CHAPTER 5

Equilibria and Stability Analyses— One-Variable Models

Chapter Goals:
- To determine the equilibria of a model with one variable
- To determine the stability of equilibria
- To find approximate values of an equilibrium when needed

Chapter Concepts:
- Equilibrium condition
- Implicit solution/Explicit solution
- Local stability analysis
- Perturbation analysis

5.1 Introduction

Determining the equilibria of a system is one of the most important steps in analyzing a dynamic model. An equilibrium is a point at which a variable (or variables) remains unchanged over time:

Definition 5.1: Equilibrium

A system at *equilibrium* does not change over time (plural: *equilibria*). A particular value of a variable is called an equilibrium value if, when the variable is started at this value, the variable never changes.

- At an equilibrium in a discrete-time model, $n(t + 1)$ must equal $n(t)$ for each variable. Equivalently, the amount by which each variable changes, $\Delta n = n(t + 1) - n(t)$, must equal zero.
- At an equilibrium in a continuous-time model, dn/dt must equal zero for each variable.

Knowing the equilibria of a model is very useful because these states are good candidates for where a system might eventually end up. We can winnow down these candidates even further by determining which equilibria are stable (attracting) or unstable (repelling).

Definition 5.2: Stability

- An equilibrium is *locally stable* if a system near the equilibrium approaches it (locally attracting).
- An equilibrium is *globally stable* if a system approaches the equilibrium regardless of its initial position.
- An equilibrium is *unstable* if a system near the equilibrium moves away from it (repelling).

In sections 5.2 and 5.3 we describe how to determine the equilibria of a model, and how to assess whether an equilibrium is stable or unstable. Section 5.4 then presents a method for approximating equilibria and stability conditions in models where exact solutions are not possible. We focus on models with a single variable in this chapter (e.g., one species or one allele frequency). The corresponding analyses for finding equilibria and determining stability in models with more than one variable will be described in Chapters 7 and 8.

5.2 Finding an Equilibrium

The method for finding equilibria is straightforward. To clarify the notation, we will place a caret over a variable, e.g., $\hat{n}$, to represent an equilibrium value

of that variable. In a discrete-time model, if $n(t)$ is at an equilibrium value $\hat{n}$, then the value of n in the next time step, $n(t + 1)$, will equal $\hat{n}$ as well. Thus, to find an equilibrium for a model, we replace every instance of $n(t)$ and $n(t + 1)$ with $\hat{n}$ in a recursion equation. Alternatively, in a difference equation, there must be no change in the variable at an equilibrium, so we set Δn to zero and $n(t)$ to $\hat{n}$. Throughout this chapter, we assume that the dynamics of a model are entirely determined by the current state of the system, $n(t)$, and do not also depend on the past history of states (as in a model with time lags) or on the actual time t (as in a model where the environment changes over time). Similarly, in a continuous-time model, there must be no change in the variable at an equilibrium, so we set dn/dt to zero and $n(t)$ to $\hat{n}$. This procedure results in one equation in one unknown (i.e., the equilibrium value $\hat{n}$); we call this equation the *equilibrium condition*. Any value of $\hat{n}$ that satisfies this condition is an equilibrium of the model. The number of equilibria in a model is determined by how many values of $\hat{n}$ satisfy the equilibrium condition.

An *equilibrium condition* is an equation that is satisfied by the equilibria of a model.

Recipe 5.1
Finding an Equilibrium, $\hat{n}$

Step 1: Obtain the equilibrium condition from the dynamical equation:

- In a discrete-time recursion equation, replace $n(t + 1)$ and $n(t)$ with $\hat{n}$. For example, the exponential growth model $n(t + 1) = R\,n(t)$ becomes $\hat{n} = R\hat{n}$.
- In a discrete-time difference equation, replace $n(t)$ with $\hat{n}$ and set Δn to zero. For example, the exponential growth model $\Delta n = (R - 1)\,n(t)$ becomes $0 = (R - 1)\hat{n}$.
- In a continuous-time differential equation, replace $n(t)$ with and set dn/dt to zero. For example, the exponential growth model $dn/dt = rn(t)$ becomes $0 = r\hat{n}$.

Step 2: Solve the equilibrium condition for $\hat{n}$. When canceling a term from both sides of an equilibrium condition, check if that

term could equal zero for some value of $\hat{n}$. If so, that value of $\hat{n}$ is an equilibrium of the model.

Step 3: Check each equilibrium by plugging it back into the original dynamical equation and confirming that the system remains constant. Also check that each equilibrium is biologically valid (e.g., is non-negative if the variable represents the number of individuals).

CAUTION: Remember that in step 2, we are solving for values of the *variables* that satisfy the equilibrium condition, not values of the *parameters*.

While the concept behind finding equilibria is straightforward, calculating the equilibria might not be. In fact, depending on your model, it can be an easy, difficult, or even impossible task. To illustrate, we start with cases in which it is easy to determine the equilibria and work up to a case where the equilibria cannot be found explicitly.

5.2.1 Exponential and Logistic Models of Population Growth

To identify equilibria of the exponential growth model in discrete time, we replace $n(t + 1)$ and $n(t)$ with $\hat{n}$ in the recursion equation, $n(t + 1)$ $Rn(t)$, to get the equilibrium condition, $\hat{n} = R\hat{n}$ (Step 1). We then solve for $\hat{n}$ (Step 2). You might be tempted to divide both sides by $\hat{n}$ to simplify this equation, leaving $1 = R$. At this point you might conclude that there is no equilibrium of the model unless R happens to equal one. This is known as a *special case of the parameters*, because it is extremely unlikely that R will equal exactly one for any real population. In general, it is a great idea to simplify an equilibrium condition by canceling out a term that multiplies both sides of the condition, but when we do so, we must check whether the canceled term could itself equal zero. For the exponential model, when we divide both sides of the equilibrium condition $\hat{n} = R\hat{n}$ by the term $\hat{n}$, the canceled term could be zero if $\hat{n} = 0$. Therefore, $\hat{n} = 0$ satisfies the equilibrium condition and is a valid equilibrium of the exponential model.

We can check to make sure that we have correctly identified an equilibrium by setting $n(t)$ to the potential equilibrium value (zero in the present case) and confirming that $n(t + 1)$ remains at this value (Step 3). Indeed, plugging $n(t) = 0$ into the recursion equation for the exponential model gives $n(t + 1) = R \times 0 = 0$. Thus, an equilibrium of the exponential model occurs when there are no individuals within the population.

An alternative way to solve the equilibrium condition $\hat{n} = R\hat{n}$ is to subtract $\hat{n}$ from both sides, giving $0 = R\hat{n} - \hat{n}$, which can be factored into $0 = (R - 1)\hat{n}$. Solving for $\hat{n}$, we can again see that $\hat{n} = 0$ is an equilibrium. Indeed, it is the only equilibrium of the model. The only other way to satisfy this equilibrium condition is to set R to a specific value, $R = 1$. Remember, however, that we are seeking values of the *variable n* at which no change is predicted, and therefore it does not make sense to say that $R = 1$ is an equilibrium. Rather, when $R = 1$, the equilibrium condition is always satisfied, and all initial values of n represent equilibria, because the population exactly replaces itself regardless of the population size.

In the logistic model, applying Recipe 5.1 to the recursion equation,

$$n(t + 1) = n(t) + r\,n(t)\left(1 - \frac{n(t)}{K}\right) \qquad \text{(recursion equation from 3.5a)}$$

gives the equilibrium condition

$$\hat{n} = \hat{n} + r\,\hat{n}\left(1 - \frac{\hat{n}}{K}\right) \qquad \text{(equilibrium condition for 3.5a).}$$

Subtracting $\hat{n}$ from both sides demonstrates that $r\hat{n}(1 - \hat{n}/K)$ must equal zero at an equilibrium. Besides the special case of zero growth ($r = 0$, in which case all populations remain constant in size), the equilibrium condition has two possible solutions; either or $\hat{n} = 0$ or $(1 - \hat{n}/K) = 0$. The second solution is satisfied when $\hat{n} = K$. Thus, we conclude that there are two states in the logistic model at which the population size will remain constant: when there are no individuals present ($\hat{n} = 0$) or when the population is at the carrying capacity ($\hat{n} = K$).

If you are well practiced in solving equations, it might be obvious that the solution to $(1 - \hat{n}/K) = 0$ is $\hat{n} = K$. Until solving such equations becomes second nature, however, there is a general recipe to find values of that satisfy any linear equation.

Recipe 5.2
Solving Linear Equations

A linear equation in a variable n is one that can be written in the form $a + bn = c + dn$, where a, b, c, and d are parameters that do not depend on n. For example, $1 - n/K = 0$ has the form of a linear equation with $a = 1$, $b = -1/K$, and $c = d = 0$.

Step 1: Move all terms involving n to one side of the equation and all terms not involving n to the other side, by adding or subtracting appropriate terms to both sides. The resulting equation is $bn - dn = c - a$.

Step 2: Factor the variable n out of every term on the side of the equation containing n to get $n\,(b - d) = c - a$.

Step 3: Divide both sides of the equation by the factor multiplying n to get the solution $n = (c - a)/(b - d)$.

For both the exponential and logistic models, we get equivalent equilibrium conditions (and thus the same equilibria) whether we use the recursion equation in discrete time, the difference equation in discrete time, or the differential equation in continuous time. For the exponential model, we can write the equilibrium condition as $0 = r\hat{n}$ using equation (3.1b), (3.2), or (3.3), if we define $r = (R - 1)$. Similarly, for the logistic model, the equilibrium condition is $0 = r\hat{n}(1 - \hat{n}/K)$ using either (3.5a), (3.5b), or (3.5c). In general, recursion and difference equations always give equivalent equilibrium conditions, because the difference equation equals the recursion equation with $n(t)$ subtracted from both sides (Recipe 2.2). Consequently, we can use either when solving for the equilibria of a discrete-time model.

It is not generally true, however, that the equilibria of a differential equation are the same as the equilibria of a recursion or difference equation. As described in Chapter 2, if there are different types of events that occur over time, the dynamical equations for continuous-time and discrete-time models might differ because they make different assumptions about the possibility of concurrent events. In continuous time, it is assumed that two things do not happen in the same instant in time. In discrete time, however, it is possible for two events to occur before the next time step (e.g., an individual could be born and die within the same year).

Consider the toy model that we built in Chapter 2 in which we tracked the number of mice in a yard, given that births, deaths, and migration occur. We obtained the dynamical equations

$$n(t+1) = (1+b)(1-d)\,n(t) + m \qquad \text{(recursion equation from 2.4)},$$

$$\Delta n = -d\,n(t) + b(1-d)\,n(t) + m \qquad \text{(difference equation from 2.5)},$$

$$\frac{dn}{dt} = b\,n(t) - d\,n(t) + m \qquad \text{(differential equation from 2.9)}.$$

These give the equilibrium conditions

$$\hat{n} = (1+b)(1-d)\,\hat{n} + m \qquad \text{(equilibrium condition for 2.4)},$$

$$0 = -d\,\hat{n} + b(1-d)\,\hat{n} + m \qquad \text{(equilibrium condition for 2.5)},$$

$$0 = b\,\hat{n} - d\,\hat{n} + m \qquad \text{(equilibrium condition for 2.9)}.$$

These equations are "implicit solutions" for $\hat{n}$, meaning that they are equations that $\hat{n}$ must satisfy. Really, we want an "explicit solution," where we can write $\hat{n}$ = *stuff*, where *stuff* is a function of the parameters only and not $\hat{n}$. Using Recipe 5.2, we can obtain explicit solutions for $\hat{n}$ from these equations:

> An *implicit solution* is an equation that $\hat{n}$ must satisfy. An explicit solution for $\hat{n}$ gives $\hat{n}$ as some function of the parameters.

$$\hat{n} = \frac{m}{1-(1+b)(1-d)} \qquad \text{(equilibrium of 2.4)},$$

$$\hat{n} = \frac{m}{d-b(1-d)} \qquad \text{(equilibrium of 2.5)},$$

$$\hat{n} = \frac{m}{d-b} \qquad \text{(equilibrium of 2.9)}.$$

The first two equilibria can both be written as $\hat{n} = m/(d - b + bd)$ and are equivalent, but the equilibrium for the continuous-time model is different. At any of these equilibria, we expect more mice at equilibrium if the migration rate of mice into the yard is higher (higher m), if the mice give birth at a higher rate (higher b), or if they die at a lower rate (lower d). In the discrete-time models, however, births occur before deaths so that mice can die in the

same time step in which they are born. This is not allowed in the continuous-time model. Consequently, there is an additional term bd in the denominator of the discrete-time models. This additional term is always positive, and hence the discrete-time model predicts a slightly lower equilibrium level of mice in the yard.

5.2.2 Haploid and Diploid Models of Natural Selection

Next, let us turn to the discrete-time model of haploid selection, described by

$$p(t+1) = \frac{W_A p(t)}{W_A p(t) + W_a(1 - p(t))} \qquad \text{(recursion equation from 3.8c).}$$

This gives the equilibrium condition

$$\hat{p} = \frac{W_A \hat{p}}{W_A \hat{p} + W_a(1 - \hat{p})} \qquad \text{(equilibrium condition from 3.8c).}$$

CAUTION: In Chapter 3, equation (3.8c) was written in an alternative form, with $q(t)$ instead of $(1 - p(t))$ in the denominator. When solving for the equilibrium value of an equation involving both $p(t)$ and $q(t)$, we have to account for the fact that these variables are interrelated. We cannot treat $q(t)$ as a constant when solving for the equilibrium values of $p(t)$, because $q(t) = 1 - p(t)$. The safest method is to replace $q(t)$ with $1 - p(t)$ when calculating equilibria.

There are many ways to solve this equilibrium condition. For example, we could start by canceling out $\hat{p}$ from both sides of the equation, making a mental note that this implies that $\hat{p} = 0$ is one equilibrium:

$$1 = \frac{W_A}{W_A \hat{p} + W_a(1 - \hat{p})} \qquad \text{(note: } \hat{p} = 0 \text{ is an equilibrium).}$$

Then we could multiply both sides by the denominator $W_A\hat{p} + W_a(1 - \hat{p})$, leaving

$$W_A \hat{p} + W_a(1 - \hat{p}) = W_A \qquad \text{(note: } \hat{p} = 0 \text{ is an equilibrium).}$$

This is a linear equation in $\hat{p}$, which can be solved using Recipe 5.2. Bringing all terms involving $\hat{p}$ to the left-hand side and factoring

$$\hat{p}(W_A - W_a) = W_A - W_a \qquad \text{(note: } \hat{p} = 0 \text{ is an equilibrium).}$$

Then we could divide both sides by $(W_A - W_a)$; the equilibrium condition would be satisfied if this factor were equal to zero, $(W_A - W_a) = 0$, which again represents a special case of the parameters (with no fitness difference between the alleles). We are left with

$$\hat{p} = 1 \qquad \text{(note: } \hat{p} = 0 \text{ is an equilibrium).}$$

Thus, the haploid model of selection has two equilibria, $\hat{p} = 0$ and $\hat{p} = 1$. Furthermore, in the special case of the parameters where $W_a = W_A$, all values of p are equilibria.

Alternatively, we could derive an equilibrium condition for the discrete-time model of haploid selection from the difference equation

$$\Delta p = \frac{(W_A - W_a)p(t)(1 - p(t))}{W_A p(t) + W_a(1 - p(t))} \qquad \text{(difference equation from 3.9)}$$

giving the equilibrium condition

$$0 = \frac{(W_A - W_a)\hat{p}(1 - \hat{p})}{W_A \hat{p} + W_a(1 - \hat{p})} \qquad \text{(equilibrium condition from 3.9).}$$

While this equilibrium condition is equivalent to the one that we just analyzed, it is much easier to solve. The right-hand side is zero only if $\hat{p} = 0$ (an equilibrium), $\hat{p} = 1$ (another equilibrium), or $W_A = W_a$ (a special case of the parameter values). In general, if the difference equation has already been factored, use it to solve for the equilibria because setting each factor to zero immediately provides a list of all possible equilibria.

Regardless of how you choose to solve for the equilibrium of the haploid model, you should always get the same answer (if not, check your math). There are only two equilibria, $\hat{p} = 0$ and $\hat{p} = 1$, which are called "boundary" equilibria because they represent the most extreme values that $\hat{p}$ (a frequency) can take. It makes sense that $\hat{p} = 0$ and $\hat{p} = 1$ are equilibria for the haploid model of selection. If allele A (or allele a) is absent at any point in time, then there is nothing in the model that will regenerate the allele. Biologically,

mutations can regenerate lost alleles, but we have yet to incorporate mutations into the model (Problem 5.4).

Now consider the diploid model of selection (equation (3.13a)). Before analyzing this model, let us discuss what equilibria we might find, so that we can hone our biological intuition. As in the haploid model of selection, if allele A (or allele a) is absent, then there is nothing in the model to regenerate it, and we therefore again expect $\hat{p} = 0$ and $\hat{p} = 1$ to be equilibria. Now, however, we have reason to suspect that another equilibrium might exist, because we saw that the allele frequency could remain constant at an intermediate value of $\hat{p}$ in Figure 4.10 (roughly at 0.66 for the parameters considered). The advantage of using the previous graphical results to anticipate the number of equilibria in the model is that it provides a good way to check our math. If we fail to find an equilibrium that we think should exist, then we've either made an error in our analysis, or we were wrong to think that the equilibrium should exist in the first place (in which case we should reevaluate our rationale for expecting the equilibrium).

Now let us identify the equilibria mathematically. By plugging in equation (3.12) for the mean fitness, we can write the recursion equation (3.13a) as

$$p(t+1) = \frac{p(t)^2 W_{AA} + p(t)q(t)W_{Aa}}{p(t)^2 W_{AA} + 2p(t)q(t)W_{Aa} + q(t)^2 W_{aa}}$$

(recursion equation from 3.13a).

To avoid errors, replace $q(t)$ with $1 - p(t)$. The equilibrium condition then becomes

$$\hat{p} = \frac{\hat{p}^2 W_{AA} + \hat{p}(1-\hat{p})W_{Aa}}{\hat{p}^2 W_{AA} + 2\hat{p}(1-\hat{p})W_{Aa} + (1-\hat{p})^2 W_{aa}}$$

(equilibrium condition from 3.13a).

It is easiest at this stage to cancel a $\hat{p}$ from both sides of the equation, noting that $\hat{p} = 0$ must be one equilibrium. For variety's sake, however, we proceed without canceling terms. A good first step is to multiply both sides by the denominator of the right, so that we don't have any fractions in the equation, leaving:

$$\hat{p}^3 W_{AA} + 2\hat{p}^2(1-\hat{p})W_{Aa} + \hat{p}(1-\hat{p})^2 W_{aa} = \hat{p}^2 W_{AA} + \hat{p}(1-\hat{p})W_{Aa}. \qquad (5.1)$$

Equation (5.1) looks messy, and it can be hard to see what to do next. A trick that often helps when factoring is to focus on one parameter at a time, simplifying all terms involving that parameter. Here we have three parameters W_{AA}, W_{Aa}, and W_{aa}, so let us start by bringing all terms involving W_{AA} to the left-hand side of the above equation. These terms are $\hat{p}^3 W_{AA} - \hat{p}^2 W_{AA}$, which can be factored into $-\hat{p}^2(1 - \hat{p})W_{AA}$. Next, we move all terms involving W_{AA} to the left-hand side. These terms are $2\hat{p}^2(1 - \hat{p})W_{AA} - \hat{p}(1 - \hat{p})W_{Aa}$, which can be factored into $(2\hat{p} - 1)\hat{p}(1 - \hat{p})W_{Aa}$. Finally, there is only one term involving W_{aa}, $\hat{p}(1 - \hat{p})^2 W_{aa}$, which is already on the left-hand side and is already factored. Putting all of these terms together, we can rewrite equation (5.1) as

$$-\hat{p}^2(1 - \hat{p})W_{AA} + (2\hat{p} - 1)\hat{p}(1 - \hat{p})W_{Aa} + \hat{p}(1 - \hat{p})^2 W_{aa} = 0. \quad (5.2)$$

Because each term contains $\hat{p}(1 - \hat{p})$, we can simplify equation (5.2) substantially by factoring:

$$\hat{p}(1 - \hat{p})(-\hat{p}W_{AA} + (2\hat{p} - 1)W_{Aa} + (1 - \hat{p})W_{aa}) = 0. \quad (5.3)$$

The equilibrium condition will be satisfied if any one of the three factors in equation (5.3) equals zero. The first two factors confirm that, indeed, $\hat{p} = 0$ and $\hat{p} = 1$ are equilibria of the diploid model of selection. Setting the third factor to zero,

$$-\hat{p}W_{AA} + (2\hat{p} - 1)W_{Aa} + (1 - \hat{p})W_{aa} = 0,$$

gives us another potential equilibrium. The third equation is linear in $\hat{p}$ and can be solved using Recipe 5.2. First, move all terms involving $\hat{p}$ to one side:

$$-\hat{p}W_{AA} + 2\hat{p}W_{Aa} - \hat{p}W_{aa} = W_{Aa} - W_{aa}.$$

Second, factor out the $\hat{p}$:

$$\hat{p}(-W_{AA} + 2W_{Aa} - W_{aa}) = W_{Aa} - W_{aa}.$$

Third, divide both sides by the factor multiplying $\hat{p}$:

$$\hat{p} = \frac{W_{Aa} - W_{aa}}{-W_{AA} + 2W_{Aa} - W_{aa}},$$

which is typically written with the positive terms first:

$$\hat{p} = \frac{W_{Aa} - W_{aa}}{2W_{Aa} - W_{AA} - W_{aa}}. \tag{5.4}$$

Let us now perform a numerical check of equation (5.4). In Figure 4.10, we saw an equilibrium at about $\hat{p} = 0.66$ using the parameters $W_{AA} = 0.6$, $W_{Aa} = 0.2$, and $W_{aa} = 1$. Plugging these parameter values into equation (5.4) gives a consistent answer of $\hat{p} = (-0.8)/(-1.2) = 2/3$.

In Figure 4.7b, we tracked the allele frequency dynamics with fitnesses equals to $W_{AA} = 1$, $W_{Aa} = 0.95$, and $W_{aa} = 0.8$. In this case, we saw that the frequency of allele A rose over time toward one, regardless of the initial allele frequency. What happened to the equilibrium (5.4)? Plugging these parameters into (5.4) gives (0.15)/(0.1) 1.5. This is a perfectly fine mathematical solution to the equilibrium condition, but it isn't a biologically valid solution, because p is a frequency and must lie between 0 and 1. This emphasizes an important step when identifying equilibria: *You should check that each equilibrium is biologically valid* (Step 3 in Recipe 5.1).

In the diploid model of selection, when is the third equilibrium (5.4) biologically valid? That is, when will $0 \le \hat{p} \le 1$? $\hat{p}$ will equal zero if $W_{Aa} = W_{aa}$ and will equal one if $W_{Aa} = W_{AA}$ (you should prove this). In these special cases, the third equilibrium falls on one of the two "boundary" equilibria that we have already identified ($\hat{p} = 0$ and $\hat{p} = 1$). More importantly, when will there be an "internal" equilibrium at which both alleles A and a are present (i.e., when will there be a polymorphism with $0 < \hat{p} < 1$)? From equation (5.4), the equilibrium frequency of allele A will be positive when

$$0 < \frac{W_{Aa} - W_{aa}}{2W_{Aa} - W_{AA} - W_{aa}} \tag{5.5}$$

It is tempting to multiply both sides of this condition by the denominator, but we must be careful:

Rule 5.1: Simplifying inequalities

CAUTION: When multiplying both sides of an inequality by a negative factor, one must reverse the inequality. Thus, $a > b/c$ is equivalent to $a\ c > b$ when c is positive but is equivalent to $a\ c$

$< b$ when c is negative. If the sign of c is not known, it is safest to avoid multiplication by c.

Subtracting terms from both sides of an inequality, however, never reverses the condition. Thus, $a > b/c$ is equivalent to $a - b/c > 0$, regardless of the signs of these terms. Similarly, one can always place terms over a common denominator without altering the condition. Thus, $a - b/c > 0$ can be written as $(a\,c - b/c > 0$. (If this is unfamiliar, try a numerical example with $a = 4$, $b = -4$, $c = -2$.)

In the case of equation (5.5), we do not know whether the denominator is positive or negative, and so it is safer not to touch it. As written, there are two ways to satisfy condition (5.5): either the numerator and denominator are both positive (case A) or they are both negative (case B).

Next, we ask when the frequency of allele A will be less than one ($\hat{p} > 1$). This is equivalent to asking when $0 < 1 - \hat{p}$, which is the same as asking when the frequency of allele a will be positive ($0 < \hat{p}$). Using equation (5.4), we can rewrite $0 < 1 - \hat{p}$ as:

$$0 < 1 - \frac{W_{Aa} - W_{aa}}{2W_{Aa} - W_{AA} - W_{aa}}. \tag{5.6a}$$

Placing the terms on the left-hand side over the same denominator ($2W_{Aa} - W_{AA}$) and simplifying gives:

$$0 < \frac{W_{Aa} - W_{AA}}{2W_{Aa} - W_{AA} - W_{aa}} \tag{5.6b}$$

Inequality (5.6b) will be satisfied either when the numerator and denominator are both positive or when they are both negative. Because the denominator is the same in (5.6b) and (5.4), this implies that there are only two cases that ensure that both $0 < \hat{p}$ and $\hat{p} < 1$.

Case A: The numerators and denominators of both (5.4) and (5.6b) are positive. For the numerators to be positive, we must have $W_{Aa} < W_{aa}$ and $W_{Aa} < W_{AA}$. For the denominators to be positive, we must have $2W_{Aa} - W_{AA} - W_{aa} < 0$. Because these conditions involve the same terms, it is worth checking

that they are mutually compatible. The easiest way to do this is to rewrite $2W_{Aa} - W_{AA} - W_{aa}$ as $(W_{Aa} - W_{AA}) + (W_{Aa} - W_{aa})$, which compares the heterozygote fitness to each of the homozygote fitnesses and allows us to see that the denominator must be positive when the numerators are positive.

Case B: The numerators and denominators of both (5.4) and (5.6b) are negative. For the numerators to be negative, we must have $W_{Aa} - W_{aa}$ and $W_{Aa} < W_{AA}$. For the denominators to be negative, we must have $2W_{Aa} < W_{AA} - W_{aa} < 0$. Convince yourself that this last condition will always hold when $W_{Aa} < W_{aa}$ and $W_{Aa} < W_{AA}$.

We conclude that a biologically valid polymorphic equilibrium exists only when the heterozygote has the highest fitness (Case A) or the lowest fitness (Case B). If the heterozygote has intermediate fitness, only the boundary equilibria are biologically valid, indicating that the allele frequency will not remain constant over time except if allele A is absent ($\hat{p} = 0$) or fixed ($\hat{p} = 1$).

5.2.3 An Example where the Equilibria Cannot be Found Explicitly

Although it is possible to determine at least some equilibria in many models, it is often the case that the equilibrium condition cannot be fully solved for all equilibria. To illustrate this problem, we add migration to a variant of the logistic equation of population growth known as the Ricker model. In the Ricker model without migration (see Problem 3.4 of Chapter 3), the number of off-spring per parent, $R(n)$, is assumed to decrease exponentially as a function of the population size. This yields the recursion equation

$$n(t + 1) = (1 + r)\, e^{-\alpha n(t)}\, n(t). \tag{5.7}$$

To find the equilibrium without migration, we solve the equilibrium condition

$$\hat{n} = (1 + r)\, e^{-\alpha \hat{n}}\, \hat{n}. \tag{5.8}$$

We can cancel $\hat{n}$ from both sides of equation (5.8), indicating that $\hat{n} = 0$ is one equilibrium. This leaves us with $1 = (1 + r)e^{-\alpha \hat{n}}$. We need to isolate $\hat{n}$, so divide both sides by $(1 + r)$ to get $1/(1 + r) = e^{-\alpha \hat{n}}$. This is not yet an explicit function for $\hat{n}$, but we can solve for $\hat{n}$ by taking the natural logarithm of both

sides, obtaining $\ln(1/(1 + r)) = -\alpha\hat{n}$ and then dividing by $-\alpha$ to get the equilibrium solution $\hat{n} = \ln(1/(1 + r))/(-\alpha)$, which depends only on the parameters. Because $\ln(1/x)$ equals $-\ln(x)$ (Rule A1.13), we can simplify this equilibrium further to get $\hat{n} = \ln(1 + r)/\alpha$.

So far, so good, but now let us extend this model to include migration. We suppose that m individuals arrive from outside the population of interest in every generation. If the migrants arrive as adults immediately before counting individuals at time $t + 1$, the recursion equation becomes

$$n(t + 1) = (1 + r)\, e^{-\alpha n(t)}\, n(t) + m, \tag{5.9}$$

whose equilibrium condition is

$$\hat{n} = (1 + r)\, e^{-\alpha \hat{n}}\, \hat{n} + m \tag{5.10}$$

Now $\hat{n}$ is no longer present in all of the terms, and it cannot be canceled. If we rewrite equation (5.10) to bring all of the terms involving $\hat{n}$ to the same side, we get $\hat{n}(1 - (1 + r)e^{-\alpha\hat{n}}) = m$. We could try taking the logarithm of both sides again, to obtain $\ln(\hat{n}(1 - (1 + r)e^{-\alpha\hat{n}})) = \ln(m)$, which can be written as $\ln(\hat{n}) + \ln(1-(1 + r)e^{-\alpha\hat{n}}) = \ln(m)$. This does not help much, though, because we still cannot write $\hat{n}$ as an explicit function of the parameters. You can try other ways of simplifying the equilibrium condition, but there is no way to isolate $\hat{n}$.

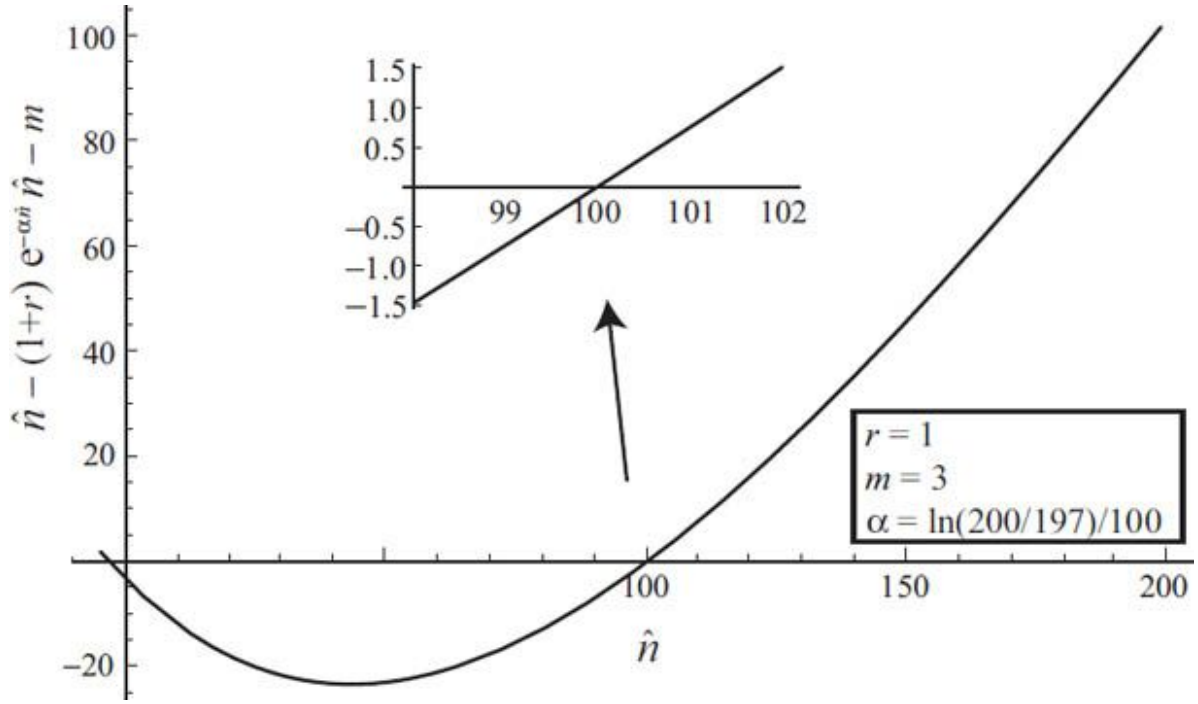

Figure 5.1: A graphical method for finding the solution to an equation. Placing all terms of equation (5.10) on the same side, $\hat{n} - (1 + r)e^{-\alpha\hat{n}}\,\hat{n} - m = 0$, which is satisfied at the equilibrium points, $\hat{n}$. These points can be found graphically for specific values of the parameters (here, $r = 1$, $m = 3$, and $\alpha = \ln(200/97)/100$) by plotting the equation on the vertical axis as a function of $\hat{n}$ on the horizontal axis. Where the curve crosses the horizontal axis, the term $\hat{n} - (1 + r)e^{-\alpha\hat{n}}\,\hat{n} - m$ equals zero, and a solution for $\hat{n}$ has been identified (inset expands the region around $\hat{n} = 100$). A curve can cross the horizontal axis at multiple points, as in this example where it crosses at both $\hat{n} = 100$ and $\hat{n} = -2.8$. Only the former equilibrium is biologically valid.

This does not imply that there is no equilibrium to the recursion equation (5.9). For example, $\hat{n} = 100$ satisfies the equilibrium condition when $r = 1$, $m = 3$, and $\alpha = \ln(200/97)/100$ (try plugging in the numbers). Rather, it means that the implicit solution for $\hat{n}$ given in equation (5.10) cannot be manipulated into an explicit solution. Nevertheless, we can use numerical methods to solve explicitly for an equilibrium of interest, as illustrated in Figure 5.1.

It is worth mentioning how we developed a model whose equilibrium condition could not be solved explicitly. Equations that are mixtures of functions like "exp," "log," and "sine" (i.e., not polynomials) plus polynomial functions like $\hat{n}$ or $\hat{n}^2$ belong to a category known as "transcendental equations." Even innocuous-looking transcendental equations like $e^{\hat{n}} + \hat{n} = 0$, cannot be solved explicitly for $\hat{n}$. So to find a model whose equilibria could not be solved explicitly, we built a model whose equilibrium condition would involve both exponential and polynomial terms.

Even equilibrium conditions that are straightforward polynomial functions of $\hat{n}$ can be impossible to solve if the order of the polynomial is high. If the order of the polynomial is two (i.e., the largest power of $\hat{n}$ is $\hat{n}^2$), then we can use the quadratic equation (Rule A1.l0) to solve for $\hat{n}$. In theory, the polynomial could also be solved if its highest power is three or four, but in practice, the solutions to such a cubic or quartic equation are so complicated that they are rarely useful. If the highest power of the equilibrium condition is greater than four and if this equation cannot be factored (e.g., $\hat{n}^5 - 3\hat{n}^3 + 1 = 0$), however, no explicit solution for $\hat{n}$ exists.

Problems solving for equilibria are further exacerbated in models with more than one variable. Indeed, you are guaranteed to find an equilibrium solution only when the recursion equations are linear in all of the variables (see Chapter 7). For example, in a model of natural selection where fitness depends on two loci rather than just one, not all of the equilibria are known explicitly (see Chapter 8).

So what should you do when you end up with a complicated equilibrium condition? First, try bringing all terms to one side of the equation and factoring it (something that software packages such as *Mathematica* are particularly adept at), because the equilibrium condition may turn out to be the product of simpler terms. Alternatively, one can try to find approximate values for the equilibria, a method that we return to at the end of this chapter (Section 5.4).

5.3 Determining Stability

Once the equilibria are identified, the next step is to determine when each equilibrium is stable versus unstable. If we plug an equilibrium back into a dynamical equation, the system will remain at that equilibrium (by definition). But what if a population starts near, but not exactly at, an equilibrium? Will it approach or move away from that equilibrium? Whenever you see the word "near," it implies that some aspect of a model is small. In this case, we assume that the distance to an equilibrium is small. Whenever a term is small, the Taylor series (Primer 1) provides an extremely useful way to approximate a model. In this section, we describe the theory used to determine whether an equilibrium is stable or not. We summarize the method in Recipe 5.3, which

provides a step-by-step recipe for carrying out a stability analysis. We then turn to a series of examples to solidify your understanding of the method.

Consider a population that starts at a point $n(t)$ where $n(t)$ is very close to an equilibrium point, $\hat{n}$. We can focus on the distance to the equilibrium by writing $n(t)$ as $n(t) = \hat{n} + \varepsilon(t)$, where ε ("epsilon") measures the *displacement* of the system from the equilibrium. The value of $\varepsilon(t) = n(t) - \hat{n}$ tells us how close the system is to the equilibrium at time t, as well as whether it is above ($\varepsilon(t) > 0$) or below ($\varepsilon(t) < 0$) the equilibrium. The key to determining stability of an equilibrium is to determine whether the distance to the equilibrium grows or shrinks over time. In the next few paragraphs, we will see how to write recursion equations for this displacement. This procedure is simplified enormously by assuming that the population is near the equilibrium, in which case the displacement, $\varepsilon(t)$, is small, and we can safely ignore higher order terms ($\varepsilon(t)^2$, $\varepsilon(t)^3$, etc.; see Primer 1).

First let us derive a recursion equation for the displacement $\varepsilon(t)$ from a general discrete-time model given by $n(t + 1) = f(n(t))$. If at time t, the system is displaced by an amount, $\varepsilon(t) = n(t) - \hat{n}$ from an equilibrium point $\hat{n}$, then in the next generation, the displacement will equal $\varepsilon(t + 1) = n(t + 1) - \hat{n}$. Using the original recursion equation $n(t + 1) f(n(t))$, this can be written

$$\varepsilon(t + 1) = f(n(t)) - \hat{n}, \tag{5.11a}$$

Equation (5.11a) is not yet in the form of a recursion equation for the displacement, however, because the right-hand side depends on the original variable $n(t)$, not the displacement $\varepsilon(t)$. To rewrite the right-hand side in terms of $\varepsilon(t)$, we use the fact that $n(t) = \hat{n} + \varepsilon(t)$ (by the definition of the displacement). Replacing $n(t)$ with $\hat{n} + \varepsilon(t)$ produces a recursion equation solely in terms of the displacement $\varepsilon(t)$:

$$\varepsilon(t + 1) = f(\hat{n} + \varepsilon(t)) - \hat{n}. \tag{5.11b}$$

Equation (5.11b) is our desired recursion, but because the system is near the equilibrium, we can assume $\varepsilon(t)$ is small and use a Taylor series approximation (Recipe P1.4) for $f(\hat{n} + \varepsilon(t))$ around the equilibrium at which $\varepsilon(t) = 0$:

$$f(\hat{n} + \varepsilon(t)) = f(\hat{n}) + \left(\frac{df}{dn}\bigg|_{n=\hat{n}}\right)\varepsilon(t) + O(\varepsilon(t)^2). \tag{5.12}$$

Here, we have used a linear approximation, because we assume that the displacement $\varepsilon(t)$ is very small, so that terms on the order of $\varepsilon(t)^2$ are negligible; we now drop these terms (represented by $O(\varepsilon(t)^2)$). The term $(df/dn)|_{n=\hat{n}}$ represents the slope of the recursion equation with respect to the variable $n(t)$ evaluated at the equilibrium point $\hat{n}$. To simplify the notation, we define $\lambda = (df/dn)|_{n=\hat{n}}$. Plugging equation (5.12) and this definition into equation (5.11b), the recursion for the displacement becomes

$$\varepsilon(t+1) \approx f(\hat{n}) + \lambda\varepsilon(t) - \hat{n}. \tag{5.13}$$

The term $f(\hat{n})$ represents the state of the system one time step after it starts at the equilibrium $\hat{n}$. But the system will not change if it starts at an equilibrium, so $f(\hat{n})$ must equal $\hat{n}$. Thus, we can simplify this recursion to

$$\varepsilon(t+1) \approx \lambda\varepsilon(t). \tag{5.14}$$

Let us now step back and think about what equation (5.14) says. A population displaced from an equilibrium by a small amount $\varepsilon(t)$ will, at the next time step, be displaced from that equilibrium by $(df/dn)|_{n=\hat{n}}$ times the original displacement. Because $(df/dn)|_{n=\hat{n}}$ is evaluated at $\hat{n}$, it is a function of the parameters only—it does not depend on the variable $n(t)$ or the displacement $\varepsilon(t)$.

Equation (5.14) is an incredibly useful result. No matter how complicated the recursion equation, we can obtain a simple approximate equation (5.14) that describes the dynamics near an equilibrium point. Even better, equation (5.14) is a linear equation in $\varepsilon(t)$ and has the same form as the model of exponential growth. In particular, we can iterate equation (5.14) for any number of generations as we did in equation (4.1); each generation, the displacement changes by a factor λ. Starting from an initial displacement $\varepsilon(0)$, the size of the displacement that we expect after t generations is

$$\varepsilon(t) = \lambda^t\varepsilon(0). \tag{5.15}$$

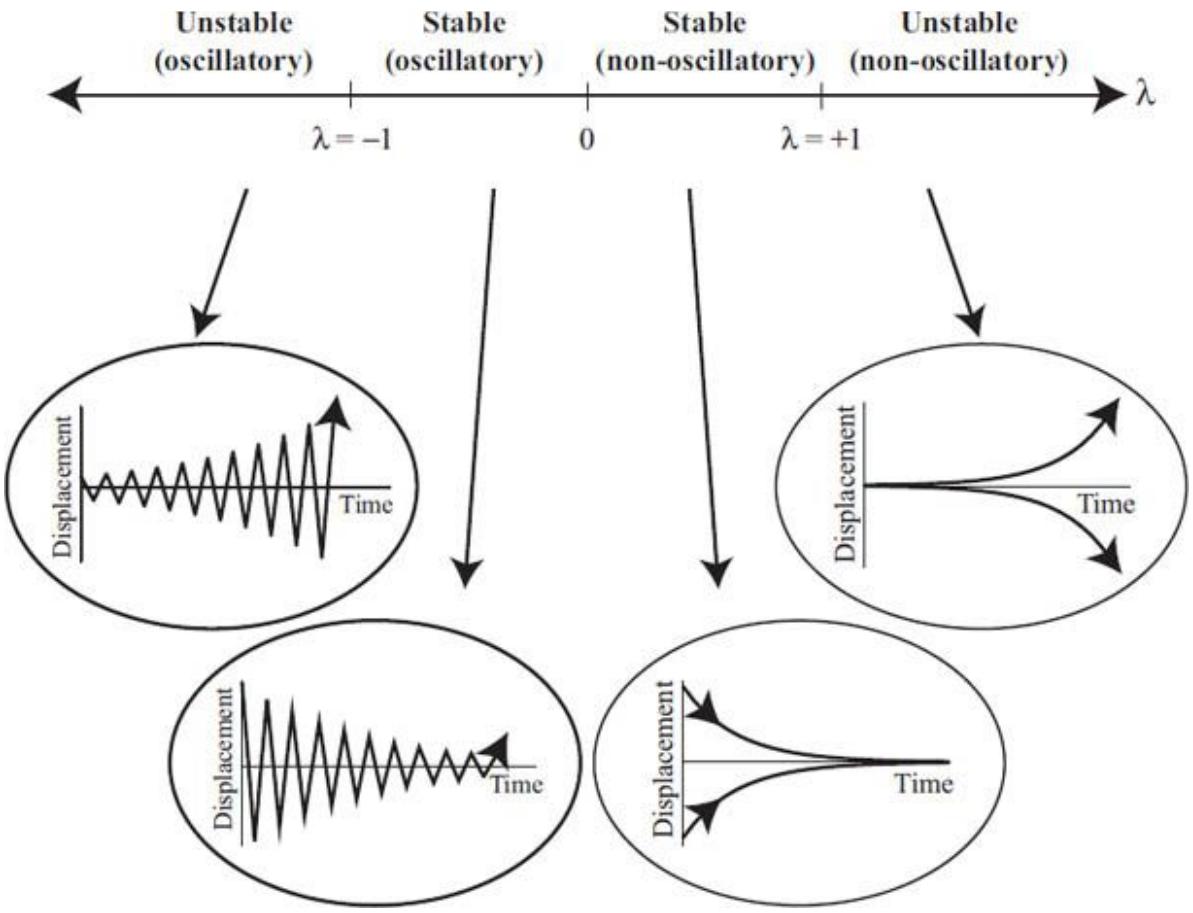

Figure 5.2: Analyzing the stability of an equilibrium in a discrete-time model. For a model whose recursion equation is $n(t+1) = f(n(t))$, the value of $\lambda = (\mathrm{d}f/\mathrm{d}n)|_{n=\hat{n}}$ determines the dynamics near the equilibrium point $\hat{n}$. The inset ovals illustrate the dynamics of the displacement from the equilibrium $\varepsilon(t)$ over time for λ values from each region.

From equation (5.15), we can infer that the behavior of a dynamical system near an equilibrium depends on the magnitude of $\lambda = (\mathrm{d}f/\mathrm{d}n)|_{n=\hat{n}}$ (Figure 5.2). The displacement will shrink over time (indicating that the equilibrium is *stable*) whenever λ is smaller than one in magnitude ($-1 < \lambda < 1$). Conversely, the displacement will grow over time (indicating that the equilibrium is *unstable*) whenever λ is greater than one in magnitude (either $\lambda > 1$ or $\lambda < -1$). A positive value of λ implies that the displacement remains on the same side of the equilibrium over time. A negative value of λ implies that the displacement flips sign and oscillates from one side of the equilibrium to the other at each time step.

In Chapter 4, we plotted the recursion equation $f(n(t))$ against the variable itself, $n(t)$, and discussed how such plots can be used to determine whether a system approaches an equilibrium. The graphical approach and the analytical

approach described above are closely related to one another. In the graphical approach, we noted that an equilibrium $\hat{n}$ must fall along the diagonal line (along which $f(n(t)) = n(t)$) and that the slope of the recursion at $\hat{n}$ provides information about the stability of the equilibrium. The term $\lambda = (\mathrm{d}f/\mathrm{d}n)|_{n=\hat{n}}$ is just the mathematical way of writing this slope. As illustrated in Figure 5.3, if the slope is larger than one ($\lambda > 1$), then a population starting slightly above or slightly below an equilibrium will move away from the equilibrium. If the slope is positive but less than one ($0 < \lambda < 1$), the population will move toward the equilibrium. If the slope is negative ($\lambda < 0$), the population will actually shoot past the equilibrium to the other side. If the slope is very negative (in particular, $\lambda < -1$), the population shoots so far past the equilibrium that it ends up even further from the equilibrium than where it started, as observed in the logistic model (Box 4.2; Figure 4.2.3).

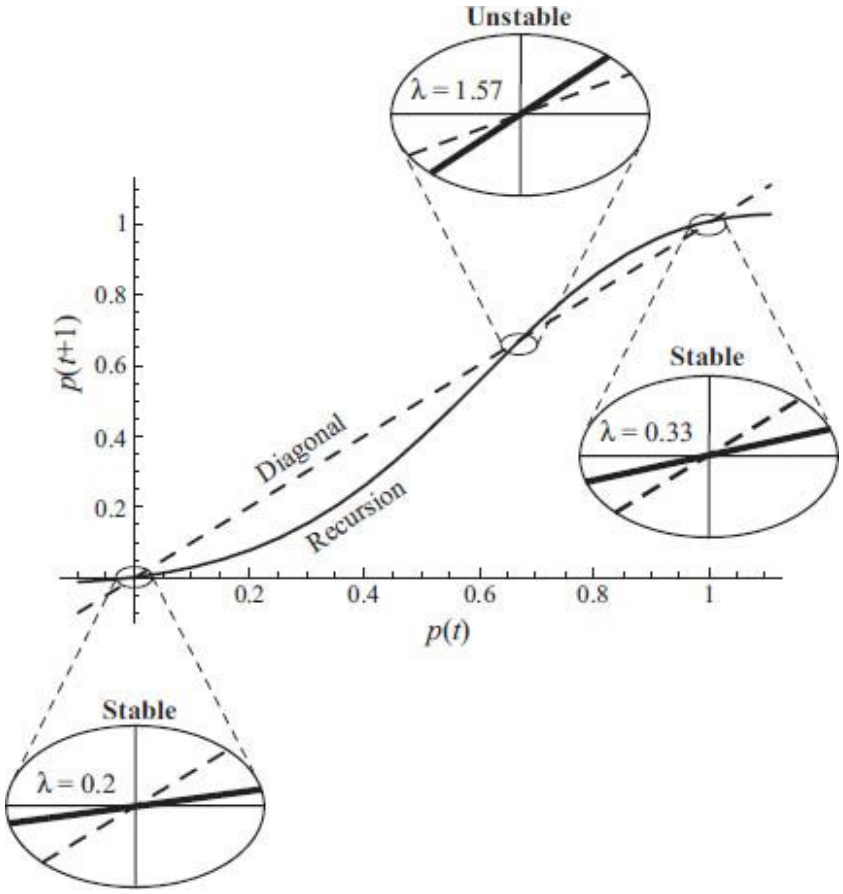

Figure 5.3: A graphical interpretation of the stability condition for the diploid model of selection in discrete time. The recursion equation (3.13a), $p(t+1) = f(p(t+1))$, is plotted against the allele frequency (as in Figure 4.10). The inset ovals show the slope of the recursion equations at each of the three equilibria. These slopes equal $\lambda = (\mathrm{d}f/\mathrm{d}p)|_{p=\hat{p}}$ and are calculated in section 5.3.2. For the equilibrium to be stable, λ must lie between –1 and +1. Parameters: $W_{AA} = 0.6$, $W_{Aa} = 0.2$, $W_{aa} = 1$.

It is important to emphasize that, as in Figure 5.3, each equilibrium is associated with its own value of $\lambda = (df/dn)|_{n=\hat{n}}$. Thus, we must calculate λ for each equilibrium of a discrete-time model and determine when that particular equilibrium is stable ($-1 < \lambda < 1$) or unstable ($\lambda > 1$ or $\lambda < -1$).

At this stage we must add two words of caution. CAUTION 1: if the displacement grows at each time step by a factor λ greater than one in magnitude, then the displacement will eventually become large, no matter how small it was initially. As the displacement gets larger, the linear approximation (5.14) for the recursion equation will get worse and worse, until eventually it is completely off. Once this happens, we must return to using the full recursion equation (in all its gory detail) to predict further changes to the system. CAUTION 2: for some equilibria, λ might be equal to +1 (or –1). In this case, you might think that the displacement would never grow or shrink, but this isn't necessarily true. Remember, we ignored the higher-order terms in the Taylor series when we derived equation (5.14). If we were to keep the next term in the Taylor series (involving the second derivative $(d^2f/dn^2)|_{n=\hat{n}}$), perhaps the balance would tip toward the equilibrium or away from it. As a result, when the magnitude of λ is one, higher-order terms in the Taylor series must be examined to determine whether an equilibrium is stable or unstable.

One can also analyze the stability of an equilibrium in a discrete-time model using a difference equation. The method is only slightly different from the one described above and is summarized in Recipe 5.3. To avoid confusion, we recommend using a recursion equation rather than a difference equation when determining stability.

Next let us consider a continuous-time model and derive a differential equation for the displacement $\varepsilon = n - \hat{n}$ from the differential equation for the original variable, $dn/dt = f(n)$. (For ease of reading, we now drop the (t) notation, but remember that both n and ε are functions of time.) By the definition of the displacement, $d\varepsilon/dt$ equals $d(n - \hat{n})/dt$. But because the equilibrium $\hat{n}$ is a constant, $d(n - \hat{n})/dt$ is just dn/dt (using Rules A2.3 and A2.1). As a result, we have $d\varepsilon/dt = f(n)$. Again, the right-hand side involves the original variable, not the displacement, but it can be rewritten as $d\varepsilon/dt = f(\hat{n} + \varepsilon)$ using the fact that $n = \hat{n} + \varepsilon$. Taking the Taylor series of the function $f(\hat{n} + \varepsilon)$ around the equilibrium at which $\varepsilon = 0$ then gives the linear approximation

$$\frac{d\varepsilon}{dt} \approx f(\hat{n}) + \left.\frac{df}{dn}\right|_{n=\hat{n}} \varepsilon(t). \tag{5.16}$$

The quantity $f(\hat{n})$ represents the rate of change of the system at an equilibrium, which is zero by definition. The term $(df/dn)|_{n=\hat{n}}$ represents the slope of the differential equation with respect to the variable n evaluated at the equilibrium point $\hat{n}$. Again, we simplify the notation by defining $r = (df/dn)|_{n=\hat{n}}$. (We use r rather than λ to emphasize the fact that it is based on the differential equation not the recursion equation.) Equation (5.16) then becomes

$$\frac{d\varepsilon}{dt} \approx r\varepsilon(t). \tag{5.17}$$

Equation (5.17) has the form of the exponential growth model in continuous time, whose general solution is given by equation (4.2). Thus, the displacement grows or shrinks over time according to the exponential function

$$\varepsilon(t) \approx e^{rt}\varepsilon(0). \tag{5.18}$$

When r is negative, the displacement has a negative growth rate and shrinks until the equilibrium is approached (a *stable* equilibrium). When r is positive, the displacement has a positive growth rate and expands over time, causing the system to move away from the equilibrium (an *unstable* equilibrium). In this case, there will come a point when the displacement has grown so much that the linear approximation (5.17) no longer accurately describes the dynamics. At this point, the full nonlinear differential equation must be used. The displacement never oscillates from side to side of the equilibrium in a continuous-time model involving one variable because the displacement follows a continuous path and cannot cross the equilibrium without remaining at the equilibrium forevermore. These conclusions are summarized in Figure 5.4.

Again, there is a close relationship between the stability analysis described above and the change versus variable plots used in the previous chapter. When the differential equation df/dn is plotted against the variable n, an equilibrium value is stable if the system grows when started below the equilibrium but shrinks when started above it. This requires that df/dn crosses the horizontal axis at $\hat{n}$ with a negative slope (Figure 5.5). This is exactly equivalent to the condition for stability, $r < 0$, because $r = (df/dn)|_{n=\hat{n}}$ is the

mathematical way of describing this slope. Conversely, the equilibrium is unstable if the variable decreases when started below the equilibrium and grows when started above it, which occurs when d*f*/d*n* crosses the horizontal axis at $\hat{n}$ with a positive slope ($r > 0$). Graphs thus help us visualize why the stability of an equilibrium is determined by the sign of $r = (df/dn)|_{n=\hat{n}}$.

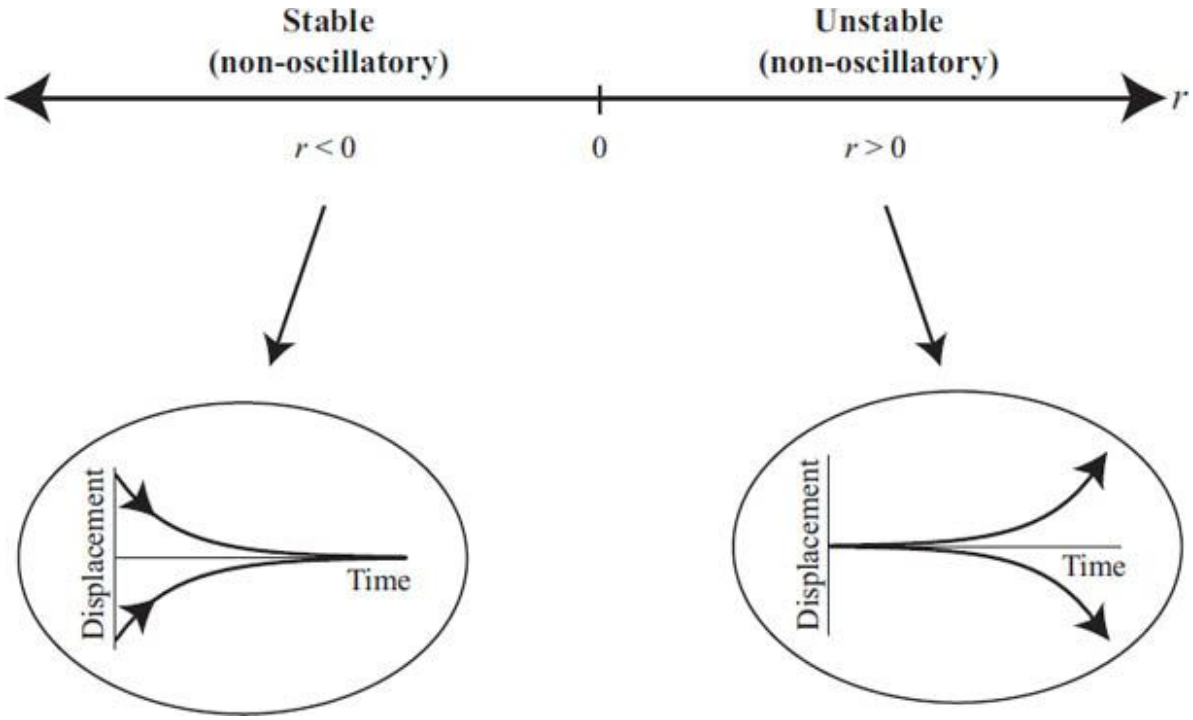

Figure 5.4: Analyzing the stability of an equilibrium in a continuous-time model. For a model whose differential equation is $dn/dt = f(n)$, the value of $r = (df/dn)|_{n=\hat{n}}$ determines the dynamics near the equilibrium point $\hat{n}$. The inset ovals illustrate the dynamics of the displacement from the equilibrium, $\varepsilon(t)$, over time for r values from each region.

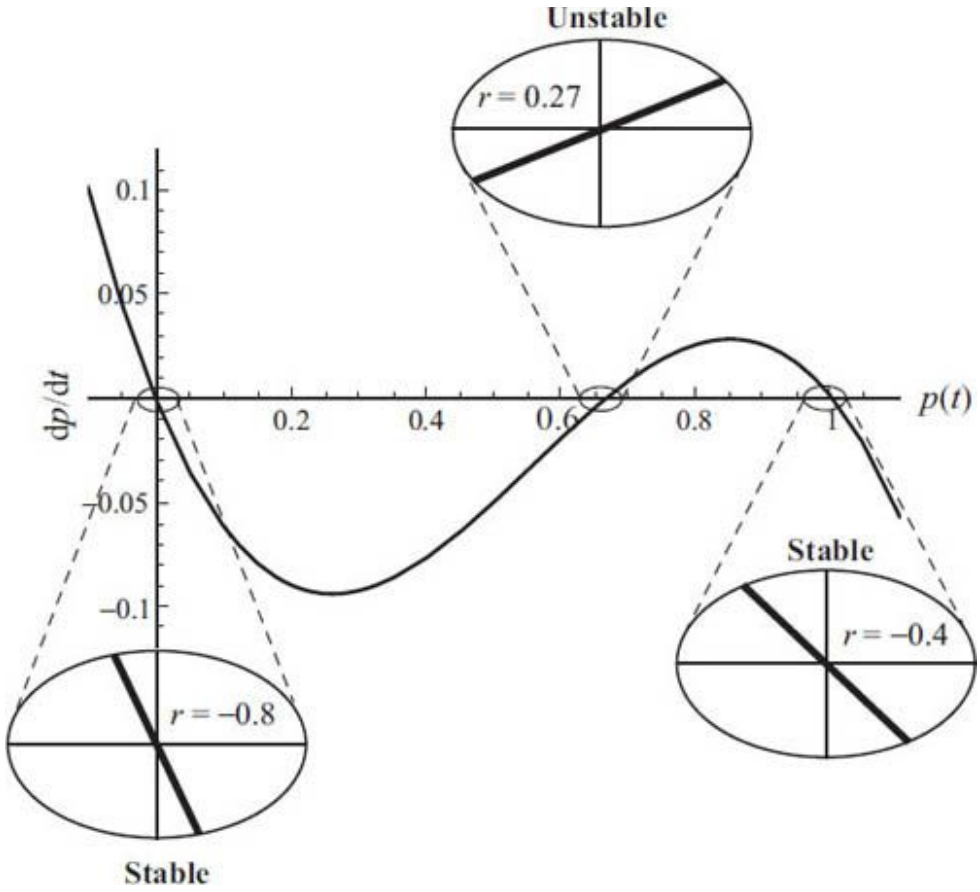

Figure 5.5: A graphical interpretation of the stability condition for the diploid model of selection in continuous time. The differential equation, $f(p) = \mathrm{d}p/\mathrm{d}t = p(1-p)(p(W_{AA} - W_{Aa}) + (1-p)(W_{Aa} - W_{aa}))$ (from Problem 3.16), is plotted against the allele frequency for the same parameters as in Figure 5.3. The inset ovals show the slope of the differential equations at each of the three equilibria. These slopes equal $r = (\mathrm{d}f/\mathrm{d}p)|_{p=\hat{p}}$, which must be negative for the equilibrium to be stable.

We have just outlined the theory behind an important modeling technique, known as a local stability analysis, used to determine whether an equilibrium is stable. A local stability analysis approximates the dynamics of a model near an equilibrium with a linear equation that can be used to predict whether the system moves toward the equilibrium (the equilibrium is then stable) or away from the equilibrium (the equilibrium is then unstable).

A *local stability anlaysis*(or *linear stability analysis*) determines whether an equilibrium is stable or unstable by approximating the dynamics of the system displaced slightly from the equilibrium.

Recipe 5.3
Performing a Local Stability Analysis

Case A: Recursion equations in a discrete-time model

Consider a recursion equation $n(t + 1) = f(n)$, where $f(n)$ is some function of the variable at time t. The local stability properties of any of its equilibria $\hat{n}$ are determined as follows:

Step 1: Differentiate $f(n)$ with respect to n to obtain df/dn.

Step 2: Replace every instance of n in this derivative with the equilibrium value $\hat{n}$ to obtain $(df/dn)|_{n=\hat{n}}$.

Step 3: Define $\lambda \equiv (df/dn)|_{n=\hat{n}}$.

Step 4: Determine the sign and magnitude of λ.

Step 5: Evaluate the stability of the equilibrium $\hat{n}$ according to Figure 5.2 or the following table:

Case A	$\lambda < 0$	$\lambda > 0$
$\lvert\lambda\rvert < 1$	*$\hat{n}$ is stable (oscillatory)*	*$\hat{n}$ is stable (nonoscillatory)*
$\lvert\lambda\rvert > 1$	*$\hat{n}$ is unstable (oscillatory)*	*$\hat{n}$ is unstable (nonoscillatory)*

"Nonoscillatory" implies that the population remains on the same side of the equilibrium over time. "Oscillatory" implies that the population alternates from side to side of the equilibrium.

Step 6: Repeat Steps 2 through 5 for each equilibrium of interest.

Case B: Difference equations in a discrete-time model

Consider a difference equation $\Delta n = f(n)$. The local stability properties of any of its equilibria $\hat{n}$ are determined as in Case A, with the exception of Step 3:

Step 3: Define $\lambda \equiv (df/dn)|_{n=\hat{n}}{}^{+1}$

Case C: Differential equations in a continuous-time model

Consider a differential equation $dn/dt = f(n)$. The local stability properties of any of its equilibria $\hat{n}$ are determined using Steps 1 and 2 above followed by:

Step 3: Define $r \equiv (df/dn)|_{n=\hat{n}}$.

Step 4: Determine the sign of r.

Step 5: Evaluate the stability of the equilibrium $\hat{n}$ according to Figure 5.4 or the following table:

Case C:	$r < 0$	$r > 0$
	$\hat{n}$ is stable	$\hat{n}$ is unstable

In one-variable, continuous-time models of the form $dn/dt = f(n)$, where $f(n)$ is a function of n but not t, the population never oscillates.

Step 6: Repeat Steps 2 through 5 for each equilibrium of interest.

A local stability analysis is an extremely powerful method that can be used to obtain insight into a variety of aspects of biological systems. In the rest of this section, we give examples of the application of Recipe 5.3. After a few examples, consider returning to this section to become truly comfortable with how and why stability analyses work.

5.3.1 Exponential and Logistic Models of Population Growth

Although we already know how the discrete-time model of exponential growth behaves from the general solution (4.1) it is instructive to return to this model for our first local stability analysis. In this case, the recursion equation is $n(t + 1) = f(n) = R\,n(t)$, and there is only one equilibrium: $\hat{n} = 0$. We now walk through Recipe 5.3 (Case A). *Step 1*: Take the derivative of $f(n)$ with respect to $n(t)$ to get $df/dn = R$. *Step 2:* Because R does not depend on n, $(df/dn)|_{n=0}$ remains R. *Step 3:* The key determinant of stability is thus $\lambda = R$. *Step 4:* Because R represents the number of surviving individuals per parent, λ must be positive. *Step 5:* We conclude that $\hat{n} = 0$ is unstable if R is greater than one; this makes sense because parents can then produce more than enough offspring to replace themselves. Conversely, the equilibrium $\hat{n} = 0$ is stable if $0 < R < 1$. These conclusions are entirely consistent with the discussion of the general solution in Chapter 4 (see also Figure 4.1).

Next, let us turn to the more interesting logistic model. In this case, the recursion equation is $n(t + 1) = f(n) = n(t) + rn(t)(1 - n(t)/K)$, and there are now two equilibria to consider: $\hat{n} = 0$ and $\hat{n} = K$. We first perform a stability analysis of the $\hat{n} = 0$ equilibrium using Recipe 5.3 (Case A). *Step 1:* Take the derivative of $f(n)$ with respect to n, giving

$$\frac{df}{dn} = 1 + r - 2\frac{rn(t)}{K}. \tag{5.19}$$

Step 2: Plugging $\hat{n} = 0$ into (5.19) gives $(df/dn)|_{n=0} = 1 + r$, which is the number of surviving offspring per parent when the population size is near zero, $R(0)$. *Step 3:* We thus set λ to $R(0)$. *Step 4:* Because $R(0)$ represents the number of surviving individuals per parent when the population size is low, λ must be positive. *Step 5:* As in the exponential model, $\hat{n} = 0$ is unstable if $R(0)$ is greater than one and stable if $R(0) < 1$. In short, the population size moves away from $\hat{n} = 0$ if parents have more surviving offspring than needed to replace themselves when the population size is low.

Now let us evaluate the stability of the second equilibrium, $\hat{n} = K$. We can skip Step 1, which is the same for all equilibria. *Step 2:* Plugging $\hat{n} = K$ into (5.19) gives $(df/dn)|_{n=K} = 1 - r$, and so, *Step 3:* $\lambda = 1 - r$. *Step 4:* λ can be positive or negative depending on the size of r. *Step 5:* The equilibrium will be stable if $-1 < \lambda < 1$. This looks harmless but the implications of this stability analysis hint at the bizarre behavior of the logistic model.

Because $R(0)$ $1 + r$ must be positive (it represents the number of surviving offspring per parent when the population is very small), the smallest that r can be is -1. For r between -1 and 0, $\lambda = 1 - r$ is greater than one, and the equilibrium is unstable. In other words, if the population size is below carrying capacity and the intrinsic growth rate is negative, then the population size will decline toward zero. What if the population size is initially above carrying capacity? The stability analysis also indicates that the population size will grow away from the carrying capacity and become larger over time! Did we make a mistake in the stability analysis? Figure 5.6a indicates not: populations with a negative r that start above K do indeed expand in size toward infinity.

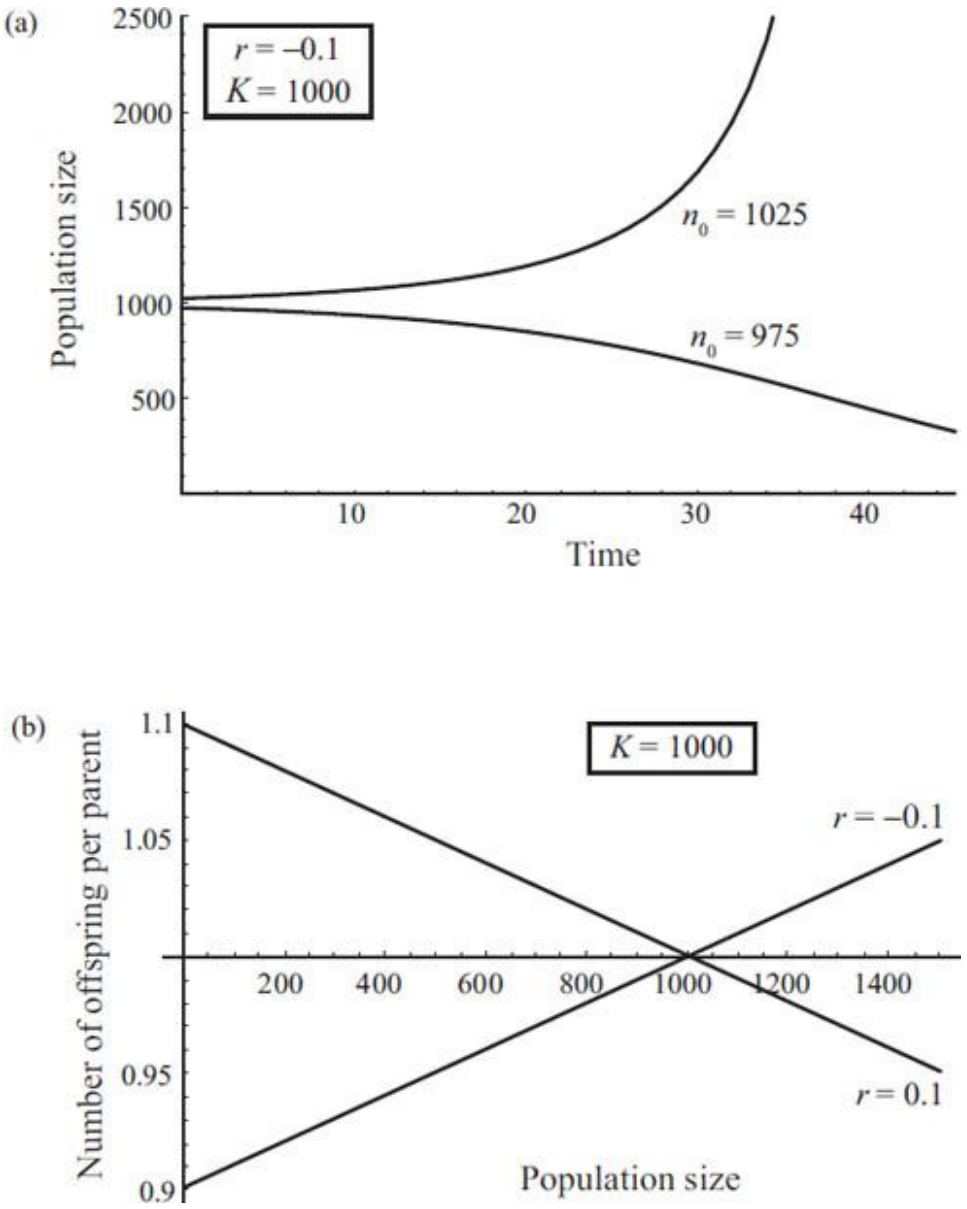

Figure 5.6: Pathological behavior of the logistic model. (a) When the growth rate is negative, a population started below the carrying capacity declines over time, but a population started above the carrying capacity increases in size ($r = -0.1$). (b) The reason for this odd behavior is that the influence of density dependence is reversed when the growth rate is negative, such that each individual leaves more surviving offspring in larger populations than in small populations (compare the line with $r = -0.1$ to the expected decline observed with $r = 0.1$). In both figures, $K = 1000$.

Why does this happen? The logistic model is based on the assumption that density dependence decreases the number of surviving offspring per parent as a linear function of the current population size: $R(n) = 1 + r\,(1 - n(t)/K)$. If the intrinsic growth rate r is negative, however, the density-dependent term in parentheses causes the number of surviving offspring per parent to *rise* as the population size increases (Figure 5.6b). If the population size is above the

carrying capacity, then both r and $1–n(t)/K$ are negative, implying that there is more than one surviving offspring per parent and explaining why the population grows. Furthermore, the problem does not go away if you assume that density dependence causes an exponential rather than linear decline in growth, leading to the Ricker model (5.7) (see Problem 5.7).

One reaction to the above results is to say that the logistic equation just cannot be used when r is negative, but this is an ad hoc restriction. There is no reason, a priori, to believe that the intrinsic growth rate of a species must always be positive; for example, r might very well decrease and become negative as a result of habitat destruction. The best way to resolve this sort of issue is to develop an explicit model of resource use as we did in Chapter 3, where resources (e.g., prey) never become negative, but the growth rate of a population can be.

For the sake of argument, let us continue and assume that r is positive. When r lies between 0 and 1, so too will $\lambda = 1 - r$, implying that $\hat{n} = K$ is stable and that populations near this equilibrium will approach the equilibrium without oscillating around it (see Figure 5.2). When r lies between 1 and 2, $\lambda = 1 - r$ will range from -1 to 0, implying that $\hat{n} = K$ is stable but that populations near this equilibrium will approach it via a series of oscillations. Finally, for r greater than 2, $\lambda = 1 - r$ becomes less than -1, indicating that the population will oscillate around the equilibrium and move further away from it over time. These conclusions are entirely consistent with Figure 4.2 and Box 4.1. Now, however, we know the exact cutoff between nonoscillatory and oscillatory behavior (i.e., $r = 1$) and between stability and instability (i.e., $r = 2$).

Before leaving the discrete-time logistic equation, it is worth discussing its behavior a bit more. The reason that oscillations are observed for high r but not low r is that, by assumption, density dependence has an effect that is proportional to r (think about the equation for $R(n) = 1 + r\,(1–n(t)/K)$). Thus, populations that grow faster when population size is low will also crash faster when population sizes are large. This may or may not be true in nature; it is certainly possible for a population with a fast intrinsic growth rate to modulate its behavior as the population size grows such that individuals invest less in reproduction and/or more in survival, causing only small changes in population size when density is high. If so, the logistic model will not describe the dynamics of such a species.

The above analysis reveals the possibility of fascinating behavior in the logistic model (e.g., oscillations), but it also reveals that the assumptions underlying the logistic equation (3.5a) constrain population growth in ways that we did not necessarily intend. We found, for example, that density dependence has a positive effect on population growth when the intrinsic growth rate is negative. Furthermore, populations with higher intrinsic growth rates necessarily crash at faster rates when the population size starts above carrying capacity. Always be on the lookout for unintended behavior in a model. If the unintended behavior results from biologically unreasonable assumptions, then you must revise the model if you can or scrap it you can't. Several ecologists have argued that the unintended behavior of the logistic is unacceptable and have instead promoted models that explicitly keep track of the resources that individuals must consume to survive and reproduce (see section 3.4).

Next, we consider the continuous-time logistic model. Using the differential equation (3.5c),

$$\frac{dn}{dt} = r\,n(t)\left(1 - \frac{n(t)}{K}\right),$$

we can define $f(n) = rn(t)(1-n(t)/K)$ and then go through the steps outlined in Recipe 5.3 (Case C).

Again, there are two equilibria of the logistic model in continuous time: $\hat{n} = 0$ and $\hat{n} = K$. Let us start with $\hat{n} = 0$. *Step 1:* Taking the derivative of $f(n)$ with respect to n gives

$$\frac{df}{dn} = r - 2\frac{r\,n(t)}{K} \tag{5.20}$$

Step 2: Plugging $\hat{n} = 0$ into (5.20) demonstrates that $(df/dn)|_{n=0} = r$. *Steps 3–5:* The equilibrium $\hat{n} = 0$ is stable when $r < 0$ (extinction predicted) and will be unstable when $r > 0$ (the population grows away from $\hat{n} = 0$).

We now repeat this procedure for the second equilibrium, $\hat{n} = K$. Again, Step 1 is the same. *Step 2:* Plugging $\hat{n} = K$ into equation (5.20) gives $(df/dn)|_{n=K} = -r$. *Steps 3–5:* As a result, the stability conditions for $\hat{n} = K$ are exactly the reverse of the stability conditions for $\hat{n} = 0$. If the population has a positive growth rate ($r > 0$), then $\hat{n} = K$ will be stable, and populations near carrying capacity will approach K over time. If the population has a negative

growth rate ($r < 0$), $\hat{n} = K$ will be unstable. Instability, however, implies that populations move away from the equilibrium whether they are slightly above or slightly below the equilibrium. Once again, we are forced to conclude that the logistic model in continuous time behaves oddly, because a population that starts above carrying capacity will increase in size and move away from K if it has a negative intrinsic growth rate.

5.3.2 Haploid and diploid models of natural selection

Determining the stability of the two equilibria, $\hat{p} = 0$ and $\hat{p} = 1$, in the haploid model of selection is a very good problem to work through for your first stability analysis (Problem 5.6), and so here we focus on the diploid model of selection in discrete time. In the diploid model, the recursion equation is

$$p(t+1) = f(p) = \frac{p(t)^2 W_{AA} + p(t)q(t)W_{Aa}}{p(t)^2 W_{AA} + 2p(t)q(t)W_{Aa} + q(t)^2 W_{aa}}, \qquad (5.21)$$

which has three equilibria $\hat{p} = 0$ and $\hat{p} = 1$, and $\hat{p}$ and given by equation (5.4).

First we analyze the stability of the equilibrium at which the A allele is absent ($\hat{p} = 0$) using Recipe 5.3 (Case A). *Step 1:* We must take the derivative of $f(p)$ with respect to the variable p. Remember, however, that $q(t)$ is a function of $p(t)$, and we must substitute $q(t) = 1 - p(t)$ before taking this derivative. Doing this, applying the quotient rule (A2.13), and rearranging, we get

$$\frac{df}{dp} = \frac{p^2 W_{AA} W_{Aa} + 2p(1-p)W_{AA}W_{aa} + (1-p)^2 W_{Aa}W_{aa}}{(p^2 W_{AA} + 2p(1-p)W_{Aa} + (1-p)^2 W_{aa})^2}. \qquad (5.22)$$

To accomplish this simplification, bring together and factor all terms that are multiplied by the same function of the parameters, e.g., by W_{AA} W_{Aa}, and repeat this for each combination of parameters.

Steps 2–3: Plugging $\hat{p} = 0$ into equation (5.22), we find that $\lambda = W_{Aa}/W_{aa}$. *Step 4:* The fitness of an individual cannot be negative (it is a measure of the number of surviving offspring per parent genotype), and therefore λ must be positive. As a result, we need only concern ourselves with determining if λ is greater or less than one. Step 5: If $W_{Aa} > W_{aa}$ then λ will be greater than one,

and $\hat{p} = 0$ will be an unstable equilibrium. Consequently, the *A* allele spreads when rare if the fitness of heterozygotes is greater than the fitness of *aa* homozygotes.

Why doesn't the fitness of *AA* individuals enter into this stability condition? The stability analysis assumes that we are very near the equilibrium so that *p* must be very small. In this case, the frequency of the *AA* genotype (p^2) must be extremely small. Therefore, most *A* alleles within the population will be present in heterozygous individuals, and so the spread of the *A* allele is governed by the fitness of heterozygotes relative to the resident *aa* individuals. Mathematically, the fitness of *AA* homozygotes is second order with respect to the deviation from the equilibrium (i.e., on the order of $\varepsilon(t)^2$) and so is ignored in the linear approximation used in the derivation of equation (5.14).

Analyzing the second equilibrium ($\hat{p} = 1$) reveals a similar picture. Plugging into $\hat{p} = 1$ (5.22), λ becomes W_{Aa}/W_{AA}. Thus, if the heterozygote is more fit than the resident *AA* homozygote ($W_{Aa} > W_{AA}$), the equilibrium will be unstable, and the *a* allele will spread. Conversely, if the heterozygote is less fit ($W_{Aa} < W_{AA}$), the equilibrium will be locally stable to the invasion of *a*.

We are left with one more equilibrium, given by equation (5.4). Plugging (5.4) into equation (5.22) and simplifying gives

$$\lambda = \left.\frac{df}{dn}\right|_{p=\hat{p}} = \frac{W_{AA}W_{Aa} + W_{aa}W_{Aa} - 2W_{AA}W_{aa}}{W_{Aa}^2 - W_{AA}W_{aa}}. \qquad (5.23a)$$

Time for a confession: we didn't derive equation (5.23a) by hand. It is straightforward to do, but it is tedious. This is exactly the sort of ugly algebra that symbolic mathematical software such as *Mathematica* and *Maple* can do in a flash. Even so, to interpret the answer that a computer spits out often involves some educated rearrangements.

To determine where λ lies (positive or negative, below or above one), it is easiest to rearrange equation (5.23a) to make the answer more apparent. We are particularly interested in interpreting (5.23a) in cases where the heterozygote is either more fit or less fit than the two homozygotes, because this is when the polymorphic equilibrium is valid. So let's measure all of the fitnesses relative to the heterozygous fitness. By dividing the top and bottom of equation (5.23a) by W_{Aa}^2, we get

$$\lambda = \frac{\frac{W_{AA}}{W_{Aa}} + \frac{W_{aa}}{W_{Aa}} - 2\frac{W_{AA}}{W_{Aa}}\frac{W_{aa}}{W_{Aa}}}{\left(1 - \frac{W_{AA}}{W_{Aa}}\frac{W_{aa}}{W_{Aa}}\right)}. \tag{5.23b}$$

We can then rewrite (5.23b) in terms (in parentheses) that are positive when the heterozygote is most fit and negative when the heterozygote is least fit:

$$\lambda = \frac{\frac{W_{AA}}{W_{Aa}}\left(1 - \frac{W_{aa}}{W_{Aa}}\right) + \frac{W_{aa}}{W_{Aa}}\left(1 - \frac{W_{AA}}{W_{Aa}}\right)}{\left(1 - \frac{W_{AA}}{W_{Aa}}\frac{W_{aa}}{W_{Aa}}\right)}. \tag{5.23c}$$

By rearranging (5.23a) in this way, we can more easily see that λ is positive whenever the heterozygote is most fit (all parenthetical terms are positive) or least fit (all parenthetical terms are negative). Because λ is positive at the polymorphic equilibrium in the diploid model of selection, the allele frequencies will never oscillate around this equilibrium.

The above rearrangements help us to see if λ is positive or negative, but a different rearrangement is needed to determine whether λ is less than or greater than one. This rearrangement is important as it will tell us when the equilibrium will be stable or unstable. The key insight is that λ will lie below one whenever $(\lambda - 1)$ is negative and above one when $(\lambda - 1)$ is positive. Often $(\lambda - 1)$ factors into easily interpretable parts:

$$(\lambda - 1) = -\frac{(W_{Aa} - W_{aa})(W_{Aa} - W_{AA})}{(W_{Aa}^2 - W_{AA}W_{aa})}. \tag{5.24a}$$

Again, this is easier to interpret if we measure fitness relative to the heterozygous fitness by dividing the top and bottom of (5.24a) by W_{Aa}^2:

$$(\lambda - 1) = -\frac{\left(1 - \frac{W_{aa}}{W_{Aa}}\right)\left(1 - \frac{W_{AA}}{W_{Aa}}\right)}{\left(1 - \frac{W_{AA}}{W_{Aa}}\frac{W_{aa}}{W_{Aa}}\right)}. \tag{5.24b}$$

If the heterozygote is most fit, then each parenthetical term is positive, and (λ – 1) becomes negative. This proves that λ is less than one, and the equilibrium is locally stable when the heterozygote is most fit. Conversely, if the heterozygote is least fit, then each parenthetical term is negative, and (λ – 1) becomes positive. This proves that λ is greater than one, and the polymorphic equilibrium is unstable when the heterozygote is least fit. We don't have to worry about other possible fitness orderings, because the equilibrium allele frequency given by equation (5.4) lies between 0 and 1 only when the heterozygote is most fit or least fit (Table 5.1).

TABLE 5.1
Stability conditions for the equilibria of the diploid model of selection

Equilibrium:	$\hat{p} = 0$	$\hat{p} = \frac{W_{Aa} - W_{aa}}{2W_{Aa} - W_{AA} - W_{aa}}$	$\hat{p} = 1$
Stable	$W_{Aa} < W_{aa}$	$W_{aa} < W_{Aa} > W_{AA}$	$W_{Aa} < W_{AA}$
Unstable	$W_{Aa} > W_{aa}$	$W_{aa} > W_{Aa} < W_{AA}$	$W_{Aa} > W_{AA}$

5.4 Approximations

For many models there comes a point at which the mathematical analysis becomes either too messy to be useful or impossible to conduct. When this occurs we are faced with two choices. First, we can resort to numerical and simulation techniques using computers, provided that we are willing to specify values for all of the parameters. Second, we can seek approximations that allow us to proceed further with the mathematical analysis. Often, our interest in a model focuses on cases where some parameter values are either very small (e.g., mutation rates) or very large (e.g., egg production in some fish species). In this section, we describe how to use such restrictions on the magnitude of parameters to find approximate values for equilibria and to perform approximate stability analyses. This material is more advanced and should be read only once you are comfortable with finding equilibria (section 5.2) and determining their stability (section 5.3).

5.4.1 Approximating equilibria

In cases where it is impossible to find explicit solutions for the equilibria, or when such solutions are so complex that they are difficult to interpret, it can be worth trying to obtain an approximation for the equilibria. Here, we describe a method based on the Taylor series (Primer 1) for finding an approximate solution for $\hat{n}$. The method is known as a *perturbation analysis*, and it is an extremely powerful and useful technique (Box 5.1).

A *perturbation analysis* identifies an approximate solution to an equation by assuming that a parameter is small.

The first step is to determine when you want the equilibrium approximation to be accurate. This involves choosing one or more parameters that you believe are small relative to other parameters in the model. We will write such small parameters in terms of a new parameter ζ ("zeta"), which is small. We use ζ to represent a small perturbation of a *parameter* from some special value (e.g., zero), whereas we used ε to represent a small displacement of the *variable* from some special value (e.g., the equilibrium). For example, you might be willing to assume that mutation rates are small or that a population is sufficiently isolated from other populations that immigration is rare relative to the number of individuals born within a population. In other cases, you might think that a parameter is very near a particular value (say, c). For example, fitnesses in a population-genetic model might be expected to be near one. To make it easier to apply the method, we will rewrite any such parameter as c plus a term that we believe to be near zero. For example, if we believe that the fitness of an allele (say, W_A) is near one, then we would write $W_A = 1 + s$, where s is assumed to be small and is replaced by ζ. Similarly, you can also consider cases where a parameter is very large, say K, by rewriting it as $K = 1/b$, where b is small and replaced by ζ.

Box 5.1: Theoretical Basis of a Perturbation Analysis

In this box, we describe a method for finding an approximate solution to an equation. To begin, we identify a solution to the equation under some special condition (e.g., when a particular parameter is zero). We then "perturb" the equation a little bit away from this special case and determine how the solution to the equation is altered. For this reason, the

method is known as a "perturbation analysis." Our focus in this chapter is to apply a perturbation analysis to an equilibrium condition in the hopes of finding an approximate solution that is close to the exact equilibrium. This method is more general, however, and can be used to approximate the solution to any equation of interest.

To apply the technique, we must have an equation that we wish to solve for a term of interest, say $\hat{n}$. We must first identify a parameter (or a set of parameters) that we are willing to assume is small. Let's call this small parameter ζ("zeta"). For example, if immigration is rare, then we could replace m with ζ in the equilibrium condition (5.10). If we have more than one parameter that we want to be small, then we can rewrite each one as some constant times ζ. Thus, by setting ζ to zero, all of the small parameters in the equation are simultaneously set to zero.

We want to find the value of $\hat{n}$ that solves an equation, but we cannot solve this equation explicitly. (To simplify the notation, we bring all of the terms in the equation of interest to one side, so that it has the form stuff = 0.) Suppose that we write $\hat{n}$ as a sum of terms:

$$\hat{n} = \hat{n}_0 + \hat{n}_1\zeta + \hat{n}_2\zeta^2 + \hat{n}_3\zeta^3 + \cdots. \tag{5.1.1}$$

At an intuitive level, we can think of each successive ζ^i term as providing a more refined estimate for the value of $\hat{n}$. At a more technical level, expression (5.1.1) is the Taylor series of the solution, $\hat{n}$, with respect to ζ around $\zeta = 0$, with $\hat{n}_i$ representing $(1/i!)(d^i\hat{n}/d\zeta^i)|_{\zeta = 0}$ (see equation (P1.12) in Primer 1). We now plug expression (5.1.1) into the equation that we wish to solve. To emphasize that this equation depends on the small parameter ζ we write it as $f(\zeta) = 0$. Our goal is to solve this equation for the $\hat{n}_i$ needed to obtain a sufficiently accurate approximation for $\hat{n}$ from expression (5.1.1).

For this method to help, we must be able to solve the original equation for the case where the small parameter is set to zero, $\zeta = 0$. That is, we must be able to solve $f(0) = 0$ for $\hat{n}_0$. If we still cannot solve this equation explicitly, even in this special case, then we must go back to the drawing board and identify other parameters that might be small.

How do we find the $\hat{n}_i$ terms needed in expression (5.1.1)? We certainly cannot find $(d^i\hat{n}/d\zeta^i)|_{\zeta = 0}$ by taking the derivative of $\hat{n}$ with respect to the parameter ζ, because we do not know $\hat{n}$. The crux of the

method is that we take the Taylor series of the equation we wish to solve, $f(\zeta)$:

$$f(\zeta) = f(0) + \left.\frac{df(\zeta)}{d\zeta}\right|_{\zeta=0}\zeta + \frac{1}{2!}\left.\frac{d^2f(\zeta)}{d\zeta^2}\right|_{\zeta=0}\zeta^2 + \frac{1}{3!}\left.\frac{d^3f(\zeta)}{d\zeta^3}\right|_{\zeta=0}\zeta^3 + \cdots. \qquad (5.1.2)$$

A perfect approximation for $\hat{n}$ would cause each term in this sum to be zero. If any term in the Taylor series (5.1.2) did not equal zero, the subsequent terms would be too small to ensure that $f(\zeta) = 0$ is satisfied by the approximation for $\hat{n}$. Thus, our goal is to find the values of $\hat{n}_i$ that cause each term in (5.1.2) to equal zero.

To accomplish this, we set $(d^i f(\zeta)/d\zeta^i)|_{\zeta=0}$ to zero for i, starting with $i = 0$ up to the order that is needed for the desired level of accuracy. We already know that $\hat{n}_0$ causes the first term to equal zero, $f(0) = 0$, because this is the solution when the small parameter ζ is absent. We then move to the next term, plugging our result for $\hat{n}_0$ into $(df(\zeta)/d\zeta)|_{\zeta=0}$, setting this to zero, and solving for $\hat{n}_1$ (or any other remaining $\hat{n}_i$). This can be repeated ad nauseum, for an ever more precise approximation for $\hat{n}$. In practice, however, we often focus on the first two terms in expression (5.1.1), which provide an approximation that is linear in terms of the small parameters. This technique is summarized in Recipe 5.4.

As an example, let us find an approximate solution to the transcendental equation $e^{\alpha\hat{n}} + \hat{n} = 5$ using Recipe 5.4. *Step 1:* In this example, there is only one parameter α, which we assume is small, $\alpha = \zeta$. *Step 2:* Plugging in (5.1.1) for $\hat{n}$ and moving all terms to the right gives

$$f(\zeta) = e^{\zeta(\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\hat{n}_3\zeta^3+\cdots)} + (\hat{n}_0 + \hat{n}_1\zeta + \hat{n}_2\zeta^2 + \hat{n}_3\zeta^3 + \cdots) - 5 = 0. \qquad (5.1.3)$$

Step 3: The first three derivatives in the Taylor series (5.1.2) are $f(0) = \hat{n}_0 - 4$, $(df(\zeta)/d\zeta)|_{\zeta=0} = \hat{n}_0 + \hat{n}_1$, and $(d^2f(\zeta)/d\zeta^2)|_{\zeta=0} = \hat{n}_0^2 + 2\hat{n}_1 + 2\hat{n}_2$. *Step 4:* Next, we determine the values of $\hat{n}_i$ that cause each of these terms to equal zero. Starting with the first term, we get $\hat{n}_0 = 4$. Using this result in the second term, $(d^2f(\zeta)/d\zeta^2)|_{\zeta=0}$ equals zero when $\hat{n}_1 = -4$. Moving to the third term, $(d^2f(\zeta)/d\zeta^2)|_{\zeta=0} = 0$ is satisfied when $\hat{n}_2 = -4$. We could continue evaluating higher-order terms in the Taylor series, but let us stop and

evaluate how we are doing. *Step 5:* To the level of accuracy obtained so far, $\hat{n} \approx 4 - 4\zeta - 4\zeta^2$, which is $\hat{n} \approx 4 - 4\alpha - 4\alpha^2$ in terms of the original parameter α.

If we assume that $\alpha = 0.01$ and we solve $e^{0.01\hat{n}} + \hat{n} = 5$ numerically (e.g., using *Mathematica*), we get $\hat{n} = 3.95961$. If we instead use our approximation, we get $\hat{n} \approx 4 - 4(0.01) - 4(0.01)^2 = 3.9596$. Not a bad match! Even if we only use the first two terms in the approximation, $\hat{n} \approx 4 - 4\alpha$, we get a decent approximation ($\hat{n} \approx 3.96$).

To make the procedure described in Box 5.1 more concrete, let us find an approximation for $\hat{n}$ in the Ricker model with exponential density dependence and migration. The equilibrium condition (5.10) cannot be solved explicitly, but it can be approximated assuming that migration is rare. Specifically, we assume that m is small and replace it with ζ. As described in Box 5.1, we then replace $\hat{n}$ in the equilibrium condition (5.10) with, $\hat{n}_0 + \hat{n}_1\zeta + \hat{n}_2\zeta^2 + \hat{n}_3\zeta^3 + \ldots$, which represents the equilibrium as a main term ($\hat{n}_0$), a small term of the same order as the migration rate ($\hat{n}_1\zeta$), and even smaller terms ($\hat{n}_2\zeta^2 + \hat{n}_3\zeta^3 + \ldots$). Making these substitutions in equation (5.10) gives

$$f(\zeta) = (\hat{n}_0 + \hat{n}_1\zeta + \cdots) - (1 + r)e^{-\alpha(\hat{n}_0 + \hat{n}_1\zeta + \cdots)}(\hat{n}_0 + \hat{n}_1\zeta + \cdots) - \zeta = 0. \tag{5.25}$$

Taking the Taylor series of (5.25) with respect to ζ near the point $\zeta = 0$ gives

$$f(\zeta) = f(0) + \left(\frac{df}{d\zeta}\bigg|_{\zeta=0}\right)\zeta + \cdots = 0, \tag{5.26}$$

where $f(0) = \hat{n}_0 - (1 + r)e^{-\alpha\hat{n}_0}\hat{n}_0$ and $(df/d\zeta)|_{\zeta=0} = \hat{n}_1 - (1 + r)e^{-\alpha\hat{n}_0}(1 - \alpha\hat{n}_0)\hat{n}_1 - 1$. [Use Rules A2.6 and A2.11 to take the derivative of (5.25) with respect to ζ.]

To ensure that equation (5.26) equals zero, it must be the case that each term in the Taylor series equals zero; if one term did not equal zero, the higher-order terms would be too small to cancel it out. Therefore, we seek the values of $\hat{n}_i$ that ensure that each term in the Taylor series is zero; these values provide us with the approximation for $\hat{n}$ that we desire.

The zeroth-order term $f(0)$ is zero when $\hat{n}_0 - (1 + r)e^{-\alpha \hat{n}_0}\hat{n}_0 = 0$, which is the same as the equilibrium condition (5.8) for the model without migration. In other words, $\hat{n}_0$ represents the term in the approximation for $\hat{n}$ that does not involve the small parameter measuring migration (ζ). As discussed after equation (5.8), the equilibrium condition without migration has two solutions, $\hat{n}_0 = 0$ and $\hat{n}_0 = \ln(1 + r)/\alpha$. Assuming that the population is able to maintain itself in the absence of migration, we focus on the second solution. If, instead, we wished to assume that the population would go extinct in the absence of migration, then we would focus on $\hat{n}_0 = 0$ (Problem 5.14).

We turn next to the linear-order term, $(df/d\zeta)|_{\zeta=0} = \hat{n}_1 - (1 + r)e^{-\alpha\hat{n}_0}(1 - \alpha\hat{n}_0)\hat{n}_1 - 1$, which must equal zero. Plugging in the solution for $\hat{n}_0 = (\ln(1 + r/\alpha)$, we get

$$\hat{n}_1 - (1 + r)e^{-\ln(1+r)}\left(1 - \alpha\frac{\ln(1 + r)}{\alpha}\right)\hat{n}_1 - 1 = 0.$$

Because $e^{-\ln(1 + r)}$ equals $1/(1 + r)$ (Rules A1.13 and A1.16), we can simplify the above to

$$\ln(1 + r)\hat{n}_1 - 1 = 0. \tag{5.27}$$

This equation is satisfied when

$$\hat{n}_1 = \frac{1}{\ln(1 + r)}. \tag{5.28}$$

Thus, to linear order in ζ (i.e., ignoring terms that are ζ^2 and smaller), an equilibrium of the Ricker model with migration is

$$\begin{aligned}\hat{n} &= \hat{n}_0 + \hat{n}_1\zeta + O(\zeta^2)\\ &= \frac{\ln(1 + r)}{\alpha} + \frac{\zeta}{\ln(1 + r)} + O(\zeta^2).\end{aligned} \tag{5.29}$$

It is more meaningful to write this approximation in terms of the original parameter $m = \zeta$ describing the migration rate:

$$\hat{n} \approx \frac{\ln(1 + r)}{\alpha} + \frac{m}{\ln(1 + r)}. \tag{5.30}$$

Earlier, we concocted an example ($r = 1$, $m = 3$, and $\alpha = \ln(200/97)/100$), where α was chosen so that the equilibrium condition (5.10) was satisfied at the equilibrium point $\hat{n} = 100$. Using a calculator to plug these parameter values into (5.30), gives $\hat{n} \approx 100.12$, which is not too far off the exact equilibrium of 100. The advantage of (5.30) is that it is an explicit approximation for $\hat{n}$, which is easy to evaluate for other parameter values, provided that m is small. Furthermore, equation (5.30) clarifies the nature of the equilibrium: it rises with the migration rate with a slope that equals $1/\ln(1 + r)$. Even greater accuracy can be obtained by taking higher order terms in the Taylor series (Problem 5.15). The procedure for using perturbation analysis to approximate an equilibrium is summarized in Recipe 5.4:

Recipe 5.4

Finding an Approximate Equilibrium

Suppose we have an equilibrium condition for $\hat{n}$, and we wish to find an approximate solution for $\hat{n}$ under the assumption that some parameter is small.

Step 1: Identify a parameter(s) that you can assume is small in your model. Write this parameter as ζ. If there is more than one small parameter, write each as some constant times ζ.

Step 2: Plug $\hat{n} = \hat{n}_0 + \hat{n}_1\zeta + \hat{n}_2\zeta^2 + \hat{n}_3\zeta^3 + \ldots$ into the equation that you wish to solve, and write this equation with all terms on the same side as $f(\zeta) = 0$.

Step 3: Calculate $d^i f(\zeta)/d\zeta^i|_{\zeta = 0}$ for $i = 0$ up to the order desired. (The zeroth derivative is just the function evaluated at zero, $f(0)$.)

Step 4: Starting with $i = 0$, solve $d^i f(\zeta)/d(\zeta^i|_{\zeta = 0} = 0$ for any $\hat{n}_i$ that it contains. Repeat for higher values of i, plugging in any $\hat{n}_i$ that have already been determined, until you have obtained a sufficiently accurate estimate for $\hat{n}$.

Step 5: Once you have determined $\hat{n}_i$ for $i = 0$ to some order k, plug these values into expression (5.1.1) to obtain an

approximation for $\hat{n}$ that is accurate to order ζ^k. To interpret your result, rewrite ζ in terms of the original parameters, by reversing Step 1.

Let us work through another example where we approximate an equilibrium using a perturbation analysis. In the models of natural selection considered so far, mutation was ignored; we basically assumed that each allele is faithfully reproduced every generation. In reality, DNA replication is not error-free, and there is some chance μ that the DNA encoding an A allele will be incorrectly replicated as an alternative allele a. Similarly, there is some chance ν that allele a will mutate into allele A. We can fix this omission by incorporating mutation into the diploid model of natural selection. First, we must specify the life cycle. We census the population at the gamete stage, after which gametes unite at random to produce diploids that experience selection, and finally mutation occurs during the production of gametes. In reality, mutations can occur at other times during the life cycle, but alternative life cycles give similar dynamics.

As described in equation (3.13a), the allele frequency in the population after selection is

$$p' = \frac{p(t)^2 W_{AA} + p(t)(1 - p(t))W_{Aa}}{p(t)^2 W_{AA} + 2p(t)(1 - p(t))W_{Aa} + (1 - p(t))^2 W_{aa}}; \qquad (5.31a)$$

this would be the frequency of allele A in the gametes if mutation were absent. With mutation, however, a fraction μ of A alleles is converted to a and vice versa. Thus, among the next generation of gametes,

$$p(t + 1) = (1 - \mu)p' + \nu(1-p'). \qquad (5.31b)$$

We obtain the equilibrium condition for this model by plugging (5.31a) into (5.31b) and setting $p(t + 1) = p(t) = \hat{p}$. The result is messy: a cubic polynomial in $\hat{p}$. As mentioned earlier, cubic polynomials can be solved, but it would take several lines of text to write down the answer.

Mutation rates are typically small, on the order of 10^{-6} per gene per generation, so let us set the mutation rate to the small parameter ζ (Step 1, Recipe 5.4). There is a new twist, however, because we have two mutation rates. To allow both mutation rates to be small, we set $\mu = \tilde{\mu}\zeta$ and $\nu = \tilde{\nu}\zeta$,

which implies that both mutation rates are proportional to the small parameter ζ. (The terms $\widetilde{\mu}$ and $\widetilde{\nu}$ are not small, they just tell us the exact factor by which the mutation rates differ from ζ.) Following Step 2, Recipe 5.4, we next replace $\hat{p}$ with $\hat{p}_0 + \hat{p}_1\zeta + \hat{p}_2\zeta^2 + \cdots$ in the equilibrium condition. Writing this equilibrium condition as $f(\zeta) = 0$, we take the Taylor series with respect to ζ near the point $\zeta = 0$, under the assumption that mutations are rare (Step 3, Recipe 5.4).

Moving to Step 4, Recipe 5.4, we set the zeroth-order term in the Taylor series to zero, $f(0) = 0$, and solve for $\hat{p}_0$. Doing so, we regain the three equilibria in the model without mutation: $\hat{p}_0 = 0$, $\hat{p}_0 = 1$, and the polymorphic equilibrium (5.4). A small rate of mutation causes a slight perturbation to each of these equilibria. Let us focus on $\hat{p}_0 = 1$ under the assumption that AA is the most fit genotype ($W_{AA} = 1$), followed by Aa ($W_{Aa} = 1 - h\,s$), and finally aa ($W_{aa} = 1 - s$). In this case, we expect allele A to rise toward fixation (Figure 4.7b) with an equilibrium frequency near one. Next, we turn to the linear order term of the Taylor series, which again we set to zero to find the approximate equilibrium. Calculating $df/d\zeta|_{\zeta=0}$ and plugging in the value for $\hat{p}_0$ that interests us ($\hat{p}_0 = 1$) gives $-\widetilde{u} + h\,s\hat{p}_1 = 0$. Consequently, $\hat{p}_1 = -\widetilde{\mu}/(h\,s)$.

Finally, in Step 5, Recipe 5.4, gathering these terms and rewriting $\widetilde{u}$ in terms of the mutation rate using the definition $\mu = \widetilde{\mu}\zeta$, the equilibrium frequency of alleles A and a are approximately

$$\hat{p} = \hat{p}_0 + \hat{p}_1\zeta + O(\zeta^2) \approx 1 - \frac{\mu}{hs},$$

$$\hat{q} = 1 - \hat{p} \approx \frac{\mu}{hs}. \tag{5.32}$$

This equilibrium is known as the "mutation-selection balance" and is a classic result in evolutionary biology (Haldane 1927). To this order of approximation, the equilibrium does not depend on the mutation rate ν between allele a and A. Intuitively, ν drops out of the equilibrium approximation because very few alleles within the population are a, and the extremely rare occasion that these few alleles mutate has a negligible influence on the equilibrium of the model. (ν would enter into $\hat{p}_2$ if we derived a more accurate approximation for the

equilibrium by solving for the next order term in the Taylor series.) Equation (5.32) makes a lot of sense: the less fit allele, a, is less common within a population when mutations are rare or when selection against it is strong.

In this example, we have assumed that the mutation rates μ and ν are small and that both are the same order of magnitude (on the order of the small parameter ζ). You can make even more sophisticated assumptions about the relative magnitudes of parameters in a perturbation analysis. For example, if there are many ways for an allele to lose its function by mutation but very few ways in which a mutant allele can regain function, you might wish to assume that the forward mutation rate μ is much higher than the backward mutation rate ν. You can express this assumption in mathematical terms by setting $\mu = \tilde{\mu}\zeta$ and $\nu = \tilde{\nu}\zeta^2$; if ζ is small, ζ^2 will always be much smaller. Alternatively, in a model with both mutation and migration, you might assume that both processes are rare but that the mutation rate is much smaller than the migration rate (e.g., by setting $m = \tilde{m}\zeta$, $\mu = \tilde{\mu}\zeta^2$, and $\nu = \tilde{\nu}\zeta^2$).

A perturbation analysis can be used to find an approximate solution to any equation, not just an equilibrium condition (Box 5.1). For example, it can be used to approximate eigenvalues, which arise in stability analyses of models with more than one variable (see Chapter 8). It can also be used to determine approximate solutions to a differential equation (Simmonds and Mann 1988). Perturbation analyses do occasionally fail, however. For example, the equations that you must solve to obtain the terms $\hat{n}_0$, $\hat{n}_1$, etc., might themselves be too complex to solve. But the technique is powerful because it allows you to state from the outset what you assume about the magnitude of the various parameters and to use this additional information to understand a model's behavior. Sup. Mat. 5.1 discusses problems that can arise when performing a perturbation analysis and how to circumvent some of these.

5.4.2 Stability when the Equilibrium Is Known by Approximation

If we only know the approximate value of an equilibrium, can we determine whether it is stable or unstable? Fortunately, the answer is yes. The underlying conceptual approach is identical to the stability analysis of an equilibrium that we know exactly (Recipe 5.3), except that we cannot evaluate $\lambda = (\mathrm{d}f/\mathrm{d}n)|_{n=\hat{n}}$ (for a discrete-time model) or $r = (\mathrm{d}f/\mathrm{d}n)|_{n=\hat{n}}$ (for a continuous-time model) exactly at the equilibrium. We can, however,

approximate λ or r using a Taylor series in the small parameter. In this section, we describe the method for a discrete-time model; continuous-time models are handled analogously.

Let's suppose, as in Box 5.1 and Recipe 5.4, that the exact equilibrium can be written as a series of terms involving some small parameter ζ, as $\hat{n} = \hat{n}_0 + \hat{n}_1\zeta + \hat{n}_2\zeta^2 + \hat{n}_3\zeta^3 + \cdots$. If the system begins slightly away from the equilibrium of interest (i.e., the variable is displaced slightly from $\hat{n}$), we would normally predict changes in the displacement over time using equation (5.14). We continue to do so, but now we substitute the series expression for the equilibrium in $\lambda = (df/dn)|_{n=\hat{n}_0+\hat{n}_1\zeta+\hat{n}_2\zeta^2+\cdots}$ rather than the exact (and unknown) value $\hat{n}$. Because λ now depends on the small parameter ζ, we write it as $\lambda(\zeta)$ to emphasize this fact.

This expression for $\lambda(\zeta)$ is exact provided that we include an infinite number of terms in the series expression for the equilibrium; of course, in practice, we cannot do this. Therefore, the key to the approach is to approximate $\lambda(\zeta)$ using a Taylor series in the small parameter ζ around the point $\zeta = 0$. This gives

$$\lambda(\zeta) = \lambda(0) + \left(\frac{d\lambda}{d\zeta}\bigg|_{\zeta=0}\right)\zeta + \frac{1}{2!}\left(\frac{d^2\lambda}{d\zeta^2}\bigg|_{\zeta=0}\right)\zeta^2 + \frac{1}{3!}\left(\frac{d^3\lambda}{d\zeta^3}\bigg|_{\zeta=0}\right)\zeta^3 + \cdots. \quad (5.33)$$

Equation (5.33) depends on the terms in our approximation, $\hat{n}_i$, but we need only know the values of $\hat{n}_i$ up to the order of the approximation desired in equation (5.33). For example, if we want a first-order approximation (i.e., terms up to and including ζ in equation (5.33)) then we typically need only $\hat{n}_0$ and $\hat{n}_1$. On the other hand, if we want a second-order approximation (i.e., terms up to and including ζ^2 in equation (5.33)) then we typically will need $\hat{n}_2$ as well.

Equation (5.33) provides an important qualitative insight. If the magnitude of $\lambda(0)$ is not near one, then the stability properties of an equilibrium will not change when the parameter that is considered small is added to a model. The only time that the higher-order terms in (5.33) can cause a change in the stability of an equilibrium is when the magnitude of $\lambda(0)$ is close enough to one that a small term proportional to ζ can tip the balance between stability and instability. (Technically, this assumes that the derivatives of $\lambda(\zeta)$ are never infinite and that the Taylor series converges, at least for values of ζ near 0 (see Primer 1), although these issues rarely arise.)

As an example, let us return to the diploid model of natural selection. In the absence of mutation, we found that the stability of the equilibrium, $\hat{p} = 1$, is determined by $\lambda = W_{Aa}/W_{AA}$. Let us assume that directional selection favors the A allele and write the fitnesses as $W_{AA} = 1$, $W_{Aa} = (1 - hs)$, and $W_{aa} = (1 - s)$. In this case, $\lambda = (1 - hs)$, which is less than one by assumption, so the equilibrium is stable. We also showed that if we add a small rate of mutation to the model, the equilibrium allele frequency becomes approximately $\hat{p} \approx 1 - \mu/(hs)$ (equation (5.32)). If we perform a stability analysis of this equilibrium using equation (5.33) with $\mu = \tilde{\mu}\,\zeta$ and $\nu = \tilde{\nu}\,\zeta$, we get $\lambda(\zeta) = \lambda(0) + d\lambda(\zeta)/d\zeta|_{\zeta = 0} + \cdots$, where the terms involving the mutation rate are so small that stability is still governed by $\lambda(0) = (1 - hs)$ unless hs is also very small. In short, the presence of a small rate of mutation does not alter the fact that an equilibrium near fixation on allele A is stable when selection favors this allele.

This is an extremely useful fact: if you know the stability of an equilibrium from one model, then you will know the stability of nearby equilibria from a variety of similar models whose recursions represent slight perturbations to the original recursions. Only when the original equilibrium lies on the boundary between stability and instability will smaller-order terms in the perturbations affect stability (for more details, see Karlin and McGregor 1972a, b).

5.5 Concluding Message

In this chapter we presented techniques that allow you to identify the equilibria of a model (summarized in Recipe 5.1) and to assess whether these equilibria are stable or unstable to small changes in the variable (summarized in Recipe 5.3). These techniques are immensely powerful and allow you to answer a broad variety of questions. For example, you can use the methods for finding equilibria to determine the long-term impact of harvesting on the size of a population (Problem 5.9). You can perform a stability analysis to determine whether a genetically modified organism is likely to spread within a population (Muir and Howard 1999, 2001). Or you can determine when migration will prevent adaptation of a population to its local environment by swamping the effects of natural selection (Problem 5.10).

We also introduced an extremely powerful technique, known as a perturbation analysis, which allows you to obtain approximate solutions to

equations that cannot be solved exactly. This technique can, for example, allow you to identify equilibria approximately, even for complicated models whose equilibrium condition cannot be solved (summarized in Recipe 5.4).

The methods described in this chapter for finding equilibria and determining their stability, while valuable, have two main limitations. The first is that they only describe the behavior of a model at or near equilibria. In the next chapter, we describe methods for finding general solutions to models involving one variable. When successful, these methods can be used to determine the global behavior of a model. The second is that the methods of this chapter have been limited to models involving a single variable. To take full advantage of these techniques, we must describe how the methods for finding equilibria and determining stability can be extended to models with more than one variable. Chapters 7 and 8 are devoted to this task.

Problems

Problem 5.1: The logistic equation (3.5a) assumes that the number of surviving offspring per parent declines linearly with population size. Ecologists have considered many other forms of density dependence (Henle et al. 2004; May et al. 1974). Find the equilibria of the following density-dependent models of population size:

(a) $$n(t+1) = \lambda\, n(t)\left(1 - \left(\frac{n(t)}{K}\right)^{\theta}\right)$$ (θ-logistic model).

(b) $$n(t+1) = \lambda\, n(t)\, e^{-\alpha n(t)}$$ (Ricker model).

(c) $$n(t+1) = \lambda\, n(t)\frac{1}{1+\alpha n(t)}$$ (Beverton-Holt model).

(d) $$n(t+1) = \lambda\, n(t)\frac{1}{(1+\alpha n(t))^{\theta}}$$ (Hassell model).

(e) $$n(t+1) = \lambda\, n(t)\frac{1}{1+\alpha\, n(t)^{\theta}}$$ (Maynard-Smith and Slatkin model).

Problem 5.2: Use the recursion equation (3.13a) for the diploid model of natural selection,

$$p(t+1) = \frac{p(t)^2 W_{AA} + p(t)q(t)W_{Aa}}{p(t)^2 W_{AA} + 2p(t)q(t)W_{Aa} + q(t)^2 W_{aa}}$$

to prove that if the fitnesses are equal to one another ($W_{AA} = W_{Aa} = W_{aa}$), then the allele frequency remains constant, regardless of its initial value. This represents a special case of the parameters.

Problem 5.3: In the haploid model of selection considered in the text, it was assumed that the fitnesses W_A and W_a were constants. In many examples of biological interest, however, the success of each type might depend on the frequency of the other type, a phenomenon known as "frequency-dependent selection." For example, allele A might produce a toxin that reduces the fitness of individuals carrying allele a, or individuals carrying allele A might produce a compound that can be consumed by a individuals. (a) Find the equilibria of the haploid model if $W_A = 1 + \alpha q$ and $W_a = 1 + \beta p$. (b) Specify when the equilibria in (a) will be biologically valid. (c) Show that you cannot obtain explicit solutions for all of the equilibria if the fitness of A decreases exponentially with the frequency of a using $W_A = e^{-\alpha q}$ and $W_a = 1 + \beta p$.

Problem 5.4: DNA replication is not entirely error-free, causing mutations to occur within a population. Here, we incorporate mutations into the haploid model of selection. Assuming that individuals carrying allele A are most fit, define fitnesses of A and a as $W_A = 1$ and $W_a = 1 - s$. Mutation causes a proportion μ of the haploid offspring produced by an A individual to become a. Mutations from a to A are ignored (such mutations will be extremely infrequent whenever the less fit allele a is rare). Under these assumptions, the frequency of the A allele among offspring will equal $p(t+1) = (1-\mu)p'$, where p' is the frequency of A after selection given by equation (3.8c):

$$p' = \frac{W_A p(t)}{W_A p(t) + W_a(1 - p(t))}.$$

(a) Determine the two equilibria for p. (b) When are these equilibria biologically valid? (c) At the polymorphic equilibrium, show that the mean fitness of the population is $\overline{W} = W_A\hat{p} + W_a(1 - \hat{p}) = 1 - \mu$, which does not depend on the strength of selection. Mutations that are more strongly selected against are less frequent at equilibrium, and these effects exactly balance, causing the selection coefficient to cancel out of $\overline{W}$. (d) Determine the stability of the equilibrium when the A allele is absent. (e) Determine the stability of the equilibrium when the a allele is absent. (f) Discuss the conditions under which each equilibrium will be locally stable. Is it possible for both equilibria to be locally stable simultaneously?

Problem 5.5: When deleterious mutations are perfectly recessive ($W_{AA} = 1$, $W_{Aa} = 1$, $W_{aa} = 1 - s$) and back mutations are absent ($\nu = 0$), the diploid model of natural selection with mutations given by equations (5.31) becomes

$$p(t+1) = (1-\mu)\frac{p(t)^2 + p(t)(1 - p(t))}{p(t)^2 + 2p(t)(1 - p(t)) + (1 - p(t))^2(1 - s)}.$$

In this example, the equilibrium can be solved exactly. (a) Solve for the three equilibria of this model. (b) Specify which equilibria are biologically valid under the assumption that s is positive.

Problem 5.6: Perform a local stability analysis of the haploid model of natural selection in discrete time, using the recursion equation (3.8c)

$$p(t+1) = \frac{W_A p(t)}{W_A p(t) + W_a(1 - p(t))}.$$

(a) Determine the conditions under which the equilibrium $\hat{p} = 0$ is stable. (b) Determine the conditions under which the equilibrium $\hat{p} = 1$ is stable. Check that your results make sense and are consistent with Figure 4.9.

Problem 5.7: If density dependence causes an exponential decline in the growth rate, as in the Ricker model (5.7), we find two equilibria, $\hat{n} = 0$ and $\hat{n} = \ln(1 + r)/\alpha$. We can use the nonzero equilibrium to rewrite the Ricker model in terms of the carrying capacity of the habitat, K, rather than the parameter α, using the definition $\ln(1 + r)/\alpha = K$. (a) Show that the Ricker equation is then equivalent to

$$n(t + 1) = (1 + r)^{1-n(t)/K}\, n(t).$$

(b) Determine the conditions under which the equilibrium $\hat{n} = 0$ is stable. (c) Determine the conditions under which the equilibrium $\hat{n} = K$ is stable. (d) Confirm that if $r < 0$, populations whose initial size is greater than $\hat{n} = K$ will grow over time, which is an undesirable property of density-dependent models that assume a constant carrying capacity regardless of the growth rate.

Problem 5.8: Mating within a population is often not random. In Problem 3.14, recursion equations were developed for a model in which each egg has a chance f of being fertilized by a sperm carrying the same allele and a chance $1 - f$ of being fertilized by a sperm drawn randomly from the gamete pool. To simplify the algebra, assume that the fitnesses are $W_{AA} = 1 - s$, $W_{Aa} = 1$, and $W_{aa} = 1 - t$. After some rearrangement, these recursions become

$$p(t + 1) = \frac{p(t) - s(1 - f)p(t)^2 - sfp(t)}{1 - s(1 - f)p(t)^2 - sfp(t) - t(1 - f)(1 - p(t))^2 - tf(1 - p(t))}.$$

(a) Find the three equilibria of this model. (b) What conditions must hold for the polymorphic equilibrium to be biologically valid? (c) Determine the stability conditions for all three equilibria. (d) Offer a biological explanation for why the stability of each equilibrium now depends on the fitnesses of both the *AA* and *aa* homozygotes. Check your answers against those given in the text for the special case when inbreeding is absent ($f = 0$). (You might wish to use a mathematical software package to carry out these calculations.)

Problem 5.9: Harvesting prevents the population size of a species from attaining its natural carrying capacity. We can add harvesting to the logistic model by assuming that the per capita harvest rate is m per day in a population whose intrinsic growth rate is r per day and whose carrying capacity is K in the absence of harvesting. (a) Derive a differential equation describing the dynamics of the population size. (b) Determine the equilibria for this model. (c) Determine the stability of these equilibria. (d) What condition must hold for the population to persist? (e) What is the maximum allowable harvest rate that ensures that the population size will remain stable at a size greater than 1000, which is considered by some to represent a minimum viable population size?

Problem 5.10: Species living at the edge of their natural range can fail to adapt to local conditions because of the constant inflow of migrants from the center of the range. Consider a haploid model of selection where selection in a marginal patch favors allele a: $W_A = 1 - s$ and $W_a = 1$. Adults migrate into the marginal patch from a more favorable area at rate m. We will assume that these migrants all carry allele A, which is favored in the core habitat (Figure 5.7).

After migration, the frequency of the locally unfit allele A becomes $p(t + 1) = (1-m)p' + m$, where p' is the frequency of allele A in the local population after selection but before migration:

$$p' = \frac{p(t)(1 - s)}{p(t)(1 - s) + (1 - p(t))}$$

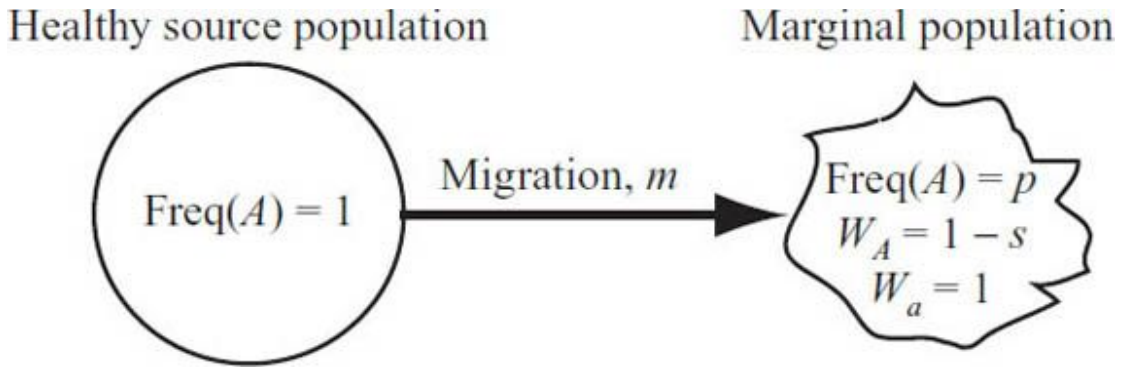

Figure 5.7: Evolution in a source and marginal habitat

(assuming random mating). (a) Find the two equilibria of this model. (b) What conditions must hold for polymorphic equilibrium to be biologically valid? (c) Determine when allele *a* will disappear from the population when rare despite the fact that it is locally favored by examining the stability of the equilibrium at $\hat{p} = 1$.

Problem 5.11: "Memes" are cultural traits, such as inventions (e.g., DVDs) and fads (e.g., wearing hats on backward), whose spread within a population can be modeled. Consider a meme that is adopted slowly, only after an individual sees two other individuals with the meme. A recursion equation for the fraction of the population with the meme *f* might be

$$f(t+1) = f(t)(1-\delta) + \alpha f(t)^2(1-f(t)),$$

where δ represents the loss of the meme and the fraction of individuals that adopt the meme is $\alpha f(t)^2$ per time step (the fact that $f(t)^2$ is squared reflects our assumption that the meme spreads only after witnessing two individuals with the meme). (a) Find the three equilibria of this model. (b) Figure 5.8 illustrates the recursion $f(t+1)$ versus $f(t)$ for $\delta = 0.4$ and $\alpha = 2.0$ along with the diagonal line (dashed) representing where $f(t+1) = f(t)$. Mark each equilibrium with an X. (c) From the slope of the recursion equation at each equilibrium (on the graph), specify which equilibria are stable (S) and which are unstable (U).

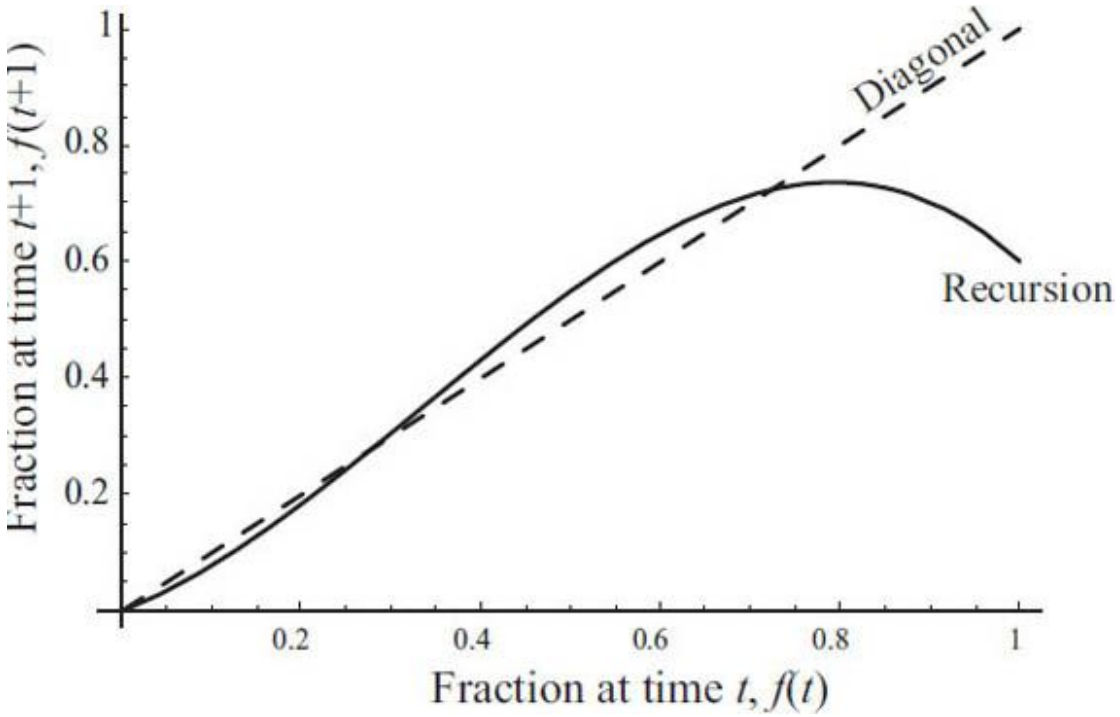

Figure 5.8: Cultural evolution and the dynamics of a "meme."

Problem 5.12: Population size might be regulated by competition for suitable territories. Consider a large number of suitable territories or patches. At time t, a fraction $p(t)$ of these patches are occupied. Of the unoccupied sites, a fraction $mp(t)$ are recolonized from occupied patches. Subsequently, each occupied site suffers a risk of local extinction e through catastrophic events such as fire or disease. These assumptions are consistent with the following discrete-time recursion equation for the fraction of occupied sites:

$$p(t+1) = (1-e)(p(t) + mp(t)(1-p(t))).$$

(a) Find the two equilibria of this model. (b) Under what conditions is there a biologically valid equilibrium with the species present? (c) Given that the equilibrium in (b) is valid, when is it stable? (d) If we assume that m is less than one so that not all patches can be immediately recolonized, can the fraction of occupied sites overshoot the equilibrium?

Problem 5.13: The extinction-recolonization model described in Problem 5.12 can also be studied in continuous time, using the differential equation

$$\frac{dp}{dt} = m\,p\,(1 - p) - e\,p.$$

(a) Find the two equilibria of this model. (b) Under what conditions is there a biologically valid equilibrium with the species present? (c) Given that the equilibrium in (b) is valid, when is it stable? (d) Is it possible for the fraction of occupied sites to overshoot the equilibrium?

Problem 5.14: For the variant of the logistic model with immigration given by the recursion equation (5.9), use a perturbation analysis to find a linear approximation for the equilibrium population size $\hat{n}$ assuming that the population would go extinct in the absence of migration (i.e., $\hat{n}_0 = 0$). Use

this approximation to show that $\hat{n}$ becomes positive when migration is present as long as the growth rate r is negative.

Problem 5.15: For the variant of the logistic model with immigration given by the recursion equation (5.9), find an approximation for the equilibrium population size $\hat{n}$ to second order in the migration rate. In other words, use the equilibrium condition (5.10) and the method described in Box 5.1 and Recipe 5.4 to extend (5.30) to include a term proportional to m^2. Into this second-order approximation, plug in the parameter values $r = 1$, $m = 3$, and $\alpha = \ln(200/97)/100$, to show that this second-order approximation gives an equilibrium population size of $\hat{n}_0 \approx 99.99$, which is very close to the true solution of 100.

Problem 5.16: Find the approximate mutation-selection balance in the diploid model of selection under the assumption that allele *A decreases* fitness. That is, use a perturbation analysis to repeat the derivation of (5.32) under the assumption that $\hat{p}_0 = 0$. Show that your answer depends on the mutation rate ν from allele a to A but not on μ. [Note: Specify the relative fitnesses that you are assuming. You can continue to measure fitness relative to the AA genotype, using $W_{AA} = 1$, $W_{Aa} = 1 - hs$, and $W_{aa} = 1 - s$, although s must be negative for A to decrease fitness. Alternatively, you can redefine the fitnesses.]

Further Reading

For more information on perturbation methods, consult

- Hinch, E. J. 1991. *Perturbation Methods*. Cambridge University Press, Cambridge.
- Simmonds, J. G., and J. E. Mann. 1988. *A First Look at Perturbation Theory*. Dover Publications, Mineola, N.Y.

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