

Figure 2.14. The discrete logistic model, (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 $x_{n+1} = x_n$.

per adult does not depend on 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 hypotheses 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 predicts 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.

The Beverton–Holt Model

The *Beverton–Holt model* was derived in the context of fisheries [22]. The growth rate is given by $g(x_n) = \frac{r}{1 + \frac{r-1}{K}x_n}$, with $r > 0$ and $K > 0$, giving

$$x_{n+1} = f(x_n) = \frac{r}{1 + \frac{r-1}{K}x_n}x_n. \quad (2.23)$$

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

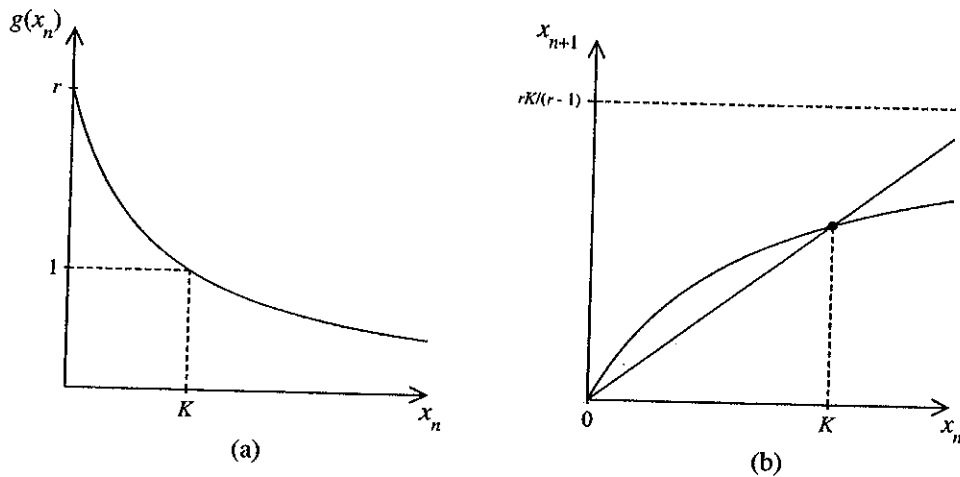


Figure 2.15. The Beverton-Holt model, (2.23). (a) Graph of $g(x_n) = r/(1 + \frac{r-1}{K}x_n)$. (b) Graphs of $x_{n+1} = f(x_n) = g(x_n)x_n$ and $x_{n+1} = x_n$.

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

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

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 $0 < x_0 \ll K$, the population initially increases quickly. 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 behavior 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 the exercises). It can be shown, then, that the solution behavior 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 reiterate that we now have two discrete-time models that can be considered analogous to

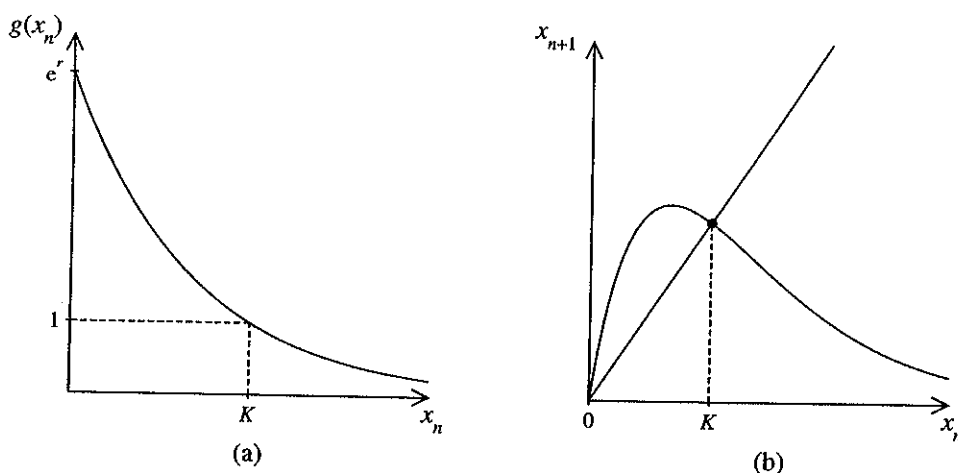


Figure 2.16. The Ricker model, (2.24). (a) Graph of $g(x_n) = \exp[r(1 - \frac{x_n}{K})]$. (b) Graphs of $x_{n+1} = f(x_n) = g(x_n)x_n$ and $x_{n+1} = x_n$.

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 [137]. In this case, $g(x) = \exp[r(1 - \frac{x}{K})]$, with $r > 0$ and $K > 0$, giving

$$x_{n+1} = f(x_n) = \exp\left[r\left(1 - \frac{x_n}{K}\right)\right]x_n. \quad (2.24)$$

We can think of the factor $\exp(r)$ as a constant reproduction factor, and of the factor $\exp(-rx_n/K)$ 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 the shape of the graph of $g(x)$ is similar to that for the Beverton–Holt model. However, the exponential function decreases more quickly 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 map (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

$$f'(x) = e^{r(1-\frac{x}{K})} \left[1 - \frac{rx}{K} \right]. \quad (2.25)$$

Then

$$f'(x_1^*) = f'(0) = e^r > 1, \quad (2.26)$$

$$f'(x_2^*) = f'(K) = 1 - r. \quad (2.27)$$

Thus, the trivial fixed point $x_1^* = 0$ is always 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 8.2 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 color in humans or wing color in moths.

Suppose we are interested in a trait determined by one gene for which there are two alleles. For example, consider wing coloration 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 have one of two *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 color 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?

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.

		Mother	
		W p_n	w $1 - p_n$
Father	W p_n	p_n^2	$p_n(1 - p_n)$
	w $1 - p_n$	$p_n(1 - p_n)$	$(1 - p_n)^2$

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 behavior 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. The development of this section was inspired by [154].

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 can always 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;
- there is an absence of mutation;
- the frequency of the allele in either sex is the same as in the entire population.

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

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

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

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

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 α be the fraction of white-winged moths surviving to produce the next generation, with $0 \leq \alpha \leq 1$. Similarly, let γ 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 $\alpha p_n^2 : 2\alpha p_n(1 - p_n) : \gamma(1 - p_n)^2$. The resulting frequency of W alleles in the next generation is then

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

$$= \frac{\alpha p_n}{(\gamma - \alpha)p_n^2 - 2(\gamma - \alpha)p_n + \gamma}. \quad (2.32)$$

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

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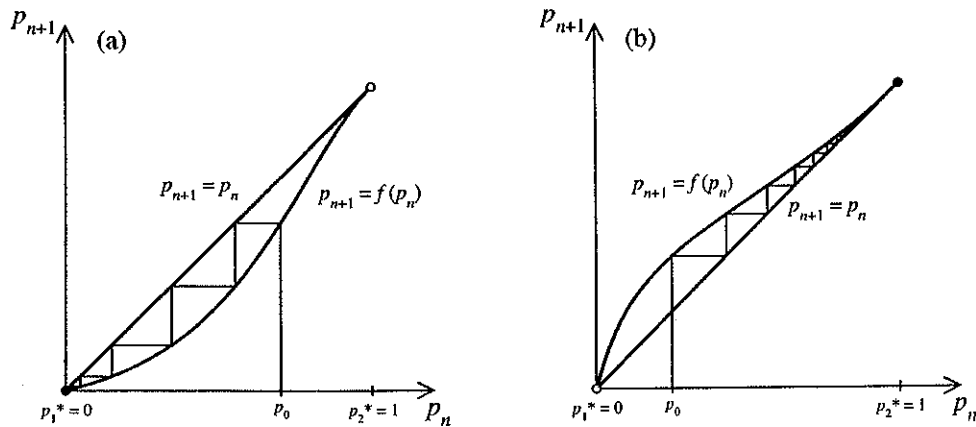


Figure 2.17. Cobwebbing diagrams for allele frequency equation (2.32). (a) $\alpha < \gamma$ ($\alpha = 0.2$ and $\gamma = 0.8$); (b) $\alpha > \gamma$ ($\alpha = 0.8$ and $\gamma = 0.2$).

$p_1^* = 0$ 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 α/γ 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 can indeed 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 α and γ . The larger the difference between α and γ , the faster the approach to extinction.

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Selection in a Population with Three Phenotypes

Let's generalize this investigation one more step into the effect of selection. Suppose that the *W* allele is no longer 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 β 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 $\alpha p_n^2 : 2\beta p_n(1 - p_n) : \gamma(1 - p_n)^2$. Questions of interest now include, under which conditions will all three phenotypes co-exist? Similarly, can gray-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 are then 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)

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

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

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

Table 2.3. Summary of the outcome of the more general allele frequency equation, (2.34).

Case	Model parameter	Fixed points and stability	Long-term behavior	Biological interpretation
I	$\alpha > \beta > \gamma$	0 is unstable 1 is stable	$p \rightarrow 1$	White-winged moths have the selective advantage and black-winged moths have the selective disadvantage; w allele becomes extinct; all moths will have genotype WW (white-winged).
II	$\alpha < \beta < \gamma$	0 is stable 1 is unstable	$p \rightarrow 0$	Black-winged moths have the selective advantage and white-winged moths have the selective disadvantage; W allele becomes extinct; all moths will have genotype ww (black-winged).
III	$\beta > \gamma > \alpha$ or $\beta > \alpha > \gamma$	0 is unstable 1 is unstable p_3^* is stable	$p \rightarrow p_3^*$	Gray-winged moths have the selective advantage; both W and w alleles remain in the population, and their frequencies reach an equilibrium; all genotypes coexist.
IV	$\beta < \gamma < \alpha$ or $\beta < \alpha < \gamma$	0 is stable 1 is stable p_3^* is unstable	$p \rightarrow 0$ or $p \rightarrow 1$	Gray-winged moths have the selective disadvantage; either the W or the w allele becomes extinct; all moths will have either genotype WW or ww (white-winged or black-winged).

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 to 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 gray-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)), gray-winged moths have the selective advantage. Consequently, both W and w alleles remain

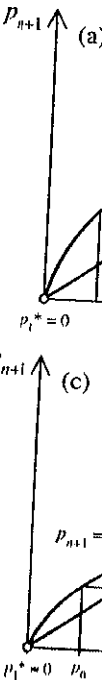


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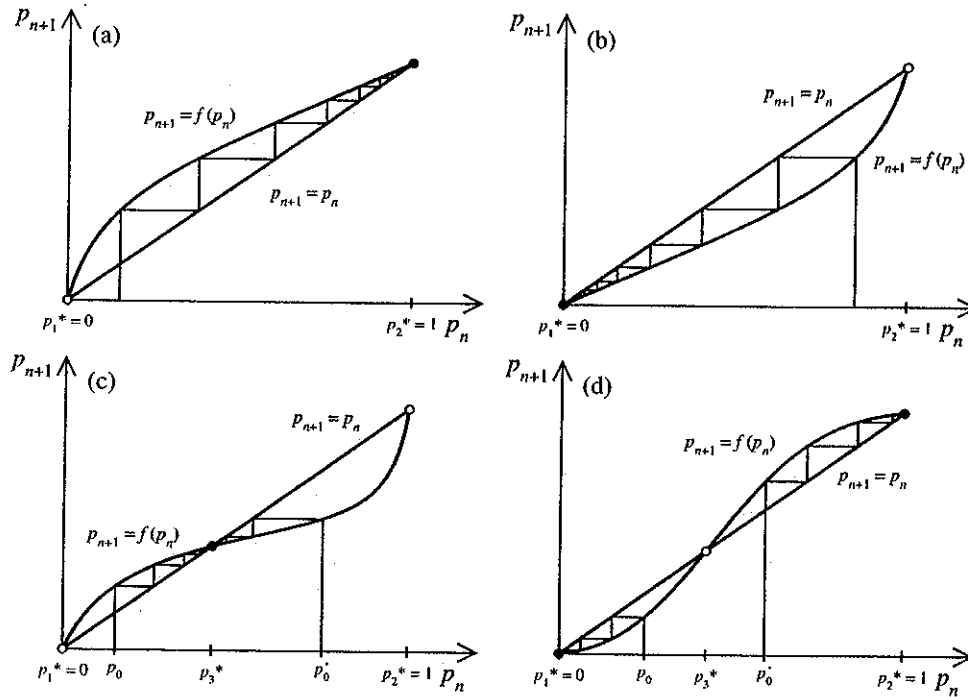


Figure 2.18. Cobweb diagrams for the more general allele frequency equation, (2.34), corresponding to the four cases summarized in Table 2.3. (a) Case I ($\alpha > \beta > \gamma$), with $\alpha = 0.8$, $\beta = 0.5$, and $\gamma = 0.1$. (b) Case II ($\alpha < \beta < \gamma$), with $\alpha = 0.1$, $\beta = 0.5$, 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 $\gamma = 0.7$.

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 α , the larger p_3^* , that is, the higher the equilibrium frequency of the W allele, as might be expected biologically.

Finally, in case IV (shown in Figure 2.18 (d)), where gray-winged moths have the selective disadvantage, we see a new and interesting dynamical behavior, 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 $p \rightarrow p_2^* = 1$ 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 $p \rightarrow p_1^* = 0$ is approached, and the W allele becomes extinct.

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 soot-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 coloration adapted quickly [101].

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 [29] and to Section 3.6 in the text by Edelstein-Keshet [51].

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 [151, 152], Strogatz developed a simple model, consisting of a system of ODEs, 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 the $|R_n|$, 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

$$R_{n+1} = a_R R_n, \quad (2.38)$$

$$J_{n+1} = a_J J_n. \quad (2.39)$$

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:

$$R_{n+1} = a_R R_n + p_R J_n, \quad (2.40)$$

$$J_{n+1} = a_J J_n + p_J R_n. \quad (2.41)$$

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

(a) R_n (b) R_n (c) R_n (d) R_n

Figure
show R_n and J_n in
phase plane. In a
 $p_R = 0.2, p_J =$
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simulate this mo
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In Figure 2
graphs in the left
show the orbits
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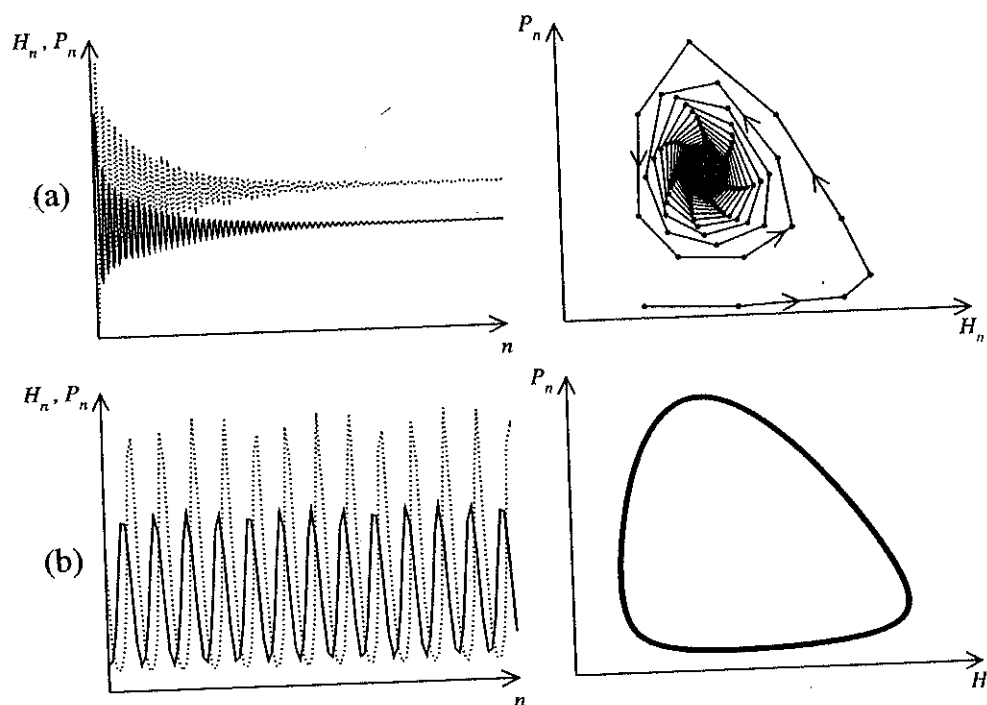


Figure 2.22. Two types of behavior exhibited by the Beddington model, (2.97)–(2.98). Graphs in the left column show H_n and P_n as functions of n ; graphs in the right column show corresponding orbits in the (H_n, P_n) phase plane. (a) The host and parasitoid coexist at a stable fixed point ($K = 200$). (b) The host and parasitoid coexist 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 at rate δ and are born at rate μ . 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 δ and μ . 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 a 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 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 10.1.

In Section 2.2.1, we fit (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 .
- (b) Simulate the model with the best fit values for k and N , and make a plot to compare the model results with the data observed by Gause. Were you able to improve upon the comparison shown in Figure 2.3?

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 $a_0 \gg M$.

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- (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, $f(x) = rx(1-x)$.

- Compute $f^2(x)$.
- Find the fixed points of $f^2(x)$. Verify that a nontrivial 2-cycle exists only for $r > 3$.
- Compute $\frac{d}{dx} f^2(x)$.
- 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, $f(x) = rx(1-x)$.

- Graph $f^4(x)$ for various values of the model parameter r . Compare to the graphs of $f(x)$ and $f^2(x)$.
- At which value of r does a 4-cycle appear?
- 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

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

Exercise 2.4.9: Fitting the Beverton–Holt model to Gause's data. In Section 2.2.1, we fit Gause's data for *P. 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 8).

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

$$f(x) = \begin{cases} \mu x & \text{for } 0 \leq x \leq 0.5, \\ \mu(1-x) & \text{for } 0.5 < x \leq 1. \end{cases}$$

- Sketch the graph of f for $\mu > 0$.
- 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 (see also [65]). 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, $d(x_n) = cx_n$. There is less information on the production of red blood cells, 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 $b > 0$ (see [105]), and

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

with $b > 0$, $\theta > 0$, and $m > 0$ (see [112]).

(a) Sketch a graph of $p_2(x_n)$ for different values of θ and m . What is the significance of b , θ , 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: Competition. Consider the following simple competition model:

$$A_{n+1} = \mu_1 A_n - \mu_3 A_n B_n,$$

$$B_{n+1} = \mu_2 B_n - \mu_4 A_n B_n,$$

where $\mu_1, \mu_2, \mu_3, \mu_4$ are positive constants.

(a) Find all fixed points.

Models

You are given the equation of the discrete logistic map, and you are to sketch the phase plane for $r > 3$.

rate map,

for $r > 3$.

unstable for

iterate map,

the graphs of

Holt model, that is, x_n in the equation $u_n = \frac{1}{x_n}$.

Section 2.2.1, Section 2.2.4, we saw that the discrete logistic map exhibits four fundamentally different cases (see Chapter 8).

discrete logistic