PRIMER 1
Functions and Approximations

Rarely is it possible to construct and analyze models in biology without making some sort of approximation or simplifying assumption. Typically, we must make compromises, and part of the art of modeling is being able to choose those compromises that are most appropriate. The reasons for this are twofold.

First, it is not always possible, or desirable, to include everything that we know about the details of a biological process in a model. The purpose of modeling is to abstract only the important parts. A crude analogy can be drawn with choosing a scale when constructing a map. If we want to use the map only for planning a driving route across the country, then it is unnecessary, and undesirable, to choose a scale that reveals all of the traffic lights, intersections, and curves in the roads in a precise way. We might not have enough information to do so anyhow. Rather, a coarser-scale map that ignores these details and that depicts the roads in a stylized fashion might be all that is possible or desirable.

Second, when it comes time to analyze a model, we are often forced to make further approximations or simplifications. Sometimes the analysis becomes too messy or difficult for extracting relevant information, and therefore we must approximate the process as best we can. Returning to our analogy, if we wanted to find the shortest route on a map, we might approximate the distance along a road that doesn't curve too much using a straight line. This would make it much easier to compare the driving distances of different alternative routes.

This primer provides a mathematical foundation for making appropriate choices for simplifying and approximating models. In the construction of models, we are often required to describe biological processes in a stylized way, by choosing functions that relate one quantity to another. Section P1.1 presents guidelines for these choices. In the analysis of models we often use straight-line approximations much as in the map analogy above, and section P1.2 presents a straightforward technique for doing so. Section P1.3 is more advanced and presents the Taylor series, a powerful mathematical concept. Taylor series are generalizations of the linear approximations of section P1.2, and they allow us to derive more accurate approximations to a function than is possible using straight lines.

P1.1 Functions and Their Forms

When modeling a biological process, we must necessarily limit ourselves to a certain frame of reference. For example, when we model the growth of a population, we typically ignore biological phenomena at a lower level (e.g., cell

growth and development) and at a higher level (e.g., extinction and specia-tion). Nevertheless, we often link a model to biological phenomena occurring at other levels without explicitly modeling the mechanistic details of these. Rather, we incorporate these other phenomena by describing them with a func-tion that behaves in a way that is consistent with our understanding of these processes or with data. Typically, the function is required to display certain desired qualitative characteristics but is otherwise arbitrary.

The modeling approach where a function is used to describe underlying bio-logical processes is called *phenomenological*. In contrast, the modeling approach where the details at another level are explicitly tracked is called *mechanistic*. In Chapter 3, the logistic model (3 5a) was phenomenological, because we described competition using a linear function, whereas the consumer-resource models (3.16)–(3.18) were more mechanistic in that they explicitly described how predators compete in the consumption of prey. The term "mechanistic" is clearly relative, however, because we still had to choose how the consumers and prey interact in a consumer-resource model (Table 3.3 presents several potential choices).The advantage of a mechanistic model is that it can be used to incorporate all of the details known to influence a biological system, which is especially appropriate if data exist that allow us to choose parameter values describing these details. The advantage of a phenomenological model is that it generally contains fewer variables and parameters and is often easier to analyze and understand, because it is less mired down by details. For a phenomeno-logical model to describe a biological process adequately, however, we must choose a function that behaves in a way that is consistent with our under-standing of the processes or data. But how do we choose an appropriate func-tion? In this section, we describe the shape of some of the most commonly encountered functions used in modeling biological processes, providing exam-ples of how and why they might be chosen.

To motivate this section, let us return to the logistic model of intraspecific competition introduced in Chapter 3. Rather than explicitly modeling the behavioral decisions made by individuals during the consumption of resources, we used a phenomenological description of competition by assuming that the number of surviving offspring per parent can be described by a function $R(n)$ that decreases as the population size increases. Specifically, we used a function that decreases linearly as population size increases. This choice was somewhat arbitrary, however, and Figure P1.1 illustrates other possible functions that still have a maximum reproductive factor of $1 + r$ and a carrying capacity of K (defined as the population size at which the parental population exactly replaces itself, $R(K) = 1$). If we wish to model a species whose reproductive fac-tor is fairly constant until the population size approaches the carrying capacity, after which point the number of surviving individuals per parent plummets, then we might wish $R(n)$ to have a shape like the thick curve in Figure P1.1. Alternatively, we might be modeling a species in which the severity of compe-tition tapers off as the population size increases, as in the dashed curve. But how do we choose functions that behave in these ways? One of the best guid-ing principles is to choose a function that is as simple as possible while still hav-ing the desired shape. In the following, we present several functions that are
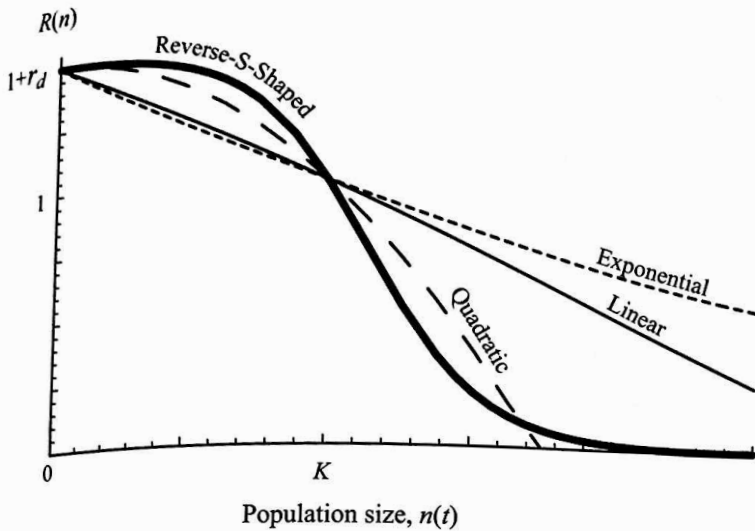
Figure P1.1: Functions describing competition. The number of surviving individuals per parent, $R(n)$, is plotted as a function of population size, $n(t)$. This function can, potentially, take on many different shapes, four of which are shown.

commonly encountered in biological models and that take on a wide variety of different shapes.

If the desired function is a line, the function will have the form

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Definition P1.1:

$$f(x) = \underbrace{b}_{\text{slope}} x + \underbrace{c}_{\text{intercept}} \qquad \text{(linear function)}$$

The slope b determines how much $f(x)$ changes (the "rise") for a given change in x (the "run"; Figure P1.2). The intercept c determines the value of $f(x)$ when $x = 0$; altering c alters the height of the line.

If the desired function curves up or down in the shape of a parabola, it will have the form

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Definition P1.2:

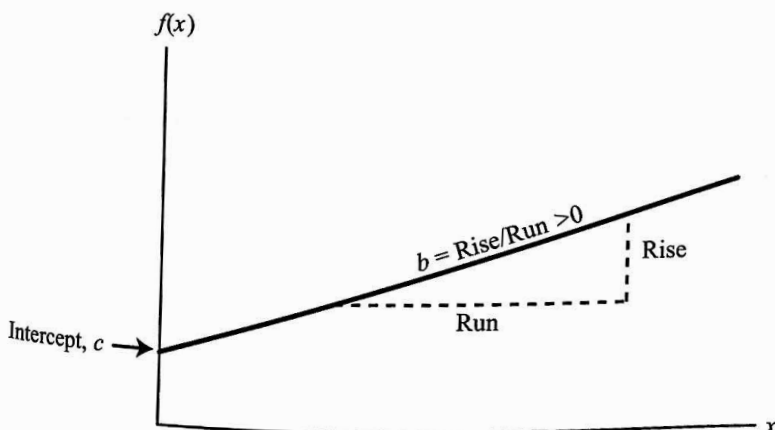$$f(x) = a\,x^2 + b\,x + c \qquad \text{(quadratic function)}$$
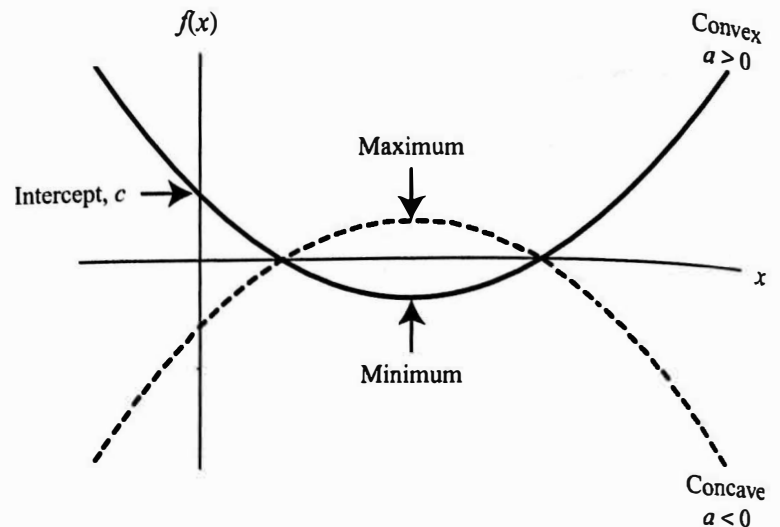

Figure P1.2: Linear functions

Figure P1.3: Quadratic functions

The shape of the quadratic function is largely determined by a. If $a > 0$, the parabola is *convex* (points up; Figure P1.3), if $a < 0$, the parabola is *concave* (points down; Figure P1.3), and if $a = 0$, then the quadratic function reduces to a linear function. The larger is the magnitude of a, the narrower the parabola. The minimum ($a > 0$) or maximum ($a < 0$) of the quadratic occurs at $x = -b/(2a)$, so that the placement of the maximum/minimum can be chosen by setting b. (Show this by finding the value of x that causes $dy/dx = 0$; Appendixes 2 and 4). Again, c is the intercept. Linear and quadratic functions are special cases of polynomial functions, where an nth-degree polynomial is a function of the form

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Definition P1.3:

$$f(x) = \sum_{i=0}^{n} a_i x^i \qquad \text{(polynomial function)}$$

Polynomials typically have $n - 1$ maxima and/or minima, and their behavior as x goes to negative or positive infinity is determined by the sign of the term with the highest power $a_n x^n$.

If the desired function rises or falls exponentially, it will have the form

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Definition P1.4:

$$f(x) = c\, e^{ax} \qquad \text{(exponential function)}$$

The shape of the function is largely determined by a. If $a > 0$, the function rises exponentially (Figure P1.4), while if $a < 0$, the function declines exponentially to zero (Figure P1.4). Again, c is the intercept.
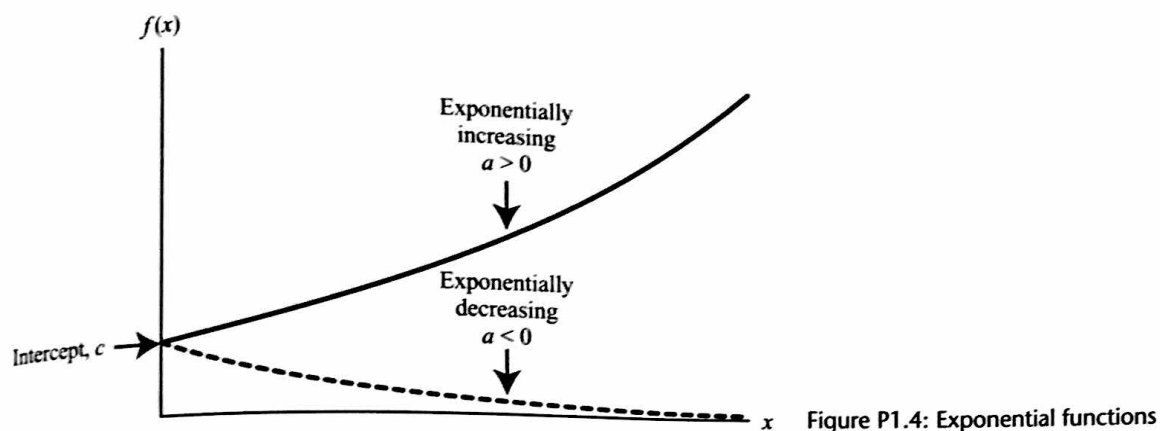
Figure P1.4: Exponential functions

If the desired function is nearly linear for small values of x but reaches a constant value as x becomes large (an "asymptote"), one possible choice is

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Definition P1.5:

$$f(x) = \frac{a\,x + c}{b\,x + d} \qquad \text{(rational function)}$$

This function starts at a height c/d (the intercept) when $x = 0$. It rises or falls linearly, at first, with slope $(a\,d - b\,c)/d^2$ (the value of df/dx when x is zero). As x becomes very large, the term $a\,x$ dominates c in the numerator, and the term $b\,x$ dominates d in the denominator. Consequently, the function eventually reaches an asymptote at $(a\,x)/(b\,x) = a/b$ (Figure P1.5). More generally, a rational function is any polynomial divided by a polynomial.

If the desired function is bell shaped, one possible choice is

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Definition P1.6:

$$f(x) = \max e^{-(x-b)^2/a} \qquad \text{(bell-shaped function)}$$
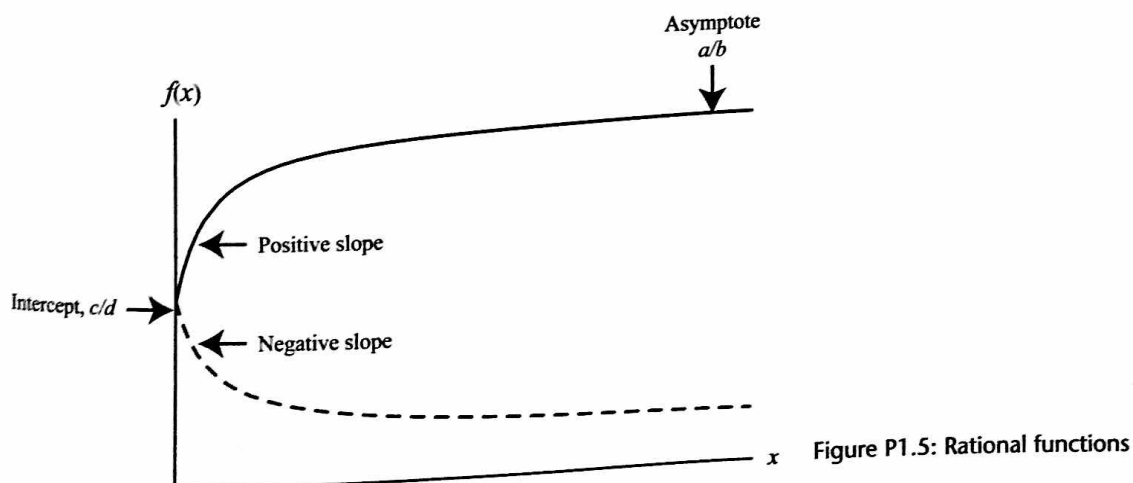
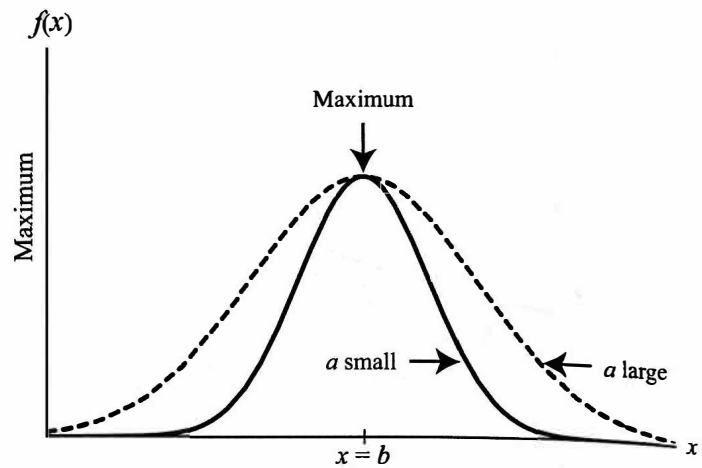---

Figure P1.5: Rational functions

Figure P1.6: Bell-shaped functions

This function has a maximum of $f(x) = \max$ when $x = b$. The shape is determined by a, with larger values of a causing the bell shape to be broader (Figure P1.6). This function is sometimes called "normal," because of its close relationship to the normal distribution in statistics (where $a = 2\sigma^2$ and $\max = 1/\sqrt{2\pi\sigma^2}$; see Definition P3.14a in Primer 3).

If the desired function is S shaped (sigmoidal), one possible choice is

Definition P1.7:

$$f(x) = \frac{c\,e^{ax}}{c\,e^{ax} + (1 - c)} \qquad \text{(S-shaped function)}$$

Here c is a fraction ($0 < c < 1$) that can be thought of as the proportion of the way up the "S" that the function is at $x = 0$. If $a > 0$, the function rises to one (Figure P1.7), while if $a < 0$, it falls to zero (reverse S shape, Figure P1.7). The larger is the magnitude of a, the sharper the S-shaped function. This function is sometimes called "logistic," because of its close relationship to the rise in population size observed in the logistic model of population growth (see Figure 3.4 and equation (6.14b)).
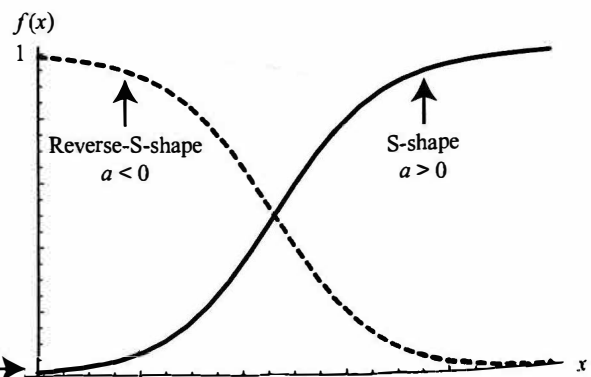

Figure P1.7: S-shaped functions

The above functions are commonly encountered in models of biological phenomena. They can be combined or manipulated to take on a shape that best matches what is understood about the biological process. They can be shifted, stretched, or flipped using Rule P1.1.

Rule P1.1: Changing the Shape of a Function

The following rules can be used to alter a function $f(x)$ to match a desired shape:

- A function can be shifted to the right by an amount d by replacing x with $(x - d)$.
- A function can be shifted to the left by an amount d by replacing x with $(x + d)$.
- The height of a function can be increased by an amount d by replacing $f(x)$ with $f(x) + d$.
- A function can be stretched along the horizontal axis by a factor d by replacing x with x/d.
- A function can be stretched along the vertical axis by a factor d by replacing $f(x)$ with $f(x) \times d$.
- A function can be reflected across the horizontal axis by replacing $f(x)$ with $-f(x)$.

For example, imagine modeling the effect of an inhibitor on the level of phosphorus within a cell. The level of phosphorus might decline exponentially at rate α from an initial level P_{max} as more of the inhibitor is applied, but it might asymptote at some minimum level P_{min} among the cells that remain alive. We could model such a process by modifying the exponential function (Definition P1.4), setting $a = -\alpha$ to reflect the fact that the function is declining at rate α, choosing the intercept such the function has the appropriate range of y values, $c = P_{max} - P_{min}$, and then shifting the height of the function up by P_{min}. Using Rule P1.1, this is accomplished by the function

$$f(x) = (P_{max} - P_{min})e^{-\alpha x} + P_{min}. \qquad (P1.1)$$

Returning to the case of disease transmission, let us identify a contact rate function that rises proportionally with the total population size N but eventually reaches a constant value in very large populations. The rational function (Definition P1.5) has the right shape, where its intercept should be zero ($c = 0$), as no contacts occur when an infected individual is isolated ($N = 0$). This gives us the function

$$f(N) = \frac{aN}{bN + d}. \qquad (P1.2)$$

Equation (P1.2) has the same form as the contact rate function used in Chapter 3 (there we divided the numerator and the denominator by b and redefined a/b and d/b using the parameters c and b, respectively).

Exercise P1.1: Determine functions $R(N)$ for the reproductive factor whose shapes are consistent with Figure P1.1. In each case, choose the parameters such that the intercept is $R(0) = 1 + r$ and the value when $N = K$ is $R(K) = 1$.

(a) A function that declines exponentially to zero.

(b) A quadratic function with a maximum at $N = 0$.

(c) A reverse-S-shaped function that declines from $1 + r$ to zero. Keep a arbitrary (allowing the steepness to vary), and use Rule P1.1 to increase the intercept to $1 + r$.

[Answers to the exercises are provided at the end of the primer.]

When summarizing complicated biological processes at other levels by a function, the hope is that a model and its results will not be very sensitive to the exact form of the function. There are, however, often multiple functions that are compatible with a set of assumptions. We saw this in Figure P1.1, where we described several possible functions to describe competition phenomenologically. Nevertheless, for low intrinsic growth rates (Figure P1.8a), these very distinct functions for $R(n)$ predict very similar population sizes over time (obtained by iterating the recursion equation $n(t + 1) = R(n)\, n(t)$ repeatedly, as we will describe in Chapter 4). It would be difficult to discern from these curves which underlying functions were used to build the model. In this case, we would be justified in not worrying too much about the exact shape of the function describing competition among individuals. This is not always true, however. Indeed, for high intrinsic growth rates, the extent of population growth depends strongly on the underlying function used to describe competition (Figure P1.8b). In this case, we must be very careful in our choice of competition function—basing the function on either a mechanistic model of competition or data. As a general rule, the less sure you are about the function used to represent a biological phenomenon, the more effort you should expend to explore alternative functions to determine the sensitivity of the results to the shape of the function. It is also a good rule of thumb to keep a model as general as possible for as long as possible, e.g., by writing $f(N)$ for the number of offspring per parent. While some analyses will require specifying the form of the function, others might not (see Chapter 12).

P1.2 Linear Approximations

The previous section focused on building functions whose shape matches what is known (or assumed) about a biological process. When analyzing models we are often confronted with a related question: Is it possible to choose a simpler function that approximates a complicated function? To be useful, the approximation must match the shape of the complex function, at least within a region of interest. Sometimes, we will want to approximate a dynamical equation when a variable lies near a particular point (e.g., when the population size
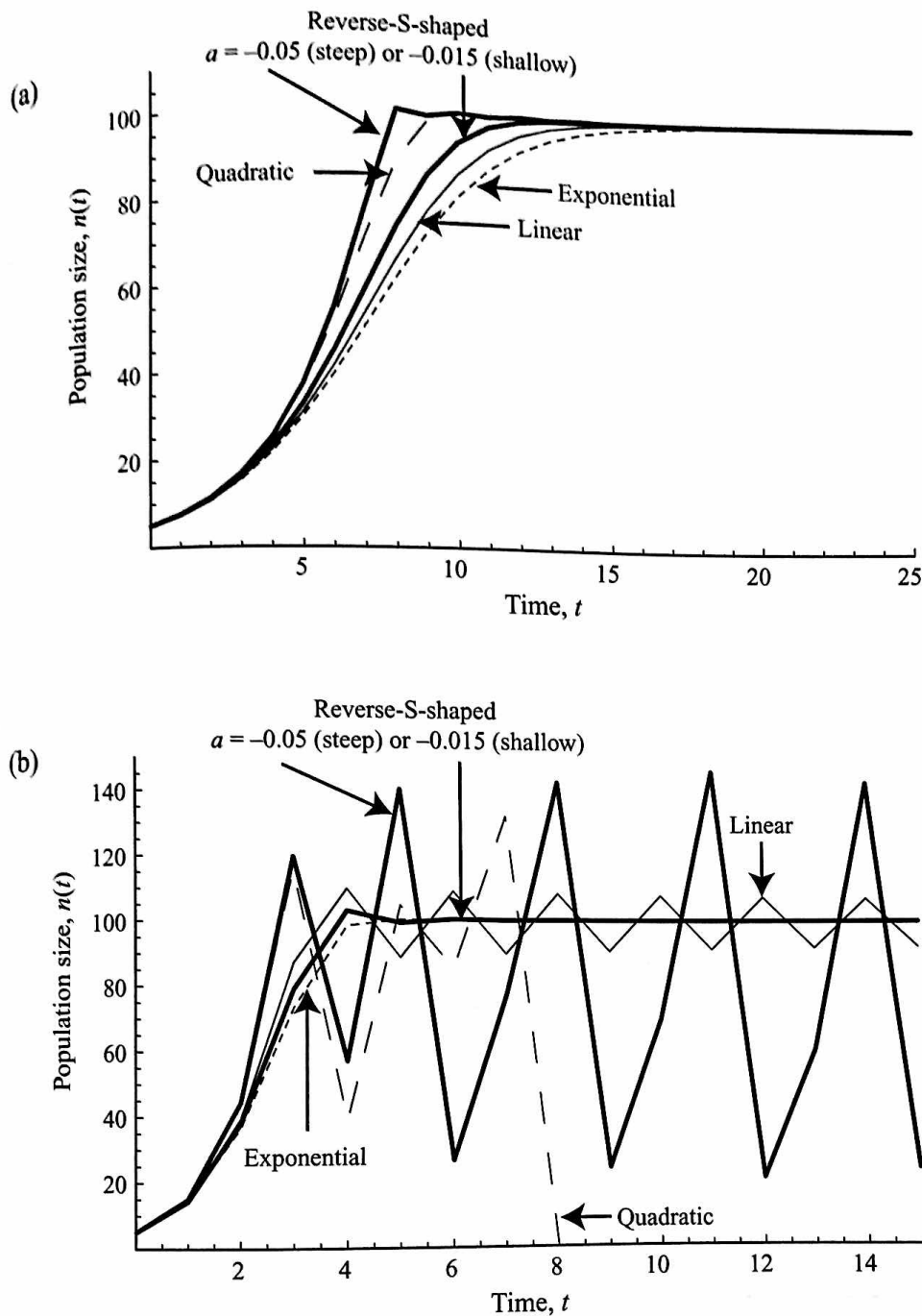
Figure P1.8: Population size over time using different functions for the reproductive factor. The population size was tracked over time (see Chapter 4) using the functions for $R(n)$ illustrated in Figure P1.1 with $K = 100$. We considered two versions of the reverse-S-shaped function: $a = -0.05$ (as in Figure P1.1) and $a = -0.015$ (a more shallow decline). (a) Low intrinsic growth rate, $r = 0.5$. (b) High intrinsic growth rate, $r = 2$. We shall discuss the odd behavior of the discrete-time logistic model in Chapter 4.

is near 0). At other times, we might wish to assume that a parameter is near a particular value (e.g., the mutation rate is near zero). Knowing how to approximate an equation accurately is arguably the most important technique in modeling and one that we will encounter throughout this book.

The most straightforward approximation is based on the idea that any curve looks roughly like a line if we look at it from a close enough distance. This is exactly the idea behind measuring distances on a map using straight lines (at least over stretches of road that aren't too curved). In particular, a function $f(x)$ can be approximated around a particular point a by a line tangent to the function at $x = a$ (see Figure A2.1 in Appendix 2). This assumes that the function is well behaved around a and does not go off to infinity or exhibit a "kink" at this point, assumptions that we make throughout this section and that we formalize in the next section.

We can use Definition P1.1 to find a formula for this tangent line, which we call $\widetilde{f}(x)$ to emphasize that it is an approximation ($\sim$) to $f(x)$. The slope of the line is given by df/dx evaluated at the point a (Appendix 2), which we write as $df/dx|_{x=a}$. To match the height of the function, we assume that $\widetilde{f}(x)$ equals $f(x)$ at $x = a$ and plug these values into Definition P1.1:

$$f(a) = \underbrace{\left(\left.\frac{df}{dx}\right|_{x=a}\right) a}_{\text{slope}} + \underbrace{c}_{\text{intercept}}.$$

Rearranging, this equation can be solved for the intercept:

$$c = f(a) - \left(\left.\frac{df}{dx}\right|_{x=a}\right)a.$$

The result is a linear function that provides a good approximation to $f(x)$ at a:

$$\widetilde{f}(x) = \underbrace{\left(\left.\frac{df}{dx}\right|_{x=a}\right) x}_{\text{slope}} + \underbrace{f(a) - \left(\left.\frac{df}{dx}\right|_{x=a}\right)a}_{\text{intercept}}.$$

Rearranging this formula further, we obtain the useful recipe:

Recipe P1.1
Approximating a Function $f(x)$ by a Line at $x = a$.
For points x near a, the function $f(x)$ can be approximated by the line

$$\widetilde{f}(x) = f(a) + \left(\left.\frac{df}{dx}\right|_{x=a}\right)(x - a). \qquad \text{(P1.3)}$$

Equation (P1.3) is also called a *linear Taylor series approximation* (see next section).

The linear approximation (P1.3) is extremely handy for simplifying compli-
cated equations. For example, consider equation (P1.1) describing the amount of
phosphorus, $f(x)$, within a cell as a function of the amount of inhibitor applied, x.
Imagine an experiment was performed using only small amounts of inhibitor,
and a roughly linear decrease in phosphorus was observed. To relate these exper-
imental data to equation (P1.1), we can use Recipe P1.1 to find a line that approx-
imates equation (P1.1) when the amount of inhibitor is small (i.e., when x is near
$a = 0$). To use Recipe P1.1, we need $f(a)$ and $df/dx|_{x=a}$ evaluated at $a = 0$. From
equation (P1.1), $f(0) = P_{max}$ and $df/dx = -\alpha (P_{max} - P_{min})e^{-\alpha x}$ (Appendix 2 reviews
the calculus needed to evaluate such derivatives). Evaluating the derivative at
$x = a = 0$, we get $df/dx|_{x=0} = -\alpha(P_{max} - P_{min})e^{-\alpha 0} = -\alpha (P_{max} - P_{min})$. This
gives us a linear approximation to equation (P1.1):

$$\widetilde{f}(x) = P_{max} - \alpha(P_{max} - P_{min}) \, x. \tag{P1.4}$$

Equation (P1.4) can then be fitted to the data using a linear regression analysis
(described in most introductory statistics books). Using the fitted line, we can
determine the intercept (giving us P_{max}) and the slope (giving us $-\alpha (P_{max} - P_{min})$).

The most subtle part about using Recipe P1.1 is to identify the term x that
we wish to vary and the point a near which we assume x lies. The following
example illustrates this process. In Chapter 3, we showed that the change in
allele frequency per generation is given by the difference equation (3.10):

$$\Delta p = \frac{s_d p(t) \, (1 - p(t))}{1 + s_d p(t)}. \tag{P1.5}$$

What is a good linear approximation to this equation assuming that selection
is weak? This question implies that we are interested in varying selection and
finding a line that is a function of s_d. Thus, s_d plays the role of x. The question
also implies that we are interested in values of s_d near 0 (weak selection). Defining
the difference equation (P1.5) as the function of interest, $f(s_d)$, we are now ready
to use Recipe P1.1. We first find the constant term by setting $s_d = a = 0$ in $f(s_d)$
to get $f(0) = 0$. We next find the derivative term by taking the derivative of $f(s_d)$
with respect to s_d, giving us

$$\frac{df}{ds_d} = \frac{d\left(\dfrac{s_d p(t) \, (1 - p(t))}{1 + s_d p(t)}\right)}{ds_d} = \frac{p(t) \, (1 - p(t))}{(1 + s_d \, p(t))^2}. \tag{P1.6}$$

(Remember, we are not varying $p(t)$ in this approximation, so it is treated as a
constant.) Evaluating this derivative at $s_d = 0$ gives $p(t) \, (1 - p(t))$. Plugging
these terms into the linear approximation (P1.3) leaves us with

$$\begin{aligned}
\widetilde{f}(s_d) &= 0 + p(t) \, (1 - p(t)) \, (s_d - 0) \\
&= s_d \, p(t) \, (1 - p(t)).
\end{aligned} \tag{P1.7}$$

This confirms the claim made in Chapter 3 that the change in allele frequency
per generation in the discrete-time model is similar to the differential equation
(3.11b), $dp/dt = s_c p(t)(1 - p(t))$, when selection is weak.