *Pourouma bicolor* at the end of 2000 or the death of a large *Doliocarpus multiflorus* vine after 1990). 4) Supra-annual patterns of fruit production (cf. *Enterolobium schomburgkii*); and/or 5) fruit preference for species eaten only when few alternative resources were present (cf. *Bursera inversa*).

Table 2. Plant resources used by woolly monkeys in periods of fruit scarcity during three different years in Tinigua Park. Plant species in three different diet categories are organized by consumption time (min). Bold plant names indicate unripe consumption.

1990	Time	1996	Time	2000	Time
FRUITS					
<i>Gustavia hexapetala</i>	686	<i>Gustavia hexapetala</i>	1382	<i>Gustavia hexapetala</i>	459
<i>Brosimum alicastrum</i>	166	<i>Pseudolmedia obliqua</i>	766	<i>Henriettella fissanthera</i>	457
<i>Brosimum guianensis</i>	102	<i>Pourouma bicolor</i>	403	<i>Ficus andicola</i>	167
<i>Doliocarpus multiflorus</i>	99	<i>Brosimum lactescens</i>	244	<i>Inga alba</i>	140
<i>Enterolobium schomburgkii</i>	98	<i>Hymenaea courbaril</i>	115	<i>Spondias venulosa</i>	138
<i>Ficus trigonata</i>	97	<i>Ocotea tomentosa</i>	110	<i>Pseudolmedia obliqua</i>	113
<i>Ficus sphenophylla</i>	80	<i>Ficus guianensis</i>	88	<i>Bursera inversa</i>	111
<i>Apeiba aspera</i>	66	<i>Brosimum alicastrum</i>	82	<i>Hymenaea courbaril</i>	66
<i>Dialium guianensis</i>	65	<i>Brosimum utile</i>	79	<i>Ficus sphenophylla</i>	65
<i>Pourouma bicolor</i>	63	<i>Apeiba aspera</i>	76	<i>Ficus nymphaeifolia</i>	65
YOUNG LEAVES					
<i>Brosimum alicastrum</i>	230	<i>Derris pterocarpus</i>	129	<i>Brosimum alicastrum</i>	334
		<i>Brosimum alicastrum</i>	81	<i>Derris pterocarpus</i>	66
		<i>Xylophragma seemannianum</i>	67	<i>Dialium guianensis</i>	58
		<i>Dialium guianensis</i>	63	<i>Adenocalymna purpurascens</i>	52
		<i>Cestrum racemosum</i>	34	<i>Clarisia biflora</i>	31
		<i>Clarisia biflora</i>	27	<i>Xylophragma seemannianum</i>	18
FLOWERS					
<i>Astrocaryum chambira</i>	25	<i>Astrocaryum chambira</i>	151	<i>Astrocaryum chambira</i>	118
		<i>Brosimum</i>	72	<i>Dalbergia sp.</i>	107

<i>alicastrum</i>			
<i>Dalbergia sp.</i>	42	<i>Pseudolmedia</i>	38
		<i>obliqua</i>	
<i>Apeiba aspera</i>	40	<i>Pseudolmedia</i>	29
		<i>laevis</i>	
<i>Phryganocydia</i>	20	<i>Brosimum</i>	28
<i>corymbosa</i>		<i>guianensis</i>	
<i>Pisonia aculeata</i>	11	<i>Pseudolmedia</i>	22
		<i>laevigata</i>	

In contrast, the leaf resources ingested during periods of fruit scarcity seemed to be more regularly recorded in the diet of the woolly monkeys (Table 2). In this case, the most important species seem to reoccur in the diet at different years (although a direct comparison among the three study years was precluded because I was unable to recognize all vine species ingested during the first year). The most important flower species consumed by woolly monkeys during periods of fruit scarcity seemed to be fairly constant among years (e.g. *Astrocaryum chambira*).

There was also variability in the fruit species consumed by other primate species during periods of fruit scarcity (Table 3). Spider monkeys used many of the fruit sources used by woolly monkeys, though the latter relied more on palms such as *Oenocarpus bataua* and *Astrocaryum chambira* than the woolly monkeys did. Capuchin monkeys in contrast to large atelines, did not consume *Gustavia hexapetala* fruits in any important amount. The capuchins instead relied heavily on *Astrocaryum chambira* fruits, which were less used by other primate species. Howler monkeys in this community drastically changed their feeding patterns during periods of fruit scarcity, feeding on very few species and consuming mainly unripe fruits (Table 3). There were also differences in the non-fruit foodstuffs eaten by different primate species at fruit scarcity periods. For example, the main plant items consumed by capuchins included the pith of *Phenakospermum guyanense*, flowers of *Astrocaryum chambira*, petioles of *Guadua angustifolia*, young buds of *Carludovica palmata*, and no leaves. In contrast, the most important items for the larger ateline monkeys were always young leaves of vines and trees (i.e. *Brosimum alicastrum*).

In the years when I conducted observations of fruiting trees, most of the activity in the frugivore community during the fruit scarcity period was focused on large fig trees and a few other species (i.e. *Cecropia membranacea*, *Oenocarpus bataua*, *Bursera inversa*, and *Apeiba aspera*). Trees of *Ficus* spp., *Cecropia membranacea* and *Bursera inversa* were consistently visited by a large coterie of frugivores including birds and primates. Table 4 shows the complete list of potential fruit sources that could be postulated as keystone resources at Tinigua, given that they produce fruit during the scarcity period or because they are consumed by frugivores in those periods.

Table 3. Fruit resources used by four primate species during at least one period of fruit scarcity (data from Angulo, 2001; Stevenson et al., 2000; Samper & Pineda unpublished, and results from this study). Fruit species are arranged in decreasing order of feeding time (handling and ingestion). Bold names indicate consumption of unripe fruits.

<i>Woolly Monkeys (90, 96, 00)</i>		<i>Spider monkeys (1990)</i>	
<i>Gustavia hexapetala</i>	2527	<i>Gustavia hexapetala</i>	323
<i>Pseudolmedia obliqua</i>	879	<i>Ficus andicola</i>	320
<i>Brosimum alicastrum</i>	492	<i>Ficus yoponensis</i>	168
<i>Pourouma bicolor</i>	466	<i>Ficus schultesii</i>	99
<i>Henriettella fissanthera</i>	457	<i>Pourouma bicolor</i>	84
<i>Hymenaea courbaril</i>	181	<i>Astrocaryum chambira</i>	82
<i>Ficus andicola</i>	167	<i>Ficus nymphaeifolia</i>	78
<i>Ficus sphenophylla</i>	145	<i>Iriarteia deltoidea</i>	62
<i>Apeiba aspera</i>	142	<i>Brosimum utile</i> (unripe?)	54
<i>Inga alba</i>	140	<i>Oenocarpus bataua</i>	52
<i>Howler Monkeys (1990)</i>		<i>Capuchin Monkeys (1990)</i>	
<i>Pseudolmedia obliqua</i>	226	<i>Astrocaryum chambira</i>	1083
<i>Brosimum alicastrum</i>	150	<i>Oenocarpus bataua</i>	379
<i>Brosimum utile</i>	148	<i>Pourouma bicolor</i>	167
<i>Gustavia hexapetala</i>	97	<i>Ficus guianensis</i>	150
<i>Ficus yoponensis</i>	67	<i>Pseudolmedia obliqua</i>	147
<i>Ficus trigona</i>	63	<i>Socratea exorrhiza</i>	100
<i>Pseudolmedia laevigata</i>	25	<i>Apeiba aspera</i>	92
<i>Dipteryx micrantha</i>	24	<i>Ficus nymphaeifolia</i>	60
<i>Ficus membranacea</i>	23	<i>Perebea xanthochyma</i>	42
<i>Pourouma bicolor</i>	18	<i>Protium glabrescens</i>	35
<i>Squirrel Monkeys (2000)</i>			
	(%)		
<i>Ficus andicola</i>	46.5		
<i>Piper fresnoense</i>	10.7		
<i>Streptochaeta spicata</i>	9.7		
<i>Henriettella fissanthera</i>	8.1		
<i>Ficus americana</i>	6.1		
<i>Cecropia membranacea</i>	4.2		

Table 4. List of plant species postulated as potential keystone resources for frugivores in the Tinigua forests because they produce or are consumed during scarcity periods. Bold names indicate some extent of unripe consumption

Species	Consumer Specificity	Resource Reliability	Resource Production	Index
Oenocarpus bataua	8	3	177.2	7.32
Cecropia membranacea	35	3	9.6	6.36
Bursera inversa	30	3	6.8	5.90
Ficus andicola	38	2	5.4	5.41
Gustavia hexapetala	5	3	56.4	4.80
Brosimum alicastrum	14	3	1.8	4.51
Ficus sphenophylla	41	1	1.9	4.48
Brosimum guianense	12	3	0.2	4.31
Iriartea deltoidea	5	3	27.7	4.26
Astrocaryum chambira	8	3	0	3.98
Apeiba aspera	4	3	6.9	3.79
Pseudolmedia obliqua	19	2	0.1	3.77
Brosimum utile	5	3	1.4	3.77
Ficus americana	30	1	8.9	3.72
Dialium guianense	3	3	0	3.58
Henriettella fissanthera	26	1	2.8	3.28
Ficus trigonata	6	2	24	3.16
Pourouma bicolor	10	2	1.7	3.07
Enterolobium schomburgkii	6	2	0.7	2.72
Ficus trigona	14	1	14.7	2.53
Hymenaea courbaril	2	2	0	2.38
Ficus guianensis	14	1	0.9	2.27
Doliocarpus multiflorus	14	1	0	2.25
Inga alba	11	1	0	2.01
Ocotea tomentosa	10	1	0	1.92
Spondias venulosa	7	1	11.5	1.90
Ficus schultesii	8	1	0	1.76
Ficus yoponensis	7	1	0	1.68
Ficus nymphaeifolia	6	1	1.3	1.62

I estimated their potential as keystone species, looking at the number of species known to feed on the fruits, their reliability during fruit scarcity periods, and their production during these periods. The potential for acting as a keystone species was ranked from 0 to 10 for each of these four parameters (from the values in table 4), so that the closer the value is to ten, the better the chance to play a keystone role (following Peres, 2000). I used the average value for the three parameters (specificity, reliability and production at fruit scarcity) to order the potential species from Tinigua in decreasing order given their potential as keystone species. I discarded parameters such as redundancy and overall abundance, because they were not contemplated in the original definition of plant keystone resources (Terborgh, 1983), and because they might obscure the actual ecological role of fruits on animal populations.

Oenocarpus bataua turned out to be the fruit species with highest rank. This palm species produced large amounts of fruit in the community every year, including some time in the scarcity period, and has been observed consumed by a relatively small coterie of consumers (8 species). The second most important species was a pioneer species, *Cecropia membranacea*, which also produced fruits every year at the beginning of the fruit scarcity period. Its production was small compared to palm species, but it is consumed by more frugivore species. The third species in this list, *Bursera inversa*, shared the same keystone traits as the former species. Nine fig species are present in the list, small-fruited figs (e.g. *F. andicola* and *F. sphenophylla*) being the most important, with large number of frugivores feeding on them, and relatively high fruit production. However, no particular fig species appears to be a reliable source producing fruits every year. *Gustavia hexapetala* produced fruits at the end of the fruit scarcity period every year, and its coterie of seed dispersers is restricted to large primates. Two *Brosimum* species were included in the list, and they were consumed mainly for their unripe fruits. Beside *O. bataua*, two other palm species were included in this list of potential keystone fruit resources (*Iriartea deltoidea* and *Astrocaryum chambira*). In spite of their high reliability in periods of fruit scarcity *Apeiba aspera* and *Hymenaea courbaril* did not rank high because they were consumed by a small set of frugivores, and their fruit production was not very high. *Doliocarpus multiflorus* showed a low reliability value probably because the main fruiting vine in the area died after the first study period. Several fruits heavily consumed by primate species such as *Gustavia hexapetala*, *Spondias venulosa*, and *Pourouma bicolor* produced fruits usually at the beginning or the end of the fruit scarcity period, and were seldom consumed by birds. *Pseudolmedia obliqua* tends to be very variable in its phenology and it does not always produce in scarcity periods. Two species were included in the list (*Henriettella fissanthera* and *Inga alba*) because of an unusual timing of fruit production during just one year. About one third of the species included in the list corresponded to plants that were consumed at least temporally for their unripe fruits, suggesting that these kinds of fruit sources might play important ecological roles during periods of fruit scarcity.

DISCUSSION

The roles of certain plant resources that are suggested to play keystone roles for frugivores in tropical forests have not been tested, mainly because there are practical limitations and ethical considerations in carrying out appropriate experimental designs. Previous studies have suggested that species producing fruits in periods of fruit scarcity can play important roles for the whole frugivore community, given that the energy that the forest is providing them is less than the energy the animals need (Terborgh, 1986). This approach has been used in studies, including this one, but in the absence of a rigorous test, conservation efforts to preserve frugivorous animals and the integrity of lowland tropical forests by means of managing suggested keystone resources could result in failure. This approach assumes that the redundant production during periods of fruit abundance results in a waste of energy that is not used by frugivores. However, there are several frugivores that are known to accumulate fat reserves during periods of fruit abundance [i.e. woolly monkeys (Di Fiore, 1997; Peres, 1994b; and see other contributions in this book)]. So far we do not know the relative importance of these reserves compared to the production of apparent keystone resources producing in fruit scarcity periods. There are also cases of primates that mainly use fruits to store enough fat during good seasons, which allow them to hibernate during the lean season (Fietz & Ganzhorn, 1999). If management policies allow harvest or logging of species producing fruits in periods of fruit abundance, there should be a threshold point at which a low maximum fruit production in the community could not allow fat storage and even these fruiting peak species could limit frugivore populations.

There is recent evidence suggesting that some rodent species are food limited, even during periods of resource abundance in the Neotropics (Adler, 1998). Furthermore, the high correlation between general fruit production and primate biomass in Neotropical forests (Stevenson, 2001), and the lack of a significant correlation between primate abundance and the density of potential keystone resources (such as figs and palms), point to the importance of the overall pattern of fruit production. With regard to primate behavior, it is a common strategy for the largest Atelines to increase movement patterns during periods of fruit abundance (possibly to locate more food) and to save energy in lean periods (e.g. Di Fiore, 1997; Stevenson et al., 2000; Strier, 1992). This strategy is also consistent with the idea that for these animals which constitute a large proportion of the frugivore biomass in undisturbed Neotropical forests, the production of fruit resources in periods of abundance is a limiting factor. Therefore, I suggest that even plant species producing fruits in periods of fruit abundance can be determinant factors for frugivore populations. Some other observations at Tinigua seem to support this argument.

For example, a large *Dolioscarpus multiflorus* vine that was frequently visited by frugivores died from unknown causes in 1991. This species was one of the most important fruits in the overall diet of woolly monkeys during the first year of observations (Stevenson et al., 1994) because the monkeys consumed large amounts

of fruits from one particular individual during the period of fruit scarcity. However, the disappearance of the vine did not cause any decrease in woolly monkey populations, which has actually increased after that event (Stevenson, 2002). It may seem naïve to expect that an individual could support the population of woolly monkeys. However, the point I wish to make is that in an analysis of potential keystone species based on consumption and timing of fruit production for that year, *D. multiflorus* would have scored high, yet its removal did not alter the population densities of its consumers. Therefore at least two questions should stay in the minds of people trying to use these assessments for conservation purposes: 1.) Does the applicability of a keystone role depend on the sampling year in a particular system? And, 2) Should we really expect changes in the community from the removal of these uncommon resources? Although these cases are non-replicated and uncontrolled events, this case suggests again that other factors could be more important for the maintenance of the frugivore community in periods of fruit scarcity. These factors may include the acquisition of fat reserves from common species at periods of abundance, as well as non-fruit resources producing food at scarcity periods (e.g. Figure 2, Stevenson et al., 2000). Among these resources young leaves of several tree and vine species, as well as flowers of *Astrocaryum chambira* seem to be most important in the Tinigua community.

Several authors have suggested restricting the use of the term keystone species to resources that are not common or abundant (Mills et al., 1993). However, if overall abundance were included in the analysis made in table 4, species such as *Oenocarpus bataua* and *Gustavia hexapetala*, that are dense in the area and heavily consumed by primates during periods of fruit shortage would not rank high in the scores as potential important keystone species. Both species are known to be among the most important fruit sources for the most abundant frugivorous primates, which comprise the largest component of the vertebrate community in terms of biomass. Therefore, it seems logical to imagine that the removal of these resources from the community could have profound negative influences on the primates, perhaps more drastic than other sources with higher scores. In conclusion, I think that in the search of keystone species, low scores should not be given to species just for being abundant, if the main purpose is to protect important resources for frugivore populations.

A recent review identifying keystone plants in Neotropical forests (Peres, 2000) used redundancy and abundance as criteria to rank keystone species. An analysis including such factors turned out to show different results compared to those presented here (data not shown). For example, no palm or fig species would have ranked among the top five species, mainly because the palm species considered here are relatively abundant, and they produce fruits outside the scarcity period as well (Fig. 1). The absence of fig species within the most important species was in part because they also produce fruits at different seasons.

How Useful is the Keystone Resources Concept in the Conservation of Tropical Forests?

Given the difficulties involved in testing keystone roles, I consider that the concept is of limited use in the conservation of complex tropical forests. An approach looking at fruit production patterns and feeding behavior can certainly provide an idea of the resources that provide energy and nutrients to frugivores.

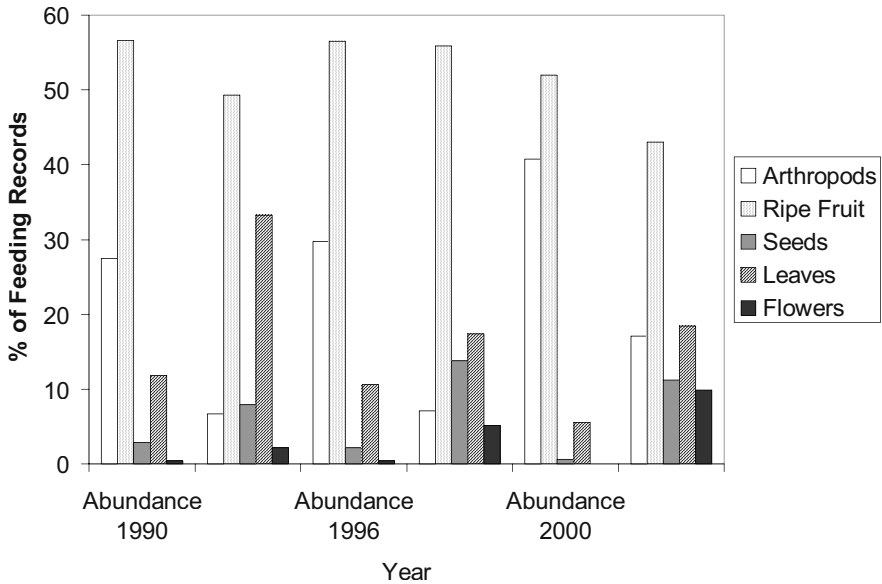


Figure 2. Comparison in diet composition of woolly monkeys in Tinigua Park between periods of fruit scarcity and fruit abundance at three different study years.

The preservation of common fruits and resources used during fruit scarcity may be a good approach to increase the chances of survival of the animals that feed on them. However, the persistence of the suggested keystone resources does not guarantee the integrity of the community if other resources are depleted.

Only three of the 29 species producing fruit in periods of scarcity at Tinigua were included in a review of potential keystone plant resources in other Neotropical forests (Peres, 2000). The majority of the plant species present at Tinigua have wide distributions, including Central America and peripheral Amazonia (Stevenson in prep.), so the disparity in keystone roles suggest that potential keystone resources may vary from place to place. For example, *Gustavia hexapetala*, the main fruit source for woolly monkeys at Tinigua, is not very important in the diet of these monkeys at other areas (Defler & Defler, 1996; Dew, 2001; Di Fiore, 1997; Di Fiore, 2001; Peres, 1994a), even though this plant species is also present at those localities.

Some palm species such as *Oenocarpus bataua*, that have been postulated as keystone species, seem to play important ecological roles in other neotropical forests (Peres, 2000), but the proportion of fruit consumers that these species have is low compared to other resources (8 vs. up to 41 species). The conservation of this palm species would probably not guarantee the survival of a diverse set of frugivores, and even the most abundant frugivore species such as the woolly monkeys will not be particularly benefited by such a management protocol.

Figs, especially small-fruited species, are visited by a large variety of frugivores, and as a group fig species tend to be present during periods of fruit scarcity (Table 2). The fact that different fig species have been postulated as keystone resources in different habitats suggests that the variability in their fruiting patterns is responsible for the keystone label when they produce during fruit scarcity periods. Fig species as a group fit the criteria of keystone plant resources. But it is puzzling why there is no positive correlation between the density of fig species and the abundance of primates in Neotropical forests (Stevenson, 2001). We found that some of the fig species that were heavily consumed during periods of fruit scarcity were completely ignored when there were other fruits available, and this low fruit preference has been found at other tropical sites (Conklin & Wrangham, 1994). This pattern of preference might be associated to low energetic contents compared to other fruits, and also argue against their potential value as keystone resources (Gautier-Hion & Michaloud, 1989). In this sense it would be interesting to know the energetic and nutrient value of figs compared to other plants with low energetic contents that are consumed in scarcity periods, such as young leaves and unripe fruits. In fact, the most consistent pattern of consumption during fruit scarcity periods, at least for primates, was feeding on young leaves and unripe fruits, suggesting that these resources are important components in the strategy to overcome fruit shortage (Stevenson et al., 2000).

There are some inherent characteristics in the life history of figs and the palm species postulated as plant keystone resources that predispose them to be consumed during periods of fruit scarcity. First, the specialized pollination system of fig by fig wasps requires multiple fruiting episodes each year to assure that the wasps will find fruiting trees in the community to lay eggs (Anstett et al., 1997). Thus, pollination system might be the cause of fruit production in periods of scarcity, perhaps independent of animal consumption and seed dispersal processes. On the other hand, most of the palm species postulated as keystone resources have large fruits which usually take longer periods to develop. Part of their importance as keystone resources, at least in Tinigua, was associated with the consumption of unripe fruits during the scarcity period (i.e. *Astrocaryum chambira*, *Oenocarpus bataua*, *Socratea exorrhiza*, and *Syagrus sancona*). If the benefit associated with seed dispersal at the start of the rainy period, when seedlings usually find better conditions for development (Garwood, 1982), applies to palm species, then there is a high probability of finding unripe fruits in scarcity periods prior to the rains. It remains to be seen if their consumption depends more on seasonal production than on nutritional factors in a variety of tropical forests.

Some other fruit sources suggested as keystone resources in this study, such as *Henriettella fissanthera* and *Inga alba*, fruited in the scarcity period only as exceptions to what seems to be their common fruiting patterns from more extensive records than those reported here. I do not know the causes for these deviations, but if they were due to unpredictable factors or chance effects, it is expected that opportunistic cases of this kind would be more frequent in diverse plant communities. Therefore we should include a potential stochastic factor in the sustainability of frugivore communities derived from the overall pattern of plant diversity.

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CHAPTER 4.

FLORISTICS, PRIMARY PRODUCTIVITY AND PRIMATE DIVERSITY IN AMAZONIA: CONTRASTING A EUTROPHIC VÁRZEA FOREST AND AN OLIGOTROPHIC CAATINGA FOREST IN BRAZIL

JEAN PHILIPPE BOUBLI

Abstract

Several factors such as rainfall, primary productivity, and plant species richness have been hypothesized to affect consumer species richness, possibly explaining differences in species richness among communities and on different continents. Primary productivity in particular has been suggested as important in determining species richness of consumer taxa, such as the primates, in the Neotropics. Here I contrast the floristics and phenological patterns of two Amazonian rainforest sites that differ markedly in primary productivity and yet have the same number of primate species: 1) an oligotrophic site—caatinga forests of Pico da Neblina National Park; and 2) a eutrophic site—várzea forests of Mamirauá. The objective of this comparison is to see how primary productivity interacts with floristics and phenology and ultimately, with primate species richness. With only 4 species each, the compared sites are characterized by low primate species richness. At both sites, low numbers of primate species are associated with an unusually low abundance of important primate food plants such as trees from the Burseraceae, Moraceae, Myristicaceae, Palmae and Sapotaceae. Moreover, in Neblina there is a long period of fruit scarcity and an overall low availability of fleshy fruits, which probably also contributes to the observed low primate species richness. In contrast, productivity in Mamirauá is high and fleshy fruits are abundant. These fruits, however, are mostly small in size and their seeds are most likely dispersed by birds, bats, fish, or water, not by primates. In this case then, primary productivity is not being largely transferred to primates as may be the case in other productive sites where preferred primate plant families are more abundant. Thus, when intertrophic interactions have a mutualistic nature such as the interaction between a fruit and a frugivore, a direct effect of primary productivity on all consumer taxa should not be expected. I suggest that in order to understand the effects of intertrophic interactions on consumer species richness in tropical rainforests it is important to first determine how the primary productivity is funnelled to the second trophic level.

Key words: Brazil, floristics, frugivory, primates, species richness, tropical forests

INTRODUCTION

One of the main tasks of ecology is to understand the patterns of species diversity among communities and on different continents (Brown, 1995, Rosensweig, 1995). As such, ecologists have been investigating several factors hypothesized to affect species diversity—i.e., abundance and diversity of predators, presence of competitors, food species diversity, primary productivity, rainfall patterns, soil quality, habitat heterogeneity, natural disturbances as well as historical, biogeographical and evolutionary factors (Ashton 1989, Begon et al., 1990, Huston 1994, Rosensweig, 1995).

A relationship between rainfall, plant productivity and plant species diversity has been hypothesized and appointed as important in determining species diversity at the second and subsequent trophic levels (Huston, 1994, Rosensweig, 1995). Kay et al (1997) have considered the effect of ‘bottom-up’ forces or plant primary productivity on primate species richness. These authors analyzed data from the neotropics and found a tight correlation between rainfall and several relevant variables namely primate species richness, tree species richness, number of wet months and primary productivity. They noticed that the curves for primate richness and productivity had similar shapes: Both increased with rainfall up to a maximum at approximately 2,500 mm/year and then fell off together at higher rainfall levels. They concluded that increased plant productivity led to increased species richness of primates because at higher productivity specialized species could maintain viability.

However, in the Amazon basin, primate species richness appears to follow a biogeographical east-west gradient with more species found near the Andes (west). Whether such pattern of species abundance follows a primary productivity gradient remains to be determined. Here, I contrast the floristics and phenological pattern of two Amazonian rainforest sites that differ markedly in primary productivity but have the same number of primate species: 1) Oligotrophic site—An extremely nutrient starved habitat represented by the white sand forests of Pico da Neblina National Park; and 2) Eutrophic site—A nutrient-rich habitat represented by várzea forest of Mamirauá as studied by Ayres (1986, 1993) with rich alluvial soils. The objective of this comparison is to see how is primary productivity interacting with floristics and phenology and thus, with primate species diversity.

*Study sites**Pico da Neblina*

Pico da Neblina study site (0°24' N/66°18' W) is located in the lowlands of Pico da Neblina National Park, in the Northwestern most part of Brazilian Amazonia on the border with Venezuela (Figure 1). The lowland area of Pico da Neblina is characterized by a high annual average rainfall (2,500 - 3,000 mm/year) and an average temperature of 26° C, with little fluctuation throughout the year (RADAM, 1978). The rainiest months are from May to September. Although, no month can be considered dry, considerably less rain falls from October to April (Figure 2). Soils

are extremely acidic at $\text{pH} = 4$ and among the poorest in the Amazon basin consisting of, for the most part, white bleached sands.

Pico da Neblina National Park is covered by dense, tall, evergreen lowland forest, submontane forests, montane forests and upland meadows. In the lowlands (~ 100 m a.s.l.), the forest is a mosaic of caatinga (forest on white sands *sensu* Klinge *et al.* 1977), terra firme (tall forest on dry land *sensu* Pires and Prance 1985) and chavascal (waterlogged forest). Igapó (seasonally-flooded forest) also occurs but is restricted to small areas along rivers.

This study focussed on an area of 500 hectares along the margins of the Cauaburi river, the main watercourse in the Park. Within this area, terra firme is the predominant forest type covering 44% of the total area with a canopy height of approximately 25 meters and emergents of up to 35 m (Boubli, 1997, 1999).

Chavascal is the second largest forest type covering 29% of the study site. This habitat is low-lying and thus, waterlogged during most of the year. Chavascal is physiologically similar to terra firme forest but has a higher occurrence of lianas (Boubli, 1997, 1999).

Caatinga corresponds to 27% of the study area. This forest is characterized by a dense understorey and a low canopy height of approximately 10 to 15 meters, with emergents of up to 25 m. Lianas are rare in this habitat. Caatinga occurs in the lower and higher parts of the study site, its structure and floristics being most likely determined by the soil. Caatinga is characteristic of areas covered by the acidic and well drained quartz sands; a bleached, white, coarse sandy soil mixed with rolled gravel (Boubli, 1997, 1999).



Figure 1. Location of the two study sites compared

Mamirauá

Mamirauá is located on the margins of Teiu lake in a young Holocene várzea near the mouth of the Japurá river, Amazonas (Figure 1). The area is characterized by several small lakes, streams, channels and swamps. In the height of the flooding season, water covers even the highest ground (Ayres 1986). Annual average rainfall is 2,850 mm with no real dry season (Ayres, 1993). However there is a considerable variation in rainfall with up to 3 times as much rain falling from December to March as compared to the period of July to October (Figure 2). Water level fluctuates as a consequence of rainfall. The total difference in water height registered at the study site was 11 m (Ayres, 1986). Water rise takes 8 months while the drop is quick at 4 months. Maximum height was reached in the months of May and June and the lowest in October.

Vegetation is of two main types: forested areas or restingas located on the higher grounds (30-40% of the area), 2) and open areas, or chavascal, relatively lower grounds (60-70%). Vegetation overlap between lower and higher restingas is only of 37% most probably because floods select against plant species unable to cope with prolonged periods of submersion.

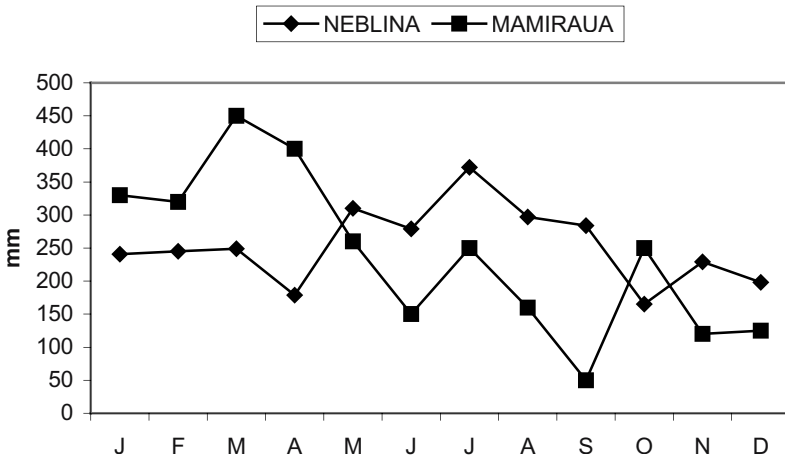


Figure 2. Rainfall at Pico da Neblina in 1995 and at Mamirauá in 1984.

METHODS

In Pico da Neblina, five botanical plots (2 ha total sampled area) in the form of belt transects (*sensu* Ludwig and Reynolds, 1988) were laid out for floristic study of the

area. The plots consisted of four 10 x 250 m plots (0.25 ha each - plots 2,3,4,5) and one continuous 10 x 1000 m plot (1 ha - plot 1). Plot 1 was placed haphazardly and was further subdivided into four 0.25 ha sub-plots (plot 1.1 to 1.4). The four smaller plots 2 to 5 were laid out such that all different forest types were represented in proportion to their contribution to the total area of the study site.

Within the plots, all trees with a diameter at breast height (DBH) equal to or greater than 10 cm were marked with aluminum tags and had their DBHs measured with a metric tape. Once a month from October 1994 to October of 1995 (but February), we scanned the crowns of 436 trees ≥ 10 cm DBH with binoculars (10 x 40) to record the presence/absence of young leaves, flowers, buds, and fruits (ripe and unripe). Trees in the phenology were chosen from a total pool of 818 trees with DBH ≥ 10 cm within the long 1 ha transect. Initially, all 818 trees from the botanical plot were used in the phenology. However, because the crowns of many trees were not visible due to thick canopy cover, we decided to reduce the sample to only those trees that offered a reasonable view of their crowns. The inclusion of poorly visible trees can greatly underestimate the production of fruits or flowers in the forest.

In Mamirauá two ha were also sampled. The first ha consisted of 16 25m x 25m quadrats placed within the area of the study site so that areas subjected to different depths were sampled. The second ha was divided into two belt transects randomly placed totaling 1000m x 10 m. All trees ≥ 10 cm DBH were marked and identified. For the phenology study, all trees from the two ha (i.e. from the 16 quadrats) were observed once a month from July 1983 to December 1984.

Fruits produced by trees in the sample plots of the compared sites were classified as fleshy or dry depending on the presence or absence respectively of animal attractants such as, aril, pulp, fleshy mesocarps etc. These data were obtained directly in the field in Pico da Neblina or, for Mamirauá, from the book *Fruits of the Guianan Flora* (Roosmalen 1985).

Both sites have been intensively studied in terms of their primate fauna. Information on primate diversity and density were obtained from these studies (Ayres 1986, Boubli 1997, 1999).

RESULTS

Floristics

Pico da Neblina

There were 1569 trees with diameter at breast height ≥ 10 cm in the sample (minimum of 229 species in 45 families) (Boubli 2002). A minimum of 229 species in 45 families were identified. In plot 1 (1ha) there were at least 161 species. The two tree species *Eperua leucantha* and *Hevea cf. brasiliensis* dominated the forest accounting for 29% of the sampled trees. High species dominance was more evident in the caatinga forest areas where the combined trees *Eperua leucantha*, *Micrandra*

sprucei and *Hevea cf. brasiliensis* accounted for 66% of all sampled trees. *Ficus* sp. trees were practically absent from the forest. Compared to Amazonian forests elsewhere, the ranking order of plant families in Pico da Neblina was peculiar in that Leguminosae *sensu latu* and Euphorbiaceae dominated the sample accounting for 52% of all marked trees (Boubli, 2002).

Of the 1569 trees ≥ 10 cm DBH in the two ha plots, at least 1,186 trees (76%) were dry fruit bearers. This high number is explained by the fact that the dominant species produced dry fruits – although more species produced fleshy fruits, the species producing dry fruits were more abundant. The 10 most common species in the two ha sample, representing 50% of all marked trees (780 individuals), produced large-seeded dry fruits protected by hard husks. The top five tree species in Importance Value (*sensu* Mori et al., 1983), *Eperua leucantha*, *Hevea cf. brasiliensis*, *Micrandra sprucei*, *Eschweilera* sp. and *Micrandra spruceana* all produced fruits with hard husks and large seeds that measured from 2 to 4 cm.

Mamirauá

In total there were 996 trees ≥ 10 cm DBH in the two ha sampled. A total of 174 species in 46 botanical families were present. Species dominance as in Pico da Neblina was not observed in Mamirauá. The most abundant species, *Eschweilera albiflora* (Lecy), *Pterocarpus amazonicus* (Fab) and *Malouetia tamaquarina* (Apo) together represented only 11% of the trees sampled.

Tree family composition also differed from other known Amazonian forests in that Euphorbiaceae was the most abundant family (14%) followed by Annonaceae and Leguminosae *sensu latu* (12% each), Lecythidaceae (6.4%), Apocynaceae (5.3%), Sapotaceae (4.5%) and Myrtaceae (4.3%). Moraceae occupied the 9th position. In the sampled forests, *Ficus* sp. was represented by only one individual.

The great majority of tree species in Mamirauá were adapted to animal dispersal (80%). However, in terms of individuals, 449 trees produced fleshy fruits. Of these, 200 produced small mostly bird, bat or fish dispersed and belonged to Annonaceae, Euphorbiaceae, Myrtaceae, and Meliaceae. Important primate food families such as Sapotaceae, Moraceae, Myristicaceae and Palmae accounted for 113 individuals or 25% of the fleshy fruit trees.

In order to put the floristic composition of both sites into perspective, I plotted in the same graph the results of this study with the combined sample of 48, 1 ha plots summarized by Terborgh and Andressen (1998) (Figure 4). Only the 16 families presented by Terborgh and Andressen were plotted here. Neblina and Mamirauá differed from Terborgh & Andressen's summary sample in that Palmae, Moraceae, Myristicaceae and Burseraceae were relatively rare families in these two sites whereas Euphorbiaceae, Guttiferae (not included in Figure 4) and Annonaceae were unexpectedly abundant.

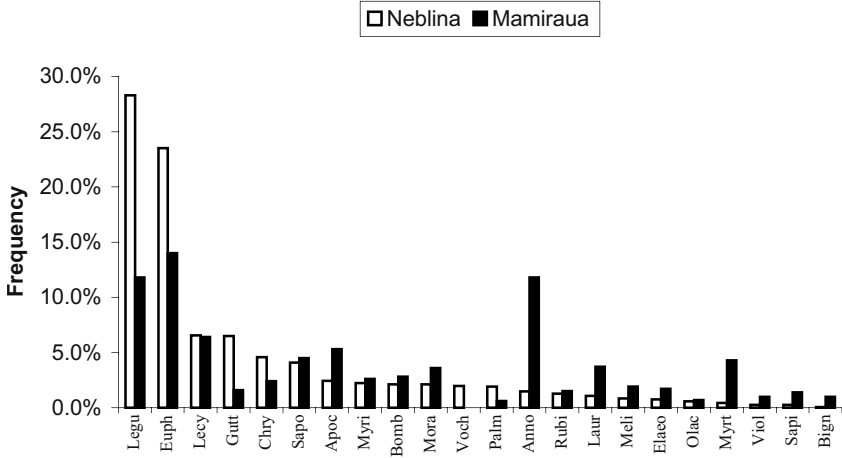


Figure 3. Plant family frequency in Pico da Neblina and in Mamirauá.

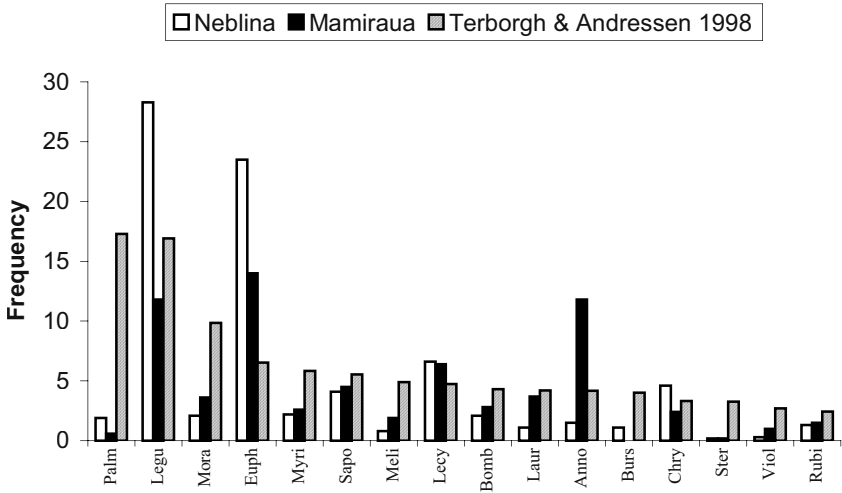


Figure 4. Plant family frequency in Pico da Neblina, Mamirauá and in a combined sample of 16 different 1 ha plots distributed throughout the Amazon basin (Terborgh and Andresen 1998).

Phenology

Pico da Neblina

Of the total sampled trees, 24% (103 individuals) produced 50% or more of their crown capacity of young leaves at least one month of the study. Maximum young leaf production occurred in the beginning of the dry season (October), immediately followed by flowers and young fruits (Boubli 1999). At the community level, leafing preceded flowering by one to two months. By March/April, most of the flushing activity had stopped. We recorded flower production on 143 (33%) trees. Buds and flowers were most abundant in December (59 and 67 individuals, respectively), the dry season. Most fruits were produced from January to July, *i.e.*, from the end of the dry season through the end of the wet season (Figure 5). Very few individual trees from the phenology sample produced fruits during the early-dry season (Figure 5). Unripe fruits were produced by 130 (30%) and ripe fruits by only 105 (24%). Unripe fruits were most abundant in the months of January and March (100 and 94 trees, respectively), whereas ripe fruits peaked in April (60 trees), the beginning of the wet season. Unripe fruits were most scarce from July through October; October 1994 being the lowest month with 2 trees with unripe fruits. Ripe fruits were most scarce from August through December; October and November being the lowest months with no trees bearing ripe fruits. There was a smaller peak of ripe fruits in June and July (14 species in each of these months) corresponding to slow-maturing fruits. Unripe fruits were present on individual trees from 1 to 8 months of the study, averaging 3 months per tree. Ripe fruits were available from 1 to 4 months, averaging 1.7 months per tree. At the peak, 13.7% of the trees bore ripe fruits.

Mamirauá

Leaves started to drop after fruiting in May. New leaf production peaked in April. There were two peaks of fruiting, in March-April after the peak in rain and the other in November-December, prior to the rains (Figure 5). Immature fruits were available from 3 to 5 months. At the peak, 14% of trees bore ripe fruits (Ayres 1993).

Fruit types

Neblina and Mamirauá had similar proportions of tree species producing dry and fleshy fruits with a predominance of the latter (Figure 6). When numbers of trees instead of species were examined however, there was a marked difference in the proportion of fleshy to dry fruit trees (Figure 7). In Neblina, 76% of the trees were dry fruit bearers whereas for Mamirauá this figure was around 40%. In Mamirauá, a large proportion of the fleshy fruits belonged to families such as Annonaceae, Myrtaceae, Melastomataceae, Elaeocarpaceae, Meliaceae, Guttiferae and Euphorbiaceae all producing small fruits dispersed preferably by birds, bats or fish (Figure 8).

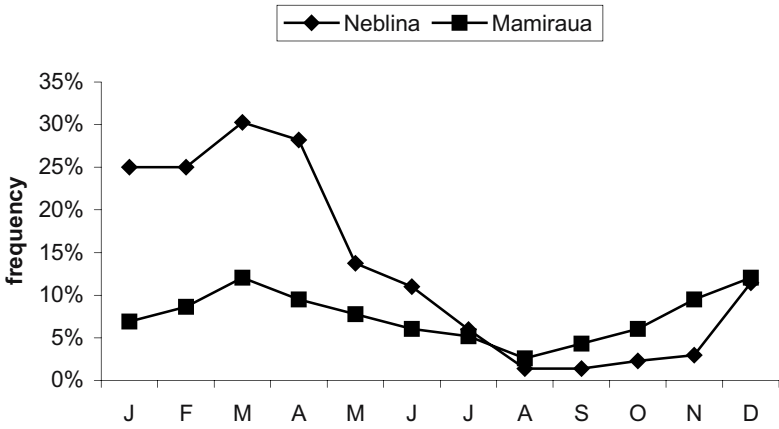


Figure 5. Fruit production in *Neblina* (1995) and *Mamirauá* (1984) (ripe and unripe fruits combined).

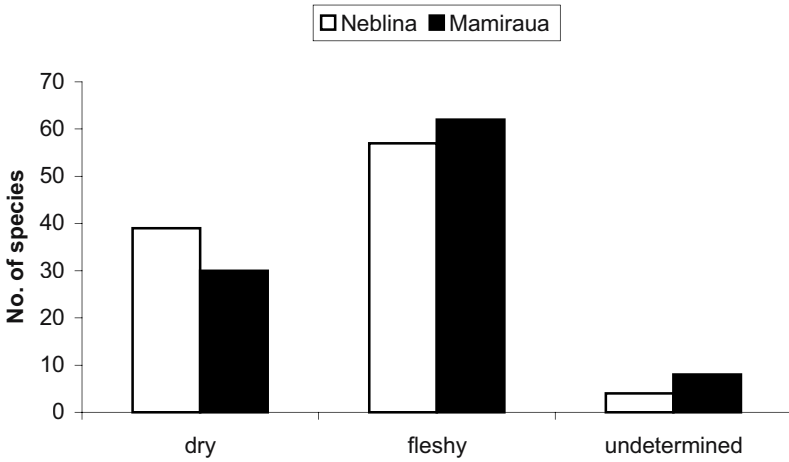


Figure 6. Proportion of tree species producing dry and fleshy fruits in *Neblina* and *Mamirauá*.

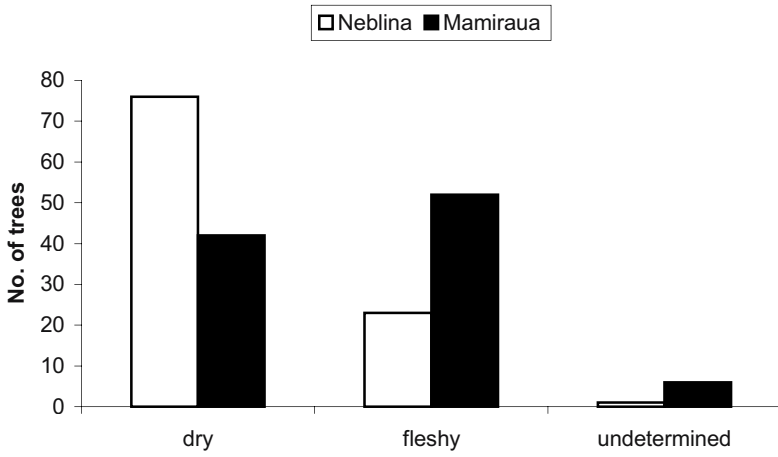


Figure 7. Proportion of individual trees producing dry and fleshy fruits in Neblina and Mamirauá.

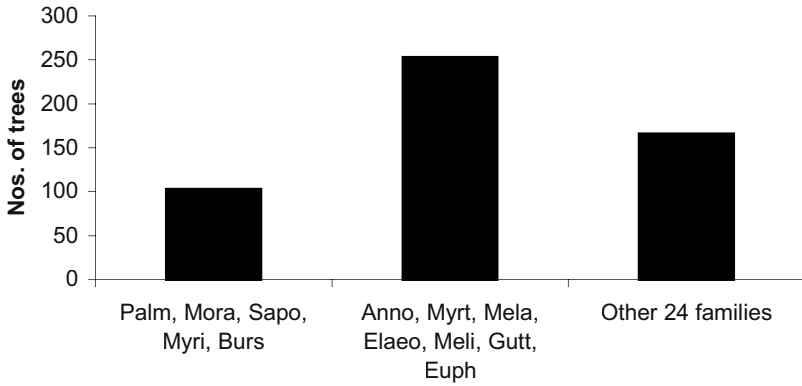


Figure 8. Numbers of trees producing fleshy fruits per family in Mamirauá.

Primary productivity

Primary productivity was not directly measured in either compared sites. However, at San Carlos de Rio Negro, a site near Neblina, and with a forest very similar to the one discussed here, Coomes (1995), found that the foliar concentrations of N were quite low (~ 13.8 mg/g) and average litterfall was 4.5 kg/ha/yr (in contrast to 13.3 kg/ha/yr in Barro Colorado Island, Panama, Foster, 1982) (Coomes, 1995). These data indicate that the San Carlos rainforest (and Neblina by extrapolation) had a low primary productivity.

In várzeas, soils are very rich from sediments brought from the Andes. Thus, nutrients are not limited. High productivity can also be inferred from the high leaf turnover since every year, most trees drop their leaves in the height of the flood (Ayres 1993). Moreover, várzea appears to provide more favorable foliage quality to arboreal folivores such as howlers, sloths hoatzins and iguanas which attain very high biomasses. All these species become rare in oligotrophic forests and are practically absent from Pico da Neblina.

Primate community

Both sites had the same number of primate species and similar primate eco-species (Ayres, 1986, Boubli, 1997). Their densities however, were much higher in Mamirauá. Except for the two small-bodied primates, i.e., titis in Neblina and squirrel monkeys in Mamirauá, the remaining species belonged to the same 3 genera present at both sites: uacaris, howlers and capuchins. Uacaris were the most frugivorous of all primates present but concentrated their diets on unripe seeds. Howlers ate a large proportion of leaves whereas capuchins and squirrel monkeys complemented their fruit diet with insects and small vertebrates (Ayres 1986, Boubli 1997). No information is available on the diet of titis from Neblina but it is possible that, like uacaris, these primates focused on unripe seeds of abundant fruit species. Densities/km² however were quite distinct (Table 1).

<i>Neblina (individuals /km²)</i>	<i>Mamirauá (individuals /km²)</i>
<i>Cacajao melanocephalus</i> (14)	<i>Cacajao calvus</i> (14)
<i>Cebus albifrons</i> (1.4)	<i>Cebus apella</i> (13)
<i>Alouatta seniculus</i> (2)	<i>Alouatta seniculus</i> (40)
<i>Callicebus torquatus</i> (1.6)	<i>Saimiri vanzolini</i> (95)

Table 1. Primate densities in Pico de Neblina and Mamirauá

DISCUSSION

In Pico da Neblina, rainfall was high and evenly distributed throughout the year, there was a high tree species and family dominance, fruit availability was quite seasonal and there was an overall low availability of fleshy fruits. Conversely, in Mamirauá, rainfall was more seasonal, no tree species or family dominance was observed, two fruiting peaks were observed and fleshy fruits were relatively more abundant.

Both sites differed considerably from other Amazonian rainforests in plant family composition as suggested by Terborgh and Andressen (1998). Important primate food plants such as trees from Sapotaceae, Moraceae, Palmae and Burseraceae (Peres, 1991, Roosmalen, 1985, Terborgh, 1983) all abundant in other Amazonian rainforests, were relatively scarce in Neblina and in Mamirauá. It is interesting to note that the east-west gradient in primate species diversity in the Amazon maps on a similar gradient in importance of plants of Moraceae, Palmae and to some extent, Sapotaceae (Steege et al., 2000).

In Neblina, low primate species richness might have been associated with the long period of fruit scarcity and the overall low availability of fleshy fruits in particular of Palmae, Moraceae, Sapotaceae, Myristicaceae and Burseraceae. Moreover, the site was possibly unsuited to primates with more folivorous proclivities such as howlers since leaf quality was possibly low (due to the low foliar concentration of N and thus, the resulting high C/N ratio, Milton, 1980).

Coley et al. (1985), hypothesized that plants growing at sites lacking in mineral nutrients would be expected to invest heavily in immobile defences such as tannins and thick cells walls. Janzen (1974) emphasized that caatinga leaves are rich in tannins explaining the scarcity of mammals and birds in the forests. Coomes (1985) found that caatinga forests had more secondary compounds because the tested species had a greater calorific value which he claimed were useful indicators for the presence of these chemicals.

The only primate found in relative abundance was the seed predator black uacari monkey that, due to dental specialization was able to break open the hard pericarps of the dominant fruit species and feed on their seeds.

Low primate species richness in Mamirauá might also have been associated with the low importance of key primate food plant families such as Palmae, Moraceae, Sapotaceae, Myristicaceae and Burseraceae. However, fleshy fruits of different plant families were relatively abundant in Mamirauá. In addition, primary productivity was supposedly high at that site, explaining the high densities attained by arboreal folivores such as howlers and sloths (Queiroz, 1995).

One possibility is that primary productivity in Mamirauá was not being translated into preferred primate fruits in that habitat. In Mamirauá, a large proportion of the fleshy fruits belonged to families such as Annonaceae, Myrtaceae, Melastomataceae, Elaeocarpaceae, Meliaceae, Guttiferae and Euphorbiaceae all producing small fruits dispersed preferably by birds, bats, fish or water.

It has been suggested that one of the most important means of seed dispersal in Amazonian flooded forests is by water. Goulding (1980) found that 35 out of 40

fruits examined in the flooded forests of Rondonia State were able to float for at least a few days. By floating, seeds can travel great distances and attain a relatively even sapatial distribution. For this reason, Ayres (1986) believes that water is possibly more efficient than other agents in dispersing seeds.

Thus, in Mamirauá, primary productivity did not appear to be affecting primate richness although it probably contibuted to their high biomass. In flooded forest habitats, the costs and benefits of seed dispersal may differ from that of Terra firme forests. In this habitat, it might be more efficient for trees to disperse their seeds via water and fish or other small vertebrate then via primates and large mammals.

In conclusion, bottom-up forces (primary productivity) may not always affect the diversity of all taxa when intertrophic interactions have a mutualistic nature such as the interaction between a fruit and a frugivore. The important task, then, is to unravel how is the primary productivity been funneled to the second trophic level.

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CHAPTER 5.

A 12-YEAR PHENOLOGICAL RECORD OF FRUITING: IMPLICATIONS FOR FRUGIVORE POPULATIONS AND INDICATORS OF CLIMATE CHANGE

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Abstract

Answering the fundamental ecological question of what determines animal abundance has become critical with the accelerating need for informed management plans for endangered species. A major difficulty in testing general hypotheses to account for variation in abundance is that periods of food scarcity, which may be responsible for limiting population size, occur on a superannual basis. Research on folivorous primates suggests that periods of food scarcity are critical in determining regional biomass; however, studies of frugivores have found no single fallback food generally used by all species. In this study we quantify fruit availability during a 12-year period in Kibale National Park, Uganda to determine patterns of fruit scarcity. Over these 12 years, temporal variability in fruit availability was high; the proportion of trees per month with ripe fruit varied from 0.14 to 15.93%. In addition, there was dramatic interannual variation in fruit availability: in 1990, on average only 1.09% of trees bore ripe fruit each month, while in 1999 an average of 6.67% of trees bore fruit each month. Over the past 12 years, fruit has become more available, fruit-scarce months have declined in frequency, and the duration of periods of fruit scarcity has decreased. If figs (*Ficus* spp.) served as a fallback food resource over these 12 years, they would have had to be available during months when few trees were fruiting. Over this 149-month period, there were 34 months when less than 1% of monitored trees fruited. Figs were not fruiting in 17 of these months, and, in only 11 of the 34 months were more than 1% of the fig trees fruiting. Rainfall data collected since 1903 indicates that the region is becoming moister, and droughts are less frequent. There has also been a significant increase in the maximum mean monthly temperature and a decrease in the minimum mean monthly temperature since we started recording these data in 1990.

Key words: Bottlenecks, conservation, fruit, frugivore, global climate change, keystone species, phenology, Uganda

INTRODUCTION

A fundamental issue in ecology is determining factors that regulate the density of animal populations. A variety of potential factors have been proposed to influence population size and density, including external factors, such as food resources, weather, predation, and disease and internal conditions, such as territoriality and aggressive behaviors (Nicholson, 1934; Andrewartha & Birch, 1954; Krebs, 1978; Boutin, 1990; Milton, 1996). The importance of understanding determinants of animal abundance has increased with the need to develop informed management plans for endangered or threatened species. With respect to primates, these theoretical issues are critical because tropical forests occupied by primates are undergoing rapid anthropogenic transformation and modification (National Research Council, 1992). Cumulatively, countries with primate populations are losing 125,140 km² of forest annually; based on global estimates of primate densities, this results in the loss of 32 million primates per year (Chapman & Peres, 2001). Other populations are being affected by forest degradation (logging and fire) and hunting.

Unfortunately, understanding and predicting factors that determine the primate abundance has proven extremely difficult. A fundamental difficulty in testing general hypotheses to account for variation in primate abundance is that periods of food scarcity, which may be responsible for limiting population size, may occur on a superannual basis. For folivorous primates, evidence suggests that bottleneck periods of food scarcity are critical in determining regional biomass. Milton (1979) and McKey (1978) proposed that year-round availability of digestible mature leaves, which are used by folivorous primates when more preferred foods are unavailable, limits their population size (see Milton et al., 1980, and Milton, 1982, 1998 for a full description of this model). By measuring overall mature leaf acceptability as the ratio of protein to fiber, several subsequent studies have found positive correlations between colobine biomass and this index of leaf quality (Waterman et al., 1988, Oates et al., 1990; Davies, 1994; Chapman et al., 2002a). By collecting all previously published data on colobine biomass and protein to fiber ratio of mature leaves and combining it with new data from a series of forest fragments, Chapman et al. (submitted) demonstrated that Milton's protein to fiber model accounted for 87% of the variance in folivore biomass.

Unfortunately, for frugivores there is no single fallback food generally used by all species in an area. For example, in Kibale National Park, Uganda, during periods of food scarcity mangabeys (*Lophocebus albigena*) eat foods more resistant to crushing; the smaller redbellied monkeys (*Cercopithecus ascanius*) rely on young leaves and insects (Lambert et al., submitted); and chimpanzees feed on terrestrial vegetation (Wrangham et al., 1993). In general, an accumulation of data on the diets of frugivorous primates over the last three decades has also led to a growing appreciation of dietary variation within species, including differences among populations, among groups in a single population, and within a single group over time (Chapman, 1987; Gautier-Hion, 1988; Chapman & Chapman, 1990; Gautier-Hion et al., 1993; Poulsen et al., 2001; Chapman et al., 2002b). As a result of this

dietary flexibility, long-term studies are needed to evaluate the importance of superannual periods of fruit scarcity to frugivores.

The objective of this study was to quantify fruit availability over a 12-year period in Kibale National Park, Uganda. This provides a means to evaluate the frequency and duration of periods of fruit scarcity, interannual variation in fruit production, the ability to infer fruit patterns from a single year study, and the potential importance of fruit scarcity periods in determining frugivore population dynamics. In addition, we consider if and when figs (*Ficus* spp.) serve as a fallback food resource over the 12 years. Figs have been frequently presented as examples of keystone plant resources in tropical forests (Terborgh, 1986; Power et al. 1996), and recently textbooks have presented figs as a clear case of the keystone species concept (Bush, 2000). The widespread acceptance of figs as keystone species has come in the absence of detailed data demonstrating their importance (Gautier-Hion & Michaloud, 1989; Peres 2000). Finally, we quantify changes in patterns of fruiting (over 12 years) and rainfall and temperature (over the last century) to examine regional patterns of global climate change and consider how such changes might influence phenology patterns.

METHODS

Study sites

Kibale National Park (766 km²) is located in western Uganda (0 13' - 0 41' N and 30 19' - 30 32' E) near the foothills of the Ruwenzori Mountains (Struhsaker, 1975, 1997; Skorupa, 1988; Chapman et al., 1997). The park consists of mature, mid-altitude, moist semi-deciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%), and plantations of exotic trees (1%; primarily *Cupressus lusitanica*, *Pinus patula*, *P. caribaea*, and *Eucalyptus* spp.; Chapman & Lambert, 2000). Mean annual rainfall in the region is 1749 mm (1990-2001, or 1547 mm from 1903-2001); the mean daily minimum temperature is 14.87 C°; and the mean daily maximum temperature is 20.18 C° (1990-2001). There are distinct wet and dry seasons that are bimodal in distribution. May to August and December to February tend to be drier than other months (Chapman et al., 1999a).

Kibale forest received the protected status of a National Park in 1993. Prior to this date, it was a Forest Reserve, gazetted in 1932 with the stated goal of providing a sustained production of hardwood timber (Osmaston, 1959). A polycyclic felling cycle of 70 years was initiated, and it was recommended that logging open the canopy by approximately 50% through the harvest of trees over 1.52 m in girth (Kingston, 1967). We have been monitoring the phenology of trees in the Kanyawara area of Kibale, which has three different forestry compartments, since 1990. K-15 is a 360-ha section of forest that experienced heavy selective felling in 1968 and 1969. Total harvest averaged 21 m³/ha or approximately 7.4 stems / ha (Skorupa, 1988); however, incidental damage was much higher and it is estimated

that approximately 50% of all trees were destroyed by logging and incidental damage (Skorupa, 1988; Chapman & Chapman, 1997). A total of 18 tree species were harvested, with nine species contributing more than 95% of the harvest volume (Skorupa, 1988). Just to the south, is the K-14 forestry compartment, a 405-ha forest block that experienced low intensity selective felling from May through December 1969 (averaging 14m³/ha or 5.1 stems/ha). Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa, 1988; Struhsaker, 1997). K-30 is a 300-ha area that has not been commercially harvested; however, prior to 1970, a few large stems (0.03 - 0.04 trees ha⁻¹) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa, 1988; Struhsaker, 1997).

Phenological Monitoring

Over 12-years three different phenological monitoring systems were used. Twenty-six 200 m x 10-m transects were established at random locations along the existing trail system at Kanyawara in January 1990 producing a sampling area of 5.2 ha (Chapman et al., 1999b). At both sites, all trees with a diameter at breast height (DBH) \geq 10 cm and within 5 m of the trail were tagged and the DBH recorded. A total of 2096 trees (67 species) were tagged. Phenological data for all trees in these plots were recorded monthly between January 1990 and April 1996. During that time 72% of the trees flowered. The majority of those individuals that did not flower were small individuals and were probably immature. Subsequently, from May 1996 to May 1998 we randomly selected 6 of these 26 plots to continue monitoring. And, 591 trees were monitored each month in an area of 1.2 ha. Finally, since May 1998 (until May 2002 analyzed here) we evaluated phenological patterns using a phenology trail system that monitored 300 individuals from 33 species (average number of individuals / species = 8.8, range = 2-12).

For each monitored tree we determined the presence of different leaf stages (i.e., leaf buds, young leaves, and mature leaves), flowers, and ripe and unripe fruit. Data were collected by Ugandan field assistants, the first and second author, and North American volunteers. Inter-observer precision in evaluating phenological status was repeatedly assessed throughout the study.

We analyzed overall patterns of fruit availability, considering (a) all species that produce fruits and (b) the 10 most abundant species. The 10 most abundant species and their densities are the following: *Uvariopsis congensis* (60.4 tree/ha), *Markhamia platycalyx* (50.0 tree/ha), *Bosqueia phoberos* (50.0 tree/ha), *Celtis durandii* (47.1 tree/ha), *Diospyros abyssinica* (40.0 tree/ha), *Funtumia latifolia* (33.8 tree/ha), *Chaetacme aristata* (17.1 tree/ha), *Strombosia scheffleri* (12.5 tree/ha), *Pancovia turbinata* (10.8 tree/ha), and *Dombeya mukole* (9.2 tree/ha). To consider if and when figs (*Ficus* spp.) could serve as a fallback food resource over the 12 years, we monitored 37 fig trees from January 1990 to April 1996, 12 from May 1996 to May 1998, and 24 since May 1998.

Rainfall data were available between 1903 to 1971 from the Government of Uganda meteorological records for the town of Fort Portal (approximately 20 km east of Kanyawara, supplied by T.T. Struhsaker), between 1972 to 1989 from T.T. Struhsaker (Kanyawara), and from 1990 to present from our data (Kanyawara). Temperature data were available from NASA (http://www.giss.nasa.gov/cgi-bin/update/name_or_map.py) from 1905 - 1948 for Fort Portal, from 1976 - 1989 from T.T. Struhsaker (Kanyawara), and from 1990 to present from our data (Kanyawara).

Ideally, to evaluate whether fruit scarcity can regulate frugivore populations, only those fruits suitable for a particular frugivore species would be considered. Unfortunately, identifying suitable fruits is extremely difficult. Many fruits eaten during periods of fruit scarcity are likely not preferred by the animals. Thus, fallback foods capable of sustaining a population may not be eaten during typical years, and their importance can only be determined through long-term observations (Chapman et al., 2002c). As a result of these difficulties, we report the fruiting patterns of all species, whether frugivores are known to eat them or not. We consider all types of fruits, since even wind-dispersed fruits are often consumed by frugivores. In Kibale approximately 80% of the tree species produce fleshy fruits that are eaten and presumably dispersed by frugivores (Chapman et al., unpublished data).

When there are appreciable differences in mean values, variation can be evaluated using the coefficient of variation (CV; Sokal & Rohlf, 1981). We use the CV to evaluate interannual variation in monthly fruit production. The CV was calculated as the standard deviation of the proportion of monitored trees bearing ripe fruit each month divided by the mean.

RESULTS

Phenology

On average, 3.97% of monitored trees bore ripe fruit each month. However, temporal variability in fruit availability was high; the proportion of trees with ripe fruit varied from 0.14 to 15.93% per month (Fig. 1). Interannual variation in fruit availability was also high (Table 1). In 1990, an average of 1.09% of trees bore ripe fruit each month; while in 1999, an average of 6.67% trees bore fruit each month. If a month of fruit scarcity is considered as one with less than 1% of monitored trees bearing ripe fruit, there is considerable interannual variation in how often frugivores experienced food shortages (Table 1). For example, 9 of the 12 months in 1990 had <1% of the trees with fruit; while in 2000, no month had less than 1% of trees fruiting.

Table 1. Interannual variation in fruit production (proportion of trees monitored each month bearing ripe fruit) in Kibale National Park, Uganda. #<1% and #<2% are the number of months in a year where there are less than 1% and 2% of the trees monitored with ripe fruit. Months with the lowest (Lowest) and highest (Highest) proportion of trees with ripe fruit are also presented.

Year	Mean	CV	#<1	#<2	Lowest	Highest
1990	1.17	1.49	9	10	1.14	6.11
1991	1.09	1.16	9	11	0.29	4.87
1992	2.06	1.03	6	9	0.44	6.62
1993	2.35	0.89	4	7	0.54	6.3
1994	4.35	0.82	0	4	1.17	10.55
1995	3.93	0.65	1	3	0.98	8.92
1996	4.49	0.91	0	2	1.1	15.93
1997	5.13	0.7	1	3	0.18	11.36
1998	2.22	0.73	4	5	0.37	5.5
1999	6.67	0.48	0	1	1.4	12.28
2000	6.14	0.51	0	1	1.17	13.06
2001	5.93	0.33	0	0	3.47	9.34

Fig. 1 suggests that in general fruit has become more available to the frugivores of Kibale over the past 12+ years; year and the proportion of trees that with ripe fruit are positively correlated ($r=0.557$, $P<0.001$). This relationship holds for two of the three phenological methods (Jan 1990 to April 1996: $r=0.506$, $P<0.001$, May 1996 to May 1998: $r=-0.133$, $P=0.526$, June 1998 to May 2002: $r=0.398$, $P=0.005$). There was also a decline in the number of fruit scarce months each year over the 12 years ($r=-0.820$, $P<0.001$).

Consistency in fruit production may be important for frugivore populations since a less variable fruiting schedule would have fewer periods of fruit scarcity and fewer periods of superabundance of fruit that cannot be utilized. Over the 12 years, there is a consistent decline in the annual coefficient of variability (Table 1; $r=-0.921$, $P<0.001$).

There was no difference in the proportion of fruiting trees ($t=0.192$, $P=0.848$) or the proportion of figs with ripe fruit ($t=0.418$, $P=0.677$) between wet and dry season months.

Frugivores, particularly the larger ones, may be able to cope with short periods of food scarcity by using stores or by losing weight. Thus, it may be long periods of fruit scarcity that are critical. There were 13 periods of fruit scarcity (<1% of monitored trees bearing ripe fruit) over the 12 years. The average period of fruit scarcity was 2.4 months, but fruit-scarce periods lasted as long as 9 months. If we define a fruit scarce month as one in which less than 2% of the trees bore ripe fruit, then there were 17 periods of fruit scarcity that had an average duration of 3.4 months, and the longest period was 16 months. Using either criteria the average

duration of the longest period of fruit scarcity in a year decreased over the 12 years (1% $r = -0.820$, $P < 0.001$, 2% $r = -0.920$, $P < 0.001$).

It seems reasonable to speculate that certain fruiting tree species may be particularly important to specific frugivores. For example, with the fruiting of an abundant species with nutritious fruits, females may build up reserves necessary for reproduction, possibly synchronizing births among females (Lee 1987, Butynski 1988). To have a robust sample to consider fruiting patterns, we consider the 10 most abundant species. These species show a diversity of fruiting patterns over the 12 years (Fig. 2a,b). *Uvariopsis congensis* exhibited a fairly regular pattern of fruiting, where approximately 60% of the entire community fruited synchronously typically in June or July (although over 50% of the population did fruit in December 1991). Despite this synchronized pattern, there were often a number of years between fruiting events. For example, *U. congensis* fruited in June 1996, but did not fruit again until July 2000. While *Celtis durandii* had very poor fruiting seasons in 1990 and 1991, subsequently greater than 30% of the trees fruited each year, typically in the October to December period, although it did not fruit in the fall of 2000. A significant proportion of the *Strombosia scheffleri* population only fruited once during the entire 12 years. *Funtumia latifolia*, *Chaetacme aristata*, and *Dombeya mukole* had irregular fruiting patterns; however, they all seemed fruit poorly in the first 3 years of the study. *Diospyros abyssinica* similarly had an irregular fruiting pattern, and never more than 12% of the population fruited in a given month. As a group, *Ficus* spp. had an irregular fruiting schedule (the sample size was not adequate to evaluate each species separately). Less than 4% of the population of *Markhamia platycalyx*, *Bosqueia phoberos*, and *Pancovia turbinata* fruited in any year. While there were many trees of these species monitored, only a few ever fruited, and these fruiting events tended to be in the first few years of the study.

Figs as Fallback Foods

On average the density of figs trees bearing fruits was 0.29 trees/ha each month. In Kibale, redtail monkeys have a home range of 24 ha, while blue monkeys and mangabeys have home ranges of 50 ha and 410 ha, respectively (Cords, 1987; Melnick & Pearl, 1987). If figs (*Ficus* spp.) served as a fallback food resource over these 12 years, they would have had to be available during months when few trees were fruiting. Over this 149-month period, there were 34 months when less than 1% of the monitored trees fruited. The average density of fruiting fig trees during these months was 0.21/ha. Thus, redtails would have had on average five fruiting trees available, and blue monkeys would have 10 fruiting fig trees in their home range. However, fallback foods should always be available when the preferred resource is lacking, so it may not be appropriate to consider the average. In the 34 months when fruit was scarce, figs were not fruiting in 17 of these months, and in only 11 of the 34 months were more than 1 % of the fig trees fruiting.

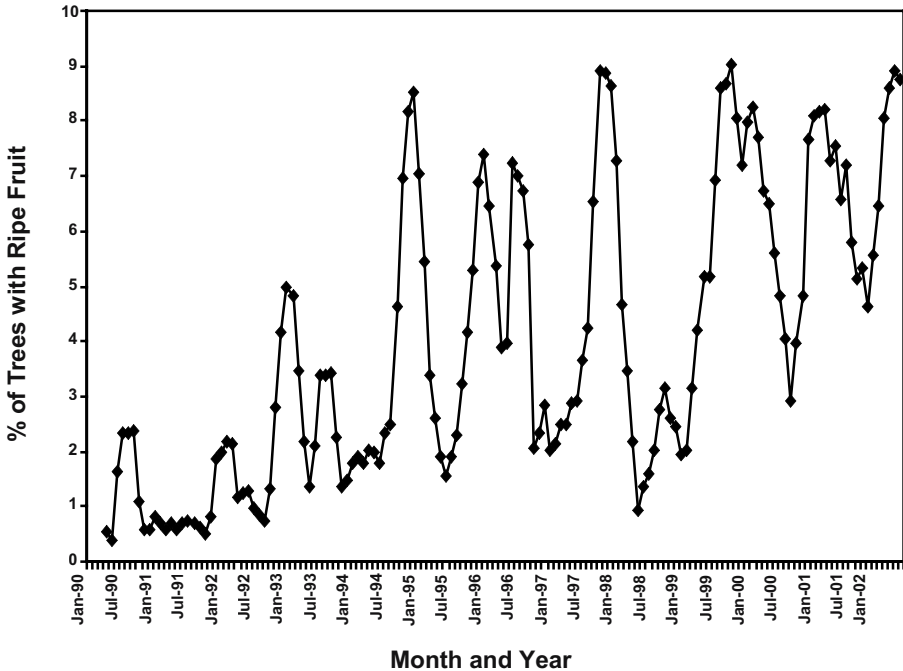


Figure 1. The 4-month running average of the percentage of trees bearing ripe fruit in Kibale National Park, Uganda over a 12-year period.

Climate Change

Rainfall data collected since 1903 indicates that the region is becoming moister (Fig. 3); year and annual rainfall are positively correlated ($r=0.415$, $P<0.001$; see also Struhsaker, 1997). If a drought year is considered one with less than 1300 mm of rain a year, then there has also been a decline in the number of drought years per decade over the last century ($r_{sp}=0.850$, $P=0.002$). There has also been an increase in the maximum mean monthly temperature since we started recording it in 1990 at the field station at Kanyawara ($r=0.767$, $P<0.001$; Fig. 4). This trend is supported by data collected since 1975 by T.T. Struhsaker and ourselves ($r=0.767$, $P<0.001$; Fig. 5). In contrast, the average monthly minimum temperature has decreased over that same period ($r=-0.652$, $P<0.001$; 1990 to 2002 $r=-0.784$, $P=0.003$; Fig. 5). Examining temperature data available from 1905 to the present (the average of the minimum and maximum daily temperatures) suggests an increase in temperature; however, the trend was not significant ($r=0.161$, $P=0.204$; Fig. 6). This analysis averaged maximum and minimum temperatures, and if these parameters are changing in opposite directions as is indicated in Fig. 5, it is not surprising that this relationship is not significant. Fig. 6 does, however, suggest that there may be some long-term cycles in temperature.

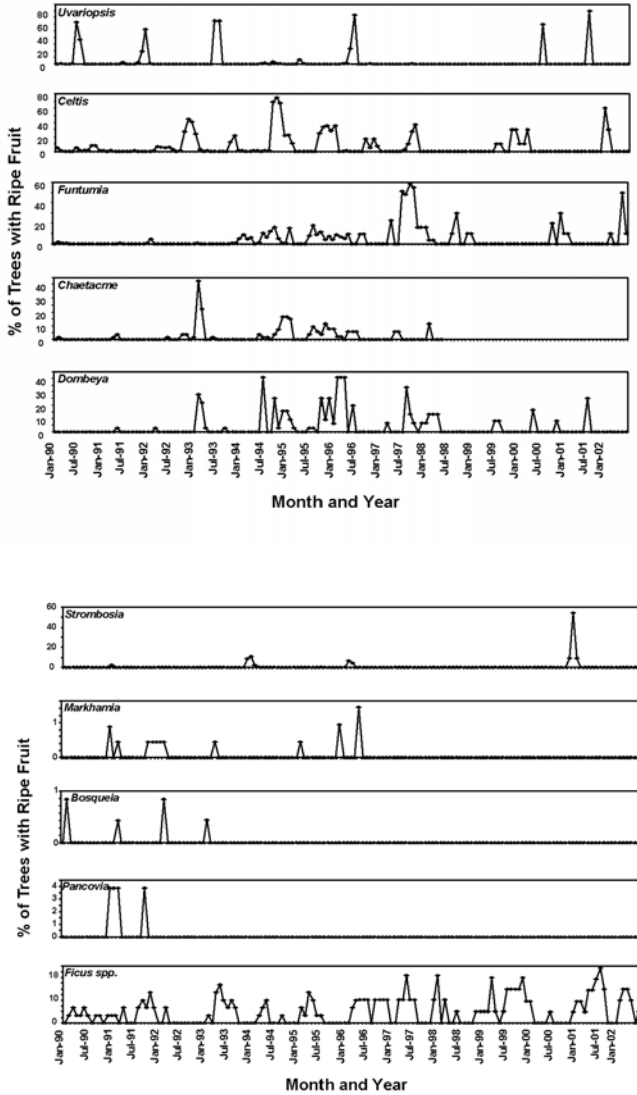


Figure 2a,b. The percentage of trees bearing ripe fruit for the 10 most common species in Kibale National Park, Uganda over a 12-year period (*Uvariopsis congensis* 60.4 tree/ha, *Markhamia platycalyx* 50.0 tree/ha, *Bosqueia phoberos* 50.0 tree/ha, *Celtis durandii* 47.1 tree/ha, *Diospyros abyssinica* 40.0 tree/ha, *Funtumia latifolia* 33.8 tree/ha, *Chaetacme aristata* 17.1 tree/ha, *Strombosia scheffleri* 12.5 tree/ha, *Pancovia turbinata* 10.8 tree/ha, and *Dombeya mukole* 9.2 tree/ha).

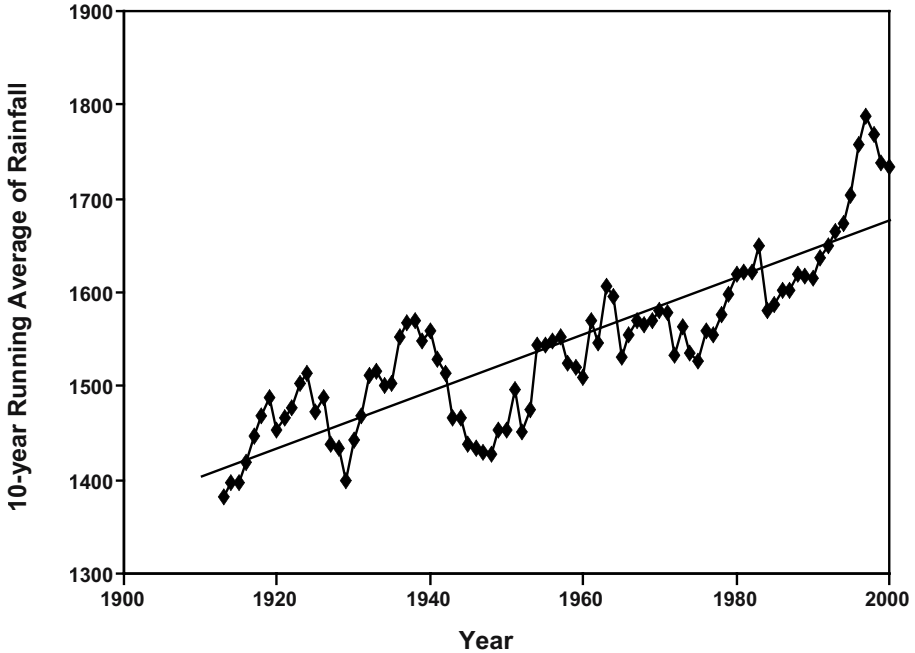


Figure 3. The 10-year running average of the annual rainfall in the area of Kibale National Park, Uganda.

Phenology

We quantified patterns of fruit availability over a 12-year period in Kibale National Park, Uganda to begin to understand the potential importance of periods of fruit scarcity in determining frugivore population dynamics. Over the 12 years there was a great deal of temporal variability in fruit availability. In addition, the frequency and duration of periods of fruit scarcity varied dramatically over the years. The nature of this variability has a number of implications for our understanding of frugivore population dynamics. First, the variability indicates conclusions from studies that are less than 3 or 4 years should be made with caution. This applies issues, such as competition, dietary adaptations, territoriality, and population regulation. For example in a 45-month study of red colobus (*Procolobus badius*) Chapman et al. (2002c) found consistent increased use of particular plant parts.

DISCUSSION

Second, over this 12-year period, there were 13 periods (34 months) when less than 1% of monitored trees fruited. The average period of fruit scarcity was 2.4 months, but fruit scarce periods lasted as long as 9 months. These data suggest that the

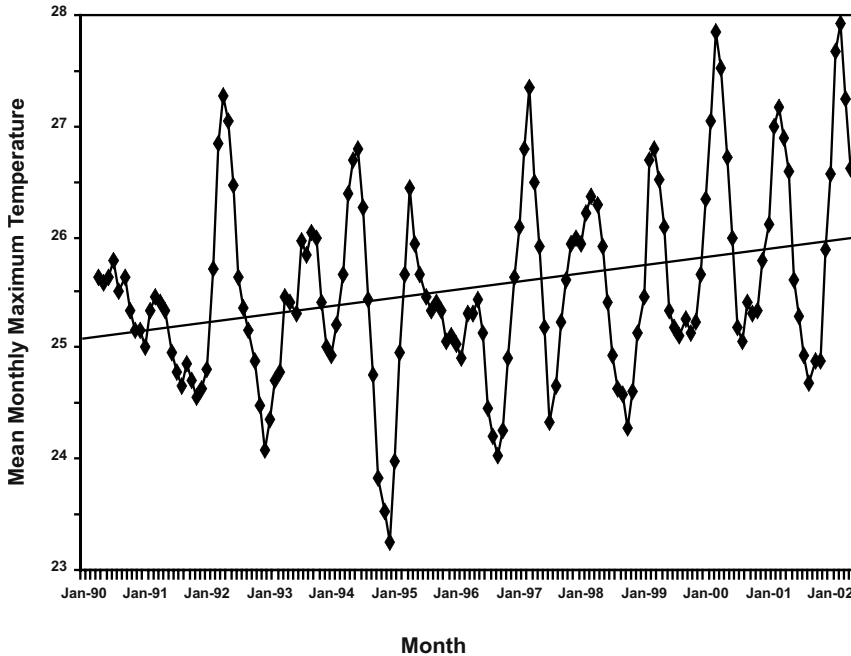


Figure 4. The 4-month running average of the monthly mean maximum temperature ($^{\circ}\text{C}$), measured at Kibale National Park, Uganda.

availability of fruit greatly exceed the consumptive capacity of the frugivores of Kibale during periods of abundance, but these periods alternate with times of scarcity when frugivores are obliged to feed on alternative resources, likely of inferior quality. Given the frequency and duration of these periods of fruit scarcity, it is quite possible that they have an important regulatory function on primate densities.

Figs as Fallback Foods

Terborgh (1986) suggested that palm nuts, figs, and nectar play an important role in the nutrition of frugivorous vertebrates during periods of fruit scarcity in one Neotropical forest. This suggestion was based on the low interannual variation in fig production, irregular timing of their fruiting period, and the high rate of fig consumption by frugivorous animals. The perception that figs constitute an important fruit resource for many frugivorous species is supported by a number of studies from different geographical regions (Janzen, 1979; Foster, 1982; Milton et al., 1982; Leighton & Leighton, 1983; Lambert & Marshall, 1991; O'Brien et al., 1998; Goodman et al., 1997; Kannan & James; 1999). Many frugivores consume

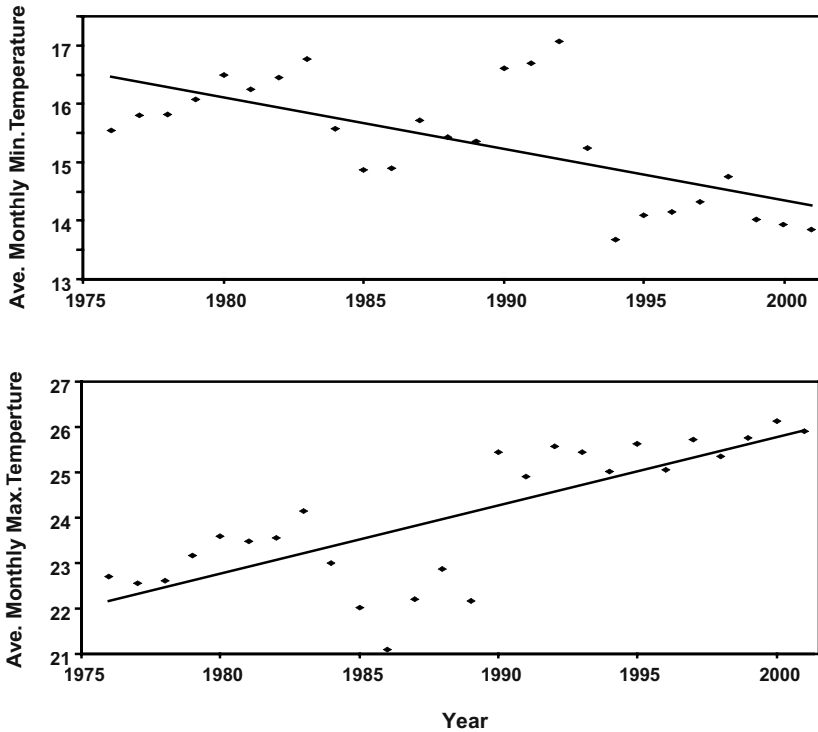


Figure 5. The average monthly (a) minimum and (b) maximum temperature ($^{\circ}\text{C}$) measured at Kibale National Park, Uganda.

figs in Kibale (Conklin & Wrangham, 1994). However, for figs to act as a fallback food for frugivores they must consistently produce abundant fruit during fruit scarce times. In this study, no figs fruited in the area we monitored in 17 out of 34 fruit-scarce months, suggesting that figs do not consistently fruit during fruit-scarce times. Thus, figs may provide fruit resources during some fruit-scarce months, but the number of trees is probably not adequate nor the fruiting phenology consistent enough to sustain all frugivore populations, particularly territorial species with relatively small home ranges. It seems likely that the role of figs as a fallback food is scale dependent. Borges (1993) studied the giant squirrel (*Ratufa indica*), a solitary, territorial species, and found figs were important only to those individuals who had access to figs in their territories. This is likely the case for the frugivorous primates of Kibale. During periods of fruit scarcity, figs can best be exploited by mobile species with large home ranges and the ability to track fruiting figs. For species with small feeding ranges, like redtail monkeys, figs are unlikely to be important resources for all groups during periods of fruit scarcity.

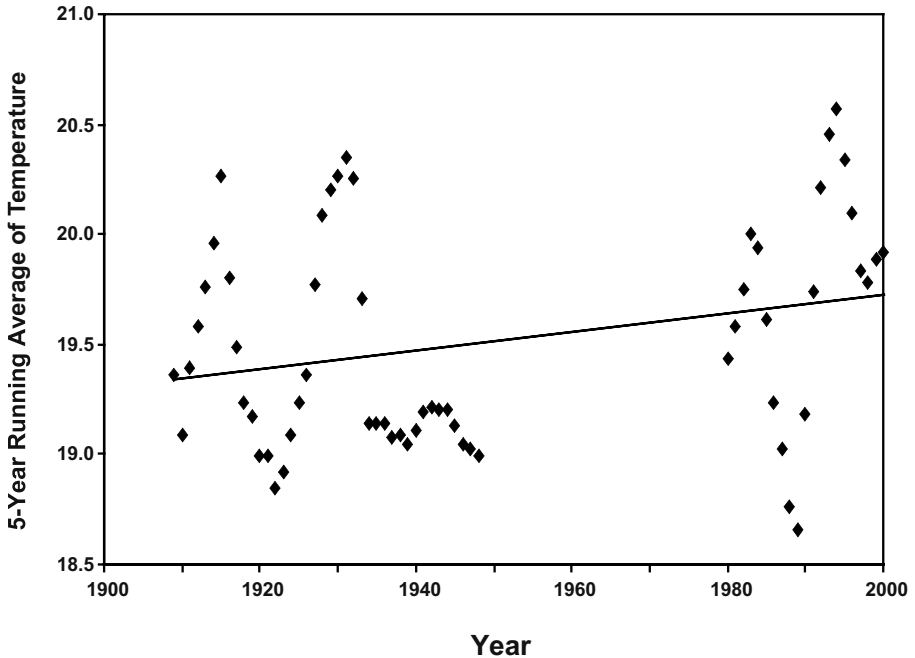


Figure 6. The average of the minimum and maximum daily temperatures ($^{\circ}\text{C}$) recorded at Fort Portal (1905-1948) and Kibale National Park, Uganda (Kanyawara 1976-2001).

Similarly, Gautier-Hion & Michaloud's (1989) study in Gabon showed that figs were infrequently eaten by most species, occurred at very low densities, and had unpredictable fruiting patterns. They concluded that fig fruits were not staple foods and could not sustain most populations of frugivorous species during periods of low fruit availability. At least for African frugivores, there may not be a single resource on which frugivore populations rely. Gautier-Hion & Michaloud (1989) determined that monkeys and large birds in Gabon depend on the fruit of two species of Myristicaceae and one species of Annonaceae. Other studies from central Africa have demonstrated that large birds may migrate to track fruit resources during fruit scarce times, whereas frugivorous monkeys shift their diets to seeds, leaves, and insects (Poulsen et al., 2002).

Climate Change

Rainfall data collected since 1903 indicate that the region is becoming moister, and droughts are less frequent. There has also been an increase in maximum mean monthly temperature and a decrease in minimum mean monthly temperature since we started recording these data in 1990. The higher temperatures and increased rainfall recorded over 12 years at Kibale may be indicative of larger global patterns. The earth's climate has warmed by approximately 0.6°C over the past 100 years

with two main periods of warming (1910 – 1945 and 1976 – present), and the 1990's is the warmest decade on record (Walther et al., 2002). Of course, ecological communities do not respond to global averages. Rather, regional changes, which are highly spatially heterogeneous, are more relevant in the context of ecological response to climatic change. The climate change documented from the Kibale region, suggests that regional changes can be much larger than the global average.

Over the past 12 years, we documented that fruit has become more available, fruit scarce months have declined in frequency, and the duration of periods of fruit scarcity has decreased. These changes correspond to local changes in climate. There is a growing body of literature that suggests that recent climatic changes have differentially affected a broad range of organisms with diverse geographical distributions (Hughes, 2000; Wuethrich, 2000; Ottersen, 2001). For example, the average first flowering date of 385 British plant species has advanced by 4.5 days over the past decade compared to the previous four decades (Fitter & Fitter, 2002). In Borneo a severe drought linked to the El Nino-Southern Oscillation event of 1997-1998, caused a substantial break in the production of inflorescences on dioecious figs, and led to the local extinction of the wasp pollinators at Lambir Hills National Park (Harrison, 2000). Changes in phenology and fruit production of trees will likely have a cascading effect on frugivorous animals and pollinating insects that are directly dependent on plant resources.

Three species, *Markhamia platycalyx*, *Bosqueia phoberos* and *Pancovia turbinata*, all fruited in the first few years of our study; however, only a small proportion of each populations fruited. These are all common species, and one would expect a greater proportion of the population to fruit. It is possible that the climatic conditions found in the early half of the century were more favorable for these species (see Struhsaker (1978) for an alternative explanation for *Markhamia platycalyx*). At our Dura River site in Kibale which is approximately 12 km south of Kanyawara and has less rainfall (1500 mm), a large proportion of the *Bosqueia phoberos* population has repeatedly fruited in recent years (Chapman et al. 2002a, Chapman unpublished data).

Conservation Implications

Unfortunately, it is relatively rare that long-term data are available from tropical forest systems. Given this and the fact that tropical forest systems are being rapidly transformed, it seems useful to speculate on the conservation implications of our findings. First, we documented that fruit production is highly variable among years, periods of fruit scarcity occur on a superannual basis and the frequency and duration of fruit-scarce periods are such that they may limit the size of frugivore populations. Thus, a study in any single year will unlikely provide the needed insights to understand relationships between frugivore numbers and fruit availability.

Second, since figs tend to occur at a low density, the importance of figs during periods of fruit scarcity will likely be limited to frugivores that have access to figs in their territories or feeding ranges. During periods of fruit scarcity, figs can best be exploited by mobile species with large home ranges and the ability to track fruiting

figs. For species with small feeding ranges, like redtail monkeys, figs are unlikely to be important resources for all groups during periods of fruit scarcity. Thus, suggestions to manage fig abundance in areas should be viewed with extreme caution, since the management strategy will only affect a small subset of the frugivore community. Also, evidence from elsewhere in Africa suggests that there may not be a single resource on which frugivore populations rely, rather the important fallback resources may vary among areas (Gautier-Hion & Michaloud, 1989; Poulsen et al., 2002).

Finally, our data build on the findings of Struhsaker (1997) and indicate that the climate of the Kibale region is changing. Whether this represents consistent long-term changes associated with global warming, or shorter-term fluctuations is not known. Regardless, the plant phenological patterns and the animals dependent on these plants are experiencing changes. Responses to this climate change are likely complex and vary among species. In general, fruit production in the Kibale region is increasing, but for certain species the current conditions appear unsuitable for flowering or fruiting. Thus, we may see the local loss of those species.

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CHAPTER 6.

AN INTERSITE COMPARISON OF FRUIT CHARACTERISTICS IN MADAGASCAR: EVIDENCE FOR SELECTION PRESSURE THROUGH ABIOTIC CONSTRAINTS RATHER THAN THROUGH CO-EVOLUTION

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Abstract

Fruit and seed characteristics are compared between a dry deciduous forest in the west and a humid littoral forest in the south-east of Madagascar to discriminate between the role of abiotic factors (humidity, climate, soil characteristics) and frugivorous vertebrates for the evolution of morphological and biochemical fruit characteristics. The sites differed in abiotic conditions but contain very similar communities of frugivorous vertebrates. Fruit selection by two lemur species (*Eulemur fulvus* and *Cheirogaleus medius*) that are important for seed dispersal and that are present at both study sites, was compared between sites to examine fixed selection criteria that could give rise to possible co-evolution between frugivores and their fruit species on the one hand or to dietary flexibility of the frugivores on the other hand. Our results show that most fruit characteristics differ significantly between study sites. Food selection by both lemur genera in relation to morphological and biochemical fruit characteristics co-varies closely with their representation at a given site. These results indicate that morphological and biochemical characteristics are more likely the result of abiotic conditions rather than of interactions between frugivorous lemurs and their food.

Key words: *Cheirogaleus medius*, *Eulemur fulvus*, frugivory, seed dispersal, lemurs, co-evolution, Madagascar.

INTRODUCTION

The study of interactions between fruits and their vertebrate consumers has generated a great deal of interest in recent decades, especially in tropical forests where most plant species depend on frugivorous animals for dispersal of their seeds (see Willson et al., 1989 for a review). Attracting frugivores is crucial for these plants in order to ensure reproduction by seed dispersal (Howe and Smallwood, 1982). Morphological fruit characteristics, such as color, pulp richness, hardness of the shell, seed size, and patterns of spatio-temporal distribution have been interpreted as co-adapted features that govern animals' choice of fruit species.

Most seed dispersal studies and reviews of correlations between frugivore food selection and fruit characteristics have produced little empirical support for tight co-evolutionary relationships (Chapman, 1995; Eriksson and Ehrlén, 1998; Fisher and Chapman, 1993; Gautier-Hion et al., 1985; Herrera, 1984; Howe, 1984; Howe and Smallwood, 1982; Lambert and Garber, 1998), as most plant species do not depend on one single species of disperser. In most cases a range of taxonomically distinct frugivores may consume and disperse the seeds of the same fruiting species (Bollen, 2003; et al., 2004; Chapman, 1995; Chapman and Chapman, 1996; Ganzhorn, 1988; Gautier-Hion et al., 1985; Herrera, 1986). Fruit traits are likely to evolve in response to other selection pressures or may perform more than one function (Willson and Whelan, 1990). Data from the fossil record suggest that morphological fruit traits often have remained relatively constant for millions of years (Chapman, 1995; Fisher and Chapman, 1993).

Primates represent a major group of mammalian seed dispersers in the tropics. Studies have demonstrated that many primate species rely heavily on fruit and that they represent a large component of the frugivore biomass (25-40%; Bourlière, 1985; Chapman, 1995; Chapman and Onderdonk, 1998; Julliot, 1996; Lambert and Garber, 1998; Terborgh, 1983). In Madagascar, lemurs have been postulated to be important seed dispersers (Birkinshaw, 1999, 2001; Dew and Wright, 1998; Ganzhorn et al., 1999a; Overdorff and Strait, 1998; Ralisoamalala, 1996; Scharfe and Schlund, 1996) in particular since the guild of frugivorous birds and bats is depauperate in this island as compared to other continents (Böhning-Gaese et al., 1999; Fleming et al., 1987; Ganzhorn et al., 1999a; Goodman and Ganzhorn, 1997; Wright, 1997; Wright and Martin, 1995).

In this study, we investigate whether morphological and biochemical fruit characteristics can be linked to abiotic conditions or whether there is evidence for co-evolution between these fruit characteristics and the main consumers that are involved in seed dispersal, i.e. *Eulemur fulvus* and *Cheirogaleus medius*. We selected two types of forest in Madagascar growing under very different climatic and edaphic conditions: evergreen littoral wet forest and dry deciduous forest. Both sites had a similar complement of frugivore species, having six genera and five species in common.

The following predictions were tested:

1. If fruit characteristics evolved mainly in response to abiotic conditions we expect different morphological and biochemical fruit characteristics at the two sites
2. If fruit characteristics co-evolved in response to selective pressure of consumers we expect that characteristics of food items at both sites do not differ, as the guild of frugivorous vertebrates is very similar at both sites.
3. The second prediction listed above requires that selection criteria of frugivores are species-specific. We therefore predict that these consumers will have a specialized diet irrespective of fruit availability, as is supposed by co-evolution.

MATERIALS AND METHODS

Study Sites

Data were collected at two sites: Sainte Luce (STL) and Kirindy/CFPF (KIR).

In STL the study site is a 377-ha fragment of humid littoral forest located in south-eastern Madagascar, 50 km north of Fort-Dauphin at 24°45' S, 47°11' E. Data collection was carried out by AB and GD in between November 1999 and February 2001 (Fig. 1; Donati 2002). Average annual rainfall is about 2690 mm, with a marked rainy season from November through February while no clear dry season could be detected (Bollen, 2003). Mean temperature is about 23°C and ranges from 12°C to 33°C. The average relative humidity is about 90% (QMM, unpubl. data). The littoral forest of STL is characterized by a relatively open or non-continuous canopy, which is 6 to 12 m in height with emergents of up to 20 m (Lewis Environmental Consultants, 1992). The diameter at breast height (DBH) of trees rarely exceeds 30-40 cm (Rabevohitra et al., 1996). Littoral forest grows on sandy soils and occurs within 2-3 km of the coast at an altitude of 0-20 m (Dumetz, 1999).



Figure 1. Location of study sites.

The forest of Kirindy/CFPP is a forestry concession of the Centre Formation Professionnelle Forestière de Morondava at 20°04'S, 44°40'E, some 60 km north of Morondava (west-Madagascar). It consists of 12,000 ha of dry deciduous forest. Annual rainfall averages about 800 mm with a long distinct dry season from April to October when most trees lose their leaves. Most rain falls between December and February. Mean temperature is around 25°C and relative humidity varies between 58% and 67% with an average of 63% (Rakotonirina, 1996; Sorg and Rohner, 1996). The canopy reaches 10-12 m in height. Trees with DBH < 30 cm predominate (Ganzhorn and Sorg, 1996; Ganzhorn et al., 1999b). The forest grows on sandy soils with a narrow band of vertisols along the seasonal Kirindy River about 20 km east of the coast at an altitude of 18-40 m (Sorg and Rohner, 1996). Here, studies were carried out by GD, JF, DS and JG between 1987 and 1997.

Frugivore Guild

Ten fruit-eating vertebrate species occur at STL, nine at KIR (Table 1). Some of these species are strictly frugivorous, while others are more granivorous or omnivorous. However, for the latter the majority of their diet (>50%) consists of fruits and/or seeds so they may be considered as possible seed dispersers. Two lemur species were studied in more detail for this study. These were *Eulemur fulvus rufus* in KIR and *E. f. collaris* in STL and *Cheirogaleus medius* at both sites. These species, particularly *E. fulvus*, are supposed to represent very important, if not essential, seed dispersers in Malagasy forests (Ganzhorn et al., 1999a).

Phenology and Pluviometry

In STL a phenological transect with a total of 423 individual trees belonging to 95 species and 439 families was set up by AB and GD and monitored between January 2000 and January 2001. Trees sampled for phenology had a DBH > 5 cm and an effort was made to obtain 5 individuals per species whenever possible. Twice a month, presence or absence of young leaves, flowers, unripe and ripe fruits were recorded. A Tru-Check Rain Gauge was installed at the campsite in December 1999. It was checked and emptied each morning around 6 a.m. during the whole study period. For KIR rainfall and phenological data were taken from Sorg and Rohner (1996) involving 80 individual trees of 56 species (26 families) monitored over several years (1978-1987). For the present phenology analysis only large overstory tree species were considered. Small trees, shrubs, vines and epiphytes were left out in order to allow comparison between sites. A sub-sample of both phenologies (STL: 54 spp., KIR: 32 spp.) was extracted to include only those plant species that had been characterized morphologically (see below).

Table 1. Frugivorous, granivorous and omnivorous vertebrate species possibly involved in seed dispersal in Sainte Luce and Kirindy. Diet: F: frugivorous, G: granivorous; Ffo: frugi-folivorous; foF: foli-frugivorous; O: omnivorous; Activity: D: diurnal, N: nocturnal, C: cathemeral; Body mass (in g) and Body length (in cm) and their potential role as seed dispersers (D) or seed predators (P) in these ecosystems.

Scientific Name	English Name	STL	KIR	Diet	Activity	Body ^a mass	Body ^{ab} length	Impact seeds
AVES								
<i>Treron australis</i>	Malagasy Green Pigeon	x	x	F	D	236	32	D
<i>Alectroenas madagascariensis</i>	Malagasy Blue Pigeon	x		F	D	173	28	D
<i>Hypsipetes madagascariensis</i>	Madagascar Bulbul	x	x	F	D	45	24	D
<i>Coracopsis nigra</i>	Lesser Vasa Parrot	x	x	G	D	246	35	P
<i>Coracopsis vasa</i>	Greater Vasa Parrot	x	x	G	D	525	50	P
MAMMALIA								
CHIROPTERA								
<i>Pteropus rufus</i>	Madagascar Flying Fox	x		F	N	500-750	23-27	D
PRIMATES								
<i>Propithecus verreauxi</i>	Verreaux's Sifaka		x	FoF	D	3000	40-47	D,P
<i>Eulemur fulvus collaris</i>	Collared Brown Lemur	x		F	C	2000-2300	40-47	D
<i>Eulemur fulvus rufus</i>	Red-fronted Brown Lemur		x	Ffo	C	1600-2100	45	D
<i>Microcebus murinus</i>	Grey Mouse Lemur		x	O	N	60	12.5	D
<i>Microcebus berthae</i>	Berthe's Mouse Lemur		x	O	N	30	12.5	D
<i>Microcebus rufus</i>	Brown Mouse Lemur	x		O	N	40-45	12.5	D
<i>Cheirogaleus major</i>	Greater Dwarf Lemur	x		O	N	443	25	D
<i>Cheirogaleus medius</i>	Fat-tailed Dwarf Lemur	x	x	O	N	119-282	20	D

^a Data from Donati (pers. comm.;2002), Fietz and Ganzhorn (1999), Ganzhorn et al. (1999a), Goodman et al. (2003), Langrand (1990). ^b Total length for birds and bats but head/body length for lemurs.

Plant and Fruit Characteristics

In STL and KIR fruits of 173 and 171 plant species belonging to 58 and 47 families respectively were sampled and characterized (Table 2).

Table 2. Plant families, genera and species sampled in Sainte Luce and Kirindy. In bold the five most important plant families per site are indicated regarding species number. There are 30 plant families in common.

Families	STL <i>N</i> sp	KIR <i>N</i> sp	TOTAL <i>N</i> genera	COMMON <i>N</i> genera
Anacardiaceae	3	4	4	1
Annonaceae	5	0	2	0
Apocynaceae	1	3	4	0
Araceae	1	0	1	0
Araliaceae	2	0	1	0
Arecaceae	5	1	2	0
Asclepiadaceae	0	1	1	0
Asteraceae	0	2	2	0
Asteropeiaceae	1	0	1	0
Bignoniaceae	3	4	5	1
Bombaceae	0	2	1	0
Families	STL <i>N</i> sp	KIR <i>N</i> sp	TOTAL <i>N</i> genera	COMMON <i>N</i> genera
Boraginaceae	0	1	1	0
Burseraceae	1	2	2	0
Buxaceae	0	1	1	0
Canellaceae	1	0	1	0
Capparaceae	1	0	1	0
Celastraceae	2	1	3	0
Combretaceae	1	6	3	1
Connaraceae	1	1	1	1
Dichapetalaceae	2	0	1	0
Ebenaceae	2	4	1	1
Elaeocarpaceae	2	0	1	0
Ericaceae	1	0	1	0
Erythroxylaceae	3	1	1	1
Euphorbiaceae	8	14	13	1

Fabaceae	3	16	17	0
Flacourtiaceae	7	1	6	1
Guttiferae	5	1	3	1
Hammamelidaceae	1	0	1	0
Hernandiaceae	0	1	1	0
Hypocrateaceae	1	0	1	0
Icacinaceae	2	0	1	0
Lauraceae	4	0	3	0
Loranthaceae	3	0	1	0
Lecythidaceae	1	1	2	0
Liliaceae	4	1	4	0
Loganiaceae	3	5	2	1
Lythraceae	0	1	1	0
Melastomataceae	1	0	1	0
Meliaceae	1	4	6	0
Menispermaceae	1	1	2	0
Monimiaceae	3	0	1	0
Moraceae	5	3	3	1
Myricaceae	1	0	1	0
Myristicaceae	2	0	1	0
Families	STL	KIR	TOTAL	COMMON
	<i>N</i> sp	<i>N</i> sp	<i>N</i> genera	<i>N</i> genera
Myrsinaceae	1	0	1	0
Myrtaceae	6	0	3	0
Ochnaceae	1	1	2	0
Olacaceae	1	1	2	0
Oleaceae	5	3	4	1
Pandanaceae	3	2	1	1
Passifloraceae	0	2	1	0
Pedaliaceae	0	1	1	0
Physenaceae	1	0	1	0
Pittosporaceae	2	0	1	0
Podocarpaceae	1	0	1	0
Ptaeroxylaceae	0	3	1	0
Rhamnaceae	0	2	2	0
Rubiaceae	23	8	20	2

Rutaceae	3	2	2	1
Sapindaceae	4	2	5	1
Sapotaceae	2	2	3	0
Sarcolaenaceae	4	2	4	0
Saxifragaceae	2	0	1	0
Scrophulariaceae	0	1	1	0
Simaroubaceae	0	1	1	0
Solanaceae	0	1	1	0
Sphaerosepalaceae	1	1	1	1
Sterculiaceae	0	3	3	0
Strelitziaceae	1	0	1	0
Tiliaceae	0	9	1	0
Ulmaceae	1	0	1	0
Verbenaceae	1	3	2	1
Violaceae	1	0	1	0
UNKNOWN	15	37		0
Sum	173	171	181	19
Maximum	23	16	20	2
Minimum	0	0	1	0
Average	3.0	1.8	2.4	-

Morphological Characteristics

Variables used to characterize fruits were:

growth form of parent plant: large tree, small tree and shrub, others (including herbs, vines and epiphytes);

fruit type: berry, drupe, capsule, pod, samara, synconia, others;

pulp type: juicy soft, juicy fibrous, dry fibrous, aril, no pulp;

(in phenology 'fleshy' fruits are characterized as juicy soft, juicy fibrous or arillate; 'non-fleshy' fruits are dry fibrous or do not have any pulp);

color: yellow-orange, red, purple, brown, green, others (comprising black, gray and white), (multicolored fruits were put in the category of the most conspicuous color present);

odor: absent, present;

number of seeds: 1-2, 3-10, 11-50, 50+;

fruit weight: <1 g, 1-10 g, 11-50 g, >50 g;

fruit length: <10 mm; 10-30 mm; >30 mm;

seed length: <10 mm, 10-20mm, >20 mm.

fruit protection: dehiscent, indehiscent with thin husk; indehiscent with thick husk;

seed protection: no protection; seed coat or lignified kernel;

dispersal type: zoochorous (exo- and endo-) or non-zoochorous including anemochorous, hydrochorous, autochorous.

The characterizations were modified based on the original classifications by Gautier-Hion et al. (1985) and Lambert and Garber (1998). Epiphytes, vines, shrubs, large (>6 m) and small trees (<6 m) but no herbs were considered. Fruits and seeds were weighed fresh using spring or electronic balances and measured using scales and calipers with 0.01 g and 0.01 mm precision, respectively.

Chemical Characteristics

Ripe fruits were dried in the sun or in a drying oven, ground to pass a 2 mm sieve, and dried overnight at 50-60°C prior to analyses. Samples were analyzed for neutral (NDF) and acid (ADF) detergent fiber (Goering and Van Soest, 1970; Van Soest, 1994; modified according to the instructions for use in an Ankom Fiber Analyzer). Neutral detergent fiber (NDF) represents the percentage of fibrous material non digestible for herbivores with unspecialized digestive systems. Acid detergent fiber is composed of cellulose and lignin. Total nitrogen was determined using the Kjeldahl procedure. Total nitrogen was not converted to crude protein as the conversion factors for heterogeneous samples are unclear (Milton and Dintzis, 1981). Extractable or soluble proteins were assessed with BioRad after extraction of the plant material with 0.1 N NaOH for 15 h at room temperature. Soluble carbohydrates and procyanidin (condensed) tannins were extracted with 50% methanol. Concentrations of soluble sugar were determined as the equivalent of galactose after acid hydrolyzation of the 50% methanol extract. This measurement correlates well with concentrations obtained with enzymatic analyses of glucose, fructose and galactose (Ganzhorn and Tomaschewski, unpubl. data). Concentrations of procyanidin tannin were measured as equivalents of quebracho tannin (Oates et al., 1977; Porter and Hemingway, 1990). Lipids were determined by the Soxhlet method. Biochemical analyses were carried out at the German Primate Center (Göttingen) and at the Institute of Zoology, Department of Ecology and Conservation (University Hamburg).

Fruit Eating

In STL diets of both lemur species were assessed by tree watches (36 hr watches from hides at 30 tree species, 1-2ind/sp), opportunistic observations, fecal analyses and analyses of fruit traps that form part of an extensive ecological study on seed dispersal and seed predation (Bollen, 2003). Additional feeding data of *Eulemur fulvus collaris* were also compiled during all-day and all-night follows (Donati, 2002; Donati et al., in press). In KIR data on fruit consumption were compiled by several researchers (contrib. to Donati et al., 1999; Fietz and Ganzhorn, 1999; Ganzhorn and Sorg, 1996; Ganzhorn et al., 1999a; Schwab, unpubl. data).

Statistical Analyses

Non-parametric tests were applied for comparisons of fruit characteristics. The role of site effects, the impact of frugivorous lemurs and their interactions on biochemical characteristics were analyzed with two-way analyses of variance. Data were arcsine transformed for these analyses. Statistical analyses were run according to Siegel (1956) with the help of SAS and SPSS software.

RESULTS

Climate and Phenology

Figure 2 shows phenology and annual precipitation for both study sites. Annual rainfall was 2690 mm in STL and 721 mm in KIR during the study period. The phenological patterns considered in this study differ slightly from the overall pattern at both sites as published previously (Bollen and Donati, 2005; Donati, 2002; Sorg and Rohner, 1996) because only a subset of the complete phenological dataset was used for comparison.

In KIR ripe fruits are available year round with a minimum in April. 'Fleshy' and 'non-fleshy' fruit species are equally (50%) represented in KIR (Fig. 2). During the dry season (May through October) non-fleshy fruits predominate. As indicated before, in STL there are no clearly defined wet or dry seasons. Fruit abundance here is highest from January through March, rather limited from April through October with a lean period from June to August. The majority (81%) of fruit species in STL are characterized as 'fleshy'. In contrast to KIR, the representation of the 'non-fleshy' fruits remains low but fairly constant (4-7%) in STL throughout the year.

Soil Conditions

In the upper layer (A horizon) soils are more acid and contain higher concentrations of organic matter, nitrogen and phosphor in STL than in KIR (Table 3). Exchange capacity has not been measured for STL. The situation at STL is similar to the data available for Ranomafana, an evergreen rainforest site at higher altitude (Ganzhorn et al., 1999b). There, growth rate of trees is higher than at Kirindy, probably due to the longer growth season. However, the probability of fruiting is reduced, indicating that fruit production is associated with higher stress for the trees of the evergreen forest. It is unclear how these different constraints affect the type of fruits produced.

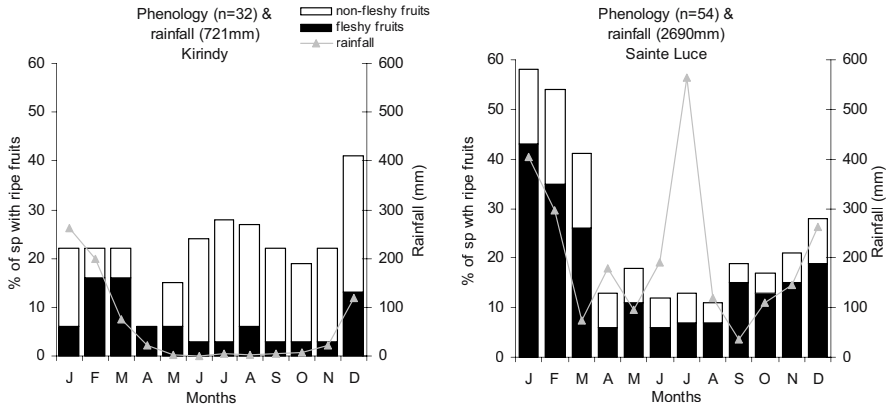


Figure 2. Monthly fruit availability and rainfall in Sainte Luce and Kirindy. Fleshy fruits are fruits characterized as juicy soft, juicy fibrous or arillate, non-fleshy fruits are dry fibrous or do not have any pulp.

Floristics

Both datasets have 30 families (40%) and 19 genera (10%) in common but no tree species (Table 2). In STL the four most important plant families were Rubiaceae (23 species), Euphorbiaceae (8), Flacourtiaceae (6), and Myrtaceae (6). They accounted for 25% of all species. In KIR Fabaceae (16), Euphorbiaceae (14), Tiliaceae (9), Rubiaceae (8), and Combretaceae (6) were the five most important plant families. They accounted for 31% of the species. The representation of these top eight families is not correlated between the two datasets ($r_s = 0.18$; $P = 0.7$, $N = 8$). The representation of large and small trees, shrubs and other growth forms in the samples did not differ between sites (Table 4).

Morphology

Five out of 11 morphological parameters differed significantly between both study sites (Table 4). In STL, berries are the dominating type of fruit followed closely by drupes. In KIR drupes are most abundant followed by berries and capsules. Fruit pulp in STL is mostly soft and juicy. In KIR the majority of fruits has a rather dry and fibrous pulp. Remarkable is the large number of odoriferous fruits in STL while in KIR only one third of the fruits was classified as odoriferous. KIR has more dehiscent fruits and thick-husked indehiscent fruits than STL where 75% of fruits are indehiscent and thin-husked. Concerning dispersal type, zoochorous fruits prevail both in KIR and STL, but KIR has more non-zoochorous fruits than STL. However this difference was no longer significant after sequential Bonferroni adjustment. There is no significant difference between study sites for color, number of seeds, fruit length, fruit mass, seed length and seed protection.

*Comparison of Diets of Eulemur and Cheirogaleus between Sites**Chemistry*

The chemical composition of mature fruits differed between sites in most chemical variables except for extractable proteins and sugars. Lipid concentrations were significantly higher in STL while NDF, ADF, total nitrogen, and procyanidin tannins were higher in KIR (Table 5). After rigorous adjustment for Type I errors (Rice, 1989), there was only a significant difference for NDF, ADF, and tannins.

Morphology

Fruits eaten by both lemur species at both sites did not differ significantly in growth form, number of seeds, fruit length, fruit mass, seed length or seed protection (Table 4). However significant differences were found with respect to pulp type and the protection of fruits consumed by *Eulemur* and *Cheirogaleus* at both sites. The observed difference corresponds to the differential availability of fruits with different types of pulp and protection at both sites.

Even though significantly fewer berries but more capsules were available in KIR than in STL (Table 4), this difference was not apparent when comparing diets of both lemurs between sites. Both species seemed to prefer berries and drupes even when these are less common and harder to find. In contrast, proportions of fruit colors did not differ significantly between samples eaten by *C. medius*, although *E. fulvus* did eat significantly more brown and green fruits in KIR and more yellow, orange and red fruits in STL. The proportion of odoriferous fruits eaten by both lemur species was higher in STL than in KIR, though the difference is not significant in the case of *C. medius*. KIR also had significantly more non-zoochorous fruits than STL, but still zoochorous fruits dominate the fruit diet of both lemur species at both sites.

Chemistry

Except for higher tannin concentrations in fruits consumed in KIR, none of the concentrations of the plant chemicals differed between fruits eaten by *C. medius* in STL and KIR (Table 6). Fruits consumed by *E. fulvus* contained higher concentrations of fiber and tannins in KIR than in STL. These results correspond with the biochemical differences in overall fruit availability between sites. Only the difference between fiber content remains significant after sequential Bonferroni.

Table 3. Soil characteristics of the littoral forest at Sainte Luce and the dry deciduous forest at Kirindy/CFPF (values are medians and range; N = 4 for both sites).

	Depth [cm]	Hori- zon	pH	C [%]	N [%]	C/N	Organic matter	P [ppm]	K [ppm]
Sainte Luce ¹	10	A	4.6	11.3	0.42	30	18.1	2.0	22
	80	B	4.1-5.9	7.2-25.5	0.21-0.84	23-41	12.4-43.9	1.0-3.0	17-49
Kirindy /CFPF ²	10	A	5.7	0.6	0.88	2.07	1.1	0	15
	80	B	5.6-7.2	0.6-4.9	0.14-1.46	0.65-4.28	1.0-8.35	0-3.0	0-17
			6.4	1.76	0.13	14	3.0	0.55	25
			6.0-6.5	0.53-2.15	0.03-0.15	13-21	0.9-3.7	0.2-0.9	12-35
			5.2	—	—	—	—	0.25	13
			4.9-6.6	—	—	—	—	0.2-0.3	6-31

¹ From Razafimanzilala (1996); ² From Felber (1984).

Table 4. Morphological characteristics of fruits collected in Sainte Luce and Kirindy and of fruits eaten by *Cheirogaleus medius* and *Eulemur fulvus* ssp. at the two sites. The χ^2 values were calculated for comparisons between sites. Several categories needed to be lumped if the sample was too small per category. * P < 0.05, **P < 0.01, ***P < 0.001. The results that remain significant after sequential Bonferroni adjustment are in bold.

	Total Database		<i>Cheirogaleus</i> Diet		<i>Eulemur</i> Diet	
	STL	KIR	STL	KIR	STL	KIR
Total number of species	173	171	36	36	107	46
<i>Growth form (N)</i>	<i>173</i>	<i>121</i>	<i>36</i>	<i>35</i>	<i>107</i>	<i>44</i>
large tree	94	69	22	19	69	27
small trees & shrubs	62	40	11	13	28	15
vine-herbs-epiphytes	17	12	3	3	10	2
unknown	0	49	0	1	0	2
χ^2	0.25; df = 2		0.37; df = 2		1.64; df = 2	
<i>Fruit type (N)</i>	<i>165</i>	<i>159</i>	<i>34</i>	<i>34</i>	<i>103</i>	<i>45</i>
berry	80	40	18	13	52	17
drupe	52	58	12	15	39	18
capsule	21	32	3	3	7	4
pod	3	16	0	1	1	2
samara	1	3	0	0	0	0
synconia	2	4	1	0	2	3
others	6	6	0	2	2	1
unknown	8	12	2	2	4	1
χ^2	25.46***; df = 4		1.54; df = 2		3.48; df = 2	
<i>Pulp type (N)</i>	<i>171</i>	<i>153</i>	<i>36</i>	<i>35</i>	<i>107</i>	<i>44</i>
juicy soft	103	43	32	14	68	9
juicy fibrous	24	38	2	9	18	14
dry fibrous	4	59	0	11	2	19
aril	11	4	1	1	8	1
no pulp	29	9	1	0	11	1
unknown	2	18	0	1	0	2
χ^2	88.90***; df = 4		22.80***; df = 3		56.86***; df = 4	
<i>Color (N)</i>	<i>172</i>	<i>116</i>	<i>36</i>	<i>31</i>	<i>107</i>	<i>36</i>
yellow orange	32	14	9	4	22	4
red	28	10	5	3	20	1
purple	16	6	7	0	12	0

	brown	44	41	6	11	25	17
	green	38	35	9	11	24	12
	others	14	10	0	2	4	2
	unknown	1	55	0	5	0	10
χ^2		10.52; df = 5		6.89; df = 3		14.14**; df = 3	
<i>Odor (N)</i>		167	152	36	33	106	44
	absent	58	104	13	19	33	27
	present	109	49	23	14	73	17
	unknown	6	18	0	3	1	2
χ^2		35.30***; df = 1		3.19; df = 1		11.84***; df = 1	
<i>Number of seeds (N)</i>		172	151	36	35	107	44
	1-2	97	72	22	16	62	17
	3-10	43	58	9	15	26	19
	11-50	12	9	0	3	5	4
	50+	20	12	5	1	14	4
	unknown	1	20	0	1	0	2
χ^2		7.02; df = 3		2.54; df = 2		7.39; df = 3	
<i>Fruit weight (N)</i>		161	146	35	33	100	39
	<1 g	69	75	23	15	40	12
	1-10 g	77	61	12	17	49	24
	11-50 g	11	9	0	1	10	2
	>50 g	4	1	0	0	1	1
	unknown	12	25	1	3	7	7
χ^2		2.38; df = 2		2.83; df = 1		1.78; df = 2	
<i>Fruit length (N)</i>		167	159	36	36	105	45
	<10 mm	42	54	12	16	23	10
	10-30 mm	96	76	22	16	62	28
	>30 mm	29	29	2	4	20	7
	unknown	6	12	0	0	2	1
χ^2		3.63; df = 2		2.19; df = 2		0.27; df = 2	
<i>Seed length (N)</i>		160	148	33	35	101	43
	<2 mm	5	5	2	0	4	1
	2-10 mm	86	93	20	24	54	22
	11-20 mm	51	42	10	8	32	17
	>20 mm	18	8	1	3	11	3
	unknown	13	23	3	1	6	3

χ^2	4.52; df = 2		0.03; df = 1		1.10; df = 2	
<i>Fruit protection (N)</i>	173	151	36	35	104	45
dehiscent	26	39	0	3	10	5
indehiscent thin husk	130	80	36	24	83	26
indehiscent thick husk	17	32	0	8	11	14
unknown	0	20	0	1	3	1
χ^2	17.68***; df = 2		9.27**; df = 1		10.05**; df = 2	
<i>Seed protection (N)</i>	158	147	35	34	101	45
none	82	79	14	18	41	24
lignified kernel/seed	76	68	21	16	60	21
unknown	15	24	1	2	6	1
χ^2	0.10; df = 1		1.16; df = 1		2.05; df = 1	
<i>Dispersal mode (N)</i>	163	150	35	35	103	45
zoochorous	130	104	34	33	9	41
anemochorous	2	11	0	0	1	1
hydrochorous	4	4	1	1	6	2
autochorous	27	31	0	1	3	1
unknown	10	20	1	1	4	1
χ^2	8.87**; df = 3		1.16; df = 1		2.05; df = 1	

Lemur Food Selection and Fruit Availability within a Site

Morphology

Cheirogaleus medius was observed feeding on 36 fruit species at both sites. The diet of *Eulemur* contained 107 and 46 fruit species in STL and KIR, respectively (Table 4). We compared the lemur food traits with the overall availability of these traits present within a site (Table 7). For the analyses of food selection for *E. fulvus* all fruits were used that had been characterized for the two forests as listed in Table 4. *C. medius* is hibernating for up to 7 months per year. Therefore, the only fruits considered for the analysis of fruit selection were those that were present during the months when this species was active (not hibernating). This resulted in different numbers than those listed in Table 4.

Table 5. Biochemical characteristics of ripe fruits at Sainte Luce and Kirindy. NDF: neutral detergent fiber; ADF: acid detergent fiber; Nitrogen: total nitrogen; Tannin: procyanidin tannin. Z-values are based on Mann-Whitney-U tests; *P < 0.05; ***P < 0.001. The results that remain significant after sequential Bonferroni adjustment are in bold.

SITE		NDF	ADF	Nitrogen	Extractable protein	Fat	Sugar	Tannin
Ste. Luce	median	31.9	22.6	0.8	2.9	3.0	18.2	0.2
	quartiles	23.9 – 47.5	17.1 – 35.7	0.6 – 1.1	1.7 – 4.4	1.8 – 5.6	7.8 – 36.3	0.0 – 0.6
		94	94	104	104	100	104	104
Kirindy	median	53.3	42.0	0.9	2.6	2.1	10.6	0.4
	quartiles	34.8 – 69.4	28.2 – 50.6	0.7 – 1.3	1.5 – 4.0	1.1 – 3.5	6.2 – 29.2	0.2 – 0.9
		41	39	45	36	52	36	37
Z		4.19***	4.08***	2.15*	0.71	2.11*	0.99	2.31*

Cheirogaleus medius. In STL fruits lighter than 10 g and fruits with soft and juicy pulp were over represented in the diet of *C. medius*. They ate only thin-husked indehiscent fruits and 34 of the 35 fruit species were classified as zoochorous (Tables 4 & 6). In KIR *C. medius* ate more drupes and berries (82%) than would be expected based on the availability of these types (62%) and 33 of the 35 fruit species were classified as zoochorous.

Eulemur fulvus ssp. In STL well-protected seeds were eaten more frequently than would be expected based on their representation in the sample, which is correlated with the importance of drupes in their diet (drupes always have a hard seed coat). As frugivores these species target mainly fruit pulp and therefore seed protection is not an important food selection criterion for them. Zoochorous fruits were also over-represented in the diet of *E. fulvus*. In KIR 62% of the fruits weighed between 1-10 g and the category "indehiscent fruit with a thin husk" comprised 74% in the diet of *E. fulvus*, compared to 50% in the forest sample. Zoochorous fruit types were also over-represented. Other morphological fruit characteristics, such as growth form, color, odor, number of seeds, fruit length and seed length, did not differ significantly between food exploited and the overall fruit availability in both forest types both for *Eulemur fulvus* and *Cheirogaleus medius*.

Table 6. Biochemical characteristics of food and non-food fruits of *Eulemur fulvus ssp.* and *Cheirogaleus medius*. For comparisons of fruit selection by *C. medius* only those fruits were considered that were present during the months when *C. medius* were active (i.e. not hibernating). Values are medians, quartiles, and sample size. Z-values are based on Mann-Whitney-U tests; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The results that remain significant after sequential Bonferroni adjustment are in bold.

	CHEIROGALEUS						difference of food
	STL			KIR			
	eaten	not eaten		eaten	not eaten		
NDF	30.6	33.4	0.90	49.8	67.4	2.80**	1.85
	24.1-41.9	24.4-50.7		29.8-54.8	52.5-72.8		
	31	58		21	16		
ADF	22.0	24.7	1.13	34.2	49.5	3.12**	1.69
	17.1-31.0	17.6-37.6		21.3-42.3	42.6-53.1		
	31	58		20	15		
total nitrogen	0.8	0.8	0.38	0.9	1.0	1.31	1.30
	0.6-1.1	0.6-1.1		0.7-1.2	0.8-1.5		
	33	64		23	18		
extractable protein	3.2	2.9	0.01	2.5	3.0	0.65	0.69
	1.5-4.7	1.8-4.3		1.7-3.1	1.9-4.1		
	33	64		20	14		
fat	2.7	3.1	0.82	2.0	2.3	0.07	1.19
	2.1-4.9	1.8-7.5		1.2-3.6	1.1-3.7		
	33	61		24	24		
sugar	31.2	14.8	2.03*	25.2	8.3	2.40*	0.16
	11.2-41.4	6.6-33.1		8.5-53.6	5.0-10.7		
	33	64		20	14		
tannins	0.2	0.2	0.70	0.3	0.6	0.40	2.09*
	0-0.4	0-0.6		0.2-0.7	0.2-1.0		
	33	64		21	14		
	EULEMUR						difference of food
	STL			KIR			
	eaten	not eaten		eaten	not eaten		
NDF	32.0	31.2	0.22	52.2	53.3	0.14	2.87**
	23.6-47.7	26.6-44.9		36.1-70.3	34.7-68.9		
	76	18		19	22		

ADF	22.4	22.6	0.75	42.0	41.6	0.29	2.91**
	17.1-35.6	20.6-35.3		25.7-48.1	27.9-52.0		
	76	18		18	21		
total	0.9	0.8	0.80	1.01	0.93	0.44	1.86
nitrogen	0.6-1.2	0.6-1.0		0.8-1.2	0.7-1.3		
	86	18		20	25		
extractable	2.8	3.3	1.24	2.5	2.7	0.09	0.22
protein	1.6-4.3	2.5-4.5		1.9-3.6	1.5-4.2		
	86	18		17	19		
fat	2.7	5.0	2.33*	2.0	2.5	0.23	1.48
	1.7-5.1	2.5-16.9		1.5-3.4	1.1-3.9		
	82	18		22	30		
sugar	19.2	11.0	1.34	16.4	10.2	0.25	0.61
	8.3-36.6	7.6-24.2		5.7-26.9	6.3-23.4		
	86	18		17	19		
tannins	0.2	0.31	1.33	0.5	0.4	0.62	2.36*
	0-0.5	0.1-1.0		0.2-1.0	0.2-0.8		
	86	18		17	20		

Chemistry

At both sites, fruits consumed by *C. medius* contained higher concentrations of sugar than fruits not consumed (Table 6). In KIR, fruits consumed by *C. medius* had lower fiber contents than fruits that had not been consumed. The only significant difference between non-food fruits and fruits consumed by *E. fulvus* consisted of lower fat concentrations in food species consumed at STL. Again, this was not significant anymore after Bonferroni adjustment for Type I errors (Rice, 1989).

Interactions between Lemur Food Selection and Site Effects on Fruit Chemistry

In order to separate possible effects due to site characteristics from effects of lemur food selection on the chemical composition of fruits, two-way analyses were run using 'site' and 'lemur food' as fixed independent factors. The results of these analyses are consistent with the conclusions above. Site-specific effects are significant for the majority of chemicals. According to the two-way ANOVA *C. medius* consistently searches for fruits with high sugar concentrations (Table 8). *E. fulvus* seems to avoid fruits with high fat contents in STL only. The site effects persisted once the food items of the two lemur species were pooled and contrasted to the fruits that had not been eaten by neither species. There were several significant interactions between site and food effects. *Cheirogaleus medius* avoids high fiber content but this clearly depends on the relative availability of fiber content at a certain site, while for *Eulemur fulvus* tannin concentrations in fruits eaten vary

differently at the two sites. Finally when both lemur species are pooled together, the lipid content of the consumed fruit species corresponds as well with the site specific availability.

Table 7. The χ^2 results of the comparison between morphological traits of lemur food species and the overall representation of these fruit traits within a site; *P < 0.05; **P < 0.01. The results that remain significant after sequential Bonferroni adjustment are in bold.

	<i>Cheirogaleus medius</i>				<i>Eulemur fulvus</i>			
	STL		KIR		STL		KIR	
	χ^2	df	χ^2	df	χ^2	df	χ^2	df
growth form	0.93	2	1.20	2	4.85	2	4.80	2
fruit type	1.28	3	11.11*	3	5.08	3	6.15	3
pulp type	11.44**	2	1.36	2	3.64	3	3.47	2
colour	3.49	4	4.19	3	3.78	5	6.44	3
odour	0.04	1	1.54	1	0.66	1	0.75	1
number of seeds	0.26	2	0.84	2	1.09	3	1.66	2
fruit mass	8.53*	2	0.78	1	0.52	2	6.77*	2
fruit length	3.72	2	2.51	2	0.66	2	4.14	2
seed length	1.97	1	1.35	1	0.03	2	2.84	2
fruit skin protection	12.31**	2	3.06	2	2.77	2	10.65**	2
seed protection	1.62	1	0.47	1	5.16*	1	0.02	1
dispersal mode	6.58*	1	8.56**	1	7.49**	1	10.46**	1

DISCUSSION

The compared forest types did not have any plant species in common with only few genera represented at both sites (19 out of 181 in our dataset; Table 2). The low similarity even at higher taxonomic levels and the different phenological pattern lead us to conclude that the two datasets are phylogenetically relatively independent. This view is supported by floristic classifications that based on phylogeographic criteria the evergreen forests of eastern Madagascar can be clearly distinguished from the deciduous formations of the west (e.g., Koechlin et al., 1974; Schatz, 2001). The difference in plant species composition and phenology can be related to adaptations in response to abiotic conditions that differ substantially between sites, such as severe water stress and a long period of drought in KIR. In contrast, the seed dispersers available at both sites do not differ markedly. Specifically, the same species of frugivorous lemurs, representing some of the most important seed dispersers of Madagascar (Birkinshaw, 1999; 2001; Dew and Wright, 1998; Ganzhorn et al., 1999a; Overdorff and Strait, 1998), occur at both study sites.

Table 8. Effects of site characteristics and whether or not an item was eaten by lemurs according to two-way analyses of variance. Analyses were performed on arcsine transformed data. Analyses were run separately for *Cheirogaleus medius*, *Eulemur fulvus*, and for fruits that had been eaten by either one or both species. Values are *F*-values; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	<i>Cheirogaleus medius</i>		
	Site	Food	Site * Food
NDF	19.88***	10.36**	4.20*
ADF	16.96**	10.94**	4.29*
nitrogen	8.68**	3.12	0.87
extractable protein	0.21	0.15	0.16
fat	2.91	0.78	2.20
sugar	0.86	9.07**	0.23
tannin	6.39*	0.15	0.25
	<i>Eulemur</i> spp.		
	Site	Food	Site * Food
NDF	19.75***	0.02	0.21
ADF	16.28***	0.06	0.16
nitrogen	5.67*	0.12	0.02
extractable protein	0.50	0.03	0.94
fat	10.51***	6.09	2.68
sugar	0.45	0.67	0.3
tannin	1.45	0.35	4.06*
	Lemurs in general		
	Site	Food	Site * Food
NDF	21.58***	2.00	3.12
ADF	18.14***	3.32	2.63
nitrogen	5.90*	1.26	0.49
extractable protein	0.10	0.50	0.21
fat	11.05***	4.66*	4.57*
sugar	0.12	5.49*	0.25
tannin	1.16	0.49	1.73

Comparison of Fruit Characteristics between Sites

In both forests the majority of plant species depend on animals for dispersal (80% in STL and 69% in KIR). This situation resembles that in other tropical forests where between 60% and 90% of fruits are zoochorous (Fleming et al., 1987; Howe and Smallwood, 1982) including typically a high percentage of berries and drupes with soft and juicy pulp (Gautier-Hion et al., 1985; Smith, 2001; Tiffney, 1984). However, the proportion of zoochorous fruits is unevenly distributed between the two study sites along with other significant morphological and chemical distinctions.

In this respect, we find in STL more fleshy zoochorous berries and drupes with thin husks while dehiscent capsules and indehiscent thick-husked drupes are more abundant in KIR. These morphological properties result in higher fiber and tannin concentrations in the fruits of KIR. Most of these traits in dataset of KIR can be interpreted as adaptations against drought and are also characteristic for the Fabaceae. This is a typical plant family of the dry deciduous forest and at the same time the most important plant family present in KIR when considering species number (Table 2). Scharfe and Schlund (1996) also concluded from their study that in the western forests of Madagascar the majority of fruits are autochorous or dispersed by mammals while in the east dispersal by birds (that eat mainly berries and drupes) and mammals prevail. Our results concur with these.

The site-related difference in the representation of fruits with an odor merits further consideration. In Malagasy forests, frugivorous diurnal and thus visually oriented bird species are poorly represented and most mammalian frugivores of Madagascar are cathemeral or nocturnal. Color is probably less relevant for these lemurs and flying foxes while olfactory clues are likely to be important (Barton et al., 1995; Bollen and Van Elsacker, 2002; Dominy et al., 2002; Hladik and Simmen, 1996; Luft et al., pers. comm.; Schilling, 1979). Since comparative data on fruit odor from other forests are lacking and taste and smell perception differ largely between individuals and species, the present results - which are based on subjective impressions of different human individuals - cannot be further interpreted. A more standardized evaluation of olfactory clues might be worthwhile in future research.

With respect to our predictions we can say that given the almost identical set of frugivores present at both sites, these large differences in morphological and biochemical fruit traits between sites are most likely not a consequence of selection for seed dispersal by animals, as far as the particular lemur species compared. They rather represent the adaptations of a plant community responding to the need for protection against water loss during the long and harsh dry season, typical for dry deciduous forest in Madagascar.

Comparison of Lemur Diets between Sites and Lemur Food Selection within a Site

Regarding feeding selection within a given site and comparison of diets between sites several patterns arise from the datasets. First of all, there are several parameters that seem less important for lemur food selection such as growth form, color, fruit length, seed length, number of seeds, seed protection and extractable proteins. They did not differ at all between sites and did not influence lemurs' feeding selection. On the contrary, clear feeding preferences were found according to fruit and dispersal type. Both lemurs selected almost exclusively zoochorous berries and drupes when fruits with abiotic dispersal were also available at both sites. Finally and most remarkably, both lemur species display a high dietary flexibility for certain parameters, both morphological (pulp type, odor, fruit skin protection) as biochemical (total nitrogen, tannins, ADF and NDF). For these parameters they would select food items in correspondence to what is most available at a given site. This seems to indicate that these species can switch their diet to what is available.

This allows them to survive in different forest types on frugivorous diets with different nutrient compositions and different morphological traits.

Overall, from a chemical perspective these lemur species did not show much evidence for fruit selection based on consistent chemical properties once site-specific characteristics were taken into account. However, in the present analyses *E. fulvus* avoids fruits with high lipid contents and fruits eaten by *C. medius* had lower fiber content than the non-food items. These criteria persist even after site-specific effects have been accounted for (Table 8). Similarly, the preference of *C. medius* for fruits with high sugar content also persists at both sites. This has been linked to their need to accumulate fat reserves for hibernation (Fietz and Ganzhorn, 1999).

The results of the present study do not support the prediction that morphological and biochemical fruit and seed characteristics result from strong specific interactions and co-evolution with lemurs. Rather they could be the consequence of abiotic conditions and can best be interpreted as the result of an opportunistic and generalist zoochorous dispersal strategy of plants. Chapman (1995) has pointed out that weak selection pressure on fruit traits could result if primates have highly flexible diets and are not the only dispersers available in an ecosystem. Furthermore, large dietary differences between neighboring primate groups or groups living a few hundred kilometers apart are not uncommon (Chapman, 1995). This matches our findings of selection criteria of *Eulemur* and *Cheirogaleus* at STL and KIR, which are located 600 km apart. Abiotic factors influence the phenology and taxonomy at a site and may then indirectly also lead to different morphological features and distinct biochemical compositions of food items available at each site.

Considering the predictions outlined above we can summarize our results as follows:

Since the frugivore communities are rather similar at the two sites, abiotic conditions rather than specific consumers are more likely to be responsible for the variety of morphological and biochemical features in fruits from different forest types.

No evidence for co-evolution between these lemurs and fruit traits could be found as diets of the same lemur species differed substantially between sites.

Within fleshy fruits, the lemur species considered did not show any persistent criteria for fruit selection in general besides few biochemical preferences but modified their diet according to fruit availability, even though mutual interactions and dependencies of fruits/seeds and their consumers exist.

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CHAPTER 7.

THE KEY TO MADAGASCAR FRUGIVORES

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Abstract

In the Malagasy ecosystem one particular animal group, lemurs, have the greatest biomass and species richness of frugivores. The peak fruit production in the Malagasy rain forests is about three months shorter compared to peak fruit production in the Amazon and the African rain forests. This suggests that the environment in Madagascar has more well-defined constraints than other continental areas with primates. In Ranomafana National Park, both the overall number of trees, and the number of tree species producing fruit drops during winter months. Particularly in large-bodied lemurs such as sifakas, drop in fruit availability corresponds to an increase in leaf eating. In addition to dietary shifts, all lemur species appear to be able to deal with the season of scarce fruit availability by conserving energy. Extreme responses to winter season are seen in small-bodied lemurs which go into hibernation up to six months every year. Unlike many primate communities in other continents, lemurs do not have synchronous birth peaks across species. In Ranomafana sympatric lemurs show that while individuals within a species have synchronized births, across species lemurs have synchronized weaning. The weaning synchrony coincides with maximum fruit availability and production of small fruits peaks when small juvenile lemurs begin to forage independently. These patterns suggest that lemurs do not appear to rely on fruits to carry them over the period of food scarcity as would be expected from classical descriptions of keystone resources. Rather, we propose that lemurs as a guild rely on fruits as a keystone resource during the warm, wet months in order for lactation and weaning to succeed. Many of the fruit tree species used by lemurs are also hardwood species favored by selective loggers. While loss of these key fruit trees may not drive lemurs into extinction immediately, it may adversely affect reproductive success years after logging.

Key Words: Frugivory, weaning synchrony, color vision, Ranomafana National Park, Madagascar.

INTRODUCTION

Madagascar, the fourth largest island in the world, rifted from Africa more than 150 million years ago, and has been isolated in its present position for over 88 million years (Krause, 1997). Over 1500 km long, Madagascar supports as rich and varied a

flora as can be found anywhere in the tropics (Schatz et al., 2002), including rain forest, dry subtropical forest and spiny desert. Botanists surveying 3 one ha plots in the Ranomafana National Park (RNP) rain forests have found 37 families and 105 species of trees (Schatz and Malcomber in Wright, 1997a). These RNP plots were not as diverse as one ha plots in Colombia (with 44 families and 197 species), but were still more diverse than an African lowland forest in Gabon (29 families and 99 species) (Gentry, 1993; Reitsma, 1988).

Many animal taxa are absent from Madagascar because of biogeographical history and ungulates, monkeys, many birds, and many bats simply never reached the island. What effect does this absence have on the ecology of the rain forest? In most rain forests the primary pollinators and seed dispersers are insects, birds and bats (Bawa et al., 1990; Fleming et al., 1987). Terborgh (1986) estimated that as much as 80% of Amazonia's mammalian biomass depends on fruit resources. As pointed out by Fleming et al. (1987), in contrast, in Madagascar 68% of the birds are insectivores and only 8% are frugivores. The only avian seed dispersers in the rain forest are the velvet asity (*Philepitta castanea*) in the understory and the Madagascar bulbul (*Hypsipetes madagascariensis*) in the canopy (Langrand, 1990; Razafindratsita, 1995). Four bird species are nectivores and pollinators. Two species of parrots and several species of pigeons are seed predators. Bats are also relatively depauperate in diversity with 28 species, and almost all are insectivorous (Peterson et al., 1995). Lemurs may be the primary pollinators and seed dispersers in the rain forests of Madagascar (Balko, 1998; Kress et al., 1992; Nilsson et al., 1993; Overdorff, 1992; Ratsimbazafy, 2002; Wright & Martin, 1995). Black and white ruffed lemurs, red-bellied lemurs and brown lemurs, medium sized (2-4kg) diurnal, diurnal primates pass vine and tree seeds intact, and these sprout faster and with less mortality than seeds not passed through a primate gut (Dew & Wright, 1998). Indeed, in the Malagasy ecosystem it is actually possible to single out one particular animal group, lemurs, which have the greatest biomass of frugivores and may qualify as keystone mutualists (Gilbert, 1980). Almost all lemur taxa eat some fruit but despite this, some fruits such as figs are much rarer in Madagascar than in other tropical forests where they are described as keystone food sources for monkeys (Goodman & Ganzhorn, 1997; Terborgh, 1983).

Although in other tropical rain forests, such as Kibale Forest (see Chapman et al., this volume), and BCI (see Milton et al., this volume), long-term phenology data show that fruit production varies greatly for individual trees, there are fruits available in those forests all year (Struhsaker, 1997). And in rain forests such as Manu Park in the Peruvian Amazon, keystone resources such as figs (large-crowned) or nectar (abundant patches) provide food for frugivores during extended periods of fruit scarcity, (Terborgh, 1983; Wright, 1989). Madagascarrain forests, unlike other forests with 12-14 species of sympatric primates, have a much longer period without fruits, up to six months a year (Wright, 1999). These long periods without fruits are reflected in the fact that few lemurs are obligate frugivores (Dew & Wright, 1998; Fleming et al., 1987; Goodman & Ganzhorn, 1997; Overdorff & Strait, 1998;

Tattersall, 1982), but nonetheless, fruits, seeds and flowers compose 40-90% of the annual diet of *Eulemur*, *Varecia*, *Eulemur ssp.*, *Propithecus*, *Microcebus*, *Cheirogaleus* and perhaps *Mirza* and *Phaner* (Atsalis, 1999; Balko, 1998; Ganzhorn & Kappeler, 1996; Ganzhorn et al., 1999; Hemingway, 1996, 1998; Overdorff, 1991, 1993; Overdorff and Strait, 1998; Powzyk, 1997; Wright & Martin, 1995).

In this paper we examine fruiting patterns in the rain forest of Madagascar, paying particular attention to the degree of seasonality of fruit production in relation to lemur life history. To understand long term patterns in detail we examine feeding and reproduction in the largest species of lemur (6kg), the Milne Edwards sifaka, *Propithecus diadema edwardsi*. The feeding behavior of this species is compared with fruit availability in the forest using fruiting phenology of 98 plant species. Finally, we compare fruiting with key life history events among several sympatric lemurs. We propose that for lemurs fruits are keystone foods critical for lactation and reproductive success rather than for survival during harsh years.

METHODS

Study Site

Ranomafana National Park, established in 1991, is 43,500 ha of continuous rain forest located in southeastern Madagascar at 21° 16'S latitude and 47° 20'E longitude (Wright, 1992, Wright and Andriamihaja, 2002). The park is 25 km from Fianarantsoa and 60 km from the Indian Ocean. Elevations range from 500-1500m within the park, and annual rainfall ranges from 1600-4017 mm (RNP records). Most of the rain falls during the months from December to March. Temperatures range from lows in June-September (4-12°C) to highs in December-February from (30-32 C). The study groups of sifakas were located in the 5km² Talatakely study site (TTS) which was selectively logged by hand in 1986-1989. The park contains moist evergreen forest and the canopy height ranges from 18m-25m. Phenology data have also been taken at an unexploited site within the continuous forest of the park 3km south of Talatakely at Vatoharanana (Hemingway, 1996; Overdorff 1991) and a third unexploited site 3km further South at Valohoaka (Balko, 1998). Botanically, RNP is one of the most diverse rain forests in the world (Lowry et al., 1997). This area has had a non-hunting tradition, and impact of human predation on lemurs and viverrids has been minimal over at least the last 50 years (Wright, 1997a).

The faunal diversity in Ranomafana National Park (RNP) is high for Madagascar (Wright, 1992, 1997a), with 114 species of birds including six species of raptors, six species of viverrid, and twelve species of primates (Table 1). (Wright 1998; Razafindratsita, 1995). Sifaka biomass estimates were 125kg/km² (Wright, 1998). Total biomass of primates at this site was 330kg/km², comparable to *terra firme* forests in Central Amazon and Lope Reserve in Gabon, but roughly half the primate biomass of the alluvial flood plain forest of Manu, Peru or Kirindy dry forest in

western Madagascar (Ganzhorn & Kappeler, 1996; Oates et al., 1990; Peres, 1993; Terborgh, 1983; Wright, 1998).

Table 1. Lemur species in the rainforest site of Ranomafana. Lemurs with an annual diet of at least 30% fruits are marked with asterisk. Only one diurnal species, *Varecia variegata* eats fruits for over 85% of its diet (Balco, 1998; Ratsimbazafy, 2002).

Species	Body Mass (g)	Biomass (kg/km ²)
<i>Avahi laniger</i> , woolly lemur	900	18
<i>Propithecus edwardsi</i> , Milne Edward's sifaka*	5800	125
<i>Cheirogaleus major</i> , fat-tailed dwarf lemur*	350	18
<i>Microcebus rufus</i> , rufous mouse lemur*	42	4
<i>Daubentonia madagascariensis</i> , aye-aye*	3500	7
<i>Lepilemur microdon</i> , sportive lemur	970	1.6
<i>Hapalemur griseus</i> , grey gentle lemur	935	20
<i>Hapalemur aureus</i> , golden bamboo lemur	1550	9.6
<i>Hapalemur simus</i> , greater bamboo lemur	2450	12
<i>Eulemur fulvus rufus</i> , brown lemur*	2200	66
<i>Eulemur rubriventer</i> , red bellied lemur*	2000	48
<i>Varecia variegata variegata</i> , ruffed lemur*	3650	9

Fruit Collection and Morphology

During the 27 month time period April 1997-June 1999, fruits were collected in the forest by TR, Paul Rasabo, ICTE botanists, and other research assistants. All fleshy fruits from canopy trees, understory trees, bushes and vines were chosen regardless of the animal consumer in order to obtain a quantitative measure of fruit availability. The parent plant was measured as to height, dbh, crown diameter, crown depth and located on a map. In the lab 10 fruits of each plant were weighed on a digital scale, measured with calipers. Color was noted. Then the fleshy aril was removed and seeds were counted, weighed and measured. For analysis the fruits were grouped according to weight. The small fruit category consisted of fruits that weighed <1g, and the large group category were fruits that weighed >1g. In addition, fruits were grouped into four color categories. "Dark" were black, purple and brown, while the category "red" were red and orange and "light" were white and yellow. The fourth category was "green," which were green colored ripe fruits, thus excluding green but unripe fruits.

Monitoring Fruit Phenology

One to three individuals of 98 species (a total of 233 trees) of fruiting trees were chosen. Morphological information including height, dbh, crown diameter, crown depth were taken on each selected tree, bush or vine. The location of each study tree was mapped on the Talatakely trail map. Twice each month from March 1997-February 1999 a botanist and several assistants observed each tree using binoculars to determine if a tree had fruits (ripe and unripe), flowers, or new leaves. A score of 1-5 was given on abundance of each category with five being high abundance.

Sifaka Fruit Feeding Patterns

Within the same trail system as the phenology trees we have been conducting studies on the behavior and ecology of four adjacent groups of Milne Edward's sifakas, *Propithecus diadema edwardsi* since 1986 (Pochron et al., 2004; Pochron & Wright, 2002; Wright, 1995, 1998, 1999). Individuals from these groups were captured with anesthetic darts, weighed, measured and given colored nylon collars for field recognition (Glander et al., 1992; Wright, 1995). The demography and changes in group composition are described in detail by Pochron & Wright (2004) and Wright (1995). For this paper, we examined the proportion of feeding time spent feeding on fruits. One individual sifaka per day was observed from awakening until asleep in the sleep tree for 2 days each month from January 1998-December 1998. During this time all foods eaten were identified, and the number of five-minute samples during which each individual fed was recorded.

RESULTS AND DISCUSSION

Seasonality in Fruiting and Fruit Feeding

Despite the similarity of Madagascar in number of species and number of stems found in tropical forests of other geographic areas (Abraham et al., 1996; Lowry et al., 1997; Sussman & Rakotozafy, 1994) the fruiting patterns in Madagascar contrast with many rain forests (Ganzhorn et al. 1999, Wright, 1999). Madagascar phenology plots, including the data shown in this paper, show a prolonged season of 4-6 months with few trees in fruit (Hemingway, 1995; Overdorff, 1993; Powzyk, 1997; Sauter, 1991) In addition, in Malagasy rain forest many canopy species produce flowers and fruit on prolonged, irregular, asynchronous or alternate year cycles (Hemingway, 1995; Morland, 1991, 1993a,b; Overdorff, 1993; Powzyk, 1997). Figure 1A shows that of the 98 species studied, the number of species that carry fruit cycles between 10 and 50. During the austral winter June-September of 1997 and 1998, the number of fruiting species remained below 25 and 20, respectively. In contrast, the times of abundant fruiting of individual trees (scores 3 to 5) are typically during austral

summer (Fig. 1A). Thus Malagasy winters are not only characterized by a drop in the number of trees producing fruit but also a lack of species producing fruits.

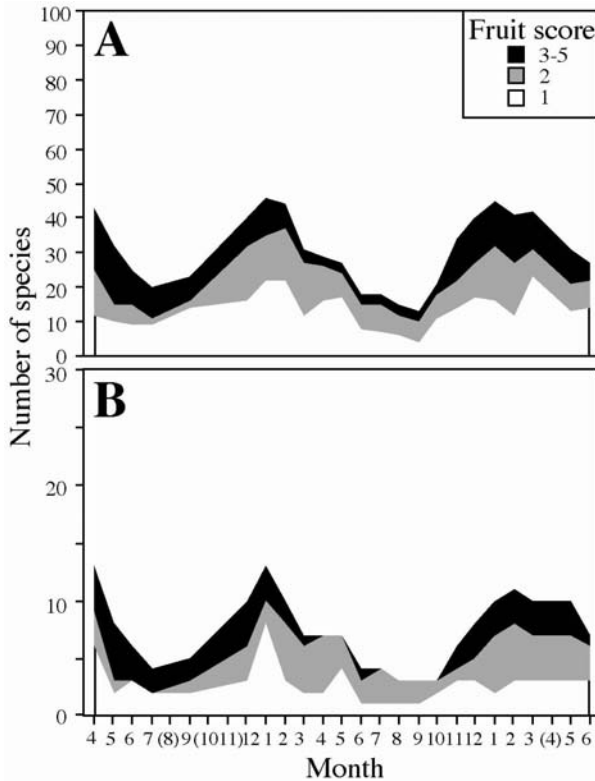


Figure 1. Phenology of fruit availability in 98 species (A) and a subset of 31 species eaten by sifakas (B) in the rain forest of Ranomafana National Park during April, 1997 to June, 1999. Note how changes in number of fruit species eaten by sifakas track the overall richness of fruiting taxa. Fruit score one represents even one fruit observed in a tree, fruit score two represents up to a quarter of the branches having fruit and score five describes branches having abundant ripe fruits. Months in parenthesis lack data.

Compared to Madagascar, where fruit availability is highly seasonal, fruiting occurs throughout the year in other tropical forests such as Kibale Forest, Uganda (Chapman et al., this volume; Struhsaker, 1997), Ketambe, Sumatra (van Schaik, 1986), Manu, Peru (Gentry & Terborgh, 1990; Terborgh, 1983) Gabon (Gautier-Hion et al., 1985), Barro Colorado Island, Panama (Foster, 1982; Milton et al., this

volume), Colombia (Stevenson, this volume), Manaus, Brazil (Lovejoy & Bierregaard, 1990), and Maraca, Brazil (Nunes, 1998) with a tendency for slightly lower fruit production in the driest months, usually for a two or three month period. The seasonal cycling of Malagasy fruit diversity (Fig. 1A) is strongly reflected in the diet of *Propithecus diadema edwardsi*. During 1998, these sifakas ate fruits of 31 species out of the studied 98. Fruiting of the 31 species resembled closely the overall seasonal patterns (Fig. 1B). However, sifakas appear to increase the relative diversity of fruit species consumed during the summer season compared to winter. Roughly 20% of concurrently fruiting species were eaten during the winter while up to 30% were eaten during the summer. This suggests that sifakas are opportunistic frugivores that track the overall fruit richness in the forest. This is further evident when the amount of fruit feeding is examined. In Figure 2 the percentage of fruit feeding minutes is plotted for 1998. Sifakas spend about half of their feeding time on fruits during the summer while the proportion of fruit feeding drops all the way to zero in July (Fig. 2). There is a high turnover of top ranking fruits in the diet among months (from the families Clusiaceae, Myrtaceae, and Lauraceae) implicating again the opportunistic nature of fruit eating in sifakas. The majority of sifakas' feeding time is spent eating leaves.

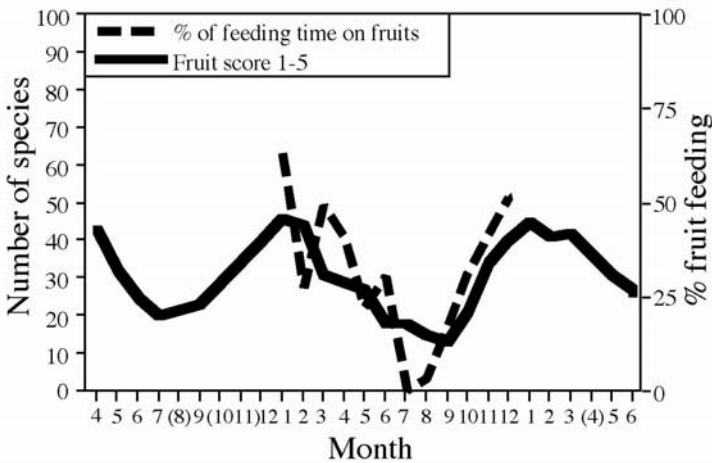


Figure 2. Distribution of fruit feeding (% of total feeding time) of sifakas during January, 1998 to December, 1998 and phenology of fruit availability

Because less than half of the 98 sampled plant species carried fruit in any single month (Fig. 1A), we also examined the overall turnover of fruiting species by calculating cumulative fruiting curves (Fig. 3). Beginning from a fruiting peak when roughly 42% of species carry fruit, in 12 months over 70% of the species have fruited, and in 24 months up to 85% of species have fruited (Fig. 3). These numbers suggest a relatively high turnover rate of fruiting species which suggests that the flexible fruit feeding of sifakas may be a good strategy in a Malagasy forest where species richness and composition of fruiting plants changes through time.

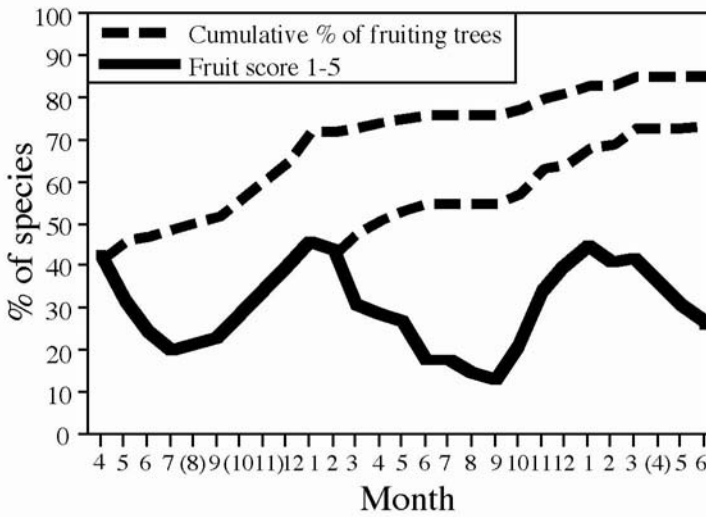


Figure 3. Cumulative fruiting curves calculated starting from 1997 and 1998 fruiting peaks. Over 70% of species fruit within a year.

Fruit Color and Size

Compared to rain forests in Asia, Africa and South America, frugivorous birds and bats are restricted to a few species in Madagascar, and fruit eating mammals are predominantly primate species (Fleming, 1987). With a lower diversity of seed dispersers than other geographic regions, one could expect plants to produce fruits of relatively uniform size and color. For example, extant seed dispersing mammals, bats and birds in Madagascar's rain forest are smaller in body size than those in African, Asian, and South American forests (Fleagle & Reed, 1995; Godfrey et al., 1997), and smaller fruit size would be expected. Indeed, only 5 out of the 98 species studied in this work had fruits larger than 50g.

Color vision capabilities also vary greatly between continental areas. In Asia and Africa primates have excellent color vision (Dominy, 2001). In South America most monkeys have color vision, but are deficient in red wave lengths (Jacobs, 1993), and Madagascar's lemurs have been shown to be largely devoid of the physiological equipment necessary for color vision (Jacobs, 1993). Indeed, in South America Janson found evidence that monkeys are attracted by the color and size of the fruit (Janson, 1983). Following this line of thinking, we might predict that fruits would be less colorful in Madagascar, where the color vision deficient lemurs are the predominant seed dispersers.

Of 87 species with data on fruit morphology, 31 had red-orange, 24 had light (yellow or white), 21 had green, and 11 had dark coloration. This suggests that plants could have coevolutionary relationships with specific seed dispersers or, alternatively, that fruit colors could bear little adaptive significance in Madagascar. At least understory plants with dark fruits, such as *Psychotria*, may rely on birds as seed dispersers. This is indicated by the fact that the smaller size of dark fruits which have an average weight of 1.52 g compared to 4.2 – 6.7 g average weights of fruits in the other color groups. While all of the fruit color groups have synchronous fruiting through time (Fig. 4), sifakas appear to prefer red-orange fruits over other colors. Sifakas ate 14 (45%) of the red-orange, 8 (33%) of the light, and 8 (38%) of the green species. No dark species were eaten.

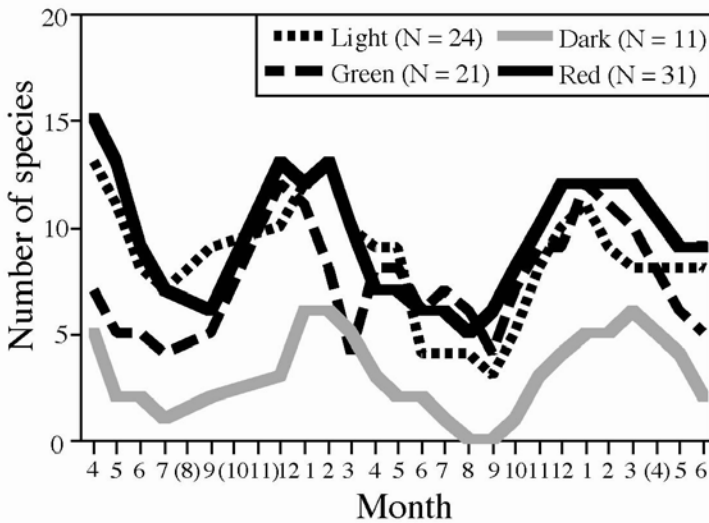


Figure 4. Fruit color and phenology of fruit availability. Note how all fruit colors fluctuate synchronously in the number of species carrying fruit.

This putative fruit color preference in sifakas, fitting the fact that Ranomafana forest has fruits of different colors, is corroborated by recent color discrimination tests showing that some lemurs can distinguish colors quite well (Gosset & Roeder, 2000; Jacobs & Deegan, 1993). One possible explanation is that even with only two classes of cone pigments (dichromatic), their behavioral performance can result from an ability to use signals from rods and cones jointly (Jacobs & Deegan, 1993).

Sifakas showed also a slight preference towards larger fruits. Of the fruiting species that had fruits heavier than 1g, 16 (39%) species were eaten by sifakas while 14 (30%) of <1g species were eaten. Species with larger fruits showed earlier seasonal fruiting peaks (Fig. 5). Correlation between large and small fruited species is 0.70 (Spearman rank correlation, $P = 0.002$) when fruiting of large fruits is shifted one month later. Correlation without temporal correction is 0.44 ($P = 0.027$) suggesting that there is at least a one month delay in the fruiting peak of species with small fruits (Fig. 5).

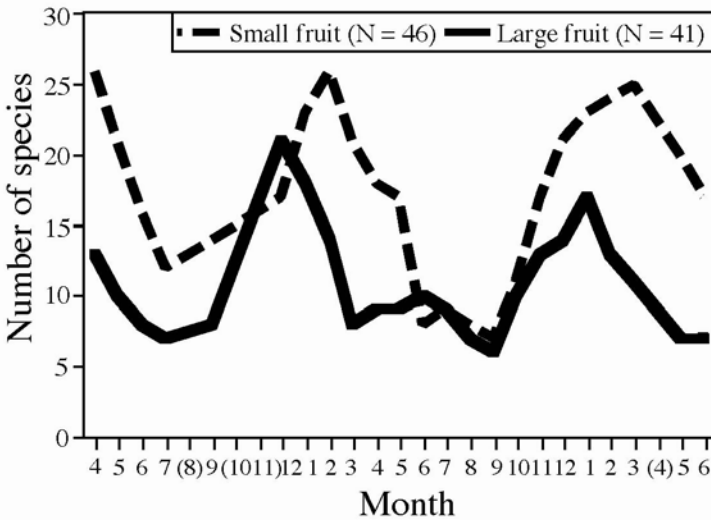


Figure 5. Fruit size and phenology of fruit availability. Note how species with large fruits peak before species with small fruits.

Lemur Response to Scarce Food Periods

The seasonal tracking of fruit feeding by sifakas (Figs 1B, 2), which reflects both the diversity and amount of available fruit, indicates that this lemur species is not dependent on fruits for individual survival during the lean season. In the case of sifakas, the drop in fruit feeding corresponds to an increase in leaf eating. In addition to dietary shifts, all lemur species appear to be able to deal with the season of scarce resources by conserving energy (Ganzhorn, 1993; Morland, 1993; Nash, 1998;

Schmid, 1998; Schmid & Ganzhorn, 1996; Wright & Martin, 1995). Extreme responses to winter season are seen in small-bodied lemurs. *Cheirogaleus spp.* go into hibernation for 4-6 months every year (Muller, 1998; Wright & Martin, 1995) and *Microcebus* also enter torpor for several days at a time (Atsalis, 1999; Fietz, 1998; Schmid, 1998). *Lepilemur ruficaudatus* has the lowest basal metabolic rate recorded for any folivorous mammal (Schmid & Ganzhorn, 1996). Additional lemur traits that can promote energy conservation are thick insulating fur, increased resting behavior, maintenance of small group size, birth of low-weight infants, and relatively small brain size (Wright, 1999).

The seasonal shift in sifaka diet does not, however, indicate that these lemurs are completely able to replace fruits with leaves in terms of energy. Sifakas lose up to 20% of their weight during winter season (Pochron & Wright, 2002, PCS unpubl. data) suggesting that fruits play an important role even in this relatively folivorous lemur. At least 30% of sifaka feeding time is on fruits annually while species of the most frugivorous lemur genera, *Eulemur rubriventer* and *Varecia variegata*, spend 70% and 90% of their annual feeding time on fruits, respectively (Balko, 1998; Overdorff, 1991). *Varecia*, a highly arboreal lemur weighing three to four kg, can be regarded as the only living lemur that is an obligate frugivore. It is also relatively specialized because fruits from five species make up to two thirds of its annual diet (Balko, 1998). This specialized frugivory is reflected in *Varecia* having large territories and extreme seasonal shifts in territory use (Balko, 1998). However, even *Varecia* has been reported to survive on leaves after total loss of fruit productivity due to cyclone damage on trees, albeit with a substantial weight loss and lack of reproduction (Ratsimbazafy, 2002; Ratsimbazafy et al., in press).

Fruits As Keystone Resources for Reproductive Output

Individual lemur species have strict breeding synchrony with a mating season typically lasting less than two weeks (Rasmussen, 1985; Sauther, 1991). This breeding synchrony is triggered by changes in photoperiodicity which makes lemurs uniquely coupled with seasonal changes among primates (Pereira, 1993; van Horn, 1975). Furthermore, in contrast to most primate communities in the Neotropics, Africa, or in Asia (Chapman et al., 1999; Gautier-Hion et al., 1985; Struhsaker, 1997; Terborgh, 1983), lemurs do not have synchronous birth peaks across species. In Ranomafana sympatric lemurs show that while individuals within a species have synchronized births, different species gave birth at different times of year (Wright, 1999, Fig. 6). However, while mating and birth seasons are not synchronized across lemur species, weaning appears to happen in all species during March-April (Fig. 6).

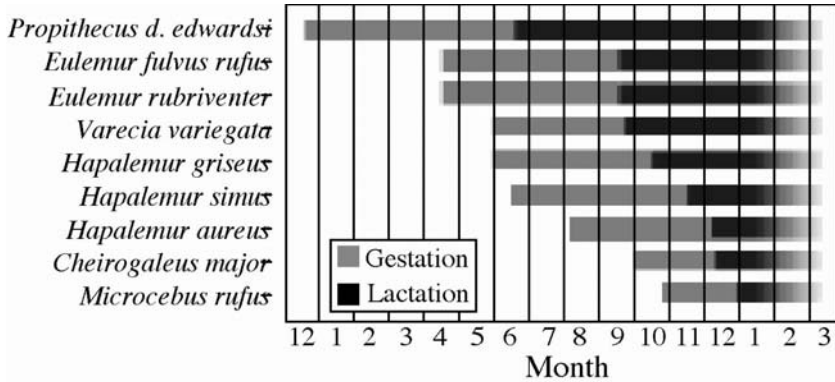


Figure 6. Reproductive schedules for 9 of 12 species of the sympatric lemur community at Ranomafana National Park. Note birth asynchrony and weaning synchrony in these rain forest species. Weaning occurs around the end of March. For information about individual species, see Table 1.

One effect of the weaning synchrony is that all lemur species lactate during the period of increasing fruit availability (Fig. 7). The smallest lemurs are able to fit their whole breeding cycle into the peak fruiting season while sifakas, the largest of the living lemurs at up to 7kg, lactate for two first months without fruits (Figs 2, 6, 7). It is noteworthy that while lactation is the most energy demanding stage of reproduction (Lee, 1997; Tilden & Oftedal, 1997), sifaka newborns are small relative to their mothers. A newborn sifaka weights around 100g which is less than 2% of the mother's weight and thus the initial cost of lactation is far less than during the peak fruiting season when the infant is over 15% of mother's weight (Wright, 1999). The peak lactation synchrony among sympatric lemurs (Fig. 7) suggests that even sifakas, while relatively opportunistic fruit eaters (Figs 1, 2), may rely on fruits as key resources for reproductive success.

It is also interesting that bigger fruits peak in abundance prior to smaller fruits in the forest (Fig. 5). The delayed peak richness of small fruits coincides with the beginning of weaning period in lemurs. Weaning marks a nutritional transition, when the infant becomes a juvenile foraging independently and is more vulnerable to the risks of malnutrition, infection and predation (Janson & van Schaik, 1993). For plants this synchrony of weaning produces a population peak of small juvenile lemurs foraging in the forest for fruits, effectively resulting in a peak of seed dispersers. Even bamboo-eating lemurs (genus *Hapalemur*) follow the weaning synchrony and include small amounts of fruit to their diet during the summer fruiting season (Tan, 1999; Grassi, 2001).

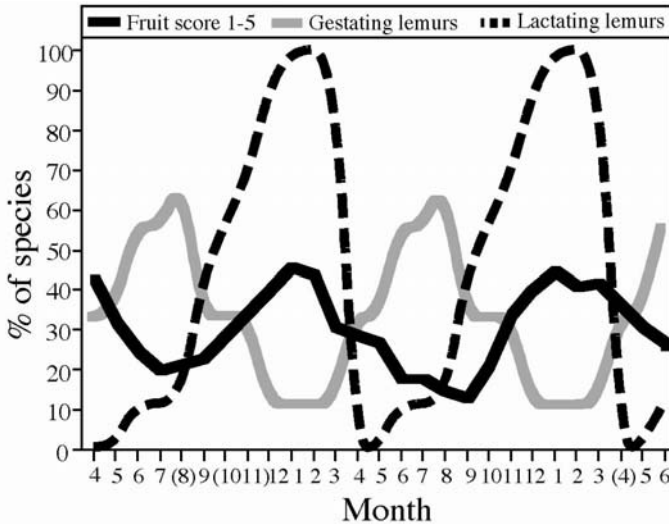


Figure 7. Percentage of plant species fruiting, lemur species gestating, and lemur species lactating. Note how lactation and fruiting peaks coincide while largest number of lemurs gestate during austral winter months when the fruit availability is low.

The peak fruit production in the Malagasy rain forest is three months shorter on average compared to peak fruit production in the Amazon forest (Stevenson, this volume; Terborgh, 1983; Wright, 1997b), and the African forest (Chapman, this volume; Gautier-Hion et al., 1985; Struhsaker, 1997). This suggests that the environment in Madagascar has more well-defined constraints than other continental areas where primates have evolved. In this respect it is informative that lemurs do not appear to rely on fruits to carry them over the period of fruit scarcity as would be expected from classical descriptions of keystone resources (Terborgh, 1983). Soil fertility overall in Madagascar is low, often lower than in other primate habitats on other continents (Ganzhorn et al., 1999). Smith and Ganzhorn (1996) compared lemurs and Australian marsupials, suggesting that both radiations were strongly influenced by these restricting environmental factors that contrast with many tropical habitats in South America, Africa and mainland Asia. Thus, even if lemur taxa had evolved to use classical keystone resources to survive winter seasons, the harsher environmental constraints of Madagascar may have weeded them out.

In conclusion, the data presented in this paper suggest that lemurs as a guild rely on fruits as a keystone resource during the warm, wet months in order for lactation and weaning to succeed. It is important to note that many of the fleshy-fruited plant species used by lemurs are also hardwood species favored by selective loggers.

While loss of key fruit trees may not drive lemurs into extinction immediately, it may adversely affect reproductive success years after logging (Pochron et al., 2004). This kind of "extinction debt" might remain unnoticed if "keystone resource" is considered in forest management and reserve planning only in the narrow sense. Thus keystone resources are probably not just the ones that help ecologically important animal guilds survive a bad season.

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CHAPTER 8.

FRUITING PHENOLOGY AND PRE- DISPERSAL SEED PREDATION IN A RAINFOREST IN SOUTHERN WESTERN GHATS, INDIA

T. GANESH AND PRIYA DAVIDAR

Abstract

The mid-elevation non-dipterocarp wet forests in southern Western Ghats, India are some of the largest stretches of undisturbed forest remaining in this biodiversity hotspot. We established a long-term study of tree phenology in this forest to study the effects of biotic and abiotic factors on phenological patterns. We measured seed predation of selected canopy trees across three years. Seed predation intensity was measured through seed fall, phenology by fruit fall, and animal abundance through transect sampling. A total of 42 tree species was sampled for phenology and 35 species for seed predation intensity. Nine of these species fruited annually, seven fruited once in two years and the remaining species fruited once in several years. Two primates and two arboreal squirrels were the major seed predators in the forest. Primates were responsible for some intact seed dispersal, while squirrels were obligate seed predators. For numerous tree species seed predators were the only seed dispersers. Seed predator abundance showed no significant changes across years except for the case of the lion tailed macaque, which appeared to show seasonal population movement. No community-wide mass fruiting phenomena were noticeable in the forest but there was significant variation in fruit availability between years. A few tree species appeared to show mast fruiting in certain years. A majority of the species suffered high levels of seed predation. Seed predation intensity decreased during mast fruiting events for certain species while for others it had no effect. There was no difference in predation intensity between annually and supra-annually fruiting species. Masting as a means of overcoming high seed predation at the population level in the Western Ghats was limited to only a few tree species.

Key words: India, mast fruiting, phenology, seed dispersal, seed predation, tropical forest.

INTRODUCTION

Seed predation is an important ecological and evolutionary force affecting plant community diversity, demography, and phenology at individual, population and community levels (Harper, 1977; Hubbell, 1980; Schupp, 1988). Seed predation is

affected by a multitude of factors ultimately related to fruit characteristics including plant spatio-temporal distribution, plant density, seed crop sizes, seed chemistry, seed size, season, ripening of fruits, soil humidity, temperature, pollination rates, predator density and the availability of alternative foods for generalist predators (see Crawley, 1992; Janzen, 1971). Fruit traits can have a major influence on predation levels since the primary functions of fruit morphology and chemistry are primarily seed protection and dispersal to safe sites.

Seed predation can also exert selective pressure to shape phenological characteristics and to favor traits such as mast fruiting that may reduce seed predation. It has been hypothesized that plants will synchronize fruiting to overwhelm seed predators (Janzen, 1974). This hypothesis has been supported by evidence from several tree species (Silvertown, 1980). However, it has not been demonstrated that masting evolved in response to predation since masting could also be a response to pollination by wind (Nilsson and Wastljung 1987; Smith et al., 1990). Masting phenomena have been consistently reported for temperate forests and the tropical rainforests of Southeast Asia but not for the Neotropics (Curran and Leighton 2000; Herrera et al., 1998; van Schaik et al., 1993).

Studies of phenology in Asia have focused primarily on dipterocarp forest trees which are wind-dispersed and which share similar fruit traits. Non-dipterocarp forests contain tree species with a variety of dispersal modes and phenological patterns (Newstrom et al., 1994). Consequently, we would expect that various forces shape their phenologies. There is at present no clear evidence of predator satiation by mast fruiting in non-dipterocarp forests. Thus, our primary research question was: does mast fruiting happen in non-dipterocarp Asian forests? Second, does mast fruiting always help reduce seed predation or are there some other benefits to the phenomenon?

In the Indian subcontinent many of the studies on phenology have come from dry tropical forests (Murali, 1992; Prasad and Hegde, 1986; Singh and Singh, 1992). The wet forests of Western Ghats have received very little attention (Kannan, 1994; Menon, 1993) and nothing is known about the mid-elevation forests of Southern Western Ghats which harbors a high proportion of endemic flora and fauna (Henry et al., 1982).

We started a long term regime of monitoring phenology, pollination, seed dispersal and floristic composition at a mid-elevation non-dipterocarp rainforest in the Western Ghats, India in 1990. The Western Ghats region is a global biodiversity hotspot. The Southern Western Ghats are the richest in terms of flora and fauna. These forests have been subjected to clearing for plantations and reservoirs, but nevertheless there are large stretches of rain forest left intact (Ramesh et al. 1997) and our site is the least disturbed site in the Western Ghats.

There is little information available on seed predation and frugivore abundance from forests in India. This paper therefore highlights information on seed predators and quantifies seed predation levels of selected tree species and relates it to fruit traits. Our specific aims were:

1. To quantify pre-dispersal seed predation of trees in a non-dipterocarp rainforest.
2. To determine whether seed predator abundance and fruit abundance are correlated.
3. To determine whether any salient fruit traits correlate with levels of seed predation.
4. To identify tree species exhibiting mast fruiting phenomena and to examine the effects of mast fruiting on predator satiation.

METHODS

Study area

The study was conducted in a wet evergreen forest at Kakachi in the Kalakad Mundanthurai Tiger Reserve. Kakachi (8°33' N. Lat. 77°23' E. Long.) is located at 1300 m elevation and receives an annual rainfall of over 3500 mm, well distributed throughout the year. Mean maximum temperature is 24° C and minimum 16° C. The terrain is highly undulating and is drained by numerous mountain streams.

The vegetation at Kakachi is characterized by three dominant tree species, *Cullenia exarillata*, *Palaquium ellipticum* and *Aglaia bourdillonii*. (Ganesh et al., 1996). About 100 tree species have been recorded from the site (100 km²) so far and over 100 species of birds and butterflies as well as 20 mammal species excluding bats. Several of these species are endemic to Western Ghats. Frugivorous birds are limited to only 6 species.

Phenology

Direct observation of phenology was done on a monthly basis by recording the percentage of the crown in flowers or fruits. Over 300 individuals from 70 spp. were followed from 1991 onwards. Fruit abundance was measured from linear fruit plots laid on the ground. Each plot measured 100 m x 0.70 m. Seventeen such plots covering a total area of 1170 m² were laid randomly in a 10 km² area. These plots were sampled once every two weeks from March 1991 to May 1994. All encountered fruit species were recorded, along with their abundances, and whether their fruits and seeds were eaten or aborted.

Animal observation

It was not always possible to closely observe fruit handling by seed predators as these animals were shy and difficult to see in the dense foliage and tall canopy. Fruit handling by seed predators was therefore observed opportunistically on all

possible occasions. Dental marks left on partially eaten fruits were studied in order to obtain indirect data from frugivores that could not be directly observed.

Animal and seed abundance

A 3 km transect was monitored once every 15 days for animal presence and abundance. The transect was walked from 7 am to 10 am. All arboreal and terrestrial mammals were recorded. Fruits were collected from 53 species of canopy and subcanopy trees between 1991 and 1993 along forest trails with a total length of about 2.5 km. This constituted nearly 69% of the tree species in Kakachi (Ganesh, 1996) and 87% of the tree species that fruited during this period. The fruits were classified into 9 categories based on their size, weight, type, seed number, protection, and color. These classifications follow Gautier-Hion et.al. (1985).

Seed predation

For 35 tree species, predation levels were estimated by placing nylon nets of 1 m² under the crown. The nets sampled roughly 10% of the canopy area for each tree. The number of nets ranged from 1 to 10 with a median of 3. Nets were sampled once a week or once every 2 weeks depending on the phenology of the species. Species with prolonged fruiting episodes were sampled once every two weeks. Five trees per species were sampled except for the 5 most common species which had up to 10 trees sampled.

Fruits fallen in the nets were collected, sorted according to the damage to the seeds and animal species involved in the damage. The proportion of seeds damaged was calculated at the end of the fruiting period giving a percentage of overall seed predation.

RESULTS

Frugivore assemblage

The frugivore assemblage at Kakachi consists of five species of non-flying arboreal mammals, one flying squirrel, two species of bat, and six species of birds. Among mammals there are two tree squirrels, the Malabar giant squirrel (*Ratufa indica*) and the nocturnal giant flying squirrel (*Petaurista petaurista*), the Nilgiri langur (*Trachypithecus johnii*), the lion-tailed macaque (*Macaca silenus*), one species of civet, the brown palm civet (*Paradoxurus jerdoni*) and two species of frugivorous bats (*Cynopterus sp.* and *Rousettus leschenaultia*).

Apart from the civet and the two bat species, the other mammals are seed predators. In particular, the giant squirrel (*Ratufa indica*) the Nilgiri langur (*trachypithecus johnii*) and the flying squirrel (*Petaurista petaurista*) are the most important seed predators at the site. These animals may disperse seeds only

accidentally either by spitting seeds after chewing the pulp as in the case of *Elaeocarpus munronii* by *S.johnii* or the accidental dropping of seeds while eating as in the case of *R.indica* feeding on *Cullenia exarillata* seeds. Avian seed predators belonging to the family Psittacidae (Parakeets) were not recorded at this site and none of the specialized avian frugivores were seed predators. Altogether, fruits of nearly 70% of the tree species at Kakachi are dispersed by these frugivores and seed predators.

Frugivore abundance

Giant squirrel (Ratufa indica): The density of *Ratufa indica* was found to be 46.71 ± 8.71 individuals per km² (n=41 censuses) and about 1 individual (mean=1.33) was encountered along the transect per census. Giant squirrels are territorial and mostly solitary.

Nilgiri langur (Trachypithecus johnii): While it was not possible to get a density estimate for these monkeys, the number of langurs sighted was 1.42 ± 0.44 per km (n=38 censuses).

Lion tailed macaque (Macaca silenus): A mean of 0.42 ± 0.19 *Macaca silenus* were recorded per km of transect (n=38 censuses). The 100ha site was usually occupied by a single troop of *M. silenus* comprising of 17 individuals. Smaller troops were encountered occasionally but it was not known whether they were part of the same troop or if they belonged to a different one.

Giant flying squirrel (Petaurista petaurista): It was not possible to estimate the density of *Petaurista petaurista*. Nevertheless, we estimated a mean number of 0.15 sightings per km (n=8).

Seasonal changes in frugivore abundance

Abundances of seed predators like *Ratufa indica* and *Trachypithecus johnii* did not differ between months (Wilcoxon signed test *R. indica*: $T=0.41$ $df=9$ $p<0.01$; *S.johnii*: $T=-1.18$ $df=9$ $p<0.05$; Fig. 1a, 1b). Lion tailed macaques were more commonly sighted during the dry season (February-May) and were sighted once during the wet season in June, 1991 (Fig. 1c). There was no significant difference in abundance of *Ratufa indica* between years (Kruskal Wallis test $H=0.03$ $df=2$, $p<0.05$) while it was significantly different for *S. johnii* ($H=14.06$ $df=2$, $p<0.01$). Fluctuations between months appeared to vary more in 1993 than in the previous years for all of the mammals.

Terrestrial seed predators like the Porcupine (*Hystrix indica*), small rodents (*Rattus sp.*), Mouse Deer (*Tragulus meminna*) and Wild Boar (*Sus scrofa*) were not sampled. Porcupine (*Hystrix indica*) and Mouse Deer (*Tragulus meminna*) were more commonly seen in the disturbed forest areas and were not common in the study site. There was little indirect evidence of the Porcupine (*H. indica*) in Kakachi.

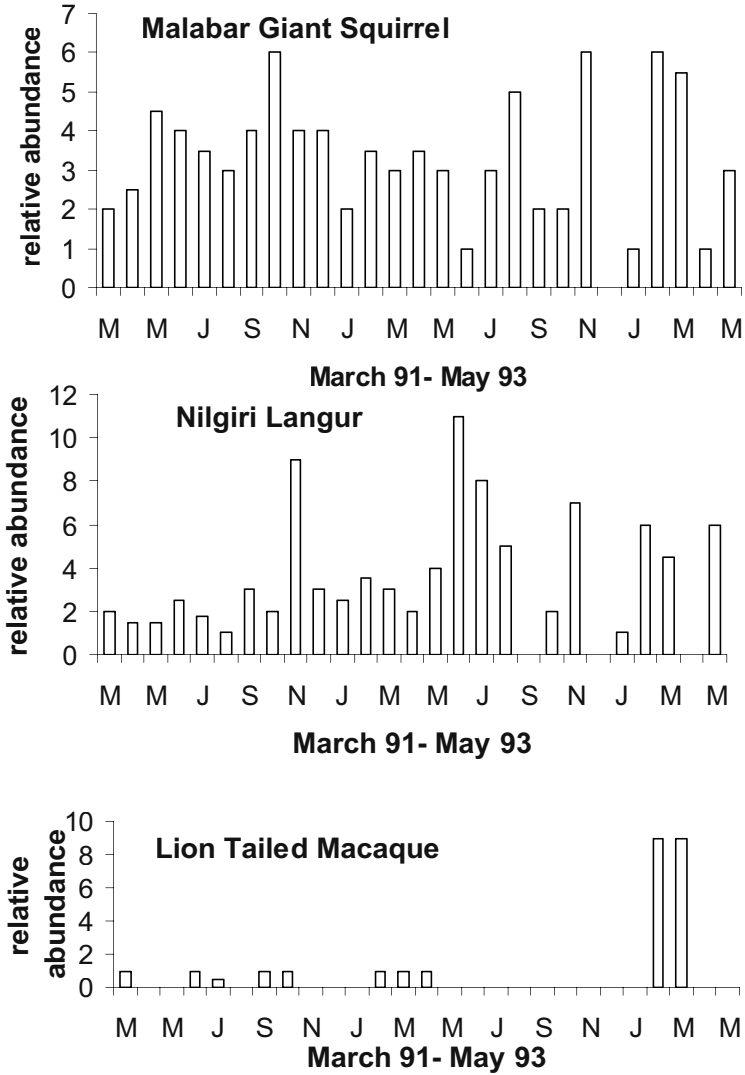


Figure 1. Abundances of seed predators as measured from transect censuses.

Community-level pre-dispersal seed predation

Seed predation levels varied from 1% (*Canarium strictum*) to almost 96% (*Aglaia sp.*) among the 35 tree species sampled. High seed predation (>70%) was found for two of the three species studied from the family Meliaceae. Members of the Elaeocarpaceae (2 spp.) and Rutaceae (2 spp.) had relatively low levels of seed predation (<30%). Members of the Lauraceae also had low levels of seed predation except for *Cryptocaria lawsoni* which was more frequently attacked by fruit galls. A large proportion (57%) of the tree species examined experienced higher than 50% seed predation during their fruiting period (Fig. 2).

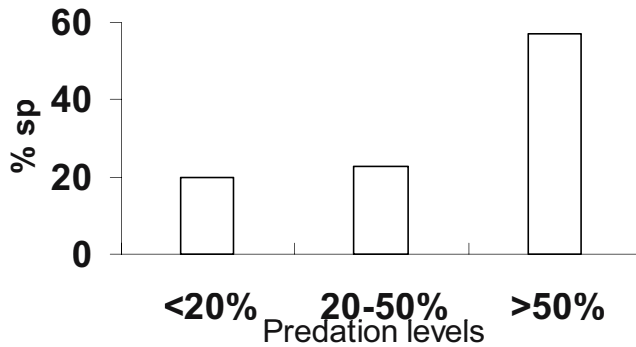


Figure 2. Frequency of seed predation across tree species.

Fruit characters and predation

Fruit characters can influence predators' choice of fruits and thereby the level of predation that a tree species suffers. Thirty two species whose seed predation levels were known were examined for fruit traits that might affect this variance in predation. Seed protection, as measured by seed coat hardness, showed a significant effect in lowering predation (Mann Whitney test $U=180$ $N=32$ $p<0.05$) while fruit protection did not have any significant effect in reducing predation (Mann Whitney test $U=30$ $N=13$ $p<0.01$). Species with protected seeds experienced a mean of $37\% \pm 8\%$ damage ($n=18$) compared to $56 \pm 5\%$ ($n=16$) for species with unprotected seeds. Species like *Canarium strictum*, and *Acronychia pedunculata*, which had very hard seeds, suffered less predation while the presence of thick, hard, and thorny exocarps, as in the cases of *Cullenia exarillata*, *Myristica dactyloides*, and *Hydnocarpus alpina*, did not lower predation levels. In the case of *C. exarillata* there was a temporal change of predators across its fruiting period. The squirrel *Ratufa indica*

preyed upon the fruit when it was unripe (all 36 observations) and preferred it less during the ripe stage (5/41 observations). The primates, *Macaca silenus* (30/41 observations) and to a lesser extent *Trachypithecus johnii* (6/41 observations) were the main predators of seeds in ripe fruit. There were no significant differences in predation between hard fruits and fleshy fruits (Mann Whitney test $U=167$ $N=33$ $p<0.05$). No significant relationship was found between seed number and predation.

Phenology

Fruit abundance in the forest as calculated from fruit traps was highly variable between years. Fruit abundance peaked in late 1993 and early 1994, and it was low during 1992 and early 1993. Fruiting species richness also increased in late 1993 and 1994 but showed less seasonal change within the year (Fig. 3). A Friedman two-way Anova corrected for tied ranks was performed to interpret the inter-year temporal variations in abundance. Results of these analyses show significant differences between years ($\chi^2 = 6$ $df = 2$, $p<0.05$). Pair-wise comparisons of years indicate that the differences between 1991 and 1992 ($\chi^2 = 0.8$ $df = 1$, $p<0.05$) and 1992 and 1993 ($\chi^2 = 1.8$, $df = 1$, $p<0.001$) were not significant but there was a significant relationship between 1991 and 1993 ($\chi^2 = 7.2$ $df = 1$, $p<0.05$).

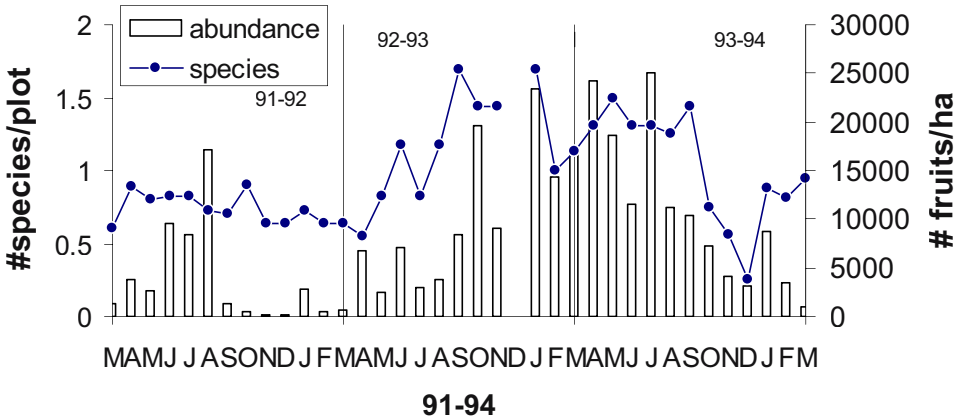


Figure 3. Fruit abundance and number of species in fruit from 1991 to 1994 in a wet evergreen forest.

Masting species

Among the 42 species of trees sampled in the plots, 9 species fruited annually while 7 species fruited twice and 19 species fruited only once. The remaining species were excluded from the above classification as the fruit plots sampled very few fruits of these species. Two species, *Tricalysia apiocarpa* and *Palaquium ellipticum*, showed clear masting patterns within the sampling period. *Tricalysia apiocarpa* mass fruited only once in 6 years with all individuals fruiting during the masting event (Fig. 4a). There was some fruiting by this species in the previous year but very few fruits were produced per tree. *Palaquium ellipticum*, on the other hand, fruited most years, producing fewer fruits per tree (Fig. 4b). In 1992 and 1993, several individuals were in fruit but none produced a large number of fruits. In 1991 and again in 1994 the species mast fruited and nearly all individuals were fruiting. This led to high overall fruit abundance in the forest. There were other species such as *Holigarna nigra* and *Callophyllum austroindicum* that fruited highly synchronously once in several years but these tree species were represented by few individuals in the sample.

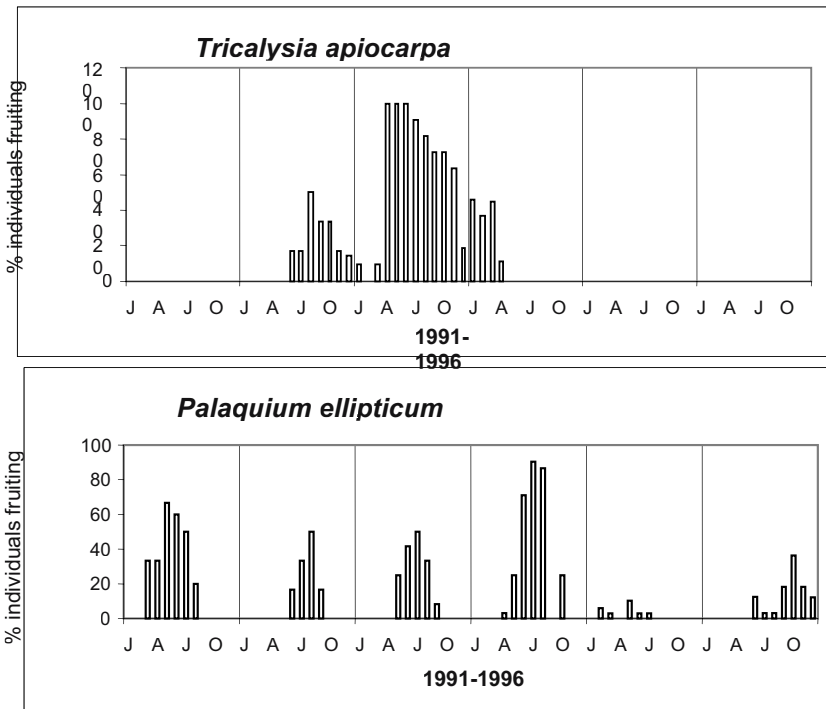


Figure 4. Fruiting phenologies of two non-dipterocarp tree species over six years.

Predation and length of fruiting season

There was a significant negative relationship between the length of the fruiting season (log) and the proportion of seeds eaten (arc sin transformed) ($r=0.50$ $n=26$ $p<0.05$). Species with short fruiting periods therefore experienced higher seed predation levels. Species for which the complete fruiting seasons were not available, such as *Callophyllum austroindicum*, were excluded from the analysis. Even within species there is a relationship between predation and length of the fruiting period. Length of the fruiting period differed between years for species like *Palaquium ellipticum*, which had fruits for a longer period in 1991 (3.6 months) than in 1992 (1.8 months) and which had correspondingly higher predation levels in 1992 (57%) compared to 1991 (11%). The proportion of individuals fruiting remained the same in both years.

Predation and frugivore abundance

There was no significant correlation between overall monthly mammal abundance and fruit abundance except for the case of *Ratufa indica*, where the relationship was negative ($r=-0.40$ $n=27$, $p<0.01$). This relationship with *R.indica* was probably more an artifact of sampling than a true decline. The abundance of lion tailed macaques in 1993 was possibly due to the higher availability of fleshy-fruits in the forest at that time.

Masting and seed predation

Annual comparison of seed predation levels was restricted to species for which a minimum of at least 100 fruits was collected from all the fruit plots pooled together within a year. Fruit plot data were used for this analysis because there were no differences between plot and net data for a particular season. (Mann-Whitney test $U=46$, $n=19$, $p<0.05$). Besides increasing the sample size, fruit plots also avoided bias in tree sampling. Mean fruit fall was calculated per plot and the corresponding proportion eaten was calculated.

If seed predation were the most important factor influencing masting, then we would expect highly preyed-upon species to show masting phenomena. Nearly 57% (20 spp.) of all the examined species suffer from high predation levels. Of these only 7 species, *Tricalysia apiocarpa*, *Palaquium ellipticum*, *Myristica dactyloides*, *Gomphandra coriaceae*, *Artocarpus heterophylla*, *Aglaia eleagnoidea*, and *Agrostistachys borneensis*, were abundant in the forest. Among these, *Gomphandra coriaceae*, *Myristica dactyloides*, *Artocarpus heterophylla*, and *P.ellipticum* fruit annually. The others mast once every several years. One species, *Aglaia eleagnoidea*, did not show masting behavior even though it did not fruit on an annual basis. There were two masting species for which we could collect data on

seed predation across the phenological period, *T. apiocarpa* and *P. ellipticum*. The first of these, *T. apiocarpa*, suffered high levels of seed predation during mini masting and during its full masting period. Although there is a slight decrease in predation rates during periods of high fruit abundance, masting does not appear to produce any significant decrease in predation levels for this species.

Figures 6a and 6b illustrate the fact that seed predation levels fall as seed availability increases for only one of the two masting species. This phenomenon was seen for *P. ellipticum* in 1991 when mast fruiting by this species corresponded with a drop in predation to a level below its three-year mean value (0.22).

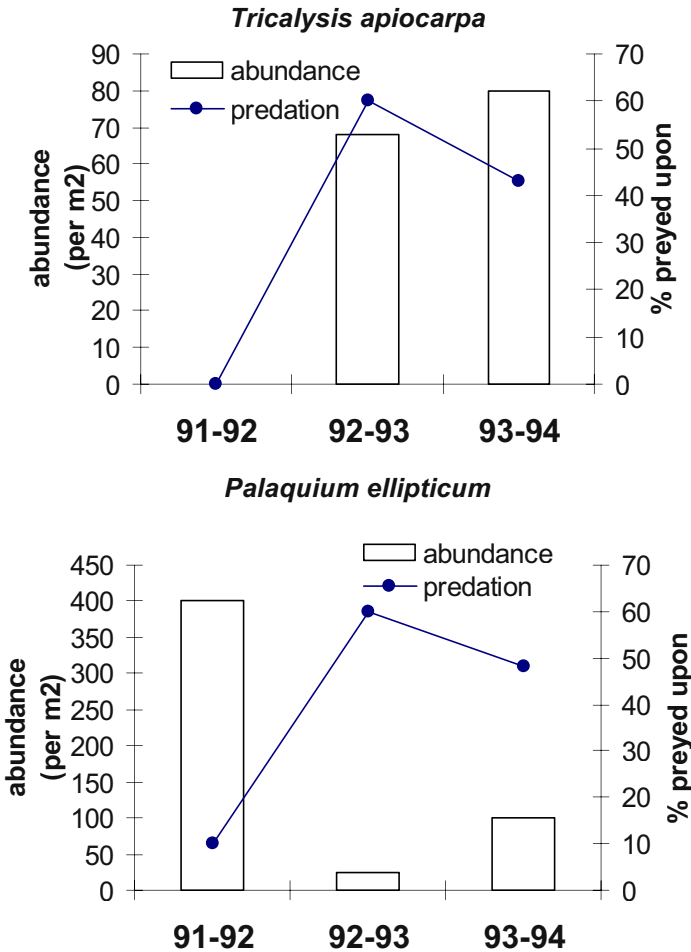


Figure 6. Fruit abundance and seed predation levels on two masting species across years.

DISCUSSION

Seed Predation

Pre-dispersal seed predation by arboreal mammals among canopy trees in Kakachi ranges from 1% to over 96%. These proportions vary between species and between years within species. Nearly all fruit species whether fleshy, hard, or protected, suffer from predation by vertebrates and 57% (20 out of 35) of the species suffer more than 50% pre-dispersal seed predation. These values are relatively higher than those reported for lowland Neotropical rainforests where post-dispersal seed predation is high (see Leigh and Alba, 1992; Terborgh et al. 1993). In Peru, seed predation is primarily restricted to post-dispersal predation (Terborgh 1990). In the M'Passa forest of Gabon, Gautier-Hion (1990) has shown a high diversity of arboreal seed predators, though levels of seed predation have not been quantified at the community level. In Southeast Asia, Leighton and Leighton (1983) note a high proportion of pre-dispersal seed predation by arboreal seed predators.

In Kakachi, pre-dispersal seed predation is higher than at sites in the Neotropics. This may be due to the high abundance of seed predators. Seeds form a major component in the diet of *Ratufa indica* (Borges 1993) and *Trachypithecus johnii* (Oates et al. 1980). The lion-tailed macaque, *Macaca silenus*, though a frugivore, also eats seeds (Menon, 1993). There is also some evidence that civets eat seeds of some species, because fragments of seeds were seen in their scats. Though seeds form only 25% of the diet of *T. johnii* (Oates et al., 1980) these squirrels consume many seeds because they are very abundant at this site. Based on his extensive survey of the Agasthyamalai hills, Oates (personal communication) found Kakachi to be the site with the highest known density of *T. johnii*. Similarly, *R. indica* seem to be at a higher density in Kakachi than in some forests (Ramachandran, 1988), but lower than in others (Borges, 1989).

A second reason for Kakachi's high levels of seed predation may be its proportion of fleshy-fruited trees, which occur at low densities compared to hard-fruited species (Ganesh, 1996). Seeds form nearly 57% of the edible biomass in fleshy fruits and are the only dietary resource for vertebrates in hard non-fleshy fruits (Ganesh, 1996). Seeds are also more nutritive and have a higher caloric value than pulp (Jordano, 1992). Even among Kakachi's dominant fleshy-fruited species like *P. ellipticum*, seeds form the major resource for seed predators which tend to discard the pulp. Gautier-Hion et al. (1993) record higher proportions of seeds in the diets of African *Cercopithecus* monkeys in Zaire than in Gabon. They attribute this to a lower availability of fleshy fruits in Zaire than in Gabon, a phenomenon which is linked to impoverished soil. The Kalakad region of the Kakachi forest also has an impoverished red loamy soil (Ganesan and Parthasarthy, unpublished data) which may be a reason for the low number of fleshy-fruited species there. Another reason for the area's high level of seed predation could be the asynchronous fruiting pattern and low fruit production of many fleshy-fruited species like *T. apiocarpa*, *Syzygium mundagam*, *Scolopia crenata*, and *Holigarna nigra*. In contrast, non-

fleshy species like *Cullenia exarillata* and *Ormosia travancorica* fruit more regularly and their fruits are available for longer periods (Ganesh, 1995).

Fruit characteristics

In Kakachi and in Gabon, fleshy fruits had protected seeds, were either red, green, or orange and were commonly dispersed by birds (Gautier-Hion et al., 1985). At Kakachi, species with protected seeds had significantly lower predation levels than those with unprotected seeds. In contrast, in Gabon, species with protected seeds suffered high levels of pre-dispersal seed predation. Species which suffered high levels of seed predation in Gabon also had a greater diversity of seed predators and a different set of dispersers, whereas, for many species in Kakachi seed predators were the only dispersers.

Seed size may influence seed predation. Larger seeds have been described as more prone to predation (Janzen, 1969; Harper, 1977). In Kakachi the sizes of seeds ranged from a few mm to about 30mm in length (Ganesh, 1996). While all seeds studied suffered predation, *Trachypithecus johnii* ate seeds of all size classes while *Ratufa indica* ate only smaller seeds. Small hard seeds are avoided by *T. johnii* and *Macaca silenus*. Two vertebrates, *M. silenus* and *R. indica* avoided eating the large seed of *Myristica dactyloides* and instead ate the aril while *T. johnii* consumed the seed. The reasons are not obvious, apart from the constraint of seed size, but seeds could have been avoided due to toxicity and/or nutrient availability (Janzen, 1969), which were not examined in this study.

Masting and phenology.

Synchronous seed production may have two important advantages. One is escape from predation pressure and the other is to take advantage of favorable climatic conditions for release and germination of seeds. There is an inherent difficulty in separating the two hypotheses, because mast fruiting could have evolved in response to either or both with the same effect. Terborgh (1990) suggested that for species that do not suffer from high seed predation, the release from predator pressure could lead them to show more random fruiting patterns. For such species masting events are of no importance with dispersal advantages overruling escape from predation. Some bird-dispersed species in Kakachi show this pattern. For instance, *Tricalysia apiocarpa* does not have a significant reduction in predation when mast fruiting even though the predation levels are high (T.Ganesh, pers. obs.). These *T. apiocarpa* trees fruit for an extended period of several months but most of the predation happens in the unripe fruits. Birds disperse whatever seeds escape this onslaught later in the trees' fruiting period.

Previous authors have stated that the influences of seed predators on fruit traits might overwhelm those imposed by seed dispersing frugivores. The case in Kakachi may be different. It appears that a combination of disperser attraction and seed predation avoidance could have evolved together to benefit from mast fruiting. The case of *Pallaquium ellipticum* in Kakachi is pertinent here. The mast fruiting of this

species attracts bats (*Cynopterus* spp.) and these bats were abundant in 1994 and to lesser extent in 1991 when this plant was mast fruiting. In other years when fruiting was low the seeds were found to be preyed upon by squirrels and monkeys. Predation levels on seeds in non-masting years were very high (Fig. 6b). This tree species did not evolve a thick protective seed coat but may have evolved a dual strategy to overcome seed predation and at the same time attract seed-dispersing fruit bats by mast fruiting. Yet another strategy would be to swamp predators early in the fruiting season so that enough fruits escape initial onslaught to remain and become ripe for seed dispersers later on in the season. One species, *Tricalysia apiocarpa*, may have evolved such a strategy. Its fruits are not preyed upon when ripe and masting appears to have no effect on seed predation (Fig. 6a). However, the sheer amount of fruits produced by this species increases the chance that there are sufficient fruits that are ripe and available to dispersers several months after fruiting begins. Masting here is therefore useful at the initial tail of the fruiting period and dispersers are more important later on in the season.

In conclusion, fruits in the rainforests of Kakachi appear to be affected strongly by vertebrate seed predation during the pre-dispersal stage. Strong protective features of fruits and seeds appear to be a result of selection imposed by vertebrate seed predators. However, masting as a phenomenon is not only applicable for swamping seed predators but perhaps also for attracting seed dispersers. Therefore, seed predation should be considered in combination with seed dispersal in the study of these plant/frugivore interactions.

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CHAPTER 9.

FAST FOODS OF THE FOREST: THE INFLUENCE OF FIGS ON PRIMATES AND HORNIBILLS ACROSS WALLACE'S LINE

MARGARET F. KINNAIRD, TIMOTHY G. O'BRIEN

Abstract

We examine relationships between fruit production and patterns of primate and hornbill densities on Sulawesi and Sumatra, Indonesia. Sumatra lies within the Asian biogeographic realm and has greater biodiversity while Sulawesi lies within Wallacea and has greater endemism. Phenological samples share 51% families, 29% genera but only 7% species. Generally, Sumatran trees are dispersed more often by small birds, bats and squirrels. Sulawesi has more wind-dispersed species. Fruiting is more seasonal on Sulawesi and is related to rainfall while Sumatran fruiting patterns show no relationship with rainfall. Sulawesi has larger trees, larger crops and smaller fruits. Average fruit production is five times higher on Sulawesi. On both islands, figs contribute disproportionately to fruit biomass. Hornbill and primate assemblages are less complex on Sulawesi but biomass of both groups is significantly higher. Hornbills and primates share 41 and 45% of diet species on Sumatra and Sulawesi, respectively. Wide-ranging hornbills on both islands decline in number or leave study areas when fig availability is low. Primates and hornbills (except *Buceros rhinoceros*) do not respond to the availability of other important diet species in the Anacardiaceae, Annonaceae, Meliaceae or Myristicaceae families. Fig availability influences resource defense and grouping patterns of primates and hornbills. We suggest that figs are a keystone guild due to their prime influence on abundance, distribution and behavior of large frugivores in Asia and Wallacea.

Key words: Figs, frugivory, hornbills, Indonesia, primates, Sulawesi, Sumatra

INTRODUCTION

Keystone plants are among the most frequently discussed types of keystone mutualists (Meffe & Carroll, 1994; Peres, 2000; Terborgh, 1986). Keystone plants provide resources such as leaves, flowers, fruits, seeds or even floral nectar or sap to a group of consumers at a level that is much larger than would be expected from their abundance alone (Peres, 2000; Power et al., 1996). Although the definition of keystone species, and therefore keystone plants, has been widely debated (Hulbert,

1997; Power & Mills, 1995; Power et al., 1996), most authors agree that the influence of such species on their communities should be strong and of critical importance to community dynamics. Because of the pivotal roles they play, the loss of keystone plants from a community or ecosystem could have dramatic effects, especially since they should have low ecological redundancy. As conservation biologists, we should be concentrating on identifying potential keystone plants and understanding the degree of complexity, and measuring the strength of interactions provided by such plants. In spite of this, there have been few detailed studies of the population ecology of potential keystone plants and how to recognize them in species-rich plant assemblages (Peres, 2000). Likewise, we know very little about the specific responses of animal communities to the availability of keystone plant resources (Shanahan et al., 2001).

The importance of figs for tropical frugivorous vertebrates, especially birds and primates, has been recognized and figs as a group have been referred to as "keystone species," "keystone mutualists," or a "keystone guild" (Bonaccorso, 1979; Kalko, 1996; Kinnaird et al., 1999; Lambert & Marshall, 1991; Leighton & Leighton, 1983; Terborgh, 1986). Shanahan et al. (2001) show that, conservatively, >10% of the world's birds and >6% of the world's mammals consume figs, making figs the most widely consumed plant genus. The attractiveness of figs for wildlife has been attributed to their asynchronous fruiting patterns, the tendency to produce large crops that ripen synchronously within a tree, the unprotected nature of the fruits and low interannual variation in fruit production (Janzen, 1979). Such fruiting patterns may make figs a reliable food source during times of general fruit scarcity (Foster, 1982; Leighton & Leighton, 1983; Terborgh, 1983; 1986); however, even when other resources are abundant frugivores regularly eat fig fruits (Lambert, 1991; Lambert & Marshall, 1991; Kinnaird et al., 1996, 1999) and in Asia, Wallacea and Australasia, a number of fig specialists have evolved (Shanahan et al., 2001). High concentrations of edible carbohydrates may contribute to the popularity of figs as a food source (Conklin & Wrangham, 1994) even though protein and lipid levels are variable and relatively low (Bronstein & Hoffmann, 1987; Conklin & Wrangham, 1994). Kinnaird et al. (1999), however, found no significant differences in protein and lipid levels for a sample of 20 figs and 35 non-fig fruits from Sulawesi. Additionally, O'Brien et al. (1998) argue that high levels of calcium make figs especially attractive to frugivorous birds and mammals.

Much of the research supporting the importance of figs to wildlife comes from the Neotropics (e.g. Foster, 1982; Kalko et al., 1996; Milton et al., 1982; Terborgh, 1983, 1986). Data from Africa are equivocal and suggest that the keystone role of figs may be context dependent (*sensu* Powers et al. 1996). Guitier-Hion and Michaloud (1989) suggest that figs are unimportant to West African birds and mammals due to their low abundance and low fruit production, while Wrangham et al. (1993) stress the importance of figs to chimpanzees, *Pan troglodytes*, and other frugivores in a Ugandan forest (For more on figs' role in Ugandan forests see Chapman et. al., this volume). In India, Borges (1993) found that fig densities were too low for them to function as keystone species. Several studies from Southeast Asia provide further evidence of the importance of figs to a diverse assemblage of

wildlife including orangutans (Leighton, 1993; Sugardjito et al., 1987), hornbills (Kinnaird et al., 1996; Leighton 1982, Leighton & Leighton 1983) and fruit doves (Lambert 1989). Van Schaik (1996) states that figs may be the single most important wildlife food resource in North Sumatran forests and suggests that wildlife densities may be higher in areas with high densities of large, strangling figs. Similarly, Kinnaird et al. (1999) conclude that the genus *Ficus* is the single most important food resource for Sulawesi's fruit-eating birds and mammals.

Shanahan et al. (2001) argue that research into figs as keystone plant resources must take into account the availability of non-fig fruits versus fig fruits, fig density, fig phenology, and frugivore mobility, and must confirm that figs are suitable for, available to and required by frugivores. Many past studies, although critical in identifying the important role of figs, were short-term, presented data from only one site, and rarely investigated the variability or strength of the interactions between figs and animal guilds, and linkages with other species in the community. Phenological studies, for example, show fig availability at times of community-wide fruit shortage but can only imply that animals will rely on figs during this time. Animal studies on the other hand may show dependence on figs by one or a guild of species, but may not measure the strength of the interaction or if it is context-dependent. Obviously the possible keystone nature of species are best tested experimentally, but such tests are difficult if not impossible in natural systems, and tend to take a long time to show direct and indirect effects (Ernest & Brown, 2001; Power & Mills, 1995).

In this study, we present long-term data on tree fruiting patterns and taxonomic diversity in conjunction with frugivore abundance, feeding ecologies and behavior. Although our study was not experimental, it does allow comparison of communities across two biogeographic regions using similar methods. In particular, we examine the roles of figs in community-wide fruiting patterns and the importance of fruit availability to hornbill and primate assemblages at forest sites on Sumatra and Sulawesi. Specifically, we ask if the contribution to food resource availability by figs at these sites is large relative to their abundance and to the resources produced by the rest of the fruit tree community. We also ask if differences in overall fig availability help explain differences in the capacities of these forests to support their frugivore assemblages, and whether figs influence movement patterns, behavior, and densities in similar ways on these different islands. Finally, by comparing patterns between Asia and Wallacea we may ask if the strength of the interactions vary with fig abundance across spatial and temporal scales and under diverse ecological conditions, or in other words, if the role of figs is context-dependent.

METHODS

Study Sites

Sulawesi – Sulawesi is the third largest island in Indonesia and is the largest and most central island of Wallacea (Figure 1). Wallacea is the remarkable

biogeographical transition zone between Asian and Australasian plants and animals. On Sulawesi, primates of Asian origin co-exist with marsupials of Australasian origin, and Australasian *Casuarina* trees occur sympatrically with Asian Dipterocarps. Due in part to its geologic history, unusual shape and geographic isolation, Sulawesi has a large percentage of endemic birds and mammals. Over 62% of Sulawesi's 127 mammal species are endemic and 27% of the island's 328 bird species are unique, making it one of the most important endemic bird areas in Indonesia (International Council for Bird Preservation 1992).

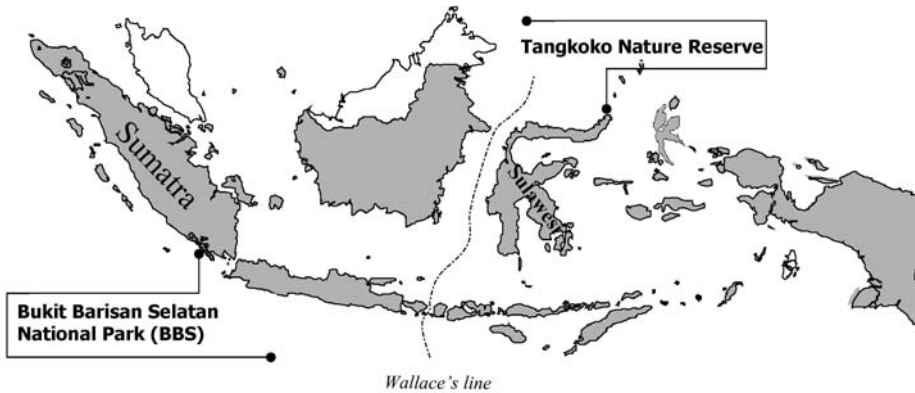


Figure 1. Location of study areas in Indonesia on both sides of Wallace's Line.

The Tangkoko Dua Sudara Nature Reserve (TDS), located on the northernmost tip of Sulawesi ($1^{\circ}34'N$, $125^{\circ}14'E$) is a critically important refuge for Sulawesi's unique bird and mammal fauna (Kinnaird et al., 1996; O'Brien & Kinnaird, 1996; 1997). TDS encompasses approximately 8,900 ha and is isolated from other forests by the sea and by agricultural lands. Forest ranges from sea level to 1,350 m elevation and is broadly classified as lowland tropical rainforest (International Union for Conservation of Nature 1991). Rainfall averages 1,700 mm per year (1992-1994) and is highly seasonal (Figure 2) with occasional droughts associated with the El Niño Southern Oscillation (ENSO; Cahill & Walker, 2000). Volcanoes dominate the reserve: Tangkoko, the recent ash cone, Batu Angus, and the twin peaks of Dua Sudara. Although threatened by agricultural encroachment and severe hunting pressure (O'Brien & Kinnaird, 1996; 2000), TDS supports the largest remaining population of endemic Sulawesi black macaques (*Macaca nigra*). Two hornbill species endemic to Sulawesi occur in TDS, the Sulawesi red-knobbed hornbill (*Aceros cassidix*) and the Tarictic hornbill (*Penelopides exarhatus*). Red-knobbed hornbills at TDS attain some of the highest densities of forest hornbills ever recorded (Kinnaird et al., 1996).

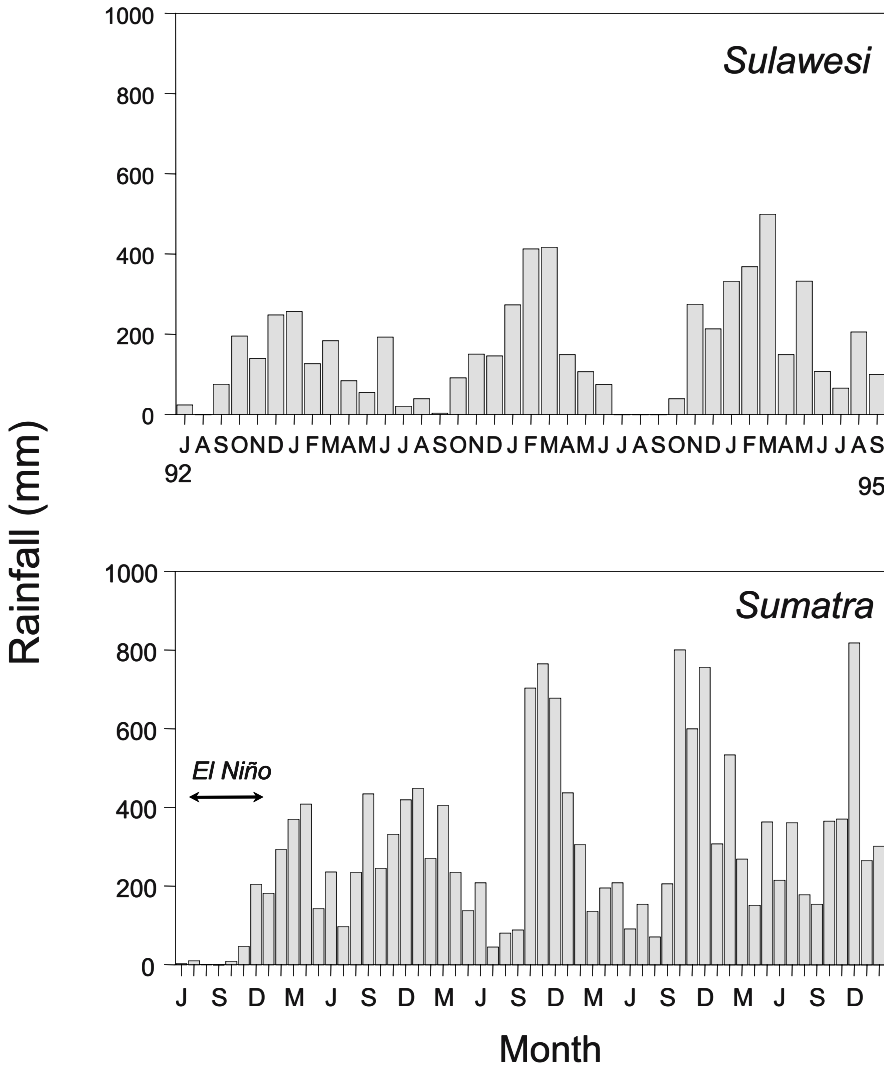


Figure 2. Monthly rainfall (in mm) for TDS and BBS.

We conducted our research from July 1992 through September 1995 within a 440-ha area on the north slope of Tangkoko Volcano. The study area is characterized by a mosaic of habitat types and disturbance regimes including (1) heavily burned areas in which the canopy has been destroyed or severely disturbed (101 ha); (2) 30-year-old regenerating agricultural plots dominated by coconut

(*Cocos nucifera*) and mango (*Mangifera indica*) trees and early successional forest species (25 ha); and (3) lightly disturbed areas with treefall gaps greater than 1 ha in size, or where light fires passed through the understory (271 ha). Forest condition in lightly disturbed areas is highly variable, including broken and closed canopy forest. Closed canopy primary forest accounts for approximately 44 ha and is characterized by large *Palaquium amboinensis*, *Cananga odorata* and *Dracontomelum dao* trees, as well as figs (*Ficus* spp.) and *Livistona rotundifolia* palms. The study area is gridded with trails at 100-m intervals.

Sumatra – Sumatra is Indonesia's second largest island and is characterized by extremely high levels of biodiversity (Whitten et al., 1997). The island's high biodiversity is due, in part, to its size, diversity of habitats, and geologically recent connection to mainland Asia. Sumatran forests are comparable to the forests of Borneo and New Guinea in tree species diversity and contain some unique plant species such as *Rafflesia arnoldii* and *Amorphophallus titanum*, the largest and tallest flowering plants in the world, respectively (Whitten et al., 1997). Sumatra has more mammal species (201) than any other Indonesian island (Payne et al., 1985) and is unusual in supporting populations of most of Asia's large and endangered mammals, including Sumatran tigers (*Panthera tigris sumatrae*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), elephants (*Elephas maximus*), and Sumatran orang-utans (*Pongo pygmaeus*). Sumatra also has an extremely rich avifauna with an estimated 486 species, but relatively few endemic bird species (21: Whitten et al., 1997).

We conducted research in the Bukit Barisan Selatan National Park (BBS) from July 1997 through February 2002 (Figure 1). BBS is the third largest protected area (3,568 km²) on Sumatra. The park is located in the extreme southwest of the island (4°31' – 5°57'S and 103°34' – 104°43'E) and extends more than 150 km along the Barisan mountain range. BBS contains some of the largest tracts of lowland rainforest remaining on the island and is the major watershed for southwest Sumatra (FAO, 1981). The park's long thin shape gives it more than 700 km of borders adjacent to villages, agriculture and plantation forestry, and poaching and encroachment for logging and agriculture are rife (Kinnaird et al., 2003; O'Brien et al., 2003a). Despite these problems, BBS provides important habitat for a major portion of Sumatra's large charismatic mammals as well as gibbons (*Hylobates agilis* and *Symphalagus syndactylus*: Kinnaird et al., 2003; O'Brien et al., 2003b) and all hornbill species known to occur on the island (O'Brien & Kinnaird, 1996). Annual precipitation ranges from 1,600 mm in dry years to 4,000 mm in wetter years (Figure 2). Although a short dry season generally occurs between June and September, rainfall exceeds 60 mm monthly and the area is considered weakly seasonal (Wright & van Schaik, 1994). Like Sulawesi, Sumatra also experiences periodic ENSO-related droughts (Kinnaird & O'Brien, 1998).

Our study was conducted in WCS/PHKA Way Canguk Research Area, a 900 ha site of lowland forest contiguous with lowland forests of the rest of the park. Intact closed canopy forest covers approximately 492 ha of the study area and is classified into two broad habitat types; the first characterized by tall trees with large diameter-breast-height (DBH) measurements (332 ha) and the second characterized by lower

stature trees with smaller DBHs (160 ha). Disturbed forest covers the remaining 460 ha, is characterized by a more open canopy, a dense understory often dominated by herbaceous plants of the Zingiberaceae family, and generally has experienced ENSO-related fires as recently as 1997. The most recent ENSO fires burned approximately 165 ha of the study area in late September and October 1997 (Kinnaird & O'Brien, 1998). The study area is gridded with trails at 200 m intervals.

Fruit Availability

We established permanent vegetation plots at both study sites to determine densities of fruiting tree species and to monitor fruiting patterns. Plots were larger in size (50 m x 50 m on Sulawesi, 10 m x 50 m on Sumatra) and fewer in number on Sulawesi (22 plots) than Sumatra (100 plots) but represent a similar amount of habitat for the two forests (5.5 ha and 5 ha for Sulawesi and Sumatra, respectively). Plots were placed in stratified random locations along trails throughout the study areas such that there was one plot for every 4-5 ha of forest on Sulawesi and every 8-9 ha of forest on Sumatra. Within plots, we measured, identified and tagged all trees > 10 cm DBH. Because fig trees were underrepresented in the plots at both sites, we established a 2.1 km x 0.02 km transect on Sulawesi and a 7.8 km x 0.1 km transect on Sumatra specifically to monitor fruiting figs.

We visually examined tagged trees for fruit at the beginning of every month. For each fruiting tree, we estimated the total fruit crop using an exponential scale developed by Leighton (1993). We then estimated the percentage of the total crop that was ripe and derived estimates of ripe and unripe fruit crops. Monthly crop production for the entire community was a simple summation; depending on the desired analyses we summed monthly crop production by consumer/disperser type (see below) and by fig and non-fig species separately. We also calculated estimates of monthly fruit biomass by multiplying a species' mean fruit wet weight (Kinnaird & O'Brien, unpublished data) by fruit crops then summing across species. Because we did not have fruit weights for all tree species, we examined the relationship between estimates of fruit biomass and monthly estimates of fruit crop to see if crop could be used as a surrogate for biomass measures of monthly fruit availability. We analysed the relationships by island, using linear regressions (Sokal & Rohlf, 1981) on subsets of non-fig ($N_{\text{Sulawesi}} = 56$, $N_{\text{Sumatra}} = 90$) and fig species ($N_{\text{Sulawesi}} = 21$, $N_{\text{Sumatra}} = 13$) for which we had wet weights. We found significant positive relationships between monthly crop size and fruit biomass for Sulawesi non-fig species ($\ln \text{biomass} = 4.29 + 0.76 \times \ln \text{crop}$; $t = 8.914$, $P < 0.0001$, $N = 24$) and fig species ($\ln \text{fig biomass} = 4.17 + 0.63 \times \ln \text{fig crop}$; $t = 6.14$, $P < 0.0001$, $N = 24$), and a similar, positive relationship for Sumatran non-fig species ($\ln \text{biomass} = 4.78 + 0.76 \times \ln \text{crop}$; $t = 7.63$, $P < 0.0001$, $N = 46$) and fig species ($\ln \text{biomass} = 3.59 + 0.66 \times \ln \text{crop}$; $t = 9.8$, $P < 0.0001$, $N = 46$). We therefore restricted most of our analysis to estimates of fruit crop.

Fruit Classification

In order to examine the effects of spatial and temporal abundance of food resources on particular frugivore densities and population fluctuation, we first classified tree species by frugivore consumers/dispersers. We considered 4 broad fruit classifications: primate, hornbill, wind, and other. The latter category included fruit species consumed by squirrels, bats, and small understory birds. Classifications were made based on our studies of primate and hornbill feeding ecology at both sites (Anggraini et al., 2000; Hadiprakarsa, 2001; Kinnaird, 1998; Kinnaird & O'Brien, 1999; Kinnaird & O'Brien, unpublished data; Kinnaird et al., 1996; Nurcahyo, 2000; O'Brien, 1997; O'Brien & Kinnaird, 1997; Suryadi et al., 1996) and published literature from other sites (Leighton, 1982; Sterck 1995). If a given tree species was consumed by both primates and hornbills, it was classified as a shared resource and monthly estimates of crops were included in fruit crop sums for separate analyses of hornbills and primates. Species classified as 'wind' or 'other' were excluded from the analysis.

Hornbills and Primates

Our study considers the hornbill and diurnal primate communities of northern Sulawesi and southern Sumatra. On Sulawesi, we focused on the island's only two hornbill species, the Sulawesi red-knobbed hornbill (*Aceros cassidix*) and the tarictic hornbill (*Penelopides exarhatus*). Sulawesi contains seven commonly recognized macaque species (Fooden, 1969; Groves, 1980) distributed across the island. Our study concerned the crested black macaque (*Macaca nigra*), which occurs only on the northern peninsula and does not overlap with any of the other macaque species. Southern Sumatra has 9 hornbill species and we concentrated on the five most common species that are known to breed in the study area: rhinoceros (*Buceros rhinoceros*), helmeted (*Rhinoplax vigil*), bushy-crested (*Anorrhinus galeritus*), wreathed (*Rhyticeros undulatus*) and white-crowned (*Berenicornis comatus*) hornbills. Southern Sumatra also has six diurnal primates; we concentrated on the most commonly occurring species, siamangs (*Symphalangus syndactylus*), agile gibbons (*Hylobates agilis*), pig-tail macaques (*Macaca nemistrina*), and banded leaf monkeys (*Presbytis melalophos*).

Density and biomass estimation

We used variable-width line-transect surveys (Burnham et al., 1980; Buckland et al., 1993) to estimate monthly densities of primates and hornbills at both study sites. Surveys were conducted just after completion of phenological sampling and took place between 0600 and 1000 hrs. On Sulawesi, we surveyed red-knobbed hornbills using 10 trails, each 2 km in length with 5 observers simultaneously walking east-west trails 200 m apart (Kinnaird & O'Brien, 1996). A second monthly survey was conducted by a single team on 4 trails, each 4.6 to 5.9 km in length to estimate tarictic hornbill and crested black macaque densities (see O'Brien & Kinnaird,

1996). On Sumatra, three teams of two observers each simultaneously surveyed 12 trails 2.2 kms in length over two mornings followed by 6 trails of 2 kms in length on a third morning. Although Sumatran trails were spaced 200 m apart as on Sulawesi, daily surveys were conducted on alternating trails separated by 400 m. As animals were detected during surveys, we noted the species, number of individuals, detection cue (visual or vocal), location of observer on transect, distance between observer and animal, and compass angle. Compass angle was later converted to angle between observer and animal.

We used DISTANCE software (Laake et al., 1993) to calculate monthly density estimates for the hornbills and crested black macaques on Sulawesi, and for the four most common hornbill species, banded leaf monkeys and pig-tail macaques on Sumatra. Where monthly observations were less than 20, we post-stratified the data and applied a pooled sighting function to monthly data sets. Final models were chosen based on AIC criteria or minimizing the variance due to model selection. Density estimates for territorial gibbons and siamangs were based on complete annual censuses of groups within the Way Canguk study area and range mapping for a subset of these groups.

Biomass estimates for individual hornbill and primate species were calculated as a weighted mean body mass for primate and hornbill species based on published estimates of male, female and juvenile body weights (Kemp, 1995; Rowe, 1996; Smuts et al., 1987), ratio of juveniles to adults and adult sex ratios. We multiplied mean body mass by densities and summed across groups to estimate the biomass of primate and hornbill aggregations for the Sulawesi and Sumatra study sites.

Finally, to test the generality of the relationship between figs and Asian frugivores, we collated density estimates of strangling figs and associated hornbill assemblages using line-transect methods at additional sites on Sulawesi (A. Cahill & J. Walker, unpubl. data), Sumba (Sitompul et al., in press), Seram, and Indonesian Borneo (Kinnaird & O'Brien, unpublished data). We also used published estimates of hornbill and fig density from peninsular Malaysia (Johns, 1983; Whitmore, 1984), Malaysian Borneo (Lambert, 1990; 1991), Indonesian Borneo (Leighton, 1982), and northern Sumatra (Kinnaird et al., 1996; van Schaik, 1996).

Behavior

To assess the degree to which hornbills and primates rely on fruit resources, we conducted studies of the feeding ecology of red-knobbed hornbills (Kinnaird & O'Brien, 1999; Suryadi et al., 1996), tarictic hornbills (O'Brien, 1997), crested black macaques (Kinnaird & O'Brien, 2000; O'Brien & Kinnaird, 1997), four Sumatran hornbill species (Anggraini et al., 2000, Hadiprakarsa & Kinnaird, in press), and siamangs (Nurcahyo 2000, O'Brien et al., 2003b). We also used our unpublished data on Sumatran hornbills delivering food to nests and on siamang diets. Finally, we referred to published literature to estimate the diets of Sumatran macaques, banded leaf monkeys and agile gibbons. Behavioral data on the defense of food resources comes from studies of intergroup interactions and territoriality of crested black macaques (Kinnaird & O'Brien, 1999; 2000), tarictic hornbills (O'Brien,

1997), siamangs (Kinnaird & O'Brien, unpubl. data) and helmeted hornbills (Kinnaird et al., 2003).

RESULTS

Tree Community Composition

Tree community composition differed between the Sumatran and Sulawesi study sites. On Sulawesi, we measured 2021 individuals from 45 families and 88 genera; 163 species were represented including 16 unidentified species. On Sumatra, we measured 2204 individuals from 49 families and 148 genera. Sumatra is far more speciose than Sulawesi, with 304 recognized species and an additional 61 unidentified but distinct species. Over half of the tree families identified (54.8%; Figure 3) occur in both study sites but the two sites share a much lower percentage of genera (29.2%) and species (7.1%). The percentages of unique families were nearly equal for the Sulawesi (21%) and Sumatra (24.2%) sites but Sumatra claims a greater percentage of unique genera (51.4%) and species (62.6%) than Sulawesi (19.5 and 30.3%, respectively).

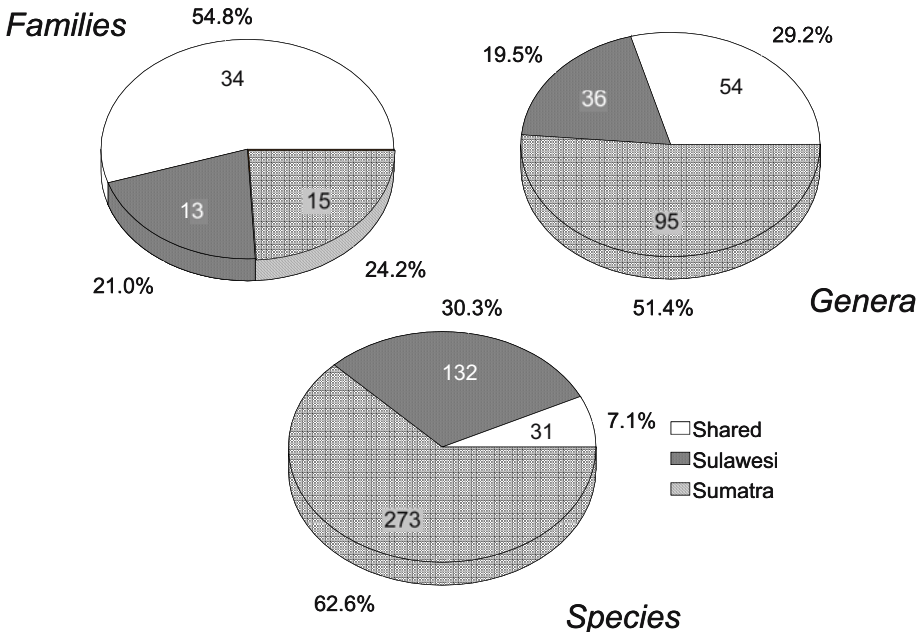


Figure 3. Proportion of tree families, genera and species in samples unique to Sumatra and Sulawesi, and those shared by Sumatra and Sulawesi.

We identified 39 fig species in the TDS study site. Of these, 21 species of figs were identified in plots and transects on Sulawesi for a density of 11.8 figs/ha (115 individuals) in our sample. A second estimate for figs in the study area eaten by hornbills and primates and based on 1.26 km² of transects in the study area is slightly lower at 8.3 figs/ha. In Way Canguk, we identified 32 fig species, including 22 species in the phenological samples, for a density of 1.37/ha (113 individuals). An independent transect survey in Way Canguk gave similar results to the density in the sample.

Fruit Consumers and Dispersers

Primates and hornbills consume the majority of fruit species on Sulawesi (63.9%) and Sumatra (52.6%; Figure 4). Sulawesi is characterized by a greater percentage of wind dispersed species than Sumatra (12.5% vs. 8.27%), while Sumatra has a much larger percentage of fruits consumed by bats, understory birds and squirrels (39.1% vs. 23.6%). Sumatra has a higher diversity of understory fruits compared to Sulawesi. Primates and hornbills show a large degree of overlap in diet species, sharing 45% of all diet species on Sulawesi and 50% on Sumatra. Shared diet species included all *Ficus* species as well as the brightly colored oily drupes of the Lauraceae and Annonaceae families and the dehiscent fruits with lipid rich arils of the Meliaceae and Myristicaceae families. Primates have similar percentages of unique diet species on Sumatra (39.3%) and Sulawesi (39%) while hornbills have a slightly higher percentage of unique diet species on Sulawesi (16.3%) relative to Sumatra (10.6%). Unique primate diet species were of the Euphorbiaceae, Flacourtiaceae, Ebenaceae, Anacardiaceae and Clusiaceae families and were generally dull in color, often hard, and found in the understory or displayed on tree trunks (cauliflorous). Alternatively, the few fruit species unique to hornbills were the larger, dehiscent arillate fruits of the Meliaceae family (i.e. *Chisocheton* spp.), one genera of the Lauraceae (*Litsea* spp.) and fruits of *Canarium* in the family Burseraceae that are protected from primates by urticating hairs.

Fruit and Tree Characteristics

The Sulawesi forest is characterized by having more trees in the larger size classes than that of Sumatra. Frequency distributions of DBH measurements differ significantly between the two sites ($\chi^2=50.99$, $df=9$, $P<0.0001$). Differences are due to greater than expected numbers of trees in the under 20 cm size class in Sumatra, and greater than expected numbers of trees in size classes over 40 cm from Sulawesi (Figure 5). As expected, trees with larger DBH measurements produce larger fruit crops, and crops tend to be larger on Sulawesi than Sumatra ($K-S z_{crop}=2.74$, $P<0.001$). Trees bearing larger crops however, have smaller fruits on both islands ($r_s = -0.30$, $P<0.001$, $N = 178$ species with crop size and fruit weight estimates). Mean fruit weight is significantly heavier on Sumatra than on Sulawesi ($\bar{x}_{Sumatra} = 14.3$ gms, $SE = 2.45$, $N = 139$; $\bar{x}_{Sulawesi} = 6.1$, $SE = 1.6$, $N = 105$;

K-S $z = 1.59$, $P = 0.013$); nearly 20% of the Sumatra fruit samples weigh > 20 gms while only 3.8% of fruits on Sulawesi reach this size (Figure 6). For example, rao (*Dracontomelum dao*) trees produce more, smaller fruits on Sulawesi compared to the fewer, larger fruits produced by these trees on Sumatra. The net effect of the small fruit-large crop relationship is that the distribution of biomass production by the fruit tree communities of Sulawesi and Sumatra is similar on a per species basis. Differences in community-wide fruit biomass should therefore be due to changes in composition of fruit community over time, and changes in the abundance of fruiting trees both by species and for the community overall.

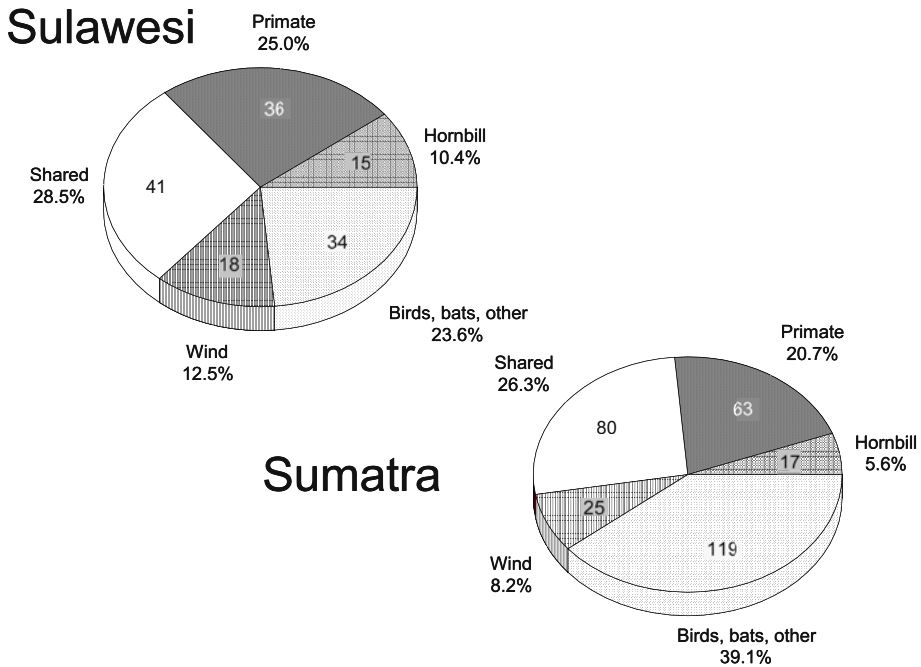


Figure 4. Numbers and percentages of fruit species dispersed by wind and animals on Sulawesi and Sumatra. Shared species are dispersed by hornbills and primates.

Spatio-temporal Patterns of Fruiting

The number of trees in fruit/ha and the total fruit crop produced/ha varied over time at both study sites (Figure 7). Both measures of fruit production were consistently higher for Sulawesi than for Sumatra. More than 40 trees/ha were in fruit during all but 2 months on Sulawesi, while Sumatra had more than 40 trees fruiting/ha during

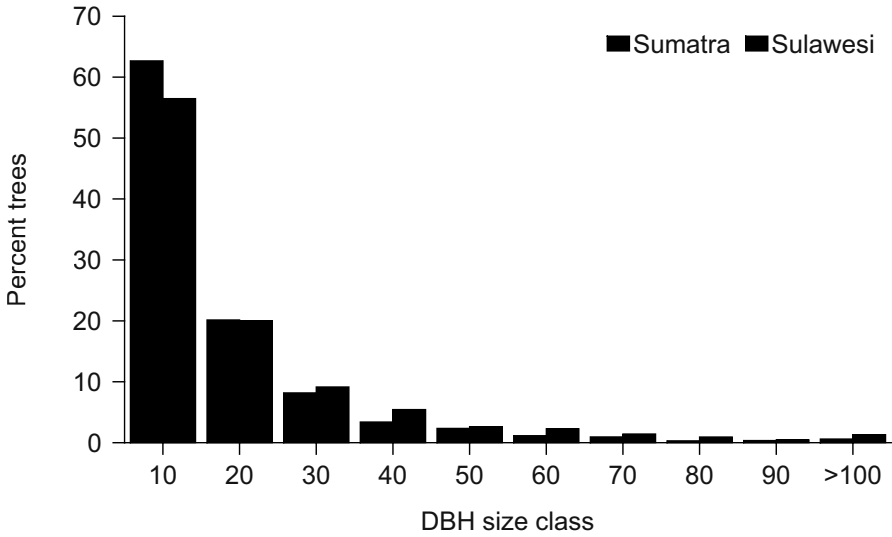


Figure 5. Size distributions of phenology trees (in 10 cm DBH classes) on Sulawesi and Sumatra.

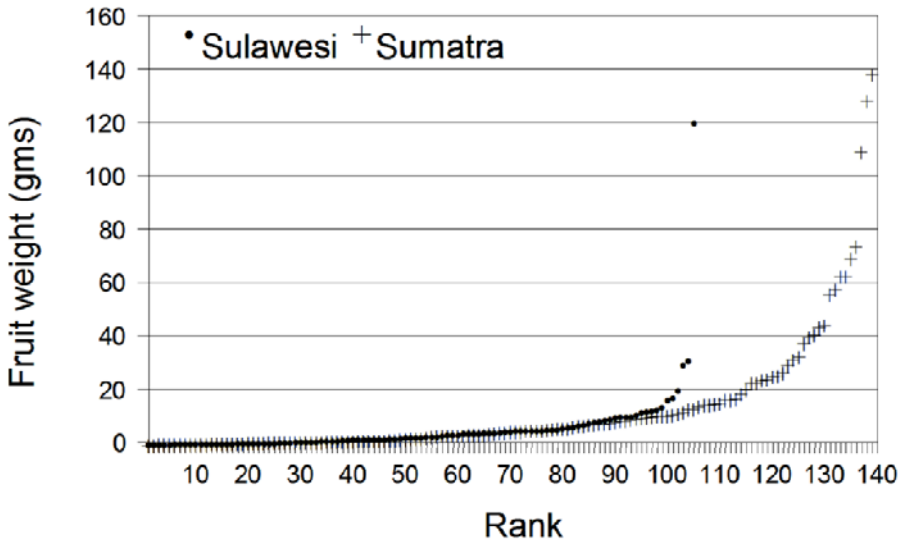


Figure 6. Ranked fruit weights for Sulawesi and Sumatra.

only 4 months. Total crop production varied by orders of magnitude between the two sites; monthly Sulawesi crops measured from hundreds of thousands to millions of fruits while Sumatran crops measured from tens of thousands to hundreds of thousands of fruits (Figure 8). Although figs made up a relatively small percentage of diet trees (hornbill + primate) in fruit at both sites each month, they were available during all months and the contribution of figs to the total monthly fruit crop was large. On average, figs accounted for 2.7% and 3.4% of all fruiting trees/month but contributed more than 64% (maximum 97%) and 50% (maximum 90%) of the total monthly crop production for Sumatra and Sulawesi, respectively.

Mean monthly fruit biomass estimates (kg fruit/ha) calculated from sub-sets of weighed fig and non-fig fruits reflect similar differences in overall fruit availability between the two islands as well as the important contribution of figs. Biomass of non-fig species is, on average, 3.8 times greater ($258.4 \text{ kg/ha} \pm 51.5$ vs $51.2 \text{ kg/ha} \pm 6.4$) on Sulawesi than Sumatra. Differences in fig biomass are less dramatic; fig biomass is 1.5 times greater on Sulawesi than Sumatra ($32.6 \text{ kg/ha} \pm 4.8$ vs $21.2 \text{ kg/ha} \pm 1.9$). However, figs contribute more to overall mean monthly fruit biomass on Sumatra than Sulawesi (41% and 14.6% of mean monthly fruit biomass, respectively). Estimates of fruit biomass by consumer type (hornbill vs primate) show similar patterns for the two sites. Sulawesi has 4.4 times more primate food per hectare per month ($191 \pm 24 \text{ kg}$. vs. $43 \pm 38 \text{ kg}$) and 3 times more hornbill food per hectare per month than Sumatra ($55 \pm 7 \text{ kg}$. vs $18 \pm 21 \text{ kg}$). Both island sites have more than twice as much biomass of primate fruits available relative to hornbill fruits.

Fruiting patterns were more seasonal in Sulawesi than Sumatra and were related to rainfall only on Sulawesi. After removing figs from the data sets, monthly crop production on Sulawesi was significantly related to the amount of rain falling one month prior to the fruit sample ($\ln \text{ crop} = 12.42 + 0.0045 \times \text{rain lag1}$; $t=4.36$, $P<0.001$, $N=24$). Fruit crops were not related to rainfall on Sumatra.

Primates of Sulawesi and Sumatra are highly frugivorous with the exception of the banded and silvered leaf monkeys (Table 1). Macaque, siamang and gibbon diets are composed of >60% fruit. Furthermore, macaques, siamangs and gibbons rely heavily on figs for > 40% of the fruit they consume. Only the leaf monkeys, species that specialize on young leaves and unripe seeds, do not consume significant amounts of fruit (Table 1). The fruit portions of macaque, siamang and gibbon diets are highly diverse. For example, crested black macaques eat the fruits of >145 fruit species including 33 species of fig while siamangs eat the fruits of >120 species including 10 species of figs. Although fig species account for only 8-23% of dietary diversity, and only 2.7 to 3.4% of monthly trees in fruit, figs fruits are top diet items for both species in all months, accounting for a major portion of the diet for both species.

For crested black macaques, fruit preference indices based on consumption relative to availability indicate that although figs are highly preferred relative to density (Figure 9; Table 2); densities of individual species are lower than many other food species. Fig preference may be linked to calcium concentrations and associated calcium:phosphorus ratios in figs, the ease of handling, and digestibility.

Black macaques handle figs more rapidly than other fruits. Of the 10 highest fruit ingestion rates (expressed as gms dry matter/min.), 6 are fig species (Kinnaird et al.,1999).

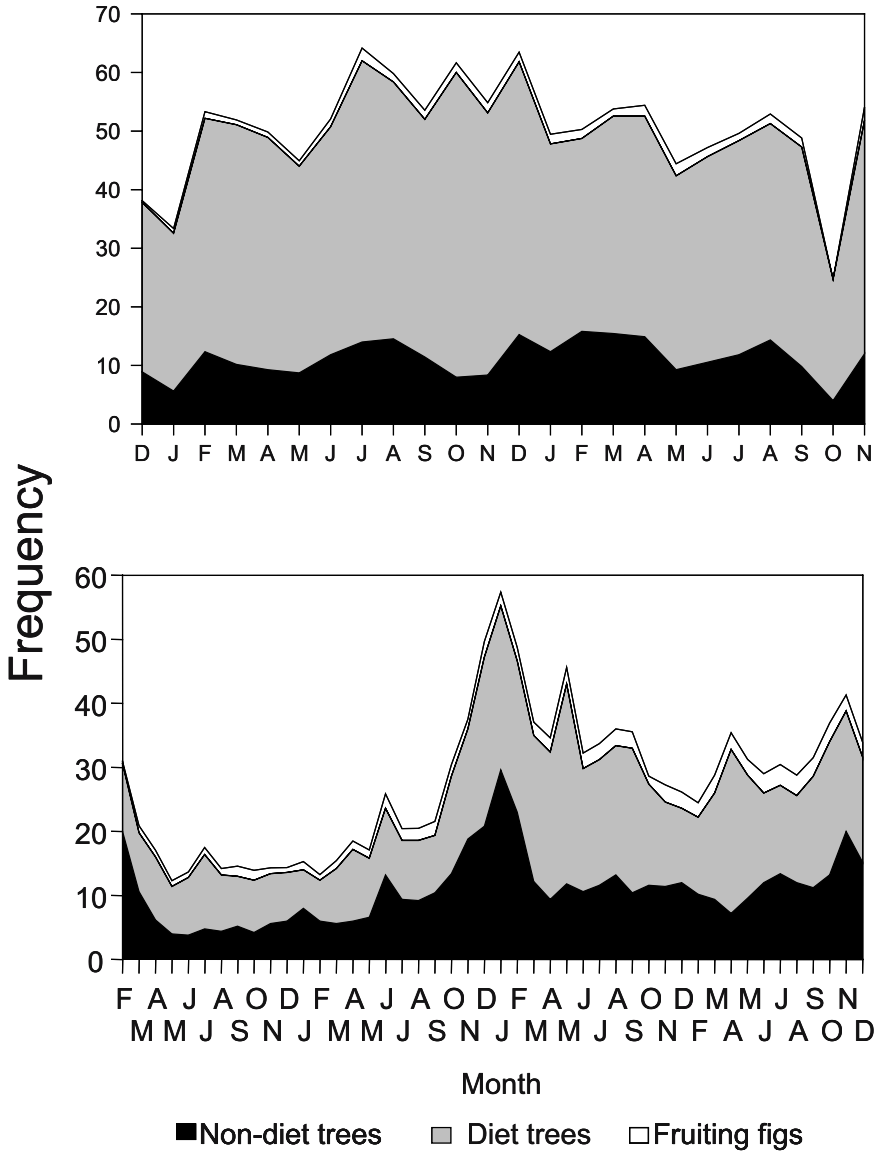


Figure 7. Monthly numbers of fruiting trees for non-diet, diet and fig species.

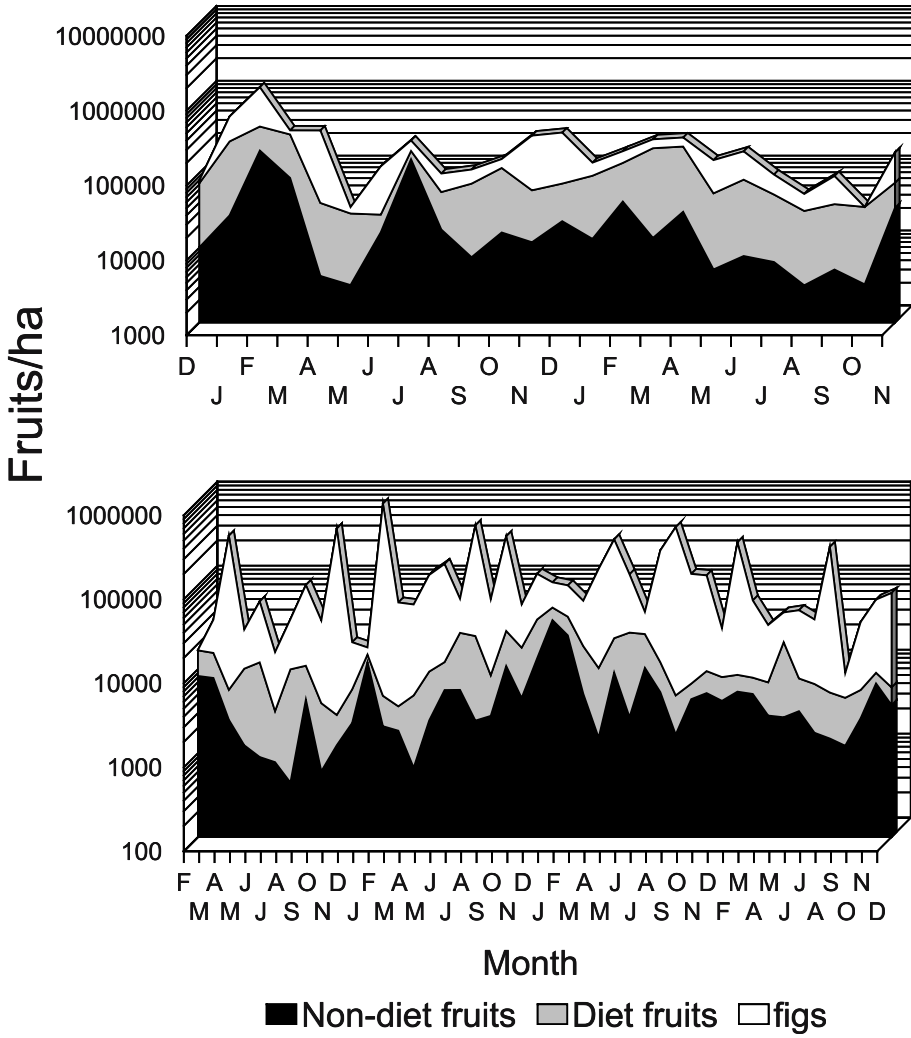


Figure 8. Estimated fruit production for non-diet, diet and fig species.

Table 1. Primate community density, biomass and diet for Sulawesi and Sumatra.

Site	Primate	Territorial	Density (ind/km ²)	Wt. (kg)		Sex ratio Ad:Juv	Biomass (kg/km ²)	% fruit in diet	% fig in fruit diet	
				♀	♂					
Sulawesi	<i>M. nigra</i>	Yes	58	6.6	10.4	3.4	47:53	365.8	68.3	44
	Total							365.8		
Sumatra	<i>H. agilis</i>	Yes	2	5.7	6	1.0	83:17	10.6	65	45
	<i>S. syndactylus</i>	Yes	15.2	10.6	10.9	1.0	66:34	125.0	63	40
	<i>P. melalophus</i>	Yes	23.7	6.6	6.7	>2	50:50	107.1	25	low
	<i>M. nemestrina</i>	No	6.7	7.8	10.4	5.0	50:50	44.5	74	?
	<i>M. fascicularis</i>	No	rare	4.1	5.9	2.5	-		64	40
	<i>T. cristatus</i>	No	rare	8.1	8.6	>2	-		10	rare
	Total							278.2		

Primates vigorously defend figs from conspecifics. Of 182 intergroup encounters between neighboring groups of crested black macaques, 54% were located at fruiting figs. Intergroup encounters escalated into fights with chases, screaming and occasionally grappling and biting as the proportion of figs in the diet increased (Figure 10). Fig consumption accounted for approximately 37% of the variability in proportion of encounters that resulted in fights. Macaques feed for longer periods and in larger foraging groups in figs than in other fruiting plants, and will shift their sleeping trees to monopolize especially fruiting figs. Among siamang groups, intergroup encounters usually involve countercalling between groups at distances less than 100 m. Almost 90% of all siamang intergroup encounters occurred at large fruiting figs.

Is there any other fruit that might elicit a similar response? For primates, rao is an important fruit tree in the family Anacardiaceae. It is a major diet item accounting for 21% of fruit consumed by crested black macaques and 22% of the fruit consumed by siamang. In both study areas, rao are relatively common at 1-2 ind./ha. Still macaques and siamang consume figs twice as often as rao, and neither siamangs nor crested black macaques defend rao.

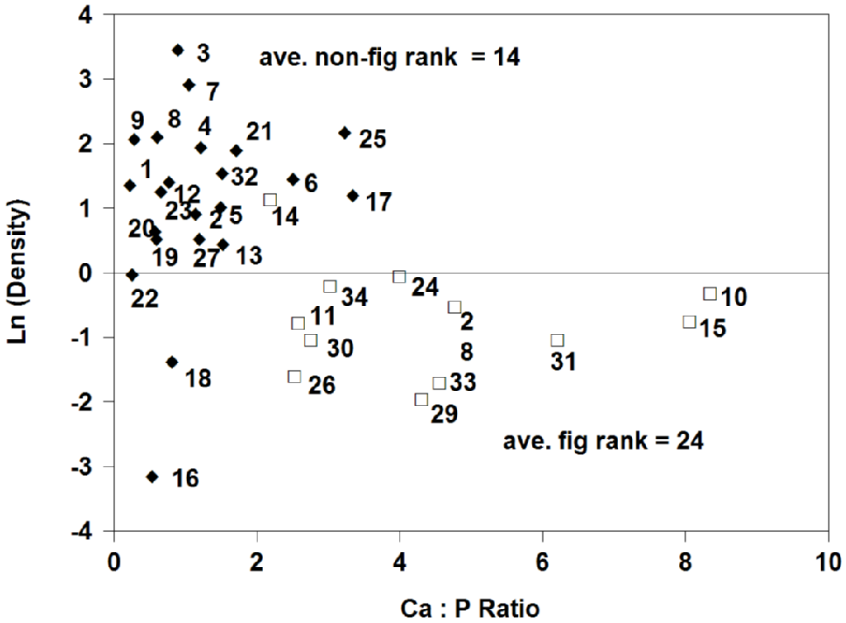


Figure 9. Distribution of fig (open squares) and non-fig (diamonds) fruits by density and Ca:P ratio. Feeding preference ranks of crested black macaques (based on Jacobson's *D*) are given for each fruit species.

Hornbill density and frugivory

As with primates, the hornbill assemblage is more diverse on Sumatra, but overall biomass is much greater on Sulawesi (6 times greater: Table 3). Sulawesi hornbill biomass is dominated by the red-knobbed hornbill with a density greater than all the other hornbills combined.

The hornbills of Sulawesi and Sumatra are more frugivorous than the primates. The diet of every species in our analysis contains > 80% fruit, with the possible exception of white-crowned hornbills (Table 3). Hornbills consume a diversity of fruit species including 56 species on Sulawesi and 74 species on Sumatra. Sulawesi hornbills are more restricted in the families they choose than Sumatra hornbills (Figure 4). Moraceae, Burseraceae, Meliaceae, Myristicaceae, and Annonaceae are the most important families at both sites. The smaller hornbills (≤ 1.5 kg) tend to be territorial, rely more on animal prey and on mid-canopy fruit trees (especially Annonaceae and Meliaceae), and the proportion of figs in their diets is relatively low (18-33% of fruit portion of diet). The larger hornbills (>1.5 kg) are wide-ranging and consume large quantities of figs (73-100% of fruit in diet).

Table 2. Density and rank of density for important diet tree families.

Family	Consumer	Sumatra	Rank	Sulawesi	Rank
Moraceae (Figs)	Both	1.3	10	8.3	6
Anacardiaceae	Primates	6.2	7.5	13.8	4
Annonaceae	Hornbill	44.4	1	29.4	1
Burseraceae	Hornbill	15.2	5	2.5	10
Lauraceae	Hornbill	17.8	4	3.2	8
Clusiaceae	Primates	6.2	7.5	10.5	5
Meliaceae	Hornbill	33	2	5.4	7
Myristicaceae	Hornbill	2.4	9	3.5	9
Ebenaceae	Primates	13.2	6	16.3	3
Euphorbiaceae	Primates	26.2	3	22.0	2

Density fluctuation and fruit resources for non-territorial hornbills

To examine the effect of fruit resources on hornbill movements in and out of the study areas, we restricted our analysis to non-territorial hornbills (*Aceros*, *Rhyticeros*, *Rhinoplax* and *Buceros* species). These genera move over wide areas as determined by variation in monthly estimates and by radio telemetry (red-knobbed hornbills and wreathed hornbills). We compared monthly densities of hornbills to measures of fig and non-fig fruit availability. Non-fig fruits only included known or expected hornbill diet items.

On Sulawesi, red-knobbed hornbill density ranged from 9 to 84 birds/km² during the 24 month study. During 22 months of this study, we also measured fruit supply. The fluctuation in hornbill numbers and distribution of hornbill observations were closely associated with figs, but not with measures of non-fig biomass. Monthly hornbill densities increased significantly with increasing fig biomass ($F=5.43$, $d.f.=3, 18$, $P=0.031$), explaining almost 50% of the variation in hornbill density. Monthly estimates of fig biomass also had a significant positive effect on mean monthly flock size (range = 1 - 101, $F=52.02$, $d.f.=1,20$, $P<0.001$), showing that hornbills congregated in flocks during periods of high fig abundance. Finally, the density of reproductive fig trees influenced the spatial distribution of red-knobbed hornbills; density was higher in hectare blocks with high fig-tree densities ($F=5.02$, $d.f.=1, 67$, $P=0.028$) after controlling for effects of habitat type and breeding season. During the breeding season, radio tracking of males attending nests in the study area showed that although males ranged widely (up to 15 km²), average daily travel distance declined significantly with increasing fig biomass.

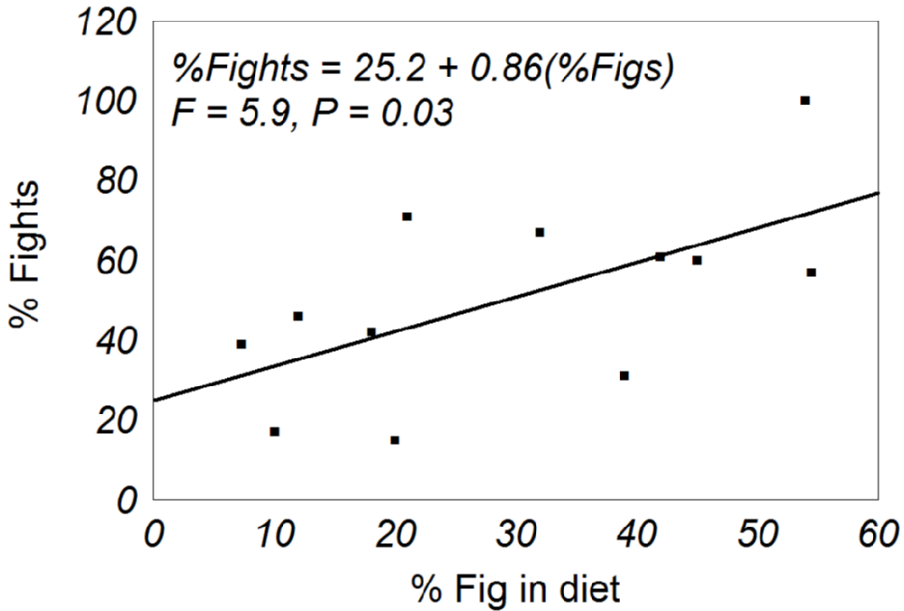


Figure 10. Regression of intergroup fights and % fig in diet for crested black macaques.

On Sumatra, wreathed hornbills appear to react strongly to fluctuations in the abundance and biomass of figs but not other hornbill fruits. Monthly density estimates of wreathed hornbills ranged from 0 to 8 birds/km² and were significantly correlated with changes in ripe fig biomass ($r = 0.37, P=0.011$). Ripe fig biomass was significantly lower ($T=2.88$ $df = 39.7, P=0.006$) in months when wreathed hornbill densities were <1.0 (14 of 46 months).

Among *Buceros* and *Rhinoplax* hornbills, the results were less clear cut. Helmeted hornbill densities fluctuated between 0 and 6.5 birds/km². Densities fell below 1 bird/km² in 9 of 46 months and density exceeded 2 birds/km² in 25 months. Helmeted hornbill densities did not show significant fluctuations with fig biomass on a monthly basis; however, they responded weakly to ripe fig biomass. Ripe fig biomass was lower in the months when density declined below 1 bird/km² ($T=1.92, P= 0.06$). Although we have no evidence that helmeted hornbills are territorial, helmeted hornbills have been observed defending fruiting figs against conspecifics (Kinnaird et al., 2003). The defense involves spectacular aerial jousts in which hornbills fly toward one another and collide casque to casque. These jousts usually involve male-male pairs and usually occur near fruiting figs. Rhinoceros hornbill density ranged from 0 to 4.1 birds/km². This species responded more strongly to monthly fluctuations in the ripe fruit crop of non-fig hornbill foods ($r = 0.34, P=0.02$) than monthly fluctuations in figs.

Table 3. Hornbill community density, biomass and diet for Sulawesi and Sumatra.

Site	Hornbill	Territorial	Density (ind/km ²)	Wt. (kg)	Biomass (kg/km ²)	% fruit in diet	% fig in fruit diet
Sulawesi	<i>A. cassidix</i>	No	51	2.36	120.36	89	88
	<i>P. exarhatus</i>	Yes	2.84	0.46	1.31	85	33
	Total				121.67		
Sumatra	<i>R. undulatus</i>	No	2.28	2.54	5.79	97	73
	<i>A. corrugatus</i>	No	rare	1.59		?	?
	<i>B. rhinoceros</i>	No	1.5	2.58	3.87	98	77
	<i>R. vigil</i>	No	2.3	3.1	7.13	98	100
	<i>B. bicornis</i>	No	rare	3.0		86	66
	<i>B. comatus</i>	Yes	0.76	1.3	0.99	>50	25
	<i>A. galeritus</i>	Yes	1.8	1.17	2.11	81	18
Total					19.89		

Fig density and hornbill communities

We next asked if hornbill density and biomass was related to the density of figs across Southeast Asia and Wallacea. We compared fig densities at eight locations in Southeast Asia and six locations in Wallacea to the density and biomass of the hornbill community at these sites. Fig density had a significant positive effect on hornbill density and abundance irrespective of the number of species involved and the mix of territorial and non-territorial species in the hornbill community (Figure 11). Hornbill density was more closely related to fig density than hornbill biomass.

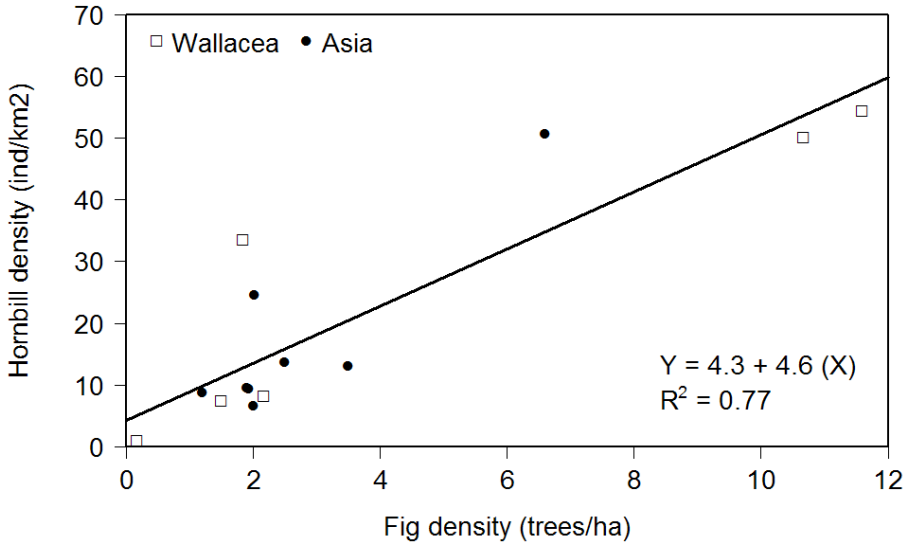


Figure 11. Regression of hornbill density on fig density for Asian and Wallacean hornbill communities.

Figs as strong interactors

We compared the percentage of major tree families in hornbill and primate fruit diets to fruit tree density for the 10 most important hornbill and primate fruits including Anacardiaceae, Annonaceae, Burseraceae, Clusiaceae, Ebenaceae, Euphorbiaceae, Lauraceae, Meliaceae, Moraceae (figs only), and Myristicaceae to test the impact of figs relative to other fruits (Table 2; Figure 12). If diet is proportional to density, we expect that hornbill and primate diets should fall along the diagonal reference line. Fruit families with points falling below the line are considered weak interactors (Powers & Mills, 1995) and those falling high above the line can be considered strong interactors. Contribution to the diets by all families are low relative to abundance, except for the Anacardiaceae, which contribute to macaque and siamang diets as expected given the density. The fig portion of the diet is above the reference line for all species indicating a strong interaction between fig fruits and diets of primates and hornbills.

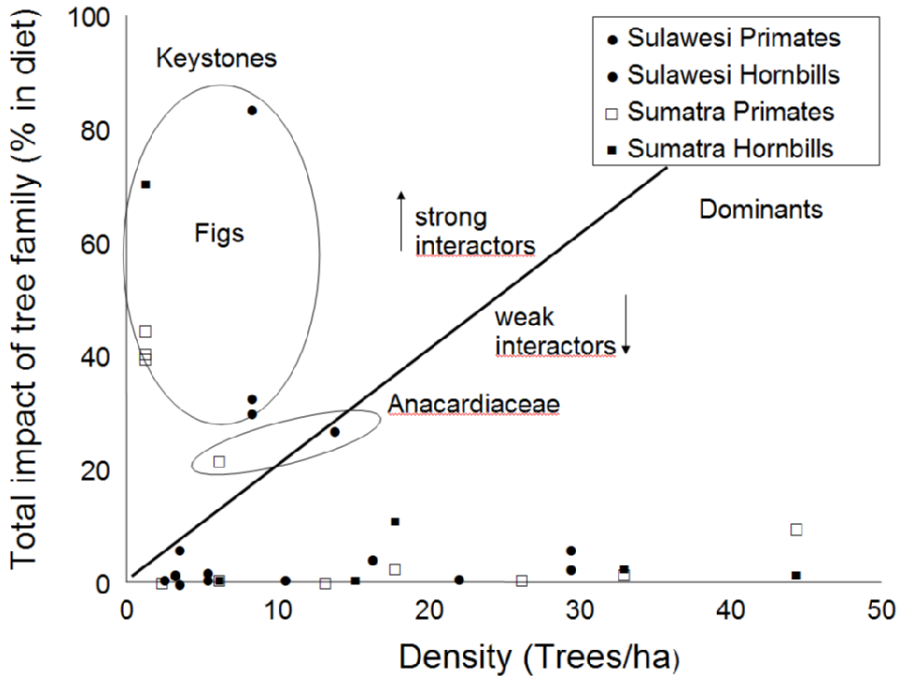


Figure 12. The impact of figs on hornbill and primate communities compared to nine other diet families. Points represent percent of family in diet relative to the density for the family. The diagonal line represents expected % in diet if fruits are consumed proportional to density. Weak interactors are defined as species that are consumed less than expected based on density and strong interactors are species that consumed more than expected based on density. The figure illustrates that common plant species may be dominant in diet but still not be keystone resources.

DISCUSSION

A popular perception of figs is that they attract a diverse group of generalist frugivores that provide poor quality dispersal services in return for a 'low quality' fig reward (Shanahan, 2001), but this is not the case (Kinnaird et al., 1999; O'Brien et al., 1998). Figs appear to be strong interactors in the sites where we work. Our studies have shown that figs affect a number of aspects of hornbill and primate ecology, including community biomass, density fluctuations, diet, movements and social behavior. Our results also point out important differences in fruiting phenologies between Wallacea and Southeast Asia and between forests dominated by dipterocarps and other forest types in Southeast Asia.

In general, fruit production is higher on Sulawesi than on Sumatra. This is true whether we measure production by the number of trees in fruit, the number of fruits produced, or the biomass of fruits produced. Higher fruit biomass may lead to the higher biomass of primates and hornbills as well as the other fruit-eating species we have observed. Sulawesi also produces more fruit consumed by primates and hornbills, as well as a host of other frugivorous birds and mammals. Not surprisingly, densities of pigeons and fruit doves are higher on Sulawesi (Kinnaird et al., 1999, unpublished data) than Sumatra (Rombang, 1999), as are the densities of wild pigs (*Sus celebensis* = 12/km², *Sus scrofa* = 5/km²; O'Brien & Kinnaird, 1996; O'Brien et al. in review). Neither site suffers from the strong and pronounced seasonal effects in fruit production comparable to Barro Colorado Island or Cocha Cashu in the Neotropics (see Milton, this volume, and Stevenson, this volume). Also, neither site suffers from prolonged periods of fruit shortage, as has been reported for dipterocarp dominated forests of Borneo (Leighton and Leighton, 1983) and Malaya (Chivers, 1974).

Fig production is more constant on Sulawesi and Sumatra than has been reported for many sites (Foster, 1982; Kinnaird & O'Brien, 1999; Leighton, 1983; van Schaik, 1996; Terborgh, 1986). On Sulawesi, the high diversity and relatively high density of strangling figs assures that on average, 1 strangling fig is in fruit every month for every 1.3 ha, resulting in 7-10 ripe figs/km² on any given day (Kinnaird et al., 1999). On Sumatra, figs occur at lower densities (@ 1 fig in fruit per month per 6 ha) but many of the strangling figs produce very large crops of large figs, and figs dominate overall fruit production. This is unlike the Neotropics (Janzen, 1979; Terborgh, 1986) where figs fruit asynchronously in populations but synchronously within trees. On Sulawesi and Sumatra we find fig communities composed of aseasonal and asynchronous species, as well as coordinated and highly seasonal species. We also see asynchronous fruiting within a tree and variable temporal fruiting patterns within trees (Kinnaird et al., 1999). Clearly, fig fruiting phenologies are complex and encompass the gamut of possibilities.

The extreme reliance on figs by non-territorial primates and hornbills suggests that seasonal movements may reflect tracking of fig resources (Kinnaird et al., 1996) rather than tracking general fruit production (van Schaik, 1996; Terborgh, 1986) or other specialized subsets of fruits (e.g. lipid rich fruits, Leighton, 1983). Resource tracking may take place over a local scale (a few km² or tens of km²: Kinnaird et al., 1996) or a regional scale (100's to 1,000's of km²: Curran & Leighton, 2000). Tracking supra-annual fruit production through migration (sometimes called nomadism) requires a reliable environmental cue that assures a shift in location will result in finding a resource (e.g. food or reproductive sites). Should an environmental cue fail to provide the proper information, the cost of long distance movement may be starvation or reproductive failure. The patterns of supra-annual fruiting that seem characteristic of trees in eastern Borneo (Leighton, 1983), western Borneo (Curran et al., 2001) and northern Sumatra (van Schaik, 1996) are much more difficult to track regionally or locally compared to seasonal variation in fruit production. Wandering over a large landscape in search of localized fruiting peaks associated with weather phenomena such as ENSO events (Curran & Leighton,

2000) does not seem an efficient strategy when ENSO events occur at 3-6 year intervals (Strahle et al., 1998; Curran & Leighton, 2000). Counter-intuitively, the asynchrony of fig fruiting may produce the most dependable fruit resource in an ecosystem characterized by short booms in fruit production followed by long periods of low fruiting. Wandering over a localized landscape of 10-50 km² in search of fruiting figs may be a more viable alternative for surviving boom and bust cycles of fruit production.

Fig specialization is more widespread in the Old World than in the Neotropics and more widespread in Asia and Australasia than in Africa (Shanahan et al., 2001; Chapman et al., this volume). In Asia, the evolution of a host of fig specialists, including hornbills, *Chloropsis* leafbirds, fairy bluebird, *Treron*, *Ducula*, and *Ptilinopus* pigeons, barbets, birds of paradise, Asian koel, channel-billed cuckoo, several parrots, gibbons, binturongs, *Pteropus* and *Cynopterus* fruit bats suggest that tracking keystone figs resources is a viable strategy. Evolution of food specialization requires a certain stability of resources such that dependencies can develop and this indirectly argues that figs represent a stable food source.

Territoriality by tropical frugivores also requires reliable fruit production in small areas, often less than 1-2 km², or the ability to subsist on alternate diet items. Territorial species that utilize supra-annual fruit resources will have to rely primarily on small fruit crops within a territory, or have the ability to shift to alternate food sources, such as animal prey, leaves or gum. Many small-bodied, territorial hornbills appear to follow this strategy, but still manage to find figs for a substantial portion of their diet (Leighton, 1982; O'Brien, 1997; Poonswad et al., 1987). Alternatively, if fig densities are sufficient, territorial defense may develop around figs whenever a species can successfully exclude conspecifics from the resources. The reliance on a diverse array of small fruit crops then becomes a strategy for getting through times of fig scarcity rather than the other way around. Given the unreliability of fruit production in Southeast Asia, it is hard to envision large frugivorous birds and mammals becoming territorial, yet all gibbon species are territorial and among Asian hornbills there are more territorial than non-territorial species. We suspect that figs play a keystone role in filling the fruit shortfall for territorial frugivores in Asian forests.

The overwhelming contribution of figs to the diets of primates (orangutans, gibbons, macaques) and hornbills, and the attempted defense of figs by primates and hornbills (Kinnaird et al., 2003; Leighton 1982) strongly suggest that figs have played a fundamental role in shaping the frugivore communities of Southeast Asia and Wallacea. This in turn may have profound indirect effects on the rest of the fruit tree community via dispersal services of frugivores that, while relying on figs, consume and disperse the seeds of other rainforest plants. Kinnaird (1998) demonstrated that Sulawesi red-knobbed hornbills moved seeds of 33 diet species to germination sites while feeding primarily on fig fruits. Studies of fruit delivery to the nest suggest similar dispersal capabilities for many other hornbill species (Kinnaird & O'Brien, unpublished data; O'Brien, 1997; Poonswad et al., 1987). Primates also are well known seed dispersers. Siamang, for example, swallow seeds of *rao* and *Polyalthia* spp whole and move them hundreds of meters throughout

their home ranges (O'Brien & Kinnaird, unpublished data; Rusmanto, 2002). Macaques typically stuff their cheek pouches with whole fruits, and move away from the parent trees where they scrape the mesocarp and deposit seeds intact. In Tangkoko, macaque groups' daily movement patterns often are between fruiting figs, and they feed on other species en route.

Finally, figs are strong interactors. They are important relative to abundance and relative to gross nutrient award. While other fruits may yield higher energetic rewards, long handling times and problems of digestibility may reduce the attractiveness of many fruits, and small fruit crops may increase search times relative to figs. Therefore, it makes sense that figs should be preferred wherever they are abundant enough to be locally reliable resources. The question then becomes what is the density threshold for reliability.

To be a territorial species and rely on figs, a species probably needs enough figs in the territory to produce at least one fruit tree every month. Territory size, therefore, may be a function of fig density. For a territorial hornbill to rely on figs for a third of the diet may require that a fig be producing ripe fruit for approximately 10 days per month. A minimum density of 12 figs/home range will suffice, on average, if the probabilities of fruiting are equal for all months. Higher densities improve the probability of ripe fig availability. At some point fig density is so low that the asynchrony and aseasonality of fig production becomes a cost rather than a benefit because figs become unreliable fruit sources or the territory becomes undefendable. The question of context dependency will only be resolved by replicated studies of territorial and nonterritorial frugivore species across a range of sites characterized by different densities of fig resources.

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CHAPTER 10.

THE FRUGIVORE COMMUNITY AND THE FRUITING PLANT FLORA IN A NEW GUINEA RAINFOREST: IDENTIFYING KEYSTONE FRUGIVORES

ANDREW L. MACK, DEBRA D. WRIGHT

Abstract

The flora at Crater Mountain Biological Research Station in Papua New Guinea is very diverse: 228 tree species (≥ 10 cm DBH) on a single hectare. However, the vertebrate fauna (169 bird and 31 mammal species) is less diverse than many tropical sites. At least 47% of bird species and 29% of mammal species are partially frugivorous. Using data on relative abundance, mass, and degree of frugivory for all frugivorous vertebrates at Crater, we generated a crude "index of importance" for each species. Using the fruit size and mass data from 400 plant species, we exclude fruits either too large or too heavy for each frugivore to disperse, yielding a "possible diet" for each species. Four species (a cassowary, a hornbill, a fruit pigeon and a flying fox) stand out as being crucial dispersers for a large subset of the plant community. The frugivore with the highest importance ranking, *Casuarius bennetti*, is highly effective as a disperser. Cassowaries appear to be a keystone frugivore, especially for large-fruited plant species (67 species > 50 g at our study site). The method employed is fairly simple and quickly identifies candidates for keystone frugivore status. However, further life history studies are recommended for confirmation of importance when using this method.

Key words: Cassowary, frugivory, keystone resources, New Guinea, phenology, tropical forests

INTRODUCTION

The concept of a keystone species (Paine, 1969) has been widely applied in ecological studies. Although Paine's initial keystone species was a predator, the term keystone has since been widely applied (e.g., to prey, herbivores, pollinators, resources, hosts, plants, modifiers, etc.; Power et al., 1996) with a concomitant obfuscation of just what constitutes a keystone (Mills, Soule, & Doak, 1993). Generally the term is applied to species (or resources) that somehow help to

maintain structure and complexity in a community or ecosystem so that removal of the species would result in an inordinate modification of that community or ecosystem. However defined, keystones have become candidates for concentrated conservation activity and monitoring because their extinction could have cascading effects and impact many other species (Simberloff, 1998). Given the limited resources for conservation, the issue of how to define and identify keystone species is more than an exercise in semantics among academics. Rather than broadly re-examine the entire keystone concept (e.g. Power et al., 1996; Simberloff, 1998; Zacharias & Roff, 2001), we focus on one particular relationship where the keystone species concept has been applied (frugivorous seed dispersers) from one understudied region (Papuan rainforests).

Although it has been long recognized that seed dispersal is important to rainforest systems (e.g. Ridley, 1930), it was not until the formulation of the "Janzen-Connell hypothesis" (Janzen, 1970; Connell, 1971) that an explicit mechanism was stated wherein seed dispersers directly affected plant diversity in rainforests. Janzen-Connell stimulated a continuing surge in seed dispersal studies. Many studies have highlighted keystone fruit resources in the maintenance of frugivore communities (e.g. Howe, 1977; Kannan & James, 1999; Shanahan, So, Compton, & Corlett, 2001; van Schaik, Terborgh, & Wright, 1993) and others in this volume). In this paper we focus on the converse, the keystone frugivores that are potentially important in the maintenance of plant communities.

Identifying potential keystone frugivores first requires clarification of criteria. Minimally, we need to identify the community of plants, the community of frugivores, and to characterize the interactions between these two groups in order to determine the degree of "reliance" of each plant species on each frugivore. By reliance we mean the projected impact on a plant population by the removal of a frugivore. This is the key criterion of the keystone species concept and the rationale for making keystones a conservation priority (Mills et al., 1993).

Empirically evaluating these criteria is exceptionally difficult, particularly in diverse and complex tropical rainforests. For example, how do we define a frugivore among the continuum of animals from those that only rarely feed upon fruit to those that feed almost exclusively upon fruit? How do you define plant "reliance" when they have their seeds dispersed by many frugivores depending on phenology, age, location, etc.? Will the removal of one frugivore only result in more fruit for another? How many plant species must "rely" on the frugivore for the frugivore to be considered a keystone? How does one account for differences in space and time; what might be a keystone in one place or time might not be in another? Clarifying such questions is simple. But obtaining answers requires knowledge of the frugivores and detailed knowledge of their surrounding flora and ecological relationships-- "inspired natural history" is required to identify keystone species (Paine, 1995).

Here we analyze some of the main criteria for identifying keystone frugivores. We use data gathered from one site in Papua New Guinea where we have a fair knowledge of both the frugivore and plant communities. New Guinea is a conservation priority because it has some of the last remaining large blocks of intact rainforest (Mittermeier, Myers, Thomsen, Fonseca, & Olivieri, 1998; Olson &

Dinerstein, 1998). Furthermore, New Guinea has an independent evolutionary history from the rest of earth's tropical forests, so studies there can test generalizations derived from the better-studied neotropics (Westoby, 1988). Our goal is to use straightforward natural history to empirically suggest candidates for keystone frugivore status in New Guinea.

METHODS

Study Site

Field data were collected from the Crater Mountain Wildlife Management Area (CMWMA), a 2700 km² conservation project in Papua New Guinea (PNG). The bulk of the area, and a much larger expanse bordering it, is essentially undisturbed primary forest. The low human population impacts some valleys with swidden gardens and adjacent areas through hunting, but there is no evidence of any local extirpation of vertebrate species, nor of introduced vertebrates other than pigs. Most data was collected at the Crater Mountain Biological Research Station (CMBRS) between 1989 and 1993. The CMBRS (145° 05' 34.5"E, 6° 43' 26.2" S) study area spans 800-1350 m elevation from hill to lower montane forest in a region characterized as the middle elevational high rainfall zone (Hyndman & Menzies, 1990) found along the southern scarp of New Guinea's central cordillera. The study area receives 6.5-7.5 m of rainfall per annum which falls relatively uniformly all year; there is no predictable dry season. The biota of the CMBRS is representative for the portion of southern New Guinea residing on the Australian craton, which is a major biogeographic province (Heads, 2001).

Floristic data

We collected floristic data from 5 ha of vegetation and phenology plots (Wright, 1998; Wright, Jessen, Burke, & Garza, 1997) and adventitiously throughout a roughly 250 ha study area from 1989-1993. We collected and identified specimens of any plant found to bear a fleshy, endozoochorous diaspore. Although it is likely that we did not sample some species of plants that produce fleshy diaspores, particularly small-fruited epiphytes, we are confident that those species missed would comprise a small percentage of the overall available fruit biomass.

For the above species we measured greatest fruit length, greatest fruit width, greatest fruit depth and fresh fruit wet mass. Linear measurements were made to the nearest 0.1 mm with Vernier calipers and masses to the nearest 0.1 g with a triple beam balance. In order to approximate the volume of a cylindrical ellipse (see Wright, 1998), fruit volume was calculated as:

$$4/3 \pi (\text{fruit length}/2) * (\text{fruit width}/2) * (\text{fruit depth}/2)$$

Frugivore data

We censused the birds and mammals of the CMBRS using a variety of techniques--visual observation, spot-lighting, mist-netting and live trapping (Sherman, Elliot, and Tomahawk traps for mammals). We have conducted field surveys at elevations above (1450 m) and below (550 m) in the study area to identify species that could occur in the margins of the study area.

Birds have been intensively observed over several years to determine species composition in the study area along with their diets (Mack & Wright, 1996). Extensive observations and regular mist-netting have continued at the site for twelve years. The species accumulation curves for all combined methods of observation are nearly level for birds and for mammals. We are confident that we have observed nearly all of the species that regularly occur in the CMBRS study area.

Data on avian diets were obtained through direct observation (Mack & Wright, 1996) and collected from the literature (e.g. Baptista, 1990; Beehler, 1989, 1983; Beehler & Dumbacher, 1996; Bell, 1983; Coates, 1985, 1990; Frith, Crome, & Wolfe, 1976; Hicks, 1988; Hicks & Hicks, 1988a, 1988b; Hopkins, 1988, 1992; Lamothe, 1979; Peckover, 1985; Pratt, 1984; Pratt & Stiles, 1985; Terborgh & Diamond, 1970; Wahlberg, 1992). Data on mammalian diets were also derived from direct observation and from the literature (e.g. Bonaccorso, 1998; Bonaccorso & Gush, 1987; Hopkins & Hiaso, 1994; Woolley & Allison, 1982).

Weights and dimensions of birds and mammals were taken from our unpublished field survey data, from many of the sources cited in the previous paragraph, and from specimens at the PNG National Museum and Art Gallery.

Possible fruit diet determined by frugivore size

Fruits weighing more than 15% or 30% of the mass of each bird and mammal species, respectively, were categorized as too large to be dispersed from the parent tree by that species. The percentage is lower for birds because of stronger aerodynamic constraints (e.g., bats can carry larger payloads than birds). We estimated the maximum fruit diameter each bird or mammal species could swallow or carry given its bill/mouth size as a gape/handling constraint (Wheelwright, 1985). We used these mass and diameter constraints to calculate what proportion of the fleshy-fruited plant species (n = 400) in our study area each frugivore species could hypothetically disperse and called these its potential diet.

"Index of importance"

The potential importance of a frugivore as a seed disperser is defined by several parameters. We created a unit-less index of relative importance. Species with

higher ranks (closer to unity) have greater importance. We expect that anything considered a "keystone" frugivore would be an outlier to the distribution of species indices. We used three parameters to generate the index:

Abundance-- an abundant but poor disperser could be more "important" than a rare but efficient disperser. For each species, abundance (a) was ranked 1-6 based on census data at the CMBRS with 1 being least common and 6 most common.

Degree of frugivory-- this is a composite of the proportion of fruit in the diet along with an estimate of whether the seeds of those fruits are potentially dispersed; e.g., seed predators rate low even though they may consume many fruits. For each species, degree of frugivory (f) was ranked as a percentage of total diet (0-100%) based on our literature search and personal observations.

Amount consumed-- this is a direct scale to body size, given the same degree of frugivory, the larger the animal the more it will consume to meet basic energetic needs (ignoring the few exceptions of taxa with similar body sizes and very different metabolic rates). For each species we used the data on body mass (m) collected by trapping at CMBRS and from literature and museum specimens. No animal weighed less than 1 gram.

These three parameters were combined and standardized to sum to unity with the following formula:

$$\text{Index} = \frac{\left[\left(\frac{a}{\sum a} \right) + \left(\frac{f}{\sum f} \right) + \left(\frac{\sqrt[3]{m}}{\sum \sqrt[3]{m}} \right) \right]}{3}$$

Analyses

Statistical analyses were performed using two computer software programs: SPSS version 10.0 and Excel 2002.

RESULTS

Diversity

Frugivorous birds and mammals are an important component of the New Guinea and Crater Mountain fauna in terms of numbers of species. Roughly 40% of bird and

30% of mammal species consume some fruit and roughly 8% of each of these taxa consume mostly fruit (Figure 1). These percentages hold whether looking at the island as a whole, at the smaller Wildlife Management Area, or at the even smaller study area.

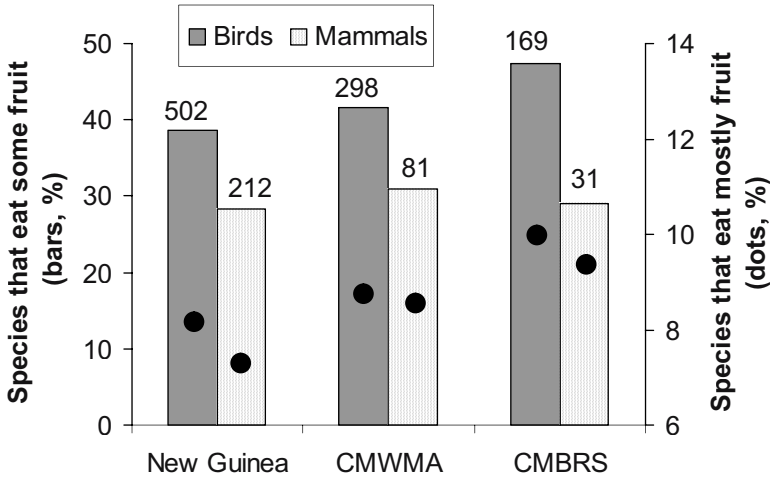


Figure 1. The percentage of bird and mammal species from New Guinea, from the Crater Mountain Wildlife Management Area (CMWMA) and from the Crater Mountain Biological Research Station study area (CMBRS) that consume some fruit (bars) and the percentage that consume almost only fruits (solid dots). Total species sample size is given above each bar. No matter which grain scale we examine, the percentages remain very similar within birds and within mammals.

Degree of frugivory

Most species that consume fruits also consume other food items (e.g., insects, nectar, vertebrates, seeds, and other plant matter). Forty seven percent and 29% of the bird and mammal species, respectively, in our study area were at least partially frugivorous. But only 10% of each were highly frugivorous (Figure 2). Some bat species eat only fruit, but some marsupials and murids (including tree kangaroos, wallabies, bandicoots, cuscus and some rodents) live partly on fruit matter and may disperse seeds (Appendix 1). Cassowaries, fruit pigeons, hornbills, some parrots, berrypeckers and some birds of paradise eat mostly fruit, but some pigeons, megapodes, parrots, honeyeaters, birds of paradise, and other passerines consume fruit along with other important dietary components (Appendix 1).

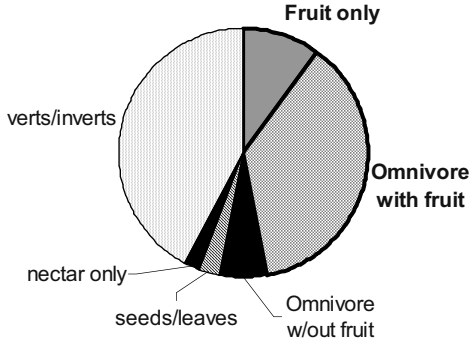
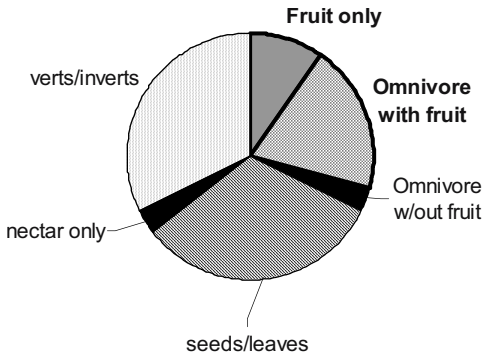
A. Birds at CMBRS**B. Mammals at CMBRS**

Figure 2. The proportion of bird (A) and mammal (B) species known to inhabit the Crater Mountain Biological Research Station that fall within each dietary category.

Sizes of fleshy fruits

We collected linear measurements and mass of fleshy fruits from 114 plant species. Using these species we found a tight correlation of fruit mass to fruit volume ($r^2 = 0.981$, $P < 0.0001$) and obtained the linear regression formula: fruit mass = $(0.9574 * \text{fruit volume}) + 1.25$. We used this formula to estimate fruit mass for an additional

286 fruit species where we had recorded linear measurements, but not mass, to yield a total sample of 400 plant species for the study area.

Mean fruit mass was 31.7 g (SD = 82.0). Most species (45%) had small fruits (< 5 g), but 17% had fruits over 50 g and 31 plant species (8%) had fruits over 100 g (Figure 3).

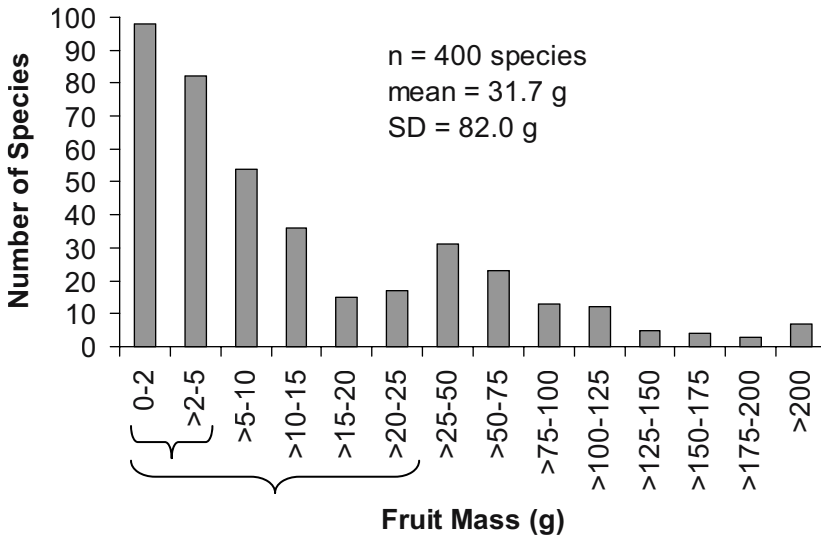


Figure 3. Size histogram for plant species with fleshy fruits at the CMBRS.

Potential diet

Of all of the bird and mammal species that eat some fruit in our study area, 82% were too small (body mass or gape limitations) to handle 30% of the fruit species. Furthermore, 18% of the flora could only possibly be moved by seven frugivore species (*Casuarium bennetti*, *Rhyticeros plicatus*, *Dobsonia magna*, *Uromys caudimaculatus*, *Phalanger gymnotis*, *Spilocuscus maculatus* and *Dorcopsulus macleayi*, Appendix 1).

Index of importance

The distribution for the Relative Importance Indices did not differ from normal (K-S test, $Z = 0.632$, $P = 0.82$, $n = 88$), and only three species stood out as being exceptionally important frugivores (more than two standard deviations from the mean-- *C. bennetti*, *R. plicatus* and *Ducula zoeae*; Figure 4).

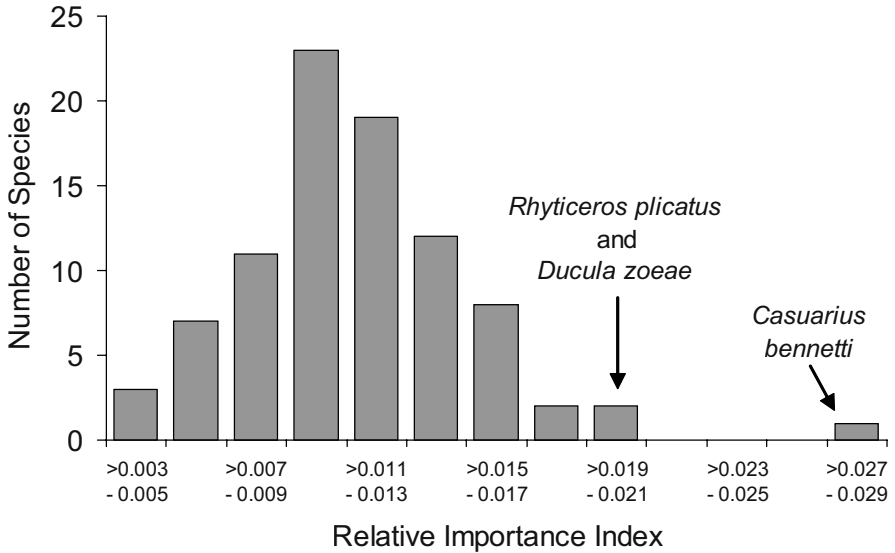


Figure 4. The Relative Importance Index, which combines measures of frugivore abundance, degree of frugivory, and amount of fruit consumed, follows a normal distribution with few outliers. Only three species are over two standard deviations from the mean.

Identifying the keystone frugivores

The most important frugivores, as defined by the number of fruit species that could potentially be dispersed, were not congruent with the most important frugivores as defined by the index (Appendix 1). When you consider both simultaneously, one species unambiguously emerges as the top candidate for keystone frugivore: *C. bennetti* (Figure 5). After the cassowary, several other species in the upper right side of the graph are also likely keystone candidates, including the hornbill *R. plicatus*, the flying fox *D. magna* and one of the fruit pigeons *D. zoeae*.

DISCUSSION

Diversity

The flora of the Crater Mountain study area is diverse (Takeuchi, 1999; Wright et al., 1997) and appears to be representative of a broad region along the southern scarp of the central cordillera of New Guinea (Hyndman & Menzies, 1990). The study area avifauna is also diverse and contains 34% of the bird species found across the

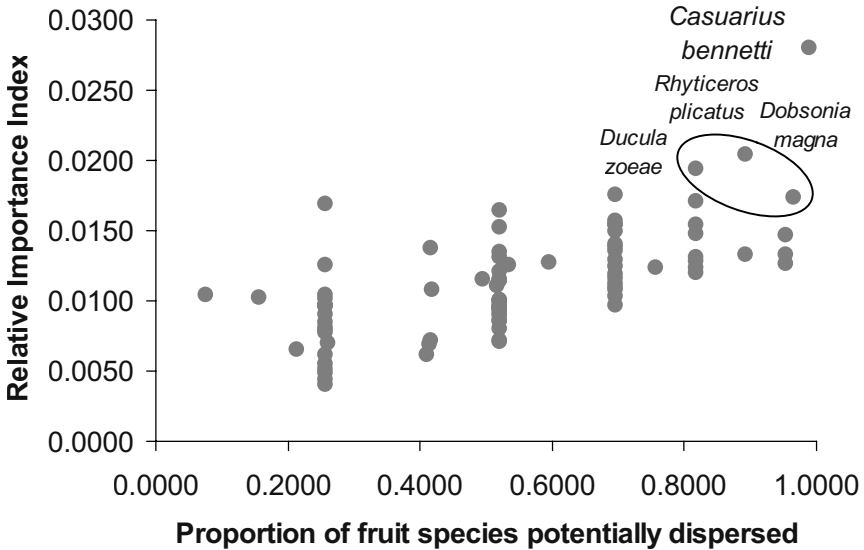


Figure 5. *Casuarius bennetti* stands out as a keystone frugivore by the Relative Importance Index and by the proportion of fruit species it can disperse. Three other species also deserve attention as possible keystone frugivores.

island of New Guinea. The mammalian fauna at the study area is relatively less diverse, with only 15% of all New Guinea mammals represented. This is partially a sampling artifact as nocturnal mammals are harder to verify than plants and birds, but it is also indicative of the patchy distributions of many New Guinea mammals. Although the data are collected from a fairly limited area in the vast forests of southern New Guinea, the diversity at this locale suggests it could be representative of a broader area.

Although the flora is diverse and is comparable to the diversity of tropical rainforest locations worldwide, the frugivore fauna is not as rich on the global scale. Many sites in the Neotropics have many more species per site than the CMBS study area. For example, the avian diversity of eastern Andean study sites of comparable size (e.g., Manu, Tambopato, Rio Napo) are roughly equivalent to the diversity of all forest birds in all of New Guinea. Likewise New Guinea completely lacks many large-bodied vertebrates that are important frugivores outside the Australasian area (e.g., primates, civets, ungulates, tapirs, ursids, etc.). New Guinea has high species diversity in fruiting plants, yet relatively low frugivore diversity. Since keystone frugivores will perform an ecosystem service that is either unique or limited to relatively few species, and their removal will extend inordinately to many taxa (Menge, Berlow, Blanchette, Navarrete, & Yamada, 1994; Mills et al., 1993), (Power et al., 1996), these data on the species richness of endozoochorous plants

versus frugivorous vertebrates alone increase the likelihood of finding important keystone frugivore species in New Guinea.

Degree of frugivory

Not all frugivores are equal in their impact on plants, they vary in the quantity of fruit they consume and their quality as seed dispersers (Howe, 1993; Jordano & Schupp, 2000; Loiselle & Blake, 1999; Wenny, 2000; Wutherich, Azocar, Garcia-Nunez, & Silva, 2001). We used extensive personal observations and a literature search to estimate the proportion (%) of each species' diet comprised of fruit and its quality as a seed disperser. Although these estimates were crude and subjective, they are the best approximations that can be made without decades of field work to quantify such parameters.

Size of fruits and potential diet

Our sample of 400 fleshy-fruited species is among the most complete for any single rainforest site (e.g. Gautier-Hion et al., 1985; Janson, 1983; Meehan, McConkey, & Drake, 2002). The fruit flora of New Guinea has relatively large fruits when compared to floras elsewhere (Mack, 1993). This potentially strengthens the importance of body size and handling capabilities of frugivores. In a flora lacking large-fruited species, more frugivores would potentially be able to disperse a larger proportion of seeds based on morphometrics. At CMBRS fruits of many plant species are simply too large to be swallowed or carried by the majority of frugivores - seventy plant species can only be moved by seven frugivore species.

Choosing Keystone Frugivores

The Relative Importance Index combines several important variables in the determination of keystone status in one number. Power et al. (1993) derived an index for determining candidates for keystone predators that also incorporated abundance (biomass), but their index incorporated a measure of community change as a consequence of trait change as well. We do this by predicting the change in plant diversity as a consequence of removing different frugivores.

The species in the right tail of the index distribution are the strongest candidates for keystone frugivore status because they have relatively high population biomass, consume primarily fruit in their diets, and are high-quality seed dispersers. At what point in the tail you make a cut-off to nominate a species for keystone status is, however, still somewhat subjective. To be conservative, we selected the three species that were outliers to the distribution of index values of all species: cassowaries, hornbills and fruit pigeons. Considering the index and ability to move large fruits, we also consider the fruit bat a strong candidate for keystone status (Figure 5).

Potential impacts of keystone frugivore removal--

The critical criterion for designation as a keystone species is some disproportionate consequence of the removal of the species (Mills et al., 1993; Paine, 1969; Power et al., 1996; Simberloff, 1998). With exceptions (e.g. Fauth, 1999; Morgan Ernest & Brown, 2001; Paine, 1969), this has been a stumbling point in much of the discussion of keystone species because the manipulations necessary to test the criterion are difficult.

At CMBRS we have made detailed studies of seed dispersal by one of the candidate keystone species, the dwarf cassowary. Mack (1995) found that seed dispersal is essential in order that seeds be moved uphill; in the absence of dispersal by frugivores, seed shadows are strongly biased downhill. Even if fruiting trees could replace themselves from undispersed seeds, their populations would eventually collapse downhill, eliminating the need to demonstrate other potential benefits of dispersal (e.g., Janzen 1970, Howe and Smallwood 1982, (Augsburger, 1984; Bond, 1994; Schupp, 1993; Wenny, 2001). In any hilly to mountainous location dispersal by frugivores is essential for the maintenance of zoochorous plant populations. This seemingly obvious and critical dependence of large-seeded plants on frugivores has been almost completely overlooked by most studies of seed dispersal (e.g. studies within Estrada & Fleming, 1986; Fleming & Estrada, 1993).

Conservation implications

Identifying keystone species can have direct applications for conservation and management. Because it is not possible to monitor and manage all components of an ecosystem, we must focus our limited resources on taxa or attributes that will be the most informative and yield the greatest conservation dividend. Considerable discussion has occurred regarding whether and to what degree the keystone species concept is useful for conservation (Mills et al., 1993; Power et al., 1996; Kotliar, 2000; Simberloff, 1998).

Determining the utility of keystones as foci of conservation effort will require more field studies and these first require the identification of keystone candidates. Once studied, candidates for keystone status might not meet all criteria, yet studies of these species would likely still result in improved conservation planning (e.g., Galetti & Aleixo, 1998). In our example, failure to properly conserve the top frugivore species at CMWMA could result in a reduction in fleshy-fruited plant diversity of almost 20%, most of which are canopy tree species. Hammann and Curio (1999) predicted a loss of up to 60% of late successional trees if "large frugivores" were extirpated from a site in the Philippines, but their group of large frugivores included 19 species and did not identify keystones among them. The extinction of large frugivores could result in significant changes over time in the flora at a Ugandan site (Chapman & Chapman, 1995). Unfortunately the same large frugivores that are likely candidates for keystone status are also heavily hunted for human consumption (e.g. Bennett & Robinson, 2000).

CONCLUSIONS

If we accept that the keystone frugivore concept is useful for study or conservation, we are left with the seemingly intractable problem of how to identify them. The amount and frequency of fruit eating, the extent of dispersal versus predation, the abundance of the frugivore and the number and strength of its interactions with plants all determine what might be considered a keystone. Yet all of these are difficult to measure individually, much less across the full spectrum of community interactions. The method employed here can be improved and does not provide definitive answers. However, it is impossible to assess the utility of the keystone frugivore concept unless we first identify candidates and then study them.

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Appendix 1. List of frugivore species at the Crater Mountain study site, Papua New Guinea. The proportion of fruit potentially dispersed refers to those fruits of the 400 species measured in the study area that are both small enough and light enough to be handled by that species.

The Relative Importance Index is a unit-less index based on the frugivore's abundance, degree of frugivory and size relative to other frugivores; larger values indicate greater importance as seed dispersers (see methods). The most important 15 frugivores in terms of number of plant species potentially dispersed are bold-faced as are the 15 most important in terms of the index. Note: the same species is not necessarily bold-faced for both categories.

Family	Genus	Species	Proportion of fruit species potentially dispersed	Relative Importance Index
<i>Mammals</i>				
Pteropodidae	<i>Dobsonia</i>	<i>magna</i>	0.9650	0.0174
Muridae	<i>Uromys</i>	<i>caudimaculatus</i>	0.9525	0.0127
Phalangeridae	<i>Phalanger</i>	<i>gymnotis</i>	0.9525	0.0133
Phalangeridae	<i>Spilocuscus</i>	<i>maculatus</i>	0.9525	0.0147
Macropodidae	<i>Dorcopsulus</i>	<i>macleayi</i>	0.8925	0.0133

Pteropodidae	<i>Nyctimene</i>	<i>cyclotis</i>	0.5950	0.0128
Pteropodidae	<i>Paranyctimene</i>	<i>raptor</i>	0.5325	0.0126
Acrobatidae	<i>Distoechurus</i>	<i>pennatus</i>	0.5200	0.0072
Peroryctidae	<i>Echymipera</i>	<i>kalubu</i>	0.5200	0.0121
<i>Birds</i>				
Casuariidae	<i>Casuaris</i>	<i>bennetti</i>	0.9875	0.0281
Bucerotidae	<i>Rhyticeros</i>	<i>plicatus</i>	0.8925	0.0205
Columbidae	<i>Ducula</i>	<i>zoeae</i>	0.8175	0.0194
Columbidae	<i>Ducula</i>	<i>chalconota</i>	0.8175	0.0171
Columbidae	<i>Ducula</i>	<i>rufigaster</i>	0.8175	0.0154
Columbidae	<i>Ducula</i>	<i>pinon</i>	0.8175	0.0148
Columbidae	<i>Otidiphaps</i>	<i>nobilis</i>	0.8175	0.0132
Corvidae	<i>Corvus</i>	<i>tristis</i>	0.8175	0.0129
Megapodiidae	<i>Talegalla</i>	<i>jobiensis</i>	0.8175	0.0124
Psittacidae	<i>Eclectus</i>	<i>roratus</i>	0.8175	0.0121
Columbidae	<i>Ptilinopus</i>	<i>magnificus</i>	0.7550	0.0124
Columbidae	<i>Columba</i>	<i>vitiensis</i>	0.6950	0.0125
Columbidae	<i>Gymnophaps</i>	<i>albertisii</i>	0.6950	0.0176
Columbidae	<i>Ptilinopus</i>	<i>ornatus</i>	0.6950	0.0141
Columbidae	<i>Ptilinopus</i>	<i>perlatus</i>	0.6950	0.0139
Columbidae	<i>Ptilinopus</i>	<i>rivoli</i>	0.6950	0.0155
Columbidae	<i>Ptilinopus</i>	<i>superbus</i>	0.6950	0.0154
Columbidae	<i>Reinwardtoena</i>	<i>reinwardtsi</i>	0.6950	0.0130
Megapodiidae	<i>Aepyodius</i>	<i>arfakianus</i>	0.6950	0.0113
Megapodiidae	<i>Megapodius</i>	<i>freycinet</i>	0.6950	0.0108
Paradisaeidae	<i>Manucodia</i>	<i>chalybata</i>	0.6950	0.0136
Paradisaeidae	<i>Paradisaea</i>	<i>raggiana</i>	0.6950	0.0157
Paradisaeidae	<i>Parotia</i>	<i>carolae</i>	0.6950	0.0110
Paradisaeidae	<i>Parotia</i>	<i>lawesii</i>	0.6950	0.0103
Psittacidae	<i>Alisterus</i>	<i>chloropterus</i>	0.6950	0.0098
Psittacidae	<i>Geoffroyus</i>	<i>simplex</i>	0.6950	0.0117
Psittacidae	<i>Psittrichas</i>	<i>fulgidus</i>	0.6950	0.0150

Sturnidae	<i>Mino</i>	<i>dumontii</i>	0.6950	0.0120
Campephagidae	<i>Coracina</i>	<i>boyeri</i>	0.5200	0.0094
Campephagidae	<i>Coracina</i>	<i>caeruleogrisea</i>	0.5200	0.0101
Columbidae	<i>Henicophaps</i>	<i>albifrons</i>	0.5200	0.0090
Columbidae	<i>Macropygia</i>	<i>nigrirostris</i>	0.5200	0.0132
Columbidae	<i>Macropygia</i>	<i>amboinensis</i>	0.5200	0.0135
Columbidae	<i>Ptilinopus</i>	<i>coronulatus</i>	0.5200	0.0116
Columbidae	<i>Ptilinopus</i>	<i>pulchellus</i>	0.5200	0.0165
Cuculidae	<i>Eudynamis</i>	<i>scolopacea</i>	0.5200	0.0072
Meliphagidae	<i>Melipotus</i>	<i>fumigatus</i>	0.5200	0.0097
Meliphagidae	<i>Philemon</i>	<i>bucerooides</i>	0.5200	0.0092
Oriolidae	<i>Oriolus</i>	<i>szalayi</i>	0.5200	0.0114
Pachycephalidae	<i>Pitohui</i>	<i>dichrous</i>	0.5200	0.0081
Pachycephalidae	<i>Pitohui</i>	<i>cristatus</i>	0.5200	0.0086
Pachycephalidae	<i>Pitohui</i>	<i>ferrugineus</i>	0.5200	0.0094
Pachycephalidae	<i>Pitohui</i>	<i>kirhocephalus</i>	0.5200	0.0101
Paradisaeidae	<i>Cicinnurus</i>	<i>regius</i>	0.5200	0.0097
Paradisaeidae	<i>Cicinnurus</i>	<i>magnificus</i>	0.5200	0.0153
Psittacidae	<i>Pseudeos</i>	<i>fuscata</i>	0.5200	0.0100
Psittacidae	<i>Trichoglossus</i>	<i>haematodus</i>	0.5200	0.0095
Ptilonorhynchidae	<i>Ailuroedus</i>	<i>melanotis</i>	0.5200	0.0086
Ptilonorhynchidae	<i>Ailuroedus</i>	<i>buccoides</i>	0.5200	0.0115
Columbidae	<i>Ptilinopus</i>	<i>naina</i>	0.5150	0.0111
Cuculidae	<i>Microdynamis</i>	<i>parva</i>	0.4950	0.0116
Meliphagidae	<i>Meliphaga</i>	<i>aruensis</i>	0.4175	0.0108
Meliphagidae	<i>Meliphaga</i>	<i>mimikae</i>	0.4150	0.0138
Meliphagidae	<i>Pycnopygius</i>	<i>ixoides</i>	0.4150	0.0072
Meliphagidae	<i>Meliphaga</i>	<i>albonotata</i>	0.4125	0.0070
Meliphagidae	<i>Meliphaga</i>	<i>analoga</i>	0.4100	0.0062
Psittacidae	<i>Loriculus</i>	<i>aurantiifrons</i>	0.2600	0.0070
Campephagidae	<i>Lalage</i>	<i>leucomela</i>	0.2550	0.0091
Columbidae	<i>Gallucolumba</i>	<i>jobiensis</i>	0.2550	0.0062

Columbidae	<i>Gallicolumba</i>	<i>rufigula</i>	0.2550	0.0078
Cuculidae	<i>Cuculus</i>	<i>saturatus</i>	0.2550	0.0051
Dicaeidae	<i>Melanocharis</i>	<i>longicauda</i>	0.2550	0.0085
Dicaeidae	<i>Melanocharis</i>	<i>nigra</i>	0.2550	0.0169
Meliphagidae	<i>Lichenostomus</i>	<i>obscurus</i>	0.2550	0.0082
Meliphagidae	<i>Pycnopygius</i>	<i>cinereus</i>	0.2550	0.0056
Meliphagidae	<i>Xanthotis</i>	<i>flaviventer</i>	0.2550	0.0102
Meliphagidae	<i>Xanthotis</i>	<i>polygramma</i>	0.2550	0.0104
Psittacidae	<i>Chamosyna</i>	<i>wilhelminae</i>	0.2550	0.0041
Psittacidae	<i>Chamosyna</i>	<i>multistriata</i>	0.2550	0.0044
Psittacidae	<i>Chamosyna</i>	<i>pulchella</i>	0.2550	0.0096
Psittacidae	<i>Chamosyna</i>	<i>placentis</i>	0.2550	0.0097
Psittacidae	<i>Cyclopsitta</i>	<i>diopthalma</i>	0.2550	0.0079
Psittacidae	<i>Cyclopsitta</i>	<i>guliemiterti</i>	0.2550	0.0126
Psittacidae	<i>Lorius</i>	<i>lory</i>	0.2550	0.0098
Psittacidae	<i>Psittaculirostris</i>	<i>desmarestii</i>	0.2550	0.0098
Psittacidae	<i>Trichoglossus</i>	<i>goldei</i>	0.2550	0.0049
Zosteropidae	<i>Zosterops</i>	<i>novaeguineae</i>	0.2125	0.0066
Zosteropidae	<i>Zosterops</i>	<i>atrifrons</i>	0.1550	0.0103
Dicaeidae	<i>Dicaeum</i>	<i>pectorale</i>	0.0750	0.0104

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CHAPTER 11.

DIET, KEYSTONE RESOURCES AND ALTITUDINAL MOVEMENT OF DWARF CASSOWARIES IN RELATION TO FRUITING PHENOLOGY IN A PAPUA NEW GUINEAN RAINFOREST

DEBRA D. WRIGHT

Abstract

I recorded plant community phenology for three years, classified each fruiting species according to pattern (continually, annually, biennially or one-year fruiting) and documented what cassowaries consumed versus this fruit availability through dung analyses. Dwarf cassowaries are 25 kg ratites whose diet consists of over 91% fruit year-round. Although the study site had aseasonal rainfall, it experienced an annual fruit lean season. During peak fruit periods cassowaries preferred predictable, synchronously fruiting annual and biennial species over continually fruiting species. However, during the lean season they had to rely on continually fruiting species, as they were almost the only fruits available over a 3-4 month period each year at the site. Cassowary diet is much more diverse than that of other specialized frugivores, perhaps because they are non-volant and can consume large quantities of fruit without the ballast limitations experienced by volant frugivores. Fruit availability and cassowary signs at three different altitudes over a 5-month period suggested that some individuals move altitudinally to follow fruit availability. I suggest that these are the females and that males remain to incubate eggs (the lean season is also the incubation season) and live mostly off their fat reserves.

Key words: *Casuarius bennetti*, cassowary, diet, phenology, specialist frugivore

INTRODUCTION

Cassowaries, the largest known specialist frugivores, are flightless ratites. There are three species in the family Casuariidae. *Casuarius casuarius*, the southern cassowary, is found in the remnant rainforests of Australia and in New Guinea; *Casuarius unappendiculatus*, the northern cassowary, is found only in New Guinea; and *Casuarius bennetti*, the dwarf cassowary, also occurs only in New Guinea. The northern and southern cassowaries weigh 50 kg and live from sea level to 500 m

a.s.l.; the dwarf cassowary weighs 25 kg and lives from 500-3300 m a.s.l. (Beehler, Pratt, & Zimmerman, 1986).

Cassowaries are particularly important to New Guinea's flora because they are probably the only non-human vertebrate large enough to disperse the many large-seeded plant species found on the island. Possible exceptions are Blyth's hornbill, *Rhyticeros plicatus*, and two species of flying fox, *Pteropus neohibernicus* and *Dobsonia moluccensis*. However, the first two species are only found below 1000 m and the dwarf cassowary's range extends to 3300 m (Beehler et al., 1986; Flannery, 1995).

Diet can be studied through direct observation (e.g., Robinson, 1986; Sun & Moermond, 1997), indirect observation (e.g., Oloo, Brett, & Young, 1994), stomach contents (e.g., Poulin, Lefebvre, & McNeil, 1994), stable isotope analysis (e.g., Fleming, Nunez, & Sternberg, 1993), or dung (fecal) contents (e.g., Fleming, 1988). In Australia habituation of southern cassowaries is possible, thus direct observations are possible (e.g., Bentrupperbaumer, 1997); however, in New Guinea cassowaries are widely hunted and thus are extremely shy and difficult to observe. In New Guinea dung analysis is the best method for determining cassowary diet because their droppings are conspicuous, persist for weeks without decay and are unmistakable for any other animal dropping in New Guinea (Mack, 1995). Cassowaries have remarkably gentle gut treatment and most items come through reasonably intact (Crome, 1975a; Stocker & Irvine, 1983; Pratt, 1983). Some fruits do not even lose their pulp (personal observation).

The diet of the southern cassowary has been studied in Australia (Crome, 1975a; Stocker & Irvine, 1983). However, in New Guinea only one relatively small study on the dwarf cassowary has been published (Pratt, 1983). Pratt examined 43 droppings that contained the seeds of 36 fruit species.

The diet of most frugivores is half fruit and half a protein-rich food such as insects (Foster, 1978). Very few animals have diets with over 90% fruit, although this is the usual definition of a specialist (or virtually obligate) frugivore (McKey, 1975; Wheelwright & Orians, 1982; Bell, 1983). Specialist avian frugivores feed their young fruit without supplementing the diet with insects, as do most other birds (Morton, 1973). They typically have a narrower diet than other frugivores, because they specialize on nutrient-rich fruits of families such as Lauraceae and Arecaceae (Snow, 1962; Wheelwright, 1983). The few examples of specialized avian frugivores include oilbirds (Snow, 1962), bearded bellbirds (Snow, 1970) and cassowaries (Crome, 1975a; Stocker & Irvine, 1983; Pratt, 1983). I wanted to find out what percentage of cassowary diet is fruit and if this varies seasonally.

Temporal patterns of fruit availability affect a frugivore's foraging efficiency. This factor is usually overlooked in frugivore studies, though it is a prominent component of nectarivore studies (Caraco, 1980; Real, 1981; Feinsinger, 1987). If the fruits in the diet are temporally and spatially predictable (e.g., they are pulsed annually or biennially, appearing during predictable months on predictable individual plants), an animal can potentially remember this information and can visit plants when they come into fruit without undirected or random searching. If fruit availability is unpredictable (e.g., asynchronously on different individuals), then a

frugivore must return to individual plants to see if they have ripe fruits, which may waste foraging time. If the above is true, one could predict that frugivores should prefer predictable annually or biennially fruiting species over unpredictable but continually fruiting species (continual fruiting as a species, but unpredictable at the individual plant level). I wanted to see if cassowaries preferred predictable species over unpredictable species.

Tropical forests typically have peaks and lows of fruits available for frugivore consumption (Terborgh, 1986; Foster, 1982). Even in aseasonal rain forests where temperature and rainfall are fairly constant, fruit supplies are not constant and frugivores face lean times (Leighton & Leighton, 1983). To get through these periods frugivores can 1) expand their home ranges to find more fruiting plants or decrease their range to save energy (van Schaik, Terborgh, & Wright, 1993; Peres, 1994a), 2) emigrate to other areas that have a different phenological schedule (Wheelwright, 1983; Debussche & Isenmann, 1992; Loiselle & Blake, 1991; Loiselle & Blake, 1993), 3) switch to other food items during the fruit scarcity (Garber, 1993; Kaplin, Munaligoga, & Moermond, 1998; Sun & Moermond, 1997), or 4) live on fat stores (Churchill, 1994). During lean times frugivores generally consume fewer fruit species than in plentiful times because fewer are available (Robinson, 1986; Sun & Moermond, 1997; but see Pyke, Pulliam, & Charnov, 1977); at one site in Peru as few as 12 plant species sustain 80% of the frugivore biomass during the lean season (Terborgh, 1986). I wanted to learn if aseasonal rainforests in Papua New Guinea (PNG) undergo an annual lean season, and if so, what strategies cassowaries use to get through these periods.

To summarize, in this study, I examined plant phenology patterns at Crater Mountain in Papua New Guinea to see if there was a fruit lean season. I examined cassowary droppings over the same three-year period to determine the extent of their dietary specialization on fruits and whether they preferred synchronous, annually or biennially available species over asynchronous, continual ones. I censused droppings and examined dropping content diversity over time in order to assess the birds' response to lean seasons. I learned which plant species sustained cassowaries during the lean season, if cassowaries switched to alternative food items when fruits were not plentiful and/or if they migrated altitudinally in response to fruit availability.

METHODS

Study Site

This study was conducted at the Crater Mountain Biological Research Station (known locally as Wara Sera) within the Crater Mountain Wildlife Management Area (WMA) of Papua New Guinea (6° 43' S, 145° 05' E). The station is 15 km east of Haia, a small village with a landing strip, in Simbu Province. The 400 ha study area ranges in elevation from 850-1350 m a.s.l. and has steep topography. Annual rainfall averages 6.7 m with no predictable wet or dry season (Wright,

1998). Vegetation is very diverse with 228 species > 10 cm DBH on a 1 ha plot (Wright, Jessen, Burke, & Garza, 1997). The surrounding area has a low human population density of about 3,600 people in the 2,700 km² Wildlife Management Area (Johnson, 1997). No people live within a one-hour hike of the study area and no hunting or vegetation clearing is permitted within this uninhabited area by agreement of the local people. The site is above the range of other species of cassowaries so that all droppings found can be unambiguously attributed to the dwarf cassowary.

Fruits

Plots-- From June through September, 1990 I delineated 40 plots measuring 50 x 10 m. Plots were randomly placed and oriented within each 200 m section of the trail system throughout the study area. All plots began 5 to 10 m off the trail. Plots were not placed on slopes greater than 75°. In February and March, 1991 I extended all plots to 50 x 20 m and added two more for a total of 4.2 ha.

Timing of Plot Visits-- I visited each plot 7 to 10 times (average 8.5 times) between June, 1990 and March, 1993, or roughly every 4 months (average 1 ha searched per month). Although some individuals could have fruited or flowered during the times I did not visit them, I thought it was more important to have a large sample area to estimate relative species abundance and overall phenology rather than to track a smaller number of individual plants. This timing allowed me to find most if not all of the reproductive events for each plant (either flowers or fruits in some stage). Generally, in tropical rainforests fruiting cycles (presence of ripe fruits) can last from 10 days to 7 months (van Roosmalen, 1985). Although ripe fruit presence can be an ephemeral stage, fruits usually take 3 or more months to develop after the plant flowers (e.g., Lucas & Corlett, 1991; Peres, 1994a). Therefore, by recording the presence of flowers and ripe, unripe, and old (rotten) fruit, I was likely to find all reproductive periods (either beginning, middle, or end) for each plant by examining them once every 4 months. To increase sample size for rare tree species (< 1 individual per ha), I also recorded phenology for individuals of these species found fruiting or flowering along 8.5 km of trails.

Data Collection-- During each plot visit, I thoroughly searched for any signs of plant reproductive activity, using binoculars for the canopy. I put a unique tag number on all angiosperms (herbs, shrubs, vines, trees, epiphytes) that had fruits or flowers within the interior 50 x 10 m strip of the plot (50 x 5 m strip before the plots were extended in early 1991). On the portions of each plot outside this interior strip, I excluded herbs and shrubs (assuming they were more numerous and so should require a smaller sample area). For each plant I recorded its position on the plot, its estimated height, and its DBH at 1.5 m (or above buttresses) if the plant was that tall. If a plant was on the border of the plot, I included it if it was rooted in the plot or, for lianas, if most of the plant was within the plot. I collected a voucher sample for all species and described and illustrated all species in a catalog. Vouchers are

deposited at the Forestry Research Institute, Lae, PNG, the University of PNG, Port Moresby, PNG, and the Harvard University Herbarium, Cambridge, USA. During each plot visit, for each marked plant, I counted the number of ripe, unripe, and old fruits on the ground and up to 1.5 m on the plant and ripe, unripe and old fruits above 1.5 m on the plant. Fruits below 1.5 m are accessible to cassowaries. If a canopy crop contained over 100 fruits, I extrapolated using crop subset counts. I also recorded whether or not each plant was producing flowers or buds.

Phenology Classifications-- For species with over five marked individuals (the minimum suggested number for documenting phenology patterns, Frankie et al., 1974), and with observations for at least 11 of the 12 annual months, I classified population phenology pattern according to regularity (sensu Newstrom, Frankie, & Baker, 1994) as: Continual if fruiting or flowering did not have a gap of 4 consecutive months. Annual if there were at least four consecutive months with: 1) no ripe or old fruits, 2) no unripe fruits if fruit diameter was under 15 mm (see below), and 3) no flowers or buds. Biennial if it was like an annual species (fruits available from one to eight contiguous months per year) but fruits were only produced every other year. One-year if it was like an annual species but with fruits produced in only one of the three years of the study. The reason for including unripe fruits for small-fruited plant species (< 15 mm when ripe) and not for large ones in this classification is that unripe small fruits are more likely to ripen in the same month than are unripe fruits of large-fruited species. When measuring fruit diameters for analyses in this section, I measured the entire aggregate for aroids and pipers and the syconium for figs because the entire aggregate/syconium has to mature before the individual fruits can ripen (Wright, 1998). If any individual of a species had any fruits or flowers during a particular month, the species was counted as fruiting or flowering that month for this classification (i.e., these phenology patterns reflect absolute periods, not peak periods).

Analyses-- I calculated the proportion of observed individuals of all species that had ripe fruits for each month of the study. Months with very small sample sizes of observed plants (fewer than 100 plants observed that had been reproductively active at some time during the study) were not included in analyses. Furthermore, if outliers in an analysis had fewer than 200 individuals observed that month (again, reproductively active at some time during the study), then I excluded those outliers from the analysis. I used ANOVAs (with arcsine square-root transformations for proportions) to look for variation by month in ripe fruits. I did the same type of analysis for the proportion of observed species, genera, and families.

I calculated the proportion of plants per species with ripe fruit per month and used a Kolmogorov-Smirnov test to see if annual and biennial species had more predictable fruiting than continual species. I used a Mann-Whitney U test to see if species with continuous fruiting patterns had smaller fruits than those with annual or multi-annual patterns. I used a Chi-square test to see if phenology pattern (continual, annual, or multi-annual) varied with plant form (liana, epiphyte, shrub defined as <3 m tall, midstory defined as 3-10 m tall, or overstory defined as > 10m

tall). All analyses were done using Systat 7.01 (SPSS, Inc.), Excel 6.0, or according to Sokal and Rohlf (1981).

Cassowaries

Dung Collections-- Dwarf cassowary droppings were collected throughout the study area both on and off trails from May 1990 to May 1993. I quantified the area searched off trails separately from the area searched on trails as the former gives a more unbiased dropping density estimate (Westcott, 1999). Droppings were from at least 2-5 adult-sized birds partially resident in the study area at most times (estimate based on footprints, sleeping areas with fresh droppings, tracking individual birds, and cassowary vocalizations; number varied with time of year). Individual sample size is unavoidably low due to the large home ranges of these ratites, and because the entire study had to be conducted on foot in rough terrain.

I only quantified contents from droppings that were less than one month old to minimize any effects of seed removal by granivores. Studies of *in situ* droppings indicate that seed predators at this site remove very few seeds from cassowary droppings, and instead consume portions of each seed in place, allowing accurate quantifications (A. Mack, personal communication). Estimated dropping age was based on regular observations of the deterioration of known-age droppings. Droppings were recorded for the month in which they were deposited, not the month in which they were found.

Determination of Dung Contents-- Most droppings (68%) were bagged, taken to the research station and then washed individually through a 1 mm screen to detect all contents. Others were left *in situ* as part of concurrent seed dispersal and seedling studies (Mack, 1995, 1998; Mack, Ickes, Jessen, Kennedy, & Sinclair, 1999), but were carefully examined to determine contents (these were minimally disturbed to avoid affecting seedling establishment).

Vouchers of all seed species found in droppings were preserved in 70% ethanol. Fruits and seeds of all angiosperms found in the forest were preserved in 70% ethanol and catalogued in a reference collection of 763 species (Wright, 1998). Seeds in droppings were identified by comparison with this reference collection. I also collected extensive data on fruit morphology for the roughly 400 species that produced fleshy fruits (fruit dimensions, average number of seeds per fruit, etc., Wright, 1998; Mack and Wright, this volume). I used fruit number, not seed number, for all analyses. Fruit number was estimated by dividing the number of seeds of a species found in a dropping by the average number of seeds per fruit for that species; fractions of fruits were rounded up to the nearest whole fruit.

Calculation of Meal Mass-- From the data collected on fresh fruit morphology (Wright, 1998), it was possible to calculate "meal mass" based on the seed content of droppings. Meal mass is defined as the pulp mass from fresh fruits that was consumed to make up each dropping (corrected for seed number per species as

above) plus the calculated fresh mass of non-fruit items (fungi, vegetation, etc.) found in that dropping. In other words, meal mass is the mass of fresh food (without the indigestible seed mass) that was consumed to make up a single dropping.

Analyses-- For each analysis I first compared data from collected droppings to *in situ* droppings to see if there was a difference for the factor being investigated. If there was not, then the combined data set was used to increase sample size and to reduce error due to small sample size. If there was a difference for the factor being tested, I checked to see if there was a bias against small or infrequently encountered items (e.g., those that may have been underestimated in *in situ* droppings). Where no bias was found, the data were combined. If a bias was detected, only collected/washed droppings were used.

I used one-way ANOVAs with Tukeys post-hoc tests to test for monthly and yearly differences. All proportional (ratio) data were arcsine square-root transformed. Two-group mean and category distribution differences were tested with Mann-Whitney U and Chi-square tests. For paired directional differences, I used Wilcoxon Signed Rank tests.

Lean Season

Elevational Study-- To see if there was evidence that cassowaries migrate to follow fruit availability, I established two camps (one at 550 m and one at 1450 m elevation) in addition to the main study site at 900 m elevation within the Crater Mountain WMA. The main study area was hill rainforest to lower montane rainforest. The 550 m site ranged from riverine rainforest to hill rainforest and was 10 km southwest of the main study area. The 1450 m site was in lower montane rainforest 6 km north of the main study area. All sites were relatively undisturbed (containing a few old gardens or tree-felling sites).

At each of the three sites I choose random compass bearings in each of three 60 degree arcs set to avoid major topographic features (cliffs, large rivers). I then searched 20 m wide by 600 m long transects along these bearings beginning 50 m from the inception point of the arcs, recording all fruits and fungi found < 1.5 m above ground (within the reach of a dwarf cassowary). I also recorded all cassowary signs (footprints, droppings, nests or sleeping areas) seen on the same 3.6 ha of transects per site.

Transects were searched in 1993 on the following dates: 1450 m: 27-29 January, 16-18 March, 5-7 May; 900 m: 2-9 February, 31 March-2 April, 18-27 May; 550 m: 13-15 February, 23-25 March, 11-12 May. I used a Spearman test to see if there was a positive correlation between fresh cassowary signs (droppings less than one month old, footprints and sightings) on the transects and the number of plants with ripe cassowary fruits at each of the sites during each time period on the transects.

RESULTS

Fruits

Sample Size—Although different transects and numbers of transects were examined each month of the study, I attempted to evenly distribute elevational representation in all monthly samples. I searched an average of 11.7 transects (1.17 ha) per month for each of the 30 months sampled (range 1-32, SD = 6.8). The following sample sizes apply for all of the phenological data presented below. Of the over 7000 marked plants that were reproductive during the study period, I examined from 132 to 3159 individuals in each of 30 months (mean = 1572, SD = 906) and from 59 to 412 species (mean = 256, SD = 102). I examined from 41 to 199 genera in each of 30 months (mean = 132, SD = 44) and from 25 to 78 families (mean = 60, SD = 13). Because I was testing for annual patterns I used the monthly values from different years as the dependent variable in ANOVA analyses. October, 1992 had a small sample size of observed plants and was eliminated from analyses.

Monthly fruit availability-- The proportion of observed individuals with ripe fruit varied by month (ANOVA, $F_{11,17} = 3.76$, $P = 0.007$; Figure 1). June had a significantly greater proportion of plants with ripe fruits than March or December (Tukey's $P = 0.007$, $P = 0.018$, respectively). The proportion of observed species with ripe fruit also varied by month (ANOVA, $F_{11,18} = 2.71$, $P = 0.03$). June had a significantly greater proportion of species with ripe fruits than December (Tukey's $P = 0.045$). Neither the proportions of observed genera or families with ripe fruits differed by month (Genera: ripe: $F_{11,18} = 1.95$, $P = 0.10$; Families: ripe: $F_{11,18} = 1.21$, $P = 0.35$).

Phenology Patterns-- Of 178 species with recorded phenology patterns, Crater Mountain had at least 8 biennial and 1 supra-biennial fruiting species (5% of the community, 12% of overstory tree species). All but one (Elaeocarpaceae) fruited together in even-numbered years (two Clusiaceae and one each in Anacardiaceae, Gnetaceae, Lauraceae, Meliaceae, Arecaceae, and Rosaceae). A few individuals of these species produced small crops during off years; however, these crops were insubstantial (less than 10% of main-year crops).

Species with continual fruiting patterns had smaller fruits than species with annual or biennial fruiting patterns (Mann Whitney $U = 2094$, $n_1 = 107$ species, $n_2 = 58$ species, $P = 0.001$). Phenology patterns varied with plant form ($\chi^2 = 41.3$, $df = 4$, $P < 0.001$, $n = 165$ species). Although lianas and epiphytes had roughly equal numbers of continual and annual fruiting species, shrubs and midstory trees had more continual than annual species. Conversely, overstory trees had more annually than continually fruiting species.

A greater proportion of individuals of species with annual and biennial phenology patterns had ripe fruit at the same time than individuals of species with continuous fruiting patterns ($K-S = 0.34$, $n = 50$ annual and biennial species and 121 continual species, $P < 0.001$). Individuals of annual and biennial species had ripe fruits more predictably than individuals of continual species.

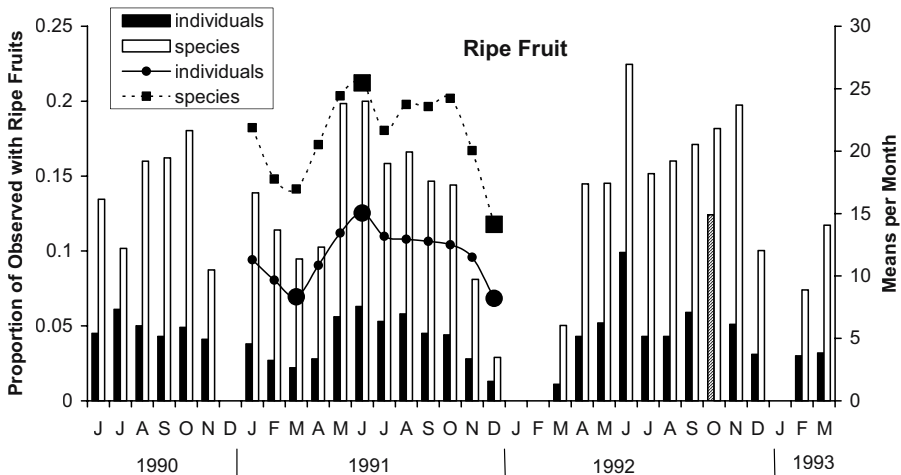


Figure 1. The proportion of observed individuals and species per month that had ripe fruit (bars) along with the means for each month for the three year period (lines) expressed as the arcsine-transformations of the proportions; i.e., the values used in ANOVA analyses. The large squares and circles represent months with significant differences. The striped bar (October 1992) represents a small sample of under 150 individuals that was an outlier in the analysis and so was excluded. December 1990, January and February 1992 and January 1993 were not sampled.

Lean Season-- An annual lean fruit season from December through March is evident not only in the numbers of species fruiting, but also in the amounts of ripe fruit and pulp mass available to consumers (Figure 2). Years of biennial masting (1990 and 1992) are also evident by the greater fruit mass produced. Annual and biennial species fruited almost entirely during the peak fruiting season so that continuous fruiting species were almost all that was available during the lean season (Figure 3).

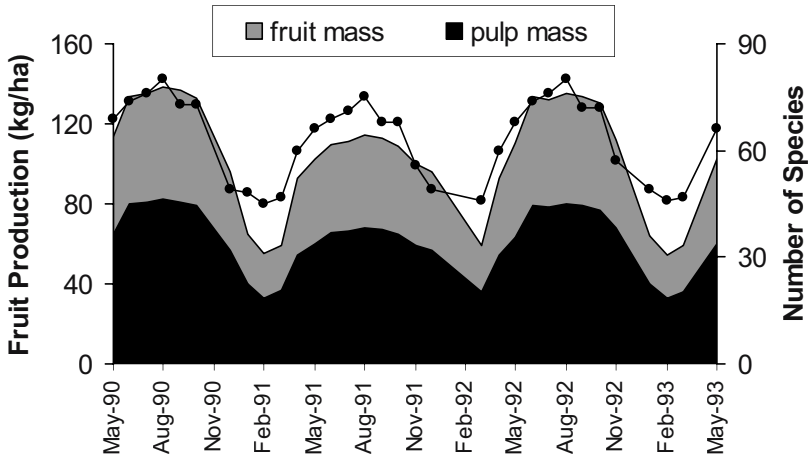


Figure 2. The minimum available fruit mass (seeds included) and pulp mass (seeds excluded) produced per ha per month of the study and the number of species (line with dots) from which these fruits came. Areas are not stacked; they are overlapping, thus the gray area represents seed mass. Not included are: species with seeds < 1 mm in diameter, with densities less than 1 per ha, with all fruits inaccessible to terrestrial frugivores (held above 1.5 m until rotted) and with non-fleshy fruits. The annual crop for each species was evenly divided among all possible months of its fruiting season so that each fruit produced was counted in only one month. This even distribution tends to level out peaks and troughs, thus the observed peaks and troughs are conservative representations.

Cassowaries

Sample Size and Dropping Age-- I analyzed a total of 855 droppings; of these 583 (68%) were collected and sieved and 272 were left *in situ*. Average dropping age was 7.4 days for all droppings (range 0-30 days, SD = 7.1 days) and 6.5 days (range 1-30 days, SD = 6.2 days) for collected droppings.

Diet Diversity-- Dung content types refer to different fruit species or to categories of non-fruit items that cassowaries consumed (e.g., beetles, snails, etc.). Remains of 192 fruit species plus mammals, birds, snakes, snails, crabs, beetles, fig wasps, maggots, parasitic worms, fungi, ferns, 1 cm diameter fibrous green stems, bark, branches, sago fibers, flowers and rocks were found in droppings (see Wright, 1998 for further detail).

Non-fruit components accounted for between 0% and 9% of total meal mass each month (Figure 4). Fungi and vertebrates were the most important non-fruit items taken (by mass) and they were taken throughout the year. Rocks were

ingested more often than non-fruit plant material or invertebrates. The proportion of non-fruit mass in the diet did not differ between months ($F(11,20) = 2.24$, $P = 0.06$) or years ($F(3,28) = 2.30$, $P = 0.1$; Figure 4). Of the 192 fruit species found in the cassowary diet, 57 (30%) had three or fewer occurrences in droppings over the three year period. Unripe fruits were taken year-round, but very rarely.

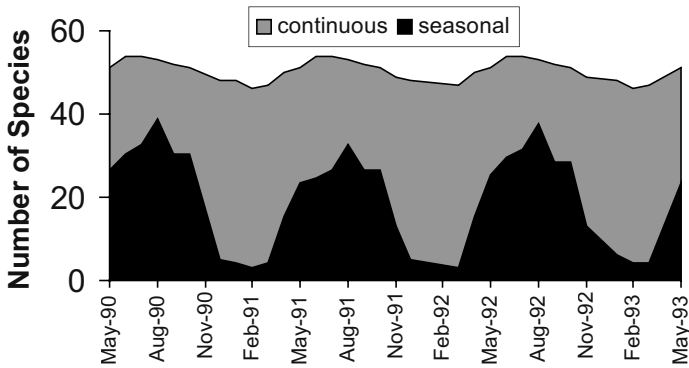


Figure 3. The number of species that have continuous fruiting versus the number that have seasonal fruiting (annual, biennial or one-year) for each month of the study. Areas are not stacked; they are overlapping. Not included are: species with seeds < 1 mm in diameter, with densities less than 1 per ha, with all fruits inaccessible to terrestrial frugivores (held above 1.5 m until rotted) or with non-fleshy fruits.

Plant Families in Cassowary Diet-- Fruits of 39 plant families were found in droppings; twelve of these families accounted for at least 15% of meal mass during some month of the study (Figure 5). I used combined dropping contents (collected and *in situ*) when calculating monthly family meal mass percentages, as there were no differences between collected and *in situ* average family meal mass data sets (Chi-square tests, $P > 0.1$). The only exceptions (July 1990 and June 1991) were due to large, common fruits, and not to small or rare fruits, as would be expected if it were a bias due to being left *in situ*.

Clusiaceae, Pandanaceae, and Moraceae were taken year-round during every year of the study (Figure 5). During the lean season Clusiaceae and Pandanaceae plus Arecaceae (palms) were consistently important and in 1993 Moraceae was also important. Combretaceae and to a lesser extent Anacardiaceae were taken from March or April through September of every year. They are important during the late lean season. Apocynaceae was consistently important from September through December, covering part of the early lean season.

Consumption of Lauraceae, and to a lesser extent Meliaceae, peaked during the plentiful season (May through August) in 1990 and 1992, probably representing a regular biennial phenological cycle (Figure 5). Although some Lauraceae fruits

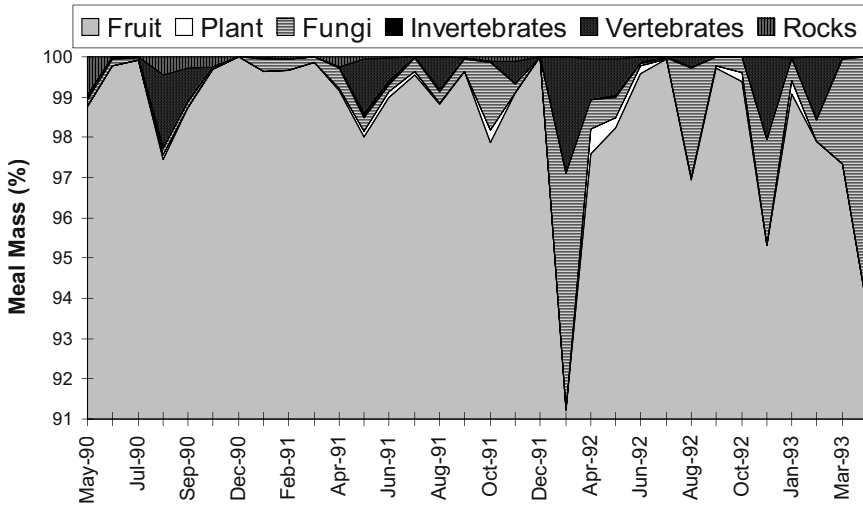


Figure 4. Cassowary diet over a three year period. Note that the Y axis begins at 91%; cassowary diet was at least 91% fruit year-round over the full three year period.

were taken at other times (including the same time period in 1991), they were not a major component of the diet during those times. During the peak fruiting period of May through September in odd-numbered years the dietary mainstays were Clusiaceae, Pandanaceae, Moraceae, Combretaceae, Anacardiaceae and Myrtaceae (note the similarity to the lean season mainstays).

During the lean season patterns could not easily be identified. Different plant families were eaten in different amounts during different years, suggesting that fruit availability is more unpredictable during this time than during the rest of the year (Figure 5). For example, from January through March 1991 Clusiaceae was extremely important; in 1992 Combretaceae fruited early and it dominated the diet during this period; and in 1993 Moraceae was important. Lauraceae was important in the cassowary diet from May through September during even-numbered years, but not in odd-numbered years when a variety of other families, including the year-round fruiteders, increased in prominence in the cassowary diet.

Plant Species in Cassowary Diet-- Over the entire study period fruits of ten species accounted for 55% of the total meal mass (fruit pulp and non-fruit item mass) of all droppings and 30 species accounted for 82% (Table 1). Although fungi are not among the 30 most important items by meal mass, fungi accounted for 16% of the items found in all droppings. Fungi plus nine fruit species accounted for 68% of the total items in droppings; fungi, vegetation, *Pandanus* flowers and 27 fruit species accounted for 87%. *Pandanus* sp. 5 and *Terminalia complanata* are notable for being in the top five species for both meal mass and overall frequency.

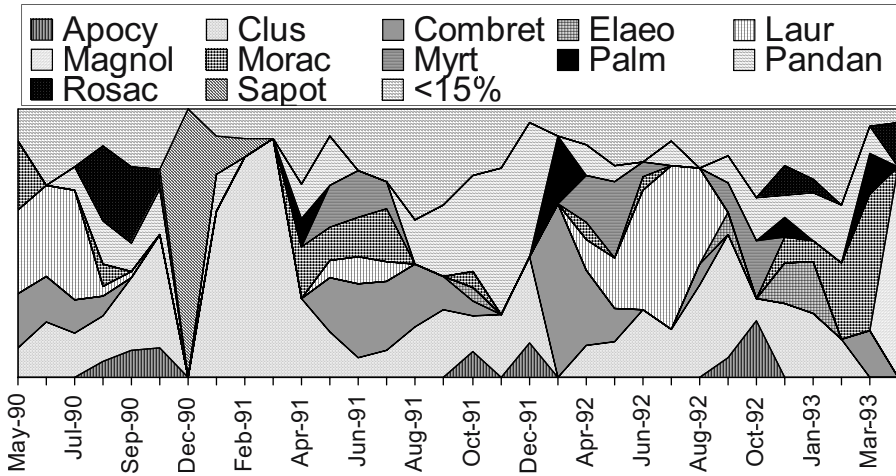


Figure 5. Proportions of each family that accounted for > 15% of the pulp mass ingested in at least one month of the study. Families that accounted for < 15% were pooled. Apocyn = Apocynaceae, Clus = Clusiaceae, Combret = Combretaceae, Elaео = Elaeocarpaceae, Laur = Lauraceae, Magnol = Magnoliaceae, Morac = Moraceae, Myrt = Myrtaceae, Palm = Arecaceae, Pandan = Pandanaceae, Rosac = Rosaceae, Sapot = Sapotaceae.

Each month the top 5 species accounted for 49-100% of the meal mass and of the frequency of items in droppings, although the same species did not always overlap in the lists of meal mass and frequency (see Wright, 1998). The biennial peaks of Lauraceae (Figure 5) were mainly caused by *Cryptocarya sp. 2* although other Lauraceae species that fruited annually were also taken in larger quantities in even-numbered years. The extreme importance of Clusiaceae during the lean period of 1991 (Figure 5) was due to the continually fruiting *Garcinia latissima*, which was eaten during all periods of every year and which accounted for 17% of the meal mass of all droppings over the three-year study (Table 1).

During each year's lean season eight fruit species (of five families) formed the core of the observed cassowary diet (they were available during each lean season) (Appendix 1). During the plentiful season, when fruits were most readily available, nine fruit species (of six families) were taken in appreciable quantities every year of the study and an additional six species were taken every even-numbered year (Appendix 1).

Table 1. The top thirty items in the cassowary diet by meal mass (see methods for definition) and by number of items over the entire study period (sample size = 855 droppings from May 1990 through May 1993). Total percentage of top ten, twenty and thirty items is given at top of table.

Meal	10 = 54.6%	30 = 81.6%		Number of	10 = 67.5%	30 = 87%	
Mass	20 = 72.5%			Items	20 = 80.4%		
Family	Genus	species	%	Family	Genus	species	%
Clus	<i>Garcinia</i>	<i>latissima</i>	17.2	Fungi	bracket		15.7
					fungi		
Pandan	<i>Pandanus</i>	<i>penicillatu</i>	6.7	Pandan	<i>Pandanus</i>	sp. 5	12
		<i>m</i>					
Laur	<i>Cryptocarya</i>	sp. 2	5.6	Myrt	<i>Syzygium</i>	sp. 2	10.2
Pandan	<i>Pandanus</i>	sp. 5	5.4	Rosac	<i>Prunus</i>	<i>gazelle-</i>	7.6
						<i>peninsulae</i>	
Combret	<i>Terminalia</i>	<i>complanata</i>	4.8	Combret	<i>Terminalia</i>	<i>complanata</i>	7.2
Apocyn	<i>Cerbera</i>	<i>floribunda</i>	3.4	Anacard	<i>Dracontomelon</i>	<i>dao</i>	3.6
Combret	<i>Terminalia</i>	<i>impediens</i>	3.1	Pandan	<i>Pandanus</i>	sp. 3	3.5
Laur	<i>Endiandra</i>	sp. 2	3.1	Magnol	<i>Elmerillia</i>	<i>tsiampacca</i>	3.1
Myrt	<i>Syzygium</i>	sp. 3	2.7	Laur	<i>Cryptocarya</i>	sp. 2	2.5
Rosac	<i>Prunus</i>	sp. 2	2.6	Arecac	?3		2.1
Anacard	<i>Dracontomelon</i>	<i>dao</i>	2.4	Rosac	?1		1.9
Clus	<i>Garcinia</i>	sp. 2	2.2	Arecac	?1		1.6
Clus	<i>Garcinia</i>	<i>celebica</i>	2.1	Elaeo	<i>Elaeocarpus</i>	sp. 2	1.4
Myrt	<i>Syzygium</i>	sp. 2	1.8	Morac	<i>Ficus</i>	1-2 cm figs	1.4
Laur	<i>Endiandra</i>	sp. 5	1.7	Elaeo	<i>Elaeocarpus</i>	<i>sphaericus</i>	1.3
Morac	<i>Ficus</i>	1-2 cm figs	1.7	Laur	<i>Endiandra</i>	sp. 5	1.3
Prot	<i>Helicia</i>	sp. 1	1.7	Combret	<i>Terminalia</i>	<i>impediens</i>	1.2
Clus	<i>Mammea</i>	<i>grandifolia</i>	1.6	Rosac	<i>Prunus</i>	sp. 2	1
Morac	<i>Ficus</i>	3 cm figs	1.4	Sapot	<i>Burckella</i>	sp. 1	1
Meliac	<i>Aglaiia</i>	<i>mackiana</i>	1.3	Morac	<i>Ficus</i>	3 cm figs	0.8
Clus	<i>Garcinia</i>	cf. <i>assugu</i>	1.2	Clus	<i>Garcinia</i>	<i>latissima</i>	0.8
Sapot	<i>Burckella</i>	sp. 1	1	Vegetation	ferns, stems		0.8
Elaeo	<i>Elaeocarpus</i>	sp. 2	1	Morac	<i>Ficus</i>	<i>trachypison</i>	0.7
Rosac	<i>Prunus</i>	<i>gazelle-</i>	1	Clus	<i>Garcinia</i>	cf. <i>assugu</i>	0.7
		<i>peninsulae</i>					
Pandan	<i>Pandanus</i>	<i>papuanus</i>	0.9	Rub	<i>Psychotria</i>	sp. 1	0.7
Morac	<i>Artocarpus</i>	sp. 1	0.9	Pandan	<i>Pandanus</i>	<i>penicillatum</i>	0.6

Clus	<i>Garcinia</i>	sp. 1 cf. <i>maluensis</i>	0.8	Clus	<i>Litsea</i>	sp. 1	0.6
Logan	<i>Neubergia</i>	<i>corynocarp</i> <i>a</i> ssp. 2	0.8	Pandan	<i>Pandanus</i>	flowers	0.6
Pandan	<i>Pandanus</i>	<i>limbatus</i>	0.8	?	catalog #	DW1146	0.6
Myrt	<i>Syzygium</i>	sp. 7	0.7	Cunon	<i>Schizomeria</i>	sp. 1	0.5

Eight droppings from cassowary chicks were found. These could be identified because they were much smaller than adult droppings, had only small items within them and often had juvenile footprints near them and larger droppings and prints from the parent were nearby. They contained seeds from 19 plant species (13 families) plus fungi; all of the items consumed were items also eaten by adults (Wright, 1998).

Seasonality of Fruits in Diet-- Of the 192 fruit species eaten, 39 species (20%) were annual. Eight species (4%) were biennial; 7 in 90/92 and 1 in 91/93. Forty-eight species (25%) were continual, and ninety-nine species (52%) were one-year only (see Wright, 1998).

One-way ANOVAs (with months as the categorical factor and meal mass proportions (arcsine transformed) for each year as the dependent variable) showed that annual fruits accounted for a larger proportion of the meal mass from April through October than from December through February ($F(11, 20) = 2.84, P = 0.02$, Tukey's $P < 0.05$ for May > February; Figure 6). Continual fruits made up a higher proportion of the diet from December through March than from April through October ($F(11, 20) = 3.44, P = 0.008$, Tukey's $P < 0.05$ for December > May, June, July; Figure 6).

Biennial fruits in 1990 and 1992 made up a larger proportion of the diet in June, July and August than from October through April ($F(9,6) = 4.27, P < 0.05$, but no Tukey's $P < 0.05$ due to the small sample size of 1 to 2 years sampled per month) and were virtually missing from 1991 and 1993 (Figure 6). The study ended in May 1993 and so biennially pulsed species for 1991 and 1993 may have been classed as one-year species in 1991 if they fruited after the end of the study in 1993. However, in 1991 one-year fruits were also in low abundance from June through December (Figure 6), so even if some of these were biennials, 1991-1993 biennials would still be rare (much rarer than 90-92 biennials). The proportion that one-year fruits contributed to meal mass varied by month ($F(11,20) = 3.11, P = 0.01$), but no discernable pattern was apparent (Tukey's $P > 0.05$).

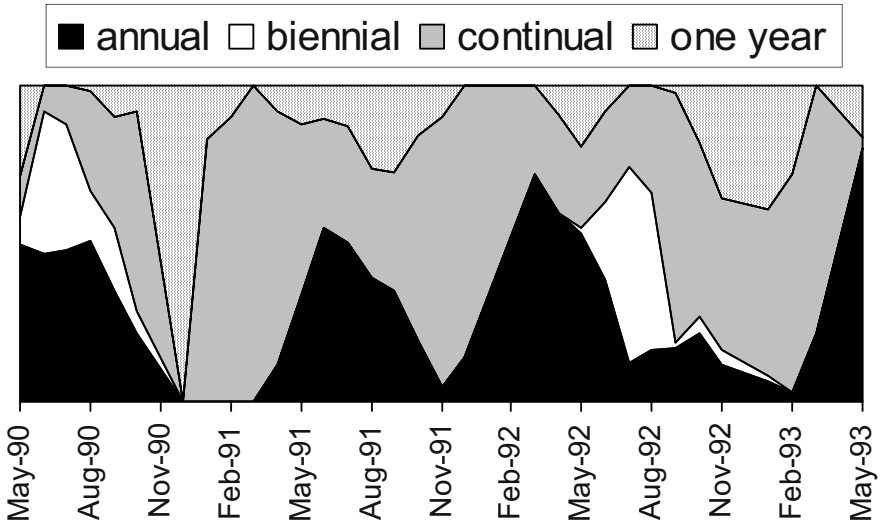


Figure 6. Proportions of annual, biennial, continual or one-year fruits that were included in the meal mass for each month of the study.

In summary, in December, January, and February 80-100 % of the meal mass for cassowaries consists of continual species that fruit year-round but unpredictably on individual plants. In March, April, and May the proportion of annual fruits increases, but continual fruits are still important (these two types make up over 90% of the meal mass). In June, July, and August during even-numbered years, biennial fruits become important (15-50% of meal mass), but annual and continual fruits are also still important; during odd-numbered years, annual and continual fruits are taken in roughly equal proportions (90% total, no biennials). During September, October, and November, the proportions of biennial and annual fruits begin to dwindle and the proportion of continual fruits increases.

These patterns may result because fruits of seasonal species (annual, biennial, and one-year) are more available from May through September than during the lean season (Wright, 1998). However, a greater proportion of seasonal species were eaten than were available in 29 months, and this was true in only 3 months for continually fruiting species (Sign test $P < 0.05$; Figure 7). Cassowaries take more seasonally fruiting species than expected by availability alone, but are unable to do this during the lean season when continually fruiting species are almost all that is available.

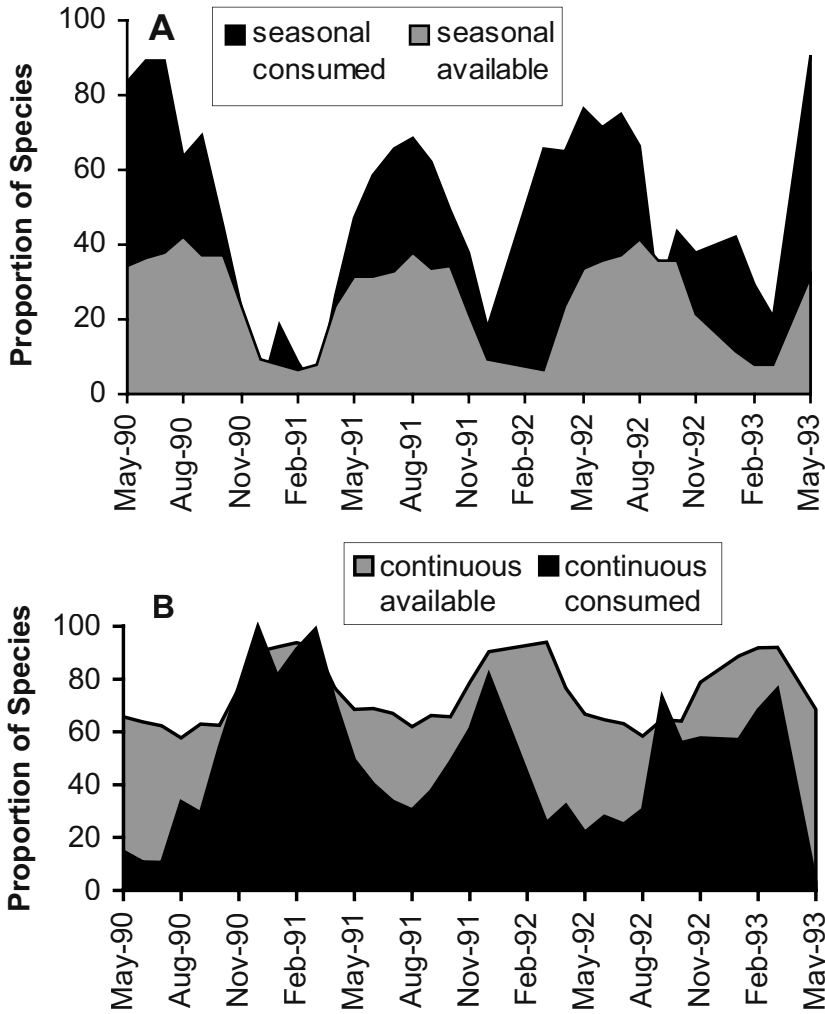


Figure 7. The proportion of species that were seasonal fruiters (annual, biennial or one-year) (in graph A) and continual fruiters (in graph B), and the proportion of these species types that were consumed by cassowaries. The gray areas of the two graphs (available species) add up to 100% and the black areas of the two graphs (consumed species) add up to 100%. A greater proportion of seasonal species were eaten than were found on the transects (available) and a lower proportion of continual species were eaten than were available throughout the study period.

Lean Season

Fewer Droppings-- Although the mass of droppings did not differ through time (Wright, 1998), droppings were less abundant within the study area from October through April than during the rest of the year, coinciding with the fruit lean season. There were 40% fewer droppings per hectare from October to April than from May to September each year (Figure 8; one-way ANOVA looking for differences between months $F = 6.33(11, 80)$, $P < 0.001$). August had more droppings per hectare than all months except for May, July, and September (Tukey's $P < 0.05$).

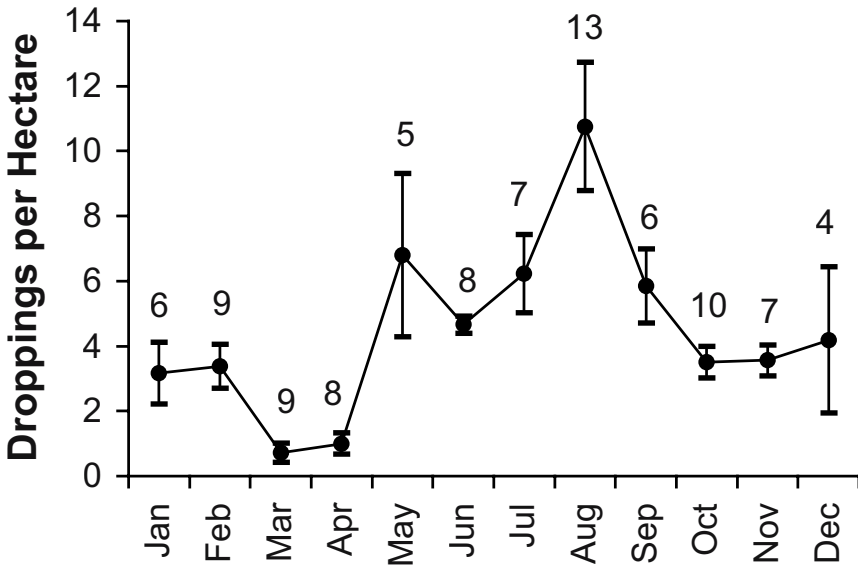


Figure 8. The mean and standard error of the number of droppings found per hectare searched off-trail during the study period. The number of hectares sampled per month is shown above each error bar. The graph combines data from all years.

Fewer Items per Dropping-- Collected droppings contained more content types (different fruit species or categories of non-fruit contents) per dropping than *in situ* droppings ($n = 855$, Mann Whitney $U = 43923$, $P < 0.001$); therefore, I used only collected droppings to determine the number of content types per dropping. The 583 collected droppings contained a total of 56,279 individual items (fruits and non-fruit items) which represented from 1 to 24 content types (fruit or non-fruit taxa) per dropping (mean = 6.2, $SD = 3.2$). Droppings collected in January contained fewer content types than those collected in April and September (5.1 versus 7.4 and 7.3), and March also had fewer content types than April, May, August, September, and

November (3.5 versus 7.4, 6.3, 6.5, 7.3 and 6.7; one-way ANOVA $F(11, 571) = 3.64$, $P < 0.001$, Tukey's $P < 0.05$). Overall, droppings collected in January through March, the fruit lean season, tended to have fewer content types than those collected in April through November, and with 30 droppings collected per month most content types were found (Figure 9).

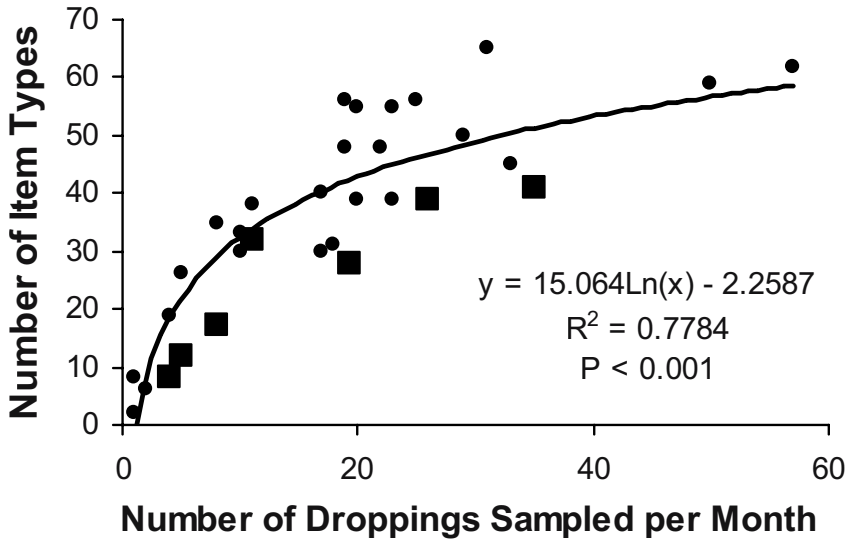


Figure 9. The number of item types (fruit and non-fruit) found in month-long samples of droppings as the number of droppings in those samples increase. The data fit a logarithmic curve. Square data points are from the main lean season (January through March).

Seasonal Altitude Shifts-- Over the three elevations and five months examined, the number of plants with ripe cassowary fruits on the transects was positively correlated with the number of cassowary signs observed on the transects (Spearman $r = 0.862$, $P = 0.001$, $n = 9$ pairs). Furthermore, there were fewer plants with ripe cassowary fruits and fewer cassowary signs at the study site (900 m) during Jan/Feb and March than in May, the beginning of the plentiful season (Figure 10).

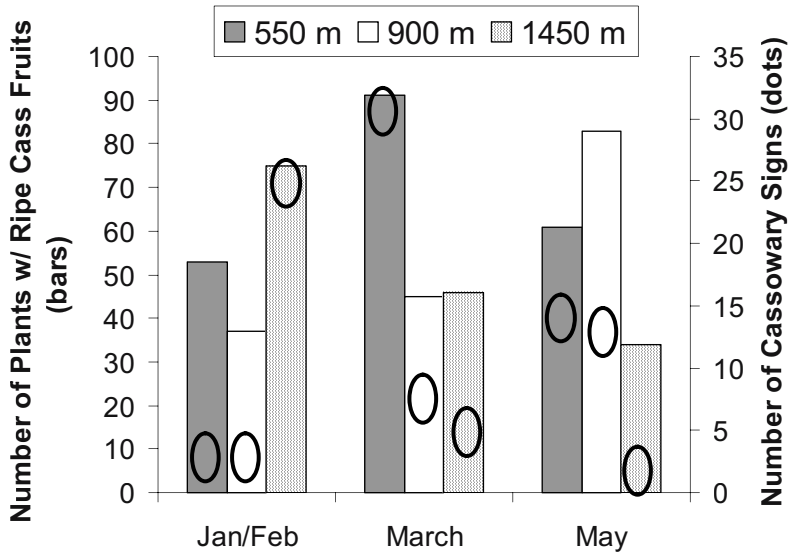


Figure 10. Cassowary fruit availability (includes only fruits cassowaries are likely to consume) versus cassowary signs (fresh droppings, tracks or actual sightings) on 3.6 ha transects over a 5 month period at three different elevations in 1993.

DISCUSSION

Cassowaries as Specialist Frugivores

Dwarf cassowary diet consisted of over 91% fruit pulp year-round over a three year period. During most months the figure was closer to 98%. Specialized frugivores are sometimes defined by what they feed their young. Using some definitions, quetzals would not be considered specialist frugivores even though the parents are obligate frugivores, because chicks are fed mostly insects, snails, and lizards with only 20-35% of their diet being fruit (Wheelwright, 1983). Oilbirds and bearded bellbirds would be considered specialist frugivores by all definitions because they feed their young strictly fruit (Bosque & Parra, 1992; Snow, 1962; Snow, 1970). Juvenile cassowaries appear to eat at least 90% fruit (based on dropping contents, Wright, 1998). Cassowaries are the largest known specialist frugivore in the world. Many heavily frugivorous bird species rely on particular plant families that are rich in nutrients (e.g., Lauraceae, Arecaceae). Quetzals feed mostly on Lauraceae

(greater than 80% of the fruit taken by frequency or mass) (Wheelwright, 1983); fruit pigeons eat 88% Lauraceae and Araliaceae fruits (Crome, 1975b; Frith, Crome, & Wolfe, 1976); Arecaceae, Lauraceae, and Burseraceae accounted for 99% of the diet of oilbirds in Trinidad over a four year period (Snow, 1962); and Lauraceae and Burseraceae accounted for 89% of the diet of bearded bellbirds (Snow, 1970).

Cassowaries have a more varied diet when compared to most specialized frugivores (Figure 11). Crome (1975a) found that double-wattled (southern) cassowaries in Australia also depend on Lauraceae fruits (20% of diet), but that Myrtaceae, Arecaceae, and Elaeocarpaceae are also important; these four families accounted for 70% of the diet over a 2.5 year period. At 1600 m a.s.l. in Papua New Guinea, Pratt (1983) found that dwarf cassowaries consume appreciable quantities of Himantandraceae, Clusiaceae, Rubiaceae, Cunoniaceae, Arecaceae, and Meliaceae in addition to Lauraceae. In my cassowary study population, Lauraceae was very important in even-numbered years during periods of peak fruit abundance, but during other times it was not important in the cassowary diet. It took seven plant families to account for only 50% of the fruits consumed by dwarf cassowaries in the present study.

Most other specialized frugivores are relatively small-bodied and volant. Cassowaries are large-bodied and non-volant. Fat storage is not a problem for cassowaries and so they can potentially consume large quantities of carbohydrate (and store it as fat) to get the other nutrients (e.g., protein) that they need. Volant frugivores cannot use this strategy and so must be more selective about what they eat; oilbird chicks consume so many carbohydrates to get the protein they need that they cannot fly because they are too fat (Snow, 1962; Thomas, Bosque, & Arends, 1993). Flightlessness and size may explain the wider diversity of plant families' fruits that cassowaries consume compared to other specialized frugivore species.

Unpredictability of Cassowary Diet

Cassowaries did prefer annually or biennially fruiting species over continually fruiting species as predicted. During plentiful periods, when both were available, they ate more of the predictable annuals and biennials than were proportionally available. This allows cassowaries to diversify their diet and to go to the same plants that they can rely upon year after year to have fruits during certain months of the year. However, even with this preference for predictable fruit species, cassowary diet was still extremely variable from year to year in addition to season to season. A large proportion of plant species only fruited in one year of the three year study and these accounted for roughly 20% of the diet. Biennial fruiters accounted for 40% of the diet when they were available. Furthermore, even though continually fruiting species were consistently taken during the lean seasons, different species were more readily available and thus consumed more than others during different years. The extreme complexity of the fruiting phenology patterns is duplicated in the cassowary diet. Even after a three year study it is difficult to find any patterns (Figure 5).

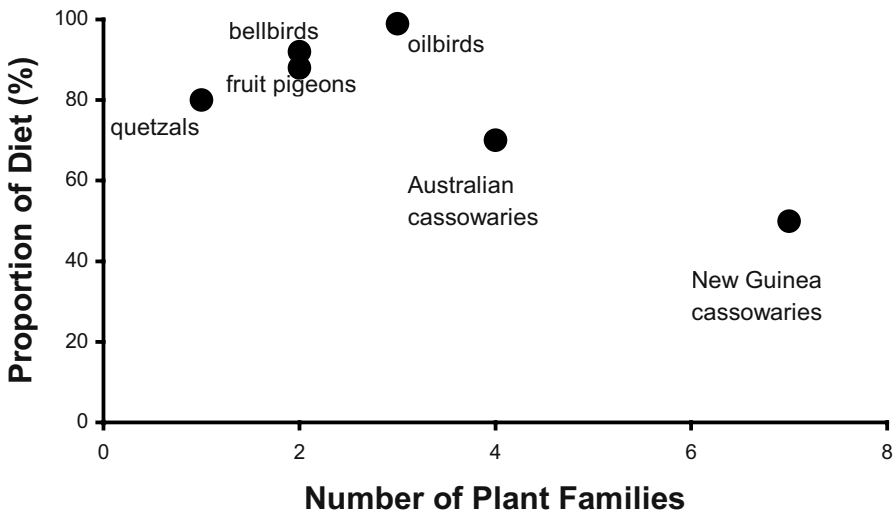


Figure 11. The diet diversity of various specialized frugivores; the greater diversity of cassowary diet may be because they do not fly. This means they can eat large quantities of fruit without calorie restrictions to get the nutrients they need instead of having to choose exceptionally nutrient-rich fruits to avoid weight gain. Data are from Wheelwright, 1983; Crome, 1975b; Frith, Crome, & Wolfe, 1976; Snow, 1962; Snow, 1970; Crome, 1975a; and this study.

Cassowaries during the Lean Season

Even though the rainfall at Crater Mountain is aseasonal and unpredictable, there is an annual predictable dearth of fruit from December through March. During this time cassowaries ate some acorns and even ate branches; they did not eat these items during other times of the year.

Diversity of cassowary dropping contents declined during the lean season. Droppings contained 40% fewer food types both within individual droppings and overall from January through March than from April through November (Figure 9, Table 2). Lean season diet for frugivores is often narrow. Capuchin and squirrel monkeys rely on figs almost exclusively during lean times (Robinson, 1986; Terborgh, 1986). Figs and palms are mainstays for many frugivores during seasonally lean periods because these plants usually have continual phenology patterns at the population level (e.g., Peres, 1994b; Kinnaird & O'Brien, this volume). Likewise, although cassowaries preferred annually fruiting species, they

depended upon continually fruiting species like figs, *Garcinia latissima*, *Pandanus spp.*, and some species of palm in the lean season. As a group, these families could be considered keystone resources for cassowaries and perhaps other frugivores in mid-elevation Papua New Guinean rainforests. It appears that despite the huge dietary diversity, a few species may be inordinately important for cassowary survival.

Crome (1975a) also found a fruit lean season for cassowaries in February and March in Australia and Pratt (1983) documented a cassowary fruit lean season from April to December at Mt. Missim in New Guinea (the opposite of our study area). Both detected fewer cassowary droppings during the lean season.

The lower number of droppings found from October through April at our study site implies that cassowaries are either migrating from the area during the lean time (December through March), increasing home range size dramatically, fasting and subsisting on stored fat and muscle, or some combination of the above. Locals report that there is a resident population of cassowaries in the study area, but that other individuals migrate altitudinally to follow fruit availability. My results are consistent with partial migration. Cassowary signs (droppings and foot-tracks on random transects, not trails, Westcott, 1999) were positively correlated with fruit availability at three elevations. When fruits were scarce in the lowlands, cassowary signs were also scarce; in the same month fruits were plentiful in the highlands and so were cassowary signs. A few months later the pattern reverses. This suggests altitudinal migration. However, because some droppings and tracks were present year-round in the main study area, all cassowaries probably do not migrate.

Males probably remain in year-round territories where they incubate and raise chicks. We found chick and adult tracks together from July through January in our study area (cassowaries are polyandrous so the adult tracks were most likely male, Crome, 1975a). January through April is the incubation season at our site, and males probably fast during much of this period. Emus, *Dromaius novaehollandiae*, the sister group to cassowaries (Noble, 1991), fast for 56 days during incubation (Davies, 1974). In Australia, Crome (1975a) found that male southern cassowaries did not come to feeding stations during their 47-53 day long incubation periods, but returned afterwards with their newly hatched chicks. Male southern cassowaries are known to fast for up to 50 days during incubation in Australia (Bentrupperbaumer, 1997). If males are going to fast during incubation, it is advantageous to do so during the lean season.

Female cassowaries, on the other hand, do not have chick-rearing and incubation duties; furthermore their fat stores may already be reduced by egg-laying once the lean season begins. Emus require 26 days to produce a single yolk and they lay the egg 10 days later (time to produce albumen and shell; Carey, 1996). If cassowaries use similar time periods, females are producing yolks just after the end of the fruiting season in December, presumably using fat stores. Once they have laid the eggs they probably need to migrate to find food to replenish their reserves. It seems that dwarf cassowaries may have a mixed strategy involving year-round residency by males, who partially subsist on fat stores in the lean season, and female migrants that track fruit availability altitudinally. However, at this point we can only

speculate. It is extremely difficult to capture adult cassowaries in New Guinea for radio tracking and the extreme topography makes telemetry a real challenge for long-ranging species. A promising new method we may use in future studies involves comparing the DNA from epithelial cells in droppings from different sites. If this works, it could verify and track individual movements over time, allowing documentation of any altitudinal migrations. However, even this will not be easy as we would be looking for the proverbial one dropping out of one thousand found and analyzed over many square km in rugged terrain.

Many animals store fat during plentiful times to get them through lean times (Robinson, 1986; Bruno & Lovari, 1989; Churchill, 1994). Animals with variable food resources put on greater fat reserves than animals with predictable, reliable food sources (Ekman & Hake, 1990; Biebach, 1996). The fruit base at Crater Mountain is certainly variable, and cassowaries can accumulate several centimeters of fat. Fat may reduce maneuverability in predator escape (Biebach, 1996) and flight, but cassowaries do not have natural predators (except for humans) and are non-volant. Emperor penguins fast for 60 days during incubation periods (Cherel, Charassin, & Handrich, 1993; Cherel, Robin, Heitz, Calgari, & LeMaho, 1992), and it appears that male cassowaries do the same (Bentrupperbaumer, 1997; Crome, 1975a). Male emus have lower metabolic rates than female emus, perhaps because of their 8 week fasting incubation period (Maloney & Dawson, 1993), which females do not endure. Ratites as a group have 35% lower basal metabolic rates than other non-passerine birds (Maloney & Dawson, 1993); this may aid survival during the fruit lean season.

Conservation Aspects

The southern cassowary and the northern cassowary (*C. casuarius* and *C. unappendiculatus*) are both on the IUCN Red List 1 for threatened animals (IUCN, 2002). *Casuarius bennetti*, the dwarf cassowary, is on the Red List 3 for near threatened animals (IUCN, 2002). In New Guinea, all three cassowary species are still avidly hunted for trade, food and feathers and have been extirpated from much of their natural range through hunting and habitat destruction. Juvenile cassowaries are especially vulnerable to human predation because they come to human whistles that sound like the calls their parent makes. Each individual cassowary disperses hundreds of seeds daily, many too large to be moved by any other animal. Without cassowaries to move seeds back uphill, the range of many fleshy fruited plant species would shrink to valley bottoms in the rugged New Guinea terrain (Mack, 1995). If these flightless birds do indeed depend on annual altitudinal migrations to sustain their populations, we need to be aware of this fact when designing reserves. Furthermore, because of the tremendous seasonal and yearly variation in their diet, we need to ensure that the full diversity of fruiting flora is kept intact if we wish to sustain cassowary populations, and especially those continuous fruited plants that fill the lean season gap.

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Appendix 1. The seasons that the top five items per month (for percentage of meal mass and/or for frequency eaten) were consumed (sample size = 855 droppings). In other words, in at least one month of the three year study period, these items were important in cassowary diet. The phenology pattern is given after the item name (A = annual, B = biennial, C = continual, OY = one-year only). Thus if an item is found under the lean season and it is A or C, it can probably be relied upon every year during the lean season. If it is B, it is taken every other year; if it is OY, it was taken only one year of the study (it may only fruit every three or more years). The first letter indicates importance by mass or by frequency (M or F), then comes the rank that month (1-5 with 1 being highest importance), then comes month, then year. Sample period is May 1990 through May 1993.

Family	Item	Phen	Sep-Nov (border)	Dec-Feb (lean)	Mar- May (lean / border)	Jun- Aug (plenty)
Anacardiaceae	<i>Dracontomelon dao</i>	A	M3S91, F1S91, F4S92		F5My90, F5A91, F5Mr92, M4Mr92	F2A90, M4A90, F2Jn90, F2Jn91, M3Jn91, F3Jy91, M5Jy91, F3A91, F3Jy92
	<i>Semecarpus papuanus?</i>	B				M4Jn90
Apocynaceae	<i>Cerbera floribunda</i>	A	M4S90, M2O90, M4O91,	M3D91		

			M2O92			
Arecaeae	<i>Calyptrocalyx</i> sp. 1	C			F5Mr91, M5Mr91, M3Mr92, M4Mr93	
	Unknown sp. 1	C		F3J91, F5F91, F5F93	F4My90, F4My91, F5A92	F4Jn90
	Unknown sp. 3	C		F5D91, F5J91, F1F91,	F1Mr91, M2Mr91, F1A91, M4A91, F2Mr92, M2Mr92, F2Mr93, M5Mr93	
Clusiaceae	<i>Calophyllum</i> cf. <i>goniocarpum</i>	C	F5O90			
	<i>Calophyllum laticostratum</i>	OY	F5S90			
	<i>Garcinia</i> cf. <i>assugu</i>	C	M5S92, M3N92, F5N92			
	<i>Garcinia celebica</i>	A	M3N91	M5D91		
	<i>Garcinia latissima</i>	C	M3S90, M1O90, M1S92, M4N92	M2D9, F4D91, M1J91, M1F91, F4F91, M1J93	M4My90, M1Mr91, F3Mr91, M1A91, M3A92, M5My92, M2Mr93, M5My93, F4My93	M3A90, M2Jn92, M2Jy92, M2A92
	<i>Garcinia</i> sp. 1 cf. <i>maluensis</i>	C		M3F93		
	<i>Garcinia</i> sp. 2	OY	M1S91, F5S91, M5N91			M3A91
	<i>Mammea grandifolia</i>	B				M2Jn90, M2Jy90, F5Jy90, M5Jn92, M4A92
Combretaceae	<i>Terminalia complanata</i>	A	F3S91		M3My90, F2My90, M1My91, F2My91, M1Mr92, F3Mr92, M1A92, F2A92, M2My92, F2My92,	M5Jn90, F1Jn90, F2Jy90, M1Jn91, F1Jn91, M1Jy91, F1Jy91, F2A91

					F4Mr93	
	<i>Terminalia impediens?</i>	A	M4S91		M5My90	M5Jy90, F4Jy90, M1A91, M3A92, F5A92
Cunoniaceae	<i>Schizomeria</i> sp. 1	A				M5A91, F4A91
Elaeocarpaceae	<i>Elaeocarpus nouhuysii?</i>	B		M2J93		
	<i>Elaeocarpus</i> sp. 5 cf. <i>sepicanus</i>	C	F3O92, F4N92			
	<i>Elaeocarpus sphaericus</i>	C	M1N92, F2N92	F2J93		
	<i>Elaeocarpus</i> sp. 2	A	F3O91, F3N91, M4S92, F2S92, M5O92, F4O92	F2D91		
Gnetaceae	<i>Gnetum</i> sp. 1	B	M5O90			
Lauraceae	<i>Cryptocarya</i> sp. 2	B				M3Jn90, F5Jn90, M4Jy90, F3Jy90, M3Jn92, F2Jn92, M1Jy92, F1Jy92, M1A92, F2A92
	<i>Endiandra</i> sp. 2	A			M2My90, M1Jn90, M4A92, M4My92	M4Jn91, M1Jn92, M4Jy92
	<i>Endiandra</i> sp. 5	A				M1Jy90, F1Jy90, M4Jn92, F1Jn92
	<i>Litsea</i> sp. 1	A				F3Jn90, M5Jy92, F2Jy92
Loganiaceae	<i>Neubergia corynocarpa</i> ssp. 2	C	M5S91		M3A91	M4A91
Magnoliaceae	<i>Elmerillia tsiampacca</i>	A			F3My90, F4My92, M1My93, F1My93	
Meliaceae	<i>Aglaiia mackiana</i>	B				M3Jy90, M5A92
	<i>Aglaiia</i> sp. 3	A				F5Jn92
Menispermaceae	<i>Chlaenandra ovata</i>	A	M3O92, F5O92			
Moraceae	<i>Artocarpus</i> sp. 1	A				M4Jy91
	<i>Ficus</i> spp.	C	F4O91,	M5F91, M5J93, M1F93,	M1My90, F1My90, M2A91,	M5Jn91, F4Jn91, M2Jy91,

			M5N92	F3F93	F4A91, M2My91, F5My91, M1Mr93, F3Mr93	F5Jy91
Myrtaceae	<i>Syzygium</i> sp. 2	A	F2S90, F2O90		F3My91, M2A92, F1A92, M1My92, F1My92	F3Jn91
	<i>Syzygium</i> sp. 3	C	M2S92, M1O92	M5J91	M4My91	M2Jn91, M3Jy91
	<i>Syzygium</i> sp. 7	A			M3My92	
Pandanaceae	<i>Pandanus papuanus</i>	C			M4Mr91, M3My91, M3Mr93	
	<i>Pandanus penicillatum</i>	C	M2S91, M2O91, M1N91, F4N91	M4D91, M4J91, M3F91, M4J93, M5F93	M5My91, M5A92	M2A90, M2A91
	<i>Pandanus limbatus</i>	C			M4My93, F5My93	M3Jy92, F4Jy92
	<i>Pandanus</i> sp. 3	A		F3D91	M5A91, F3A91, F3My92, F5Mr93	F2Jy91, F1A91, F3Jn92
	<i>Pandanus</i> sp. 5	C	M5S90, F3S90, M3O90, F1O90, F4S91, M1O91, F2O91, M2N91, F1N91, M3S92, F1S92, M4O92, F1O92	M1D91, F1D91, M3J91, F1J91, F3J93, F4F93	M3Mr91, F2Mr91	F4A90
Proteaceae	<i>Helicia</i> sp. 1	A	M3O91, F5O91, M4N91, F5N91			
Rosaceae	<i>Prunus</i> sp. 1	B	M2S90, F1S90			M5A90, F1A90, F4A92
	<i>Prunus</i> sp. 2	A	M1S90, F4S90, M4O90, F4O90, M2N92			M1A90, F3A90
	Unknown sp. 1	OY	F3N92	F1J93	M2My93,	

					F3My93	
Rubiaceae	<i>Psychotria</i> sp. 1				F4Mr92	
Sapotaceae	<i>Burckella</i> sp. 1	OY		M2J91, F2J91, M2F91, F3F91		
	<i>Payena</i> sp. 1	C		F1D90		
Unknown	Catalog DW166	A	F3O90			
	Catalog DW176	C		M4F91		
	Catalog DW890	OY	M5O91			
	Catalog DW1146	OY				F3A92
	Catalog DW1159	OY				F5Jy92
	Catalog DW1189	OY	F5S92			
	Catalog DW1255	OY		M3J93, F5J93		
	Catalog DW1270	OY		M2F93, F1F93		
Non-Fruit	Bracket Fungi	C	F2S91, F1O91, F2N91, F3S92, F2O92, F1N92	F2D90, F4J91, F2F91, F4J93, F2F93	F4Mr91, F3A91, M5Mr92, F1Mr92, F3A92, F5My92, F1Mr93, M3My93, F2My93	F5A90, F5Jn91, F4Jy91, F5A91, F4Jn92, F1A92
	Pandanus flowers	OY			F1My91	
	Vegetation-- ferns, stems	C			F4A92	

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CHAPTER 12.

KEYSTONE FRUIT RESOURCES AND AUSTRALIA'S TROPICAL RAIN FORESTS

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Abstract. The keystone species concept has contributed greatly to our thinking about how communities are structured and to our approaches to the development of conservation strategies. While keystone species have been proposed for tropical rain forest systems, the extraordinary diversity and complexity of these systems suggests that their potential for harboring keystones will be small. In this chapter we ask whether particular species of fleshy fruited plants might play a keystone role in Australia's tropical rain forests. We use fruiting phenology survey data from a range of upland and highland sites to identify potential keystone taxa. We identified a number of traits that might make a species a keystone fruit resource. These include, the proportion of the total lean season fruit biomass produced, the proportion of the lean season months in which fruiting was recorded, the inter-annual reliability of lean-season fruiting, the proportion of sites in which the species was recorded, and the proportion of frugivores recorded eating the species. All species recorded during the surveys were scored according to these keystone traits. In total 197 species from 123 genera and 57 families were recorded from across the sites. Fruiting phenology was similar across all sites with a single peak and a single trough in fruit diversity and abundance. Only 11 species (6%) contributed significantly (>2.5%) to lean season (April – July) biomass. Just 11 species were recorded at more than half of the sites and only one was detected in all studies. The ideal keystone species would be all things to all frugivores in all places and at all times. No such species was identified in this study. Individual species' keystone score varied across keystone categories and across sites. Keystone scores increased with taxonomic level considered: genera and families that might rank as keystone taxa were among the most speciose. Our results suggest that the relative importance of any particular fleshy fruited species to the rain forest community is context dependent. Frugivores feeding in the canopy focus on different fruits to those on the ground, and, community structure determines a species' relative contribution in different places and at different times.

Key words: Australia, *Ficus*, frugivory, fruiting phenology, keystone species concept, rainforest.

INTRODUCTION

Fleshy fruited, animal-dispersed plants are a striking feature of tropical humid forests throughout the world, often representing a majority of tree species in rain forest communities (Foster & Janson, 1982; Hilty, 1980; Webb & Tracey, 1981). As the chapters in this volume demonstrate, the dominance of these plants and their high levels of fruit production are reflected in diverse frugivore communities reliant on the fruits produced (Gautier-Hion, 1985; Peres, 2000; Snow, 1981; Terborgh, 1986). Despite their apparent richness in terms of both species and productivity, evidence from tropical rain forests around the world point to these ecosystems as being highly seasonal in many respects, including their levels of fruit production (Crome, 1975; Foster, 1982; Gautier-Hion & Michaloud, 1989; Leighton & Leighton, 1983; Terborgh, 1986; Wallace & Painter, 2002). In addition to seasonal fluctuations, long-term studies point to dramatic multi-year fluctuations in fruit production associated with large-scale weather patterns, e.g. El Niño, which negatively impact frugivore population dynamics on longer time scales (Foster, 1982; Wright et al., 1999). Understanding the consequences of these fluctuations for rain forest frugivore guilds, whether from a theoretical or an applied perspective, requires an understanding of the variation and importance of particular fruit resources in these interactions.

A critical concept in guiding thinking about the role of particular species or taxa in ecosystem dynamics over the last few decades has been the keystone species concept. The keystone species concept was first articulated and defined by Paine, (1966, 1969) with respect to predatory species, specifically those that preferentially consumed and limited the populations of species that would otherwise have dominated their ecosystems. The concept has subsequently been applied to a variety of roles and interactions in all the major ecosystems of the world (Power et al., 1996). Recent definitions identify two characteristics of keystone species, without limiting the manner in which their impacts are felt within communities (Power et al., 1996); keystone species are those which 1) have a large impact on a community or ecosystem, and 2) whose impact is disproportionately large relative to their abundance within that community. Despite criticism of the concept's broad definition, loose application, and the rush to apply it to management, largely in the absence of empirical evidence (Hurlbert, 1998; Mills et al., 1993; Simberloff, 1991), the keystone species concept has remained popular and influential in both ecological and management circles. In ecology the concept has focused attention on the control of ecosystem structure and variation in the strength of interaction between species in food webs, e.g. Berlow (1999), and Ernest & Brown (2001). In conservation biology the concept demands recognition of the disproportionate impacts individual species might have within ecosystems (Paine, 1995; Power et al., 1996). While identification and protection of keystones is seen as a potential means of managing for the protection of many species (Mills et al., 1993; Simberloff, 1998) but also for the management of ecosystem function and resilience more generally (Walker, 1995). In tropical rain forests, particular fruit taxa and fruit-frugivore mutualisms

have been described as keystone and this trait has been linked to conservation and management efforts (Leighton & Leighton, 1983; Mills et al., 1993; Terborgh, 1986; Wallace and Painter, 2001).

The suggestion that tropical rain forests with their extraordinary diversity and complexity should to a large extent be structured by just a handful of “keystone” species is in many ways a surprising one. The sheer weight of plant diversity encountered in these forests automatically means most species have a relative abundance that would categorise them as rare and, a priori, relegates their influence on ecosystem processes to that of a relatively minor one. Such high levels of diversity should also result in similarly high levels of functional redundancy (Lawton & Brown, 1993; Walker, 1992) and consequent ecosystem resilience in the face of perturbation (Walker, 1995). This redundancy would be expected to mitigate against the existence of keystone species, particularly in frugivore-fruiting plant mutualistic systems, which potentially include a majority of the vertebrate and woody plant species in most rain forest communities.

Despite these considerations, a number of authors have argued that particular fleshy fruited species or higher taxa are rain forest keystone fruit resources. Examples include figs (Kinnaird & O’Brien, this volume; Leighton and Leighton, 1983; Terborgh, 1986), palms (Terborgh, 1986) and a variety of individual plant species (other chapters in this volume; reviewed in Peres, 2000). These suggested keystone examples have been proposed on a variety of grounds, including 1) contributing significantly to total fruit production or the diets of frugivores generally during the year, 2) contributing significantly to total fruit production or the diets of frugivores during periods of resource scarcity, or 3) providing a reliable, if not abundant, resource during times of paucity (Peres, 2000). However, the generality of the “keystoneness” of some of these taxa must be viewed with some suspicion as many of the studies consider only a single site and just one or several seasons. Even very simple fruit-frugivore systems show enormous variation over a variety of time-scales (Herrera, 1998) and fruit production in rain forests is no different (Wright et al., 1999). It is not unreasonable to expect that similar geographical variation also occurs. Indeed, the keystoneness of even one of the most widely accepted rain forest examples, *Ficus*, appears to be context dependent with variation in its keystoneness identified at pan-tropical, regional and landscape scales (Gautier-Hion & Michaloud, 1989; Kinnaird & O’Brien, this volume; Peres, 2000; Shanahan et al., 2000).

In this paper we ask whether particular species of fleshy fruited plants might play a keystone role in Australia’s tropical rain forests. We examine data on fruiting phenology from upland and highland tropical Australian rain forests. We then use this data to identify the fruiting taxa which at a regional scale appear most likely to sustain the frugivore community during times of resource stress. We consider whether any of the species identified might be considered “keystone” resources or whether they are better identified simply as “key” or critical resources and we consider the utility of the keystone concept in ecosystems as complex as tropical rain forests.

At the outset we suggest a number of ways in which a plant taxon might become a “key” resource. These include fruiting during the lean season, doing so consistently across years and survey locations, contributing significantly to the lean season fruit biomass, and providing a resource that is utilised by a wide range of the frugivore community. Because frugivores differ in their ability to access resources we consider these attributes for the ground and for the canopy separately as well as in combination.

METHODS

Study Area

The study sites are situated in the Wet Tropics region of Australia, on the east coast of northern Queensland. (Figure 1). The region consists of narrow coastal plains flanked by rugged mountains (to 1622 m) with extensive upland areas gradually sloping down to the west. The region has a tropical climate with mean annual rainfall ranging between 1200 mm to over 8000 mm on the higher coastal ranges. Throughout the region, rainfall is strongly seasonal with over 70% occurring in the months of December to March (Figure 2).

Vegetation

The vegetation of the wet tropics region is broadly composed of closed canopy rain forest and open Eucalyptus woodlands and forests. Continuous areas of rain forest account for approximately 6300 km² of the region (Tracey, 1982) and are the focus of this study. The rain forests are found in a largely continuous strip in the wetter and mountainous areas where the rainfall exceeds 1500 mm (Figure 1) (Beadle, 1981). Approximately three quarters of the pre-European rain forest cover remains, with clearing concentrated mostly on the rich soils of the coastal lowlands and tablelands (Winter et al., 1987). Dominant woody plant families in North Queensland rain forests canopies are Myrtaceae, Lauraceae, Proteaceae, Elaeocarpaceae and Rutaceae, (Hyland et al., 2003). Fleshy fruited species are particularly abundant with 80-90% of tree species, sometimes as many as 95%, in a plot producing, vertebrate dispersed fruit (Webb and Tracey, 1981; Hyland et al., 2003).

Fauna

The composition of the rain forest fauna differs markedly from those of much of the Pale- and Neotropics in that frugivores represent a relatively small proportion of the vertebrate community. Of approximately 130 rain forest bird species and 89 mammal species we consider only 45 to be regularly frugivorous or granivorous. This is in stark contrast with other rain forests where frugivores may comprise the greater proportion and biomass of the vertebrates (Gautier-Hion et al., 1985; Peres, 2000; Terborgh, 1983).

Description of sites and survey methods

In this study we examine data derived from five separate fruit phenology studies from the wet tropics region. These studies were conducted in different areas (Figure 1), in different years and for different purposes. Three were located on the Atherton Tablelands (Dennis, 1997; Westcott & Bradford, unpubl.; Westcott, Bradford & Dennis, unpubl), one on the Paluma Range (Moore, 1991) and one on the Windsor Tablelands (F. Crome, data held by CSIRO), (Figure 1). Each study was conducted in upland and highland rain forests between 700 and 1200 m in altitude. All study sites had some previous history of selective logging, up to 30 years previously in all but that of the Crome et al. study where no logging had occurred. Because the studies were all conducted independently the methods and data collected vary slightly. The differences are outlined below.

In the Windsor Tableland survey phenology data was collected quarterly from March 1983 to December 1986 from all trees greater than 10 cm diameter at breast height in 54 circular plots, each plot 25 m in diameter. The canopy of each tree was assessed for ripe fruit and the species recorded.

The Paluma Range survey was undertaken as part of a study by Moore (1991). Phenology data was collected between June 1987 and December 1989. Six transects each 300 m by 2 m were assessed every month and for each fruit fall the fruit species and fruit abundance on the ground was recorded.

In the "Hypsi" study, Dennis, (1997) surveyed an area on the eastern edge of the Atherton Tablelands monthly from May 1990 to December 1992. Seven 300 m x 2 m transects were walked in a previously logged forest within a single forest type. For each fruit fall the fruit species and fruit abundance on the ground was recorded.

The Cassowary survey (Westcott & Bradford, unpubl.), was undertaken from February 1998 to May 2000 on the eastern Atherton Tablelands. Each month approximately 10 kilometres of roads, old logging tracks and walking tracks were walked for the purpose of collecting fresh cassowary dung. All fruit falls encountered were recorded and the species identified.

MGB's survey (Westcott, Bradford & Dennis, unpubl.), was undertaken from July 2000 to September 2002 at sites spread across the Atherton Tablelands. Each month, 12, 250 m x 5 m transects were walked in forest over five forest types and three geological types. Fruit abundance was assessed on the ground and in the canopy. The ground survey consisted of recording the species and abundance of fruit encountered on the transects. The canopy survey consisted of estimating the

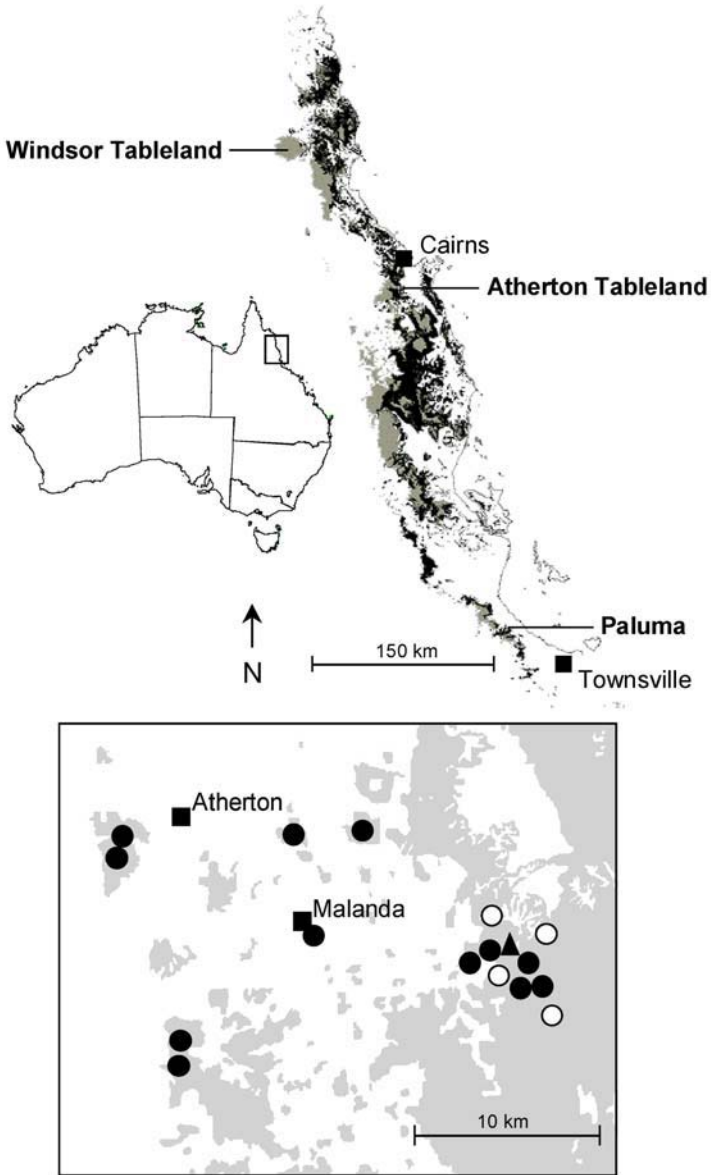


Figure 1. Map of the Wet Tropics Region of Australia showing the location of the study sites. Shaded areas represent closed forest. Inset, detail of the distribution of sites on the Atherton Tableland. Shaded circles = MGB sites, unshaded circles = cassowary sites, and triangle = Hypsi site.

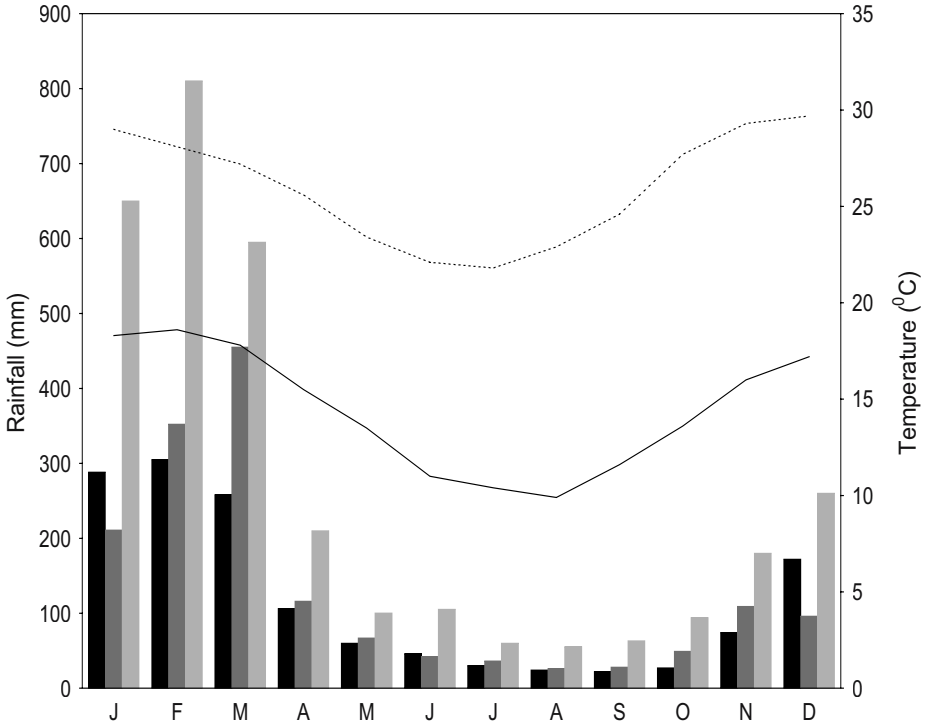


Figure 2. Temperature and rainfall data from upland and highland areas of the Wet Tropics Region. Mean monthly rainfall (columns) for Atherton, 72 year mean, (black), Windsor Tableland, six year mean, (dark grey) and Paluma township, 32 year mean, (light grey). Mean monthly daily minimum and maximum temperatures for Atherton (13 year mean) (Anon. 1990).

abundance of ripe fruit present in the entire crown of all trees, shrubs, vines and epiphytes whose foliage overhung the transect. Species was recorded and ripe crop size was estimated using Connell and Green's, (2000) approximately logarithmic scale: 0 fruit = 0, <10 fruit = 1, 10 - 100 = 2, 100 - 1000 = 3, 1000 - 10 000 = 4, >=10 000 = 5. The score was applied to the entire plant independent of plant size.

Analyses

The differences in data collected and in sampling frequency place limits on the degree to which the data from the different studies can be combined. In the following analyses and discussion all analyses of species richness are conducted

using the data from Moore, (1991), Dennis, (1997), the Cassowary surveys and MGB's surveys. These four studies provide a picture of fruiting phenology from the Central to the Southern Wet Tropics (Figure 1). The Windsor Tableland quarterly species richness data is used only to provide a general comparison from a northern site. Analyses of the biomass of fruit fall rely on the data from only three of the studies: Moore (1991), Dennis (1997) and MGB's surveys. Again, these studies provide a picture of the central to southern part of the region. Analyses of canopy biomass were derived from the data collected on the Atherton Tablelands in MGB's surveys alone.

Biomass was estimated using abundance records from the surveys and mean fruit masses, measured for all but 33 (15%) species. For these 33 species fruit mass was estimated by regressing mean fruit mass on mean fruit volume for 107 species for which we had length, width, depth and mass data. Volume was calculated as for an ellipsoid:

$$(4/3)\pi((\text{length}/2)(\text{width}/2)(\text{depth}/2)).$$

For spherical fruits length was substituted for width and depth, for cylindrical fruits width was substituted for depth. To increase the accuracy of the estimation across all fruit volumes three separate regression equations were derived for different parts of the fruit size range. Biomass was then calculated as (the number of fruits of a species on the transect) x (the mean mass of 10– 50 fruits) and then converted to kg/ha to allow direct comparisons between studies. In some instances we examine the differences in phenology for large, medium and small fruit independently, since fruit size can be an important determinant of the frugivores able to use a fruit. We define large fruit as those > 20ml, medium as >4ml and <20ml, and small fruit as <4ml.

To assess the keystone-ness of a taxon we examined and scored the performance of each species in the following ways:

1) the proportion of the total lean season fruit biomass produced by the taxon. This is a measure of the contribution to available resources provided by the taxon.

2) the proportion of the four lean season months in which the taxon was recorded fruiting. This provides a measure of the temporal extent of fruiting during the lean season in which a taxon provided resources. For example, all species that were recorded fruiting in May and no other month would score 0.25 regardless of how many years they were recorded fruiting in May.

3) the inter-annual reliability of lean-season fruiting, scored as the proportion of all lean-season monthly surveys in which a taxon was recorded. This provides an indication of the probability that a fruit could be encountered in any month's surveys across all studies and years.

4) the geographic scale of contribution, scored as the proportion of studies in which the taxon was recorded, and,

5) the consumer specificity, scored as the proportion of frugivores recorded eating the taxon.

As indicated in Table 1, we sub-divided some of these categories to distinguish between keystone-ness in the canopy and on the ground.

The scores for each species, genus, and family were then calculated for the following classes of keystone-ness: 1) lean season keystone – ground only, 2) lean season keystone – canopy only, and 3) lean-season keystone, both canopy and ground combined. Because it is difficult a priori to assess the relative importance of any one scoring category, we assigned equal weighting to each. To achieve this we allowed a maximum score of 1.00 for each data category: contribution to biomass, temporal availability, geographic availability, and consumer specificity. In addition, the two temporal availability scores, i.e. proportion of lean season months and inter-annual reliability of fruiting during the lean season, were summed and divided by two. The overall score for canopy was calculated as:

$(\text{relative contribution to biomass} + (\text{proportion of months} + \text{reliability})/2 + \text{consumer specificity})/3 * 100.$

The overall ground score was calculated as:

$(\text{relative contribution to biomass} + (\text{proportion of months} + \text{reliability})/2 + \text{geographic scale} + \text{consumer specificity})/4 * 100.$

The total overall score was the combination of these:

$((\text{canopy} + \text{ground biomass contribution})/2 + (\text{ground and canopy temporal measures})/4 + \text{geographic scale} + \text{consumer specificity})/4 * 100.$

RESULTS

Fruit Mass Estimation

Across the full fruit volume range a single linear regression explained 94% of the variation in mass ($F_{(1, 105)}=1636, p<0.0001, r^2=0.94$). However, while the overall fit of this regression was good, it substantially over or under-estimated in some parts of the fruit volume range. To overcome this and to improve the fit across the entire fruit size range, separate regression equations were fitted in different parts of the range: fruit $\leq 1\text{ml}$: mass = $0.017 + 1.051 \text{ volume}$, $F_{(1,35)}=85.13, p<0.0001, r^2=0.92$;

fruit $1 < \text{ml} \leq 20 \text{ml}$: $\text{mass} = 0.302 + 0.944 \text{volume}$, $F_{(1,38)}=408.12$, $p < 0.0001$, $r^2=0.70$; fruit $20 < \text{ml}$, $\text{mass} = 3.226 + 0.806 \text{volume}$, $F_{(1,38)}=408.12$, $p < 0.0001$, $r^2=0.91$. Using these regressions there was no detectable difference between the estimated and measured masses of fruits for the 107 species for which measured weights were available (paired t-test, $t=-0.56$, $df=106$, $p=0.57$). Combined with the high mean:variance ratios of measured fruit masses, this indicates that our estimated fruit sizes are reasonable.

Fruiting Phenology and Productivity

Across the studies 197 species from 123 genera and 57 families were recorded with 78 (range 59-100) species, 53 (range 41-64) genera and 33 (range 24-45) families recorded in the average month (Figure 3). Ninety three (76%) of 123 genera and 25 (44%) of 57 families were represented by just a single species. Six genera were represented by five or more species: *Endiandra* (13), *Syzygium* (11), *Ficus* (10), *Elaeocarpus* (9), *Cryptocarya* (9), and *Acronychia* (5). Seven families were represented by 10 or more species: Lauraceae (30), Myrtaceae (16), Elaeocarpaceae (15), Proteaceae (12), Rutaceae and Sapindaceae (11), and Moraceae (10).

There were substantial differences between the areas in the species richness of fruiting trees, though it must be remembered that the studies differed in both the area (range 3600 –26 507 m²) and number of years sampled (range 2-4). The Windsor Tableland study recorded 47 species, 36 genera and 22 families. Eighteen, ± 1.06 S.E., species fruited in an average month. The three Atherton Tableland studies combined recorded 139 species, 93 genera and 48 families. There were 34.08 ± 2.85 S.E. species fruiting in any given month. At Paluma Range 38 species, 31 genera and 23 families were recorded, 6.48 ± 7.2 SE in an average month.

Seasonal Patterns of Species Richness

On the ground, the pattern of fruiting richness was highly seasonal with a peak in richness occurring between the middle of the dry season to the early wet season, roughly October to January (Figure 3). Lowest fruit richness occurred between April and July, a cool to cold time of the year dominated by consistent but light rain of orographic origin (Figure 1.). The annual cycle in species richness was closely tracked in terms of richness at the genus and family level (Figure 3). The average species fruited for 4.22, ± 0.21 S.E., months in a year, while genera and families had representative species fruiting in 4.73, ± 0.30 S.E., and 6.43, ± 0.50 S.E., months respectively. Across the studies in an average month 20.45 ± 3.82 S.E. species were recorded as fruiting.

The richness of species fruiting in the canopy followed the same general annual cycle as that on the ground (Figure 3). There was an extended period of high species richness from July to November, or in the Windsor Tableland study, during the September quarter. The highest species richness in the canopy was recorded in August rather than December, as occurred on the ground. While fewer species were

recorded in the canopy, the magnitude of annual variation was similar to that on the ground.

Productivity

Productivity, like species richness, was seasonal (Figure 4). Both in the canopy and on the ground there was a distinct, prolonged low in productivity roughly from February through to July. Despite the differences in the study sites and the fact that there was no temporal overlap between studies, the pattern of productivity on the ground remained remarkably consistent (Figure 4). Across the studies in the average month 10.7 kg/ha (± 9.4 SD) of fruit was encountered in the ground surveys. In the canopy study an average of 111 kg/ha (± 38 S.D) was recorded. Total biomass of fruit in the canopy peaked early, in August, and then declined slowly through the dry into the beginning of the wet season, in January. In contrast, biomass on the ground increased through the dry season and peaked in December.

On the ground large, medium, and small fruits showed the same general annual pattern of productivity though large fruit biomass increased more rapidly and remained at high levels for three months whereas small fruits only remained at high levels for one month and medium fruit for two. (Figure 5). In the canopy, large and small fruits showed similar annual patterns of biomass, increasing from June through until they reach their peak in December. Medium fruits peaked in biomass early in the dry season, in August, and then declined through until April and May.

Identifying Keystone Fruiting Resources

Species relative abundance

On our transects the average species was represented by 2.9 individuals/ha, (± 6.8 S.D., range 1 - 71). The species with the greatest average density was the vine *Pothos longipes* Schott (Araceae) with an estimated density of 71 stems/ha. The species scoring above 40% in the overall scores (Table 1 – total score) with the highest density was *Syzygium gustavioides* (F.M.Bailey) B.Hyland (Myrtaceae) with 9.3 individuals/ha, next was *Ficus pleurocarpa* F.Muell. (Moraceae) with 5 individuals/ha. With a forest-wide average of 837 stems/ha >10 cm DBH in these forest types (CSIRO, unpubl. data) it would seem that none of the potential keystones we considered are dominant within the ecosystem.

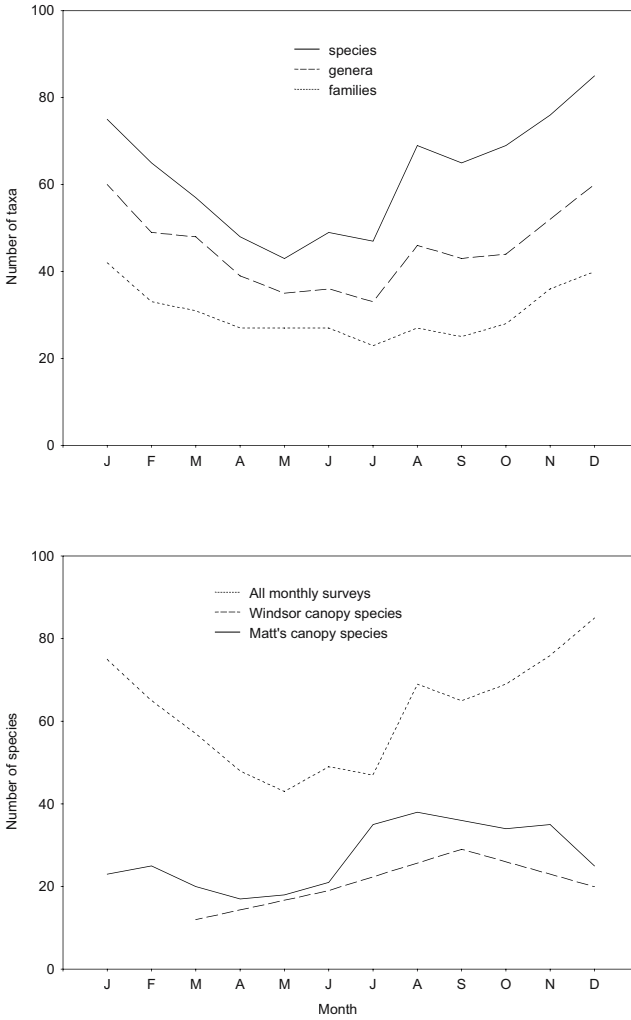


Figure 3. Annual cycle of fruiting richness a) on the ground across all transects except WindsorTableland, showing number of species, genera and families observed, b) in the canopy at WindsorTableland and the Atherton Tableland versus all sites on the ground.

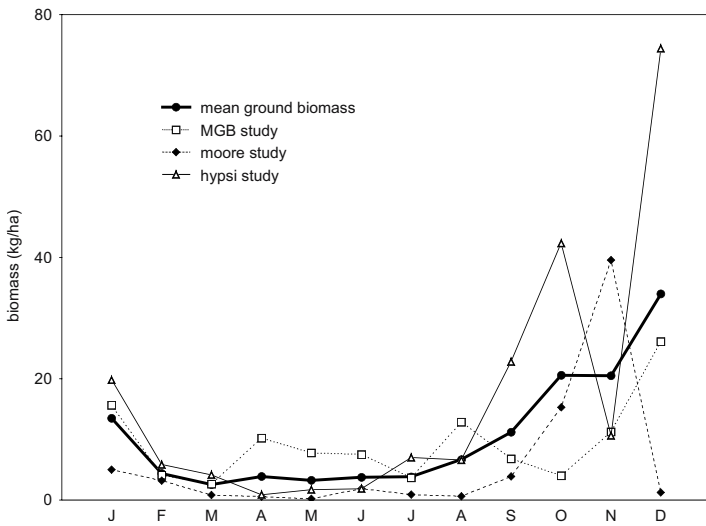
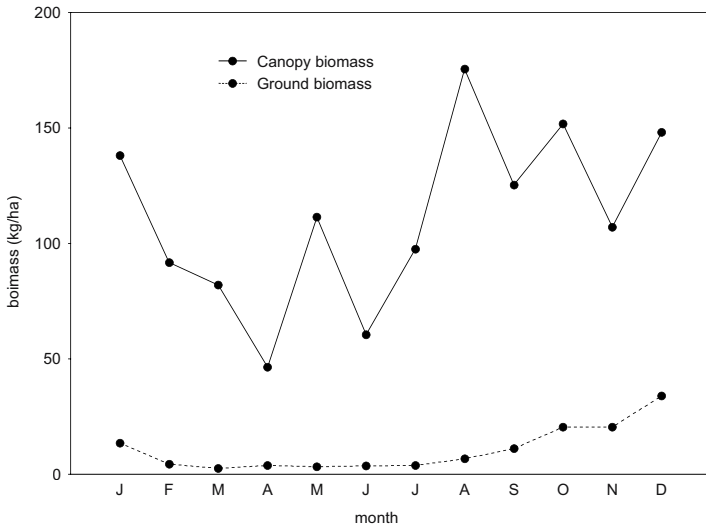


Figure 4. Comparison of annual patterns of productivity in the canopy and on the ground. Canopy data comes from MGB's surveys on the Atherton Tableland while the ground data comes from the three studies where biomass could be calculated.

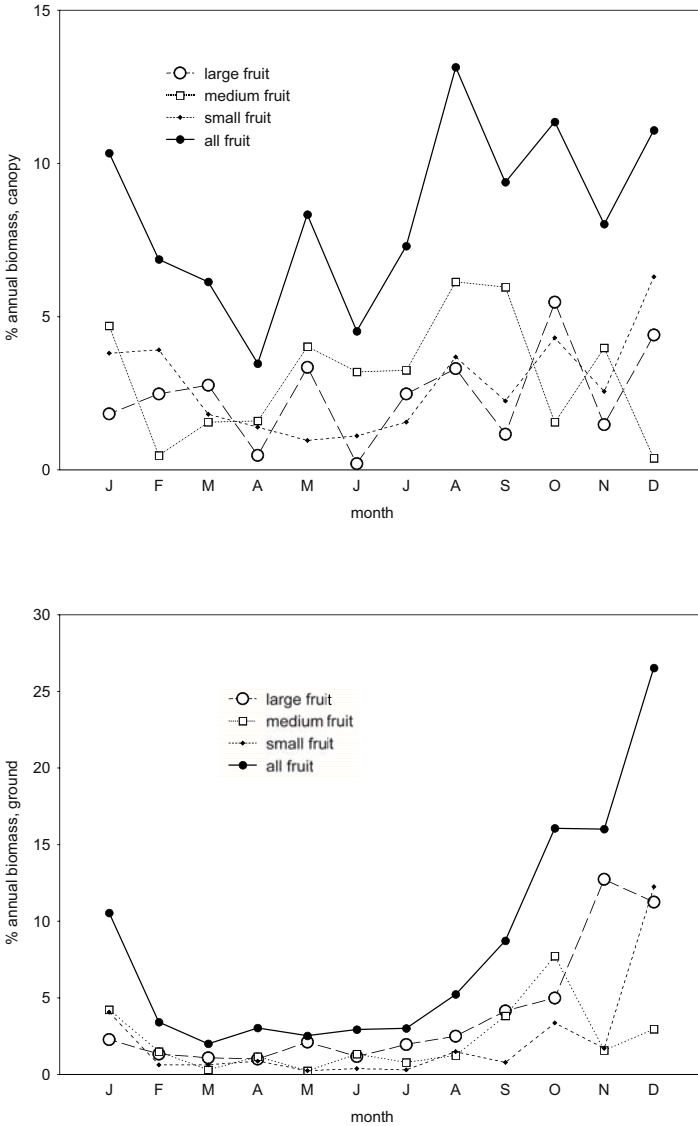


Figure 5. Contributions of fruits of different size to annual patterns of productivity. Small fruits are those with a volume <4ml, medium fruits are 4ml > volume < 20ml, large fruits are those with a volume > 20ml.

Taxa Fruiting During Resource Lows

While a decline in fruit resources between February and July is obvious from both the ground and canopy data in terms of fruit diversity and biomass (Figure 3), we define the lean season as comprising only the last four months of this period for the following reasons. In February and March frugivores are coming out of a period of plenty with good reserves and in a relatively benign climate. By April fruit availability and fat reserves are lower, the weather is wet and it is the coldest time of the year. That this is the hardest time of the year for frugivores is suggested by anecdotal evidence on cassowary rescue and intervention (P. Latch, Queensland Parks and Wildlife Service) and from musky rat kangaroo, *Hypsiprimnodon muschatus*, mortality, condition and reproductive data (Dennis & Marsh, 1997).

Across the studies, 92 (47%) species, 64 (52%) genera, and 38 (67%) families fruited during the months April to July. Only nine (5%) species, six (5%) genera and two (4%) families fruited at no other time of the year. Species that fruited during the leanest months tended to have longer fruiting seasons ($\bar{x} = 5.6$ versus 2.2 months, $t=8.97$, $df=164$, $p<0.000$). The biomass of their crops, corrected for differences in season length, did not differ from those of species fruiting at other times of the year ($t=-0.64$, $df=164$, $p=0.5$).

Contribution to Lean Season Biomass

On the ground and across all studies 9 species (5%), 11 genera (9%), and 9 families (16%) contributed >2.5% of the recorded lean-season biomass and in doing so accounted for 67%, 82%, and 85% respectively of the recorded crop (Table 1. "canopy" & "ground" biomass). The average proportion of the overall biomass contributed by any particular taxon tended to be small: species, $\bar{x} = 0.006$ (± 0.02 S.D.), genus $\bar{x} = 0.009$ (± 0.04 S.D.), family $\bar{x} = 0.02$ (± 0.05 S.D.). Only *Cryptocarya angulata* C.T.White (Lauraceae) (18%), *Castanospermum australe* A.Cunn. & Fraser ex Hook. (Fabaceae) (12%) and *Syzygium gustaviodes* (10%) produced $\geq 10\%$ of the lean season biomass.

In the canopy 11 (11%) species contributed >2.5% to the lean season biomass, accounting for 84% of canopy fruit biomass recorded during this period. *Ficus pleurocarpa* F.Muell. (Moraceae) contributed the most with 18% followed by *Cryptocarya angulata* with 15%. All other species scored less than 10%. The average proportion of canopy biomass contributed by a taxon was small: species, $\bar{x} = 0.006$ (± 0.02 S.D.), genus $\bar{x} = 0.014$ (± 0.05 S.D.), family $\bar{x} = 0.02$ (± 0.06 S.D.). A comparison of the species contributing >2.5% of recorded lean season canopy biomass with those contributing >2.5% of ground lean season biomass at the same sites reveals only five of 5 species in common. These were *Cryptocarya angulata*, *Castanospermum australe*, *Syzygium gustaviodes*, *Cryptocarya oblata* F.M.Bailey (Lauraceae), and *Elaeocarpus grandis* F.Muell. (Elaeocarpaceae).

Reliability

In the canopy 11 species were recorded in more than 50% of the lean season monthly surveys, while on the ground 16 species scored more than 50% (Table 1 “surveys”). Six species, *Syzygium gustavioides*, *Cryptocarya angulata*, *Acronychia vestita* F.Muell. (Rutaceae), *Siphonodon membranaceus* F.M.Bailey (Celastraceae), *Endiandra sankeyana* F.M.Bailey (Lauraceae), and *Elaeocarpus grandis*, were more than 50% likely to be recorded in a lean season survey both on the ground and in the canopy. Twenty-six and 44 species fruited in 25% or more of all lean season surveys in the canopy and on the ground respectively.

Spatial Ubiquity

Surprisingly few species were recorded at more than half of the four sites in which monthly data was collected, n=11, with only one, *Halfordia kendack* (Montrouz.) Guillaumin (Rutaceae), being recorded at all four (Table 1. “sites”). Twelve genera were recorded at three of four sites with just three, *Dendrocnides*, *Gmelina* and *Opisthiolepis* being recorded at all four. Thirteen families were recorded at more than half of the four sites while six were recorded at all four. These six were Lauraceae, Rutaceae, Elaeocarpaceae, Rhamanaceae, Piperaceae, and Pittosporaceae. The average proportion of the four sites at which a species, genus or family was recorded during the lean season were 39, 50 and 56% respectively.

Consumer Specificity

To provide a measure of consumer specificity for each fruit species recorded on our transects we collated data on observations of frugivores feeding on particular fruit species (Table 1. “% consumers”). This data came from published observations, from unpublished observations of professional and amateur biologists, and from our own field work (Dennis & Westcott, in prep). In total 2295 unique frugivore species– fruit species interactions were used. Foraging observations were available for 167 species or 85% of the species recorded on the transects. The average species was recorded being fed upon by 4 frugivore species (range 0-24 species). Averages for genera and families were 6 (0-36) and 12 (0-36) respectively. The species fed upon by the most frugivores were *Ficus obliqua* G. Forst. (Moraceae) (24), *Polyscias elegans* (C.Moore & F.Muell.) Harms (Araliaceae) (22), *Polyscias murrayi* (F.Muell.) Harms (Araliaceae) (20), and *Alphitonia petriei* Braid & C.T.White (Rhamanaceae) (20). The genera with the greatest number of recorded frugivores were *Ficus* (36), *Polyscias* (30), and *Alphitonia* (22). The three highest ranked families were Moraceae (36), Araliaceae (31) and Lauraceae (31).

Table 1. Scores for species, genera and families with a total score greater than 40/100. Categories are explained in the methods.

Species	canopy %			ground %				% consumers	overall scores		
	biomass	Mos.	survey s	biomass	Mos.	surveys	sites		canopy	ground	total
<i>Cryptocarya angulata</i>	0.85	1.00	0.75	1.00	1.00	0.75	0.50	0.04	59	60	59
<i>Ficus pleurocarpa</i>	1.00	1.00	0.75	0.04	1.00	0.44	0.50	0.40	76	42	55
<i>Siphonodon membranaceus</i>	0.08	1.00	1.00	0.36	1.00	0.69	0.75	0.06	38	50	49
<i>Syzygium gustavioides</i>	0.44	0.75	0.63	0.57	1.00	1.00	0.50	0.04	39	53	47
<i>Halfordia kendack</i>	0.01	0.75	0.38	0.08	1.00	0.53	1.00	0.09	22	48	45
<i>Elaeocarpus grandis</i>	0.28	1.00	0.50	0.17	1.00	0.50	0.25	0.38	47	39	40
Genus											
<i>Ficus</i>	0.79	1.00	0.75	0.04	1.00	0.44	0.75	0.79	82	57	68
<i>Cryptocarya</i>	1.00	1.00	0.75	1.00	1.00	0.50	0.50	0.42	76	67	68
<i>Syzygium</i>	0.33	0.75	0.63	0.52	1.00	0.67	0.50	0.42	48	57	53
<i>Endiandra</i>	0.15	0.75	0.75	0.17	1.00	0.63	0.75	0.35	42	52	51
<i>Elaeocarpus</i>	0.41	1.00	0.63	0.20	1.00	0.35	0.50	0.44	55	45	50
<i>Acronychia</i>	0.02	0.75	0.63	0.03	1.00	0.54	0.75	0.33	35	47	46
<i>Alphitonia</i>	0.01	0.50	0.25	0.18	0.75	0.31	0.75	0.48	29	48	44
<i>Beilschmiedia</i>	0.06	0.50	0.38	0.20	1.00	0.50	0.75	0.25	25	49	43
<i>Siphonodon</i>	0.05	1.00	1.00	0.31	1.00	0.69	0.50	0.06	37	43	42
Family											
Lauraceae	1.00	1.00	1.00	1.00	1.00	0.58	1.00	0.67	89	86	89
Moraceae	0.64	1.00	0.75	0.03	1.00	0.44	0.75	0.81	78	58	67
Elaeocarpaceae	0.34	1.00	1.00	0.16	1.00	0.50	1.00	0.46	60	59	65
Rutaceae	0.02	1.00	1.00	0.20	1.00	0.58	1.00	0.56	53	64	64
Myrtaceae	0.29	0.75	0.75	0.37	1.00	0.63	0.75	0.58	54	63	61
Araliaceae	0.27	0.50	0.50	0.02	1.00	0.63	0.75	0.69	48	57	56
Rhamnaceae	0.01	0.75	0.25	0.13	1.00	0.21	1.00	0.50	34	56	53
Celastraceae	0.04	1.00	1.00	0.22	1.00	0.69	0.75	0.15	40	49	49
Piperaceae	0.00	0.25	0.00	0.03	1.00	0.54	1.00	0.33	15	53	45
Euphorbiaceae	0.05	0.75	0.13	0.04	1.00	0.50	0.50	0.58	36	47	43
Rubiaceae	0.01	1.00	1.00	0.00	0.50	0.25	0.50	0.44	48	33	41
Rosaceae	0.03	0.25	0.13	0.06	0.75	0.38	0.75	0.46	22	46	41

DISCUSSION

Phenology and Resource Bottlenecks

Fruiting phenology showed a clear and consistent pattern across all the studies. Fruit was most abundant and diverse through the dry and early wet seasons, roughly from October through January. Both biomass and diversity decreased through the wet season to a lean period between April and July. This general pattern was consistent across the studies despite their spread across the region, vegetation types, and years. That this is a period of resource scarcity for frugivores is confirmed by observations such as the departure of migratory species, reports of starving cassowaries to management agencies, and high levels of mortality and poor condition in monitored frugivore populations, e.g. (Dennis & Marsh, 1997). While the studies considered here demonstrate a consistent annual pattern of fruiting at mid to high elevations, Crome's (1975) coastal study indicates that the lean season may be earlier (Jan – May) in at least one coastal site, which displayed a season of abundance beginning in June/July, peaking in August and September and declining through to December.

While the same phenological patterns could be discerned in the canopy and on the ground there were also some differences. The canopy study identified many fewer species than did the ground studies overall. This is not surprising given that there were a greater number of ground studies and they encompassed a wider geographical spread. However, fewer fruit species were detected in the canopy than on the ground even in simultaneous surveys on the same transects. This difference is most likely due to the greater difficulty of detecting fruit in the canopy and to transport by animals and water onto the transect from elsewhere.

Species Contributions to Keystoneness

Only a small proportion of species contributed significantly to lean season biomass - just 11 and 10 species each contributed more than 2.5% to the canopy and ground biomass respectively. These individual species contributions could be very large. *Cryptocarya angulata*, for example, contributed 15% and 18% to available fruit biomass in the canopy and on the ground respectively. This is a surprising result as it suggests that despite the diversity of these forests, certain species do make a contribution to resource availability that far outstrips their abundance and makes the possibility of particular species acting in a keystone role all the more plausible.

What is perhaps even more intriguing is that there is only a weak relationship between a species' contribution to biomass in the canopy and its contribution to biomass on the ground. Just five of 15 species contributed more than 2.5% of the total biomass in both places. In the one study where these data were collected simultaneously there was a significant and positive relationship between canopy and ground biomass when all species are included ($r^2=0.44$, $F_{1,64}=31.71$, $p>0.001$). This

relationship, however, is driven almost entirely by just 3 species. When these species are excluded, contribution to canopy biomass does not explain a species contribution to ground biomass ($r^2=0.004$, $F_{1,61}=0.29$, $p=0.59$). *Ficus pleurocarpa* is an excellent example of such a pattern, providing 18% of the canopy biomass but only 1% of the ground biomass. Consequently, fruit species can serve canopy and terrestrial frugivores in very different ways, even at the same site. This differential in the kind of service provided is no doubt largely a function of removal rates in the canopy.

If species are to have a keystone role in the rain forests of a region then they might be expected to be widely distributed and therefore be recorded in studies from across the region. Just 11 (6%) species were recorded in more than half of the studies and only one, *Halfordia kendack*, was detected in all studies. This raises questions about the spatial generality of any keystone role for these species. Most identifications of keystone roles are performed at a local scale and then generalised to ecosystem and regional scales (reviewed in Peres, 2000). Though many of the species recorded in our study have a general distribution throughout the region (Hyland et al., 2003) combined with reasonable abundances where they do occur (CSIRO unpubl. data, this study), the failure to detect them in 50% and more of studies suggests that in complex ecosystems such as these, local distributions of particular species will be patchy, and, at the local scale of resolution particular species may often be unavailable to fulfill a potential keystone role. How this absence of a potential keystone resource impacts the frugivore community will be a function of the relative scales of frugivore movements and keystone dispersion within the local environment. For some frugivore species, e.g. musky rat kangaroo (Dennis, 1997), honeyeaters and bowerbirds (Westcott and Dennis, unpubl. data), these movement scales will potentially be smaller than the dispersion of the fruit species. In temperate systems where keystone roles have been shown using comparative or experimental studies (e.g. studies cited in Power et al., 1996; Berlow, 1999), communities are much simpler and suggested keystone species tend to be readily discernible at most spatial scales.

Assessing Keystone Scores

Translating our scores into an *a priori* decision about the keystone status of any single taxa without the benefit of corroborating field evidence on effects of the loss of particular species is a difficult task. We have arbitrarily chosen a cutoff score of 40, a score that was attained by just six species (Table 1). If considered in terms of their "client" frugivores these six fruits fall into two very distinct classes. *C. angulata*, *H. kendack*, and *F. pleurocarpa* all share characteristics that make them available to a wide range of frugivores and are potential keystones to the frugivore community generally. *C. angulata* appears only infrequently in our feeding database, due to a lack of sampling effort. The genus *Cryptocarya*, however, ranks 10th of 392 genera in terms of number of frugivore species recorded consuming it, 42% of all frugivores

(Dennis and Westcott, in prep.). Medium to small *Cryptocarya* species, like *C. angulata*, are recorded as being consumed by between 10 and 24 species, within the top 12% of 795 species scores (Dennis and Westcott, in prep.). Taken together this would suggest that *C. angulata* is fed upon by all but the smallest volant canopy frugivores. *H. kendack* is a small to medium sized fruit available to all but the smallest frugivores. *F. pleurocarpa* is fed on by the full range of frugivores both in the canopy and on the ground and ranks 8th of 795 species for which we have data in terms of the number of frugivores recorded consuming it (Dennis and Westcott, in prep.). Due to the softness of its flesh when ripe, it is available to even the smallest of frugivores. *Elaeocarpus grandis* differs slightly from the preceding species in that it is a medium to large fruit, $\bar{x} = 7.7$ gm, fed upon by nearly all medium to large frugivores.

The second class of species is comprised of *Siphonodon membranaceus* and *Syzygium gustavioides*. These are large fruits that are fed upon primarily by seed predators such as parrots in the canopy and rats on the ground. Both musky rat kangaroos, *Hypsiprimnodon moschatus*, and white-tailed rats, *Uromys caudimaculatus*, feed on the seed and tend to discard the flesh but often leave the seed only partially chewed and still viable (Dennis, 1997). White-tailed rats, other rodents, and parrots in the canopy feed on the seeds and occasionally the flesh of *S. membranaceum*. Cassowaries and musky rat-kangaroos occasionally feed on *S. membranaceum* flesh but only in small quantities and generally only during the lean season. The general availability and reliability of both these species across study areas and during the lean season suggests that they represent an important component of the diet of granivores during the lean months, although the biomass of *S. membranaceum* was relatively low. Whether this translates into a keystone role is uncertain.

Of course the ideal keystone species would be all things to all frugivores in all places and at all times. Examination of the scores of the top ranked species in Table 1 shows no such über-fruits; individual species perform variably across the different categories. For example, *F. pleurocarpa* was fed upon by a large number of frugivores, and provided a significant and reliable contribution in the canopy but not on the ground. *S. membranaceus* was reliable in terms of where and when it was found but made only a small contribution to biomass and was fed upon by only a small number of frugivores. This suggests that any keystone role played by a particular species will be one that is received by a select group of frugivores, e.g. granivorous frugivores in the case of *S. membranaceum*, or will be provided only in certain places or to species that can move at appropriate spatial scales, e.g. *F. pleurocarpa*.

A critical component of the definition of a keystone species is that its removal from the system would result in significant changes in the structure of that ecosystem. Such an effect would be most expected when resources are scarce, hence our concentration on lean season fruiting. Despite focusing on the lean season it seems unlikely that loss of the species that ranked most highly would radically alter the structure of the frugivore community. The loss of *C. angulata* and *F.*

pleurocarpa would represent an overall reduction in fruit biomass of 16 and 9% respectively and would impact across the frugivore spectrum. This might reduce populations of all frugivores but is unlikely to radically restructure the guild. Most other fruit species are characterised by one or more of the following: 1) low biomass input, 2) lack of temporal reliability, or 3) lack of geographic availability. This suggests that in many local communities within the Wet Tropics Region these species are already effectively absent and yet ecosystem collapse is not evident. Why isn't it? Probably the simplest explanation is that there are high levels of redundancy. Across the studies, ninety-four species were recorded fruiting during lean months, with 50 species potentially fruiting in an average lean season month. In addition, many frugivores, e.g. honeyeaters and flying-foxes, are able to switch dietary focus to include other, non-fruit resources. Combined with the departure of migratory species, the result is relatively less demand from the frugivore community as a whole.

Key Genera and Families?

While the keystone species concept is usually couched at the species level (Powers et al., 1996) it has been common in rain forest studies for keystones to be defined in terms of higher taxonomic levels (Terborgh, 1986; White et al., 1995), life-forms (Nadkarni, 1994) or even communities (Bond, 1993). In this study the genera and families that might rank as keystone taxa were all large. At the genus and the family level, taxon size explained 39 and 38% of the variation in overall keystone score (genus: $F_{1, 108}=70.35$, $p>0.001$; family, $F_{1,47}=28.82$, $p>0.001$). The genera that scored more than 50% represented the five largest genera of the 1085 plant genera of the Australian tropical rain forests (Hyland et al., 2003). The families that scored more than 50% were amongst the 35 largest of the 208 plant families of the region (Hyland et al., 2003). These results suggest that the numerical dominance of large taxa leads inevitably to their relatively high aggregate scores. Perhaps this is unsurprising but it highlights the contribution of speciose genera such as *Cryptocarya*, *Syzygium*, *Ficus*, *Endiandra* and *Elaeocarpus* and families such as the Myrtaceae, Lauraceae, Euphorbiaceae and Rubiaceae in these systems.

Summary

The search for clear, strong interactions between species has characterised much of the history of frugivory and seed dispersal research in tropical rain forests. The search for tight, reliable coevolutionary relationships between fruits and frugivores dissolved with the recognition that these relationships in general were loose and shifting alliances (Wheelwright, 1991; Howe, 1993). If in much simpler temperate ecosystems keystone-ness is recognized to be context dependent (Paine, 1995; Power et al., 1996), perhaps we should not be surprised if in tropical rain forests, replete with redundancy, the search for keystone fruit resources also boils down to a suite of

interactions that vary in strength across both spatial and temporal scales. While there may be circumstances where single species can be identified as playing keystone roles, the complexity of tropical forests, the huge variation in their community composition and in the relative productivity of particular species across even small spatial scales, mitigates against particular taxa playing identifiable keystone roles that can be generalised to larger spatial scales.

This portrayal could be interpreted as implying that in tropical forest ecosystems interactions between species are mostly weak. This is not our intention. Even if true, this does not necessarily imply that these weak interactions are not or cannot be important in different places or at times. In a review of published food-web studies Berlow, (1999) found that while the average reported interaction was weak, the variation inherent in these “weak” interactions was of the same magnitude as the strongest effects. Consequently, species whose average effect is weak may in certain contexts and times prove fundamental to sustaining community structure and frugivore populations. In our data set, *F. pleurocarpa* made a relatively low contribution to on-ground biomass but scored reasonably well in other on-ground keystone categories gaining 7th ranking overall. Yet Dennis, (1997) reported that in one particularly lean season on his study site *F. pleurocarpa* sustained the *H. moschatus* population, for which he considered it a keystone.

Have we identified a set, or even a single keystone fruit resource for Australia’s upland tropical rain forests? We suspect not. The data suggest that the best candidates for this status are *C. angulata* and *F. pleurocarpa*. However, despite their contributions to lean season fruit biomass these species, like most others, were effectively absent at some sites or in some years. While we feel that this makes it difficult for them to truly act as keystone species it certainly does not reduce their importance as a lean season resource, a result that can be used to advantage in planning rehabilitation and management strategies, especially for small and isolated reserves.

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