Mathematical Modeling I - preliminary

Hao Wang

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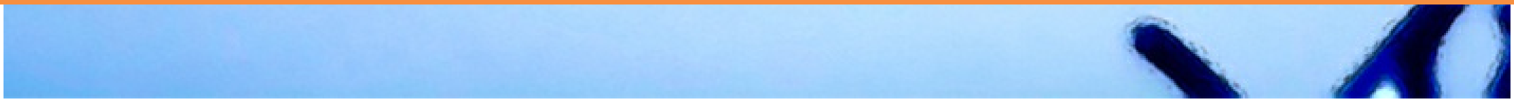

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Contents

Preface

Mathematical Modeling I – preliminary is designed for undergraduate students. Two other followup books, Mathematical Modeling II – advanced and Mathematical Modeling III – case studies in biology, will be published. II and III will be designed for both graduate students and undergraduate students. All the three books are independent and useful for study and application of mathematical modeling in any discipline.

1 Introduction

Mathematical models are of broad use in physics, life sciences, engineering, economics, management, social sciences, and many other disciplines. However, all mathematical models are "wrong", but some are useful to help us better understand real-world systems. Models should be made for specific goals with clear assumptions since they are only "valid" under certain conditions.

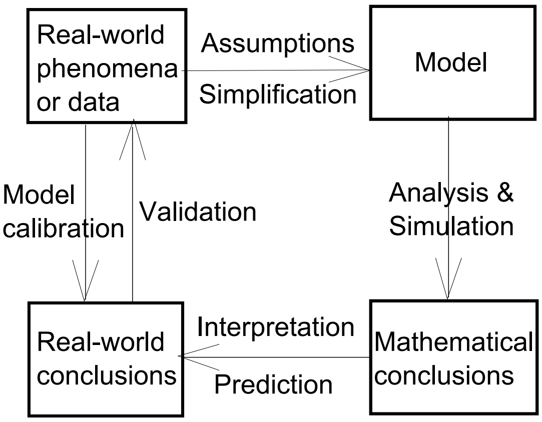


Figure 1: A flow chart of the modeling process

Modeling Process:

Step 1. Identify the problem with specific goals and questions

Step 2. Post assumptions unambiguously

Step 3. Define variables and construct the model

Step 4. Analyze and simulate the model

Step 5. Validate the model with real phenomena or empirical data

Step 6. Apply the model to make predictions

Step 7. Possibly calibrate and extend the model

We can always improve the model with more details, but meanwhile we want to keep the model as simple as possible such that we can obtain useful and in-depth results.

There have been many famous yet simple mathematical models in literature, such as the following ones:

- Newton's law $F = ma$, where F is force, m is mass, a is acceleration.
- Ohm's law $V = IR$, where V is voltage, I is current, R is resistance.
- Kepler's third law $T = cR^{3/2}$, where T is the orbital period of the planet, R is the mean distance from the planet to the sun.

- Einstein's relativity theory $E = Mc^2$, where E is energy, M is mass, c is light speed.
- Metabolic theory of ecology $B = B_0 M^{3/4}$, where B is organism metabolic rate, B_0 is a mass-independent normalization constant, M is organism mass.
- Logistic population model $\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$, where N is population size, r is the maximum per capita growth rate, K is carrying capacity.

2 Discrete-time models

2.1 Motivation

Discrete-time models are constructed to describe phenomenon in terms of fixed time steps. In general, we consider a sequence of quantities, $x_0, x_1, x_2, \ldots$, where x_i denotes the quantity after i time steps. If x_{n+1} depends only on x_n, a discrete-time (in abbreviation, discrete) model is expressed by

$$x_{n+1} = f(x_n), \quad n = 0, 1, 2, \ldots$$

with some initial condition x_0. This discrete model is called a difference equation.

This discrete model gives

$$\begin{array}{rcl} x_1 & = & f(x_0) \\ x_2 & = & f(x_1) = f(f(x_0)) = f^{[2]}(x_0) \\ x_3 & = & f(x_2) = f(f(x_1)) = f(f(f(x_0))) = f^{[3]}(x_0) \\ & \vdots & \end{array}$$

The resulting sequence $x_0, x_1, x_2, x_3, \ldots$ is called an orbit of the map f.

x_n in the discrete model can represent the population size of lemmings in month n, or the number of bacterial cells in a culture on day n, or the concentration of oxygen in the lung after the nth breath.

The difficulty is how choose the map f:

- Start with a knowledgable guess and necessary assumptions.
- Make adjustments to get a better model by comparing behavior of the current model to reality.
- A good model should be in close agreement with the real-world data.

2.2 An example – bacterial reproduction

Bacterial cells divide into more cells after one sampling time. The number of bacterial cells in the next measurement will be some multiple of the current number. We assume that this multiple is a constant over several sample times. Note that this assumption is obviously invalid for many sampling times due to resource and space limitations.

Denote B_n as the cell number observed at the nth sampling time, then the model can be written as

$$B_{n+1} = rB_n \quad \text{(Malthus model, 1798)}$$

where the constant r is called the growth rate.

Solution: Given the initial cell number B_0,

$$\begin{aligned} B_1 &= rB_0 \\ B_2 &= rB_1 = r^2 B_0 \\ B_3 &= rB_2 = r^3 B_0 \\ &\vdots \\ B_n &= r^n B_0 \end{aligned}$$

which is the solution of this discrete model.

In reality, the growth rate r usually depends on the cell number because of competition for resource and space. $r = r(B_n)$ is a decreasing function of B_n. The more general model than Malthus model is of the form

$$B_{n+1} = r(B_n)B_n.$$

For instance, Verhulst model assumes

$$r(B_n) = \frac{2}{1+\frac{B_n}{K}}$$

and thus the model becomes

$$B_{n+1} = \frac{2B_n}{1+\frac{B_n}{K}}.$$

The function $r(B_n)$ is a decreasing function of B_n with the maximum 2 occurring at $B_n = 0$. When $B_n = K$, $r(B_n) = 1$, one-half of its maximum.

Solution: Direct iteration does not work. However, if we introduce a new variable $R_n = 1/B_n$, then the sequence $R_0, R_1, R_2, \ldots$ satisfies the linear relationship

$$R_{n+1} = \frac{R_n}{2} + \frac{1}{2K}.$$

Hence,

$$\begin{aligned}
R_n &= \frac{R_{n-1}}{2} + \frac{1}{2K} \\
&= \frac{1}{2}\left(\frac{R_{n-2}}{2} + \frac{1}{2K}\right) + \frac{1}{2K} \\
&= \frac{R_{n-2}}{2^2} + \frac{1}{2K}\left(1+\frac{1}{2}\right) \\
&= \frac{1}{2^2}\left(\frac{R_{n-3}}{2} + \frac{1}{2K}\right) + \frac{1}{2K}\left(1+\frac{1}{2}\right) \\
&= \frac{R_{n-3}}{2^3} + \frac{1}{2K}\left(1+\frac{1}{2}+\frac{1}{2^2}\right) \\
&\vdots \\
&= \frac{R_0}{2^n} + \frac{1}{2K}\underbrace{\left(1+\frac{1}{2}+\cdots+\frac{1}{2^{n-1}}\right)}_{\text{a geometric series}} \\
&= \frac{R_0}{2^n} + \frac{1}{2K}\cdot\frac{1\cdot(1-(\frac{1}{2})^n)}{1-\frac{1}{2}} \\
&= \frac{R_0}{2^n} + \frac{1-(\frac{1}{2})^n}{K}.
\end{aligned}$$

Equivalently,

$$B_n = \frac{1}{\frac{1}{2^n B_0} + \frac{1-(\frac{1}{2})^n}{K}}.$$

The asymptotic behavior is

$$B_n \to K, \quad \text{as} \quad n \to \infty.$$

2.3 Solution and equilibrium of a discrete model

The solution of a linear discrete model $x_{n+1} = rx_n$ (r is a constant) is $x_n = r^n x_0$, $n = 0, 1, 2, 3, \ldots$, since $x_n = rx_{n-1} = r^2 x_{n-2} = \cdots = r^{n-1}x_1 = r^n x_0$.

The long-term behavior as $n \to \infty$ is given as follows:

If $r > 1$, $x_n = r^n x_0 \to \infty$ as $n \to \infty$.

If $r = 1$, $x_n = x_0 \to x_0$ as $n \to \infty$.

If $-1 < r < 1$, $x_n = r^n x_0 \to 0$ as $n \to \infty$.

If $r = -1$, $x_n = (-1)^n x_0 = \begin{cases} x_0, & n \quad \text{even}, \\ -x_0, & n \quad \text{odd}, \end{cases}$ and thus no convergence as $n \to \infty$.

If $r < -1$, $x_n = r^n x_0$, thus $|x_n| = |r|^n |x_0| \to \infty$ as $n \to \infty$, thus no convergence as $n \to \infty$. In addition, r^n is positive when n is even, negative when n is odd.

Now we start to discuss equilibrium or fixed point.

Definition 1 *A number x^* is called an equilibrium or fixed point of $x_{n+1} = f(x_n)$, if $x_n = x^*$ for all $n = 1, 2, 3, \ldots$ when $x_0 = x^*$. That is, $x_n = x^*$ is a constant solution to the discrete model.*

For the model $x_{n+1} = rx_n$, an equilibrium satisfies $x^* = rx^*$. If $r \neq 1$, $x^* = 0$ is the only equilibrium. If $r = 1$, every number is an equilibrium.

Now let's look at a slightly more complicated discrete model

$$x_{n+1} = rx_n + b,$$

where r and b are constants. An equilibrium x^* satisfies $x^* = rx^* + b$. If $r \neq 1$, $x^* = \frac{b}{1-r}$. If $r = 1$, $x^* = x^* + b \Rightarrow b = 0$, then there are two subcases: every number is an equilibrium if $b = 0$; no equilibrium exists if $b \neq 0$.

As a summary, results for equilibria are listed below:

- $x^* = \frac{b}{1-r}$ is the only equilibrium if $r \neq 1$.
- Every number is an equilibrium if $r = 1$ and $b = 0$.
- no equilibrium exists if $r = 1$ and $b \neq 0$.

Solution of the model $x_{n+1} = rx_n + b$:

$$\begin{aligned}
x_n &= rx_{n-1} + b \\
&= r(rx_{n-2} + b) + b \\
&= r^2 x_{n-2} + b(1 + r) \\
&= r^2(rx_{n-3} + b) + b(1 + r) \\
&= r^3 x_{n-3} + b(1 + r + r^2) \\
&\vdots \\
&= r^n x_0 + b(1 + r + r^2 + \cdots + r^{n-1}) \\
&= r^n x_0 + b \cdot \frac{1 \cdot (1 - r^n)}{1 - r} \qquad (\text{if} \quad r \neq 1) \\
&= r^n x_0 + \frac{b}{1 - r} - \frac{b}{1 - r} r^n \\
&= r^n \left(x_0 - \frac{b}{1 - r} \right) + \frac{b}{1 - r}.
\end{aligned}$$

If $r = 1$, $x_{n+1} = x_n + b$, then $x_n = x_{n-1} + b = x_{n-2} + 2b = \cdots = x_0 + nb$.

As a summary, the solution is

$$\begin{aligned} x_n &= r^n\left(x_0 - \frac{b}{1-r}\right) + \frac{b}{1-r} \qquad \text{if} \quad r \neq 1; \\ x_n &= x_0 + nb \qquad \text{if} \quad r = 1. \end{aligned}$$

Now let's discuss the long-term behavior for the case $b \neq 0$, since $b = 0$ reduces the model to $x_{n+1} = rx_n$ which has been discussed before.

Then if $r \neq 1$, $x_n = r^n\left(x_0 + \frac{b}{1-r}\right) + \frac{b}{1-r}$. There are two cases:

- When $|r| < 1$, $x_n \to \frac{b}{1-r}$ (the only equilibrium) as $n \to \infty$. We call the equilibrium $x^* = \frac{b}{1-r}$ stable.
- When $|r| > 1$, x_n is not convergent as $n \to \infty$. We call the equilibrium $x^* = \frac{b}{1-r}$ unstable.

If $r = 1$, $x_n = x_0 + nb \to \begin{cases} \infty & \text{if} \quad b > 0 \\ -\infty & \text{if} \quad b < 0 \end{cases}$ as $n \to \infty$. We have known that no equilibrium exists in this case ($r = 1, b \neq 0$).

2.4 Cobwebbing

Revisit the nonlinear bacterial reproduction model

$$B_{n+1} = \frac{2B_n}{1 + \frac{B_n}{K}} \triangleq F(B_n).$$

Equilibria B^* satisfy $B^* = \dfrac{2B^*}{1 + \frac{B^*}{K}} \Rightarrow B^* = 0$ or $B^* = K$. In the first panel of Figure 2, we plot the curve $F(B_n)$ and the diagonal line, whose intersections are equilibria. The red curves represent two sample solutions. For the left one, we start from $B_0 = 0.2$, then plot a vertical line and find its intersection with the curve $F(B_n)$. The y value of the intersection is B_1. Plot a horizontal line from the intersection (B_0, B_1) and then find the intersection (B_1, B_1) with the diagonal line. From this intersection, we plot a vertical line and find the intersection (B_1, B_2) with the curve $F(B_n)$. Repeat this process, we can find the orbit $\{B_0, B_1, B_2, ...\}$. Graphically we can see that this orbit is increasing and tends to the equilibrium $B^* = K$. For the right solution, we start from $B_0 = 1.8$ and use the same graphic approach to see that the orbit is decreasing but also tends to the equilibrium $B^* = K$. This graphical method is called cobwebbing.

The second panel of Figure 2 exhibits the above two solutions in cobwebbing analysis. Both solutions tend to the equilibrium $B^* = K$ (in this simulation $K = 1$). Actually all solutions with $B_0 > 0$ tend to K. Hence, the equilibrium $B^* = K$ is called stable, while the trivial equilibrium $B^* = 0$ is called unstable. We will discuss the stability theorem in the next section.

In reality there should be a threshold size below which bacteria go extinct due to predation. Hence, a more complicated nonlinear bacterial reproduction model is given as

$$B_{n+1} = \frac{rB_n^2}{1+(\frac{B_n}{K})^2} \triangleq F(B_n).$$

Equilibria B^* satisfy $B^* = \dfrac{rB^{*2}}{1+(\frac{B^*}{K})^2} \Rightarrow B^* = 0$ or $1 = \dfrac{rB^*}{1+(\frac{B^*}{K})^2}$.

The second case leads to a quadratic equation $B^{*2} - rK^2B^* + K^2 = 0$ whose roots are $B^* = K\left(\frac{rK}{2} \pm \sqrt{(\frac{rK}{2})^2 - 1}\right)$. There are three cases:

If $rK > 2$, there are three equilibria $B^* = 0$, $B^* = K\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)$, $B^* = K\left(\frac{rK}{2} + \sqrt{(\frac{rK}{2})^2 - 1}\right)$.

If $rK = 2$, there are two equilibria $B^* = 0$, $B^* = K$.

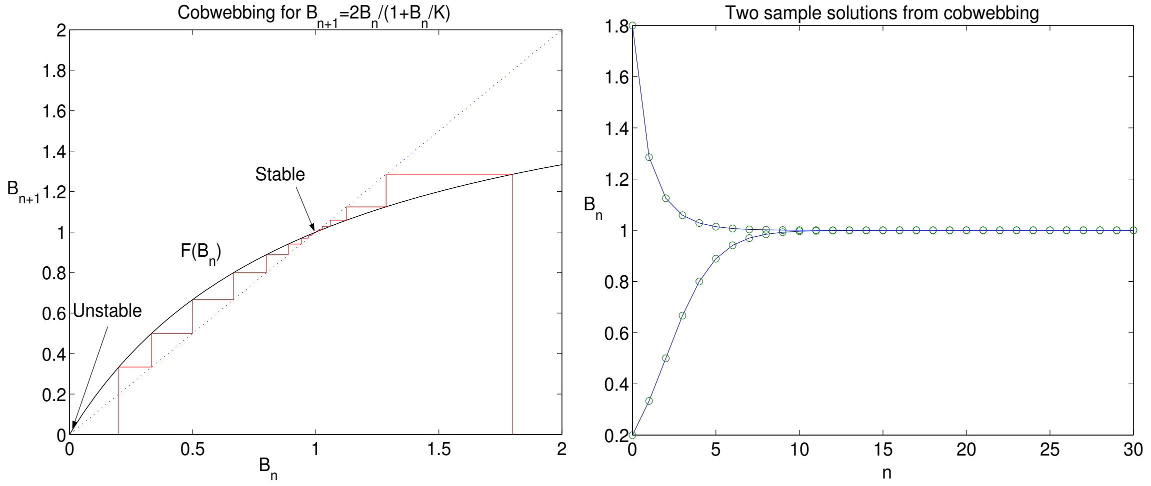


Figure 2: Cobwebbing analysis for the model

If $rK < 2$, there is only one equilibrium $B^* = 0$.

See the first two panels of Figure 3 for the case $rK > 2$, the third panel for the case $rK = 2$, and the fourth panel for the case $rK < 2$.

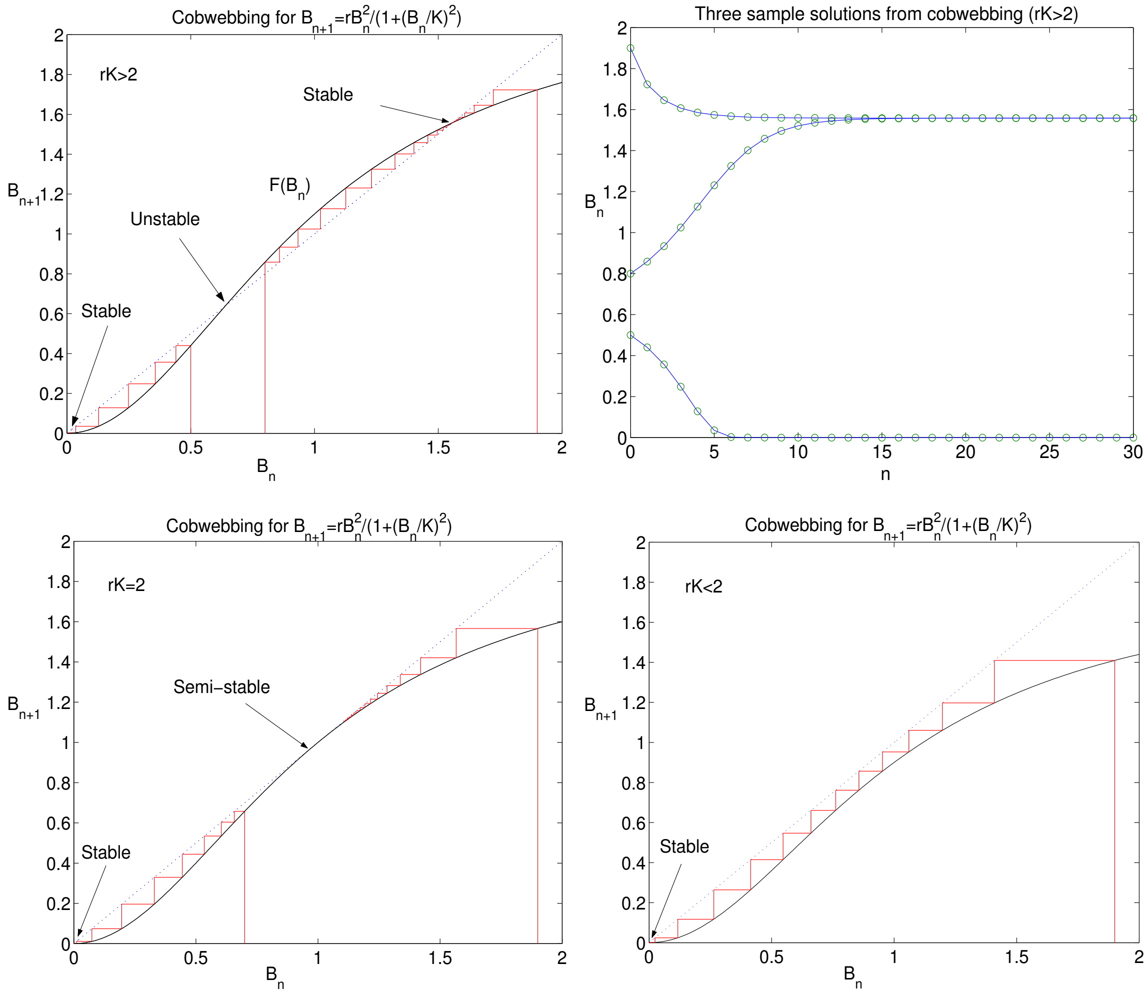


Figure 3: Cobwebbing analysis for the model $B_{n+1} = \frac{rB_n^2}{1+(B_n/K)^2}$

For the case $rK > 2$, we can observe from the cobwebbing that solutions with $B_0 > K\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)$ tend to $K\left(\frac{rK}{2} + \sqrt{(\frac{rK}{2})^2 - 1}\right)$, while solutions with $B_0 < K\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)$ tend to 0 (extinction). The equilibria $B^* = 0$ and $B^* = K\left(\frac{rK}{2} + \sqrt{(\frac{rK}{2})^2 - 1}\right)$ are stable, while the equilibrium $B^* = K\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)$ is unstable. The interval $(0, K\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right))$ is a pit of extinction. The extinction scenario, generated by the stable trivial equilibrium is the main difference between the model with predation and the model without predation.

For the case $rK = 2$, solutions with $B_0 \geq K$ tend to K, while solutions with $0 \leq B_0 < K$ tend to 0. The equilibrium $B^* = K$ is semi-stable (stable from right, unstable from left), while the equilibrium $B^* = 0$ is stable.

For the case $rK < 2$, all solutions tend to 0. The only equilibrium $B^* = 0$ is stable.

2.5 General theory and analytical methods

In this section, we discuss the linear stability analysis for a discrete-time model $x_{n+1} = f(x_n)$.

Let x^* be an equilibrium of the model $x_{n+1} = f(x_n)$, that is, $x^* = f(x^*)$. Consider a perturbation of x^*: $x_n = x^* + y_n$ with tiny y_n. Substitute it into the model to obtain $x^* + y_{n+1} = f(x^* + y_n)$. Apply Taylor's series to obtain $x^* + y_{n+1} = f(x^*) + f'(x^*)y_n + \text{higher order terms}$, which leads to $y_{n+1} = f'(x^*)y_n + \text{higher order terms}$. For tiny y_n, higher order terms are negligible compared the first order term $f'(x^*)y_n$: $y_{n+1} \approx f'(x^*)y_n$. We call $y_{n+1} = f'(x^*)y_n$ the linearized equation, where $f'(x^*)$ is a constant. Given the initial condition y_0, the solution is

$$y_n = (f'(x^*))^n y_0.$$

There are four cases for the deviation y_n:

- $f'(x^*) > 1$: the deviation has geometric growth, thus the equilibrium x^* is unstable.
- $0 < f'(x^*) < 1$, the deviation has geometric decay, thus the equilibrium x^* is stable.
- $-1 < f'(x^*) < 0$: the deviation has geometric decay with sign switch, thus the equilibrium x^* is stable.
- $f'(x^*) < -1$, the deviation has geometric growth with sign switch, thus the equilibrium x^* is unstable.

As a summary of all the above cases, we arrive at the following theorem:

Theorem 1 *(Stability Criterion) Let x^* be an equilibrium of $x_{n+1} = f(x_n)$, then we have the results:*

If $|f'(x^*)| < 1$, x^* *is stable.*

If $|f'(x^*)| > 1$, x^* *is unstable.*

If $|f'(x^*)| = 1$, *there is no conclusion about the stability of* x^*. *Higher order terms need to be examined to determine stability.*

The constant $f'(x^*)$ is called the eigenvalue of the map f at x^*.

Let's look at a few examples to apply this theorem.

Example 1 *Consider the discrete logistic equation $y_{n+1} = ry_n(1 - y_n/K)$, where the parameters $r \geq 0$, $K > 0$. Find all equilibria and determine their stability.*

Solution: Let $x_n = y_n/K$, then $x_{n+1} = rx_n(1-x_n)$. Note that $x_n \geq 0$ represents population size, and $r \geq 0$ is the maximum growth rate. Equilibria satisfy

$$x^* = rx^*(1-x^*)$$

which leads to $x^* = 0$ or $x^* = \frac{r-1}{r}$. The nontrivial equilibrium $x^* = \dfrac{r-1}{r} > 0$ if and only if $r > 1$.

To check stability, we compute the eigenvalue:

$$f'(x^*) = r(1-2x^*).$$

For the trivial equilibrium $x^* = 0$, the eigenvalue $f'(0) = r$, thus $x^* = 0$ is stable if $0 \leq r < 1$ and unstable if $r > 1$.

For the nontrivial equilibrium $x^* = \frac{r-1}{r}$, the eigenvalue $f'(\frac{r-1}{r}) = 2 - r$, thus $x^* = \frac{r-1}{r}$ is stable if $1 < r < 3$ (from $|2-r| < 1$) and unstable if $r > 3$ (from $|2-r| > 1$ and $r > 1$).

Example 2 *Consider the Beverton-Holt model* $x_{n+1} = \dfrac{rx_n}{1 + \frac{r-1}{K}x_n}$ *with* $r > 0$ *and* $K > 0$. *Find all equilibria and determine their stability.*

Solution: Equilibria x^* satisfy

$$x^* = \frac{rx^*}{1 + \frac{r-1}{K}x^*}$$

which leads to $x^* = 0$ or $x^* = K$ (if $r \neq 1$). Note that for $r = 1$ the model becomes $x_{n+1} = x_n$, which is not interesting.

To check stability, we compute the eigenvalue

$$f'(x^*) = \frac{r}{(1 + \frac{r-1}{K}x^*)^2}.$$

For the trivial equilibrium $x^* = 0$, the eigenvalue $f'(0) = r$, thus $x^* = 0$ is stable if $0 < r < 1$ and unstable if $r > 1$.

For the nontrivial equilibrium $x^* = K$, the eigenvalue $f'(K) = \dfrac{1}{r}$, thus $x^* = K$ is stable if $r > 1$ and unstable if $0 < r < 1$.

Example 3 *Revisit the bacterial reproduction models:w*

Model I:

$$B_{n+1} = rB_n;$$

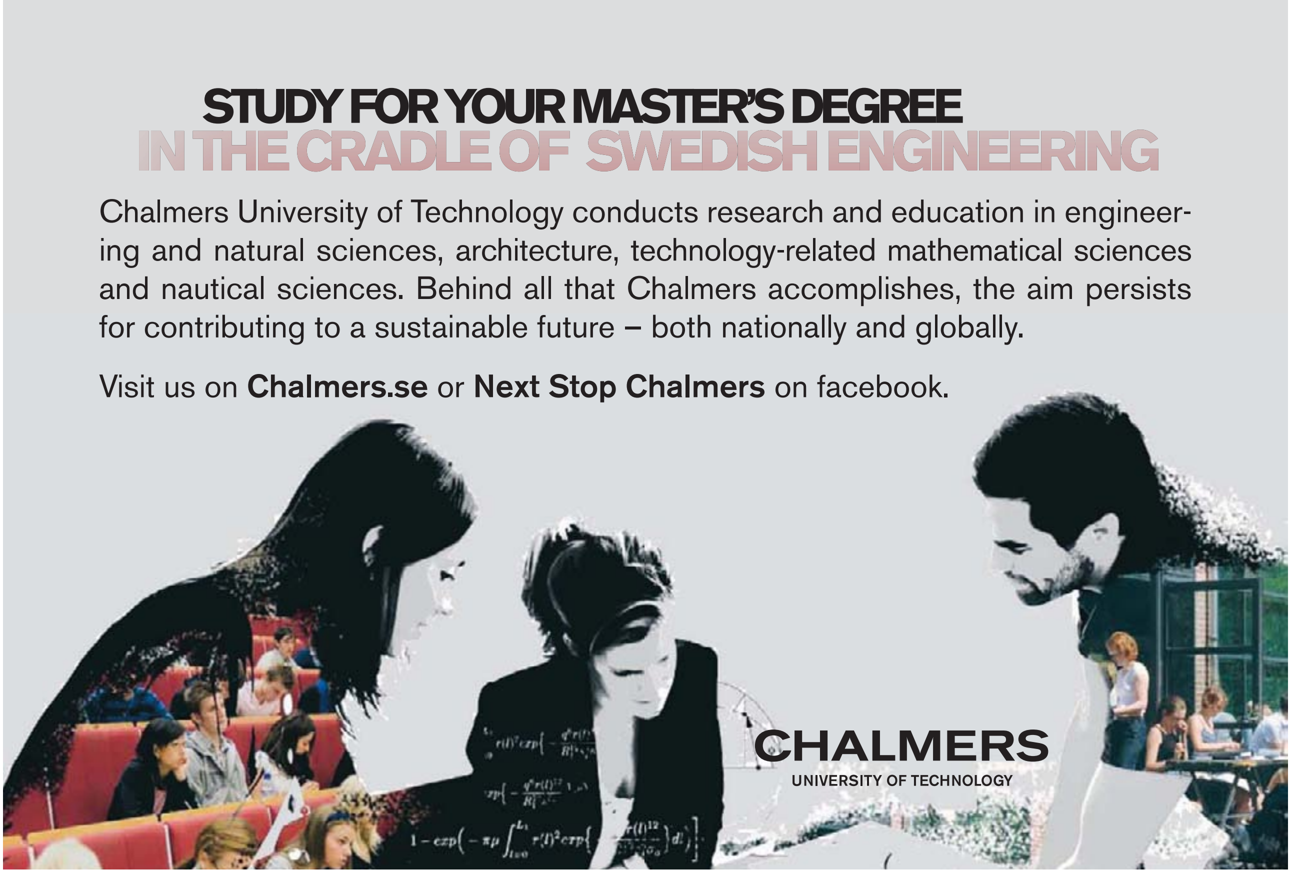
Model II:

$$B_{n+1} = \frac{2B_n}{1+\frac{B_n}{K}};$$

Model III:

$$B_{n+1} = \frac{rB_n^2}{1+(\frac{B_n}{K})^2}.$$

Solution: For Model I, equilibria B^* satisfy $B^* = rB^*$. If $r \neq 1$, $B^* = 0$ is the only equilibrium. If $r = 1$, every nonnegative number is an equilibrium. The eigenvalue is $f'(B^*) = r$. For the case $r \neq 1$, $B^* = 0$ is stable if $0 < r < 1$, unstable if $r > 1$. This result is consistent to cobwebbing analysis. For the case $r = 1$, $|f'(B^*)| = 1$ for all equilibria, there is no conclusion about stability from the stability theorem. Actually this case is a trivial case $B_{n+1} = B_n$ whose solutions are obvious.



For Model II, equilibria B^* satisfy $B^* = \frac{2B^*}{1+\frac{B^*}{K}}$ which has two roots $B^* = 0$ or $B^* = K$. The eigenvalue at B^* is $f'(B^*) = \dfrac{2}{(1+\frac{B^*}{K})^2}$. For the trivial equilibrium $B^* = 0$, $|f'(0)| = 2 > 1$, thus $B^* = 0$ is unstable. for the nontrivial equilibrium $B^* = K$, $|f'(K)| = \dfrac{1}{2} < 1$, thus $B^* = k$ is stable. The results are consistent to cobwebbing analysis.

For Model III, equilibria B^* satisfy $B^* = \dfrac{rB^{*2}}{1+(\frac{B^*}{K})^2}$ whose roots are $B^* = 0$, $B^* = K\left(\frac{rK}{2} - \sqrt{\left(\frac{rK}{2}\right)^2 - 1}\right)$, $B^* = K\left(\frac{rK}{2} + \sqrt{\left(\frac{rK}{2}\right)^2 - 1}\right)$.
Hence, there are three equilibria if $rK > 2$. The eigenvalue at B^* is $'(B^*) = \frac{2rB^*}{[1+(\frac{B^*}{K})^2]^2}$.

For $B^* = 0$, $|f'(0)| = 0 < 1$, thus $B^* = 0$ is stable.

For $B^* = K\left(\dfrac{rK}{2} - \sqrt{\left(\dfrac{rK}{2}\right)^2 - 1}\right)$, the eigenvalue

$$
\begin{aligned}
& f'\left(K\left(\frac{rK}{2} - \sqrt{\left(\frac{rK}{2}\right)^2 - 1}\right)\right) \\
&= \frac{2rK\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)}{\left[1 + \left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)^2\right]^2} \\
&= \frac{2rK\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)}{\left(\frac{r^2K^2}{2} - rK\sqrt{(\frac{rK}{2})^2 - 1}\right)^2} \\
&= \frac{2}{rK\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)} \\
&= \frac{2\left(\frac{rK}{2} + \sqrt{(\frac{rK}{2})^2 - 1}\right)}{rK\left(\frac{rK}{2} - \sqrt{(\frac{rK}{2})^2 - 1}\right)\left(\frac{rK}{2} + \sqrt{(\frac{rK}{2})^2 - 1}\right)} \\
&= \frac{rK + 2\sqrt{(\frac{rK}{2})^2 - 1}}{rK} \\
&= 1 + \frac{2\sqrt{(\frac{rK}{2})^2 - 1}}{rK} \\
&> 1,
\end{aligned}
$$

thus $B^* = K\left(\dfrac{rK}{2} - \sqrt{\left(\dfrac{rK}{2}\right)^2 - 1}\right)$ is unstable.

We can apply the same idea to obtain

$$f'\left(K\left(\frac{rK}{2}+\sqrt{\left(\frac{rK}{2}\right)^2-1}\right)\right)=1-\frac{2\sqrt{(\frac{rK}{2})^2-1}}{rK}.$$

Since $0<\frac{2\sqrt{(\frac{rK}{2})^2-1}}{rK}=\frac{\sqrt{(\frac{rK}{2})^2-1}}{\frac{rK}{2}}=\frac{\sqrt{(\frac{rK}{2})^2-1}}{\sqrt{(\frac{rK}{2})^2}}<1$, then

$$0<f'\left(K\left(\frac{rK}{2}+\sqrt{\left(\frac{rK}{2}\right)^2-1}\right)\right)=1-\frac{2\sqrt{(\frac{rK}{2})^2-1}}{rK}<1,$$

thus $B^*=K\left(\frac{rK}{2}+\sqrt{\left(\frac{rK}{2}\right)^2-1}\right)$ is stable.

For the case $rK<2$, the only equilibrium is $B^*=0$ which is stable. The case $rK=2$ is the degenerate case in which there are two equilibria $B^*=0$ (stable) and $B^*=K$ (semi-stable).

All these results are consistent to cobwebbing analysis.

Example 4 *Consider the annuity for retirement with* 0.5% *as the monthly interest rate and a monthly withdrawal of* $\$2000$. *Develop a discrete-time model to describe the annuity problem. Determine equilibria and stability. How much of an initial deposit is needed to deplete the annuity in* 30 *years?*

Solution: Let x_n be the amount in the account after n months, then the discrete-time model is provided by

$$x_{n+1}=x_n(1+0.5\%)-2000$$

which can be simplified as

$$x_{n+1}=1.005x_n-2000$$

with the initial deposit x_0.

Equilibria x^* satisfy $x^*=1.005x^*-2000$ which leads to $x^*=400000$. The eigenvalue is $f'(x^*)=1.005>1$, thus the only equilibrium $x^*=400000$ is unstable.

Recall that the solution of $x_{n+1} = rx_n + b$ is

$$\begin{aligned} x_n &= r^n \left(x_0 - \frac{b}{1-r} \right) + \frac{b}{1-r} \qquad \text{if} \quad r \neq 1; \\ x_n &= x_0 + nb \qquad \text{if} \quad r = 1. \end{aligned}$$

In this example, $r = 1.005 \neq 1$ and $b = -2000$, thus we use the first formula to obtain

$$0 = a_{360} = 1.005^{360} \left(x_0 - \frac{-2000}{1-1.005} \right) + \frac{-2000}{1-1.005}$$

from which we solve for the initial deposit: $x_0 = 333580$.

As a conclusion, an initial deposit of $\$333580$ allows the withdrawal of $\$2000$ per month from the account from 30 years. The total withdrawal is $\$720000$, and at the end of 30 years the account is depleted.

For discrete models, we have three ways to judge stability of equilibrium values:

1. Solving the model;
2. Cobwebbing analysis;
3. Stability criterion.

2.6 Optimization of discrete models

The basic optimization model is given as

$$\text{Optimize (maximize or minimize)} \quad f(X)$$

subject to

$$\begin{pmatrix} g_1(X) \\ g_2(X) \\ \vdots \\ g_n(X) \end{pmatrix} \left\{ \begin{matrix} \geq \\ = \\ \leq \end{matrix} \right\} \begin{pmatrix} b_1 \\ b_2 \\ \vdots \\ b_n \end{pmatrix}$$

Here,

- X is a vector with a group of decision variables whose values are discrete.
- $f(X)$ is called the objective function.
- $g_1(X), g_2(X), ..., g_n(x)$ are called constraint functions, and their associated side conditions are called constraints.

Goal: We seek the vector $X = X_0$ to optimize the objective function $f(X)$ and meanwhile to satisfy all constraints $g_i(X) \left\{ \begin{matrix} \geq \\ = \\ \leq \end{matrix} \right\} b_i,\ i = 1, 2, ..., n$.

Example 5 *A carpenter wants to decide how many chairs and how many benches he should make each month. One chair contributes to \$20 net profit, and one bench contributes to \$18 net profit. A chair requires 10 board-feet of lumber and 5 hours of labor, and a bench requires 20 board-feet of lumber and 4 hours of labor. Every month the carpenter has lumber up to 1000 board-feet and labor up to 360 hours.*

Solution: Let x_1 and x_2 are the number of chairs and the number of benches produced each month, respectively. The optimization problem can be described as

$$\text{Maximize the total net profit} \quad f(x_1, x_2) = 20x_1 + 18x_2$$

subject to

$$\begin{aligned} 10x_1 + 20x_2 &\leq 1000 \quad \text{(lumber)} \\ 5x_1 + 4x_2 &\leq 360 \quad \text{(labor)} \\ x_1 &\geq 0 \quad \text{(nonnegativity)} \\ x_2 &\geq 0 \quad \text{(nonnegativity)} \end{aligned}$$

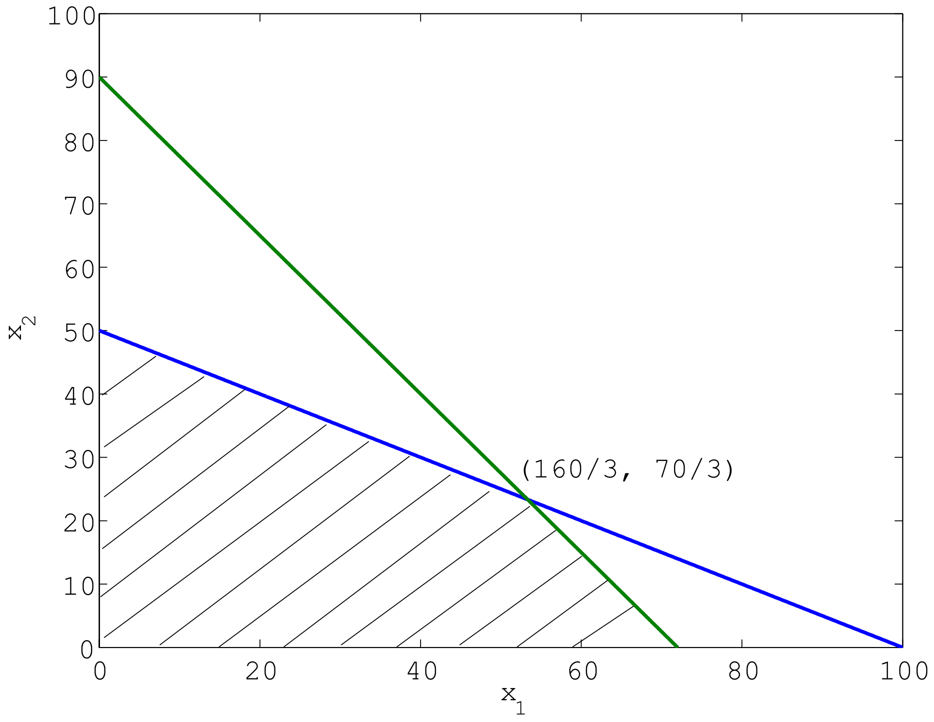


Figure 4: The convex set (shaded region) formed by constraints.

If an optimal solution to a linear problem (both the object function and all constraints are linear) exists, it must occur among the extreme points of the convex set formed by the set of constraints (see the shaded region of Figure 4). A set C is convex if for any two vectors $x, y \in C$, $(1-r)x + ry \in C$ for all $0 \leq r \leq 1$.

The shaded region generated by constraints has four extreme points: $(0,0)$, $(72,0)$, $(0,50)$, $(160/3, 70/3)$. We evaluate the objection function at each extreme point: $f(0,0) = 0$, $f(70,0) = 1440$, $f(0,50) = 900$, $f(160/3, 70/3) = 1486.7$. Hence, the maximum monthly profit is $1486.7, occurring at the internal extreme point $(160/3, 70/3)$, about 53 chairs and 23 benches.

Note: The maximum monthly profit can occur at a boundary extreme point. For instance, if we assume that one chair contributes to $20 net profit and one bench contributes to $15 net profit, then the maximum monthly profit occurs at $(70,0)$.

3 Continuous-time models

3.1 Motivation and derivation of continuous models

We derive a continuous model from a discrete model for population prediction. Let $N(t)$ be the population size at time t. In a small time period Δt, a percentage b of the population is born, and a percentage d of the population dies. Thus the change of the population size during the time period Δt is

$$N(t+\Delta t) - N(t) = bN(t)\Delta t - dN(t)\Delta t.$$

Note that b and d have the unit per time, and they are called growth and death rates. Divide both sides by Δt to obtain

$$\frac{N(t+\Delta t) - N(t)}{\Delta t} = (b-d)N(t).$$

Let $\Delta t \to 0$, we have

$$\frac{dN(t)}{dt} = (b-d)N(t)$$

using the definition of derivative. Let $\alpha = b - d$, then the model becomes

$$\frac{dN}{dt} = \alpha N.$$

Give the initial condition $N(t_0) = N_0$, the continuous-time model $\dfrac{dN}{dt} = \alpha N$ is defined for $t \geq t_0$.

Solution: We apply separation of variables to obtain

$$\int \frac{dN}{N} = \int \alpha dt$$

which leads to

$$\ln N = \alpha t + C$$

for some constant C. We then use the initial condition $N(t_0) = N_0$ to obtain $\ln N_0 = \alpha t_0 + C$, thus $C = \ln N_0 - \alpha t_0$. Substitute it back into the solution, then $\ln N = \alpha t + \ln N_0 - \alpha t_0$, which leads to $\ln(N/N_0) = \alpha(t - t_0)$, and thus

$$N(t) = N_0 e^{\alpha(t-t_0)},$$

which is the solution of the continuous model.

We apply this model to the Chinese census data: the 2000 census for the population of China was 1262600000 and in 1980 it was 981235000. Substitute these values into the solution by letting $t_0 = 1980$ and $N_0 = 981235000$:

$$1262600000 = 981235000 e^{\alpha(2000-1980)},$$

from which we solve for $\alpha : \alpha = 0.0126$. Hence the model becomes

$$N(t) = 981235000 e^{0.0126(t-1980)},$$

which can be used to predict future population. For example, in 2010 the Chinese population size should be $N(2010) = 981235000 e^{0.0126(2010-1980)} = 1432000000$, overestimate the realistic number 1338300000. How about the year 2100? $N(2100) = 981235000 e^{0.0126(2100-1980)} = 4450700000$, obviously unsustainable in China. Clearly the model is oversimplified.

We improve the model with limited growth. The constant α should be a decreasing function of the population size N and becomes zero when N reaches the sustainable maximum populations size M. The simplest to incorporate the population ceiling is

$$\alpha = r(M - N)$$

which is

- positive when $N < M$;
- zero when $N = M$;
- negative when $N > M$.

Therefore, the improved model is provided by

$$\frac{dN}{dt} = r(M - N)N,$$

called logistic population growth model.

Solution: We apply separation of variables to obtain

$$\int \frac{dN}{(M-N)N} = \int r dt$$

$$\int \frac{1}{M}\left(\frac{1}{M-N} + \frac{1}{N}\right) dN = \int r dt$$

$$\frac{1}{M}(-\ln|M-N| + \ln N) = rt + C$$

$$\ln N - \ln|M-N| = M(rt + C)$$

Use the initial condition $N(t_0) = N_0 < M \Rightarrow \ln N_0 - \ln(M - N_0) = M(rt_0 + C)$, from which we solve for $C : C = \frac{1}{M}\ln\frac{N_0}{M-N_0} - rt_0$. Hence,

$$\ln N - \ln|M-N| = M\left(rt + \frac{1}{M}\ln\frac{N_0}{M-N_0} - rt_0\right)$$

Consider the case $N < M$ which is usually valid according to the definition of M, then

$$\ln\frac{N(M-N_0)}{N_0(M-N)} = rM(t-t_0)$$

$$N(M-N_0) = N_0(M-N)e^{rM(t-t_0)}$$

$$N(M-N_0) + N_0 N e^{rM(t-t_0)} = N_0 M e^{rM(t-t_0)}$$

$$N(t) = \frac{N_0 M e^{rM(t-t_0)}}{M - N_0 + N_0 e^{rM(t-t_0)}}$$

$$N(t) = \frac{MN_0}{N_0 + (M-N_0)e^{-rM(t-t_0)}}$$

This is the solution of the improved model with limited growth. We can easily observe that

$$N(t) \to M \quad \text{as} \quad t \to \infty.$$

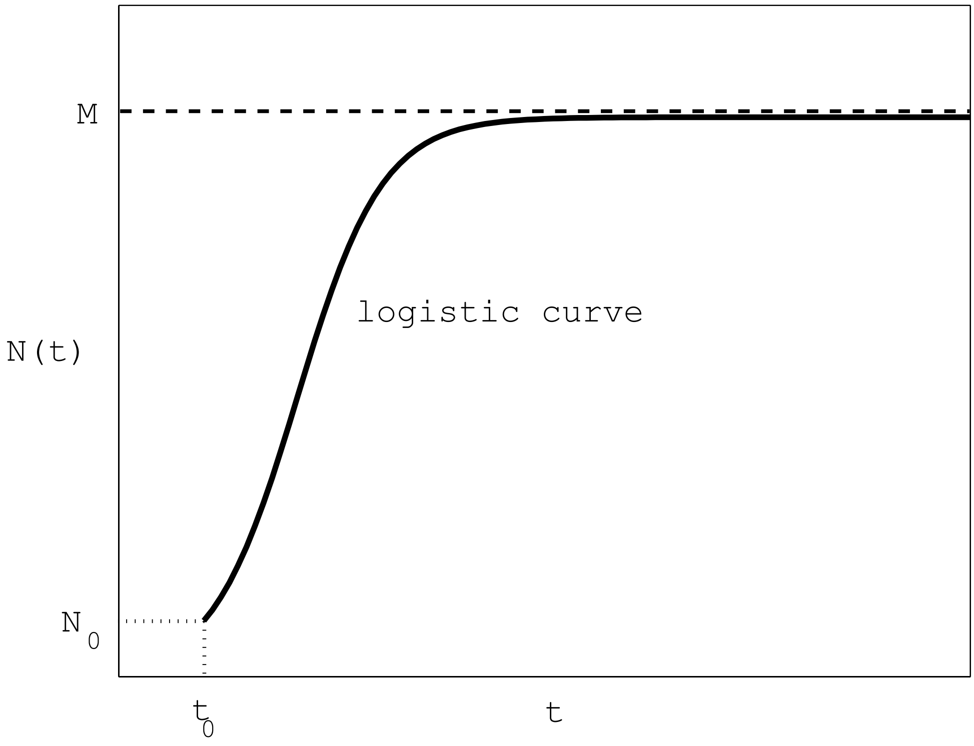


Figure 5: The logistic curve: the solution of the model $\frac{dN}{dt} = r(M-N)N$ with the initial condition $N(t_0) = N_0$.

3.2 Differential equation models

Consider a general first-order differential equation:

$$\frac{dx}{dt} = f(t,x).$$

Definition 2 *The collection of short line segments of slope $f(t,x)$ at selected points (t,x) in tx-plane is called a slope field. Solution curves follow these tangents.*

If $f(t,x)$ is independent of t, i.e. $\frac{dx}{dt} = f(x)$, then the differential equation is called autonomous. The values of x such that $\frac{dx}{dt} = 0$ are called equilibrium values or steady states or fixed points. A phase line is a plot on the x axis that shows all fixed points together with the intervals where we can determine the signs of $\frac{dx}{dt}$ and $\frac{d^2x}{dt^2}$, from which we know the monotonicity and concavity of solution curves.

Given an initial condition $x(t_0) = x_0$, the solution curve of the initial value problem (IVP) $\frac{dx}{dt} = f(t,x), x(t_0) = x_0$ passes through the point (t_0, x_0) and has slope $f(t_0, x_0)$ there.

Let's look at a simple example to perform the phase line analysis.

Example 6 *For the autonomous differential equation* $\frac{dx}{dt} = x(x-1)$, *determine equilibrium values and perform the phase line analysis.*

Equilibrium values are $x^* = 0$ and $x^* = 1$, i.e. the equation has two constant solutions $x = 0$ for all t and $x = 1$ for all t.

It is easy to determine that

$\frac{dx}{dt} = x(x-1)$ is positive if $x < 0$ or $x > 1$; negative if $0 < x < 1$.

We can compute $\frac{d^2x}{dt^2} = \frac{d}{dt}(\frac{dx}{dt}) = \frac{d}{dt}(x(x-1)) = (2x-1)\frac{dx}{dt} = (2x-1)x(x-1)$, which is positive if $x > 1$ or $0 < x < 1/2$; negative if $1/2 < x < 1$ or $x < 0$. According to these facts, we can plot the phase line as in Figure 6.

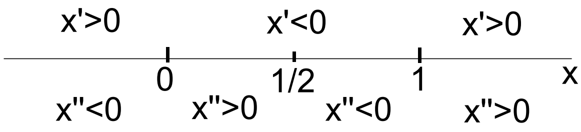


Figure 6: The phase line analysis of $\frac{dx}{dt} = x(x-1)$.

Without solving the differential equation, we can also sketch representative solution curves using the phase line (see Figure 7). It is not difficult to observe that Figures 6&7 are consistent.

The equilibrium $x = 0$ is stable since solution curves near $x = 0$ tend toward to $x = 0$ as t increases. The equilibrium $x = 1$ is unstable since solution curves near $x = 1$ (except $x = 1$ itself) move away from $x = 1$ as t increases. Note that the phase line is enough to judge stability of equilibrium values. Strict definitions of stability can be found in most ordinary differential equation textbooks.

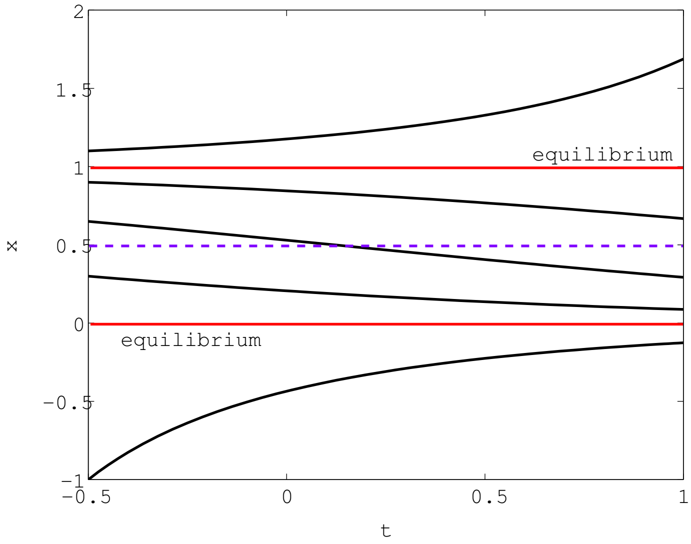


Figure 7: Some representative solution curves of $\dfrac{dx}{dt} = x(x-1)$.

3.3 Some basic theorems

For the differential equation $\dfrac{dx}{dt} = f(t, x)$, we have the following basic theorems that can be useful for the preliminary analysis of a differential equation model.

Theorem 2 *(Existence and Uniqueness) Under some mild conditions (* $f(t, x)$ *and* $\dfrac{df}{dx}(t, x)$ *are continuous with respect to* t *and* x *) most differential equation models satisfy, we have the following basic results for* $\dfrac{dx}{dt} = f(t, x)$*:*

- ***Existence of solutions*** *Each point in tx-plane has a solution passing through it.*
- ***Uniqueness of solutions*** *Only one solution passes through each point* (t, x)*.*
- ***Continuous dependence*** *Solution curves through nearby initial points remain close over a short time.*

Theorem 3 *(Stability Criterion) Let* x^* *be an equilibrium of an autonomous equation* $\frac{dx}{dt} = f(x)$*. Then*

- x^* *is stable when* $f'(x^*) < 0$*;*
- x^* *is unstable when* $f'(x^*) > 0$*;*
- *there is no conclusion about the stability of* x^* *when* $f'(x^*) = 0$.

Note that $f'(x^*)$ is called the eigenvalue of x^*.

Example 7 *Determine equilibrium values and their stability for the differential equation*

$$\frac{dx}{dt} = (x+1)(x-2).$$

Solution: Equilibrium values are $x^* = -1$ and $x^* = 2$.
$f(x) = (x+1)(x-2) = x^2 - x - 2$,
then $f'(x) = 2x - 1$, thus $f'(x^*) = 2x^* - 1$.
$f'(-1) = -3 < 0$, hence the equilibrium solution $x = -1$ is stable.
$f'(2) = 3 > 0$, hence the equilibrium solution $x = 2$ is unstable.

Example 8 *Revisit the logistic population growth model* $\frac{dN}{dt} = r(M-N)N$ *to determine equilibrium values and their stability.*

Solution: Equilibrium values are $N^* = M$ and $N^* = 0$.
$f(N) = r(M-N)N = rMN - rN^2$,
then $f'(N) = rM - 2rN$, thus $f'(N^*) = rM - 2rN^*$.
$f'(M) = -rM < 0$, hence the equilibrium solution $N = M$ is stable.
$f'(0) = rM > 0$, hence the equilibrium solution $N = 0$ is unstable.

Similar to discrete models, we have three ways to judge stability of equilibrium values of autonomous differential equations (a group of continuous models):

1. Solving the model;
2. Phase line analysis;
3. Stability criterion.

3.4 Separation of variables

Consider the nonautonomous differential equation

$$\frac{dx}{dt} = f(t, x),$$

which is separable if

$$f(t, x) = p(t)q(x).$$

Note that $p(t)$ or $q(x)$ may be a constant function. For a separable equation, we can express it as

$$\frac{dx}{dt} = p(t)q(x) \quad \Rightarrow \quad \int \frac{dx}{q(x)} = \int p(t)dt,$$

from which we can obtain the general solution to the differential equation.

Example 9 *Solve the differential equation* $\dfrac{dx}{dt} = t^2 + (xt)^2$.

Solution: This equation is separable because we can rewrite it as

$$\frac{dx}{dt} = t^2(1 + x^2),$$

then

$$\int \frac{dx}{1 + x^2} = \int t^2 dt,$$

$$\tan^{-1}(x) = t^3/3 + C,$$

$$x = \tan(t^3/3 + C),$$

where C is a constant determined by the initial condition.

Example 10 *Solve* $\dfrac{dx}{dt} = \dfrac{t}{e^{t+x}}$.

Solution: This equation is separable because it is equivalent to

$$\frac{dx}{dt} = \frac{t}{e^t}\frac{1}{e^x}.$$

Thus,

$$\int e^x dx = \int \frac{t}{e^t} dt$$

$\Rightarrow e^x = \int te^{-t}dt = \text{integration by parts} = -(te^{-t} - \int e^{-t}dt) + C = -(te^{-t} + e^{-t}) + C = -(t+1)e^{-t} + C$. Hence, the general solution is $x(t) = \ln[-(t+1)e^{-t} + C]$, where the constant C depends on the initial condition.

For instance, given the initial condition $x(0) = 0$, then

$$x(0) = \ln[-1 + C] = 0,$$

which leads to $C = 2$. Then the solution of the IVP

$$\begin{cases} \dfrac{dx}{dt} = \dfrac{t}{e^{t+x}}, \\ (0) = 0, \end{cases}$$

is $x(t) = \ln[-(t+1)e^{-t} + 2]$.

Example 11 *Solve the IVP* $\begin{cases} \dfrac{dx}{dt} = \dfrac{e^x}{t^2 x}, \\ (1) = 0. \end{cases}$

Solution: We apply separation of variables to obtain

$$\int xe^{-x}dx = \int t^{-2}dt,$$

$$-(xe^{-x} - \int e^{-x}dx) = -t^{-1} + C,$$

$$-(xe^{-x} + e^{-x}) = -t^{-1} + C,$$

$$-(x+1)e^{-x} = -t^{-1} + C.$$

Then use the initial condition $x(1) = 0$ to obtain $-(0+1)e^{-0} = -1^{-1} + C$, which gives $C = 0$. Hence, the solution to IVP is

$$-(x+1)e^{-x} = -\frac{1}{t} - \frac{1}{2},$$

which provides an implicit formula for $x(t)$. There is no explicit formula for $x(t)$ since the resulting algebraic equation is a transcendental equation.

3.5 Linear equations

Let's start with a lake pollution problem, which is a common and extremely severe issue in many lakes around the world. We let $V(t)$ be the lake volume at time t, and $p(t)$ be the amount of pollutant in the lake at time t. Then the concentration of pollutant is the ratio

$$c(t) = \frac{p(t)}{V(t)}.$$

Over the time interval $[t, t + \triangle t]$, the change in the amount of pollutant $\triangle p$ is the amount of pollutant that enters the lake minus the amount that leaves:

$$\triangle p = \text{amount input} - \text{amount output}.$$

If water enters the lake with a constant concentration c_{in} at a rate r_{in}, then

$$\text{amount input} = r_{in} c_{in} \triangle t.$$

If water leaves the lake at a constant rate r_{out}, since the concentration of pollutant in lake is $\frac{p(t)}{V(t)}$, then

$$\text{amount output} = r_{out} \frac{p(t)}{V(t)} \triangle t.$$

Thus,

$$\triangle p = r_{in} c_{in} \triangle t - r_{out} \frac{p(t)}{V(t)} \triangle t,$$

$$\frac{\triangle p}{\triangle t} = r_{in} c_{in} - r_{out} \frac{p(t)}{V(t)}.$$

Let $\triangle t \to 0$, we have

$$\frac{dp}{dt} = r_{in}c_{in} - \frac{r_{out}}{V}p.$$

Suppose $V(0) = V_0$ is the volume of the lake initially, then $V(t) = V_0 + (r_{in} - r_{out})t$, then the model becomes

$$\frac{dp}{dt} = r_{in}c_{in} - \frac{r_{out}}{V_0 + (r_{in} - r_{out})t}p.$$

We can rewrite this differential equation as

$$\frac{dp}{dt} + \frac{r_{out}}{V_0 + (r_{in} - r_{out})t}p = r_{in}c_{in},$$

$$\frac{dp}{dt} + g(t)p = r_{in}c_{in},$$

where $(t) = \frac{r_{out}}{V_0 + (r_{in} - r_{out})t}$, is the lake pollution model.

This is an example of a linear first-order differential equation. Can we solve this equation to find the amount $p(t)$ of pollutant in the lake at time t? The answer is positive. We will discuss the general method and then come back to the lake pollution example.

In general, the first-order linear equation is of the form

$$a_1(t)x' + a_0(t)x = b(t),$$

$$x' + \frac{a_0(t)}{a_1(t)}x = \frac{b(t)}{a_1(t)},$$

$$x' + P(t)x = Q(t),$$

which is the standard form of the linear equation. The method is to multiply both sides by an integrating factor

$$\mu(t) = e^{\int P(t)dt}.$$

(Note that we introduce no arbitrary constant of $\int P(t)dt$ since only one function is needed for $\mu(t)$.) Then the equation becomes

$$\mu(t)x' + P(t)\mu(t)x = \mu(t)Q(t).$$

Because $\mu'(t) = p(t)\mu(t)$, then the equation becomes

$$(\mu(t)x(t))' = \mu(t)Q(t),$$

$$\mu(t)x(t) = \int \mu(t)Q(t)dt + C,$$

then we obtain the general solution $x(t) = \dfrac{C}{\mu(t)} + \dfrac{1}{\mu(t)}\displaystyle\int \mu(t)Q(t)dt = Ce^{-\int P(t)dt} + \underbrace{e^{-\int P(t)dt}\int e^{\int P(t)dt}Q(t)dt}_{\text{t in the first factor is different from t in the second factor}}$.

Example 12 *(Lake pollution problem) Return to the lake pollution example:*

$$\frac{dp}{dt} + g(t)p = r_{in}c_{in},$$

where $g(t) = \dfrac{r_{out}}{V_0 + (r_{in} - r_{out})t}$.

Let $\alpha = r_{in}c_{in}$, *then* $\dfrac{dp}{dt} + g(t)p = \alpha$.

Solution: Multiple both sides by an integrating factor

$$\mu(t) = e^{\int g(t)dt} = e^{\int \frac{r_{out}}{V_0+(r_{in}-r_{out})t}dt} = e^{\frac{r_{out}}{r_{in}-r_{out}}\ln|V_0+(r_{in}-r_{out})t|},$$

then

$$\frac{d}{dt}(\mu(t)p(t)) = \alpha\mu(t),$$

$$\mu(t)p(t) = \int \alpha\mu(t)dt + C,$$

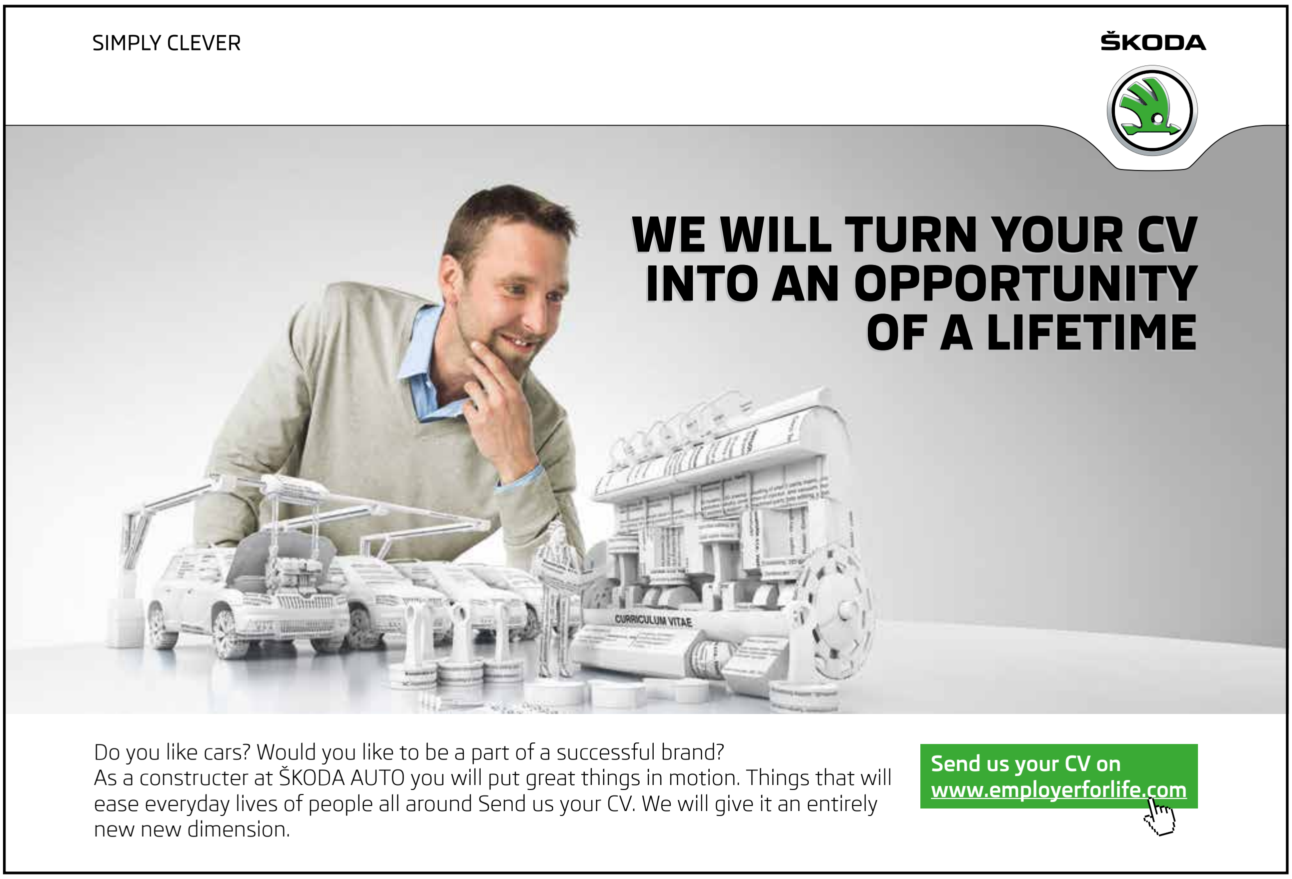
$$p(t) = \frac{C}{\mu(t)} + \frac{\alpha}{\mu(t)}\int \mu(t)dt,$$

where $\mu(t) = e^{\frac{r_{out}}{r_{in}-r_{out}}\ln|V_0+(r_{in}-r_{out})t|}$ and C is a constant determined by the initial condition. Note that $\mu(t)$ in the second term cannot be canceled out.

If we assume that $V_0+(r_{in}-r_{out})t>0$ for all t in the studied interval $[0,T]$, then $\mu(t)=e^{\frac{r_{out}}{r_{in}-r_{out}}\ln(V_0+(r_{in}-r_{out})t)}=e^{\ln(V_0+(r_{in}-r_{out})t)^{\frac{r_{out}}{r_{in}-r_{out}}}}=(V_0+(r_{in}-r_{out})t)^{\frac{r_{out}}{r_{in}-r_{out}}}$.

Then $\mu(t)dt=\int(V_0+(r_{in}-r_{out})t)^{\frac{r_{out}}{r_{in}-r_{out}}}dt=\frac{1}{r_{in}-r_{out}}\frac{1}{\frac{r_{out}}{r_{in}-r_{out}}+1}(V_0+(r_{in}-r_{out})t)^{\frac{r_{out}}{r_{in}-r_{out}}+1}=\frac{1}{r_{in}-r_{out}}\frac{r_{in}-r_{out}}{r_{in}}(V_0+(r_{in}-r_{out})t)^{\frac{r_{in}}{r_{in}-r_{out}}}=\frac{1}{r_{in}}(V_0+(r_{in}-r_{out})t)^{\frac{r_{in}}{r_{in}-r_{out}}}$. No arbitrary constant is needed in the above calculation since C is already incorporated in the expression of $p(t)$.

Therefore, the solution is
$p(t)=C(V_0+(r_{in}-r_{out})t)^{\frac{r_{out}}{r_{out}-r_{in}}}+\alpha(V_0+(r_{in}-r_{out})t)^{\frac{r_{out}}{r_{out}-r_{in}}}\frac{1}{r_{in}}(V_0+(r_{in}-r_{out})t)^{\frac{r_{in}}{r_{in}-r_{out}}}=C(V_0+(r_{in}-r_{out})t)^{\frac{r_{out}}{r_{out}-r_{in}}}+\frac{\alpha}{r_{in}}(V_0+(r_{in}-r_{out})t)$.



Example 13 *Find the general solution of the linear equation*

$$tx' + x = \cos(t), \quad t > 0.$$

Solution: Rewrite the linear equation in the standard form

$$x' + \frac{1}{t}x = \frac{\cos(t)}{t},$$

thus $P(t) = \frac{1}{t}, Q(t) = \frac{\cos(t)}{t}$. An integrating factor satisfies

$$\mu(t) = e^{\int P(t)dt} = e^{\int \frac{1}{t}dt} = e^{\ln t} = t.$$

Multiply both sides of the linear equation by $\mu(t)$ to obtain

$$tx' + x = \cos(t),$$

$$(tx)' = \cos(t),$$

$$tx = \int \cos(t)dt + C,$$

$$tx = \sin(t) + C,$$

$$x = \frac{\sin(t)}{t} + \frac{C}{t}, \quad t > 0.$$

Hence, the general solution is $(t) = \frac{\sin(t)}{t} + \frac{C}{t}$ for $t > 0$.

Example 14 *Solve the IVP*

$$\begin{cases} x' + x = e^t, & t \geq 0 \\ x(0) = 1. \end{cases}$$

Solution: An integrating factor is $\mu(t) = e^{\int 1dt} = e^t$. Multiply both sides of the linear equation by e^t to obtain

$$e^t x' + e^t x = e^{2t},$$

$$(e^t x)' = e^{2t},$$

$$e^t x = \int e^{2t} dt + C,$$

$$e^t x = \frac{1}{2} e^{2t} + C,$$

$$x = \frac{1}{2} e^t + C e^{-t}.$$

The general solution is $x(t) = \frac{1}{2} e^t + C e^{-t}$. The initial condition $x(0) = 1$ implies that $\frac{1}{2} + C = 1$, thus $C = \frac{1}{2}$. Therefore, the solution to IVP is

$$x(t) = \frac{1}{2} e^t + \frac{1}{2} e^{-t} = \frac{e^t + e^{-t}}{2} = \cosh(t)$$

(a hyperbolic cosine function).

3.6 Optimization of continuous models

We study the optimization problem:

$$\mathrm{Optimize} f(X)$$

subject to constraints

$$g_i(X) \left\{ \begin{array}{c} \geq \\ \leq \end{array} \right\} b_i \quad \text{for all} \quad i \in I,$$

where the objective function f is continuous but nonlinear. We discuss a representative example to show how to construct and solve an optimization problem.

Example 15 *A PC company plans to introduce two new products: 21-inch all-in-one computer and 27-inch all-in-one computer. The cost of a 21-inch all-in-one computer is \$500, the cont of a 27-inch all-in-one computer is \$600, and the fixed cost is \$100,000. The suggested retail price of a 21-inch all-in-one computer is \$900, and the suggested retail price of a 27-inch all-in-one computer is \$1050. In the competitive market, for each additional computer of a particular type sold, the selling price falls by \$0.10. Furthermore, the selling price for each 21-inch computer is reduced by \$0.03 for each 27-inch computer sold, and the selling price for each 27-inch computer is reduce by \$0.04 for each 21-inch computer sold. If we assume that all computers made by this company can be sold at the above prices, how many computers of each type should the company manufacture to maximize its profit?*

Solution: We define the variables for the two types of computers ($i = 1, 2$):

x_1 — number of 21-inch all-in-one computers
x_2 — number of 27-inch all-in-one computers
P_i — selling price of x_i
R — revenue obtained from computer sales
C — cost to produce the computers
P — net profit from the sales of the computers

We have two independent variables x_1 and x_2, all other variables defined above can be expressed as functions of x_1 and x_2:

$$P_1 = 900 - 0.1x_1 - 0.03x_2$$

$$P_2 = 1050 - 0.04x_1 - 0.1x_2$$

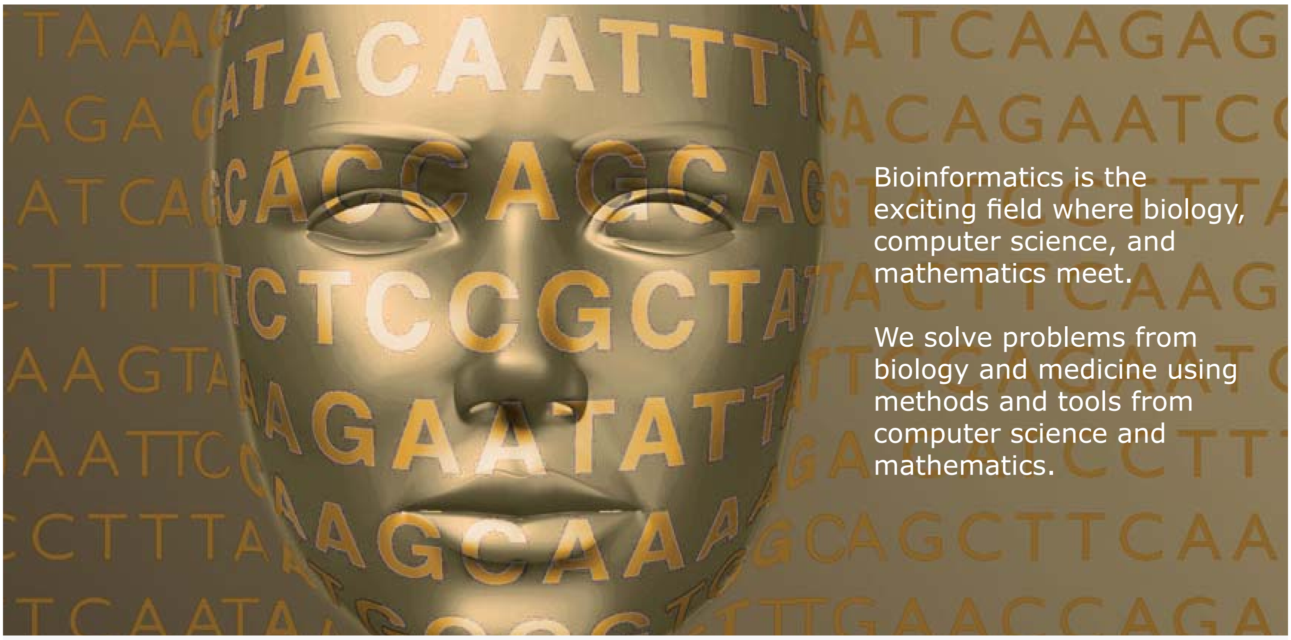
$$R = P_1x_1 + P_2x_2$$

$$C = 100000 + 500x_1 + 600x_2$$

$$P = R - C$$

and

$$x_1 \geq 0, \quad x_2 \geq 0.$$



Optimization problem:

To maximize the profit function

$$\begin{aligned}
P(x_1, x_2) &= R - C \\
&= (P_1 x_1 + P_2 x_2) - (100000 + 500x_1 + 600x_2) \\
&= (900 - 0.1x_1 - 0.03x_2)x_1 + (1050 - 0.04x_1 - 0.1x_2)x_2 \\
&\quad -(100000 + 500x_1 + 600x_2) \\
&= 400x_1 - 0.1x_1^2 + 450x_2 - 0.1x_2^2 - 0.07x_1x_2 - 100000
\end{aligned}$$

The necessary conditions of obtaining the maximum net profit are

$$\frac{\partial P}{\partial x_1} = 0 \quad \text{and} \quad \frac{\partial P}{\partial x_2} = 0,$$

that is,

$$\begin{aligned}
\frac{\partial P}{\partial x_1} &= 400 - 0.2x_1 - 0.07x_2 &= 0 \\
\frac{\partial P}{\partial x_2} &= 450 - 0.2x_2 - 0.07x_1 &= 0
\end{aligned}$$

$$\Rightarrow \quad x_1 \approx 1382, \quad x_2 \approx 1766.$$

At $x_1 = 1382$, $x_2 = 1766$, the total net profit is

$$P(1382, 1766) = \$573790.$$

This should be the maximum profit or the minimum profit. We have three ways to judge whether it is the maximum profit:

1) Compute $P(x_1, x_2)$ at some positive integers $\bar{x}_1$ and $\bar{x}_2$ (we can choose $(\bar{x}_1, \bar{x}_2)$ near $(1382, 1766)$), and compare with $P(1382, 1766)$. It is easy to see that $(\bar{x}_1, \bar{x}_2) < P(1382, 1766)$, thus $P(1382, 1766)$ is the maximum profit.
2) Use the second-derivative test from multivariable calculus:

$$\frac{\partial^2 P}{\partial x_1^2}(1382, 1766) = -0.2 < 0$$

and

$$\left[\frac{\partial^2 P}{\partial x_1^2}\frac{\partial^2 P}{\partial x_2^2} - \left(\frac{\partial^2 P}{\partial x_1 \partial x_2}\right)^2\right](1382, 1766) = 0.0351 > 0.$$

These two inequalities imply that $P(1382, 1766)$ is the maximum profit.

3) Sketch $P(x_1, x_2)$ for $x_1 \geq 0,\ x_2 \geq 0$, which can show that the profit $P(x_1, x_2)$ at $(1382, 1766)$ is indeed the maximum profit.

Another important type of optimization problems is listed as follows:

maximize or minimize $f(x)$ subject to $g(x) = c$. Here $x \in \mathbb{R}^n$.

To find the local maxima and minima of the function $f(x)$ subject to equality constraints $g(x) = c$, we introduce a new variable λ called a Lagrange multiplier and study the Lagrange function defined by $L(x, \lambda) = f(x) + \lambda[g(x) - c]$, where the λ term may be either added or subtracted. If $f(x)$ is a maximum or minimum, then there exists λ such that (x, λ) is a stationary point for the Lagrange function. Note that the method of Lagrange multipliers provides a necessary condition for optimality, that is, not all stationary points of the Lagrange function yield a solution of the optimization problem.

Example 16 *Maximize* $f(x_1, x_2) = x_1 + x_2$ *subject to the constraint* $x_1^2 + x_2^2 = 1$.

Solution: We apply the method of Lagrange multipliers to obtain the Lagrange function

$$L(x_1, x_2, \lambda) = f(x_1, x_2) + \lambda(g(x_1, x_2) - c) = x_1 + x_2 + \lambda(x_1^2 + x_2^2 - 1).$$

Stationary points satisfy

$$\begin{aligned} \frac{\partial L}{\partial x_1} = 1 + 2\lambda x_1 &= 0 \\ \frac{\partial L}{\partial x_2} = 1 + 2\lambda x_2 &= 0 \\ \frac{\partial L}{\partial \lambda} = x_1^2 + x_2^2 - 1 &= 0 \end{aligned}$$

$\Rightarrow \lambda = \pm\sqrt{2}/2$ which lead to two stationary points $(-\sqrt{2}/2, -\sqrt{2}/2)$ and $(\sqrt{2}/2, \sqrt{2}/2)$.

We evaluate the objective function $f(x_1, x_2)$ at these stationary points:

$$f(-\sqrt{2}/2, -\sqrt{2}/2) = -\sqrt{2}$$

and

$$f(\sqrt{2}/2, \sqrt{2}/2) = \sqrt{2}.$$

Hence, similar to the example 15, we can judge that the maximum is $\sqrt{2}$, occurring at $(\sqrt{2}/2, \sqrt{2}/2)$.

4 Sensitivity analysis

Sensitivity analysis is to study how the variation in the output of a mathematical model depends on different sources of variation in the input of a mathematical model.

One common type of sensitivity analysis is to determine how a focused quantity (depending on variables) is related to perturbation of each parameter.

Sensitivity analysis is of important use in many ways. For instance, we perform sensitivity analysis to test robustness of model predictions, or to understand (relative) importance of parameters to the focused quantity and check their relationships (positively or negatively related, strength of relationships).

Definition 3 *The normalized forward sensitivity index of a variable,* u*, that depends differentiably on a parameter,* p*, is defined as*

$$\gamma_p^u := \frac{\partial u}{\partial p} \times \frac{p}{u}.$$

We now look at some examples to show how to use sensitivity analysis.

Example 17 *We consider the logistic population growth model*

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right).$$

Assume the experiment (or field observation) is terminated at $t = 10$, *how does the final population size depend on the parameters* r *and* K *?*

Here, given the initial condition $x(0) = 1$, *and the default parameter values are* $r = 0.1$, $K = 5$, *compute the normalized forward sensitivity index of the final population size that depends on* r *or* K *.*

Solution: We apply Separation of Variables to find the solution

$$x(t) = \frac{K}{1 + (K-1)e^{-rt}}.$$

In the end of the experiment, the final population size is

$$x(10) = \frac{K}{1 + (K-1)e^{-10r}}.$$

The r-related sensitivity index is

$$\begin{aligned}
\gamma_r^{x(10)} &= \frac{\partial x(10)}{\partial r} \times \frac{r}{x(10)} \\
&= \frac{-K[(K-1)(-10)e^{-10r}]}{(1 + (K-1)e^{-10r})^2} \frac{r}{K/[1 + (K-1)e^{-10r}]} \\
&= \frac{10r(K-1)e^{-10r}}{1 + (K-1)e^{-10r}}.
\end{aligned}$$

At default parameter values, $\gamma_r^{x(10)}|_{r=0.1,K=5} = 0.5954.$

$$\begin{aligned}
\gamma_K^{x(10)} &= \frac{\partial x(10)}{\partial K} \times \frac{K}{x(10)} \\
&= \frac{1 + (K-1)e^{-10r} - Ke^{-10r}}{(1 + (K-1)e^{-10r})^2} \frac{K}{K/[1 + (K-1)e^{-10r}]} \\
&= \frac{1 - e^{-10r}}{1 + (K-1)e^{-10r}}.
\end{aligned}$$

At default parameter values, $\gamma_K^{x(10)}|_{r=0.1,K=5} = 0.2558.$

The sign of the sensitivity index means positive or negative dependence of the studied quantity on the parameter. The absolute value of the sensitivity index indicates how sensitive the studied quantity depends on the parameter. Positive $\gamma_r^{x(10)}$ and positive $\gamma_K^{x(10)}$ mean that the final population size is positively related to r and K. And $|\gamma_r^{x(10)}| > |\gamma_K^{x(10)}|$ means that the final population size is more sensitive to r (growth rate) than to K (carrying capacity), or r has larger effect on the final population size than K.

Note 1: If we cannot find an explicit expression for u, we can still compute γ_p^u numerically:

$$\gamma_p^u = \frac{\partial u}{\partial p} \times \frac{p}{u} \approx \frac{u(p+\triangle p) - u(p)}{\triangle p} \frac{p}{u(p)},$$

in which $\triangle p$ should be tiny, for example, 1% of the default p value. We can use Matlab solver to obtain u at p and u at $p + \triangle p$, then we can compute γ_p^u numerically. Of course, the above discussion is under default parameter values, which are needed in Matlab simulations.

Note 2: The sensitivity index can be applied to any mathematical model, for instance, a discrete equation, a system of differential equations, a system of discrete equations, etc.

Example 18 *Revisit the discrete bacterial reproduction model:*

$$B_{n+1} = \frac{rB_n^2}{1 + \left(\frac{B_n}{K}\right)^2}.$$

Determine sensitivity of the stable internal equilibrium with respect to the parameters r and K. The default parameters values are $r = 1$, $K = 4$.

Solution: Equilibrium values satisfy

$$B^* = \frac{rB^{*2}}{1 + \left(\frac{B^*}{K}\right)^2}$$

$\Rightarrow B^* = 0, B^* = K\left(\frac{rK}{2} - \sqrt{\left(\frac{rK}{2}\right)^2 - 1}\right), B^* = K\left(\frac{rK}{2} + \sqrt{\left(\frac{rK}{2}\right)^2 - 1}\right)$. As we have discussed in Chapter 2, the stable internal equilibrium is $B^* = K\left(\frac{rK}{2} + \sqrt{\left(\frac{rK}{2}\right)^2 - 1}\right)$. The sensitivity indices are

$$
\begin{aligned}
\gamma_r^{B^*}|_{r=1,K=4} &= \frac{\partial B^*}{\partial r}\times\frac{r}{B^*}\Big|_{r=1,K=4}\\
&= K\left(\frac{K}{2}+\frac{2\cdot\frac{rK}{2}\cdot\frac{K}{2}}{2\sqrt{\left(\frac{rK}{2}\right)^2-1}}\right)\cdot\frac{r}{K\left(\frac{rK}{2}+\sqrt{\left(\frac{rK}{2}\right)^2-1}\right)}\Bigg|_{r=1,K=4}\\
&= 4\left(2+\frac{8}{2\sqrt{3}}\right)\cdot\frac{1}{4(2+\sqrt{3})}\\
&\approx 1.15,
\end{aligned}
$$

$$
\begin{aligned}
\gamma_K^{B^*}|_{r=1,K=4} &= \frac{\partial B^*}{\partial K}\times\frac{K}{B^*}\Big|_{r=1,K=4}\\
&= \left[\left(\frac{rK}{2}+\sqrt{\left(\frac{rK}{2}\right)^2-1}\right)+K\left(\frac{r}{2}+\frac{2\cdot\frac{rK}{2}\cdot\frac{r}{2}}{2\sqrt{\left(\frac{rK}{2}\right)^2-1}}\right)\right]\\
&\quad\cdot\frac{K}{K\left(\frac{rK}{2}+\sqrt{\left(\frac{rK}{2}\right)^2-1}\right)}\Bigg|_{r=1.K=4}\\
&= \left[(2+\sqrt{3})+4\left(\frac{1}{2}+\frac{2}{2\sqrt{3}}\right)\right]\cdot\frac{1}{2+\sqrt{3}}\\
&\approx 2.15.
\end{aligned}
$$

Hence, the stable internal equilibrium is positively related to the parameters r and K, and it is more sensitive to K than to r.

Example 19 *We consider nearly pristine coral reefs where much of the prey use coral as refuge and are inaccessible to the predators. Singh, Wang, Morrison, Weiss (2012) constructed a mathematical model with an explicit refuge to illustrate a new biologically plausible mechanism that can explain stable inverted biomass pyramids in nearly pristine coral reefs. New modeling components include a refuge of explicit size, a refuge size dependent functional response, and refuge size dependent prey growth rate. The prey-predator model in a coral reef is provided by*

$$\begin{aligned} \frac{dx}{dt} &= a(r)x\left(1-\frac{x}{K}\right)-bf(x,r)y, \\ \frac{dy}{dt} &= cbf(x,r)y-dy, \end{aligned}$$

where x *is the prey biomass,* y *is the predator biomass,* b *is the maximum predation rate,* K *is the prey carrying capacity,* r *is the refuge size in coral reef,* c *is the biomass conversion efficiency, and* d *is the predator death rate. The functions in the model are the prey growth rate function* $a(r) = 0.003 + \left(\frac{0.004r^1 2}{0.1+r^1 2}\right)$*;*

the predation response function $f(x,r) = \frac{1}{1+e^{-10(x-r)}}$.

Compute sensitivity indices of the biomass ratio (predator to prey) at the coexistence equilibrium with respect to all parameters.

Note: We will learn how to analyze such a model in Chapter 6. Usually explicit solutions cannot be obtained, thus qualitative analysis is of necessary use.

Solution: Similar to the case of one differential equation, equilibrium points (x^*, y^*) satisfy

$$\begin{aligned} \frac{dx}{dt} &= 0 \\ \frac{dy}{dt} &= 0 \end{aligned}$$

$\Rightarrow$

$$\begin{aligned} a(r)x(1-x/K)-bf(x,r)y &= 0 \\ cbf(x,r)y-dy &= 0 \end{aligned}$$

$\Rightarrow$ three possibilities: $(0,0)$, $(K,0)$, and the coexistence equilibrium $(\bar{x},\bar{y})$ where $\bar{x} = r - \frac{1}{10}\ln\left(\frac{bc}{d}-1\right) > 0,\ \bar{y} = \frac{a(r)c}{d}\bar{x}\left(1-\frac{\bar{x}}{K}\right) > 0$. The biomass ratio at the coexistence equilibrium is

$$BR = \frac{\bar{y}}{\bar{x}} = \frac{a(r)c}{d}\left(1 + \frac{1}{10K}\ln\left(\frac{bc}{d} - 1\right) - \frac{r}{K}\right),$$

from which we can compute $\gamma_r^{BR}, \gamma_c^{BR}, \gamma_d^{BR}, \gamma_K^{BR}, \gamma_b^{BR}$. Given default parameter values: $r = 0.9, c = 0.15, d = 0.0005, K = 2.0, b = 0.24$, we can obtain the sensitivity table:

Parameters	Sensitivity index
r	1.55
c	0.61
d	-0.61
K	0.11
b	0.05

The biomass ratio is most sensitive to variation in the refuge size (r) and least sensitive to variation in the predation response (b). The signs of the sensitivity indices illustrate that the biomass ratio is an increasing function of r (per unit area coral reef refuge size), b (maximum predation rate), c (biomass conversion efficiency) and K (prey carrying capacity) and a decreasing function of d (predator death rate).

5 Systems of difference equations (discrete)

5.1 Analytical methods

We consider a two-dimensional discrete-time system:

$$\begin{aligned} x_{n+1} &= f(x_n, y_n), \\ y_{n+1} &= g(x_n, y_n). \end{aligned}$$

The qualitative analysis of a higher dimensional discrete-time system is, although more complicated, similar to a two-dimensional discrete-time system.

Same logic as the scalar case, equilibria (x^*, y^*) satisfy

$$\begin{aligned} x^* &= f(x^*, y^*), \\ y^* &= g(x^*, y^*). \end{aligned}$$

Stability of an equilibrium (x^*, y^*) can be determined by the following theorem:

Theorem 4 *(Linear stability analysis) Let* (x^*, y^*) *be an equilibrium of*

$$\begin{aligned} x_{n+1} &= f(x_n, y_n), \\ y_{n+1} &= g(x_n, y_n), \end{aligned}$$

and f, g *are at least twice continuously differentiable. Let*

$$J(x^*, y^*) = \begin{pmatrix} \frac{\partial f}{\partial x_n}(x^*, y^*) & \frac{\partial f}{\partial y_n}(x^*, y^*) \\ \frac{\partial g}{\partial x_n}(x^*, y^*) & \frac{\partial g}{\partial y_n}(x^*, y^*) \end{pmatrix}$$

be the Jacobian matrix of $\begin{pmatrix} f \\ g \end{pmatrix}$*, evaluated at* (x^*, y^*)*. Then*
(x^*, y^*) *is stable if all eigenvalues of* J *have magnitude less than one;*
(x^*, y^*) *is unstable if at least one of the eigenvalues has magnitude greater than one.*

Note 1: Eigenvalues λ of J are obtained from the characteristic equation $\det(J - \lambda I) = 0$ where I denotes the identity matrix.

Note 2: Magnitude of a real eigenvalue is absolute value, while magnitude of a complex eigenvalue $|a + bi| = \sqrt{a^2 + b^2}$.

Note 3: This stability theorem can be easily extended to a higher dimensional system. For a system of m difference equations, the Jacobian matrix will be $m \times m$, and there will be m eigenvalues (counting multiplicity).

Note 4: For a two-dimensional system, the characteristic equation $\det(J - \lambda I) = 0$ is equivalent to $\lambda^2 - (\mathrm{tr} J)\lambda + \det J = 0$. We can show that $|\mathrm{tr} J| < 1 + \det J < 2$ (Jury conditions) are sufficient and necessary conditions for all eigenvalues of J to have magnitude less than one, then the equilibrium (x^*, y^*) is stable.

If additionally $(\mathrm{tr} J)^2 - 4 \det J > 0$, then (x^*, y^*) is a stable node (real eigenvalues);
If additionally $(\mathrm{tr} J)^2 - 4 \det J < 0$, then (x^*, y^*) is a stable spiral (complex eigenvalues).

We will apply the above definition and theorem to analysis some discrete-time systems.

5.2 Some examples

Example 20 *We consider love affairs between Romeo and Juliet. Let* x_n *be Romeo's love/hate for Juliet on day* n*, and let* y_n *be Juliet's love/hate for Romeo on day* n*.* $x_n > 0$ *implies Romeo loves Juliet,* $x_n < 0$ *implies Romeo hates Juliet, and* $x_n = 0$ *implies Romeo is neutral to Juliet. The larger* $|x_n|$*, the stronger feeling of love/hate. Parallel assumptions hold for* y_n*. A simple linear model is provided by*

$$\begin{aligned} x_{n+1} &= ax_n + by_n, \\ y_{n+1} &= cx_n + dy_n, \end{aligned}$$

where a *and* d *are response rates to their own feelings,* b *and* c *are response rates to the feelings of the other. The sign of* b *or* c *determines a particular romantic style. Analyze this linear model mathematically.*

Solution: Equilibria (x^*, y^*) satisfy

$$\begin{aligned} x^* &= ax^* + by^* \\ y^* &= cx^* + dy^* \end{aligned}$$

$\Leftrightarrow$

$$\begin{aligned} (a-1)x^* + by^* &= 0 \\ cx^* + (d-1)y^* &= 0 \end{aligned}$$

$\Leftrightarrow$

$$\begin{pmatrix} a-1 & b \\ c & d-1 \end{pmatrix} \begin{pmatrix} x^* \\ y^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

Two cases: i) $\det\begin{pmatrix} a-1 & b \\ c & d-1 \end{pmatrix} \neq 0$; ii) $\det\begin{pmatrix} a-1 & b \\ c & d-1 \end{pmatrix} = 0$. We discuss these two cases one by one.

i) If $\det\begin{pmatrix} a-1 & b \\ c & d-1 \end{pmatrix} \neq 0$, then $(x^*, y^*) = (0,0)$ is the only equilibrium. Stability of this unique equilibrium is determined by the Jacobian matrix $J = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \Rightarrow \mathrm{tr}J = a + d$, $\det J = ad - bc$. According to Jury conditions, $(0,0)$ is stable if $|a+d| < 1 + ad - bc < 2$.

If $\det\begin{pmatrix} a-1 & b \\ c & d-1 \end{pmatrix} = 0$, then $(a-1)(d-1) - bc = 0$, that is $\dfrac{a-1}{c} = \dfrac{b}{d-1}$, thus the two algebraic equations are identical, we only need to solve from one equation, e.g. the first equation: $^* = \frac{1-a}{b}x^*$, which is the only condition for equilibria to

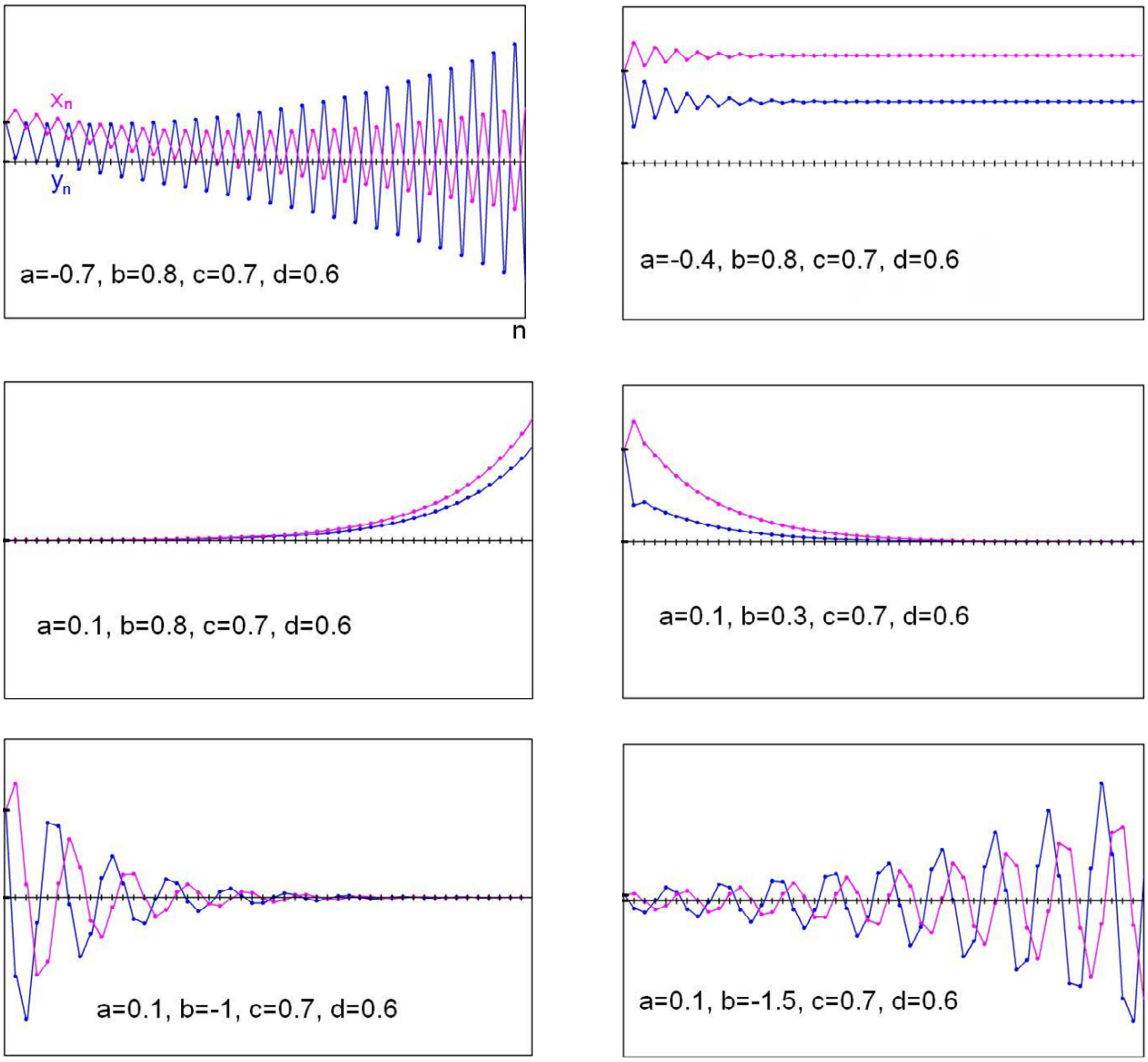


Figure 8: Different showcases of Romeo and Juliet's love affairs.

satisfy. Hence, all points of the form $(x^*, y^*) = (x^*, \frac{1-a}{b}x^*)$ are equilibria. All equilibria have the same Jacobian matrix because the system is linear. Therefore, any equilibrium $(x^*, \frac{1-a}{b}x^*)$ is stable if $|a+d| < |1+ad-bc < 2|$ which is equivalent to $|a+d| < a+d < 2$ (since $\det\begin{pmatrix} a-1 & b \\ c & d-1 \end{pmatrix} = 0 \Rightarrow ad-bc+1 = a+d$). However, the first Jury condition is never satisfied, then at least one eigenvalue has magnitude greater than or equal to one. To determine stability, We need to examine more details.

Actually when $a+d>0$, $|a+d| = a+d$, at least one eigenvalue has magnitude one with the proof:
$\lambda^2 - (\mathrm{tr}J)\lambda + \det J = 0 \Rightarrow \lambda^2 - (a+d)\lambda + ad - bc = 0 \Rightarrow$

$$\begin{aligned}
\lambda &= \frac{a+d \pm \sqrt{(a+d)^2 - 4(ad-bc)}}{2} \\
&= \frac{a+d \pm \sqrt{(a+d)^2 - 4(a+d-1)}}{2} \\
&= \frac{a+d \pm \sqrt{(a+d-2)^2}}{2} \\
&= \frac{a+d \pm (a+d-2)}{2}
\end{aligned}$$

which leads to eigenvalues $\lambda_1 = a+d-1,\ \lambda_2 = 1$. In general, we may need to look at higher order terms of the right hand side of the system when one or a few eigenvalues have magnitude one and all other eigenvalues have magnitudes less than one. Fortunately the system here is linear (no high order terms), then the stability is determined by the eigenvalue whose magnitude is not one. Hence, all equilibria $(x^*, \frac{1-a}{b}x^*)$ are stable if $|a+d-1| < 1 \Leftrightarrow 0 < a+d < 2$.

When $a+d<0$, $|a+d| > a+d$, the eigenvalues $\lambda_1 = a+d-1 < -1, \lambda_2 = 1$. Since $|\lambda_1| = |a+d-1| > 1$, then the stability theorem implies that all equilibria $(x^*, \frac{1-a}{b}x^*)$ are unstable.

Figure 8 shows various possible relations between Romeo and Juliet, depending on different parameter values. We only vary the parameters in the first equation since x_n and y_n are symmetric. From the figure, we can observe that when Romeo and Juliet have opposite response rates of their own feelings (first and second panels), or when the response rates of the feeling of the other have opposite signs (fifth and sixth panels), oscillations occur, that is, Romeo and Juliet love or hate each other alternatively. When all response rates are nonnegative, there are two possibilities: the feeling variables are increasing functions of time when at least one response rate of the feeling of the other is large ($b = 0.8$ in the third panel), that is, Romeo and Juliet love each other more and more if one of them loves the other deeply; the feeling variables are decreasing functions of time when both response rates of the feeling of the other are small ($b = 0.3$ in the fourth panel), that is, Romeo and Juliet love each other less and less if both of them only love each other a little bit.

Example 21 *We consider host-parasitoid interactions (see Figure 9). Parasitoids lay eggs on hosts, and thus hosts are separated into two groups. Parasitized hosts give rise to the next generation of parasitoids, while non-parasitized hosts give rise to the next generation of hosts. Write up a simple model for host-parasitoid interactions and perform mathematical analysis.*

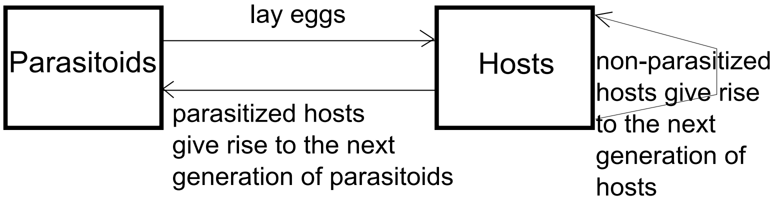


Figure 9: A flowchart of host-parasitoid model.

Solution: Let H_n be the number of hosts at generation n, P_n be the number of parasitoids at generation n. Let $f(H_n, P_n)$ be the fraction of hosts that are not parasitized, then the number of hosts not parasitized is $f(H_n, P_n)H_n$, and the number of hosts parasitized is $[1 - f(H_n, P_n)]H_n$. To simplify the model, we assume that the host population grows geometrically in the absence of the parasitoids with the reproduction rate $b > 1$, and that the average number of eggs laid in one host that give rise to adult parasitoids is $c > 0$. With these assumptions, we obtain the discrete model:

$$\begin{aligned} H_{n+1} &= bf(H_n, P_n)H_n, \\ P_{n+1} &= c[1 - f(H_n, P_n)]H_n. \end{aligned}$$

If we assume that the fraction of hosts not parasitized is a decreasing function of the parasitoid population and independent of the host population, then we can choose $f(H_n, P_n) = e^{-aP_n}$. Hence, the model becomes

$$\begin{aligned} H_{n+1} &= bH_n e^{-aP_n}, \\ P_{n+1} &= cH_n[1 - e^{-aP_n}], \end{aligned}$$

which is the classic Nicholson and Bailey's model.

Equilibria satisfy

$$\begin{aligned} H^* &= bH^* e^{-aP^*}, \\ P^* &= cH^*[1 - e^{-aP^*}], \end{aligned}$$

which leads to $(H^*, P^*) = (0, 0)$ and $(H^*, P^*) = (\frac{b \ln b}{ac(b-1)}, \frac{\ln b}{a})$ (it makes sense since $b > 1$).

We determine stability by evaluating the Jacobian matrix

$$J(H^*, P^*) = \begin{pmatrix} be^{-aP^*} & -abH^* e^{-aP^*} \\ c[1 - e^{-aP^*}] & acH^* e^{-aP^*} \end{pmatrix}$$

at each equilibrium: $J(0,0) = \begin{pmatrix} b & 0 \\ 0 & 0 \end{pmatrix}$ which leads to eigenvalues $\lambda_1 = b > 1, \lambda_2 = 0$, thus $(0,0)$ is unstable; $J(\frac{b \ln b}{ac(b-1)}, \frac{\ln b}{a}) = \begin{pmatrix} 1 & -\frac{b \ln b}{c(b-1)} \\ \frac{c(b-1)}{b} & \frac{\ln b}{b-1} \end{pmatrix}$ whose trace and determinant are $\mathrm{tr} J = 1 + \frac{\ln b}{b-1}$, $\det J = \ln b + \frac{\ln b}{b-1}$. Since $b > 1$, $|\mathrm{tr} J| < 1 + \det J$, the first Jury condition is satisfied. Since $\det J > 1$ for all $b > 1$, then the second Jury condition ($1 + \det J < 2$) is never satisfied (the inequality has the opposite direction without equal). Hence, $(\frac{b \ln b}{ac(b-1)}, \frac{\ln b}{a})$ is unstable. A natural question appears: where do solutions go? A stable cycle or chaotic attractor! This is out of the scope of this book.

Note: If $1 + \det J = 2$, then the situation can be more complicated. Besides the Jacobian matrix, high order terms need to be examined to determine stability. Same logic holds for the first Jury condition.

A sample simulation will be provided in Chapter 8 (see Figure 20).

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6 Systems of differential equations (continuous)

6.1 Some motivation examples

Example 22 *(A competition model) Consider a pond that supports two fish types: trout and bass. They compete for food. Let* $x(t)$ *be the population of trout at time* t *and* $y(t)$ *be the population of bass at time* t*. The model is provided by*

$$\begin{aligned} \frac{dx}{dt} &= ax - bxy, \qquad \text{(growth-competition)} \\ \frac{dy}{dt} &= my - nxy, \qquad \text{(growth-competition)} \end{aligned}$$

where $a, b, m, n > 0,\ x, y \geq 0$*. The parameters* a *and* m *represent the per capita growth rates of trout and bass, respectively. The parameters* b *and* n *represent the competition strengths between trout and bass.*

The mathematical analysis of this model will be discussed later. This model only considers the between-species competition. To incorporate both between-species and within-species competitions, we have the following well-known model.

Example 23 *(The Lotka-Volterra competition model) Let* $y_1(t)$ *be the population of species 1 and* $y_2(t)$ *be the population of species 2. The model incorporating both between-species and within-species competitions can be provided by*

$$\begin{aligned} \frac{dy_1}{dt} &= r_1 y_1(1 - y_1 - a_1 y_2), \\ \frac{dy_2}{dt} &= r_2 y_2(1 - y_2 - a_2 y_1), \end{aligned}$$

where $r_1, r_2, a_1, a_2 > 0,\ y_1, y_2 \geq 0$*. The right hand side of either equation is formulated as growth – within species competition – between species competition. This model is usually called the Lotka-Volterra competition model.*

We will return to this example as well after we study basic analytical methods.

Example 24 *(A basic epidemic model) Epidemic models are constructed for understanding the spread of an infectious disease in a host population.*

We define the variables and the parameters as follows:

S *— the number of susceptible individuals*

I *— the number of infected&infectious individuals*

R *— the number of recovered individuals*

$\beta > 0$ *— the transmission coefficient*

$\alpha > 0$ *— the recovery rate*

$\gamma > 0$ *— the rate for the loss of immunity*

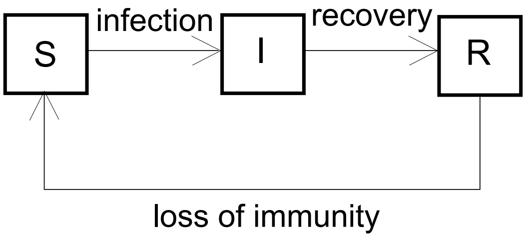


Figure 10: A flowchart of SIR epidemic model.

Infected individuals can infect susceptible individuals and can be recovered. It is possible for recovered individuals to lose their immunity after some time. The classical SIR (susceptible-infected-recovered) model describing the above process is provided by

$$\begin{aligned} S' &= -\beta SI + \gamma R, \\ I' &= \beta SI - \alpha I, \\ R' &= \alpha I - \gamma R, \end{aligned}$$

where βSI *is the rate of new incidences via direct contact between* S *and* I*, using the mass-action form.*

$(S+I+R)' = 0 \Rightarrow S+I+R = \text{constant}$, say N, then

$$\begin{aligned} S' &= -\beta SI + \gamma(N - S - I), \\ I' &= \beta SI - \alpha I, \\ R &= N - S - I, \end{aligned}$$

which is actually a two-dimensional system of differential equations since the third equation is an algebraic equation.

If we assume permanent immunity, then $\gamma = 0$, then

$$\begin{aligned} S' &= -\beta S I, \\ I' &= \beta S I - \alpha I, \\ R' &= \alpha I, \end{aligned}$$

or equivalently

$$\begin{aligned} S' &= -\beta S I, \\ I' &= \beta S I - \alpha I, \\ R &= N - S - I, \end{aligned}$$

6.2 Nondimensionalization

Nondimensionalization is a technique to reduce the number of free parameters without losing any property of the model. We discuss this technique in two examples.

Example 25 *Nondimensionalize the logistic growth model* $N' = rN\left(1 - \frac{N}{K}\right)$.

Let $\tilde{N} = \dfrac{N}{K}$ which has no unit, then

$$\frac{N'}{K} = r\frac{N}{K}\left(1 - \frac{N}{K}\right),$$

which leads to

$$\tilde{N}' = r\tilde{N}(1 - \tilde{N}).$$

Let $\tilde{t} = rt$ which has no unit, then

$$\frac{\tilde{N}}{dt} = \frac{d\tilde{N}}{d\tilde{t}}\frac{d\tilde{t}}{dt} = r\frac{d\tilde{N}}{d\tilde{t}},$$

thus

$$r\frac{d\tilde{N}}{d\tilde{t}} = r\tilde{N}(1 - \tilde{N}),$$

$$\frac{d\tilde{N}}{d\tilde{t}} = \tilde{N}(1 - \tilde{N}).$$

If we delete tilde, then we obtain the nondimensionalized model $N' = N(1 - N)$ which has no parameters!

Example 26 *Nondimensionalize the competition model*

$$\begin{aligned} x' &= ax - bxy, \\ y' &= my - nxy. \end{aligned}$$

Let $\tilde{x} = \dfrac{n}{a}x$, $\tilde{y} = \dfrac{b}{a}y$, $\tilde{t} = at$, $\mu = \dfrac{m}{a}$, all of which have no units, then the model becomes

$$\begin{aligned} \tilde{x}' &= \tilde{x} - \tilde{x}\tilde{y}, \\ \tilde{y}' &= \mu\tilde{y} - \tilde{x}\tilde{y}. \end{aligned}$$

Delete tilde to obtain the nondimensionalized model:

$$\begin{aligned} x' &= x - xy, \\ y' &= \mu y - xy, \end{aligned}$$

which has only one parameter!

6.3 Analytical methods

For a system of differential equations, usually we cannot solve it explicitly, thus qualitative analysis is useful to understand dynamical behaviors of a system. In this section, we study the qualitative analysis of a system of two differential equations:

$$\begin{aligned} x_1' &= f_1(x_1, x_2), \\ x_2' &= f_2(x_1, x_2). \end{aligned}$$

Let $x = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$, $f(x) = \begin{pmatrix} f_1(x) \\ f_2(x) \end{pmatrix} = \begin{pmatrix} f_1(x_1, x_2) \\ f_2(x_1, x_2) \end{pmatrix}$, we have the vector form:

$$x' = f(x).$$

Actually, for any number of autonomous differential equations, we can always write the system as this vector form.

Nullclines

The x_1-nullcline is the set of points (x_1, x_2) such that $x_1' = f_1(x_1, x_2) = 0$.
The x_2-nullcline is the set of points (x_1, x_2) such that $x_2' = f_2(x_1, x_2) = 0$.

Equilibrium points (or fixed points or steady states)

All equilibrium points (x_1^*, x_2^*) satisfy

$$\begin{aligned} f_1(x_1^*, x_2^*) &= 0, \\ f_2(x_1^*, x_2^*) &= 0, \end{aligned}$$

the intersection(s) of x_1- and x_2-nullclines.

Stability of equilibrium points

Jacobian matrix at (x_1^*, x_2^*): $J(x_1^*, x_2^*) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1}(x_1^*, x_2^*) & \frac{\partial f_1}{\partial x_2}(x_1^*, x_2^*) \\ \frac{\partial f_2}{\partial x_1}(x_1^*, x_2^*) & \frac{\partial f_2}{\partial x_2}(x_1^*, x_2^*) \end{pmatrix}$ Characteristic equation: $\det(J(x_1^*, x_2^*) - \lambda I) = 0$ whose roots λ_1, λ_2 are eigenvalues.

Stability criterion:

The equilibrium point (x_1^*, x_2^*) is (asymptotically) stable if all eigenvalues have negative real parts.

The equilibrium pint (x_1^*, x_2^*) is unstable if at least one of the eigenvalues has positive real part.

For a system of two differential equations, the condition “all eigenvalues have negative real parts” is equivalent to $\det J(x_1^*, x_2^*) > 0$ and $\mathrm{tr} J(x_1^*, x_2^*) < 0$.

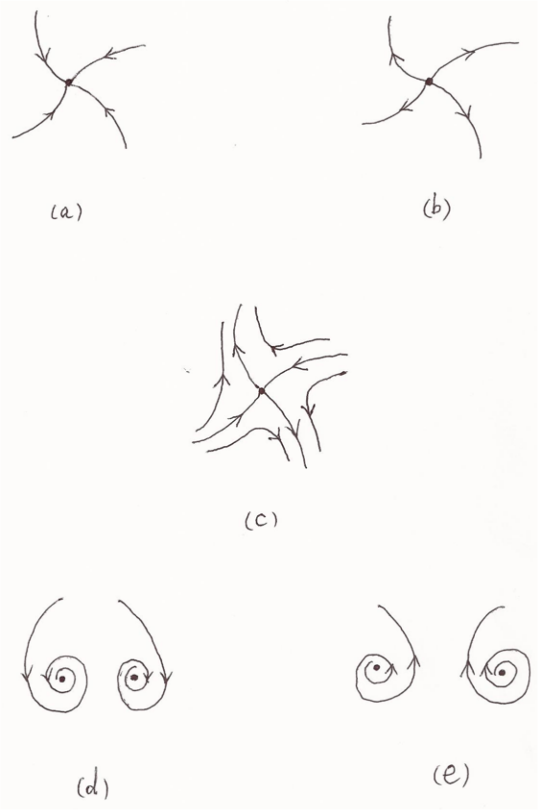


Figure 11: Types and stability of an equilibrium point.

Besides stability, we can classify equilibria in more detail (see Figure 11).

- When both eigenvalues are real and negative, then the equilibrium point (x_1^*, x_2^*) is a stable node (see panel (a)).
- When both eigenvalues are real and positive, then the equilibrium point (x_1^*, x_2^*) is an unstable node (see panel (b)).
- When one eigenvalue is negative (real) and one eigenvalue is positive (real), then the equilibrium point (x_1^*, x_2^*) is a saddle (unstable) (see panel (c)).
- When both eigenvalues are complex and have negative real parts, then the equilibrium point (x_1^*, x_2^*) is a stable spiral (see panel (d), counterclockwise versus clockwise).
- When both eigenvalues are complex and have positive real parts, then the equilibrium point (x_1^*, x_2^*) is an unstable spiral (see panel (e), counterclockwise versus clockwise).

Note: For a system of two differential equations, complex eigenvalues are complex conjugates which have the same real parts, thus the following two cases are impossible: i) one complex eigenvalue has positive real part while the other complex eigenvalue has negative real part; ii) one eigenvalue is complex while the other eigenvalue is real.

Revisit Example 22:

$$\begin{aligned}\frac{dx}{dt} &= ax - bxy,\\ \frac{dy}{dt} &= my - nxy,\end{aligned}$$

where $a, b, m, n > 0$, $x, y \geq 0$.

Equilibrium points (x^*, y^*) satisfy

$$\begin{aligned}ax^* - bx^*y^* &= 0\\ my^* - nx^*y^* &= 0\end{aligned}$$

There are two possibilities: $(0, 0)$, $(m/n, a/b)$.

We can determine their stability by checking the Jacobian matrix

$$J(x, y) = \begin{pmatrix} a - by & -bx \\ -ny & m - nx \end{pmatrix}.$$

At each equilibrium point (x^*, y^*), $J(x^*, y^*) = \begin{pmatrix} a - by^* & -bx^* \\ -ny^* & m - nx^* \end{pmatrix}$.

For the equilibrium $(0,0)$,

$$J(0,0) = \begin{pmatrix} a & 0 \\ 0 & m \end{pmatrix}$$

$$\det(J(0,0) - \lambda I) = 0$$

$$\det \begin{pmatrix} a-\lambda & 0 \\ 0 & m-\lambda \end{pmatrix}$$

$$(a-\lambda)(m-\lambda) = 0$$

Eigenvalues: $\lambda_1 = a > 0,\ \lambda_2 = m > 0$. Thus, the equilibrium $(0,0)$ is an unstable node.

For the equilibrium $(m/n, a/b)$,

$$J(m/n, a/b) = \begin{pmatrix} 0 & -bm/n \\ -na/b & 0 \end{pmatrix}$$

$$\det(J(m/n, a/b) - \lambda I) = 0$$

$$\det \begin{pmatrix} -\lambda & -bm/n \\ -na/b & -\lambda \end{pmatrix} = 0$$

$$\lambda^2 - am = 0$$

$$\lambda = \pm\sqrt{am}$$

Since $am > 0$, we obtain two real eigenvalues: $\lambda_1 = \sqrt{am} > 0, \lambda_2 = -\sqrt{am} < 0$. Thus the equilibrium $(m/n, a/b)$ is a saddle (unstable).

Revisit Example 23:

$$\begin{aligned} \frac{dy_1}{dt} &= r_1 y_1(1 - y_1 - a_1 y_2), \\ \frac{dy_2}{dt} &= r_2 y_2(1 - y_2 - a_2 y_1), \end{aligned}$$

where $r_1, r_2, a_1, a_2 > 0,\ y_1, y_2 \geq 0$.

Equilibrium points $(\bar{y}_1, \bar{y}_2)$ satisfy

$$\begin{aligned} r_1\bar{y}_1(1-\bar{y}_1-a_1\bar{y}_2) &= 0 \\ r_2\bar{y}_2(1-\bar{y}_2-a_2\bar{y}_1) &= 0 \end{aligned}$$

There are four possibilities: $(0,0), (1,0), (0,1), (y_1^*, y_2^*)$ where y_1^*, y_2^* satisfy

$$\begin{aligned} 1-y_1^*-a_1y_2^* &= 0 \\ 1-y_2^*-a_2y_1^* &= 0 \end{aligned}$$

$\Rightarrow y_1^* = \frac{1-a_1}{1-a_1a_2}, \; y_2^* = \frac{1-a_2}{1-a_1a_2}.$

Jacobian matrix

$$\begin{aligned} J(\bar{y}_1, \bar{y}_2) &= \begin{pmatrix} \frac{\partial f_1}{\partial y_1} & \frac{\partial f_1}{\partial y_2} \\ \frac{\partial f_2}{\partial y_1} & \frac{\partial f_2}{\partial y_2} \end{pmatrix}_{(\bar{y}_1, \bar{y}_2)} \\ &= \begin{pmatrix} r_1(1-2y_1-a_1y_2) & -r_1a_1y_1 \\ -r_2a_2y_2 & r_2(1-2y_2-a_2y_1) \end{pmatrix} \\ &= \begin{pmatrix} r_1(1-2\bar{y}_1-a_1\bar{y}_2) & -r_1a_1\bar{y}_1 \\ -r_2a_2\bar{y}_2 & r_2(1-2\bar{y}_2-a_2\bar{y}_1) \end{pmatrix}. \end{aligned}$$

For the equilibrium point $(0,0)$, the Jacobian matrix $J(0,0)=\begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix}$ has eigenvalues $\lambda_1 = r_1 > 0, \lambda_2 = r_2 > 0$, thus the equilibrium $(0,0)$ is an unstable node.

For the equilibrium point $(1,0)$, the Jacobian matrix $J(1,0)=\begin{pmatrix} -r_1 & -r_1a_1 \\ 0 & r_2(1-a_2) \end{pmatrix}$ has eigenvalues $\lambda_1 = -r_1 < 0, \lambda_2 = r_2(1-a_2)$. Thus the equilibrium $(1,0)$ is asymptotically stable (a stable node) if $a_2 > 1$, and it is unstable (a saddle) if $a_2 < 1$.

For the equilibrium point $(0,1)$, the Jacobian matrix $J(0,1)=\begin{pmatrix} r_1(1-a_1) & 0 \\ -r_2a_2 & -r_2 \end{pmatrix}$ has eigenvalues $\lambda_1 = r_1(1-a_1), \lambda_2 = -r_2 < 0$. Thus the equilibrium $(0,1)$ is asymptotically stable (a stable node) if $a_1 > 1$, and it is unstable (a saddle) if $a_1 < 1$.

For the coexistence/internal equilibrium point (y_1^*, y_2^*), the Jacobian matrix

$$\begin{aligned}
J(y_1^*, y_2^*) &= \begin{pmatrix} r_1(1-2y_1^*-a_1y_2^*) & -r_1a_1y_1^* \\ -r_2a_2y_2^* & r_2(1-2y_2^*-a_2y_1^*) \end{pmatrix} \\
&= \begin{pmatrix} r_1(1-\frac{2-2a_1}{1-a_1a_2}-\frac{a_1-a_1a_2}{1-a_1a_2}) & -r_1\frac{a_1-a_1^2}{1-a_1a_2} \\ -r_2\frac{a_2-a_2^2}{1-a_1a_2} & r_2(1-\frac{2-2a_2}{1-a_1a_2}-\frac{a_2-a_1a_2}{1-a_1a_2}) \end{pmatrix} \\
&= \begin{pmatrix} \frac{r_1(1-a_1a_2-2+2a_1-a_1+a_1a_2)}{1-a_1a_2} & \frac{r_1(a_1^2-a_1)}{1-a_1a_2} \\ \frac{r_2(a_2^2-a_2)}{1-a_1a_2} & \frac{r_2(1-a_1a_2-2+2a_2-a_2+a_1a_2)}{1-a_1a_2} \end{pmatrix} \\
&= \frac{1}{1-a_1a_2}\begin{pmatrix} r_1(a_1-1) & r_1a_1(a_1-1) \\ r_2a_2(a_2-1) & r_2(a_2-1) \end{pmatrix}.
\end{aligned}$$

Now we check the conditions $\mathrm{tr}J(y_1^*, y_2^*) < 0$ and $\det J(y_1^*, y_2^*) > 0$. All eigenvalues have negative real parts if and only if

$$\mathrm{tr}J = \frac{r_1(a_1-1)+r_2(a_2-1)}{1-a_1a_2} < 0$$

and

$$\det J = \frac{r_1r_2(a_1-1)(a_2-1)}{(1-a_1a_2)^2} - \frac{a_1a_2r_1r_2(a_1-1)(a_2-1)}{(1-a_1a_2)^2} = \frac{r_1r_2(a_1-1)(a_2-1)}{1-a_1a_2} > 0.$$

We consider four cases:

(i) $a_1 > 1$ and $a_2 > 1 \Rightarrow \dfrac{r_1 r_2 (a_1 - 1)(a_2 - 1)}{1 - a_1 a_2} < 0$, the second inequality is violated, thus the coexistence equilibrium (y_1^*, y_2^*) is unstable.

(ii) $a_1 < 1$ and $a_2 < 1 \Rightarrow$ both inequalities are valid, thus the coexistence equilibrium (y_1^*, y_2^*) is asymptotically stable.

(iii) $a_1 > 1$ and $a_2 < 1 \Rightarrow$ it is difficult to determine whether any of the two inequalities are valid.

(iv) $a_1 < 1$ and $a_2 > 1 \Rightarrow$ it is difficult to determine whether any of the two inequalities are valid.

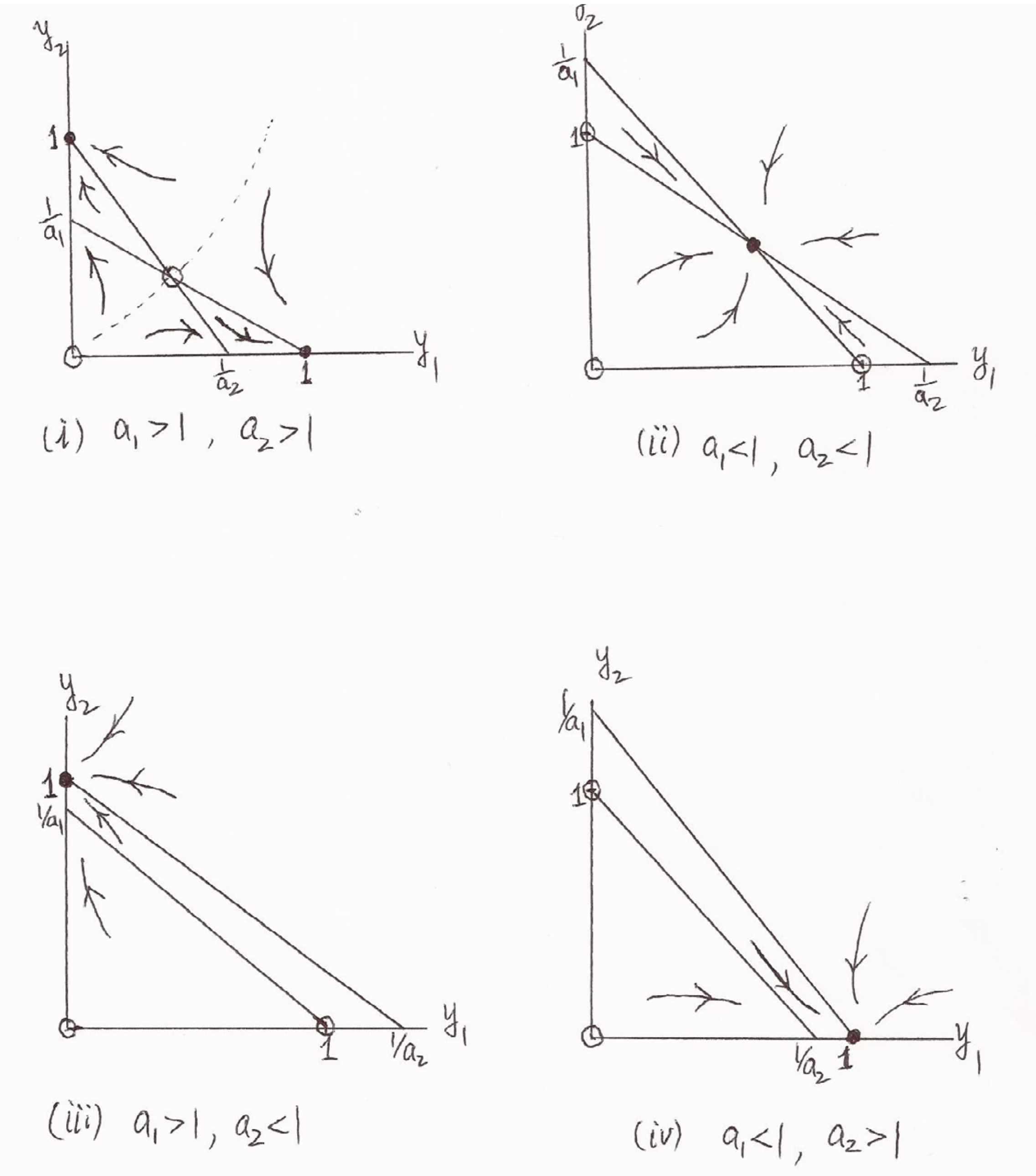
Since populations y_1, y_2 are nonnegative, we only consider the first quadrant of the phase plane (y_1-y_2 plane). We need to examine whether y_1^*, y_2^* are nonnegative.

For case (iii) and case (iv), $y_1^* y_2^* = \frac{(1-a_1)(1-a_2)}{(1-a_1 a_2)^2} < 0$, thus either y_1^* or y_2^* is negative. This means that the coexistence equilibrium (y_1^*, y_2^*) is unfeasible.

For case (i) and case (ii), the coexistence equilibrium (y_1^*, y_2^*) is obviously feasible in the first quadrant.

As a conclusion, there are four cases under different values of a_1 and a_2.
y_1-nullcline: $f_1(y_1, y_2) = 0 \Leftrightarrow y_1 = 0$ or $1 - y_1 - a_1 y_2 = 0$.
y_2-nullcline: $f_2(y_1, y_2) = 0 \Leftrightarrow y_2 = 0$ or $1 - y_2 - a_2 y_1 = 0$.
Intersections of different nullclines provide equilibrium points.

We plot phase portraits for the four cases in Figure 12 accordingly. Nullclines and equilibria are sketched with some representative solutions. Solid points represent stability while circles represent instability. The dotted curve in the first panel represents the separatrix (stable manifold of the internal saddle) for the attracting basins of the two stable equilibrium points. This panel indicates that when both species are strong in between-species competition ($a_1 > 1, a_2 > 1$), who wins the competition depends on the initial population sizes. All solutions in the second panel tend to the only stable equilibrium (y_1^*, y_2^*). This panel indicates that when the between-species competition is weak ($a_1 < 1, a_2 < 1$), the two competing species can coexist. All solutions in the third panel tend to the only stable equilibrium $(0, 1)$, and the intersection of the two internal nullclines is in the second quadrant. This panel indicates that when species 1 is stronger than species 2 ($a_1 > 1 > a_2$), species 1 always wins the competition. All solutions in the fourth panel tend to the only stable equilibrium $(1, 0)$, and the intersection of the two internal nullclines is in the fourth quadrant. This panel indicates that when species 1 is weaker than species 2 ($a_1 < 1 < a_2$), species 2 always wins the competition. These results are all reasonable in biology, thus the simple Lotka-Volterra competition model captures the main qualitative features of species competition.



(i) $a_1 > 1$, $a_2 > 1$ (ii) $a_1 < 1$, $a_2 < 1$

(iii) $a_1 > 1$, $a_2 < 1$ (iv) $a_1 < 1$, $a_2 > 1$

Figure 12: Phase portrait of the Lotka-Volterra competition model.

Revisit Example 24:

$$\begin{aligned} S' &= -\beta S I \\ I' &= \beta S I - \alpha I \end{aligned}$$

$$\frac{d}{dt}\begin{pmatrix} S \\ I \end{pmatrix} = \begin{pmatrix} -\beta S I \\ \beta S I - \alpha I \end{pmatrix}$$

which is simple but still a nonlinear system.

Equilibria (S^*, I^*) satisfy

$$\begin{aligned} -\beta S^* I^* &= 0, \\ \beta S^* I^* - \alpha I^* &= 0. \end{aligned}$$

The first equation implies that $S^* = 0$ or $I^* = 0$.
When $S^* = 0$, the second equation implies that $I^* = 0$.
When $I^* = 0$, the second equation is always satisfied, thus S^* can be any nonnegative number.
Hence, we have infinitely many equilibria $(\bar{S}, 0)$, $\bar{S} \geq 0$.

To determine the type and stability of equilibria, we need to consider the Jacobian matrix at each equilibrium and compute eigenvalues. The Jacobian matrix $J(S, I) = \begin{pmatrix} -\beta I & -\beta S \\ \beta I & \beta S - \alpha \end{pmatrix}$ $\Rightarrow$ $J(\bar{S}, 0) = \begin{pmatrix} 0 & -\beta \bar{S} \\ 0 & \beta \bar{S} - \alpha \end{pmatrix}$ $\Rightarrow$ Eigenvalues are $\lambda_1 = 0$ (neutral for stability), $\lambda_2 = \beta \bar{S} - \alpha \begin{cases} > 0 & \text{if} \quad \bar{S} > \alpha/\beta; \\ < 0 & \text{if} \quad \bar{S} < \alpha/\beta. \end{cases}$

Based on the value of $\bar{S}$, should the model have a group of equilibria unstable and a group of equilibria stable?

$$\frac{dI}{dS} = \frac{dI/dt}{dS/dt} = \frac{\beta SI - \alpha I}{-\beta SI} = -1 + \frac{\alpha}{\beta S},$$

then $I = \int \left(-1 + \frac{\alpha}{\beta S}\right) dS = -S + \frac{\alpha}{\beta} \ln S + C$.

If the initial point is (S_0, I_0), then $I_0 = -S_0 + \frac{\alpha}{\beta} \ln S_0 + C \Rightarrow C = I_0 + S_0 - \frac{\alpha}{\beta} \ln S_0$. Hence, $I = \frac{\alpha}{\beta} \ln S - S + (I_0 + S_0 - \frac{\alpha}{\beta} \ln S_0)$.

Phase portrait is sketched in Figure 13 that shows the following observations:

If $S_0 > \alpha/\beta$, then I initially increases, reaching its maximum at $S = \alpha/\beta$, and then decreases. Therefore, there is an outbreak (or epidemic) in this case.

If $S_0 < \alpha/\beta$, then no epidemic is possible, and I decreases from the beginning.

Obviously, the value α/β represents the critical population size for causing an epidemic.

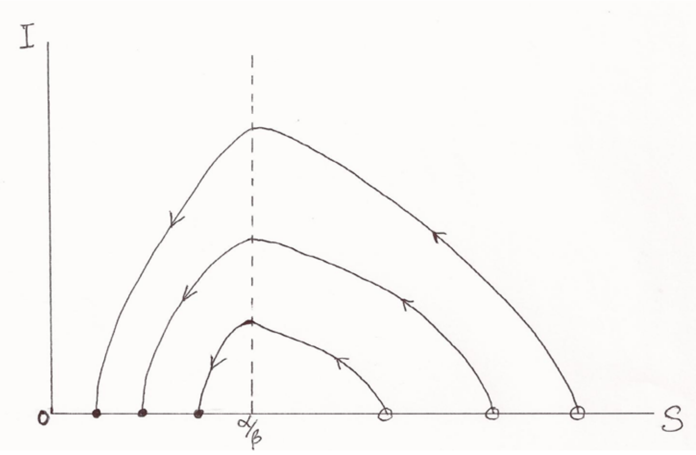


Figure 13: Phase portrait of the SIR epidemic model.

We look at one more example, which will be discussed again in Chapter 7.

Example 27 *Analyze the model*

$$\begin{aligned}\frac{dx_1}{dt} &= -x_2 + x_1(\mu - x_1^2 - x_2^2),\\ \frac{dx_2}{dt} &= x_1 + x_2(\mu - x_1^2 - x_2^2).\end{aligned}$$

Solution:
x_1-nullcline: $-x_2 + x_1(\mu - x_1^2 - x_2^2) = 0$,
x_2-nullcline: $x_1 + x_2(\mu - x_1^2 - x_2^2) = 0$,
both of which are not straight lines.

Equilibria (x_1^*, x_2^*) satisfy

$$\begin{aligned}-x_2^* + x_1^*(\mu - x_1^{*2} - x_2^{*2}) &= 0\\ x_1^* + x_2^*(\mu - x_1^{*2} - x_2^{*2}) &= 0\end{aligned}$$

$\Leftrightarrow$

$$\begin{aligned}x_1^*(\mu - x_1^{*2} - x_2^{*2}) &= x_2^*\\ x_2^*(\mu - x_1^{*2} - x_2^{*2}) &= -x_1^*\end{aligned}$$

$\Rightarrow$

$$(x_1^{*2} + x_2^{*2})(\mu - x_1^{*2} - x_2^{*2}) = 0$$

$\Rightarrow$

$$x_1^{*2}+x_2^{*2}=0 \quad \text{or} \quad \mu-x_1^{*2}-x_2^{*2}=0$$

$\Rightarrow$

$$x_1^*=x_2^*=0.$$

The system has only one equilibrium point $(0,0)$.

To determine its stability, we examine its Jacobian matrix:

$$J(x_1,x_2)=\begin{pmatrix} \mu-3x_1^2-x_2^2 & -1-2x_1x_2 \\ 1-2x_1x_2 & \mu-x_1^2-3x_2^2 \end{pmatrix}$$

$$J(0,0)=\begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}$$

$$\det(J(0,0)-\lambda I)=0$$

$$\det\begin{pmatrix} \mu-\lambda & -1 \\ 1 & \mu-\lambda \end{pmatrix}=0$$

$$(\mu-\lambda)^2+1=0$$

$$(\mu-\lambda)^2=-1$$

$$(\lambda-\mu)^2=-1$$

$$\lambda-\mu=\pm i$$

$$\lambda=\mu\pm i$$

Eigenvalues are two complex conjugates: $\lambda_1=\mu+i$, $\lambda_2=\mu-i$.

Hence, the only equilibrium point $(0,0)$ is

- a stable spiral when $\mu<0$,
- an unstable spiral when $\mu>0$.

This example provides the canonical form for the Hopf bifurcation, from which the limit cycle occurs. We will discuss basic bifurcations in Chapter 7.

Stability of an equilibrium we discuss in this book is local stability (initial points are close to the equilibrium). Global stability of an equilibrium in a two dimensional system can be determined by Poincaré-Bendixson theorem (to claim all possibilities) and Dulac criterion (to exclude limit cycles).

6.4 Higher dimensional systems

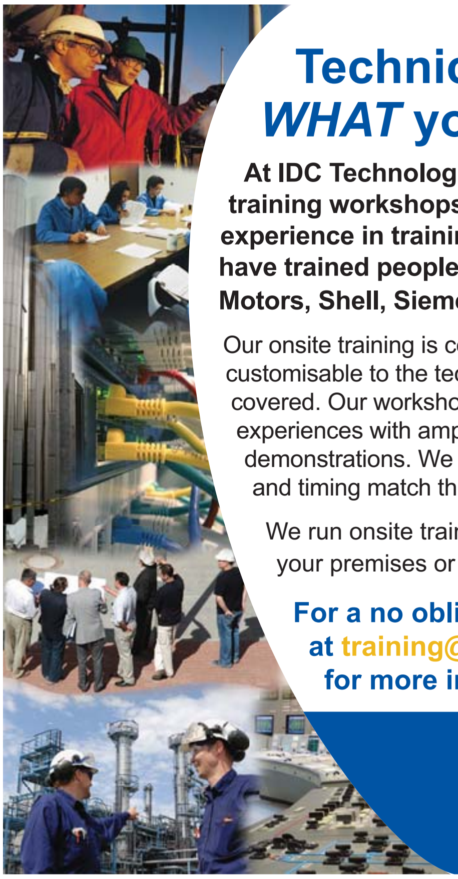
In this section, we briefly mention the analysis of a system with dimension three or higher. The general system can be expressed as

$$\begin{aligned} \frac{dx_1}{dt} &= f_1(x_1, \cdots, x_n) \\ &\vdots \\ \frac{dx_n}{dt} &= f_n(x_1, \cdots, x_n) \end{aligned}$$

In the vector notation, the system is $\frac{dx}{dt} = f(x)$, where $= \begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix}$, $f(x) = \begin{pmatrix} f_1(x) \\ \vdots \\ f_n(x) \end{pmatrix} = \begin{pmatrix} f_1(x_1, \cdots, x_n) \\ \vdots \\ f_n(x_1, \cdots, x_n) \end{pmatrix}$.

Equilibria x^* satisfy $f(x^*) = 0 \Leftrightarrow$

$$\begin{aligned} f_1(x^*) &= 0 \\ &\vdots \\ f_n(x^*) &= 0 \end{aligned}$$



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$\Leftrightarrow$

$$\begin{array}{rcl} f_1(x_1^*, x_2^*, \cdots, x_n^*) & = & 0 \\ & \vdots & \\ f_n(x_1^*, x_2^*, \cdots, x_n^*) & = & 0 \end{array}$$

Stability of each equilibrium x^* is determined by the associated Jacobian matrix

$$J(x^*) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1}(x^*) & \cdots & \frac{\partial f_1}{\partial x_n}(x^*) \\ \vdots & \cdots & \vdots \\ \frac{\partial f_n}{\partial x_1}(x^*) & \cdots & \frac{\partial f_n}{\partial x_n}(x^*) \end{pmatrix}$$

$\det(\lambda I - J(x^*)) = 0 \Rightarrow$ Eigenvalues $\lambda_1, \lambda_2, \cdots, \lambda_n$ (some of them may be same) $\Rightarrow$ Stability of x^* and local solution behaviors.

The characteristic equation $\det(\lambda I - J(x^*)) = 0$ is a polynomial with degree n. Here $n \geq 3$, thus it is likely that we cannot obtain all eigenvalues explicitly. We usually apply Routh-Hurwitz theorem that provides conditions for all eigenvalues to have negative real parts.

Global stability of an equilibrium in a system with dimension three or higher is extremely complicated and may be determined by Lyapunov functions or theory of monotone dynamics systems or compound matrices if lucky.

7 Bifurcation analysis

Bifurcation analysis is an important technique to understand the role of key parameters in the output of the studied model and to examine the robustness of theoretical results. In this textbook, we only consider one bifurcation parameter. Multiple bifurcation parameters are more complicated but follow similar ideas. We will discuss one-dimensional flows (generated from one equation) for typical bifurcation types: saddle-node bifurcation, transcritical bifurcation, pitchfork bifurcation. We will also discuss two-dimensional flows (generated from a system of two equations) for typical bifurcation types: saddle-node bifurcation, transcritical bifurcation, pitchfork bifurcation, Hopf bifurcation. Note that Hopf bifurcation can only occur in a system of two or more equations. These typical bifurcation types frequently appear in higher dimensional equations as well.

7.1 Saddle-node bifurcation

The saddle-node bifurcation occurs when equilibrium points are created and destroyed. As the bifurcation parameter varies, two equilibrium points move toward each other, collide, and finally disappear.

Example 28 *For the equation* $\dfrac{dx}{dt} = r + x^2$, *discuss how equilibrium points and their stability change as the parameter* r *varies.*

Solution: When $r < 0$, there are two equilibrium points: $x = \sqrt{-r}$ (unstable), $x = -\sqrt{-r}$ (stable).

When $r = 0$, the only equilibrium point $x = 0$ is half-stable.

When $r > 0$, no equilibrium points exist.

These three cases are plotted in Figure 14.

We can plot these results in a bifurcation diagram (the last panel of Figure 14) which sketches the key dynamical features (equilibria, limit cycles, etc.) versus the bifurcation parameter. The saddle-node bifurcation occurs at $r = 0$.

Example 29 *For the equation* $\dfrac{dx}{dt} = r - x^2$, *discuss how equilibrium points and their stability change as the parameter* r *varies. Plot the bifurcation diagram.*

We leave this problem to readers since the process is same as Example 28.

Other names of saddle-node bifurcation include fold bifurcation, turning-point bifurcation.

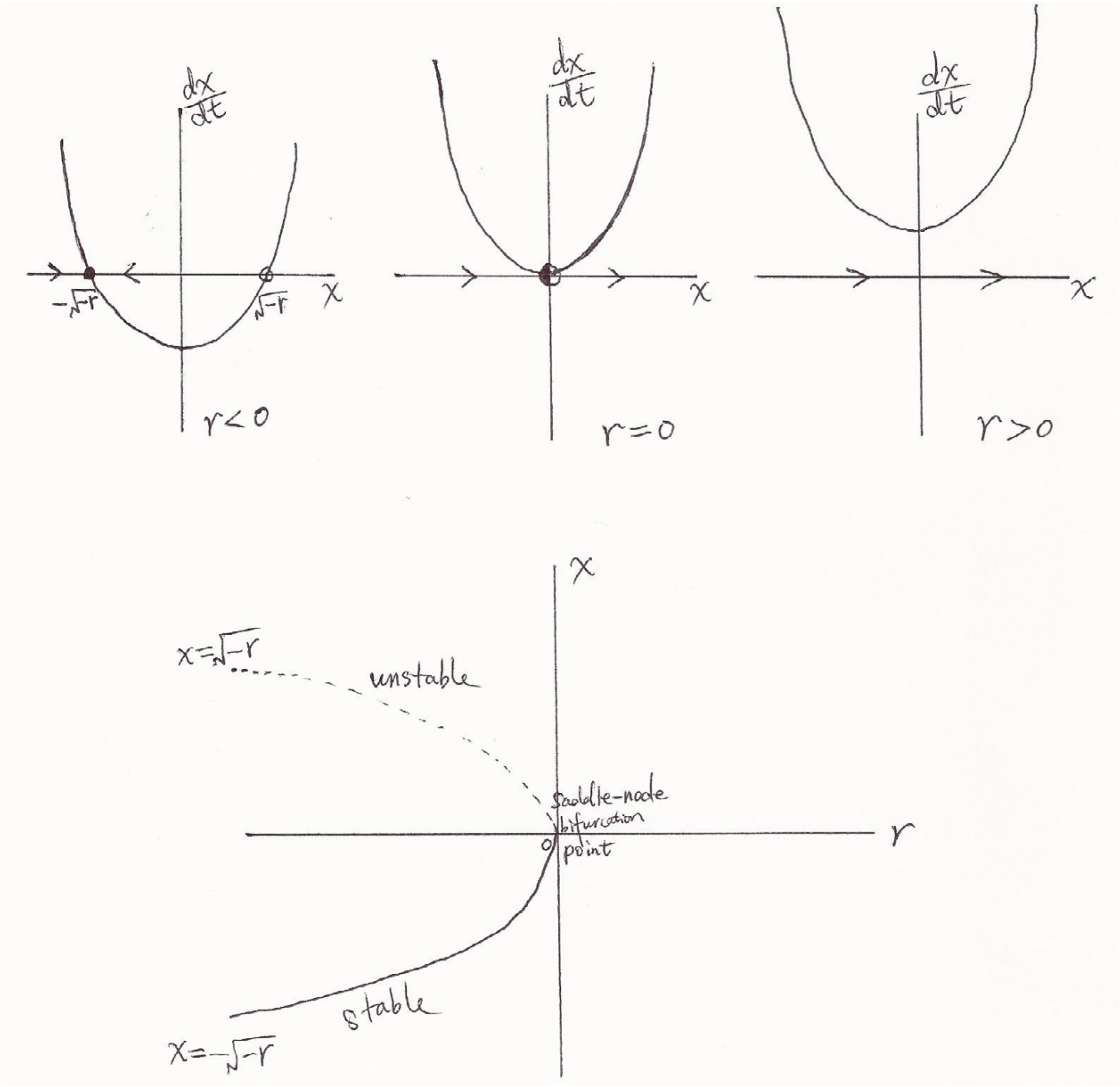


Figure 14: Three cases of Example 28 and the bifurcation diagram.

7.2 Transcritical bifurcation

The transcritical bifurcation occurs when an equilibrium point always exists but changes its stability as the bifurcation parameter varies.

Example 30 *Perform bifurcation analysis of the equation* $\dfrac{dx}{dt} = rx - x^2$.

Solution: Equilibrium points are $x = 0$ and $x = r$.

When $r < 0$, the equilibrium point $x = 0$ is stable and the equilibrium point $x = r$ is unstable.

When $r = 0$, the equilibrium point $x = 0$ and the equilibrium point $x = r$ collide and are half-stable.

When $r > 0$, the equilibrium point $x = 0$ is unstable and the equilibrium point $x = r$ is stable.

These three cases are plotted in Figure 15.

The equilibrium point $x = 0$ exists for all values of r. As r increases from negative to positive, the two equilibrium points exchange their stabilities. We conclude these results in a bifurcation diagram (the last panel of Figure 15). The transcritical bifurcation occurs at $r = 0$.

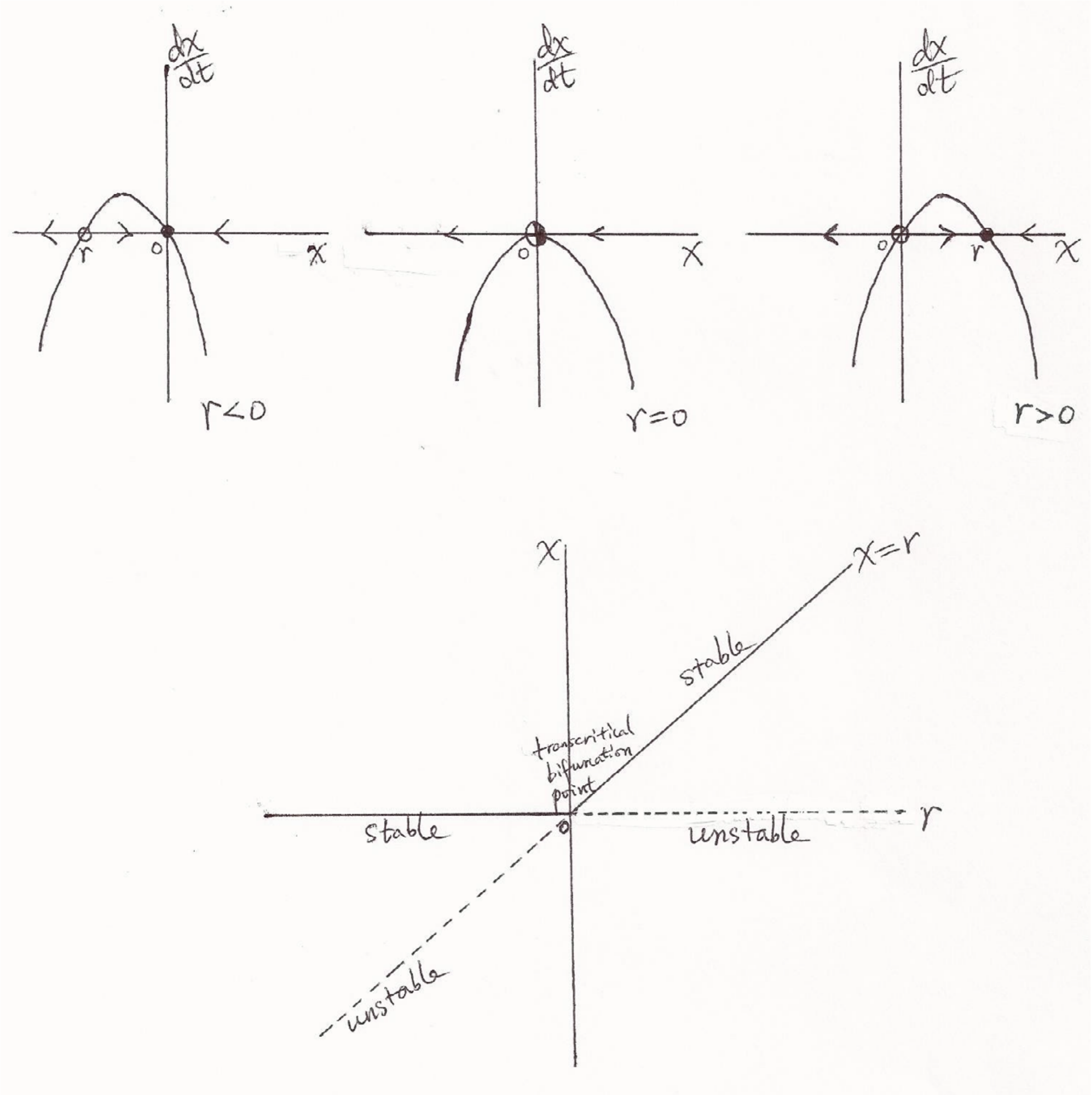


Figure 15: Three cases and the bifurcation diagram of Example 30.

7.3 Pitchfork bifurcation

There are two types of pitchfork bifurcation: supercritical and subcritical. The supercritical pitchfork bifurcation occurs when the following dynamical switch occurs: As the bifurcation parameter varies, a forever existing equilibrium changes its stability from stable to unstable, and two new equilibrium points appear and are stable. The subcritical pitchfork bifurcation occurs when the following dynamical switch occurs: As the bifurcation parameter varies, a forever existing equilibrium changes its stability from unstable to stable, and two new equilibrium points appear and are unstable.

Example 31 *Perform bifurcation analysis of the equation* $\dfrac{dx}{dt} = rx - x^3$ *(supercritical case).*

Solution: When $r \leq 0$, $x = 0$ is the only equilibrium and stable.

When $r > 0$, there are three equilibria: $x = 0$ is unstable, and $x = \pm\sqrt{r}$ are stable.

The first two panels of Figure 16 show the phase portraits of these two cases.

We conclude the supercritical pitchfork bifurcation (occurring at $r = 0$) in a bifurcation diagram (the third panel of Figure 16). We can observe that as the bifurcation parameter r increases from negative to positive, the trivial equilibrium changes its stability from stable to unstable, and two new stable equilibria appear.

Example 32 *Perform bifurcation analysis of the equation* $\frac{dx}{dt} = rx + x^3$ *(subcritical case).*

Solution: When $r > 0,\ x = 0$ is the only equilibrium and unstable.

When $r \leq 0$, there are three equilibria: $x = 0$ is stable, and $x = \pm\sqrt{-r}$ are unstable.

The fourth and fifth panels of Figure 16 show the phase portraits of these two cases.

We conclude the subcritical pitchfork bifurcation (occurring at $r = 0$) in a bifurcation diagram (the last panel of Figure 16). We can observe that as the bifurcation parameter r decreases from positive to negative, the trivial equilibrium changes its stability from unstable to stable, and two new unstable equilibria appear.

The supercritical pitchfork bifurcation is also called a forward bifurcation. The subcritical pitchfork bifurcation is also called an inverted or backward bifurcation.

7.4 Generic saddle-node bifurcation

In this section, we discuss the generic form of saddle-node bifurcation which can be extended from the normal from of saddle-node bifurcation (Section 7.1). Similar ideas can be applied to discuss generic transcritical or pitchfork bifurcation.

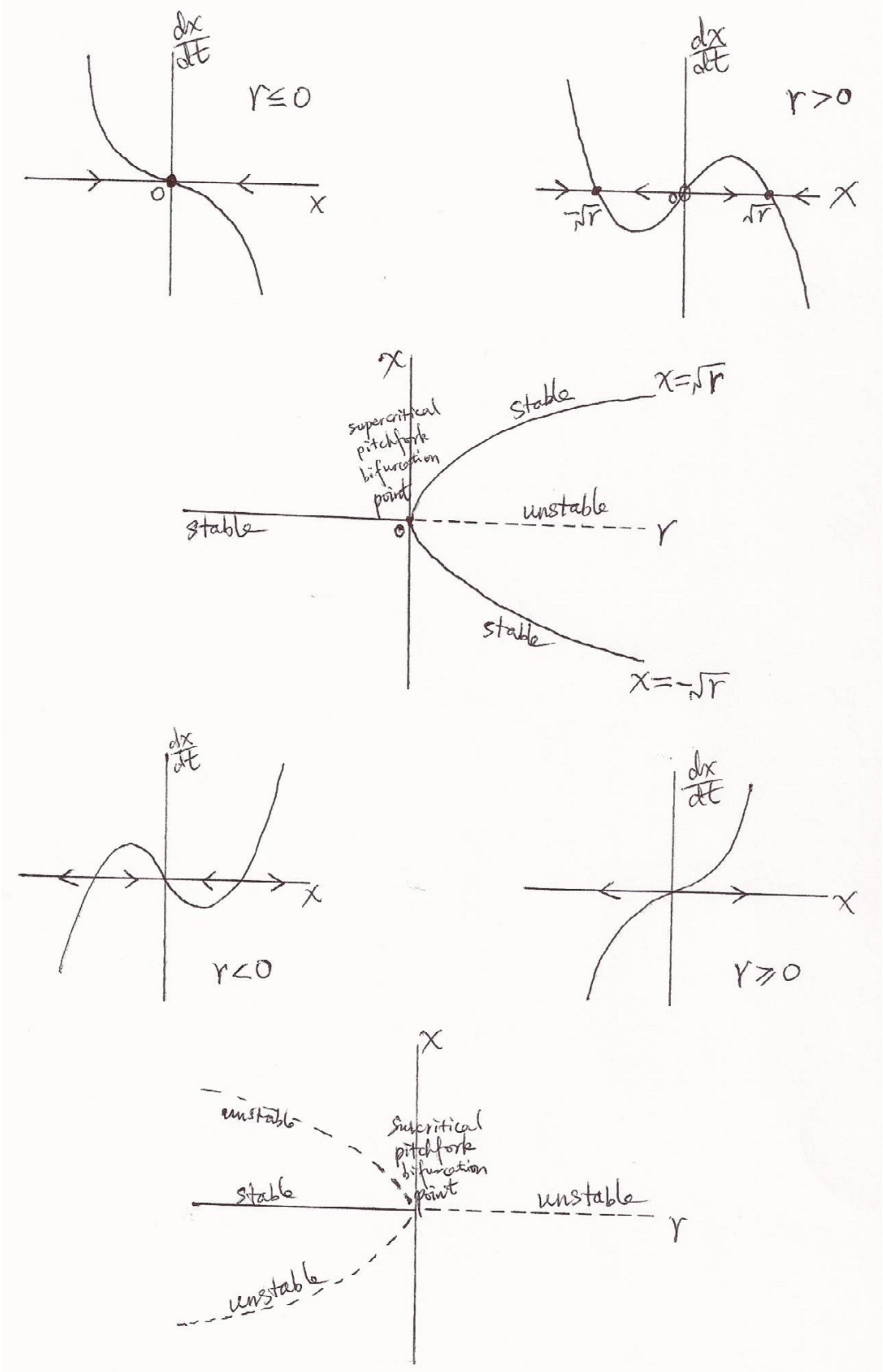


Figure 16: The first three panels are for supercritical pitchfork bifurcation and the last three panels are for subcritical pitchfork bifurcation.

The normal form of saddle-node bifurcation is $\frac{dx}{dt} = r + x^2$. We first discuss the extension of this normal form with a higher order term, and then we discuss the generic form.

Lemma 1 *The equation* $\frac{dx}{dt} = r + x^2 + O(x^3)$ *is locally topologically equivalent near the origin to the equation* $\frac{dx}{dt} = r + x^2$.

Topological equivalence means that one object can be continuously deformed to the other, i.e. there is a homeomorphism of one onto the other, i.e. there is a one-to-one map between them that is continuous in both directions. This lemma claims that adding a higher order term will not change the existence of saddle-node bifurcation. The proof can be found in "Elements of Applied Bifurcation Theory" by Yuri A. Kuznetsov.

Generic case: $\frac{dx}{dt} = f(x,r), x \in \mathcal{R}^1, r \in \mathcal{R}^1$, with s smooth function f, and at $r = 0$, the equilibrium $x = 0$ has the eigenvalue $\lambda = f_x(0,0) = 0$ (saddle-node bifurcation condition).

Expand $f(x,r)$ as a Taylor series with respect to x at $x = 0$:

$$f(x,r) = f_0(r) + f_1(r)x + f_2(r)x^2 + O(x^3).$$

Equilibrium condition: $f(0,0) = 0$, i.e. $f_0(0) = 0$;

Saddle-node bifurcation condition: $f_x(0,0) = 0$, i.e. $f_1(0) = 0$.

When solutions are near the bifurcation point, the generic equation becomes the normal equation plus higher order terms.

Theorem 5 *Suppose that a one-dimensional system* $\frac{dx}{dt} = f(x,r), x \in \mathcal{R}^1, r \in \mathcal{R}^1$, *with smooth* f, *has the equilibrium* $x = 0$ *at* $r = 0$. *Assume that*

(A1) $\lambda = f_x(0,0) = 0$

(A2) $f_{xx}(0,0) \neq 0$

(A3) $f_r(0,0) \neq 0$

where (A2) and (A3) are for invertibility. Then there exist invertible coordinate and parameter changes transforming the system into

$$\frac{d\hat{x}}{d\tau} = \hat{r} \pm \hat{x}^2 + O(\hat{x}^3).$$

Theorem 5 together with Lemma 1 implies that the generic case $\dfrac{dx}{dt} = f(x, r)$ with (A1),(A2),(A3) and the equilibrium $x = 0$ at $r = 0$, is locally topologically equivalent near the origin to one of the normal forms:

$$\frac{d\hat{x}}{d\tau} = \hat{r} \pm \hat{x}^2.$$

Is this useful? No doubt!

Even if we cannot compute bifurcation points by hand, the existence conditions of bifurcations provide underlying ideas for programming of bifurcation diagrams (Matlab, xppaut, etc.).

Example 33 *Determine whether the equation* $\dfrac{dx}{dt} = r - x - e^{-x} \triangleq f(x, r)$ *possesses saddle-node bifurcation.*

Solution: At $r = 0$, $x = 0$ is not an equilibrium, since $f(0, 0) = -1 \neq 0$.

Rewrite the equation as $\dfrac{dx}{dt} = (r - 1) + 1 - x - e^{-x}$.

Let $\bar{r} = r - 1$, then $\dfrac{dx}{dt} = \bar{r} + 1 - x - e^{-x} \triangleq \bar{f}(x, \bar{r})$.

Now $\bar{f}(0,0) = 0$, i.e. $x = 0$ is an equilibrium at $\bar{r} = 0$. We can check the three conditions in Theorem 5:

(A1) $\lambda = \bar{f}_x(0,0) = -1 + e^{-x}|_{(0,0)} = 0$

(A2) $\bar{f}_{xx}(0,0) = -e^{-x}|_{(0,0)} = -1 \neq 0$

(A3) $\bar{f}_{\bar{r}}(0,0) = 1 \neq 0$

Hence, there exists a saddle-node bifurcation as the bifurcation parameter $\bar{r}$ (or r) varies. The bifurcation value of the parameter for the original equation is $r = 1$ (i.e. $\bar{r} = 0$). The bifurcation diagram can be plotted using Matlab or xppaut.

7.5 Saddle-node, transcritical, and pitchfork bifurcations in two-dimensional systems

We start our discussion from an example.

Example 34 *Perform bifurcation analysis of a simple decoupled system:*

$$\begin{aligned} \frac{dx}{dt} &= \mu - x^2, \\ \frac{dy}{dt} &= -y. \end{aligned}$$

Solution: If $\mu > 0$, there are two equilibria $(\sqrt{\mu}, 0), (-\sqrt{\mu}, 0)$. Their stability can be determined by their Jacobian matrices:

$J(\sqrt{\mu}, 0) = \begin{pmatrix} -2\sqrt{\mu} & 0 \\ 0 & -1 \end{pmatrix} \Rightarrow (\sqrt{\mu}, 0)$ is a stable node;

$J(-\sqrt{\mu}, 0) = \begin{pmatrix} 2\sqrt{\mu} & 0 \\ 0 & -1 \end{pmatrix} \Rightarrow (-\sqrt{\mu}, 0)$ is a saddle.

If $\mu = 0$, the system has a unique equilibrium $(0,0)$. The Jacobian matrix is $J(0,0) = \begin{pmatrix} 0 & 0 \\ 0 & -1 \end{pmatrix}$ which cannot tell the stability. However, we can solve the decoupled system easily to obtain that the equilibrium $(0,0)$ is a saddle-node (one side like a saddle and one side like a stable node). This may be the reason for the name "saddle-node" bifurcation.

If $\mu < 0$, no equilibria exist since $\mu - x^2 < 0$.

These three cases are plotted in Figure 17.

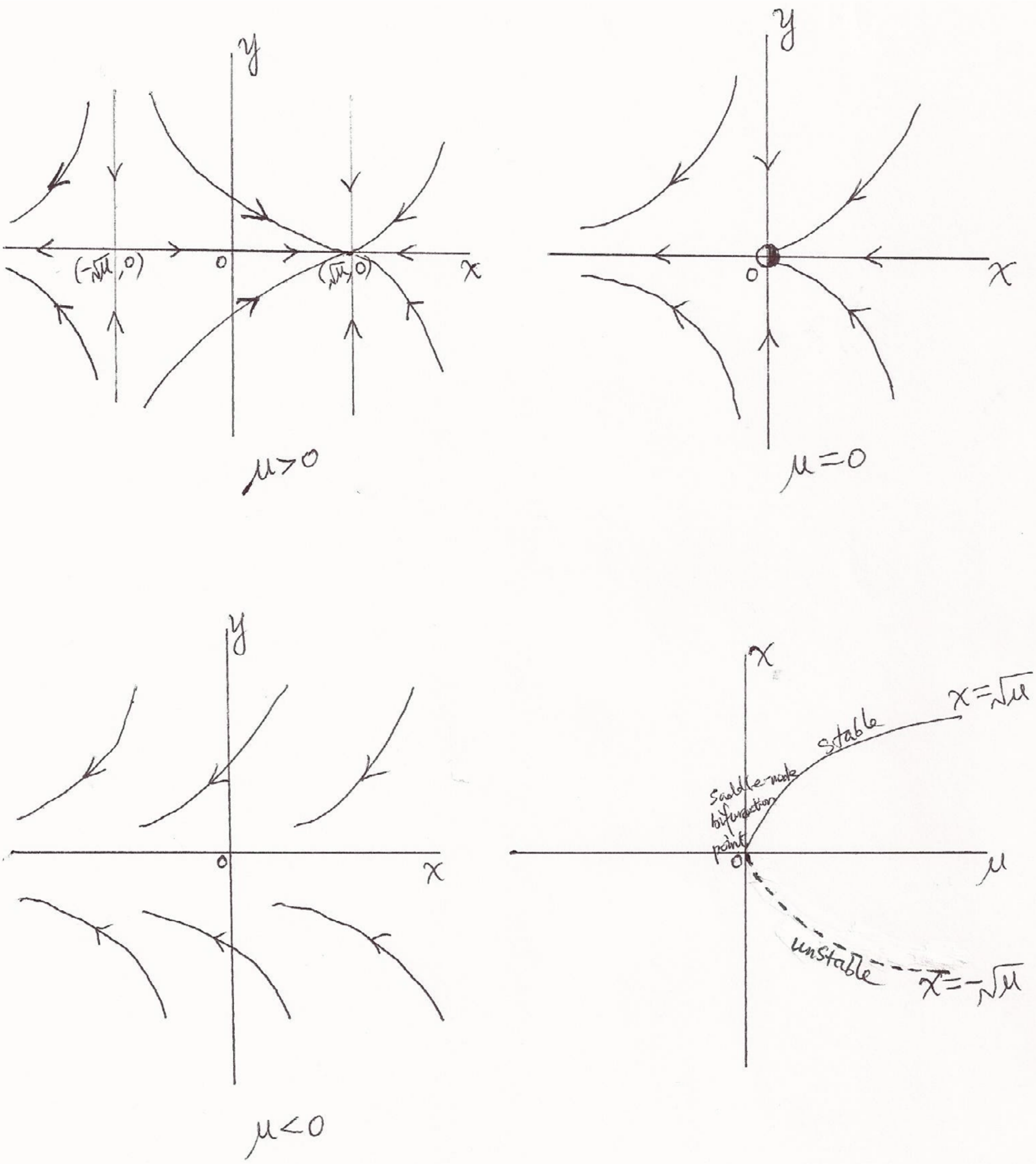


Figure 17: Three cases and the bifurcation diagram of Example 34.

As μ decreases from positive to negative, the saddle and the node approach each, then collide when $\mu = 0$, and finally disappear when $\mu < 0$. We conclude these results in a bifurcation diagram (the last panel of Figure 17) in which we plot x versus μ since the change of equilibria occurs in x -coordinate. The bifurcation diagram is the same as the one-dimensional case $\dfrac{dx}{dt} = \mu - x^2$.

Typical examples for transcritical and pitchfork bifurcations of two dimensional flows are listed below:

(transcritical)

$$\begin{aligned}\frac{dx}{dt} &= \mu x - x^2\\ \frac{dy}{dt} &= -y\end{aligned}$$

(supercritical pitchfork)

$$\begin{aligned}\frac{dx}{dt} &= \mu x - x^3\\ \frac{dy}{dt} &= -y\end{aligned}$$

(subcritical pitchfork)

$$\begin{aligned}\frac{dx}{dt} &= \mu x + x^3\\ \frac{dy}{dt} &= -y\end{aligned}$$

More complicated examples can be found in “Nonlinear dynamics and chaos” by S.H. Strogatz.

7.6 Introduction of Hopf bifurcations

As the bifurcation parameter varies, a real eigenvalue passes through $\lambda = 0$ (see the first panel of Figure 18). This is the case for saddle-node, transcritical, or pitchfork bifurcation.

As the bifurcation parameter varies, two complex conjugate eigenvalues simultaneously cross the imaginary axis into the right half-plane (see the second panel of Figure 18). This is the case for Hopf bifurcations.

Hopf bifurcation has two main types: supercritical and subcritical.

Example 35 *Perform bifurcation analysis for the system*

$$\begin{aligned}\frac{dr}{dt} &= \mu r - r^3\\ \frac{\theta}{dt} &= \omega + br^2\end{aligned}$$

in polar coordinates where μ *is the bifurcation parameter. (supercritical case)*

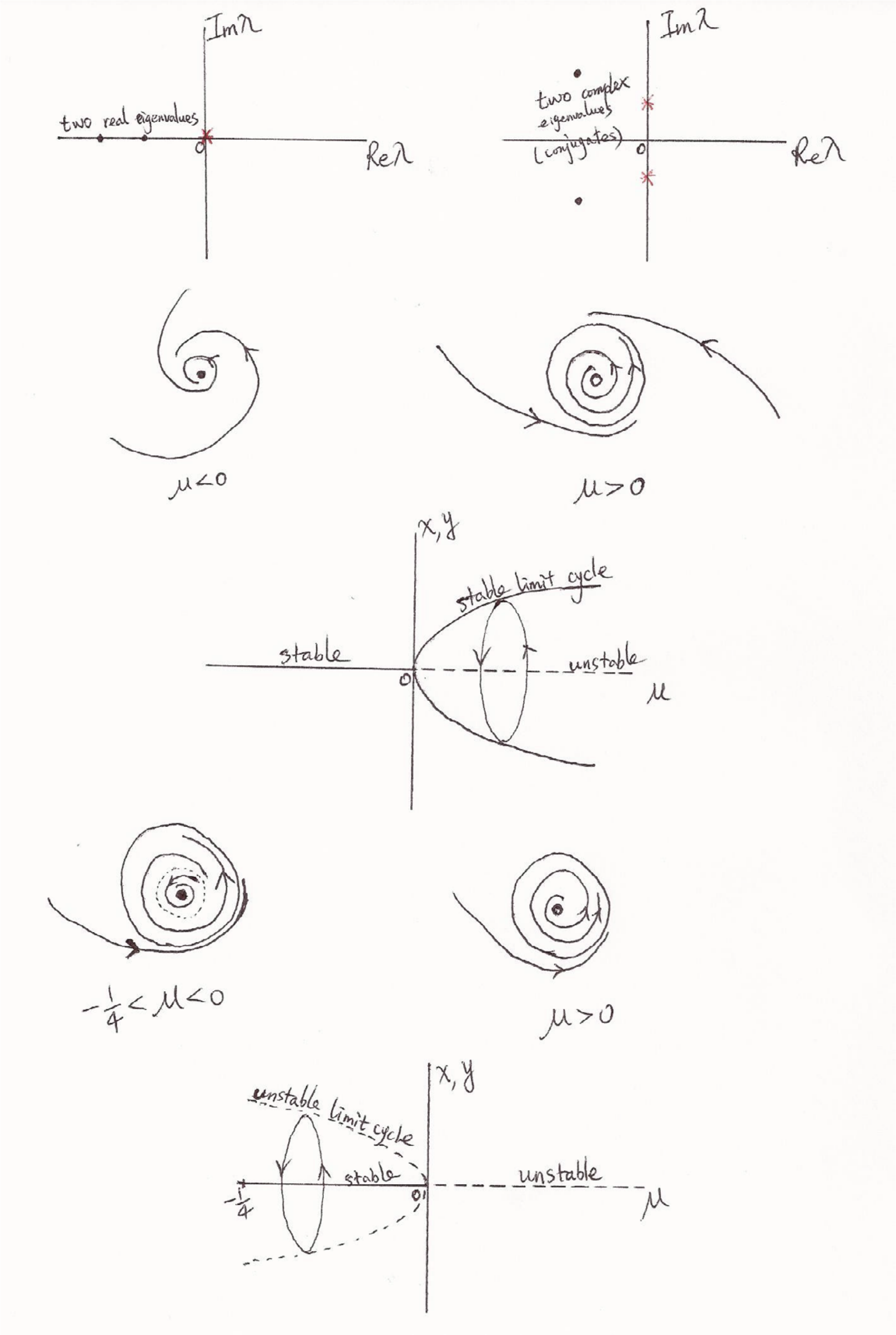


Figure 18: Two complex planes, and two phase portraits and the bifurcation diagram of supercritical Hopf bifurcation (Example 35), and two phase portraits and the bifurcation diagram of subcritical Hopf bifurcation (Example 36).

Solution: In Cartesian coordinates, $x = r\cos\theta, y = r\sin\theta$, then

$\frac{dx}{dt} = \frac{dr}{dt}\cos\theta - r\frac{d\theta}{dt}\sin\theta = (\mu r - r^3)\cos\theta - r(\omega + br^2)\sin\theta = (\mu - (x^2+y^2))x - (\omega + b(x^2+y^2))y$; similar for $\frac{dy}{dt}$. Hence the system becomes

$$\begin{aligned}\frac{dx}{dt} &= \mu x - \omega y + \text{cubic terms}\\ \frac{dy}{dt} &= \omega x + \mu y + \text{cubic terms}\end{aligned}$$

The Jacobian matrix at the origin (the trivial equilibrium) is

$$A = \begin{pmatrix} \mu & -\omega \\ \omega & \mu \end{pmatrix}$$

Eigenvalues $\lambda = \mu \pm i\omega$ cross the imaginary axis from left to right as μ increases from negative to positive values.

When $\mu < 0$, the origin is a spiral sink.

When $\mu > 0$, the origin is a spiral source, and all solutions tend to a limit cycle.

The third and fourth panels of Figure 18 exhibit the phase portraits of these two cases.

We conclude these results in a bifurcation diagram (the fifth panel of Figure 18). The supercritical Hopf bifurcation occurs at $\mu = 0$. It is usually difficult to prove existence of a limit cycle and its stability, but we can definitely check them numerically.

Example 36 *Perform bifurcation analysis for the system*

$$\begin{aligned}\frac{dr}{dt} &= \mu r + r^3 - r^5\\ \frac{d\theta}{dt} &= \omega + br^2\end{aligned}$$

in polar coordinates where μ is the bifurcation parameter. (subcritical case)

Solution: Similar to Example 35, we can obtain the system in Cartesian coordinates $x = r\cos\theta, y = r\sin\theta$, and perform local stability analysis.

When $-1/4 < \mu < 0$, the origin is a spiral sink. There is an unstable limit cycle and a stable limit cycle. Bistability occurs with the unstable limit cycle as the separatrix.

When $\mu > 0$, the origin is a spiral source, and there is a stable limit cycle.

The sixth and seventh panels of Figure 18 exhibit the phase portraits of these two cases.

We conclude these results in a bifurcation diagram (the last panel of Figure 18). The subcritical Hopf bifurcation occurs at $\mu = 0$.

Readers may be curious about the case $\mu \leq -1/4$. Actually $\mu = -1/4$ is a saddle-node bifurcation of limit cycles (a type of global bifurcations). When $\mu < -1/4$, no limit cycles exist. When $\mu = -1/4$, one limit cycle exists and is half-stable. When $-1/4 < \mu < 0$, two limit cycles exist (one stable, one unstable). We do not expand the details of this global bifurcation since we only discuss local bifurcations in this textbook.

7.7 Normal form of Hopf bifurcation

The normal form of supercritical case is provided by

$$\begin{aligned} \frac{dx}{dt} &= \mu x - y - x(x^2 + y^2) \\ \frac{dy}{dt} &= x + \mu y - y(x^2 + y^2) \end{aligned}$$

The normal form of subcritical case is provided by

$$\begin{aligned} \frac{dx}{dt} &= \mu x - y + x(x^2 + y^2) \\ \frac{dy}{dt} &= x + \mu y + y(x^2 + y^2) \end{aligned}$$

Supercritical case:

The system has the equilibrium $(0, 0)$ for all μ values (additional equilibria are possible). The Jacobian matrix $J(0,0) = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}$ ⇒ Eigenvalues $\lambda = \mu \pm i$.

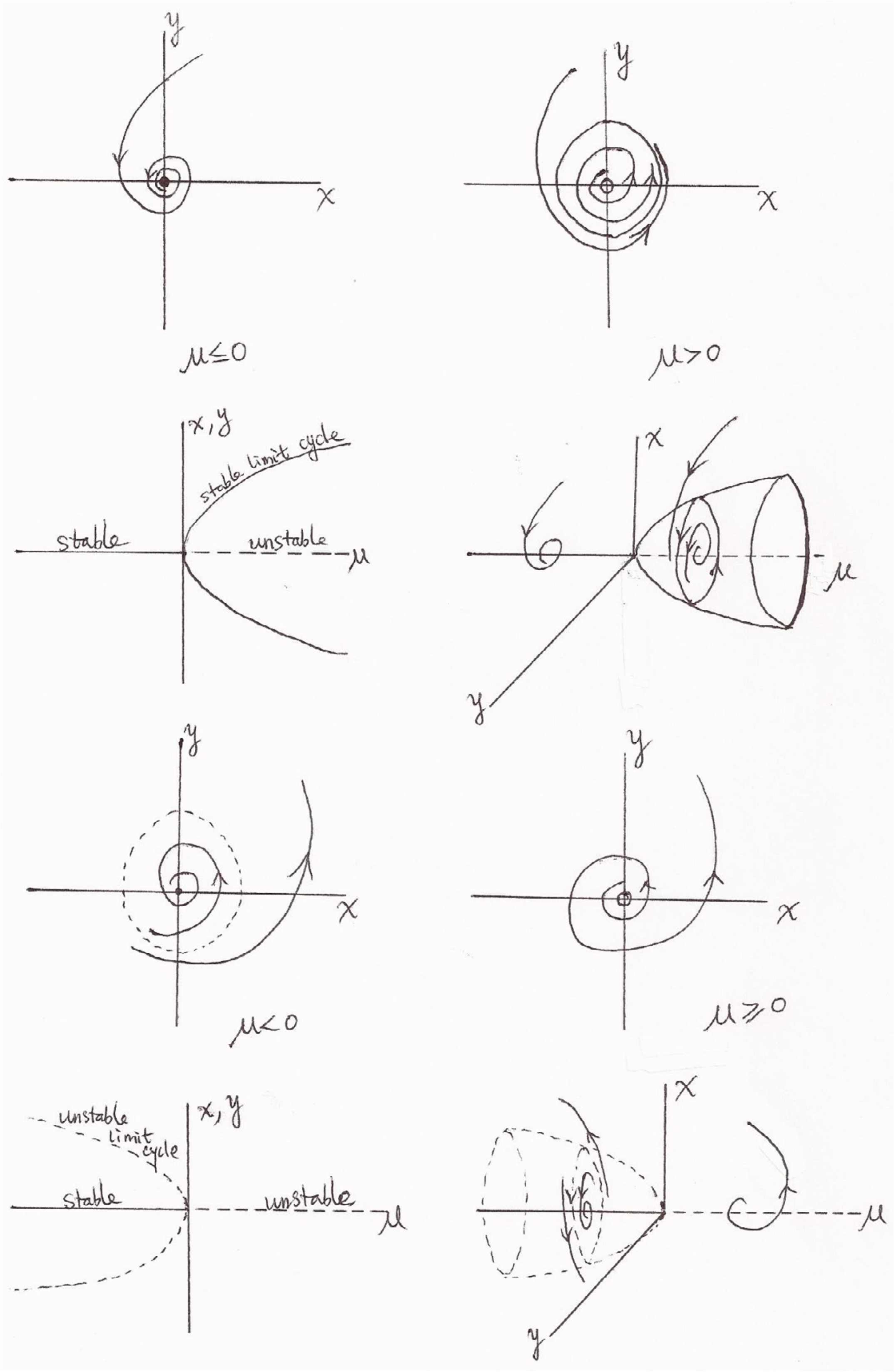


Figure 19: Two phase portraits and two bifurcation diagrams of supercritical Hopf bifurcation (normal form), and two phase portraits and two bifurcation diagrams of subcritical Hopf bifurcation (normal form).

Introduce the complex variable $z = x + iy$, then $\bar{z} = x - iy$, $|z|^2 = z\bar{z} = x^2 + y^2$.

$$\frac{dz}{dt} = \frac{dx}{dt} + i\frac{dy}{dt} = \mu(x+iy) + i(x+iy) - (x+iy)(x^2+y^2) = (\mu+i)z - z|z|^2.$$

Let $z = re^{i\theta}$, where $r = \sqrt{x^2+y^2} \geq 0, \tan\theta = y/x$, then

$$\frac{dz}{dt} = \frac{dr}{dt}e^{i\theta} + ri\frac{d\theta}{dt}e^{i\theta}.$$

Hence,

$$\frac{dr}{dt}e^{i\theta} + ir\frac{d\theta}{dt}e^{i\theta} = (\mu+i)z - z|z|^2 = z(\mu+i-|z|^2) = re^{i\theta}(\mu+i-r^2).$$

There are two groups in this equality: $e^{i\theta}$ and $ie^{i\theta}$. Setting the coefficients of them equal on both sides to obtain

$$\begin{aligned} \frac{dr}{dt} &= r(\mu - r^2) \\ \frac{d\theta}{dt} &= 1 \end{aligned}$$

The second equation implies that all orbits keep rotating in the counterclockwise direction with a constant speed.

When $\mu < 0$, we have $\frac{dr}{dt} < 0$ for $r > 0$ (actually $r > 0$ is always true except for the origin where $r = 0$), and thus the only equilibrium (of the original system) $r = 0$ is a spiral sink.

When $\mu = 0$, we have $\frac{dr}{dt} = -r^3 < 0$ for $r > 0$, and thus the only equilibrium $r = 0$ is still a spiral sink.

When $\mu > 0$, we have $\frac{dr}{dt} = r(\mu - r^2) > 0$ for $0 < r < \sqrt{\mu}$. In this case, there are two possibilities from $\frac{dr}{dt} = 0$: $r = 0$ and $r = \sqrt{\mu}$ (since $r \geq 0$, the negative one is not feasible). $r = 0$ is corresponding to an unstable equilibrium, and $r = \sqrt{\mu}$ is corresponding to a stable limit cycle.

The first two cases above are combined in the first panel of Figure 19, and the third case is plotted in the second panel of Figure 19.

We conclude the above results in bifurcation diagrams (the third and fourth panels of Figure 19). Similar analysis can be done for the subcritical case, for which we also plot phase portraits (the fifth and sixth panels of Figure 19) and bifurcation diagrams (the seventh and eighth panels of Figure 19).

7.8 Generic Hopf bifurcation

We start this section with a lemma.

Lemma 2 *The system*

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} \pm (x^2+y^2)\begin{pmatrix} x \\ y \end{pmatrix} + O\left(\left\|\begin{pmatrix} x \\ y \end{pmatrix}\right\|^4\right)$$

is locally topologically equivalent near the origin to the system

$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} \pm (x^2+y^2)\begin{pmatrix} x \\ y \end{pmatrix}.$$

Any generic two-dimensional system undergoing a Hopf bifurcation can be transformed into one of the normal forms (supercritical "-" in cubic terms, subcritical "+" in cubic terms) plus some higher order terms.

Consider $\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = f(x, y, \mu)$, with a smooth vector function f, which has at $\mu = 0$ the equilibrium $(0, 0)$ with eigenvalues $\lambda = \pm i\omega_0$, $\omega_0 > 0$.

Theorem 6 *Suppose a two-dimensional system* $\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = f(x, y, \mu)$ *with smooth* f*, has the equilibrium* $(0, 0)$ *with eigenvalues* $\lambda(\mu) = \alpha(\mu) \pm i\beta(\mu)$ *for all sufficiently small* $|\mu|$*. Assume the following conditions are satisfied:*

(B1) $\alpha(0) = 0,\ \beta(0) = \omega_0 > 0$ *(key Hopf bifurcation condition).*

(B2) $l_1(0) \neq 0$*, where* l_1 *is the first Lyapunov coefficient (nondegeneracy condition).*

(B3) $\alpha'(0) \neq 0$ *(transversality condition).*

Then there exist invertible coordinate and parameter changes and a time reparametrization transforming the system $\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = f(x, y, \mu)$ *into*

$$\frac{d}{d\tau}\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} = \begin{pmatrix} \bar{\mu} & -1 \\ 1 & \bar{\mu} \end{pmatrix}\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} \pm (\bar{x}^2 + \bar{y}^2)\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} + O\left(\left\| \begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} \right\|^4\right).$$

Theorem 6 together with Lemma 2 leads to the following theorem.

Theorem 7 *(Topological normal form of Hopf bifurcation) Any generic (=(B2)+(B3)) two-dimensional, one-parameter system* $\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = f(x, y, \mu)$*, having at* $\mu = 0$ *the equilibrium* $(0, 0)$ *with eigenvalues ((B1)* ⇔*)* $\lambda_1(0) = i\omega_0$, $\lambda_2(0) = -i\omega_0$, $\omega_0 > 0$, *is locally topologically equivalent near the origin to one of the following normal forms:*

$$\frac{d}{d\tau}\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} = \begin{pmatrix} \bar{\mu} & -1 \\ 1 & \bar{\mu} \end{pmatrix}\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} \pm (\bar{x}^2 + \bar{y}^2)\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}.$$

Example 37 *Consider a predator-prey model*

$$\begin{aligned} \frac{dx}{dt} &= rx(1-x) - \frac{cxy}{\alpha + x} \\ \frac{dy}{dt} &= \frac{cxy}{\alpha + x} - dy \end{aligned}$$

to examine whether Hopf bifurcation exists.

See the solution in “Elements of Applied Bifurcation Theory” by Yuri A. Kuznetsov.

The bifurcations we discussed so far are popular ones, but there are many other bifurcations we have not discussed, for example, saddle-node bifurcation of limit cycles, infinite-period bifurcation, homoclinic bifurcation, etc.

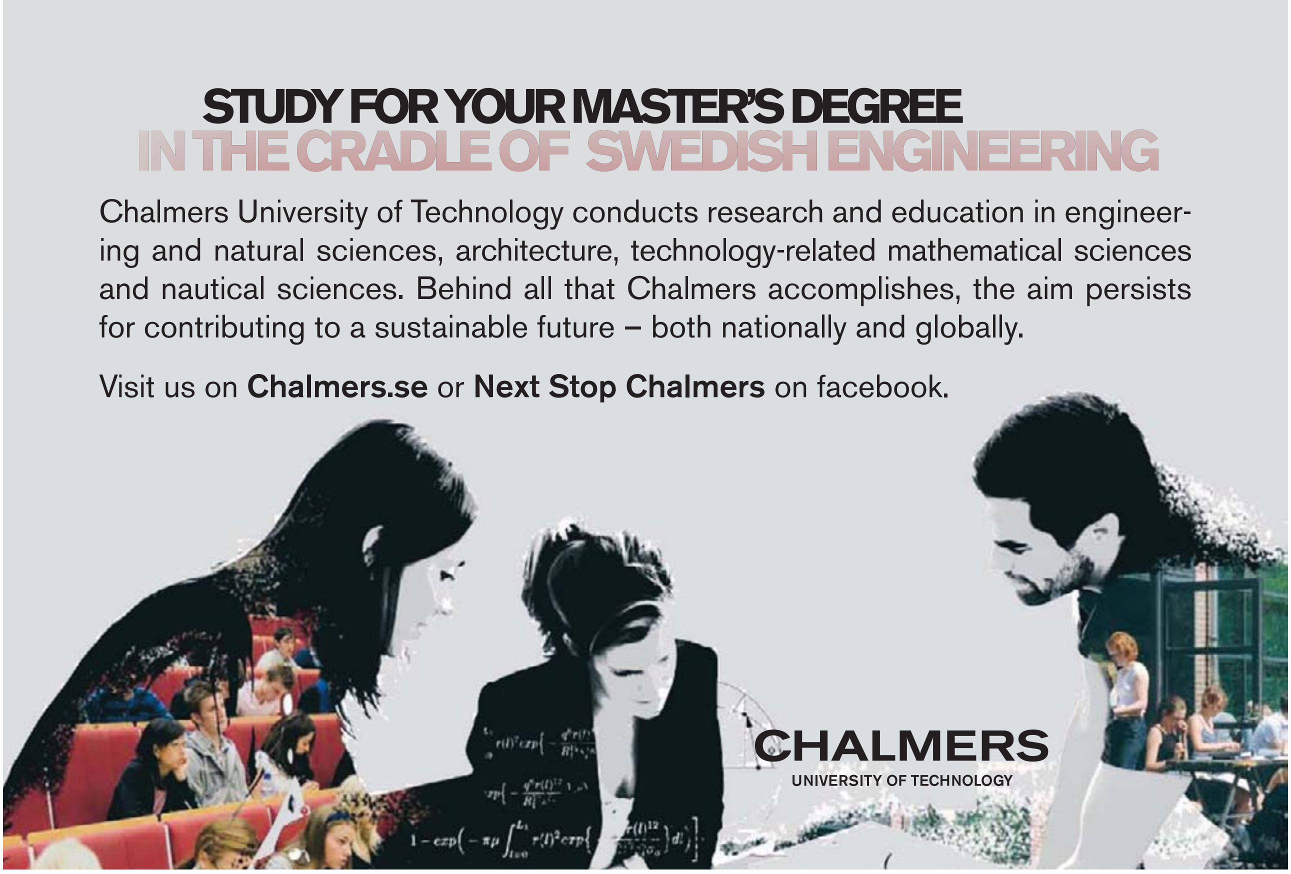
8 Matlab programming

All basic Matlab knowledge can be learned from Matlab manual. All Matlab commands and the way to use them can be found from Matlab help files. In this chapter, we use Matlab to run simulations for some typical examples that are relevant to contents we have learned so far. Readers can modify these sample Matlab files for similar models. To change the model dimension, we need to change the dimensions of vectors and matrices.

The Matlab .m file for the host-parasitoid model is listed below.

```
% TwoDifferenceEquations.m – this MATLAB file simulates the host-parasitoid model
k=1.8; %parameter input
a=1; %parameter input
c=1; %parameter input
x0=1; %input initial population of host
y0=1; %input initial population of parasitoid
n=30; %input time period of run
x=zeros(n+1,1);
y=zeros(n+1,1);
t=zeros(n+1,1);
x(1)=x0;
y(1)=y0;
for i=1:n
t(i)=i-1;
x(i+1)=k*x(i)*exp(-a*y(i));
y(i+1)=c*x(i)*(1-exp(-a*y(i)));
end
t(n+1)=n;
figure
subplot(221)
plot(t,x,t,x,’o’)
title(’Host population’)
subplot(222)
```

```
plot(t,y,t,y,’*’)
title(’Parasitoid population’)
subplot(223)
plot(t,y,t,x,t,x,’o’,t,y,’*’)
title(’Host and parasitoid populations’)
subplot(224)
plot(x,y,’o-’)
title(’Host vs parasitoid’);
```



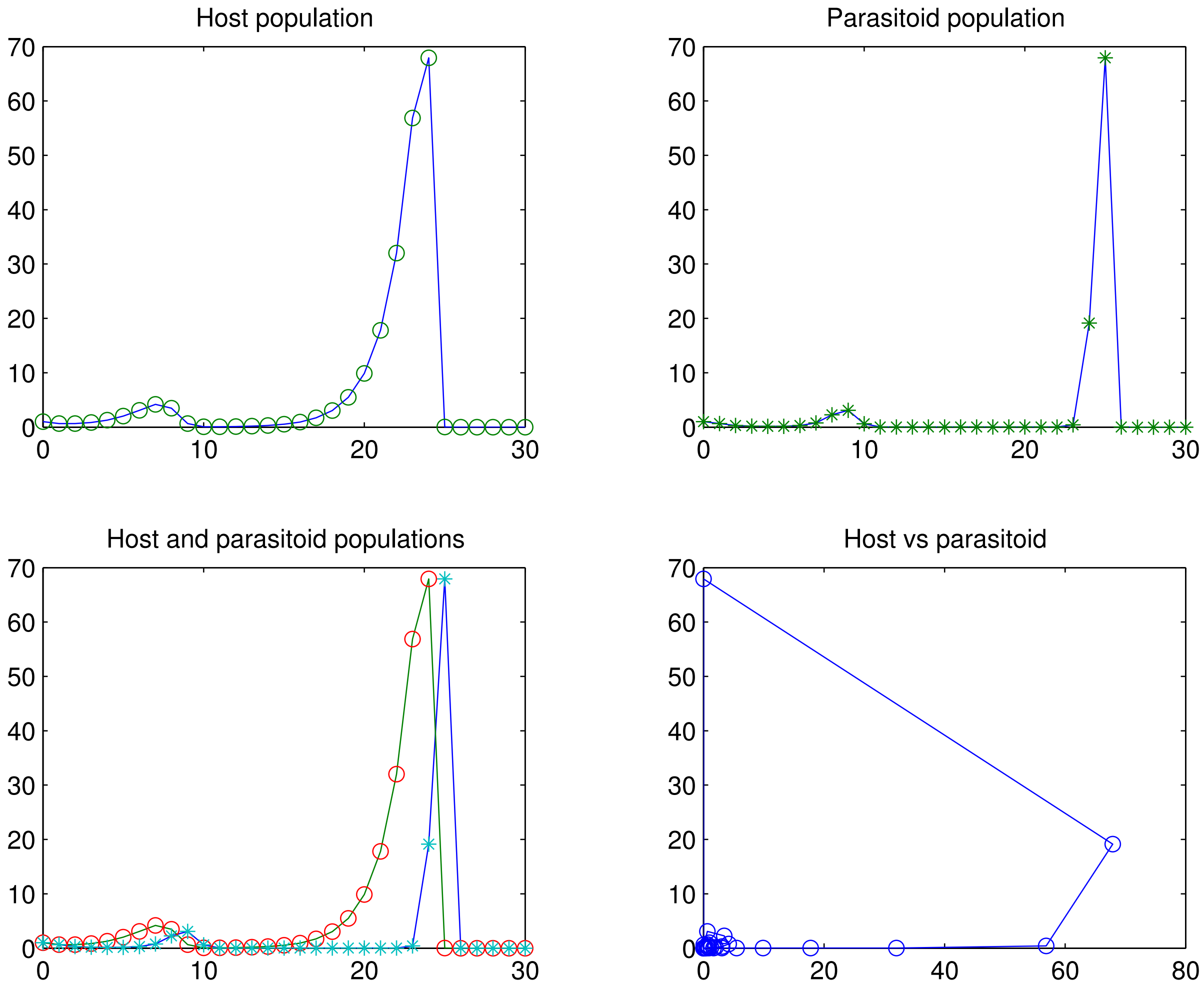


Figure 20: The sample simulation for the host-parasitoid model.

The simulation results of this program are sketched in Figure 20. Readers can simply modify this program to run simulations for any model with a group of difference equations.

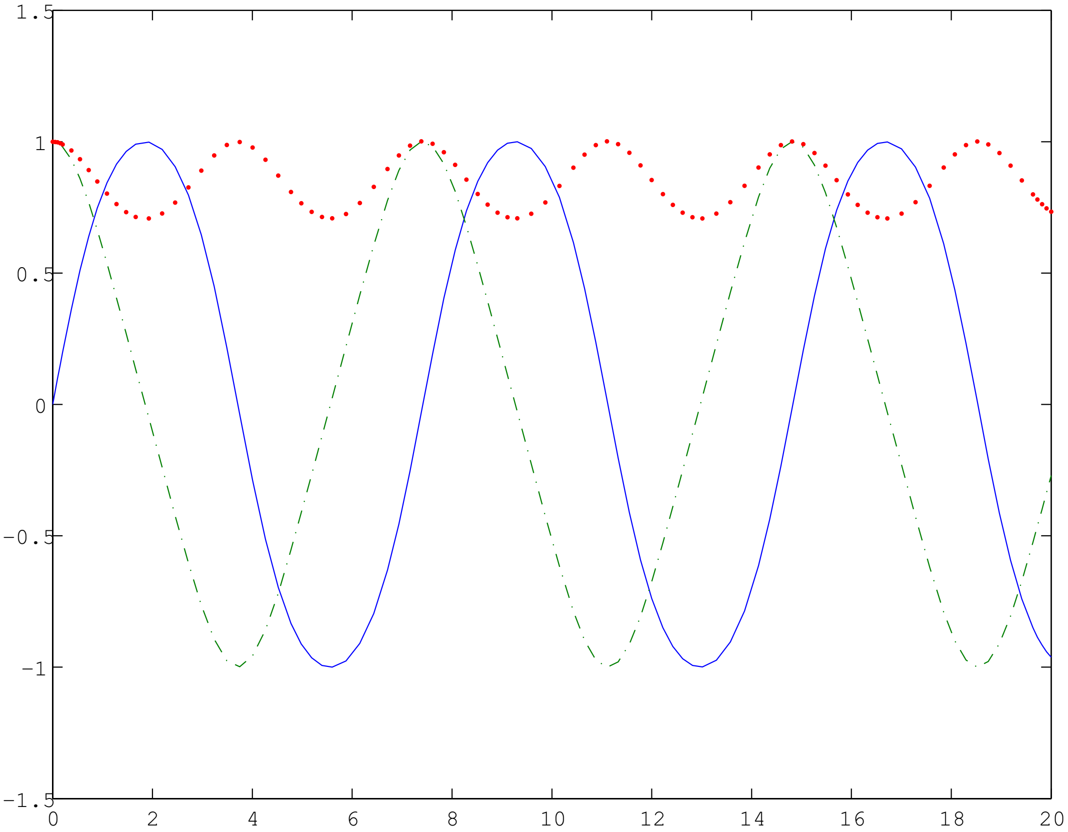


Figure 21: The sample simulation for a system of three differential equations.

Matlab programs for a system of differential equations are simple. We provide an example of three differential equations below.

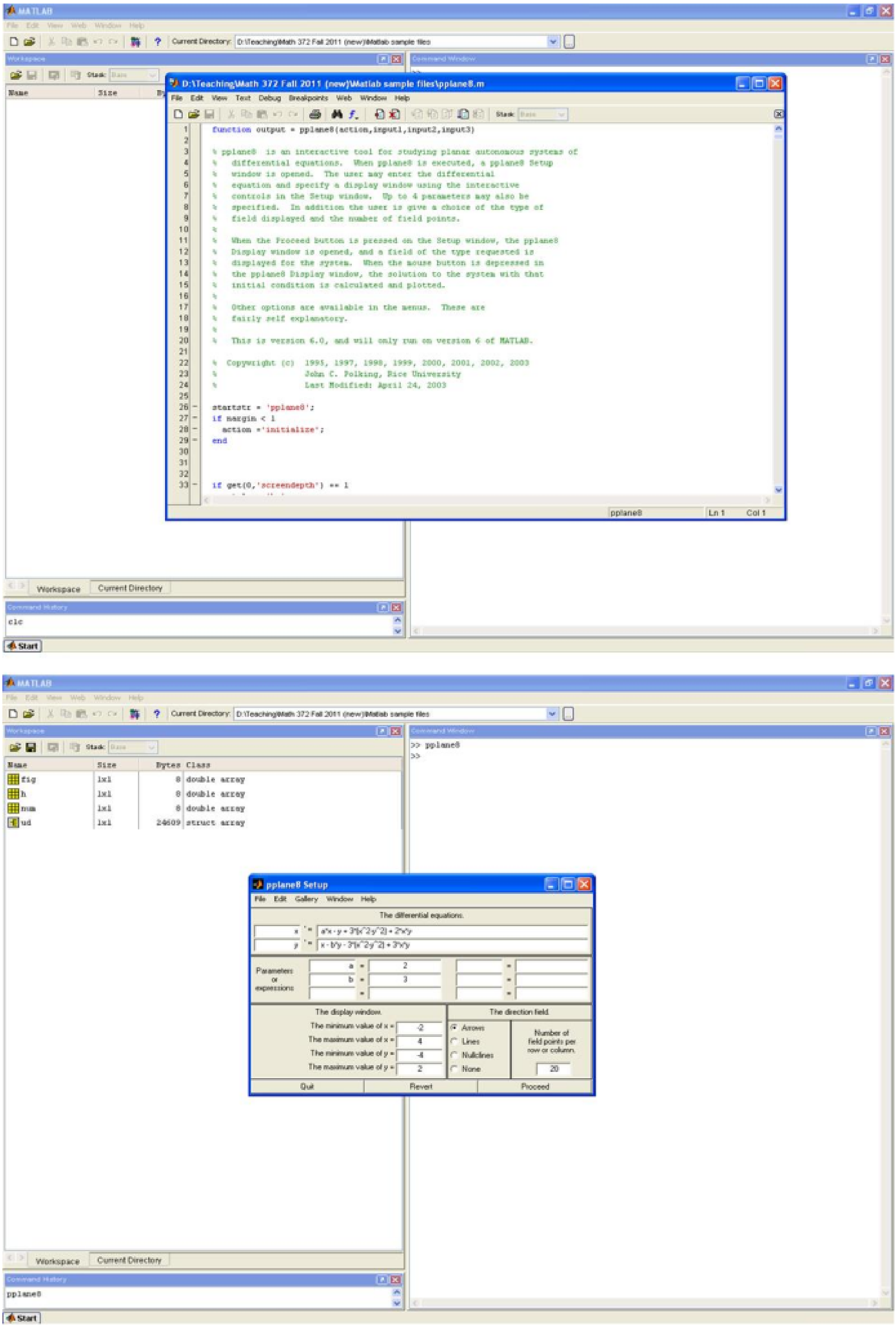
```
%ThreeDmodel.m
function dy = ThreeDmodel(t,y)
dy = zeros(3,1); % a column vector
dy(1) = y(2) * y(3);
dy(2) = -y(1) * y(3);
dy(3) = -0.5 * y(1) * y(2);

%ThreeDifferentialEquations.m
options = odeset(’RelTol’,1e-3,’AbsTol’,[1e-3 1e-3 1e-4]);
[T,Y] = ode45(@ThreeDmodel,[0 20],[0 1 1],options);
plot(T,Y(:,1),’-’,T,Y(:,2),’-.’,T,Y(:,3),’.’)
```

The simulation result is sketched in Figure 21.

pplane8.m, copyright by John C. Polking at Rice University, is a useful program for a system of two differential equations, more specifically for planar autonomous systems. We can use it to simply plot equilibria, nullclines, sample solutions, etc.. pplane8.m can be downloaded from John C. Polking's website. We show how to use pplane8.m in Figures 22 and 23. We first download pplane8.m into our own computer and run it in Matlab. A user friendly interface shows up. We can define our two dimensional system, parameters, plotting window size, and the type of direction field. Click "proceed" on the right-bottom corner to obtain the phase plane in which we can plot all dynamical features we want, such as equilibria and nullclines. We can also sketch sample solutions by simply clicking on the phase plane. The point we click will be used as the initial point for the generated solution.

pplane8.m can be applied to plot phase portraits of all the two dimensional examples in Chapters 6 and 7.



```
function output = pplane8(action,input1,input2,input3)

% pplane8  is an interactive tool for studying planar autonomous systems of
%   differential equations.  When pplane8 is executed, a pplane8 Setup
%   window is opened.  The user may enter the differential
%   equation and specify a display window using the interactive
%   controls in the Setup window.  Up to 4 parameters may also be
%   specified.  In addition the user is give a choice of the type of
%   field displayed and the number of field points.
%
%   When the Proceed button is pressed on the Setup window, the pplane8
%   Display window is opened, and a field of the type requested is
%   displayed for the system.  When the mouse button is depressed in
%   the pplane8 Display window, the solution to the system with that
%   initial condition is calculated and plotted.
%
%   Other options are available in the menus.  These are
%   fairly self explanatory.
%
%   This is version 6.0, and will only run on version 6 of MATLAB.

%  Copyright (c)  1995, 1997, 1998, 1999, 2000, 2001, 2002, 2003
%                 John C. Polking, Rice University
%                 Last Modified: April 24, 2003

startstr = 'pplane8';
if nargin < 1
  action ='initialize';
end



if get(0,'screendepth') == 1
```

```
clc
```

Name	Size	Bytes	Class
fig	1x1	8	double array
h	1x1	8	double array
num	1x1	8	double array
ud	1x1	24609	struct array

```
>> pplane8
>>
```

x ' = a*x - y + 3*(x^2-y^2) + 2*x*y

y ' = x - b*y - 3*(x^2-y^2) + 3*x*y

a = 2

b = 3

The minimum value of x = -2

The maximum value of x = 4

The minimum value of y = -4

The maximum value of y = 2

● Arrows

○ Lines

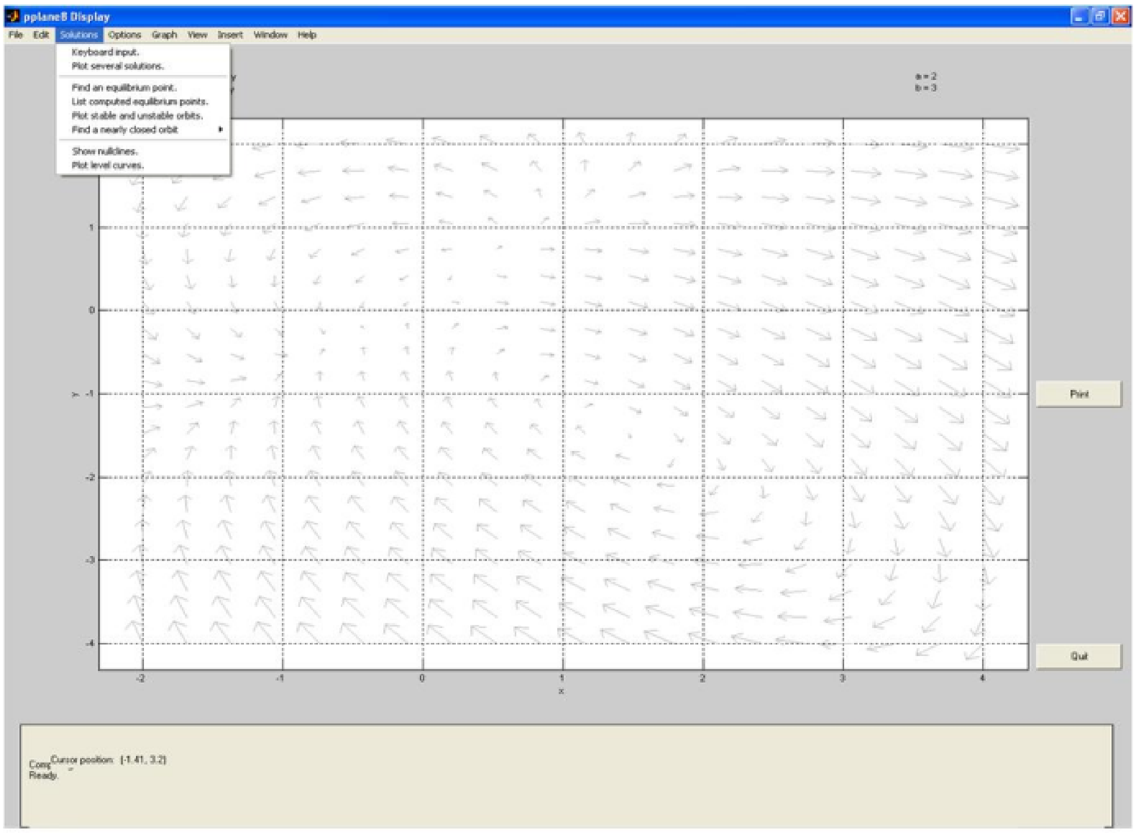
○ Nullclines

○ None

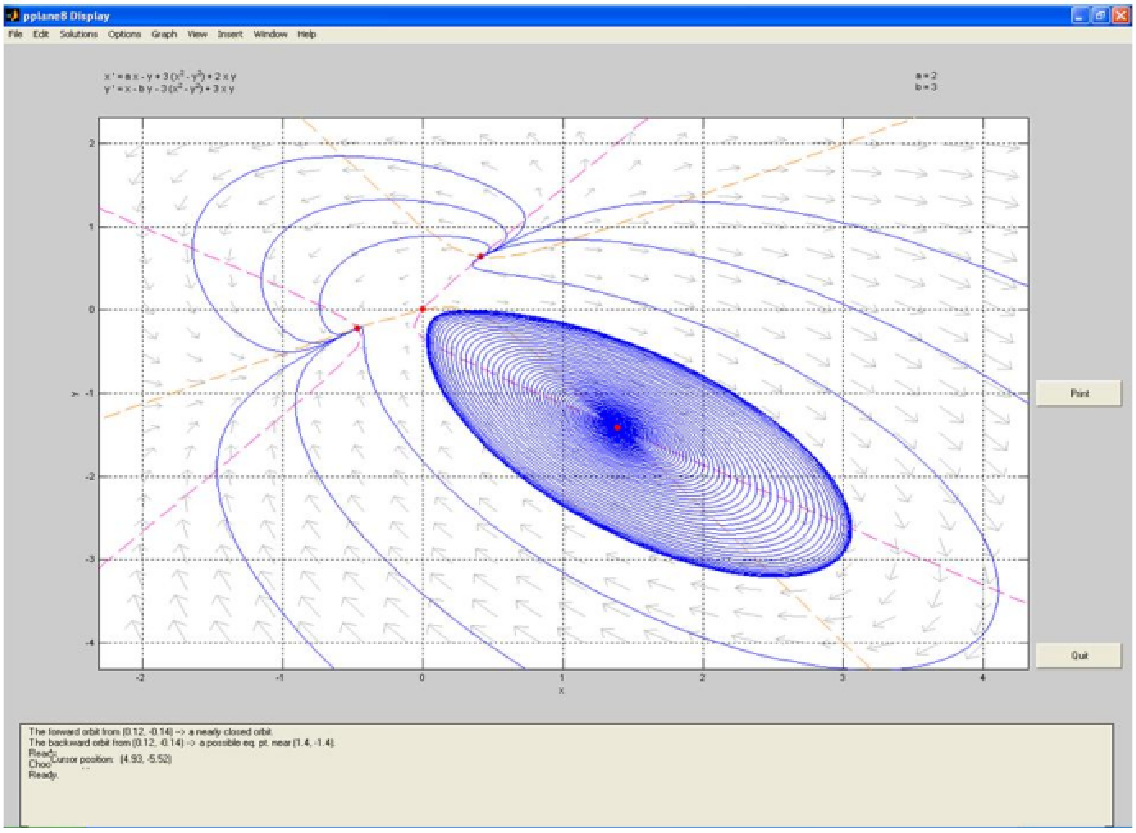
Number of field points per row or column. 20

```
pplane8
```

Figure 22: pplane8.m guidance.



```
CompCursor position:  [-1.41, 3.2]
Ready.
```



```
The forward orbit from [0.12, -0.14] --> a nearly closed orbit.
The backward orbit from [0.12, -0.14] --> a possible eq. pt. near [1.4, -1.4].
ReadyCursor position:  [4.93, -5.52]
Choo
Ready.
```

Figure 23: pplane8.m guidance – continued.

Two sample .m files to plot the Hopf bifurcation are provided below. The first one defines the model, and the second one sketches the Hopf bifurcation diagram using a “for” loop.

```
%bif_odef.m
function xprime=bif_odef(t,x)

global R;
us=12;
Km=2000;
A=15;
B=70;
Gs=.44*A;
Gw=.63*A;
alpha=0.5;
l=0.01;
ut=us/6;
Gt=5*Gw/6+Gs/6;

xprime=[ut*x(1)*(1-x(1)/Km)-alpha*A*x(1)*x(2)/(alpha*x(1)+B)
R*x(2)*(A*alpha*x(1)/(alpha*x(1)+B)-Gt)-l*x(2)^2
];
```

```
%bif_odemain.m
rect = [200 80 700 650]; %fix the window size and position
set(0, ’defaultfigureposition’,rect);

global R;

option=odeset(’AbsTol’,1e-8,’RelTol’,1e-5);
inc=[0:0.1:50]’;
time=[ inc ] ;
limit=[ 400:1:500];
for R=0:0.01:1;
IC=[1000,20];
[t,U] = ode23s(’bif_odef’,time,IC,option);
u2=U(limit,2);
usmin=min(u2);
usmax=max(u2);
plot(R, usmax,’b.’,’MarkerSize’, 5);
plot(R, usmin,’r.’,’MarkerSize’, 5);
hold on
```

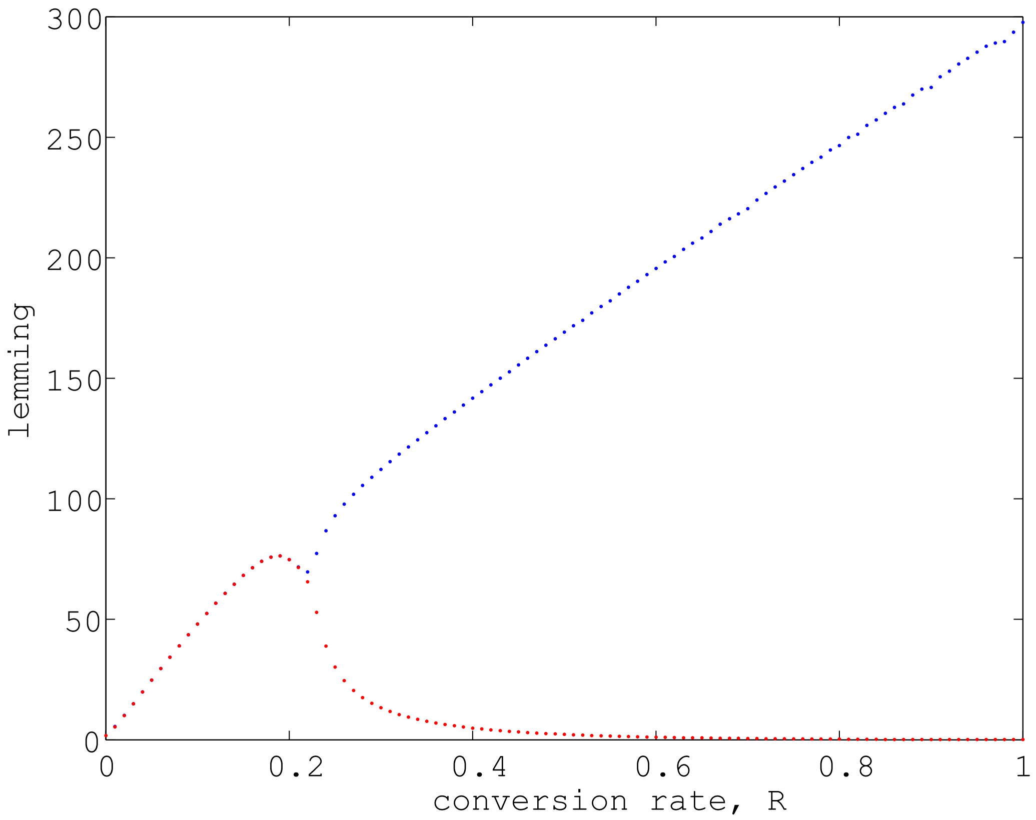


Figure 24: A sample Hopf bifurcation diagram.

```
end
xlim([0 1]);
ylim([0 300]);
xlabel(’conversion rate, R’);
ylabel(’lemming’);
```

The Hopf bifurcation, sketched by these two .m files, is shown in Figure 24. The main idea is to take maxima and minima of the tail of the solution. We need to run the simulation for a sufficiently long time such that the solution is stabilized, and we need to choose the length of the tail reasonably long such that at least one period of the limit cycle is included.

9 Data fitting

In this chapter, we focus on the most popular and simplest technique – least-square method – to perform data fitting. Given a model and a data set, how to obtain optimal parameter values to fit data? If the model with optimal parameter values cannot fit data well, then either the model is problematic or the data is not accurate.

The least-square data fitting method is defined as follows:

Consider a system of differential equations

$$y' = f(t, y, p), \quad y \in \mathcal{R}^n, \quad f \in \mathcal{R}^n, \quad p \in \mathcal{R}^m,$$

where p is the vector of m parameters. Given a group of k data points:

$$(t_1, y_1), (t_2, y_2), \cdots, (t_k, y_k),$$

we can compute optimal parameter values for the parameters p by minimizing the error

$$error(p) = \sum_{i=1}^{k} |y(t_i, p) - y_i|^2.$$

Sample .m files to apply this technique are provided below. The first file is to define the model, the second file is to compute the error function defined in least-square method, and the third file is to find optimal parameter values and use them to run the solution for a comparison with data.

```
%PPmodel.m
function value = PPmodel(t,y,p)
%Predator-prey model
%Parameters: p(1)=a, p(2) = b, p(3) = c, p(4) = d.
value=[p(1)*y(1)-p(2)*y(1)*y(2)
p(3)*y(1)*y(2)-p(4)*y(2)];
```

```
%PPerror.m
function error = PPerror(p)
%Error function for the predator-prey model
clear y;
years = 0:20;
DataX = [20.0 45.1 70.2 78.3 36.4 21.5 18.6 21.7 22.8 25.9 27.0 40.1 57.2 77.3 52.4 19.5 11.6 8.7 15.8 16.9 25.0];
DataY = [5.0 6.1 10.2 35.3 60.4 42.5 19.6 13.7 8.8 9.9 7.0 8.1 12.2 20.3 46.4 51.5 30.6 16.7 10.8 11.9 9.0];
[t,y] = ode23(@PPmodel,years,[DataX(1); DataY(1)],[],p);
```

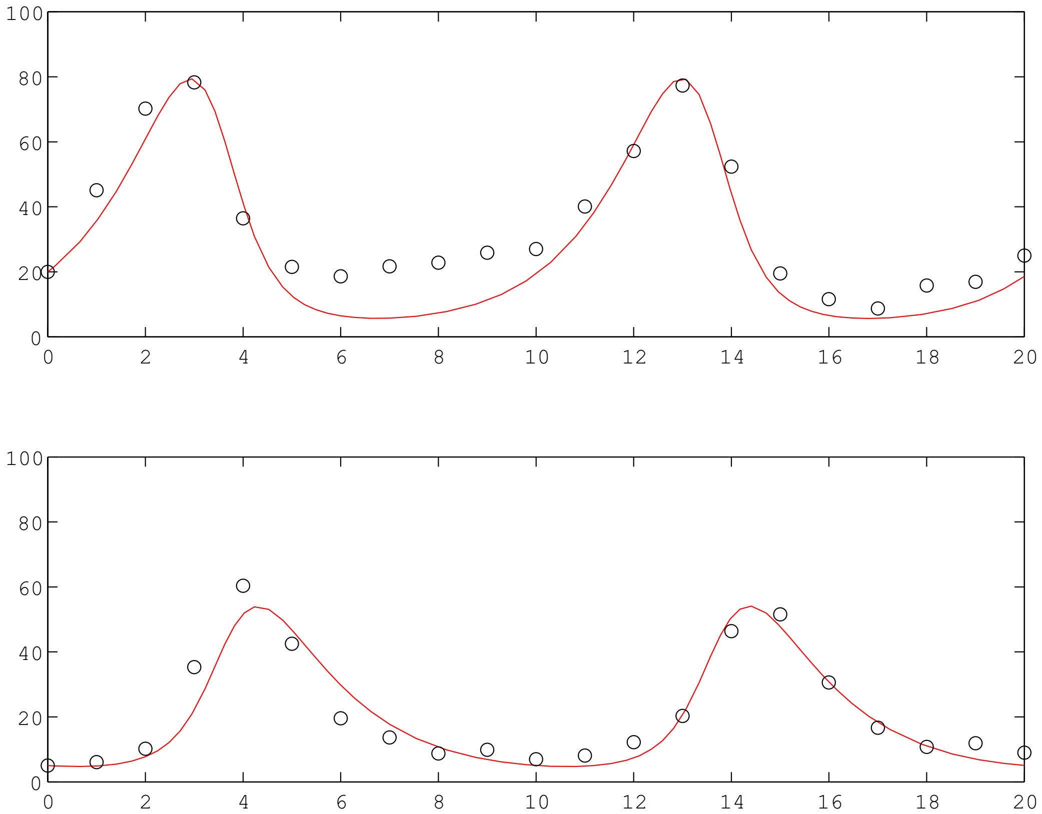


Figure 25: Least-square data fitting of the Lotka-Volterra predator-prey model to a data set.

```
value = (y(:,1)-DataX’).^2+(y(:,2)-DataY’).^2;
error = sum(value);

%LeastSquareDataFitting.m
%Parameter estimation and run the simulation to compare with data
guess = [0.5; 0.02; 0.02; 0.8];
[p,error] = fminsearch(@PPerror, guess)
[t,y] = ode23(@PPmodel,[0, 20],[20.0; 5.0],[],p);
years = 0:20;
DataX = [20.0 45.1 70.2 78.3 36.4 21.5 18.6 21.7 22.8 25.9 27.0 40.1 57.2 77.3 52.4 19.5 11.6 8.7 15.8 16.9 25.0];
DataY = [5.0 6.1 10.2 35.3 60.4 42.5 19.6 13.7 8.8 9.9 7.0 8.1 12.2 20.3 46.4 51.5 30.6 16.7 10.8 11.9 9.0];
subplot(2,1,1)
plot(t,y(:,1),’r’,years,DataX,’ko’)
axis([0 20 0 100])
subplot(2,1,2)
plot(t,y(:,2),’r’,years,DataY,’ko’)
axis([0 20 0 100])
```

The least-square data fitting for the Lotka-Volterra predator-prey model is shown in Figure 25. We can observe that the model fits the data well with the optimal parameter values.

The optimal values of the parameters a, b, c, d can be read from the command window of Matlab as below. The vector p gives optimal parameter values a, b, c, d in the order.

```
>>
p =

0.7571
0.0374
0.0234
0.6547

error =

2.0503e+003
```