Chapter 2

Discrete-Time Models
2.1 Introduction to Discrete-Time Models

In this chapter, we use discrete-time models to describe dynamical phenomena in biology. Discrete-time models are appropriate when one can think about the phenomenon in terms of discrete time steps, or when one wishes to describe experimental measurements that have been collected at fixed time intervals.

In general, we are concerned with a sequence of quantities,

\[ x_0, x_1, x_2, x_3, x_4, \ldots, \]

where \( x_i \) denotes the quantity at the \( i \)-th measurement or after \( i \) time steps. For example, \( x_i \) may represent

- the size of a population of mosquitoes in year \( i \);
- the proportion of individuals in a population carrying a particular allele of a gene in the \( i \)-th generation;
- the number of cells in a bacterial culture on day \( i \);
- the concentration of oxygen in the lung after the \( i \)-th breath;
- the concentration in the blood of a drug after the \( i \)-th dose.

You can undoubtedly think of many more such examples. Note that the time step may or may not be constant. In the example of the bacterial culture, the time step is fixed to be a day, but in the example of the oxygen concentration in the lung, the time step is variable from breath to breath. Also, time steps can be anywhere from milliseconds to years, depending on the biological problem at hand.

We can now ask ourselves, what does it mean to build a discrete-time model? In the context of our sequence of quantities \( x_i \), a discrete model is a rule describing how the quantities change. In particular, a discrete model describes how \( x_{n+1} \) depends on \( x_n \) (and perhaps \( x_{n-1}, x_{n-2}, \ldots \)). Restricting ourselves to the case where \( x_{n+1} \) depends on \( x_n \) alone, a model then can be thought of as an updating function (Adler, [1]), of the form

\[ x_{n+1} = f(x_n), \quad (2.1) \]

Equation (2.1) often is referred to as a map.

Given some initial condition \( x_0 \), the updating function can be iterated to give \( x_1 = f(x_0), x_2 = f(x_1), x_3 = f(x_2), \) and so on. The resulting simulated sequence \( x_0, x_1, x_2, \ldots \) is called an orbit of the map. A good model should be able to produce orbits that are in close agreement with observed experimental data.
Finding the precise function $f$ that describes experimental data well or that gives a certain desired type of behaviour is not always straightforward. It is often said that modelling (here, finding the right function $f$) is more of an art than a science. One starts with a particular function $f$, and then makes adjustments. Insight into how a function $f$ should be adjusted to get a better model can often be obtained from knowledge of the behaviour of the current model.

Simple but powerful analytical tools are available to help determine possible types of behaviour of a given model. In this chapter, we will give an introduction to some commonly used tools. We divide the chapter into two main sections. Section 2.2 deals with scalar discrete-time equations of the form (2.1), while Section 2.3 deals with systems of discrete-time equations. Throughout the chapter, applications of discrete-time equations to real biological systems, such as population growth and genetics, are discussed. More applications can be found in the exercises at the end of this chapter.

### 2.2 Scalar Discrete-Time Models

#### 2.2.1 Growth of a Population and the Discrete Logistic Equation

In this section, we build a simple model describing the growth of a population of *Paramecium aurelia*. A paramecium is a unicellular organism found in large numbers in freshwater ponds. It is a member of the group of organisms called Protozoa, and feeds on small organisms such as bacteria and other protozoa.

We will build the model based on a classic data set collected by Gause [39]. In Table 2.1, the mean density of *Paramecium aurelia*, measured in individuals per 0.5 cm$^3$, is tabulated as a function of time, measured in days. The corresponding graph of the data is shown in Figure 2.1. The population was grown in isolation, and provided with a constant level of nutrients.

Let $p_n$ be the mean density of this population on day $n$. A good starting point for building a model for $p_n$ is to think of the word equation

\[
\text{future value} = \text{present value} + \text{change},
\]

which readily translates to the following mathematical equation

\[
p_{n+1} = p_n + \Delta p_n. \tag{2.2}
\]

The goal of the modelling process then is to find a reasonable approximation for $\Delta p_n$ that more or less reproduces the given set of data.
Table 2.1. Growth of Paramecium aurelia in isolation. Here, density is the number of individuals per 0.5 cm$^3$. Data taken from Gause [39].

<table>
<thead>
<tr>
<th>Day $(n)$</th>
<th>Mean density of P. Aurelia $(p_n)$</th>
<th>Change in density $(\Delta p_n = p_{n+1} - p_n)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>14</td>
<td>20</td>
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<td>3</td>
<td>34</td>
<td>32</td>
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<tr>
<td>4</td>
<td>56</td>
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<td>5</td>
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<td>6</td>
<td>189</td>
<td>77</td>
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<tr>
<td>7</td>
<td>266</td>
<td>64</td>
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<tr>
<td>8</td>
<td>330</td>
<td>86</td>
</tr>
<tr>
<td>9</td>
<td>416</td>
<td>91</td>
</tr>
<tr>
<td>10</td>
<td>507</td>
<td>73</td>
</tr>
<tr>
<td>11</td>
<td>580</td>
<td>30</td>
</tr>
<tr>
<td>12</td>
<td>610</td>
<td>$-97$</td>
</tr>
<tr>
<td>13</td>
<td>513</td>
<td>80</td>
</tr>
<tr>
<td>14</td>
<td>593</td>
<td>$-36$</td>
</tr>
<tr>
<td>15</td>
<td>557</td>
<td>3</td>
</tr>
<tr>
<td>16</td>
<td>560</td>
<td>$-38$</td>
</tr>
<tr>
<td>17</td>
<td>522</td>
<td>43</td>
</tr>
<tr>
<td>18</td>
<td>565</td>
<td>$-48$</td>
</tr>
<tr>
<td>19</td>
<td>517</td>
<td>$-17$</td>
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<tr>
<td>20</td>
<td>500</td>
<td>85</td>
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<tr>
<td>21</td>
<td>585</td>
<td>$-85$</td>
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<tr>
<td>22</td>
<td>500</td>
<td>$-5$</td>
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<tr>
<td>23</td>
<td>495</td>
<td>30</td>
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<tr>
<td>24</td>
<td>525</td>
<td>$-15$</td>
</tr>
<tr>
<td>25</td>
<td>510</td>
<td>-</td>
</tr>
</tbody>
</table>

Finding a suitable form for $\Delta p_n$ is not always easy. But let’s examine the data more closely. Initially, the population increases slowly; values of $\Delta p_n$, tabulated in the third column of Table 2.1, are relatively small. As time progresses, values of $\Delta p_n$ increase and reach a maximum approximately halfway through the experiment. After that, they decrease again. We can attribute the decrease in the growth rate to intra-specific competition for nutrients and space. At the end of the experiment, the population appears to be levelling off when it reaches a mean density of approximately 540 individuals per 0.5 cm$^3$ (roughly, $\Delta p_n$ is negative when $p_n > 540$ and $\Delta p_n$ is positive when $p_n < 540$). To keep things relatively simple, we will ignore the fluctuations in the population. Note that the choice of using 540 for the limiting density may not be the best. However, it will do for a first approximative model. For clarity then, we continue to use this number in the following discussion, but keep in mind that there may be room for improvement.
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Based on the above observations, we must find a suitable form for $\Delta p_n$ that is small when $p_n$ is close to 0 and 540, and positive for intermediate values of $p_n$. The following quadratic expression fits the bill:

$$\Delta p_n = k(540 - p_n)p_n.$$  \hfill (2.3)

Note that this expression ensures that $\Delta p_n < 0$ when $p_n > 540$ and $\Delta p_n > 0$ when $p_n < 540$. Substituting (2.3) into (2.2), we obtain the following model for the population:

$$p_{n+1} = p_n + k(540 - p_n)p_n,$$  \hfill (2.4)

where the value of the parameter $k$ remains to be determined.
Figure 2.2. Testing equation 2.4 against the data shown in Table 2.1. The slope of the line of best fit is approximately 0.00145.

The experimental data contains enough information to allow us to obtain an estimate for \( k \) from the data set. In particular, note that we have hypothesized that \( \Delta p_n = p_{n+1} - p_n \) is proportional to the product \((540 - p_n)p_n\), with the parameter \( k \) being the constant of proportionality. To test our hypothesis, we plot \( \Delta p_n = p_{n+1} - p_n \) versus \( p_n(540 - p_n) \) and check whether there is reasonable proportionality. The graph is shown in Figure 2.2.

Although the data looks scattered, we can fit it nicely with a straight line passing through the origin, consistent with our hypothesis. The line of best fit has slope approximately 0.00145 (in Chapter 7, you will learn how to obtain lines of best fit using Maple). Thus, setting \( k = 0.00145 \), we obtain the following model for the growth of the population:

\[
p_{n+1} = p_n + 0.00145(540 - p_n)p_n. \tag{2.5}
\]
Last but not least, we compare the behaviour of our model with the observed data. Starting with the same initial condition, \( p_0 = 2 \), we can iterate equation 2.5, and obtain the sequence \( \{p_0, p_1, p_2, \ldots\} \). The simulated data and the observed data are shown together in Figure 2.3. We see that the agreement looks good. Recall that the choice to use 540 in the model was rather arbitrary, and improvement in the fit may be possible by adjusting this number (see exercises).

In general, we can write the model just developed as

\[
x_{n+1} = x_n + k(N - x_n)x_n,
\]  

\( (2.6) \)
where $N$ is the maximum population that can be sustained by the environment. $N$ often is referred to as the carrying capacity of the population. As we have just seen, this model can be used to describe the growth of a population in an environment with limited resources. The model can be used for other purposes as well. In particular, it can be used to describe the spread of an infectious disease, such as the flu or the common cold, through a small, closed population of size $N$. Here, $x_n$ is the number of infected individuals after $n$ time steps (e.g., days). Then $(N - x_n)$ is the number of individuals who have not yet become ill. The parameter $k$ is a measure of the infectivity of the disease, as well as the contact rate between healthy and infected individuals. Similarly, the model can be used to describe the spread of a rumour through a population of size $N$. In this case, $x_n$ is the number of individuals who have heard the rumour, and $N - x_n$ is the number of individuals who have not yet heard the rumour. The parameter $k$ measures how juicy the rumour is. The larger $k$, the juicier the rumour, and the faster its spread through the population.

Equation 2.6 generally is rewritten as follows:

$$x_{n+1} = x_n + k(N - x_n)x_n$$
$$= (1 + kN)x_n - kx_n^2$$
$$= (1 + kN)\left(1 - \frac{k}{1 + kN}x_n\right)x_n$$
$$= (1 + kN)\left(1 - \frac{x_n}{(1 + kN)/k}\right)x_n$$
$$= r \left(1 - \frac{x_n}{K}\right)x_n,$$

(2.7)

where

$$r = 1 + kN,$$

(2.8)

$$K = \frac{1 + kN}{k}.$$  

(2.9)

Since this model is similar in appearance to the continuous-time model known as the logistic model or the Verhulst model (you will encounter this model in section 3.1), the model here is known as the discrete logistic model.

Although the discrete logistic model provides a nice fit to Gause's data, it has the unfortunate (but mathematically interesting) property that it does not exhibit logistic growth (exponential growth initially, after which growth levels off until the population's carrying capacity is reached) for all choices of the model parameters.

In Section 2.2.4, we will discuss possible alternatives to the discrete logistic model. We first make a mathematical detour. In Section 2.2.2, we introduce techniques that can be used to analyze discrete-time equations of the form

$$x_{n+1} = f(x_n).$$
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Figure 2.4. Cobwebbing for the logistic equation, (2.7). Parameter values used are \( r = 2.8 \) and \( K = 1 \).

In Section 2.2.3, we use these techniques to explore in some detail the dynamical behaviour of the discrete logistic equation in various parameter regimes.

### 2.2.2 Cobwebbing, Fixed Points, and Linear Stability Analysis

With the fast computers of today, it is easy to generate many orbits by varying initial conditions and model parameters, and get a feel for the dynamics of the model. However, it is easy to miss some subtle behaviour. We often can gain valuable insight into the model dynamics from sophisticated, but easy to learn, mathematical techniques. We will examine a few of these techniques in this section.

We begin with **cobwebbing**, which is a graphical solution method allowing one to quickly visualize the orbits and their longterm behaviour without explicitly calculating each and every iterate along the way.
We demonstrate the cobwebbing technique in Figure 2.4. Figure 2.4 shows the graphs of a function $x_{n+1} = f(x_n)$, using $r = 2.8$ and $K = 1$, and the straight line $x_{n+1} = x_n$. We choose our first iterate, $x_0$, on the horizontal axis. The next iterate is $x_1 = f(x_0)$, which we can just read off the parabola. Visually, this is shown by a vertical line from $x_0$ on the horizontal axis to the point $(x_0, x_1)$ on the parabola. The next iterate, $x_2$, can be obtained in a similar way from $x_1$. We first need to locate $x_1$ on the horizontal axis. We already have $x_1$ on the vertical axis, and the easiest way to get it onto the horizontal axis is to reflect it through the diagonal line $x_{n+1} = x_n$. Visually, this is shown by a horizontal line from $x_1$ on the vertical axis to the point $(x_1, x_1)$ on the diagonal line, and then a vertical line from the point $(x_1, x_1)$ on the diagonal line to $x_1$ on the horizontal axis. This process is repeated for subsequent iterates.

In summary, one starts by travelling from $x_0$ vertically to the parabola, then horizontally to the diagonal line, vertically to the parabola, and so on, as indicated by the solid portion of the vertical and horizontal lines on the cobwebbing diagram in Figure 2.4. In this particular case, the orbit converges to the right-most intersection of the parabola and the diagonal line.

Any intersection of the parabola and the diagonal line represents a special point. Let $x^*$ be such a point. Then $f(x^*) = x^*$. We call any such point a fixed point (or an equilibrium point or a steady state) of the model. If any iterate is $x^*$, then all subsequent iterates also are $x^*$. A question of interest is what happens when an iterate is close to, but not exactly at, a fixed point. Do subsequent iterates move closer to the fixed point or further away? In the former case, the fixed point is said to be stable, whereas in the latter case, the fixed point is said to be unstable.

Examples of both stable and unstable fixed points are shown in Figure 2.5. The three fixed points shown are $x_1^*$, $x_2^*$, and $x_3^*$. Choosing an initial condition $x_0$ just to the left of $x_2^*$, we see that the orbit moves away from $x_2^*$, and towards $x_1^*$. Similarly, choosing the initial condition $x_0$ just to the right of $x_2^*$, we see that the orbit again moves away from $x_2^*$, but now towards $x_3^*$. Choosing the initial condition $x_0$ near $x_1^*$ or $x_3^*$ results in the orbit moving towards $x_1^*$ or $x_3^*$, respectively. We say that $x_2^*$ is an unstable fixed point of the model $x_{n+1} = f(x_n)$, and $x_1^*$ and $x_3^*$ are stable fixed points.

From Figure 2.5, note that the slope of $f$ at the stable fixed points $x_1^*$ and $x_3^*$ is less than 1 (the slope of the straight diagonal line), whereas the slope of $f$ at the unstable fixed point $x_2^*$ is greater than 1. We can formalize these ideas via a linear stability analysis.

We choose the $n$-th iterate to be close to a fixed point $x^*$ of (2.1),

$$x_n = x^* + y_n,$$

(2.10)
with \( y_n \) small, so that \( x_n \) can be thought of as a perturbation of \( x^* \). The question of interest now is what happens to \( y_n \), the deviation of \( x_n \) from \( x^* \), as the map is iterated. If the deviation grows, then the fixed point \( x^* \) is unstable, and if the deviation decays, then it is stable. We can find the map for the deviation by substituting (2.10) into (2.1) to obtain
\[
x^* + y_{n+1} = f(x^* + y_n).
\] (2.11)

We expand the right hand side using a Taylor series about \( x^* \) to obtain
\[
x^* + y_{n+1} = f(x^*) + f'(x^*)y_n + \mathcal{O}(y_n^2).
\] (2.12)

Since \( x^* \) is a fixed point, we can replace \( f(x^*) \) on the right hand side by \( x^* \). If, in addition, we neglect all the terms in the Taylor series that have been collected in the term \( \mathcal{O}(y_n^2) \), then we are left with the following map for the deviation,
\[
y_{n+1} = f'(x^*)y_n.
\] (2.13)

We recognize that \( f'(x^*) \) is some constant, \( \lambda \) say. The map for the deviation thus is the linear map
\[
y_{n+1} = \lambda y_n.
\] (2.14)

Figure 2.5. Illustration of stable and unstable fixed points of the difference equation \( x_{n+1} = f(x_n) \). The fixed points \( x_1^* \) and \( x_3^* \) are stable (indicated by a filled circle), and the fixed point \( x_2^* \) is unstable (indicated by an open circle).
Figure 2.6. Behaviour of the general linear map, (2.14), as a function of the iterates \( n \), for the cases (a) \( \lambda > 1 \); (b) \( 0 < \lambda < 1 \); (c) \(-1 < \lambda < 0 \); (d) \( \lambda < -1 \).

We can write \( y_{n+1} \) explicitly in terms of \( \lambda \) and the initial condition \( y_0 \):

\[
\begin{align*}
y_1 &= \lambda y_0, \\
y_2 &= \lambda y_1 = \lambda(\lambda y_0) = \lambda^2 y_0, \\
&\vdots \\
y_n &= \lambda^n y_0.
\end{align*}
\]

The behaviour of the deviation \( y_n \), and the subsequent conclusion regarding the stability of the fixed point \( x^* \), can be summarized as follows:

- \( \lambda > 1 \): geometric growth; fixed point \( x^* \) is unstable;
- \( 0 < \lambda < 1 \): geometric decay; fixed point \( x^* \) is stable;
- \(-1 < \lambda < 0 \): geometric decay with sign switch; fixed point \( x^* \) is stable;
- \( \lambda < -1 \): geometric growth with sign switch; fixed point \( x^* \) is unstable.

The four cases are illustrated in Figure 2.6. Note that no conclusion can be reached about the stability of the fixed point \( x^* \) when \( \lambda = \pm 1 \). These two cases require advanced treatment, involving a careful examination of the neglected terms that were collected in the term \( \mathcal{O}(y_{n+1}^2) \) in (2.12), which is beyond the scope of this book. For treatment of these cases, the reader is referred to Kuznetsov [66].
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More generally, we can summarize the results of the analysis in the following Theorem:

**Theorem 2.1.** Let \( x^* \) be a fixed point of the map \( x_{n+1} = f(x_n) \). Then,

- \( x^* \) is stable when \( |f'(x^*)| < 1 \);
- \( x^* \) is unstable when \( |f'(x^*)| > 1 \);
- there is no conclusion about the stability of \( x^* \) when \( |f'(x^*)| = 1 \).

That is, the linear stability of a fixed point \( x^* \) is determined by the slope of the map at the fixed point, as intuited earlier. The parameter \( \lambda = f(x^*) \) generally is referred to as the *eigenvalue* of the map at \( x^* \).

### 2.2.3 Analysis of the Discrete Logistic Equation

We now return to the discrete logistic equation, (2.7), and apply the tools discussed in the previous section to this map. We begin with eliminating the parameter \( K \) by using the transformation \( \bar{x}_n = \frac{x_n}{K} \) to obtain, after dropping the overbars,

\[
x_{n+1} = f(x_n) = rx_n(1-x_n).
\]

(2.15)

Note that if we have \( x_n > 1 \), then \( x_{n+1} < 0 \). To avoid such situations, we impose the restriction \( 0 \leq r \leq 4 \) (can you think of the reason for why this should be so?), so that \( x_n \in [0, 1] \) for all \( n \) provided \( x_0 \in [0, 1] \).

The fixed points of the map can be found exactly by setting \( f(x^*) = x^* \) and solving for \( x^* \). There are two fixed points. The trivial fixed point, \( x^* = 0 \), always exists, while the nontrivial fixed point, \( x^* = \frac{r-1}{r} \), is positive only when \( r > 1 \).

To determine the stability of the fixed points, we need \( f'(x) \), which is

\[
f'(x) = r(1-2x).
\]

(2.16)

At the trivial fixed point, \( x^* = 0 \), the eigenvalue is \( f'(0) = r \). That is, the trivial fixed point is stable for \( 0 \leq r < 1 \), and unstable for \( 1 < r \leq 4 \). At the nontrivial fixed point, \( x^* = \frac{r-1}{r} \), the eigenvalue is \( f'(\frac{r-1}{r}) = 2 - r \). That is, the nontrivial fixed point is stable for \( 1 < r < 3 \), and unstable for \( 3 < r \leq 4 \).
Figure 2.7. Partial bifurcation diagram for the rescaled logistic map, \((2.15)\). Shown are the fixed points and their stability as a function of the model parameter \(r\). Solid lines indicate stability of the fixed point, and dashed lines indicate instability. The filled circles represent bifurcation points.

The existence and stability of the fixed points is summarized in the bifurcation diagram of the fixed points versus the parameter \(r\), shown in Figure 2.7. Reading the diagram from left to right, note that the trivial fixed point becomes unstable as soon as the nontrivial fixed points come onto the scene at \(r = 1\), when the eigenvalue moves through +1. The nontrivial fixed point is stable initially, but loses its stability at \(r = 3\), when the eigenvalue moves through −1.

The two points \(r = 1\) and \(r = 3\) are known as bifurcation points. A bifurcation point is a parameter value at which there is a qualitative change in the dynamics of the map. The bifurcation at \(r = 1\) is called a transcritical bifurcation, referring to an exchange of stability when two branches of fixed points meet (the two branches meeting here are \(x^* = 0\) and \(x^* = \frac{r-1}{r}\)). The bifurcation at \(r = 3\) is called a flip bifurcation or a period-doubling bifurcation. We will see shortly how the dynamics of the map changes at this flip bifurcation.
There are many other types of bifurcations. A detailed discussion of bifurcation theory is beyond the scope of this book, and the interested reader is referred to Alligood et al. [3], Kuznetsov [66], and Strogatz [101].

We can easily read off the longterm behaviour of the logistic map from the bifurcation diagram. As before, let us think of $x_n$ as the size of a population (now scaled by the factor $K$). We can distinguish three cases (indicated along the bottom of Figure 2.7). In the first case, for $0 \leq r < 1$, the population goes extinct, no matter what the size of the initial population, $x_0$, is. In the second case, for values of $r$ between 1 and 3, the population reaches a nonzero steady state. The larger the value of $r$, the larger the steady-state population. What happens when the parameter exceeds 3 is not clear. Before investigating this third case however, it pays to perform a graphical analysis complementing the results from the linear stability analysis.
Figure 2.9. (a) and (b) Case 1 ($0 < r < 1$), for $r = 0.9$. The only fixed point $\bar{x} = 0$ is stable, and the population goes extinct. (c) and (d) Case 2 ($1 < r < 3$), for $r = 2$. The fixed point $\bar{x} = 0$ is unstable, the nontrivial fixed point is stable, and the population size stabilizes.

Figure 2.8 shows how the shape of the parabola $f(x_n) = rx_n(1 - x_n)$ depends on the value of the model parameter $r$. Note that the roots remain fixed at $x_n = 0$ and $x_n = 1$. However, the maximum of the parabola is $r/4$, and thus increases with $r$.

For the first case, $0 < r < 1$, the parabola lies entirely below the diagonal line $x_{n+1} = x_n$, and the only point of intersection is at the origin. That is, the only fixed point is the trivial fixed point. Since the slope of $f$ at the origin clearly is positive but less than 1, the trivial fixed point is stable. Any population will go extinct, eventually. This situation is illustrated in Figures 2.9 (a) and (b).

When $r = 1$, the parabola is tangent to the diagonal line $x_{n+1} = x_n$ at the origin. This event marks the transition to the second case. As soon as $r > 1$, the slope of $f$ at the origin exceeds 1 (that is, the fixed point at the origin has switched from being stable to unstable), and there is an additional point of intersection, namely the nontrivial fixed point, $x^* = \frac{r-1}{r}$. The slope of $f$ at the nontrivial fixed point is always less than 1. Initially, for $1 < r < 3$ (case 2), the slope of $f$ at the nontrivial fixed point is greater than $-1$, and so the fixed point is stable. Any population will eventually reach a steady-state size. This situation is illustrated in Figure 2.9 (c) and (d).
When \( r = 3 \), the slope of \( f \) at the nontrivial fixed point is \(-1\), and this event marks the transition to the third case. When \( 3 < r \leq 4 \) (the third case), the slope of \( f \) at the nontrivial fixed point is less than \(-1\), and so the fixed point now is unstable, as we had inferred earlier from linear stability analysis (Theorem 2.1).

We now continue with the graphical analysis and cobwebbing to determine what happens in the third case. In Figure 2.10, we show the dynamics of the map for three values of \( r \) between 3 and 4. The plots in the left column of Figure 2.10 show values of the iterates \( x_n \) as a function of \( n \) for various values of \( r \). Corresponding cobwebbing diagrams are shown in the right column of Figure 2.10 (to clarify the cobwebbing diagrams shown in (b) and (d), only the last few iterates are used).
In Figures 2.10 (a) and (b), for \( r = 3.2 \), we observe that the population eventually oscillates between two values. We refer to the oscillation as a \( 2\)-cycle. In Figures 2.10 (c) and (d), for \( r = 3.55 \), we eventually observe a \( 4\)-cycle, or an oscillation between four population sizes. Values of \( r \) can be found at which the map exhibits an \( 8\)-cycle, a \( 16\)-cycle, and so on. But not all values of \( r > 3 \) give periodic oscillations. An example of an aperiodic oscillation is shown in Figures 2.10 (e) and (f), for \( r = 3.88 \). The orbit appears chaotic, and indeed, it can be shown that the logistic map exhibits chaos in the mathematical sense. A careful mathematical definition of chaos is beyond the scope of this book, and the interested reader is referred to Alligood et al. [3] and Strogatz [101] for more information. For the purposes of our discussion, it suffices to observe that the simple model under investigation can exhibit some very complicated dynamics.

We can broaden our analysis to determine the origin of the 2-cycle. When an orbit converges to a 2-cycle, it oscillates between two values, say \( u \) and \( v \) (see Figure 2.10 (b)), with

\[
\begin{align*}
  f(u) &= v, \\
  f(v) &= u,
\end{align*}
\]

or, equivalently,

\[
\begin{align*}
  f(f(u)) &= u, \\
  f(f(v)) &= v.
\end{align*}
\]

Recalling the definition of a fixed point (\( x \) is a fixed point of \( f(x) \) if \( f(x) = x \)), we see that the above equations imply that \( u \) and \( v \) are fixed points of the second-iterate map, \( f(f(x)) = f^2(x) \).

The graph of the second-iterate map \( f^2 \) is shown in Figure 2.11 for various values of the parameter \( r \). For values of \( r < 3 \) (Figure 2.11 (a)), the second-iterate map has two fixed points, namely the origin, which is unstable, and the nontrivial fixed point, \( x^* = \frac{r}{r + 1} \), of the original logistic map, which is stable (note that any fixed point of the logistic map automatically also is a fixed point of the second-iterate map). That is, no interesting 2-cycles exist for these values of \( r \). As \( r \) increases, the maxima of the second-iterate map rise and the local minimum descends, until at \( r = 3 \) (Figure 2.11 (b)), the local minimum is tangent to the diagonal line \( x_{n+2} = x_n \). At this point, two new stable fixed points of the second-iterate map emerge, namely \( u \) and \( v \), corresponding to the 2-cycle (Figure 2.11 (c)). At the same time, the nontrivial fixed point \( x^* \) becomes unstable (this is in accordance with our findings from the analysis of the original logistic map). The bifurcation at \( r = 3 \) is called a period-doubling or flip bifurcation.
2.2. Scalar Discrete-Time Models

Initially, $u$ and $v$ are close together, so the 2-cycle is barely noticeable. But as $r$ increases, $u$ and $v$ move away from each other, and the 2-cycle becomes more pronounced. The stability of $u$ and $v$ corresponds to the stability of the 2-cycle. That is, the 2-cycle is stable initially, since the graph of $f^2$ at $u$ and $v$ is shallow. As $r$ increases beyond $1 + \sqrt{6}$ (see Exercise 2.4.6), the slope of $f^2$ at $u$ and $v$ becomes less than $-1$, indicating that the 2-cycle becomes unstable. At this point (another flip bifurcation), the 4-cycle arises. We could continue the analysis by graphing $f^4$ for various values of $r$, but this is left as an exercise for the reader.

We can update the bifurcation diagram shown in Figure 2.7 by including information about the 2-cycle, as shown in Figure 2.12.

Ideally, we should also include information about the 4-cycle, the 8-cycle, and so on. The algebra to do so becomes unwieldy rather quickly. However, we can use the computer to create a similar diagram. The idea is to let the computer program determine the long-term behaviour of the map for many values of the parameter $r$. For example, for $r = 2$, the iterates converge to $\bar{x} = \frac{1}{2}$, the stable fixed point of the map for this value of $r$. If we had computed 2000 iterates, say, from an arbitrary initial condition, then the last 100 or so iterates will all have a value virtually indistinguishable from $\frac{1}{2}$. So, plotting these last 100 iterates above $r = 2$ on a diagram of $\bar{x}$ versus $r$ just gives a point, $(r, \bar{x}) = (2, \frac{1}{2})$. If we choose $r = 3.2$ (cf. Figure 2.10 (a)), the last 100 iterates or so will jump back and forth between the values of the corresponding 2-cycle. Plotting these iterates above $r = 3.2$ gives two points, and so on. A lot of computation, using many values of $r$ close together, eventually leads to the *orbital bifurcation diagram*, also known as the *Feigenbaum diagram*, shown in Figure 2.13. Note that since the computations only detect stable behaviour (stable fixed points, stable 2-cycles, and so on), the orbital bifurcation diagram differs from the bifurcation diagrams shown in Figures 2.7 and 2.12 in that the branches of unstable behaviour, indicated by dashed lines, no longer are shown.
Figure 2.12. Updated bifurcation diagram for the logistic map shown earlier in Figure 2.7. Shown are the fixed points, as well as the 2-cycle for values of $r > r_1 = 3$. The 2-cycle is stable up to $r_2 = 1 + \sqrt{6}$, and unstable thereafter.

Figure 2.13. Orbital bifurcation diagram for the logistic map.
2.2. Scalar Discrete-Time Models

By examining the orbital bifurcation diagram, it can be seen that the 4-cycle exists only over a small range of $r$, the 8-cycle over an even smaller range of $r$, etc. It can be shown (see for example Holmgren [54]) that the bifurcation points leading to higher-order cycles converge at $r \approx 3.57$. Beyond $r \approx 3.57$, the map becomes chaotic, that is, the iterates no longer appear to follow a predictable pattern, although they are confined to take on only certain values (for example, when $r = 3.6$, the iterates never take on values below 0.324 or above 0.900, but they can take on any intermediate value). We say that the attractor of the map is a *strange attractor*. By computing the orbital bifurcation diagram over a smaller range of $r$, say for $3 < r < 4$, with higher resolution, many interesting features of the map can be observed, such as *periodic windows* surrounded by chaos. A periodic window is a small range of $r$ where the attractor is periodic again. For example, near $r = 3.83$, one can find 3-cycles. From this periodic window, the transition back to chaos occurs through a series of period-doubling or flip bifurcations, leading to 6-cycles, 12-cycles, and so on.

The logistic map is a well-studied map, and there are many interesting mathematical investigations that can be pursued. We will stop here, and refer the interested reader to Devaney [28] and Strogatz [101].

In the 1970's, May noticed that maps defined by simple mathematical formulas can lead to extraordinarily complicated dynamics [70]. He hypothesized that some of the complicated, noisy data observed in time series of populations might have a deterministic component based on simple rules. Cushing and his team (http://math.arizona.edu/~cushing/research.html) have followed up on this hypothesis, and have investigated nonlinear dynamics in populations of flour beetles by means of controlled experiments. These studies have established several important tenets concerning the modelling of biological populations. They have found that mathematical models can be used to make quantitatively accurate descriptions and predictions, that theoretical predictions of mathematical models can be documented in real biological populations, and that mathematical models can offer explanations of dynamics patterns that were previously unavailable to biologists. Thus, their work has lent credibility to the use of models such as described in this chapter. It should be no surprise then that these models continue to be used on a regular basis.
2.2.4 Alternatives to the Discrete Logistic Equation

In the previous section, we saw that the behaviour of the discrete logistic equation, (2.7), is quite complex. For many choices of the model parameters, the solution does not exhibit logistic growth (exponential growth initially, followed by a levelling off of the growth rate, until the population reaches a steady state). Also, for some choices of parameter values, the model gives unrealistic results. For example, if the population \( x_n > K \) in any year, then the population is extinct (negative) the next year. For these reasons, it is worthwhile to examine alternative models that do not have these problems and that are widely used.

In particular, we examine the Beverton-Holt and Ricker models. Before discussing these models in detail, we note that these two models and the discrete logistic equation belong to a class of models that can be written in the following general form:

\[
x_{n+1} = f(x_n) = g(x_n)x_n.
\]  

(2.21)

Many other population models can be written in this form. Of course, the simplest model belonging to this class is the geometric growth model, using \( g(x_n) = r \), so that

\[
x_{n+1} = rx_n
\]  

(2.22)

where \( r > 0 \). We have encountered this model previously, as equation (2.14) in the discussion of linear stability analysis. When \( r > 1 \), \( x_n \to \infty \) as \( n \to \infty \); when \( r < 1 \), \( x_n \to 0 \) as \( n \to \infty \). In this case, the growth rate \( g(x_n) = r \) is constant, that is, the number of offspring per adult does not depend in the current population. We say that growth in the geometric model is density independent.

Regulatory mechanisms that control the growth of populations need to be included in any realistic model. There are many hypothesis regarding the mechanisms at play in regulating the size of populations. For example, populations are influenced by changes in the weather, a limited food supply, competition for resources such as nutrients and space, territoriality, predation, diseases, etc. The discrete logistic equation as well as the Beverton-Holt and Ricker models contain self-regulatory mechanisms that are density dependent, that is, the growth rate \( g(x_n) \) depends nontrivially on the current population \( x_n \). The models differ in their form of density dependence.

In the case of the discrete logistic model, we have \( g(x_n) = r(1 - x_n/K) \). Thus, the growth rate decreases linearly, as shown in Figure 2.14(a). It is because \( g(x_n) < 0 \) when \( x_n > K \) that the model predict extinction within a year whenever \( x_n > K \) (see Figure 2.14(b)). Thus, any good alternative to the discrete logistic model should have \( g(x_n) > 0 \). Both the Beverton-Holt and Ricker models satisfy \( g(x_n) > 0 \). We now discuss these models in some detail.
2.2. Scalar Discrete-Time Models

2.2.1 Scalar Discrete-Time Models

The discrete logistic equation, (2.7). (a) Graph of \( g(x_n) = r(1 - x_n/K) \). (b) Graphs of \( x_{n+1} = f(x_n) = g(x_n)x_n \) and \( x_{n+1} = x_n \).

**The Beverton-Holt model**

The *Beverton-Holt model* was derived in the context of fisheries [15]. Here, \( g(x_n) \) is inversely proportional to \( x_n \). In particular, \( g(x_n) = \frac{r}{1 + \frac{r}{K}x_n} \), with \( r > 0 \) and \( K > 0 \), giving

\[
x_{n+1} = f(x_n) = \frac{r}{1 + \frac{r}{K}x_n} x_n.
\]  \hspace{1cm} (2.23)

The graph of \( g(x) \), for \( r > 1 \), is shown in Figure 2.15(a), and the resulting Beverton-Holt map is shown in Figure 2.15(b). We see that the Beverton-Holt map increases monotonically, approaching the asymptote \( x_{n+1} = rK/(r - 1) \).

Fixed points of the Beverton-Holt map are the nontrivial fixed point at the origin, \( x_1^* = 0 \), and the nontrivial fixed point at the carrying capacity, \( x_2^* = K \). To determine the stability of the fixed points, we need

\[
f'(x) = \frac{r}{(1 + \frac{r}{K}x)}.
\]

Then

\[
f'(x_1^*) = f'(0) = r,
\]

\[
f'(x_2^*) = f'(K) = \frac{1}{r}.
\]
Thus, when \( r > 1 \), the trivial fixed point, \( x_1^* = 0 \), is unstable, and the nontrivial fixed point, \( x_2^* = K \), is stable (when \( 0 < r < 1 \), the stability reverses). Cobwebbing confirms our analytical result. In fact, it is easy to verify with cobwebbing that convergence to \( x_2^* = K \) is monotonic. That is, starting from a small initial condition \( 0 < x_0 << K \), the population increases fast initially. Growth slows down when the population approaches the carrying capacity \( K \). Similarly, when the initial condition \( x_0 > K \), the population decreases smoothly to \( K \). Complex behaviour such as cycles and chaos is not possible.
The Beverton-Holt model is one of the few nonlinear models for which a solution in closed form can be written down (see exercises). It can be shown then that the solution behaviour of the Beverton-Holt model is precisely that of the continuous version of the logistic model (equation (3.6), discussed in detail in section 3.1). In fact, the Beverton-Holt model is the time-one-map of the continuous logistic equation, and as such, we can consider it to be another discrete analog of the continuous logistic equation. We defer derivation of the Beverton-Holt equation via the time-one-map to section 3.6.2. In the meantime, we iterate that we now have two discrete-time models that can be considered analogous to the continuous logistic equation. In particular, we have the discrete logistic equation, which is analogous in the sense that the form of the equation is the same, and the Beverton-Holt model, which is analogous in the sense that the form of the solution is the same.

In Section 2.2.1, we fit the discrete logistic equation, (2.7), to Gause’s classic data for the growth of Paramecium aurelia (cf. Figure 2.1). As we have just seen, it may be more appropriate to fit the Beverton-Holt model to the data instead. This is left as an exercise for the reader.

**The Ricker model**

The Ricker model also has its roots in fisheries [91]. In this case, \( g(x) = \exp \left[ r \left( 1 - \frac{x}{K} \right) \right] \), with \( r > 0 \) and \( K > 0 \), giving

\[
x_{n+1} = f(x_n) = \exp \left[ r \left( 1 - \frac{x_n}{K} \right) \right] x_n.
\]

(2.24)

We can think of the factor \( \exp(r) \) as a constant reproduction factor, and of the factor \( \exp \left( -rx_n/K \right) \) as a density-dependent mortality factor. The larger the population \( x_n \), the more severe the mortality factor.

The graph of \( g(x) \) is shown in Figure 2.16(a), and the resulting Ricker map is shown in Figure 2.16(b). Comparing Figures 2.15(a) and 2.16(a), we see that shape of the graph of \( g(x) \) is similar to that for the Beverton-Holt model. However, the exponential function decreases faster than the inverse function, and as a result, the Ricker map has a single local maximum (it sometimes is referred to as a single-hump map), as is the case in the discrete logistic equation (see Figure 2.14(b)). However, the Ricker map remains positive for all values of \( x_n \). Thus, the model can exhibit complex dynamics such as cycles and chaos, but it never yields unrealistic (negative) populations.

Fixed points of the Ricker map are given by the trivial fixed point at the origin, \( x_1^* = 0 \), and the nontrivial fixed point at the carrying capacity, \( x_2^* = K \). To determine the stability of the fixed points, we need

\[
f'(x) = e^{r(1 - \frac{x}{K})} \left[ 1 - \frac{rx}{K} \right].
\]

(2.25)
Figure 2.16. The Ricker equation, (2.24). (a) Graph of $g(x_n) = \exp\left[r\left(1 - \frac{x_n}{K}\right)\right]$. (b) Graphs of $x_{n+1} = f(x_n) = g(x_n)x_n$ and $x_{n+1} = x_n$.

Then

$$f'(x_1^*) = f'(0) = e^r > 1,$$

$$f''(x_2^*) = f'(K) = 1 - r.$$  \hfill (2.26)

Thus, the trivial fixed point $x_1^* = 0$ always is unstable. Since $|1 - r| < 1$ when $0 < r < 2$, the nontrivial fixed point is stable for $0 < r < 2$ and unstable for $r > 2$. Numerical simulation of the model shows that the nontrivial fixed point is reached from any initial condition $x_0 > 0$ when $0 < r < 2$, that is, the nontrivial fixed point is globally asymptotically stable. When $r > 2$, cycles and chaos are observed.

Further detailed analysis of the Ricker model mirrors the investigation of the discrete logistic equation in the previous section, and is the subject of Section 7.2 in the chapter on Maple.
2.2.5 Models in Population Genetics

We now move away from population biology and show another application of discrete-time equations, namely in the study of population genetics. Population genetics concerns itself with the genetic basis for evolution in a population.

We begin with a review of some terminology in the study of genetics. We consider diploid organisms, whose genetic material rests on two sets of chromosomes, one obtained from each parent. Chromosomes contain genes, which are the fundamental units of heredity, carrying information from one generation to the next. Due to mutations, a gene can exist in different forms, or alleles. Two homologous alleles, one originating from each parent, interact to produce a trait, such as eye colour in humans, or wing colour in moths.

Suppose we are interested in a trait determined by one gene for which there are two alleles. For example, consider wing colouration in moths. Let the two alleles be denoted by W and w. That is, individual moths may have one of three genotypes (allelic composition): WW, Ww, and ww. Individuals with WW or ww are called homozygous; those with Ww are called heterozygous. Let’s further suppose that individuals individuals have one of three phenotypes (outward expression of the genetic code): individuals with genotype WW and Ww develop white wings, whereas individuals with genotype ww develop black wings. In this case, the W allele is capable of expressing the colour trait at the expense of the w allele; we say it is dominant. Similarly, the w allele fails to have an impact when paired with the W allele; we say it is recessive.

A question of interest in population genetics is how the genetic make-up of a population changes over time. In particular, how do allele frequencies change, if at all, across the generations? Do recessive alleles disappear gradually? What happens when there is selection?

We divide this section into three parts. First, we develop a model to track the frequency of the W allele in the population, and derive a well-known result in population genetics known as the Hardy-Weinberg law. We then introduce selection, and examine the effect of selection in a population with two phenotypes and a population with three phenotypes. The model for the latter case exhibits a type of behaviour not encountered previously, namely bistability. Throughout this section, we restrict ourselves to the study of organisms with discrete generations, so that discrete-time equations are appropriate.
Table 2.2. Punnett square summarizing how the frequencies of the $W$ and $w$ alleles in the current generation give rise to three different genotypes in the next generation.

The Hardy-Weinberg law

Let $p_n$ be the frequency of the $W$ allele in the population, that is, the number of alleles $W$ divided by the total number of alleles in the population, during the $n$-th generation. Similarly, let $q_n$ be the frequency of the $w$ allele during the $n$-th generation. Of course, since $p_n + q_n = 1$, it is sufficient to track only $p_n$, since $q_n$ always can be recovered via $q_n = 1 - p_n$.

To derive a model for $p_n$, we need to make a number of assumptions. To begin, we assume the following:

- mating is completely random (white moths don’t preferentially mate with other white moths nor with black moths);
- all genotypes are equally fit, that is, all genotypes are equally likely to survive to breed;
- absence of mutation.
To compute $p_{n+1}$, it helps to construct a *Punnett square*, as shown in Table 2.2, which summarizes the frequencies of the alleles in the current generation, and the resulting frequencies of the three different genotypes in the next generation. Thus, the frequencies of the next generation with genotypes WW, Ww (= wW), and ww are $p_n^2$, $2p_n(1 - p_n)$, and $(1 - p_n)^2$, respectively. The frequency of the W allele in the next generation is equivalent to the probability of obtaining a W allele by randomly choosing one allele from a random individual. The probability of obtaining a W allele from an individual with genotype WW is 1; from an individual with genotype Ww it is $\frac{1}{2}$, and from an individual with genotype ww it is 0. Computing a weighted average of these probabilities thus yields the following expression for the frequency of the W allele:

$$p_{n+1} = \frac{1 \cdot p_n^2 + \frac{1}{2} \cdot 2p_n(1 - p_n) + 0 \cdot (1 - p_n)^2}{p_n^2 + 2p_n(1 - p_n) + (1 - p_n)^2} \quad (2.28)$$

$$= \frac{p_n}{(p_n + 1 - p_n)^2} \quad (2.29)$$

$$= p_n. \quad (2.30)$$

We see that allele frequencies do not change from generation to generation, provided the assumptions stated above hold, of course. This conclusion is known as the *Hardy-Weinberg law*.

**Selection in a population with two phenotypes**

The assumptions stated in the previous section imply that there is no selection. What happens when there is selection? For example, suppose that white-winged moths are more conspicuous, and therefore more likely to be eaten by birds than black-winged moths. Will white-winged moths become extinct? What if white-winged moths have the selective advantage instead? Will black-winged moths become extinct?

Let $\alpha$ be the fraction of white-winged moths surviving to produce the next generation, with $0 \leq \alpha \leq 1$. Similarly, let $\gamma$ be the fraction of black-winged moths surviving, with $0 \leq \gamma \leq 1$. Choosing $\alpha > \gamma$ gives white-winged moths a selective advantage, while $\alpha < \gamma$ gives black-winged moths a selective advantage.

Just before reproduction, the genotype ratio WW : Ww : ww is $\alpha^2 p_n^2 : 2\alpha p_n(1 - p_n) : \gamma(1 - p_n)^2$. The resulting frequency of W alleles in the next generation then is

$$p_{n+1} = \frac{1 \cdot \alpha p_n^2 + \frac{1}{2} \cdot 2\alpha p_n(1 - p_n) + 0 \cdot \gamma(1 - p_n)^2}{\alpha p_n^2 + 2\alpha p_n(1 - p_n) + \gamma(1 - p_n)^2} \quad (2.31)$$

$$= \frac{\alpha p_n}{(\gamma - \alpha)p_n^2 - 2(\gamma - \alpha)p_n + \gamma}. \quad (2.32)$$
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Note that when \( \alpha = \gamma \), that is, when there is no selective advantage, we recover the Hardy-Weinberg equilibrium, namely \( p_{n+1} = p_n \). But when \( \alpha \neq \gamma \), we have a nonlinear equation that warrants further investigation.

Let’s begin by finding the fixed points \( p^* \) of this equation, and determining their stability with a linear stability analysis. First, we look for values of \( p^* \) such that \( f(p^*) = p^* \), where

\[
f(p) = \frac{\alpha p}{(\gamma - \alpha)p^2 - 2(\gamma - \alpha)p + \gamma}.
\]

It is easy to show that this equation has two distinct roots, corresponding to two fixed points, namely \( p_1^* = 0 \) and \( p_2^* = 1 \). In terms of the genetic problem at hand, \( p_1^* = 0 \) means that the W allele has become extinct and all moths have black wings, whereas \( p_2^* = 1 \) means that the w allele has become extinct and all moths have white wings. Intuitively, we expect \( p_1^* = 0 \) to be stable when black-winged moths have the selective advantage (\( \alpha < \gamma \)), and \( p_2^* = 1 \) to be stable when white-winged moths have the selective advantage (\( \alpha > \gamma \)).

To determine the stability of these fixed points with linear stability analysis, we find

\[
f'(p) = \frac{-\alpha ((\gamma - \alpha)p^2 - \gamma)}{((\gamma - \alpha)p^2 - 2(\gamma - \alpha)p + \gamma)^2}.
\]

so that \( f'(p_1^*) = f'(0) = \frac{\alpha}{\gamma} \) and \( f'(p_2^*) = f'(1) = 1 \). The appearance of the ratio \( \alpha/\gamma \) looks promising in light of our intuition discussed above. Let’s check the details. When \( \alpha < \gamma \), we have \( 0 < \frac{\alpha}{\gamma} < 1 \), and so we conclude that the fixed point \( p_1^* = 0 \) is stable. That is, when black-winged moths have the selective advantage, the W allele indeed can become extinct if its frequency becomes sufficiently small (since the linear stability analysis only is local, we cannot conclude that the W allele will become extinct per se). Similarly, when \( \alpha > \gamma \), the fixed point \( p_1^* = 0 \) is unstable. Since \( f'(p_2^*) = 1 \), the linear stability analysis does not yield a conclusion about the stability of the other fixed point, \( p_2^* = 1 \) (see Theorem 2.1). A graphical stability analysis will be helpful.

Cobwebbing diagrams for the allele frequency equation (2.32) are shown in Figure 2.17. In Figure 2.17(a), the case \( \alpha < \gamma \) is shown. Indeed, any initial condition \( p_0 \) with \( 0 \leq p_0 < 1 \) leads to the fixed point \( p_1^* = 0 \). We conclude that \( p_1^* = 0 \) is stable, and \( p_2^* = 1 \) is unstable (for any \( 0 < p_0 \leq 1 \), which are the only biologically sensible initial conditions). In Figure 2.17(b), the case \( \alpha > \gamma \) is shown. Here, the situation is reversed. The fixed point \( p_1^* = 0 \) is unstable, and \( p_2^* = 1 \) is stable (again, for any \( 0 < p_0 \leq 1 \)).

In summary, selection on the level of phenotype (white-winged versus black-winged), when one allele is dominant and the other recessive, eventually leads to extinction of one of the alleles. How fast the allele is driven to extinction depends on the relative strength of the model parameters \( \alpha \) and \( \gamma \). The larger the difference between \( \alpha \) and \( \gamma \), the faster the approach to extinction.
2.2. Scalar Discrete-Time Models

Figure 2.17. Cobwebbing diagrams for allele frequency equation (2.32). (a) \( \alpha < \gamma \) (\( \alpha = 0.2 \) and \( \gamma = 0.8 \)); (b) \( \alpha > \gamma \) (\( \alpha = 0.8 \) and \( \gamma = 0.2 \)).

Selection in a population with three phenotypes

Let’s generalize this investigation into the effect of selection one more step. Suppose that the W allele no longer is dominant, and that the three genotypes, WW, Ww, and ww, give rise to three distinct phenotypes. For ease of discussion, we will assume that individuals with genotypes WW and ww will develop white and black wings, respectively, as before, and that individuals with genotype Ww will develop gray wings. Furthermore, introduce the parameter \( \beta \) to represent the selective pressure on gray-winged moths, with \( 0 \leq \beta \leq 1 \). Just before reproduction, the genotype ratio WW : Ww : ww is \( p_2^n : 2p_n(1 - p_n) : \gamma(1 - p_n)^2 \). Questions of interest now include: under which conditions will all three phenotypes co-exist? Similarly, can grey-winged moths be driven extinct? If so, will white-winged moths or black-winged moths survive?

As before, it suffices to study the iterative map for the frequency of W alleles, which is

\[
p_{n+1} = \frac{1 \cdot \alpha p_n^2 + \frac{1}{2} \cdot 2\beta p_n(1 - p_n) + 0 \cdot \gamma(1 - p_n)^2}{\alpha p_n^2 + 2\beta p_n(1 - p_n) + \gamma(1 - p_n)^2} \quad (2.33)
\]

\[
= \frac{(\alpha - \beta)p_n^2 + \beta p_n}{(\alpha - 2\beta + \gamma)p_n^2 + 2(\beta - \gamma)p_n + \gamma}. \quad (2.34)
\]

This more general allele frequency equation looks a bit more intimidating than the previous one, but doing the analysis is still quite reasonable. In particular, fixed points \( p \) satisfy \( p^* = f(p^*) \), where

\[
f(p) = \frac{(\alpha - \beta)p^2 + \beta p}{(\alpha - 2\beta + \gamma)p^2 + 2(\beta - \gamma)p + \gamma}.
\]
yielding a cubic equation in $p$. One fixed point can be found by inspection, namely $p_1^* = 0$. We then are left with a quadratic equation, and its roots are $p_2^* = 1$, and

$$p_3^* = \frac{\gamma - \beta}{\alpha - 2\beta + \gamma}.$$  

It is easy to check that $p_3^* \in (0, 1)$ only when $\beta < \alpha, \gamma$ or when $\beta > \alpha, \gamma$. Otherwise, $p_1^* = 0$ and $p_2^* = 1$ are the only biologically relevant fixed points. We can now proceed to determine the stability of the fixed points. As before, we require $f'(p)$, which is

$$f'(p) = \frac{(\alpha\beta - 2\alpha\gamma + \beta\gamma)p^2 + 2\gamma(\alpha - \beta)p + \beta\gamma}{((\alpha - 2\beta + \gamma)p^2 + 2(\beta - \gamma)p + \gamma)^2}.$$  

Then (with a little help from Maple to simplify the algebra)

$$f'(p_1^*) = f'(0) = \frac{\beta}{\gamma}, \quad (2.35)$$  

$$f'(p_2^*) = f'(1) = \frac{\beta}{\alpha}, \quad (2.36)$$  

$$f'(p_3^*) = -\frac{\alpha\beta - 2\alpha\gamma + \beta\gamma}{\alpha\gamma - \beta^2}. \quad (2.37)$$  

We can now determine the fate of the moth population under different conditions by studying the outcome of the model with different parameter sets. It can be shown that there are four fundamentally different cases, as summarized in Table 2.3 (the reader is asked work out the details in the exercises). Representative cobweb diagrams for each case are shown in Figure 2.18.

Cases I and II are straightforward, and the results are rather intuitive. In case I, white-winged moths (genotype WW) have the selective advantage and black-winged moths (genotype ww) have the selective disadvantage, so that the $w$ allele is driven to extinction. Consequently, both grey-winged and black-winged moths are driven to extinction, and the only moths remaining are the white-winged moths (Figure 2.18(a)). Case II is just the opposite, with black-winged moths having the selective advantage and white-winged moths the selective disadvantage so that the only moths remaining are black-winged moths (Figure 2.18(b)).

A bit more interesting are cases III and IV. In case III (shown in Figure 2.18(c)), grey-winged moths have the selective advantage. Consequently, both $W$ and $w$ alleles remain in the population ($p \rightarrow p_3^*$, which lies between 0 and 1), and all three genotypes coexist. The equilibrium frequency for the $W$ allele, $p_3^*$, depends on the relative strength of the three selective pressure parameters. The larger the value of $\alpha$, the larger $p_3^*$; that is, the higher the equilibrium frequency of the $W$ allele, as might be expected biologically.
2.2. Scalar Discrete-Time Models

<table>
<thead>
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<td>$\alpha &gt; \beta &gt; \gamma$</td>
<td>$p_1^* = 0$ is unstable $p_2^* = 1$ is stable</td>
<td>$p \to p_2^* = 1$</td>
<td>White-winged moths have the selective advantage and black-winged moths have the selective disadvantage; $w$ allele becomes extinct; all moths have genotype WW (white-winged).</td>
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<tr>
<td>II</td>
<td>$\alpha &lt; \beta &lt; \gamma$</td>
<td>$p_1^* = 0$ is stable $p_2^* = 1$ is unstable</td>
<td>$p \to p_1^* = 0$</td>
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<td>III</td>
<td>$\beta &gt; \gamma &gt; \alpha$ or $\beta &gt; \alpha &gt; \gamma$</td>
<td>$p_1^* = 0$ is unstable $p_2^* = 1$ is unstable $p_3^*$ is stable</td>
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<tr>
<td>IV</td>
<td>$\beta &lt; \gamma &lt; \alpha$ or $\beta &lt; \alpha &lt; \gamma$</td>
<td>$p_1^* = 0$ is stable $p_2^* = 1$ is stable $p_3^*$ is unstable</td>
<td>$p \to p_1^* = 0$ or $p \to p_2^* = 1$</td>
<td>Grey-winged moths have the selective disadvantage; either the $W$ or the $w$ allele becomes extinct; all moths have either genotype WW or ww (white-winged or black-winged).</td>
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Table 2.3. *Summary of the outcome of the more general allele frequency equation,* (2.34).

Finally, in case IV (shown in Figure 2.18(d)), where grey-winged moths have the selective disadvantage, we see a new and interesting dynamical behaviour, known as *bistability*. There are two stable fixed points, separated by an unstable fixed point. As time progresses, either one of the stable fixed points is approached, depending on the initial condition. If the initial frequency of the $W$ allele is greater than $p_3^*$, then $p \to p_3^* = 1$ is approached. That is, provided the frequency of the $W$ allele is sufficiently large initially, it will become dominant. If it is less than $p_3^*$, then $p \to p_1^* = 0$ is approached, and the $W$ allele becomes extinct.
Figure 2.18. Cobweb diagrams for the more general allele frequency equation, (2.34), corresponding to the four cases summarized in Table 2.3. (a) Case I ($\alpha > \beta > \gamma$), with $\alpha = 0.8$, $\beta = 0.5$, and $\gamma = 0.1$; (b) Case II ($\alpha < \beta < \gamma$), with $\alpha = 0.1$, $\beta = 0.5$, and $\gamma = 0.8$; (c) Case III ($\beta > \alpha, \gamma$), with $\alpha = 0.1$, $\beta = 0.9$, and $\gamma = 0.3$; (d) Case IV ($\beta < \alpha, \gamma$), with $\alpha = 0.9$, $\beta = 0.1$, and $\gamma = 0.7$.

It turns out that the ideas presented here find application in a real-life situation. The peppered moth (*Biston betularia*) is common in both Europe and North America. Normally, the moth has a “peppered” appearance, but sometimes it is completely black (melanic). On lichen-covered tree trunks, the normal form is camouflaged, while the melanic form is rather conspicuous and at a selective disadvantage. During the industrial revolution in England, lichen were killed by pollution, resulting in much darker tree trunks. Consequently, the selective pressure on the two forms of the moths reversed, and the frequencies of the allele for the gene responsible for wing colouration adapted quickly [64].

In this section, we have only scratched the surface of the types of problems in the area of population genetics that can be studied with discrete-time equations. For further exploration, the reader is referred to Chapter 4 in the text by Britton [20], and Section 3.6 in the text by Edelstein-Keshet [32].
2.3 Systems of Discrete-Time Equations

2.3.1 Love Affairs: Introduction

Consider the relationship between two lovers, say Romeo and Juliet (with apologies to Shakespeare). It is not unreasonable to think that their feelings for each other are dynamic. In [100, 101], Strogatz developed a simple model, consisting of a system of ordinary differential equations, describing the dynamic love affair. Here, we will consider a discrete-time version of the model.

Let $R_n$ be Romeo’s love/hate for Juliet on day $n$, and let $J_n$ be Juliet’s love/hate for Romeo on day $n$. We will agree upon the following interpretation of the values of $R_n$ (similarly for $J_n$): when $R_n > 0$, Romeo loves Juliet, when $R_n < 0$, Romeo hates Juliet, and when $R_n = 0$, Romeo is neutral towards Juliet. The larger $|R_n|$, the stronger the feeling of love/hate.

Next, let’s assume that Romeo and Juliet respond to their own feelings in a linear fashion. In particular, assume

$$R_{n+1} = a_R R_n,$$  \hspace{1cm} (2.38)
$$J_{n+1} = a_J J_n.$$  \hspace{1cm} (2.39)

It seems reasonable to take $a_R, a_J > 0$ so that we’re not dealing with wild mood swings (love one day, hate the next, and so on). Depending on the magnitude of the $a$ parameter, there are two romantic styles. If $0 < a_R, a_J < 1$, then the initial feeling becomes neutral as time progresses. If $a_R, a_J > 1$, then the initial feeling intensifies.

Now we add simple linear terms that represent the response of Romeo and Juliet to the feelings of the other, to get the following system of equations:

$$R_{n+1} = a_R R_n + p_R J_n,$$  \hspace{1cm} (2.40)
$$J_{n+1} = a_J J_n + p_J R_n.$$  \hspace{1cm} (2.41)

The $p$ parameters describe how their love/hate changes in response to the current feeling of the other. We allow $p_R, p_J \in \mathbb{R}$. In this case, the sign of the $p$ parameter determines a particular romantic style. For example, if $p_R > 0$, then Romeo gets excited by Juliet’s love for him, while he gets discouraged by Juliet’s hate for him. In contrast, if $p_R < 0$, then Juliet’s hate for him contributes to his love for her, while Juliet’s love for him contributes to his hate for her.
Both Romeo and Juliet thus have four romantic styles. The outcome of their love affair depends on the particular combination of romantic styles, the relative size of the $a$ and $p$ parameters, and the initial feelings for each other. It is easy (and instructive too) to simulate this model, for example on a spreadsheet, and experiment with different sets of parameters. Here, we present four case studies, illustrating typical types of behaviour of the system.

In Figure 2.19, we show two side-by-side graphs for each of the four case studies. Graphs in the left column show $R_n$ and $J_n$ as functions of $n$. Graphs in the right column show the orbits in the $(R_n, J_n)$ phase plane. In these graphs, time $n$ is suppressed, and successive coordinates $(R_n, J_n)$ are plotted. The direction of the orbit as $n$ increases is indicated with arrows.

In Figure 2.19(a), both Romeo and Juliet can be considered cautious lovers. If they were to respond to their own feelings only, their feelings for each other would become neutral ($0 < a_R, a_J < 1$). Although they respond in kind to each other, they only do so tentatively ($p_R$ and $p_J$ are both positive, but relatively small). Different initial conditions all lead to the same outcome: as $n \to \infty$, $R_n, J_n \to 0$, that is, the love affair fizzes, and both Romeo and Juliet become neutral to each other.

In Figure 2.19(b), the $p$ parameters have been increased slightly, so that Romeo and Juliet both respond more decisively to the feelings of the other. In the case shown, the love affair results in a love fest, with both $R_n, J_n \to +\infty$ as $n \to \infty$. With different initial conditions, the love affair may result in war instead, with both $R_n, J_n \to -\infty$ as $n \to \infty$.

In Figure 2.19(c), we consider a case where both Romeo and Juliet remain true to their initial feelings ($a_R, a_J = 1$), but their $p$ parameters have opposite sign (do opposites attract?). Here, the love affair exhibits growing oscillations, that is, Romeo and Juliet experience a perpetual cycle of love and hate, with their feelings ever intensifying as time progresses.

Finally, in Figure 2.19(d), we achieve an equilibrium of perpetual love, albeit one in which Juliet loves Romeo more than Romeo loves Juliet.

One can continue to vary the model parameters and initial conditions to investigate the outcome of the love affair. This becomes tiring quickly, and unsatisfying. Instead, it would be nice to be able to predict the outcome of the love affair given a set of model parameters. We can do so by extending the concept of fixed points and their stability from scalar equations to systems of equations, which we do in the next section. We return to Romeo and Juliet in Section 2.3.3, where we apply the results of linear stability analysis.
2.3. Systems of Discrete-Time Equations

2.3.2 Fixed Points and Linear Stability Analysis for Systems of Discrete-Time Equations

In this section, we extend the concept of fixed points and their stability from scalar equations to systems of equations. For ease of notation, we present the material for a two-dimensional system, but the results are generalized readily to higher-dimensional systems, as we will see shortly.
Consider the following two-dimensional discrete-time system:

\[ x_{n+1} = f(x_n, y_n), \quad (2.42) \]
\[ y_{n+1} = g(x_n, y_n). \quad (2.43) \]

Fixed points of this system are all points \((x^*, y^*)\) satisfying \(f(x^*, y^*) = x^*\) and \(g(x^*, y^*) = y^*\).

To determine the stability of a fixed point, consider a small perturbation from the fixed point by letting

\[ x_n = x^* + u_n, \quad (2.44) \]
\[ y_n = y^* + v_n, \quad (2.45) \]

where both \(u_n\) and \(v_n\) are understood to be small, so that \(x_n\) and \(y_n\) can be thought of as perturbations of \(x^*\) and \(y^*\), respectively. Similar to the situation for one-dimensional discrete-time equations, discussed earlier, the question of interest is what happens to \(u_n\) and \(v_n\), the deviations of \(x_n\) and \(y_n\) from \(x^*\) and \(y^*\), respectively, as the map is iterated.

We can find the map for the deviation \((u_n, v_n)\) by substituting (2.44)–(2.45) into (2.42)–(2.43) to obtain

\[ x^* + u_{n+1} = f(x^* + u_n, y^* + v_n), \quad (2.46) \]
\[ y^* + v_{n+1} = g(x^* + u_n, y^* + v_n). \quad (2.47) \]

We expand the right hand side using a Taylor series about \((x^*, y^*)\) to obtain

\[ x^* + u_{n+1} = f(x^*, y^*) + \frac{\partial f}{\partial x}(x^*, y^*)u_n + \frac{\partial f}{\partial y}(x^*, y^*)v_n + \mathcal{O}(u_n^2, v_n^2), \quad (2.48) \]
\[ y^* + v_{n+1} = g(x^*, y^*) + \frac{\partial g}{\partial x}(x^*, y^*)u_n + \frac{\partial g}{\partial y}(x^*, y^*)v_n + \mathcal{O}(u_n^2, v_n^2). \quad (2.49) \]

Since \((x^*, y^*)\) is a fixed point, we can replace \(f(x^*, y^*)\) and \(g(x^*, y^*)\) on the right hand side by \(x^*\) and \(y^*\), respectively. If, in addition, we neglect all the terms in the Taylor series that have been collected in \(\mathcal{O}(u_n^2, v_n^2)\), then we are left with the following map for the deviation,

\[ u_{n+1} = \frac{\partial f}{\partial x}(x^*, y^*)u_n + \frac{\partial f}{\partial y}(x^*, y^*)v_n, \quad (2.50) \]
\[ v_{n+1} = \frac{\partial g}{\partial x}(x^*, y^*)u_n + \frac{\partial g}{\partial y}(x^*, y^*)v_n. \quad (2.51) \]

As before, we recognize that the partial derivatives appearing here are evaluated at the fixed point \((x^*, y^*)\), and so they are all constants. We thus have a linear map, which can be rewritten in matrix form:

\[ u_{n+1} = J u_n, \quad (2.52) \]
2.3. Systems of Discrete-Time Equations

where

$$u_n = \begin{pmatrix} u_n \\ v_n \end{pmatrix},$$

(2.53)

and

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

(2.54)

is the Jacobian matrix of the original map, evaluated at the fixed point \((x^*, y^*)\) (earlier, we used \(J\) to denote Juliet’s love/hate for Romeo; however, the meaning should be clear from the context of the equation).

Since we started with a 2-dimensional system of equations, (2.42)–(2.43), \(u\) is a 2-vector, and the Jacobian matrix is a 2 \(\times\) 2 matrix. In general, if we start with an \(m\)-dimensional system, \(u\) is an \(m\)-vector, and the Jacobian matrix has dimension \(m \times m\). Thus, now that we have switched to matrix notation, the results that follow not only apply to 2-dimensional systems, but to \(m\)-dimensional systems in general.

Motivated by the form of the solution for scalar equations, we look for solutions of the form

$$u_n = \lambda^n c,$$

(2.55)

where \(c\) is a constant vector. Substituting (2.55) into (2.52) gives

$$\lambda^{n+1} c = \lambda^n J c.$$

(2.56)

Cancelling \(\lambda^n\) and rearranging gives

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

(2.57)

where \(I\) denotes the identity matrix, and \(0\) denotes the zero vector.

We recognize this last equation as the eigenvalue problem from linear algebra for the matrix \(J\): a nonzero vector \(c\) satisfying the equation is an eigenvector corresponding to the eigenvalue \(\lambda\).

In order to obtain a nonzero vector \(c\), we need

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

(2.58)

known as the characteristic equation of the matrix \(J\). Since \(J\) is an \(m \times m\) matrix, setting \(\det(J - \lambda I) = 0\) gives a polynomial equation of degree \(m\) for \(\lambda\). This polynomial is known as the characteristic polynomial of the matrix. In general, the characteristic polynomial has \(m\) distinct roots, \(\lambda_1, \lambda_2, \ldots, \lambda_m\). The superposition principle then yields the following general solution of (2.52) for the deviation \(u_n\):

$$u_n = \sum_{i=1}^{m} A_i \lambda_i^n c_i,$$

(2.59)
where the $A_i$'s are arbitrary constants (determined by initial conditions), and $c_i$ is the eigenvector corresponding to the eigenvalue $\lambda_i$.

We now are in a position to evaluate the dynamics of the deviation $u_n$. As was the case for scalar equations, the dynamics are determined by the size of the eigenvalues $\lambda_i$ relative to 1. In general, if all eigenvalues $|\lambda_i| < 1$, then $|u_n| \to 0$ as $n \to \infty$. If at least one of the eigenvalues $|\lambda_i| > 1$, then $|u_n| \to \infty$ as $n \to \infty$.

The implication for the stability of the fixed points of the original map thus can be summarized in the following theorem:

**Theorem 2.2.** Let $x^*$ be a fixed point of the $m$-dimensional map $x_{n+1} = f(x_n)$, where $x \in \mathbb{R}^m$ and $f : \mathbb{R}^m \to \mathbb{R}^m$. Let $J$ be the Jacobian matrix of $f$, evaluated at $x^*$. Then

- $x^*$ is stable if all eigenvalues of the Jacobian matrix $J$ have magnitude less than 1;

- $x^*$ is unstable if at least one of the eigenvalues has magnitude greater than 1.

It is not always necessary to calculate the eigenvalues of the Jacobian matrix $J$ explicitly. In particular, Jury [59] derived necessary and sufficient conditions for all eigenvalues of the Jacobian matrix to have magnitude less than 1. The so-called Jury conditions can be written down in terms of the coefficients of the characteristic polynomial. They are easy to write down and apply for 2- and 3-dimensional systems, but quickly become unwieldy for high-dimensional systems.

For 2-dimensional systems, the characteristic polynomial can be written as

$$\lambda^2 - tr\,J\lambda + det\,J = 0.$$  \hfill (2.60)

In the exercises, the reader is asked to verify that the following Jury conditions

$$|tr\,J| < 1 + det\,J < 2.$$ \hfill (2.61)

are necessary and sufficient conditions for all eigenvalues of $J$ to have magnitude less than 1, that is, for the fixed point in question to be stable. The Jury conditions for systems of higher dimension can be found in the paper by Jury [59], and also in the text by Edelstein-Keshet [32].
For 2-dimensional systems, the Jury conditions can be visualized in \((\text{tr} J, \text{det} J)\) space, as shown in Figure 2.20. In particular, the Jury conditions hold on the interior of the stability triangle, determined by the intersection of the three following regions:

\[
\begin{align*}
\text{det} J &< 1, & (2.62) \\
\text{det} J &> \text{tr} J - 1, & (2.63) \\
\text{det} J &> -\text{tr} J - 1. & (2.64)
\end{align*}
\]
The system undergoes a bifurcation as parameter values are varied and \((\text{tr } J, \det J)\) crosses one of the boundaries of this triangle. On the boundary of the triangle, one of the Jury conditions is violated through equality, and at least one of the eigenvalues is precisely +1. A treatment of bifurcations is beyond the scope of this book, but the reader is referred to [66] for details.

### 2.3.3 Love Affairs: Model Analysis

We now return to the love affair of Romeo and Juliet, and attempt to understand the outcome of their affair as observed in the four case studies discussed in Section 2.3.1 in terms of the stability of any fixed points.

Fixed points \((R^*, J^*)\) of the system for Romeo and Juliet, (2.40)–(2.41), must satisfy

\[
R^* = a_R R^* + p_R J^*, \tag{2.65}
\]

\[
J^* = a_J J^* + p_J R^*. \tag{2.66}
\]

Rearranging, we obtain the following linear system for \(R^*\) and \(J^*\):

\[
(a_R - 1)R^* + p_R J^* = 0, \tag{2.67}
\]

\[
p_J R^* + (a_J - 1)J^* = 0, \tag{2.68}
\]

which can be written as

\[
\begin{bmatrix}
  a_R - 1 & p_R \\
  p_J & a_J - 1
\end{bmatrix}
\begin{bmatrix}
  R^* \\
  J^*
\end{bmatrix}
= \begin{bmatrix}
  0 \\
  0
\end{bmatrix}. \tag{2.69}
\]

We have a homogeneous linear system. Thus, this system has a unique solution, namely \((R^*, J^*) = (0, 0)\), provided that \(\det(A) \neq 0\), where

\[
A = \begin{bmatrix}
  a_R - 1 & p_R \\
  p_J & a_J - 1
\end{bmatrix}. \tag{2.70}
\]

It can be verified easily that this condition holds for the three case studies shown in Figure 2.19(a)–(c). When \(\det(A) = 0\), as is the case for the fourth case study, shown in Figure 2.19(d), there is an infinite number of solutions or fixed points. We begin by discussing the results of the first three case studies, and defer discussion of the fourth case study to later.

Orbits shown in the phase planes in Figure 2.19(a)–(c) suggest that the fixed point \((R^*, J^*) = (0, 0)\) is stable in the first case study, while it is unstable in the second and third case studies. We can easily verify this with a linear stability analysis. Since the original system, (2.40)–(2.41), already is linear, there is little work to be done.
2.3. Systems of Discrete-Time Equations

The Jacobian matrix is simply

\[ J = \begin{bmatrix} a_R & p_R \\ p_J & a_J \end{bmatrix}, \]  

with

\[ \text{tr} J = a_R + a_J, \]  

\[ \det J = a_R a_J - p_R p_J. \] (2.72)

Applying the Jury conditions, (2.61), we require

\[ |a_R + a_J| < 1 + a_R a_J - p_R p_J < 2 \] (2.74)

for the fixed point \((R^*, J^*) = (0, 0)\) to be stable.

Indeed, for the first case study \((a_R = 0.5, a_J = 0.7, p_R = 0.2, p_J = 0.5, \text{ shown in Figure 2.19(a)})\), both Jury conditions are satisfied, and hence the fixed point is stable, as we had guessed. For the second case study \((a_R = 0.5, a_J = 0.7, p_R = 0.7, p_J = 0.9, \text{ shown in Figure 2.19(b)})\), the first Jury condition is violated, and hence the fixed point is unstable, also as we had guessed. For the third case study, \((a_R = a_J = 1.0, p_R = 0.2, p_J = -0.2, \text{ shown in Figure 2.19(c)})\), it is the second Jury condition that is violated, verifying that indeed the fixed point is unstable in this case as well. The oscillatory nature of the love affair results from the fact that the eigenvalues no longer are real in this case, but complex conjugates.

Last but not least, we examine the fourth case study in more detail. Recall that in this case, the fixed point \((R^*, J^*) = (0, 0)\) no longer is unique, since \(\det(A) = 0\), where \(A\) is the matrix defined in (2.70). Instead, from (2.69), we note that there is a continuum of fixed points satisfying \((a_R - 1)R^* + p_R J^* = 0\) or, equivalently, \(p_J R^* + (a_J - 1)J^* = 0\) (since \(\det(A) = 0\), one of the equations in (2.69) is redundant; we can choose either one of the two to work with). Choosing to work with the first equation, we obtain

\[ J^* = \frac{1 - a_R}{p_R} R^*. \] (2.75)

Thus, all points of the form

\[ (R^*, J^*) = (R^*, \frac{1 - a_R}{p_R} R^*) \] (2.76)

are fixed points. For example, in our case \((a_R = 0.5, a_J = 0.8, p_R = 0.2, p_J = 0.5)\), all fixed points are of the form

\[ (R^*, J^*) = (R^*, \frac{1 - 0.5}{p_R} R^*) = (R^*, 2.5 R^*), \] (2.77)

that is, if the fixed points are stable, Romeo and Juliet will either both love or hate each other, with Juliet’s feeling always 2.5 as strong as Romeo’s. We will verify shortly that the fixed points indeed are stable with our choice of parameter values. For now, we investigate which of the infinite number of fixed points is approached as \(n \to \infty\).
Consider the original system, using the specific model parameters from the fourth case study:

\[
R_{n+1} = 0.5R_n + 0.2J_n, \tag{2.78}
\]

\[
J_{n+1} = 0.5R_n + 0.8J_n. \tag{2.79}
\]

Note that \(a_R + p_J = 0.5 + 0.5 = 1\) and \(p_R + a_J = 0.2 + 0.8 = 1\). In terms of the love affair, we can interpret these conditions as follows: the total amount of love/hate that Romeo and Juliet feel for each other initially is preserved on all subsequent days. Each day, Romeo’s love/hate for Juliet is split 50/50 between Romeo and Juliet. Similarly, Juliet’s love/hate for Romeo is split unequally, with 20% transferred to Romeo, and the remaining 80% retained by Juliet herself.

The reader is asked in the exercises to show that \(\det(A) = 0\) whenever Romeo and Juliet preserve their love/hate from day to day, that is, whenever \(a_R + p_J = 1\) and \(p_R + a_J = 1\). In what follows, we will restrict ourselves to the situation in which Romeo and Juliet are in love/hate-preserving mode.

Although the insight just obtained perhaps is a bit unromantic, it does allow us to determine the final outcome of Romeo and Juliet’s relationship. Since the total amount of love/hate between Romeo and Juliet initially is \(R_0 + J_0\), and it is preserved, we must have \(R^* + J^* = R_0 + J_0\), provided that the fixed point is stable. Thus,

\[
R^* + J^* = R^* + \frac{1 - a_R}{p_R} R^* = R^* + \frac{p_J}{p_R} R^* = \frac{p_R + p_J}{p_R} R^* = R_0 + J_0, \tag{2.80}
\]

yielding the following solution for the fixed point that is approached,

\[
R^* = \frac{p_R}{p_R + p_J}(R_0 + J_0), \tag{2.81}
\]

\[
J^* = R_0 + J_0 - R^*. \tag{2.82}
\]

For our choice of parameter values and initial conditions \((R_0 = J_0 = 1)\), we obtain \(R^* \approx 0.571429\) and \(J^* \approx 1.428571\).

We now investigate the stability of the fixed points. In the exercises, the reader is asked to show that the two eigenvalues of the Jacobian matrix are

\[
\lambda_1 = 1, \tag{2.83}
\]

\[
\lambda_2 = a_R + a_J - 1 > -1. \tag{2.84}
\]

The first eigenvalue, \(\lambda_1\), is precisely equal to 1, reflecting the fact that the first Jury condition is just violated through equality. Because the original system is linear, the stability of the fixed points is determined by the magnitude of the second eigenvalue, \(\lambda_2\) (remember, this is not the case for nonlinear systems!). The fixed points are stable provided \(|\lambda_2| < 1\), that is, provided \(a_R + a_J < 2\), which simply is the second Jury condition. For our choice of parameter values, \(\lambda_2 = 0.5 + 0.8 - 1 = 0.3\), that is, the fixed points are stable (as expected from the solution shown in Figures 2.19).
2.3.4 Host-Parasitoid Models

Host-parasitoid models are a classic example of the use of discrete-time systems in population dynamics. These types of models address the life cycles of two interacting species of insects, one a host, and the other a parasitoid.

Adult parasitoids are free-living, parasitic insects, and the females lay their eggs in or on the bodies of the host insects. Parasitoid eggs develop into parasitoid larvae, at the expense of their host. Hosts that have been parasitized thus give rise to the next generation of parasitoids, while only hosts that are not parasitized will give rise to the next generation of hosts.

We will limit our attention to hosts and parasitoids with one non-overlapping generation per year so that discrete-time equations are appropriate.

Let $H_n$ and $P_n$ be the number of the hosts and parasitoids, respectively, at generation $n$. Further, let $f(H_n, P_n)$ be the fraction of hosts that are not parasitized. This fraction is a function of the rate of encounter of the two insect species, and will be specified shortly. We thus have the following:

\[
\begin{align*}
  f(H_n, P_n)H_n &= \text{number of hosts not parasitized}, \\
  [1 - f(H_n, P_n)]H_n &= \text{number of hosts parasitized}.
\end{align*}
\]

The two following assumptions allow us to complete the basic host-parasitoid model:

1. The host population grows geometrically in the absence of the parasitoids, with reproductive rate $k > 1$;

2. The average number of eggs laid in a single host that give rise to adult parasitoids is $c$.

We obtain

\[
\begin{align*}
  H_{n+1} &= kf(H_n, P_n)H_n, \\
  P_{n+1} &= c[1 - f(H_n, P_n)]H_n.
\end{align*}
\]
We now develop the functional form of \( f(H_n, P_n) \). We assume that encounters between hosts and parasitoids occur at random and are independent (the latter means that parasitoids do not distinguish between hosts that have parasitized and hosts that have not yet been parasitized). The law of mass action, which will be treated in depth in section ??, states that the number of encounters is proportional to the product \( H_n P_n \), that is, \( aH_nP_n \), where \( a \) is the constant of proportionality representing the searching efficiency of the parasitoids. The average number of encounters per host thus is
\[
\nu = \frac{aH_nP_n}{H_n} = aP_n. \quad (2.87)
\]
Of course, not all hosts experience this many encounters. Some will experience more, others less. Let
\[
p(i) = \text{the probability that a host experiences } i \text{ encounters.} \quad (2.88)
\]
Since we assumed that encounters are random and independent, they are said to follow a Poisson process, and we can use the Poisson distribution for \( p(i) \) [1]. In particular,
\[
p(i) = \frac{\nu^i e^{-\nu}}{i!}. \quad (2.89)
\]
Recalling that we defined \( f(H_n, P_n) \) to be the fraction of hosts not parasitized, we have
\[
f(H_n, P_n) = p(0) = \frac{\nu^0 e^{-\nu}}{0!} = e^{-\nu} = e^{-aP_n}. \quad (2.90)
\]
Substituting (2.90) into (2.85)–(2.86), we obtain Nicholson-Bailey’s classic model [82],
\[
\begin{align*}
H_{n+1} &= kH_ne^{-aP_n}, \quad (2.91) \\
P_{n+1} &= cH_n[1 - e^{-aP_n}]. \quad (2.92)
\end{align*}
\]
It can be shown (see exercises) that the Nicholson-Bailey model has two fixed points, namely the trivial fixed point, \( (H_1^*, P_1^*) = (0, 0) \), and the following nontrivial fixed point:
\[
(H_2^*, P_2^*) = \left( \frac{k \ln k}{ac(k - 1)}, \frac{\ln k}{a} \right), \quad (2.93)
\]
provided \( k > 1 \). The trivial fixed points represents the situation in which both the host and the parasitoid are extinct. We are interested in situations where there is co-existence of the two insect species. Hence, of interest is the stability of the nontrivial fixed point.

The Jacobian matrix, evaluated at the nontrivial fixed point, is
\[
J(H_2^*, P_2^*) = \begin{bmatrix}
\frac{1}{c(k-1)} & -\frac{k \ln k}{c(k-1)} \\
\frac{k \ln k}{c(k-1)} & \frac{\ln k}{k-1}
\end{bmatrix}, \quad (2.94)
\]
2.3. Systems of Discrete-Time Equations

Figure 2.21. The Nicholson-Bailey model, (2.91)–(2.92), exhibits growing oscillations. The left panel shows a typical solution for $H_n$ and $P_n$ as functions of $n$. The right panel shows the orbit in the $(H_n, P_n)$ phase plane. Model parameters used are $k = 1.05$, $a = 0.005$, and $c = 3$, and initial conditions are $H_0 = 50$ and $P_0 = 10$.

so that

$$\text{tr} J = 1 + \frac{\ln k}{k - 1};$$ \hspace{1cm} (2.95)

$$\text{det} J = \ln k + \frac{\ln k}{k - 1};$$ \hspace{1cm} (2.96)

Since $k > 1$, the first of the Jury conditions, (2.61), always is satisfied. Since $\text{det} J > 1$ for all $k > 1$ (see exercises), the second Jury condition never can be satisfied. We conclude that the nontrivial fixed point, $(H_2^*, P_2^*)$, always is unstable.

Instability of the nontrivial steady state in itself does not preclude coexistence of the two insect species. For example, coexistence could come in the form of a stable cycle. However, for the Nicholson-Bailey model, no choice of parameter values leads to coexistence. Instead, the model exhibits growing oscillations, an example of which is shown in Figure 2.21. We observe that parasitoid levels can become extremely low. That is, the model predicts extinction of the parasitoids. Of course, as soon as the parasitoids have gone extinct, the hosts grow geometrically.

It appears that the model is not very realistic. Indeed, it cannot be used to predict long-term dynamics of a host-parasitoid interaction. However, the model has been used successfully to describe short-term oscillations in host-parasitoid systems. For example, Burnett [23] used the model to fit data for approximately two dozen generations of populations of the greenhouse whitefly *Trialeurodes vaporaiorum* and the parasitoid *Encarsia formosa* grown under laboratory conditions.
The work of Nicholson and Bailey [82] was an important milestone in the modelling of host-parasitoid systems, showing that host-parasitoid interactions can result in large-amplitude oscillations when host density is limited solely by the parasitoid. Further, the Nicholson-Bailey model is used as a starting point for many contemporary models. These models all include features that have a stabilizing effect on the nontrivial fixed point.

For example, Beddington et al. [12] modified the equation for the host population, so that its growth is density-dependent instead of geometric in the absence of parasitoids. In particular, they replaced

\[ H_{n+1} = kH_n \]

in (2.91) with

\[ H_{n+1} = e^{r(1-H_n/K)}H_n, \]

where \( K \) is the carrying capacity of the host insect population, and \( r \) determines the rate of approach to the carrying capacity. Their full host-parasitoid model thus reads:

\[ H_{n+1} = e^{r(1-H_n/K)}H_n e^{-aP_n}, \]
\[ P_{n+1} = cH_n[1 - e^{-aP_n}]. \] (2.97) (2.98)

Two simulations of this model are shown in Figure 2.22. The simulation shown in Figure 2.22(a) shows co-existence at a stable fixed point, and the one in Figure 2.22(b) shows co-existence in a stable cycle. The determination of fixed points and their stability is tedious, and the reader is referred to [12] for details.

Ecological processes other than intraspecific competition in the host population also can stabilize the system. Examples are intraspecific competition in the parasitoid population, spatial heterogeneity of the environment, parasitoid dispersal among host patches, and so forth. It has proven extremely difficult to ascertain which, if any, of these mechanisms operate in nature, and research continues in this fascinating area of mathematical biology. One reason why host-parasitoid systems continue to receive much attention is their potential for biological control, where parasitoids are introduced to reduce the host population of a pest on agricultural crops. Questions of interest are what the qualities of a parasitoid should be, what can go wrong, etc. Readers interested in learning more about host-parasitoid systems and biological control are referred to the books by Godfray [41] and Hassell [48], and the article by Murdoch [75].
2.3. Systems of Discrete-Time Equations

Figure 2.22. Two types of behaviour exhibited by the Beddington model, (2.97)–(2.98). Graphs in the left column show $H_n$ and $P_n$ as functions of $n$; graphs in the right column show corresponding orbits in the $(H_n, P_n)$ phase plane. (a) The host and parasitoid co-exist at a stable fixed point ($K = 200$); (b) The host and parasitoid co-exist in a stable cycle ($K = 250$). Other model parameters are $r = 1.1$, $a = 0.005$, and $c = 3$. 
2.4 Exercises for Discrete-Time Models

Exercise 2.4.1: (German population)

Write down a simple discrete birth-death model describing the following situation. Individuals die with rate $\delta$ and are born with rate $\mu$. On December 31, 1998, Germany had a population of 82,037,000. In 1999 there were 770,744 live births and 846,330 deaths (source: Statistisches Bundesamt). Find $\delta$ and $\mu$. What will happen to the German population in the future? How should the model be altered to be more realistic?

Exercise 2.4.2: (Drug prescriptions)

Consider the following model for drug prescription:

$$a_{n+1} = a_n - ka_n + b,$$

where $a_n$ is the amount of a drug (in mg, say) in the bloodstream after administration of $n$ dosages at regular intervals (hourly, say).

(a) Discuss the meaning of the model parameters $k$ and $b$. What can you say about their size and sign?

(b) Find the fixed points of the model and their stability via linearization.

(c) Perform a cobwebbing analysis for this model. What happens to the amount of drug in the bloodstream in the long run? How does the result depend on the model parameters?

(d) How should $b$ be chosen to ensure that the drug is effective, but not toxic?

Exercise 2.4.3: (Improving the fit of the logistic model to the data)

Note to the instructor: This question requires nonlinear fitting techniques, which are not treated in this chapter, nor in the chapter on Maple. However, students may be asked to attempt this question after studying the project on cell competition in Section 9.1.

In Section 2.2.1, we fit equation (2.4) to Gause’s data. Recall that the choice to use the number 540 in this equation was rather arbitrary. Consider the more general model,

$$p_{n+1} = p_n + k(N - p_n)p_n.$$

(a) Use nonlinear fitting techniques to determine the best fit of both model parameters, $k$ and $N$. 
Exercise 2.4.4: (Fluctuations in the population of *P. aurelia*)

In Section 2.2.1, we ignored the fluctuations in the population of *P. aurelia* at carrying capacity. Discuss possible reasons for the appearance of the fluctuations.

Exercise 2.4.5: (Whale population)

Consider the survival of a population of whales, and assume that if the number of whales falls below a minimum survival level *m*, then the species will become extinct. In addition, assume that the population is limited by the carrying capacity *M* of the environment. That is, if the whale population is above *M*, then it will experience a decline because the environment cannot sustain that large a population level.

(a) Let *a*$_n$ represent the whale population after *n* years. Discuss the model

\[ a_{n+1} = a_n + k(M - a_n)(a_n - m), \]

where *k* > 0. Does it make sense in terms of the description above?

(b) Find the fixed points of the model, and determine their stability via linearization. You may assume that *M* = 5000, *m* = 100, and *k* = 0.0001.

(c) Perform a graphical stability analysis. Are your results consistent with the results from (b)?

(d) Sketch the graphs of *a*$_n$ versus *n* for various initial conditions.

(e) The model has two serious shortcomings. What are they? Hint: consider what happens when *a*$_0$ < *m*, and when *a*$_0$ \(\gg\) *M*?

(f) Think of a possible way to fix the model so as to overcome the shortcomings. You are encouraged to be creative, innovative – you do not need to write down the equation of an improved model; it is sufficient to describe your ideas with words and/or sketches of graphs.

Exercise 2.4.6: (Second-iterate map)

This exercise deals with the second-iterate map, *f*$_2$(x), for the logistic map, *f*(x) = *rx*(1 - *x*).

(a) Compute *f*$_2$(x).
(b) Find the fixed points of $f^2(x)$. Verify that a nontrivial 2-cycle exists only for $r > 3$.

e) Compute $\frac{dx}{dx} f^2(x)$.

d) Verify that the nontrivial 2-cycle is stable for $3 < r < 1 + \sqrt{6}$, and unstable for $r > 1 + \sqrt{6}$.

Exercise 2.4.7: (Fourth-iterate map)

This exercise deals with the fourth-iterate map, $f^4(x)$, for the logistic map, $f(x) = rx(1-x)$.

(a) Graph $f^4(x)$ for various values of the model parameter $r$. Compare to the graphs of $f(x)$ and $f^2(x)$.

(b) At which value of $r$ does a 4-cycle appear?

(c) At which value of $r$ does the 4-cycle become unstable?

Exercise 2.4.8: (Exact solution for the Beverton-Holt model)

The Beverton-Holt model, (2.23), is one of the few nonlinear models which has a solution in closed form, that is, $x_n$ in terms of the model parameters and the initial condition $x_0$. Use the transformation $u_n = \frac{1}{x_n}$ to show that the solution can be written as

$$x_n = \frac{rx_0}{1 + \frac{r}{K} x_0}.$$

Exercise 2.4.9: (Fitting the Beverton-Holt model to Gause’s data)

In Section 2.2.1, we fit Gause’s data for Paramecium aurelia with the discrete logistic equation. In Section 2.2.4, we learned about alternatives to the discrete logistic equation. In particular, we saw that the Beverton-Holt model would be a suitable alternative model to describe populations undergoing logistic growth. Fit the Beverton-Holt model to the data in Table 2.1.

Hint: The use of line-fitting techniques with Maple will be helpful (see Chapter 7).

Exercise 2.4.10: (The tent-map)

The tent-map is an approximation to the discrete logistic equation: $x_{n+1} = f(x_n)$ with

$$f(x) = \begin{cases} \mu x & \text{for } 0 \leq x \leq 0.5 \\ \mu(1-x) & \text{for } 0.5 < x \leq 1 \end{cases}$$
(a) Sketch the graph of $f$ for $\mu > 0$.

(b) Find the steady states and their stability.

(c) Find orbits of period 2.

(d) Plot $f$ for $\mu = 2$. Carefully try to find an orbit of period 3.

**Exercise 2.4.11: (Blood cell population)**

In this exercise, we will investigate a model for the size of the red blood cell population in the human body. Let $x_n$ be the number of red blood cells in the human body on day $n$. We wish to write down an updating function for the number of red blood cells on day $n + 1$. We will think of the updating function in terms of destruction and production of red blood cells. If we let $d(x_n)$ represent the number of red blood cells lost due to cell death on day $n$, and $p(x_n)$ the number of red blood cells gained due to production by the bone marrow on day $n$, then we can write

$$x_{n+1} = x_n - d(x_n) + p(x_n),$$

that is, the number of red blood cells tomorrow is the number of red blood cells today minus those destroyed plus those produced.

It is widely accepted that a constant fraction $c$ of cells is destroyed each day, that is, $d(x_n) = cx_n$. Information on the production of red blood cells is more sketchy, but the qualitative features of $p(x_n)$ are generally assumed to be as for the Ricker curve. That is, if there are not many red blood cells, then the bone marrow is rather productive, whereas if there are already many red blood cells, the bone marrow is less productive. Two possible forms for $p(x_n)$ are

$$p_1(x) = axe^{-bx},$$

with $a > 0$ and $b > 0$, and

$$p_2(x) = \frac{b\theta^m x}{\theta^m + x^m},$$

with $b > 0$, $\theta > 0$, and $m > 0$.

(a) Sketch a graph of $p_2(x_n)$ for different values of $\theta$ and $m$. What is the significance of $b$, $\theta$, and $m$?

(b) It is known that the production of red blood cells involves a delay of several days. How would you modify the above model to take account of the delay?

**Exercise 2.4.12: (Population genetics)**
The general allele frequency equation, (2.34), exhibits four fundamentally different outcomes, summarized in Table 2.3. Prove that indeed there are four fundamentally different cases.

**Exercise 2.4.13: (Spotted owls and hawks)**

Consider the following competitive hunter model for spotted owls and hawks:

\[
O_{n+1} = (1 + k_1)O_n - k_3 O_n H_n,
\]
\[
H_{n+1} = (1 + k_2)H_n - k_4 O_n H_n,
\]
where \(k_1, k_2, k_3, k_4\) are positive constants.

(a) Find all fixed points.

(b) Determine the stability of the fixed points for the specific case \(k_1 = 0.2, k_2 = 0.3, k_3 = 0.001\), and \(k_4 = 0.002\).

**Exercise 2.4.14: (Spread of infectious disease)**

Consider the following model for the spread of an infectious disease (such as the flu or the common cold) through a population of size \(N\):

\[
I_{n+1} = I_n + kI_n(N - I_n),
\]
\[
I_0 = 1,
\]
where \(I_n\) is the number of infected (and infectious) individuals on day \(n\), \(k\) is a measure of the infectivity and how well the population mixes.

(a) What does the model predict? You may assume that \(kN < 2\).

The above model does not take into account recovery of individuals. Consider recovery with immunity (that is, once a person recovers, (s)he cannot get sick a second time), and assume that an individual recovers in exactly \(d\) days.

(b) Modify the model to incorporate immunity. Explain (justify) your model. What additional assumptions have you made?

**Exercise 2.4.15: (Jury conditions)**

Let \(J\) be the Jacobian matrix, (2.54), corresponding to the general two-dimensional discrete-time system, (2.42)-(2.43).
2.4. Exercises for Discrete-Time Models

(a) Show that the characteristic polynomial for $J$ can be written as
\[ \lambda^2 - tr \, J \lambda + \det J = 0. \]

(b) Show that necessary and sufficient conditions for both eigenvalues of $J$ to have magnitude less than 1 are the following Jury conditions:
\[ |tr \, J| < 1 + \det J < 2. \]

Exercise 2.4.16: (Romeo and Juliet in love/hate-preserving mode)

Consider the discrete-time model developed for the relationship between Romeo and Juliet, (2.40)–(2.41), and assume that the amount of love/hate that Romeo and Juliet feel for each other initially is preserved on all subsequent days, that is, $a_R + p_J = 1$ and $a_J + p_R = 1$.

(a) Show that $\det(A) = 0$, where the matrix $A$ is defined in (2.70).

(b) Show that the two eigenvalues of the Jacobian matrix are
\[ \lambda_1 = 1, \]
\[ \lambda_2 = a_R + a_J - 1. \]

Exercise 2.4.17: (Host-parasitoid systems: the Poisson distribution)

Assuming that the average number of encounters with a parasitoid per host is $\nu$, the Poisson distribution states that
\[ P(i) = \text{the probability that a host experiences } i \text{ encounters} \]
\[ = \frac{\nu^i e^{-\nu}}{i!}. \]

Show that
\[ \sum_{i=0}^{\infty} P(i) = 1. \]

Exercise 2.4.18: (Host-parasitoid systems: the Nicholson-Bailey model)

Consider the Nicholson-Bailey model, (2.91)–(2.92).

(a) Show that fixed points of the Nicholson-Bailey model are the trivial fixed point, $(H_1^*, P_1^*) = (0, 0)$, and the following nontrivial fixed point:
\[ (H_2^*, P_2^*) = \left( \frac{k \ln k}{ac(k - 1)}, \frac{\ln k}{a} \right), \]
provided $k > 1$. Why is the restriction $k > 1$ necessary?
(b) Determine the stability of the trivial fixed point, \((H_1^*, P_1^*)\).

(c) In the text, we investigated the stability of the nontrivial fixed point, \((H_2^*, P_2^*)\), and stated that

\[
\ln k + \frac{\ln k}{k - 1} > 1
\]

for all \(k > 1\). The inequality implies that the second Jury condition cannot be satisfied, that is, the nontrivial fixed point always is unstable. Prove the inequality.

Hint: Consider \(f(k) = k \ln k - k + 1\), and show \(f(k) > f(1) = 0\) for \(k > 1\).

Exercise 2.4.19: (Host-parasitoid systems: the Beddington model)

Consider the Beddington model, (2.97)–(2.98).

(a) Determine all fixed points.

(b) Determine the stability of the fixed points. Under which conditions on the model parameters are fixed points stable; unstable?

(c) Use Maple to iterate the model, and confirm the results of the stability analysis.