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A Biologist's Guide to Mathematical Modeling in Ecology and Evolution

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CHAPTER 6

General Solutions and Transformations— One-Variable Models

Chapter Goals:

- To describe methods for obtaining general solutions for models with one variable
- To describe transformation methods for simplifying models

Chapter Concepts:

- Transformation
- Affine model
- Brute force iteration
- Separation of variables

6.1 Introduction

In Chapter 5 we focused on finding equilibria of models and determining the local stability properties of these equilibria. In a small fraction of models, it is possible to go beyond identifying equilibria and their stability by finding the *general solution* of the equations:

Definition 6.1: General Solution

A description of the state of the system for all future points in time that depends only on the parameters, the initial state, and the amount of time that has passed.

We have already seen an example of a general solution for a discrete-time recursion equation. The recursion equation $n(t + 1) = Rn(t)$ can be iterated by hand to get the general solution (4.1):

$$n(t) = R^t n(0). \quad (6.1)$$

Any model where the variable is multiplied by the same factor each generation to obtain the value of the variable in the next generation has a general solution of this form. We will describe recipes that can be followed to find the general solution for any linear model with one variable (this chapter) or multiple variables (Chapter 9). Because these recipes exist, there is some hope of finding the general solution for any linear model (although the equations can become so complicated that we might get bogged down along the way). For nonlinear models, however, there may or may not be a general solution, and it is a bit of a black art to be able to massage equations in just the right way to obtain a general solution.

Many of the techniques in this chapter involve *transformations* from the original set of variables to another set of variables. Transformations often simplify the dynamical equations. For example, in some cases, it is possible to “see” how to obtain a general solution only after a transformation is performed. More generally, however, transformations can be used to gain more insight into models and to obtain approximate dynamical equations when an exact general solution cannot be obtained.

A *transformation* rewrites the dynamical equations of a model in terms of a new set of variables, which is chosen to simplify the equations or to provide more biological insight than the original set of variables.

In section 6.2 we describe transformations in a general context. Sections 6.3 and 6.4 then discuss how to obtain general solutions to linear and nonlinear models in discrete time, typically with the help of a transformation. Finally, sections 6.5 and 6.6 do the same for models in continuous time. Throughout, we focus on models with one variable, leaving the corresponding analyses for models with multiple variables until Chapter 9.

6.2 Transformations

As you get more experience analyzing models, you will come to appreciate techniques that simplify the calculations and that help extract useful biological information. One of the most powerful techniques involves transforming the variables of a model. To perform a transformation, we define a new set of variables in terms of the original variables in the model. We then derive “transformed” dynamical equations that describe how these new variables change over time. For example, if we have a differential equation describing the size of a population, N , over time, $dN/dt = f(N)$, we might define a new variable y as $y = \ln(N)$ or perhaps $y = a + bN$. We could then determine how the new variable changes over time by rewriting the differential equation in terms of the new variable. This transformation changes how we keep track of the system (in terms of y rather than N), but it does not alter the underlying process being modeled.

The utility of transformations is that, when chosen well, the equation describing the dynamics of the new variable can be much simpler than the original equation. Given a choice between analyzing a simple equation in terms of y or a complicated equation in terms of N , it makes sense to go the simple route. Not only does this save effort, but it can also be the only way to “see” how to solve a model. Furthermore, transformations often provide insight into why a model behaves the way that it does. And once we have analyzed the simpler transformed equation, we can then transform back to the original variable to understand the dynamics of the original variable.

In fact, we have already introduced several transformations in this book. In Chapter 3, we described a useful transformation in models of selection, going from the number of individuals carrying allele A and allele a to the proportion p carrying allele A (Box 3.1). And in Chapter 5, we described how the stability of an equilibrium can be assessed by performing a transformation from the original variable to a new variable describing the displacement from an equilibrium, $\varepsilon(t) = n(t) - \hat{n}$. We then transformed the recursion equation involving the original variable $n(t)$ into a recursion equation involving the new variable $\varepsilon(t)$. This transformed recursion equation was particularly helpful because we could approximate it with a linear equation (5.14) in $\varepsilon(t)$ under the assumption that the system is near the equilibrium.

This all sounds great, but you are probably asking yourself: how do I choose an appropriate transformation? This is a good question, which, unfortunately, does not have a simple answer. Different transformations work best in different situations. In this chapter, we discuss some methods and transformations that often work for obtaining general solutions. We also discuss clues that you can

use to guide your choice of transformation. Using these clues and being willing to play around trying different transformations increases the likelihood that you will hit upon a useful one.

6.3 Linear Models in Discrete Time

With only one variable in discrete time, there are two types of linear models that we need to solve: those of the form

$$n(t + 1) = Rn(t), \quad (6.2a)$$

and those that also involve a constant,

$$n(t + 1) = Rn(t) + m. \quad (6.2b)$$

Equations of the first form arise when a process or processes act independently on every individual on a per capita basis. For example, each individual might give birth, die, or emigrate out of a population, leading the total number of births, deaths, or emigrants to be proportional to the total number of individuals within the population, $n(t)$. In contrast, equations of the second form, known as *affine* models, arise when there is a constant input or outflow from the system that does not depend on the current state $n(t)$. For example, there might be a constant number of migrants into a population from a source population, as in the toy model of mice migrating in from surrounding fields (equation (2.4) has the same form as (6.2b) with $R = (1 + b)(1 - d)$). Or there might be a constant number of individuals that are harvested from a population per time step, causing m to be negative. Equation (6.2b) could also be used to describe the number of red blood cells in the body on day t , where R is the fraction of red blood cells that are not eliminated by the liver and m is the number of new red blood cells produced by the bone marrow per day. The important point is that in affine models with recursion equations like (6.2b), the variable is replenished or eliminated by a process that is not dependent on the current value of the variable.

An *affine model* depends linearly on the variables and contains a constant term representing any input or outflow to the system.

According to equation (6.2a), every time step that passes causes the previous solution to be multiplied by R , so $n(1) = Rn(0)$, $n(2) = Rn(1) = R^2n(0)$, etc. Consequently, at any future point in time, $n(t) = Rn(t - 1) = \dots = R^t n(0)$, and we get the general solution (6.1). If we try this technique with (6.2b), it also works, but the general solution is not pretty. Equation (6.2b) tells us also that $n(2)$ must be $Rn(1) + m$. Using equation (6.2b) to substitute in for $n(1)$, we get $R(Rn(0) + m) + m = R^2n(0) + Rm + m$. It is not yet clear what is happening as we iterate (6.2b). If we calculate $n(3)$ in the same manner, we get $n(3) = Rn(2) + m = R(R^2n(0) + Rm + m) + m = R^3n(0) + R^2m + Rm + m$. Thus, it appears that the general solution has the form

$$n(t) = R^t n(0) + m \sum_{i=0}^{t-1} R^i. \quad (6.3a)$$

Brute force iteration is a method to solve recursion equations by repeatedly plugging in the recursion equation for the value of the variable in the previous time step.

This method, known as *brute force iteration*, again works in this situation. But this is not always the case; often brute force iteration generates a complicated mess of equations that do not follow any obvious pattern, especially when there is more than one variable.

Life is much simpler if we first transform the affine model (6.2b) into a linear model without constants (6.2a). The transformation that accomplishes this goal defines a new variable $\delta(t)$ as the distance between the original variable $n(t)$ and the equilibrium of the system. Using this transformation, we can solve any affine model:

Recipe 6.1

Solving a Linear Discrete-Time Model with a Constant Term

Affine recursion equations of the form $n(t + 1) = \rho n(t) + c$ can be solved as follows:

Step 1: Solve for the equilibrium $\hat{n}$. Here, $\hat{n} = c/(1 - \rho)$.

Step 2: Define a new variable $\delta(t)$ as the distance of the system from the equilibrium, $\delta(t) = n(t) - \hat{n}$. Reversing this equation implies that $n(t) = \delta(t) + \hat{n}$.

Step 3: The recursion equation for the transformed variable is $\delta(t + 1) = \rho \delta(t)$. To prove this, use the recursion equation for $n(t + 1)$ to write a recursion for $\delta(t + 1)$:

$$\delta(t + 1) = n(t + 1) - \hat{n} = \rho n(t) + c - \hat{n}.$$

Replacing $n(t)$ with $\delta(t) + \hat{n}$ gives $\delta(t + 1) = \rho \delta(t) + \rho \hat{n} + c - \hat{n}$. Plugging in the equilibrium from Step 1 and factoring causes the last three terms to equal zero (try this).

Step 4: The general solution for the distance to the equilibrium is thus $\delta(t) = \rho^t \delta(0)$.

Step 5: The general solution for the original variable is found by using the result from Step 4 in $n(t) = \delta(t) + \hat{n}$, resulting in $n(t) = \rho^t \delta(0) + \hat{n}$. Rewriting $\delta(0)$ in terms of $n(0)$ gives the general solution:

$$\begin{aligned} n(t) &= \rho^t (n(0) - \hat{n}) + \hat{n} \\ &= \rho^t n(0) + (1 - \rho^t) \hat{n}. \end{aligned}$$

As this recipe always works, Steps 2–4 can be skipped, and the above equation can be used after having identified $\hat{n}$ and ρ .

The advantage of a good transformation is that it can reveal an underlying simplicity to the dynamics that might be impossible to see in the original variable. For example, in an affine model, the fact that $\delta(t + 1) = \rho \delta(t)$ tells us that the distance to the equilibrium changes by a factor ρ at every time step. Thus, there is exponential growth away from ($\rho > 1$) or decay toward ($\rho < 1$) the equilibrium. This is not at all apparent when looking at the original equation (6.2b).

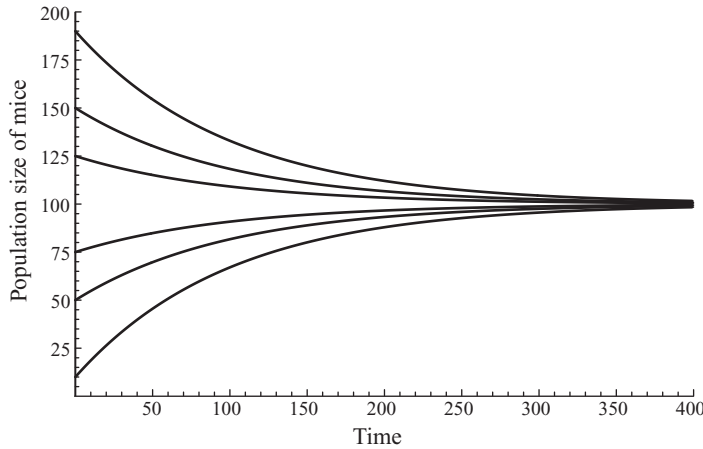


Figure 6.1: The general solution for the model of cats eating mice. The cat-mouse model given by equation (2.4) is equivalent to (6.2b), where $R = (1 + b)(1 - d)$. For $d = 0.1$, $b = 0.1$, and $m = 1$, the predicted equilibrium occurs at $\hat{n} = m/(1 - R) = 100$ and $R = 0.99$. According to the general solution (6.3b), the distance from the equilibrium declines by a factor, $R = 0.99$, at every time step regardless of the initial starting position.

All we have to do to apply Recipe 6.1 is to find $\hat{n}$ and ρ . The equilibrium condition for (6.2b) is $\hat{n} = R\hat{n} + m$, which has one equilibrium at $\hat{n} = m/(1 - R)$. The term ρ represents the factor multiplying the variable, which in this case equals R . Consequently, Recipe 6.1 indicates that the distance from the equilibrium has the general solution $\delta(t) = R^t\delta(0)$, which decays exponentially over time if $R < 1$ and grows exponentially over time if $R > 1$. Plugging $\hat{n}$ and ρ into Step 5 gives the general solution for equation (6.2b):

$$n(t) = R^t n(0) + \left(1 - R^t\right) \frac{m}{1 - R}. \quad (6.3b)$$

The general solution (6.3b) is certainly nicer than (6.3a), which involved a summation, but it is a bit disconcerting that the two solutions for the same model look so different. In fact they aren't different. Using Rule A1.19, the sum $\sum_{i=0}^{t-1} R^i$ equals $(1 - R^t)/(1 - R)$, which we can insert into (6.3a) and rearrange to get (6.3b). Thus, brute force iteration gives the same general solution as using a transformation. The advantage of using a transformation is that the steps are straightforward and the answer is simple without having to evaluate a sum. Even more importantly, the transformation gave us insight into how the model behaves—the system moves closer to or further from the equilibrium by the same factor R at each step (Figure 6.1).

6.4 Nonlinear Models in Discrete Time

Unfortunately, there is no general recipe to follow for solving nonlinear models in discrete time, even when there is only one variable. One look at the extraordinarily complex dynamics of the logistic model (Figure 4.2), and it is no surprise that there isn't a general solution. But even the diploid model of natural selection, which is pretty nicely behaved (Figure 4.7), does not have a general solution. If a model exhibits chaotic dynamics, then you can rest assured that there is no general solution. For most nonlinear models, however, it is hard to tell whether or not a general solution exists. Typically, we must try

a bunch of different transformations to see if any of them dramatically simplify the recursion equation.

The haploid model of selection is a good example where the dynamics can be simplified by using a transformation. As described in Chapters 3 and 5, the recursion equation for this model is

$$p(t + 1) = \frac{W_A p(t)}{W_A p(t) + W_a q(t)}, \quad (6.4)$$

and the equilibria are $\hat{p} = 0$ and 1. Equation (6.4) is a nonlinear function of the allele frequency $p(t)$, and it is not clear that it can be solved. First, we could try brute force iteration, using (6.4) to define $p(t + 2)$ as a function of $p(t + 1)$, plugging in (6.4) for $p(t + 1)$ as a function of $p(t)$, and simplifying to infer how each generation of selection affects the recursion. This method does generate a general solution, but it is cumbersome.

Let us try a transformation instead. You might first consider a transformation that measures the distance to an equilibrium. Well, $p(t)$ already measures the distance to the equilibrium of $\hat{p} = 0$. We could rewrite (6.4) in terms of the distance to the other equilibrium, $\hat{p} = 1$. This distance is measured by $q(t) = 1 - p(t)$, whose recursion equation is

$$q(t + 1) = 1 - \frac{W_A p(t)}{W_A p(t) + W_a q(t)} = \frac{W_a q(t)}{W_A p(t) + W_a q(t)}. \quad (6.5)$$

But equation (6.5) is no simpler than (6.4).

What other transformations might you try? Let us step back a bit and think about the model. It is a symmetrical model in the sense that we could reverse which allele is called A and which allele is called a and get the same recursion. It is a good idea when seeking a transformation to preserve symmetry. That is, transformations like $x(t) = 2p(t) - 3q(t)$ or $x(t) = e^{p(t)} - q(t)$ are unlikely to help because they break the symmetry of the model by weighting the frequency of alleles A and a differently. One possible symmetric transformation is $d(t) = p(t) - q(t)$. Let us see if this transformation simplifies the model:

$$\begin{aligned} d(t + 1) &= p(t + 1) - q(t + 1) \\ &= \frac{W_A p(t)}{W_A p(t) + W_a q(t)} - \frac{W_a q(t)}{W_A p(t) + W_a q(t)} \\ &= \frac{W_A p(t) - W_a q(t)}{W_A p(t) + W_a q(t)}. \end{aligned} \quad (6.6a)$$

This is a mixed-up recursion equation, with the variable d on the left and the variables p and q on the right. To fix this, we can plug $q(t) = 1 - p(t)$ into $d(t)$ to get $d(t) = 2p(t) - 1$, which implies that $p(t) = (d(t) + 1)/2$. Substituting $q(t) = 1 - p(t)$, then $p(t) = (d(t) - 1)/2$, and factoring, gives

$$d(t + 1) = \frac{W_A - W_a + W_A d(t) + W_a d(t)}{W_A + W_a + W_A d(t) - W_a d(t)}. \quad (6.6b)$$

This is even worse than the original recursion equation.

As tempting as it is to give up, let us forge ahead and try one more symmetrical transformation $f(t) = p(t)/q(t)$:

$$\begin{aligned} f(t+1) &= \frac{p(t+1)}{q(t+1)} = \frac{W_A p(t)}{W_a q(t)} \\ &= \frac{W_A}{W_a} f(t). \end{aligned} \quad (6.7)$$

Wow! We now have a simple recursion that has the same form as the exponential growth model (6.2a), with R equal to W_A/W_a . Therefore, we can apply the general solution for the exponential model to this model: $f(t) = (W_A/W_a)^t f(0)$. Once we have the general solution in terms of the transformed variable, we can “back transform” to obtain the general solution in terms of the original variable. Because $q(t)$ equals $1 - p(t)$, $f(t) = p(t)/(1 - p(t))$, which can be rearranged to describe the old variable $p(t)$ in terms of the new variable $f(t)$ as $p(t) = f(t)/(f(t) + 1)$. Therefore,

$$\begin{aligned} p(t) &= \frac{f(t)}{1 + f(t)} = \frac{\left(\frac{W_A}{W_a}\right)^t \frac{p(0)}{q(0)}}{1 + \left(\frac{W_A}{W_a}\right)^t \frac{p(0)}{q(0)}} \\ &= \frac{W_A^t p(0)}{W_A^t p(0) + W_a^t q(0)}, \end{aligned} \quad (6.8)$$

where we have multiplied the top and the bottom by $W_a^t q(0)$ to get the last line. Equation (6.8) is the same general solution that we would have obtained by brute force iteration.

There is an additional advantage gained from having performed this transformation. Equation (6.7) provides insight into the nature of selection in the haploid model of selection. It tells us that selection alters the ratio of one allele frequency to the other by a constant factor equal to the ratio of their fitnesses. Consequently, the ratio of the allele frequencies undergoes exponential growth (when $W_A > W_a$) or decline (when $W_A < W_a$) over time.

The fact that equation (6.7) is so simple also allows us to broaden the scope of the results. For example, so far we have assumed that the fitnesses of the two alleles are constant over time, but what if they vary from generation to generation? Suppose that at time t the fitnesses of alleles A and a are $W_{A,t}$ and $W_{a,t}$, respectively. Equation (6.7) indicates that the ratio of the allele frequencies is multiplied by $W_{A,t}/W_{a,t}$ each generation. Thus, we can iterate (6.7) to obtain the general solution

$$f(t) = \left(\prod_{i=0}^{t-1} \frac{W_{A,i}}{W_{a,i}} \right) f(0) \quad (6.9a)$$

(the Π indicates a product, as described in Appendix 1). From Rule A1.26, we can rewrite the product in (6.9) in terms of the geometric mean of the relative fitnesses over the time span from 0 to $t-1$:

$$f(t) = \left(\text{Geometric mean} \left(\frac{W_A}{W_a} \right) \right)^t f(0)$$

or, equivalently,

$$f(t) = \left(\frac{\text{Geometric mean}(W_A)}{\text{Geometric mean}(W_a)} \right)^t f(0). \quad (6.9b)$$

The geometric mean of t numbers averages a set of numbers like the arithmetic mean, except that we multiply the numbers together and take the t^{th} root of the result (geometric mean $\sqrt[t]{x_1 x_2 \dots x_t}$) rather than add the numbers together and divide the result by t (arithmetic mean $(x_1 + x_2 + \dots + x_t)/t$). If the numbers are non-negative (as with fitnesses), the geometric mean is always less than or equal to the arithmetic mean and is much more sensitive to low values. For example, if fitness is zero in any one generation, then the geometric mean fitness is zero, even if the arithmetic mean fitness is high.

Equation (6.9b) tells us that allele A spreads over time and $f(t)$ increases if the geometric mean fitness of individuals carrying A is greater than the geometric mean fitness of individuals carrying a . Cannings (1971) demonstrated this result in more general terms and pointed out that an allele with less fitness variability over time tends to have a higher geometric mean fitness and is thus selectively favored over alleles with the same arithmetic mean fitness but greater temporal variability in fitness (Problem 6.1).

To find a general solution, it is a good idea to try multiple approaches: brute force iteration, transformations, and/or using a mathematical software package (e.g., using the command “RSolve” in *Mathematica*). The truth of the matter, however, is that most nonlinear recursion equations do not have a general solution. We turn next to differential equations in continuous time, which can be solved for a much broader array of models. One way to obtain a rough general solution for a discrete-time model is to approximate the recursion equation by a differential equation and then use the methods described next. This approximation works well as long as the changes that occur over a time step are small (Box 2.6).

6.5 Linear Models in Continuous Time

As with discrete-time equations, linear differential equations have two forms:

$$\frac{dn}{dt} = rn \quad (6.10a)$$

and an affine form:

$$\frac{dn}{dt} = rn + m. \quad (6.10b)$$

Equation (6.10a) implies that changes in the system arise from processes occurring to each individual independently, causing a constant rate of change per capita (due to births, deaths, emigration, etc.). In contrast, equation (6.10b) also allows an inflow or outflow of individuals (or whatever the variable describes) at a rate that does not depend on the value of the variable. For example,

equation (6.10b) was used by Ho et al. (1995) to model the rate of HIV turnover within the bloodstream (see section 1.3.2). In their model, the number of viruses within the plasma, V , was the variable (in place of n), and viruses were cleared from the bloodstream at a per capita rate c (in place of r). Regardless of the current number of viruses within the plasma, however, infected CD4+ cells produced new viruses at a constant rate P (in place of m).

Both differential equations (6.10a) and (6.10b) can be solved using the method known as a *separation of variables* (Recipe 6.2).

Recipe 6.2

Solving Differential Equations Using a Separation of Variables

Differential equations that can be written as $dn/dt = f(n)g(t)$ can be solved as follows:

Step 1: Rewrite the differential equation as $(1/f(n))dn = g(t)dt$.

Step 2: Take the indefinite integral of both sides $\int (1/f(n))dn = \int g(t)dt$, integrating the left-hand side with respect to the dependent variable n and the right-hand side with respect to the independent variable t . Don't forget to add a constant of integration.

Step 3: Attempt to solve the resulting equation for n .

Step 4: Use an initial condition (e.g., at $t = 0$, there are $n(0)$ individuals) to determine the constant of integration.

A *separation of variables* is a technique for solving differential equations that are some function of the dependent variable multiplied by some other function of the independent variable.

Let us first solve the exponential-growth model (6.10a) using a separation of variables. We begin by writing the differential equation in the form $dn/dt = f(n)g(t)$. We could choose $f(n) = rn$ and $g(t) = 1$ or we could choose $f(n) = n$ and $g(t) = r$; either way we would get the same answer. We arbitrarily make the first choice. The two integrals we have to evaluate are then $\int (1/f(n))dn = \int (1/(rn))dn = (1/r) \ln(n) + c_1$ and $\int g(t)dt = \int 1 dt = t + c_2$. Setting these equal to one another and merging together the constants of integration by defining $c_2 - c_1 = c$, we get $(1/r) \ln(n) = t + c$.

Now we proceed to solve for n by multiplying both sides by r and taking the exponential of both sides, getting $n = e^{r(t+c)} = e^{rt} e^{rc}$. Setting t to zero, indicates that $n(0) = e^{rc}$. Replacing e^{rc} with $n(0)$, we obtain the general solution for the continuous-time model of exponential growth:

$$n = e^{rt} n(0). \quad (6.11)$$

This is the same solution as equation (4.2), which we obtained by educated guesswork.

You might feel uncomfortable (reasonably enough) breaking apart a differential equation in Step 1 of Recipe 6.2 as if dn/dt represented a regular fraction. The best way to ensure that a mathematical shortcut works is to check that the solution satisfies the original equation. In this case, we can take the derivative of the solution $n = e^{rt} n(0)$ with respect to t to get $dn/dt = d(e^{rt} n(0))/dt = r e^{rt} n(0)$.

According to our general solution, $e^{rt}n(0)$ is equivalent to n . Making this replacement correctly gives the differential equation that we were trying to solve: $dn/dt = rn$. Thus, a separation of variables was successful in producing a general solution (6.11) that satisfies the differential equation (6.10a). The general solution to the exponential-growth model is widely used in all aspects of life, including in the calculation of interest by banks (Box 6.1).

It is worth comparing the general solutions for the continuous-time model, $n = e^{rt}n(0)$ and the discrete-time model, $n = R^t n(0)$, of exponential growth. If R were equal to e^r , the two solutions would be identical and would predict the same trajectory for the population size. But if we defined r as the per capita per generation change in population size, then we would set $R = 1 + r$ in the discrete-time model (see Chapter 3). According to the Taylor series (P1.14), $e^r = 1 + r + \frac{1}{2}r^2 + \dots$ is always greater than $(1 + r)$ (Figure 6.2a). Thus, for the same per capita per generation change in population size, populations grow faster in continuous time than in discrete time (Figure 6.2b). Intuitively, this is because every offspring in continuous time can immediately reproduce and add to future growth, whereas offspring must wait until the next time step to reproduce in the discrete-time model.

Equation (6.10b) describing exponential growth with a constant inflow or outflow can be solved directly using the method of separation of variables. We leave this task to Problem 6.4, as it represents the next most complicated problem for you to tackle. Alternatively, we can transform (6.10b) into the form of (6.10a) to obtain a linear differential equation without a constant term, whose solution we have already calculated:

Recipe 6.3

Solving a Linear Continuous-Time Model with a Constant Term

Linear differential equations of the form $dn/dt = \rho n + c$ can be solved as follows:

Step 1: Solve for the equilibrium $\hat{n}$. Here, $\hat{n} = -c/\rho$.

Step 2: Define a new variable δ as the distance of the system from the equilibrium, $\delta = n - \hat{n}$. Reversing this equation implies that $n = \delta + \hat{n}$.

Step 3: The differential equation for δ is the same as the differential equation for n , because $dn/dt = d(\delta + \hat{n})/dt = d\delta/dt = \rho n + c$ given that $\hat{n}$ is a constant. Replacing n with $\delta + \hat{n}$ and factoring leaves a differential equation of the form $d\delta/dt = \rho \delta$, which does not involve a constant term.

Step 4: From equation (6.11), the general solution for the distance to the equilibrium is $\delta(t) = e^{\rho t}\delta(0)$.

Step 5: The general solution for the original variable is found by replacing δ with $n - \hat{n}$, and simplifying to get $n(t) = e^{\rho t}n(0) + (1 - e^{\rho t})\hat{n}$.

Next, we turn to nonlinear models in continuous time.

Box 6.1: Getting the Most for Your Money

The exponential growth model can help you make wiser financial decisions. If, for example, you inherit \$10,000 and decide to invest it in a five-year fixed-term account, you might be offered 4% interest per year from your bank. But how is this interest calculated? At one of our banks (a major Canadian bank), this interest is calculated on an annual basis, meaning that you would have \$10,000 until the very end of the year, at which point \$400 ($0.04 \times \$10,000$) would be added to the account. Other banks (and even other types of accounts at the same bank) calculate interest on a different schedule. If you found a bank that offers a 4% annual interest rate compounded monthly, then your \$10,000 would grow at the end of the first month by \$33.33 ($(0.04/12) \times \$10,000$).

How much would your money be worth at the end of a five-year fixed term at these two banks? To answer this question, we can use the general solution (6.1), $n(t) = R^t n(0)$. Here, the variable $n(t)$ represents the amount of money in your account, the time step represents the period over which interest is calculated (one year for the first bank, one month for the second bank), and R is the factor by which money grows over the time step ($R_{\text{annual}} = 1 + 0.04$ for the first bank, $R_{\text{monthly}} = 1 + (0.04/12)$ for the second bank). After the five-year term, the amount of money you would have in each bank equals

$$(1 + 0.04)^5 \times \$10,000 = \$12,166.53 \quad (4\% \text{ annual interest rate compounded yearly}),$$

$$\left(1 + \frac{0.04}{12}\right)^{12 \times 5} \times \$10,000 = \$12,209.97 \quad (4\% \text{ annual interest rate compounded monthly}).$$

Thus, you would earn \$43.44 more over five years from the second bank. You could earn an extra \$3.92 if you found a bank that compounded interest daily:

$$\left(1 + \frac{0.04}{365}\right)^{365 \times 5} \times \$10,000 = \$12,213.89 \quad (4\% \text{ annual interest rate compounded daily}).$$

As you can see, the more often the interest is compounded, the more the account grows over time. The best that you could do, given a 4% annual interest rate, would be to find a bank that compounds interest continuously. To calculate how much more you would earn, we must use the general solution (6.11) to the continuous-time exponential model, $n = e^{rt} n_0$. Measuring time in years, r represents the annual growth rate (4%), and after five years the amount of money in your account would be

$$e^{0.04 \times 5} \times \$10,000 = \$12,214.03 \quad (4\% \text{ annual interest rate compounded continuously}).$$

You would gain an additional 14 cents if your savings were compounded continuously rather than daily.

The continuous-time formula can also be arrived at directly from the discrete-time compounding formula. In particular, if the interest was compounded a total of k times during the year, then after 5 years your account would contain

$$\left(1 + \frac{0.04}{k}\right)^{k \times 5} \times \$10,000 \quad (4\% \text{ annual interest rate compounded } k \text{ times/year}).$$

(continued)

Box 6.1 (continued)

As k gets larger and larger (i.e., as the compounding becomes more and more frequent), this quantity gets closer and closer to $e^{0.04 \times 5} \times \$10,000$. Indeed, in the limit as k goes to infinity, $\lim_{k \rightarrow \infty} (1 + x/k)^k = e^x$ (see Box 7.4).

These calculations demonstrate that, if all else is equal, you should choose a bank that compounds your savings as often as possible. The converse argument holds for loans, however. You should choose a bank that compounds your loans as infrequently as possible. The same Canadian bank that calculates interest on an annual basis for investments calculates interest for outstanding Visa bills on a daily basis! By compounding investment accounts on an annual basis, but calculating loans on a daily basis, the bank earns a substantial amount of money.

Often, banks offer different interest rates. These are difficult to compare when the interest rates are compounded differently. The general solutions to the exponential growth model can help choose the bank whose rate is truly in your best interest. For example, if one bank offers a mortgage loan with an interest rate of 4.75% compounded monthly, would this be better or worse than a mortgage loan with an interest rate of 4.8% compounded annually? By compounding monthly, the total amount by which the 4.75% loan would grow over the course of the year would be $R_{\text{annual}} = (1 + 0.0475/12)^{12} = 1.04855$, i.e., a 4.855% increase, which means that you would owe more money over the course of a year than had you taken out the loan at 4.8% compounded annually. The difference seems pretty trivial, but home mortgages typically involve a lot of money paid back over a long period of time. To get the best interest rate possible, ask your banker to translate their offered rate of interest to the “effective interest rate” (EIR), giving the total factor by which your account or mortgage would grow over a year if you did not withdraw or deposit funds.

6.6 Nonlinear Models in Continuous Time

Most differential equations arising in biology are nonlinear functions of the variable of interest. Fortunately, these can still be solved using a separation of variables, as long as they can be written in the form $dn/dt = f(n)g(t)$. Many models in biology have this form because changes to the system are assumed to depend only on the current composition of the system and not on the exact time, so that $g(t) = 1$ and $dn/dt = f(n)$. For such models, Recipe 6.2 can be applied.

We have already seen two examples of differential equations of the appropriate form, the logistic model

$$\frac{dn}{dt} = r n \left(1 - \frac{n}{K} \right) \quad (6.12)$$

and the haploid model of selection

$$\frac{dp}{dt} = s p (1 - p). \quad (6.13)$$

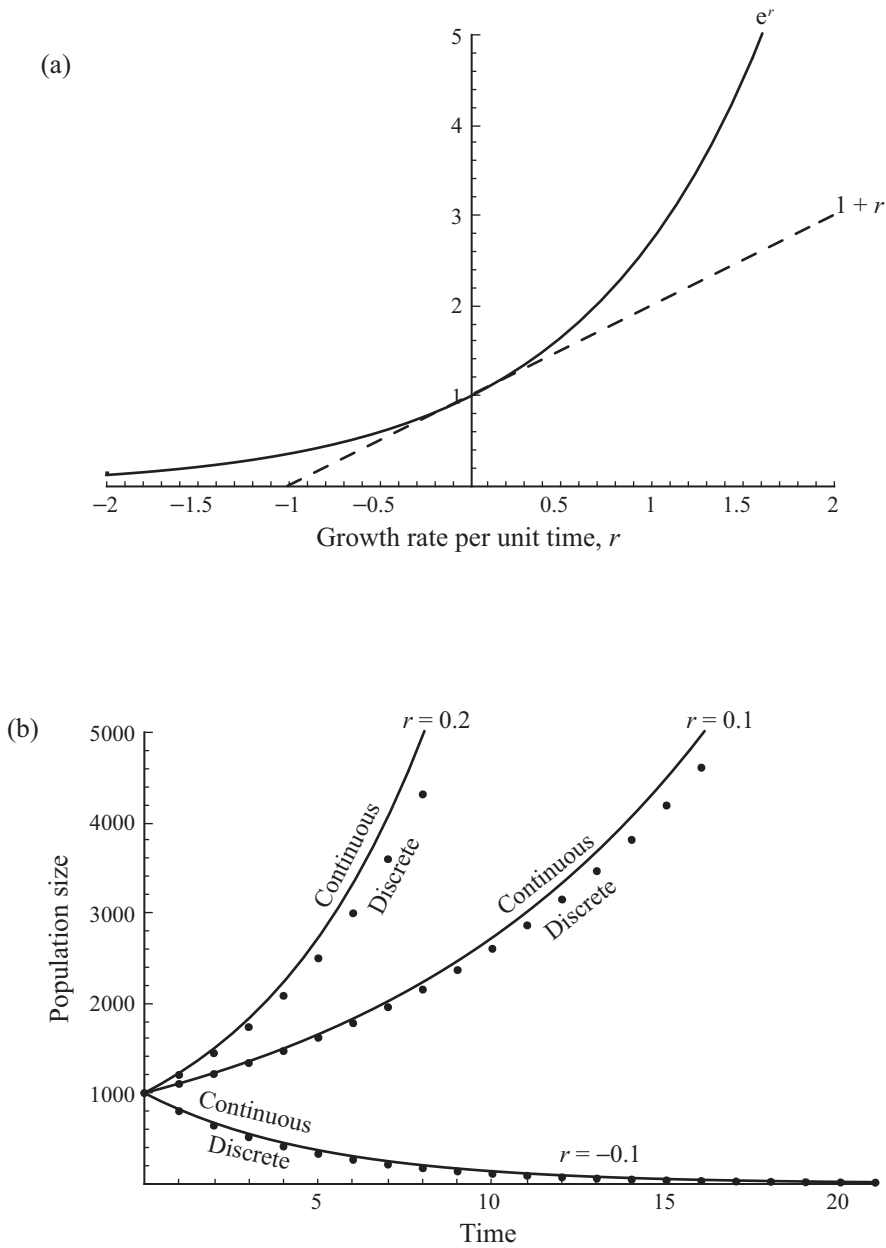


Figure 6.2: A comparison of exponential growth in discrete and continuous time. (a) e^r is larger than $1 + r$ for any value of the growth rate, r . (b) Consequently, the population size is predicted to be larger in the continuous-time model of exponential growth, $n = e^{rt} n(0)$ (solid), than in the discrete-time model, $n = (1 + r)^t n(0)$ (dots), given the same value of r .

These models seem different, but in fact they are closely related. Take a close look at equations (6.12) and (6.13). The model of selection on haploids represents a special case of logistic growth with $n = p$, $K = 1$, and $r = s$. This realization makes our life easier because if we solve (6.12) then we have solved (6.13) as well.

So let us apply Recipe 6.2 to the logistic model. First, we define $f(n) = rn(1 - n/K)$ and $g(t) = 1$. The integrals we have to evaluate are then

$$\int \frac{1}{f(n)} dn = \int \frac{1}{rn\left(1 - \frac{n}{K}\right)} dn$$

and $\int g(t) dt = \int 1 dt = t + c_3$. The first integral is a bit complicated, but it can be solved in a number of ways, including consulting tables of integrals (e.g., Appendix 1; Rule A2.22) or using software packages like Maple or *Mathematica*.

We will solve this integral, however, using partial fractions. Whenever you have a fraction like

$$\frac{1}{rn\left(1 - \frac{n}{K}\right)},$$

involving the product of two linear functions in the denominator (here, rn and $1 - n/K$), we can always break the fraction into two pieces using Rule A1.9. In this example,

$$\frac{1}{rn\left(1 - \frac{n}{K}\right)} = \frac{1}{rn} + \frac{\frac{1}{rK}}{\left(1 - \frac{n}{K}\right)}$$

These two terms can be integrated separately. We've already calculated

$$\int \frac{1}{rn} dn = \frac{1}{r} \ln(n) + c_1$$

for the exponential-growth model. The second term integrates to

$$\frac{1}{rK} \int \frac{1}{\left(1 - \frac{n}{K}\right)} dn = -\frac{1}{r} \ln\left(1 - \frac{n}{K}\right) + c_2.$$

Adding these terms together, setting them equal to $\int g(t) dt = \int 1 dt = t + c_3$, and merging the constants of integration leaves us with

$$\frac{1}{r} \ln(n) - \frac{1}{r} \ln\left(1 - \frac{n}{K}\right) = t + c.$$

We next proceed to Step 3: solving this equation for the population size. Multiplying both sides by r and using Rule A1.14 to gather together the logarithmic terms leaves us with $\ln(n/(1 - n/K)) = rt + rc$. Taking the exponential of both sides gives $n/(1 - n/K) = e^{rt+rc} = e^{rt}e^{rc}$. This result is the same as the exponential-growth model except for the term in the denominator on the left, $1 - n/K$. This term measures the proportional distance to the carrying capacity (for example, if $n = K/3$, then the population is $2/3$ away from the carrying capacity). Thus, this result suggests that the population size grows exponentially when measured relative to the distance of the population from the carrying capacity. Solving this equation for n (Recipe 5.2) gives us the solution to the continuous-time logistic model:

$$n(t) = \frac{e^{rt}e^{rc}}{1 + e^{rt}e^{rc}/K} \quad (6.14a)$$

To solve for c , we could use either equation (6.14a) or the previous equation $n/(1 - n/K) = e^{rt}e^{rc}$, but the latter is easier because c appears only once. Setting $t = 0$, we find that $n_0/(1 - n_0/K) = e^{rc}$. Making this replacement for e^{rc} in equation (6.14a), we get the general solution for the population size:

$$\begin{aligned} n(t) &= \frac{e^{rt}\left(\frac{n_0}{1 - n_0/K}\right)}{1 + \frac{e^{rt}}{K}\left(\frac{n_0}{1 - n_0/K}\right)} \\ &= \frac{e^{rt}n_0}{1 - \frac{n_0}{K} + \frac{e^{rt}n_0}{K}}. \end{aligned} \quad (6.14b)$$

To simplify the fractions, we have multiplied the top and bottom by $1 - n_0/K$ in the last line.

Again, it is a good idea to check the general solution for n by taking its derivative and making sure that we can rewrite it as (6.12). We can also compare equation (6.14b) to numerical solutions of the differential equation (see the on-line Lab exercise on solving differential equations; Figure 6.3). Both checks confirm that (6.14b) satisfies the differential equation for the logistic model.

Now let us take advantage of the fact that the haploid model of selection is a special case of the logistic model with $n = p$, $K = 1$, and $r = s$ to solve this model too:

$$p(t) = \frac{e^{st}p_0}{1 - p_0 + e^{st}p_0}. \quad (6.15a)$$

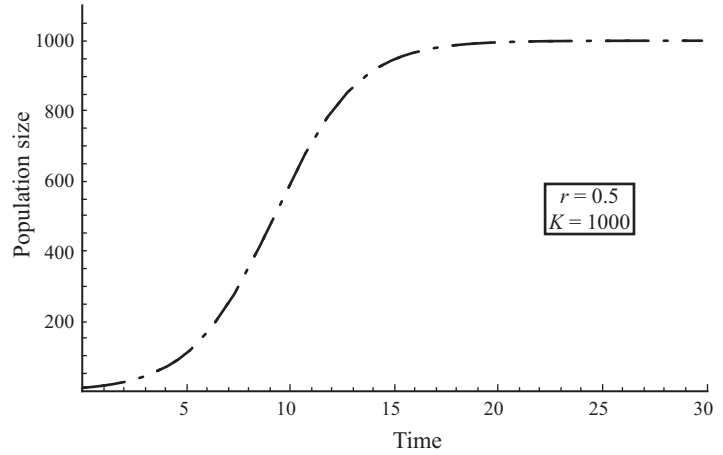


Figure 6.3: The general solution and a numerical solution of the logistic model in continuous-time. NDSolve was used in *Mathematica* to provide a numerical solution to the differential equation (6.12) (long-dashed curve). This is compared to the analytical solution (6.14b) (short-dashed curve). The two curves match precisely.

Recalling that the selection coefficient s describes the difference in growth rates between the two alleles, $r_A - r_a$ (Box 3.1), equation (6.15a) can be written as

$$p(t) = \frac{e^{(r_A - r_a)t} p_0}{(1 - p_0) + e^{(r_A - r_a)t} p_0}. \quad (6.15b)$$

Multiplying the top and bottom by $e^{r_a t}$,

$$p(t) = \frac{e^{r_A t} p_0}{e^{r_a t}(1 - p_0) + e^{r_A t} p_0}. \quad (6.15c)$$

Equation (6.15c) is analogous to the discrete-time model (6.8), but with e_j^r replacing W_j .

At this point, it might seem puzzling that the haploid model of selection is a special case of the logistic model in continuous time but that the haploid model and logistic model behave so differently in discrete time. Unlike the continuous-time model, there is no choice of parameters that converts the logistic model in discrete time into the haploid model of selection (compare equations (3.5b) and (3.9)). Furthermore, while there is a general solution (6.8) describing the haploid model at any future point in discrete time, there is no general solution for the logistic model in discrete time. The oscillations and chaos exhibited by the logistic model cannot be described by any simple function of time. The underlying reason why the haploid model and logistic model behave so differently in discrete time is that their nonlinearity arises in different ways. In the haploid model of selection, the nonlinearity arises because the allele frequencies are normalized to sum to one. Because each allele frequency is positive, the normalizing factor (the mean fitness) is positive, and the allele frequencies remain positive after normalization (see equation (6.4)). Because no allele frequency can ever become negative, the allele frequencies cannot overshoot either equilibrium, $\hat{p} = 0$ or $\hat{p} = 1$. In contrast, the logistic recursion

equation is nonlinear because the number of surviving offspring per parent is assumed to depend on the population size. There is no normalization procedure in the logistic model, and the population size is free to rise above and fall below the carrying capacity. It is because the equilibrium can be overshoot in the logistic model that chaos is possible.

We have described how a separation of variables can be used to solve differential equations of the form $dn/dt = f(n)g(t)$. Even for such differential equations, however, a separation of variables is not guaranteed to yield a solution. The integrals in Step 2 of Recipe (6.2) might be impossible to evaluate. Even when the integrations can be performed, they can yield an equation for the variable n that cannot be explicitly solved (e.g., in the diploid model of natural selection; see Problem 6.7). On the other hand, just because a differential equation cannot be written in the form $dn/dt = f(n)g(t)$ does not mean that it cannot be solved. Indeed, entire books are devoted to methods for solving various types of differential equations (see further reading). In Box 6.2, we provide the solutions to other forms of differential equations that are commonly encountered in biological models (see Problems 6.9–6.12).

6.7 Concluding Message

In this chapter we have discussed the utility of transformations as well as how to obtain general solutions to some models with one variable. A general solution predicts the state of a system at any future point in time, as a function of the initial state of the system, the parameters, and the amount of time that has passed. Thus, a general solution describes the behavior of a model in one formula and can be used to answer any question about the model. For example, the long-term behavior of a system can be determined by allowing time to increase to infinity in the general solution. Also, the form of the general solution often provides insight into the fundamental manner by which a biological system changes. In the haploid model of selection, for instance, we learned that each generation of selection alters the ratio of allele frequencies by a factor equal to the ratio of their fitnesses.

For models involving a single variable, we have discussed several methods for obtaining a general solution. For a linear model, there is always a general solution, whether the model involves a constant input or output term (an *affine* model) or not (Recipe 6.1 and 6.3; equations (6.1) and (6.11)). The picture is not so rosy for nonlinear models. Except for a small subset of models in continuous time (see, for example, Box 6.2), there is no recipe to follow that is guaranteed to yield a general solution. Various techniques, from brute force iteration to transformations, must be tried in the hopes of hitting upon a general solution. As a rough guiding principle, general solutions are most likely to exist for models with only one stable equilibrium, but even such models cannot always be solved (e.g., the logistic model in discrete time). When a general solution is elusive, plotting numerical solutions (Chapter 4) alongside a stability analysis (Chapter 5) can be used to obtain as comprehensive a picture as possible.

Box 6.2: Some Additional Methods for Solving Differential Equations

Many methods exist to solve differential equations (see further reading). In this box, we summarize some useful techniques that help solve differential equations that are commonly encountered in biological models.

Linear differential equations have the form

$$\frac{dn}{dt} = f(t)n + g(t). \quad (6.2.1)$$

The solution to a linear differential equation is

$$n = e^{\mu(t)} \left(\int e^{-\mu(t)} g(t) dt + c \right), \quad (6.2.2)$$

Where $\mu(t) = \int f(t)dt$. This equation and its solution apply, for example, to a population that experiences immigration or harvesting at a variable rate over time, $g(t)$ (independent of the current population size) and that undergoes exponential growth or decline at a variable rate $f(t)$ (see Problems 6.9 and 6.13).

Homogeneous differential equations have the form

$$\frac{dn}{dt} = F\left(\frac{n}{t}\right), \quad (6.2.3)$$

where F is any function that depends only on the ratio n/t and not on n or t independently. Homogeneous equations can be solved by defining a new variable $v = n/t$. The differential equation for v will then be

$$\frac{dv}{dt} = \frac{d\left(\frac{n}{t}\right)}{dt} = \frac{1}{t} \frac{dn}{dt} - \frac{n}{t^2}.$$

Plugging in the equation for dn/dt and replacing n with $v t$ allows us to simplify this equation to

$$\frac{dv}{dt} = \frac{F(v) - v}{t},$$

which is always separable and can be solved using Recipe 6.2, even if the original differential equation for n was not separable.

Bernoulli differential equations have the form

$$\frac{dn}{dt} = n f(t) + n^a g(t). \quad (6.2.4)$$

(continued)

Box 6.2 (continued)

Bernoulli equations can be solved by defining a new variable $v = n^{1-a}$. The differential equation for v will then be

$$\frac{dv}{dt} = \frac{d(n^{1-a})}{dt} = (1 - a)n^{-a} \frac{dn}{dt}.$$

Plugging in dn/dt for the Bernoulli equation gives

$$\frac{dv}{dt} = (1 - a)(n^{1-a} f(t) + g(t)).$$

By definition, n^{1-a} is v , so a Bernoulli equation can be rewritten as

$$\frac{dv}{dt} = (1 - a)(v f(t) + g(t)). \quad (6.2.5)$$

This is a linear differential equation and has the solution (6.2.2) once f and g are redefined to include the constant term $(1 - a)$ in (6.2.5). The logistic equation (6.12) is a special case of (6.2.4) with $f(t) = r$, $a = 2$, and $g(t) = -r/K$ (Problem 6.10). The power of this method is that it allows us to obtain solutions to a generalized logistic equation in which the intrinsic growth rate r and/or the carrying capacity K vary over time (Problem 6.12).

Problems

Problem 6.1: Consider the haploid model of selection with two alleles A and a , where the fitness of allele A relative to that of allele a alternates from generation to generation between $W_A = 3/2$ and $W_A = 1/2$. (a) Calculate the arithmetic average fitness of the two alleles over a time period from 0 to $t - 1$, which may be even or odd (Rule A1.21). (b) Calculate the geometric average fitness of the two alleles over the same time span (Rule A1.26). (c) Over the long term, which allele will spread?

Problem 6.2: In the presence of mutations, allele frequencies change over time even when selection is absent. Assume that a fraction μ of A alleles is converted to a each generation, while a fraction ν of a alleles is converted to A each generation. The frequency of A is then described by the recursion equation $p(t + 1) = (1 - \mu)p(t) + \nu q(t)$. (a) Determine the equilibrium for this model of mutation (don't forget to rewrite q in terms of p). (b) Determine the general solution for this model using recipe 6.1. (c) How rapidly does the allele frequency approach the equilibrium, assuming that the mutation rates are very low?

Problem 6.3: Here, we expand the exponential growth model to consider the case where the per capita number of surviving offspring, R , declines as an inverse function of the current population size $R = R_1 n(t)^{-b}$, where R_1 represents the number of surviving

offspring when there is only one individual in the population. (a) By brute force iteration, determine the general solution for the resulting recursion equation $n(t+1) = R_1 n(t)^{1-b}$. Simplify your result using Rules A1.1 and A1.19. (b) Check the result from (a) when $b = 1$, by noting that $n(t+1)$ then equals R_1 regardless of the initial population size. (c) Assuming that $0 < b < 1$, let t go to infinity in your general solution and determine the population size toward which the system will head. (You can check this result by finding the equilibrium for the recursion equation.)

Problem 6.4: Messenger RNA levels within the cell reflect the production of new mRNA molecules by transcription of genes and the decay of existing mRNA transcripts. Let m represent the number of new transcripts produced per second and r represent the rate of decay of existing transcripts. The change in the number of mRNA molecules within the cell can then be described by the differential equation (6.10b):

$$\frac{dn}{dt} = -rn + m.$$

(a) Solve for the equilibrium of this differential equation, $\hat{n}$. (b) By blocking the production of new transcripts ($m = 0$), Iyer and Struhl (1997) estimated the half-life of mRNA transcripts for the histidine gene of yeast, *his3*, to be 660 seconds. Use the general solution for the exponential decay model $n(t) = e^{-rt} n(0)$ to estimate r given $m = 0$ and $n = n_0/2$ after 660 seconds. (c) Iyer and Struhl (1997) also determined that the normal number of mRNA transcripts within yeast cells was about 7. Assuming that the normal transcript levels are at equilibrium, use your answers to (a) and (b) to estimate the rate of transcriptional initiation m for *his3*. (d) Solve the differential equation by the method of a separation of variables. Use the initial condition, $n = n_0$ at $t = 0$, to replace the constant of integration. [Show your work.] (e) If the mRNA became degraded by heat such that $n_0 = 0$, how long would it take for the cell to regain approximately half of the normal level of mRNA molecules ($n = \hat{n}/2$)? Does this time depend on the rate of mRNA decay r or the rate of transcription initiation m ? (f) Using your estimates for r and m from (b) and (c), plot the general solution from (d) giving the expected number of mRNA molecules as a function of time (using *Mathematica* or any other method). Check that your answer to (e) is consistent with this plot. [Note that these methods were the very ones used by Iyer and Struhl (1997) to characterize mRNA decay rates and rates of transcriptional initiation.]

Problem 6.5: Habitat degradation can cause the growth rate of a population to decline over time. This can be modeled by modifying the exponential growth model such that r becomes $r_0 - \delta t$, where δ represents the rate of habitat destruction. The size of a population then follows the differential equation

$$\frac{dn}{dt} = (r_0 - \delta t)n.$$

(a) Using the method of a separation of variables, solve for the population size at time t given that the population was at size n_0 at time $t = 0$. (b) Using your answer to (a), determine the predicted extinction time as the time it would take for the

population to decline to a single individual ($n_0 = 1$). [The quadratic formula will give you two solutions for t . Choose the appropriate root and explain your choice.]

Problem 6.6: By differentiating $p(t)$ with respect to time, check that the solution to the model of haploid selection, (6.15a), satisfies the differential equation (6.13).

Problem 6.7: Consider the diploid model of selection in continuous time. As shown in Problem 3.16, the differential equation for the A allele frequency can be written as

$$\frac{dp}{dt} = s p(1 - p)(p + h(1 - 2p)),$$

where $W_{AA} = 1 + s$, $W_{Aa} = 1 + h s$, and $W_{aa} = 1$.

(a) Try solving this differential equation using DSolve in *Mathematica*. (b) The answer to (a) is not pretty and involves an InverseFunction, which is *Mathematica*'s way of saying that it cannot find an explicit solution for p even though it knows a function that p must satisfy. Find this function by performing a separation of variables (use *Mathematica* for help with the integral). (c) Show that this function cannot be simplified even if allele A is recessive ($h = 0$) or dominant ($h = 1$) but that it can be simplified when selection is additive ($h = 1/2$). (d) By comparing the above differential equation to (6.13), infer the general solution for the continuous-time model of diploid selection when selection is additive ($h = 1/2$).

Problem 6.8: Within a population, say of university students, one can model the spread of infectious diseases, like colds, using the flow diagram in Figure 6.4.

The parameter c represents the *per capita* rate at which an infected individual contacts a susceptible individual, a is the probability of transmission of the disease per contact, and σ is the rate at which individuals recover from the disease. In this model, the population is assumed constant over the time frame of interest (e.g., we can treat the number of students as roughly constant over a school year), and individuals who recover from the disease are assumed to be susceptible again. This assumption is reasonable for colds, which are caused by a large number of different viruses. The following differential equations can be used to track the number of susceptible individuals S and infected individuals I over time:

$$\frac{dS}{dt} = -a c S I + \sigma I, \quad (\text{Q6.1a})$$

$$\frac{dI}{dt} = a c S I - \sigma I. \quad (\text{Q6.1b})$$

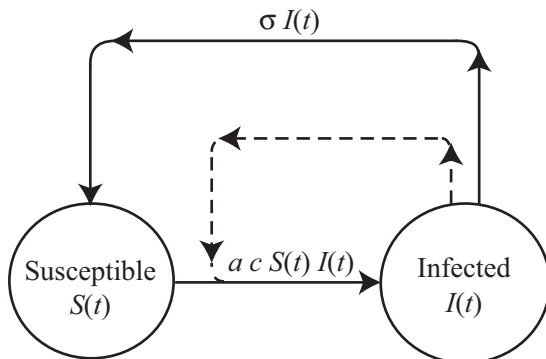


Figure 6.4: Flow diagram for a susceptible-infected model.

(a) Use the quotient rule (see Box 3.1) and the above equations to prove that the proportion of infected individuals, $P = I/(S + I)$, satisfies the differential equation

$$\frac{dP}{dt} = \alpha P(1 - P) - \sigma P \quad (\text{Q6.2})$$

where $\alpha = ac(S + I)$ represents the infectivity of the disease, a , times the total rate of contact among individuals in the population. Because we assume that the total population size $S + I$ remains constant, the differential equation (Q6.2) depends only on the fraction of infected individuals, P . (b) Determine the equilibria for (Q6.2) and determine when each equilibrium is valid given that P represents a proportion. (c) Determine the local stability condition for each equilibrium. Describe in words what these conditions imply. (d) Assuming that the force of infection α is greater than the recovery rate σ and using the information obtained from parts (b) and (c), sketch the shape that the differential equation must have in a plot of dP/dt (vertical axis) versus P (horizontal axis). Use this sketch to determine which equilibrium is globally stable over the range $0 \leq P \leq 1$. (e) Determine the general solution for (Q6.2). [There are multiple ways of doing this, including using a separation of variables. The simplest method is to show how (Q6.2) and the logistic equation (6.12) are related.]

Problem 6.9: Sink populations are defined as populations that are maintained by migration from another source population. Here we consider a sink population with a negative intrinsic growth rate that receives immigrants at rate m per year, which is decreasing over time due to habitat deterioration in migration corridors, $m = m_0 - \delta t$. A differential equation describing this situation is

$$\frac{dn}{dt} = rn + (m_0 - \delta t).$$

(a) Use the solution for a linear model from Box 6.2 to obtain the general solution for this model. (b) Plot the result using the parameters $r = -0.01$, $m_0 = 0.5$, $\delta = 0.02$, and initial population size $n_0 = 40$. (c) Explain why the curve has the shape that it does and specify when you expect the sink population to go extinct.

Problem 6.10: Solve the logistic model in continuous time using the recipe for solving a Bernoulli differential equation, $dn/dt = n f(t) + n^a g(t)$ where $f(t) = r$, $a = 2$, and $g(t) = -r/K$ (see Box 6.2). Check your answer against the solution (6.14b).

Problem 6.11: Solve the haploid model of selection in continuous time, $dp/dt = sp(1 - p)$, under the assumption that the selection coefficient varies sinusoidally with time, $s = s_0 + \sigma \sin(\theta t)$, as might be the case in a seasonal environment. Use the fact that the model is a Bernoulli differential equation with $a = 2$ (Box 6.2) and the fact that $\int e^{f(t)} (df(t)/dt) dt = e^{f(t)} + c$ (see Rule A2.6). Use the initial allele frequency p_0 to solve for the constant of integration, c . Check that your answer is consistent with (6.15a) when $\sigma = 0$. If $s_0 > 0$, what happens as time goes to infinity?

Problem 6.12: By decreasing the density of resources available, habitat degradation could act to reduce the reproductive potential of a species or to increase the amount of territory needed to sustain each individual. Here we alter the logistic model by allowing r or K to decrease over time. (a) Solve the logistic equation in continuous time when $r(t) = r_0(1 - \delta t)$ but $K(t) = K_0$ is constant. (b) Solve the logistic equation

in continuous time when $K(t) = K_0/(1 + \delta t)$ but $r(t) = r_0$ is constant. (c) Plot and compare your solutions starting from $n_0 = 500$ individuals with $r_0 = 1$, $K_0 = 1000$, and $\delta = 0.1$. Use the fact that the logistic equation with time varying parameters, written as $dn/dt = n r(t) - n^2 r(t)/K(t)$, corresponds to a Bernoulli differential equation (Box 6.2). [Hint: Rules A2.23 and A2.29 can help with the integrals. Do not forget to include the constant of integration.]

Problem 6.13: The cat-mouse model discussed in Chapter 2 is described by the differential equation $dn/dt = b n - d n + m$. (a) Solve this differential equation using a separation of variables, assuming that the initial number of mice is n_0 . (b) Solve using the solution to a linear differential equation (6.2.2). (c) Check that these two solutions are consistent with each other.

Problem 6.14: Here we generalize the exponential growth model (6.1) to allow the environment to vary over time, causing the number of surviving individuals per parent, R_t , to depend on time. (a) By brute force iteration, solve the model of exponential growth $n(t + 1) = R_t n(t)$. (b) Rewrite your solution to (a) in terms of the geometric mean value of R_t over the time span from 0 to $t-1$. (c) Based on these calculations, what would you expect to happen over the long term if the environment fluctuated such that $R_t = 1/3$ in every odd time step and $R_t = 2$ in every even time step?

Further Reading

For further information on solving differential equations, consult

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