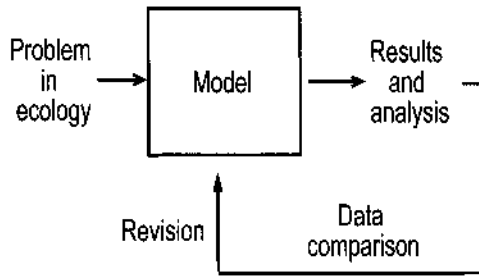


# *Introduction to Ecological Modeling*

In ecology we want to quantify theories about population growth, animal behavior, life histories, environmental influences, and so on. A mathematical model is an analytical statement that quantifies and explains a certain phenomenon or observation.

## 1.1 Mathematical Models

By a **mathematical model** we usually mean an equation, or set of equations, or some other relationships that describe some phenomenon that we observe in science, engineering, economics, or some other area, that provides a quantitative prediction of observations. By **mathematical modeling** we mean the process by which we formulate and analyze model equations and compare observations to the predictions that the models makes. This process includes introducing the important and relevant quantities or variables involved in the model; making model-specific assumptions about those quantities; solving the model equations, if possible; comparing the solutions to real data, and interpreting the results. Often, the solution method involves computer simulation or approximation. The comparison to data may lead to revision and refinement until we are satisfied that the model describes the phenomenon accurately and is predictive of similar observations. This process is depicted schematically in Fig. 1.1. In summary, mathematical modeling involves physical intuition, formula-



**Figure 1.1** Schematic of the modeling process.

tion of equations, solution techniques, analysis, and tests of validity. A good mathematical model is simple, applies to many situations, and is predictive. Stated in a different way, in the modeling process the overarching objective is to make sense of the natural world as we observe it, by inventing caricatures of reality. Scientific exactness is sometimes sacrificed for mathematical tractability. Models help us clarify verbal descriptions of nature and the mechanisms that make up natural laws, and they help us determine which processes are important and which are unimportant.

One issue is the level of complexity of a model. With modern computer technology it is tempting to build complicated models that include every possible effect we can think of, with large numbers of parameters and variables. *Simulation models* (also called *agent-based models*) like these have their place, but computer output does not always allow us to discern which are the important processes and which are not. In building a model, it is usually a good idea to err on the side of simplicity and then build in complexity as needed or desired.

Mathematical models are classified in several ways: stochastic vs. deterministic, continuous vs. discrete, static vs. dynamic, quantitative vs. qualitative, descriptive vs. explanatory, and so on. In this book we are interested in modeling the underlying reasons for the phenomena we observe (explanatory) rather than fitting the data with formulas (descriptive) as is often done in statistics. For example, fitting measurements of the size of an animal over its lifetime by a regression curve is descriptive, and it gives some information. But describing the dynamics of growth by a differential equation relating growth rates, food assimilation rates, and energy maintenance requirements tells more about the underlying processes involved.

The reader is already familiar with many mathematical models. For example, in an elementary science course we learn that Newton's second law,  $F = ma$  (force equals mass times acceleration), governs mechanical systems. The law of

mass action in chemistry describes how fast chemical reactions occur, and the logistics equation models growth and competition in a population.

The first step in the modeling process is to select relevant variables (independent and dependent) and parameters that describe the problem. Biological quantities have *dimensions* such as time, mass, and degrees, or corresponding *units* such as seconds, kilograms, and degrees Celsius. The equations we write down as models must be dimensionally correct. Apples cannot equal oranges. Verifying that each term in a model equation has the same dimensions is the first task in obtaining a correct model. We should always be aware of the dimensions of the quantities, both variables and parameters, and we should always try to identify the biological meaning of the terms in the equations we obtain. Another general rule is always to allow the biological issues to drive the mathematics, not vice versa.

### Example 1.1

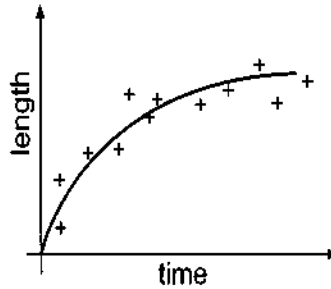
Suppose that we want to know how fast a certain species of fish grow. One strategy is to go to the lab and every few days measure the length of each member of a cohort of newly hatched eggs. We can record at each time the average length  $L$  of the fish and plot the data points on a set of time-length,  $tL$ , axes. These data points are shown as pluses in Fig. 1.2. Then we can fit a curve to the data that has the same shape as the data. For example, we might determine constants  $a$  and  $b$  for which the curve

$$L = b(1 - e^{-at}) \tag{1.1}$$

fits the data. Equation (1.1) is a satisfactory model for the growth. It is a *descriptive model* that explains *how* the growth occurs, but it gives no clue as to *why* it occurs in this way. An *explanatory model*, on the other hand, is a model that provides reasons for the shape of the growth curve. That is, it gives mechanisms that explain the growth. In this case, as we observe later, the explanatory model is a differential equation which states that the growth rate is equal to the rate at which nutrients are assimilated minus the rate at which they are used for body maintenance and respiration. Out of this explanatory model comes equation (1.1) automatically; and there is an underlying mechanism based on energetics that tells us why the growth occurs in the way it does.  $\square$

### Example 1.2

MATLAB has simple commands to plot curves. Let us consider the two growth formulas  $L_1 = 5(1 - e^{-0.5t})$  and  $L_2 = 8(1 - e^{-0.5t})$  for times  $0 \leq t \leq 10$ . We



**Figure 1.2** A set of data points (+) and a curve of the form  $L = b(1 - e^{-at})$ ,  $a, b > 0$ , that fits the data. Such a curve, which is a descriptive model, can be found by regression, which is discussed in a later section.

can use MATLAB to plot these curves on the same axes using the commands

```
t=0:0.05:10;
L1=5*(1-exp(-0.5*t));
L2=8*(1-exp(-0.5*t));
plot(t,L1,t,L2)
```

The command `plot(t,L1)` graphs just a single curve. To make two plots side by side, use the `subplot` command:

```
subplot(1,2,1), plot(t,L1)
subplot(1,2,2), plot(t,L2)
```

The command `subplot(n,m,p)` creates an  $n \times m$  array of plots, putting the current plot in the  $p$ th position.  $\square$

## EXERCISES

- Suppose that a marine animal essentially has a spherical shape with radius  $r$ . If it assimilates nutrients at a rate proportional to its surface area, and if it uses nutrients at a rate proportional to its volume, what would be its size (radius) if its intake and use rates are in balance?
- Darlington's rule* is a descriptive model that relates the number of species  $S$  of birds on an island of area  $A$  ( $\text{mi}^2$ ) near a mainland. The rule is  $S = cA^b$ , where  $c$  and  $b$  are constants found by fitting the curve to data. For example, in the West Indies,  $c = 8.76$  and  $b = 0.113$ .
  - Plot the West Indies model on the  $AS$  axes (with  $A$  the abscissa, or horizontal axis). Then plot the model on a set of  $\log A$ ,  $\log S$  axes, where the logarithm is base 10.

- (b) Can you give reasons why the curve has the shape it has?
3. The immigration rate of bird species (species per time) from a mainland to an offshore island is  $I_m(1 - S/P)$ , where  $I_m$  is the maximum immigration rate,  $P$  is the size of the source pool of species on the mainland, and  $S$  is the number of species already occupying the island. Further, the extinction rate is  $ES/P$ , where  $E$  is the maximum extinction rate. The growth rate of the number of species on the island is the immigration rate minus the extinction rate.
- (a) Plot the immigration and extinction rates vs.  $S$ , and determine the number of species for which the net rate of growth is zero, or the number of species is in equilibrium. (This exercise requires generic plots of functions. A *generic plot* is a plot of the *form* of the equation, regardless of what the constants may be. For example, we know that  $y = mx + b$  plots as a straight line regardless of  $m$  and  $b$ , so a generic plot is just a straight line. We could indicate on the plot, if possible, what the constants mean; for example,  $b$  is the  $y$  intercept.)
- (b) Suppose that two islands of the same size are at different distances from the mainland. Birds arrive from the source pool, and they have the same extinction rate on each island. However, the maximum immigration rate is larger for the island farther away. Which island will have the larger number of species at equilibrium?
4. If a herbivore enters a patch where food has density  $F$  (items per area), one can model the rate of consumption  $C$  (items per time), the rate at which food items are eaten, by the equation

$$C = \frac{adF}{1 + a\tau dF}, \quad (1.2)$$

where  $a$  is the search rate of the herbivore (area per time),  $d$  is the fraction of the food items discovered of those present, and  $\tau$  is the time it takes to consume a single item. This equation, called a **type II functional response**, will be derived later.

- (a) Make a table of the quantities in model (1.2) and indicate the dimensions of each as well as a suitable set of units for a field mouse hunting for small edible food items.
- (b) What is the shape of the graph of  $C$  vs.  $F$  for  $F$  taking on all positive values? At what value of  $C$  does the rate *saturate* as  $F$  gets very large? What is the ecological meaning of this saturation value? Why is this response an example of a law of diminishing returns?

- (c) At what food density is the consumption rate half its saturation value?
- (d) The **risk** of any one food item being consumed is  $R = C/F$ . What are the dimensions of  $R$ ? What is the shape of the graph of the risk  $R$  vs.  $F$ ?
- (e) If the fraction  $d$  of items discovered is a linear function of food density  $F$  (i.e.,  $d = \gamma F$ ), find  $C$  as a function of  $F$  and plot the shape of the curve. This model for  $C$  is called a **type III functional response**. What are the dimensions of the proportionality constant  $\gamma$ ?
- (f) A simple consumption rate where there is no handling time is the linear rate,  $C = adF$ , which is called a **type I functional response**. Sketch this consumption rate and the risk vs.  $F$ .
- (g) Contrast the shapes of the three consumption curves as well as the shapes of the associated curves for risk.
- (h) Discuss situations where these responses might be appropriate or inappropriate.

## 1.2 Rates of Change

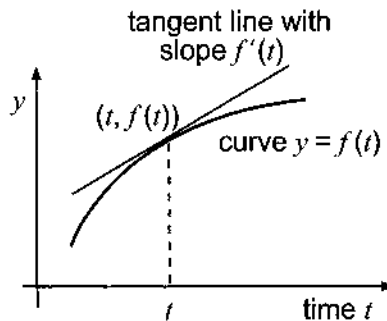
There are two fundamental concepts in calculus, the derivative and the integral. In this section we review key ideas about the derivative. Derivatives allow us to calculate how fast certain quantities, such as population, temperature, and growth, are changing. The derivative is also the slope of the tangent line to a curve at a point, and it permits us to approximate the curve near that point with a straight line. Going one step further, we discuss the higher-order approximations given by Taylor polynomials.

The **derivative** of a quantity measures how fast the quantity is changing with respect to another quantity, which is usually time. If  $t$  is time and the quantity  $y$  is a function of  $t$ , we write

$$y = f(t), \tag{1.3}$$

where  $f$  is the name of the function. For definiteness, think of  $y$  as being a population, or numbers of animals in a given region. A word about notation—when there is no confusion, we sometimes write (1.3) as  $y = y(t)$ , using the same letter to denote the quantity, or dependent variable, and the name of the function. Often, the right side of (1.3) is given by a specific formula.

At a certain *fixed* value of time,  $t = t_0$ , we can ask how fast the population  $y$  is changing at that instant. The answer is given by the derivative, which we



**Figure 1.3** Generic plot of a function  $y = f(t)$  and a tangent line at a time  $t$ . The slope of the tangent line at the point  $(t, f(t))$  is the derivative, and its value measures how fast the function is changing at that instant.

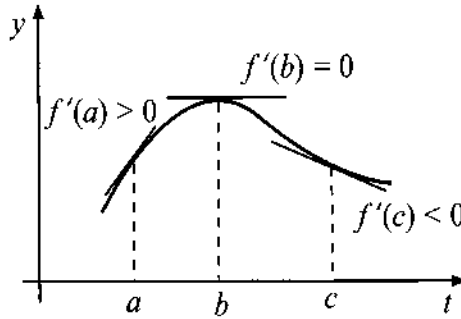
denote by  $f'(t_0)$ . Graphically, the derivative measures the slope of the tangent line to the graph of  $y = f(t_0)$  at the point  $(t_0, f(t_0))$ , as shown in Fig. 1.3. The slope measures how fast the quantity, in this case the population  $y$ , is changing. Clearly, we can consider the slope of the tangent line at any arbitrary value  $t$ , which is  $f'(t)$ . Thus, we can regard the derivative itself as a function of  $t$ . If the derivative is large, the slope is steep and  $y$  is changing rapidly, and if the derivative is small, the slope is shallow and  $y$  is changing slowly. If the derivative is positive at a value  $t = a$ ,  $f'(a) > 0$  and the graph of  $f$  must be rising at that instant; and if the derivative of  $f$  is negative at a time  $t = c$ ,  $f'(c) < 0$  and the graph is decreasing, or falling, at that time. If  $f'(b) = 0$ , the graph of  $f$  is flat at  $(b, f(b))$ , possibly signaling a maximum or a minimum value of the population. See Fig. 1.4.

Another common notation for the derivative  $f'(t)$  is

$$f'(t) = \frac{dy}{dt}. \quad (1.4)$$

This notation is suggestive that the derivative is a ratio of  $dy$  and  $dt$ , where  $dy$  is an infinitesimally small change in population and  $dt$  is an infinitesimally small change in time. This is clarified below. Thinking in this way, the derivative has dimensions of population per time. The derivative is called the **rate of change**, measuring how fast the quantity  $y$ , in this case, population, is changing instantaneously at a fixed time  $t$ . Many of the laws of biology are expressed in terms of rates, or derivatives. These often arise as differential equations, which are equations that relate an unknown function to its rates.

It is important to understand how the derivative is defined. Let us fix an instant of time  $t_0$  and ask how much the population changes from  $t_0$  to  $t_0 + h$ ,



**Figure 1.4** A function  $y = f(t)$  will have a positive derivative at times where the function is increasing, and a negative derivative at times where the function is decreasing. At a point where the function has a local maximum (or a local minimum), the derivative, or slope, is zero.

where  $h$  is a small amount of time. The actual change is  $f(t_0 + h) - f(t_0)$ , so the average change in the population over this interval is

$$\text{average change} = \frac{f(t_0 + h) - f(t_0)}{h}. \quad (1.5)$$

Geometrically, on the graph of  $y = f(t)$ , this average change is the slope of the line connecting the two points  $(t_0, f(t_0))$  and  $(t_0 + h, f(t_0 + h))$ . The derivative is the limiting value of the average change as the interval of time  $h$  approaches zero. In symbols,

$$f'(t_0) = \lim_{h \rightarrow 0} \frac{f(t_0 + h) - f(t_0)}{h}. \quad (1.6)$$

Notice that if  $h$  is very small,

$$f'(t_0) \approx \frac{f(t_0 + h) - f(t_0)}{h},$$

which means that the derivative is approximated by the average change over a very small interval of time. Rewriting this expression with  $t = t_0 + h$  gives

$$f(t) \approx f(t_0) + f'(t_0)h. \quad (1.7)$$

This important equation states that the actual population  $f(t)$  at time  $t = t_0 + h$  can be approximated by the population at time  $t_0$ , provided that we know the derivative, or how fast the population is changing, at time  $t_0$ . The right side of expression (1.7) is called the **linear approximation** or **linearization**, and it implies that the curve  $y = f(t)$  can be approximated near a fixed time  $t_0$  by the tangent line through the point  $(t_0, f(t_0))$ . The right side of (1.7), using  $h = t - t_0$ , is  $f(t_0) + f'(t_0)(t - t_0)$ , which is the equation of a straight line.



If  $y = N(t)$  represents a population, we say that  $N'(t)$  is the **growth rate**. It measures how fast the population is changing. The *relative growth rate*, or *per capita growth rate*, is defined by the ratio

$$\text{per capita growth rate} = \frac{N'(t)}{N(t)}. \quad (1.8)$$

The per capita growth rate, which has units of  $\text{time}^{-1}$ , measures how fast the population is changing relative to the current value of the population. To say that the growth rate of a population is 3% and the per capita growth rate is 3% is to say two very different things. Really, saying that a population grew 3% actually says very little. Is it a large change in the population? Is it a small change?

### 1.2.1 Taylor Polynomials

The approximation of  $f(t)$  at a value  $t = a$  by its linearization (a straight line) can be improved by including higher-order derivatives. The linear approximation, which we denote by

$$P_1(t) = f(a) + f'(a)(t - a),$$

agrees with both  $f(a)$  and  $f'(a)$  at the value  $t = a$ , and it approximates  $f(t)$  near  $t = a$ . To get more accuracy, we can also require the approximation to have the same concavity at  $t = a$ . Recall that the concavity is measured by the second derivative. Therefore, let us try a parabolic approximation and define

$$P_2(t) = f(a) + f'(a)(t - a) + c_2(t - a)^2,$$

where  $c_2$  is to be determined so that  $P_2''(a) = f''(a)$ . By direct differentiation we get  $P_2''(a) = 2c_2$ . So we choose  $c_2 = \frac{1}{2}f''(a)$ . Then

$$P_2(t) = f(a) + f'(a)(t - a) + \frac{1}{2}f''(a)(t - a)^2,$$

which is a **quadratic**, or parabolic, **approximation**. To do even better, we can try to add a cubic term to make the third derivatives equal also. So, let

$$P_3(t) = f(a) + f'(a)(t - a) + \frac{1}{2}f''(a)(t - a)^2 + c_3(t - a)^3.$$

Requiring that  $P_3'''(a) = f'''(a)$  forces  $P_3'''(a) = 3 \cdot 2c_3 = f'''(a)$ , which means that  $c_3 = 1/(2 \cdot 3)f'''(a)$ . Therefore,

$$P_3(t) = f(a) + f'(a)(t - a) + \frac{1}{2}f''(a)(t - a)^2 + \frac{1}{2 \cdot 3}f'''(a)(t - a)^3,$$

which is called the **cubic approximation**. We can continue this process indefinitely, assuming that  $f$  has the required derivatives, to obtain

$$P_n(t) = f(a) + f'(a)(t-a) + \frac{1}{2}f''(a)(t-a)^2 + \frac{1}{2 \cdot 3}f'''(a)(t-a)^3 \\ + \cdots + \frac{1}{n!}f^{[n]}(a)(t-a)^n,$$

where  $f^{[n]}(a)$  denotes the  $n$ th derivative of  $f$  at  $t = a$ . These approximating polynomials,  $P_1(t)$ ,  $P_2(t)$ ,  $P_3(t)$ , ...,  $P_n(t)$ , are called the **Taylor polynomials**. These polynomials approximate  $f(t)$  for values  $t$  near  $t = a$ ; generally, the higher the degree of polynomial, the more accurate the approximation and the larger the interval over which the approximation is good. As an aside, we define  $P_0(t) = f(a)$ , which is a constant function.

### Example 1.3

Let  $f(t) = \ln t$ . Find a cubic approximation to  $\ln t$  at  $t = 1$ . We need the derivatives of  $f$  at  $t = 1$ :

$$f(t) = \ln t, \quad f'(t) = \frac{1}{t}, \quad f''(t) = -\frac{1}{t^2}, \quad f'''(t) = \frac{2}{t^3}.$$

Here  $a = 1$ , and therefore

$$f(1) = \ln 1 = 0, \quad f'(1) = 1, \quad f''(1) = -1, \quad f'''(1) = 2.$$

Therefore, the cubic approximation is

$$P_3(t) = f(1) + f'(1)(t-1) + \frac{1}{2}f''(1)(t-1)^2 + \frac{1}{2 \cdot 3}f'''(1)(t-1)^3 \\ = (t-1) - \frac{1}{2}(t-1)^2 + \frac{1}{3}(t-1)^3.$$

We urge the reader to use a calculator and plot both  $f(t) = \ln t$  and  $P_3(t)$  on the same set of axes. For example, we can approximate  $\ln 1.5$  by  $P_3(1.5) = 0.4167$ . The actual value is  $\ln 1.5 = 0.4055$ , so we make an error of magnitude 0.0112.  $\square$

One can show (see most calculus texts) that the exact error in the Taylor approximation  $P_n(t)$  at  $t$  involves the next-higher derivative of  $f$  and is given by

$$\text{error} = \frac{1}{(n+1)!}f^{[n+1]}(c)(t-a)^{n+1},$$

where the  $(n + 1)$ st derivative of  $f$  is evaluated at some point  $c$  *between*  $a$  and  $t$ ; we don't know the value of  $c$ , but we can use this formula to estimate an upper bound on the error in an interval  $[a - \delta, a + \delta]$ . We have

$$|\text{error}| \leq \frac{M}{(n+1)!} (2\delta)^{n+1},$$

where  $M$  is the maximum value of  $|f^{[n+1]}(t)|$  over  $[a - \delta, a + \delta]$ .

### Example 1.4

Returning to Example 1.3, the maximum error in  $P_3(t)$  over the interval  $[0.5, 1.5]$  (so  $\delta = 0.5$ ) is bounded by

$$\frac{M}{(4)!},$$

where  $M = \max |f^{[4]}(t)| = \max |-6t^{-4}| \leq 6(0.5)^{-4} = 16$ . Therefore, the absolute error is bounded by  $16/24 = 0.667$ .  $\square$

### Example 1.5

The logistic growth law for a population  $x$  is given by

$$g(x) = rx \left(1 - \frac{x}{K}\right),$$

where  $r$  is the growth rate and  $K$  is the carrying capacity. The populations  $x = 0$  and  $x = K$  have zero growth rate and are therefore called **equilibrium populations**. We find the linearization of the growth rate at the carrying capacity  $K$ . First,

$$g'(x) = r - 2\frac{r}{K}x; \quad g'(K) = -r.$$

Therefore, the linearization is

$$P_1(x) = g(K) + g'(K)(x - K) = -r(x - K).$$

Later, we show that we can use this simple linear approximation for  $g(x)$  to examine the behavior of the population at values near the carrying capacity.  $\square$

If a function  $f$  has infinitely many continuous derivatives at  $t = a$ , we can form the Taylor polynomial  $P_n(t)$  for arbitrarily large  $n$ . In the limit as  $n \rightarrow \infty$ , we have the infinite sum

$$\sum_{k=0}^{\infty} \frac{1}{k!} f^{[k]}(a)(t-a)^k.$$

Here, to get the first term, when  $k = 0$  we use  $0! = 1$  and  $f^{[0]}(a) = f(a)$ , both by convention. This series is called the **Taylor series** for  $f(t)$  centered about  $t = a$ . One can show that it converges *either* for all real numbers  $t$ , for only  $t = a$ , or for  $t$  in a symmetric interval  $|t - a| < r$  about  $a$ ; the radius  $r$  is called the *radius of convergence*. When the series converges for a value  $t$ , it converges to  $f(t)$ , and we write

$$f(t) = \sum_{k=0}^{\infty} \frac{1}{k!} f^{[k]}(a)(t - a)^k.$$

### Example 1.6

The Taylor series for the functions  $e^{rt}$  and  $\sin at$  about  $t = 0$  are, respectively,

$$e^{rt} = \sum_{k=0}^{\infty} \frac{1}{k!} (rt)^k, \quad (1.9)$$

$$\sin at = \sum_{k=0}^{\infty} \frac{(-1)^k}{(2k+1)!} (at)^{2k+1}. \quad (1.10)$$

Both converge for all values of  $t$ . The function  $f(t) = 1/(1 - t)$  has a Taylor series about  $t = 0$  given by

$$\frac{1}{1 - t} = \sum_{k=0}^{\infty} t^k = 1 + t + t^2 + t^3 + \dots, \quad (1.11)$$

which is called the **geometric series**. The geometric series converges in the interval  $|t| < 1$ . Taylor series are used extensively in mathematical biology and in other sciences to make approximations.  $\square$

We end this section with two interesting models that require only calculus techniques for their analysis.

## 1.2.2 Foraging Theory

There are different theories about animals' foraging strategies. For a broad introduction, the reader should consult Stephens & Krebs (1986), which has become a standard reference on the topic. Here we investigate which is the best of two strategies. The idea is that a forager is consuming prey items from a single patch that has two types of prey items, 1 and 2. Each type has a total energy associated with it ( $E_1$  and  $E_2$ ), a time that it takes for the forager to handle an item ( $h_1$  and  $h_2$ ), and a rate that the particular type of item is

encountered ( $r_1$  and  $r_2$ ), the latter measured in items per unit of time. The question is: What is the rate at which energy is gained by a generalist who consumes each item as it is encountered vs. a specialist who consumes only the item with the higher-energy payoff? Without loss of generality, we assume that eating item 1 has a higher-energy payoff, or  $E_1 > E_2$ .

To compare these strategies, we first calculate the *rate*  $R_s$  at which energy is gained by the specialist from consuming *only* item 1 over a time period  $T$ , which is the total time available to the forager. Clearly, the total time  $T$  must be the sum of the time  $S$  spent searching and the time  $H$  it takes to handle the food items encountered. So  $T = S + H$ . But during the time searching  $S$ , the forager encounters  $r_1 S$  food items and gains total energy  $E_1 r_1 S$ ; the total time it takes to handle those items is  $H = h_1 r_1 S$ . Therefore,

$$T = S + h_1 r_1 S,$$

or

$$S = \frac{T}{1 + h_1 r_1}.$$

Thus, the rate that energy is gained by selecting only item 1 is

$$R_s = \frac{E_1 r_1 S}{T} = \frac{E_1 r_1}{1 + h_1 r_1}.$$

For the generalist who consumes both items, the total time  $T$  is

$$T = S + H_1 + H_2,$$

where  $H_1$  and  $H_2$  are the total times to handle all items of type's 1 and 2, respectively. Then

$$T = S + h_1 r_1 S + h_2 r_2 S,$$

which gives

$$S = \frac{T}{1 + h_1 r_1 + h_2 r_2}.$$

The total energy gained is  $E_1 r_1 S + E_2 r_2 S$ . It follows that the rate at which energy is gained by the generalist in selecting both items is

$$R_g = \frac{E_1 r_1 S + E_2 r_2 S}{T} = \frac{E_1 r_1 + E_2 r_2}{1 + h_1 r_1 + h_2 r_2}.$$

It is interesting to compare  $R_g$  and  $R_s$ . By direct algebra it is easy to show that  $R_s > R_g$  implies that

$$r_1 > \frac{E_2}{h_2 E_1 - h_1 E_2},$$

which occurs when the encounter rate for the most profitable item is sufficiently high. The right side can be thought of as a cut off value when a forager should switch from being a generalist to a specialist.

### Optimum Time in a Patch

Now let's look at a different foraging situation. Suppose that there are several patches, all the same, each with the same food items, and the energy gain  $G(t)$  for a forager in a given patch is a function of the *residence time*  $t$  spent in that patch, but with diminishing returns. In other words, the energy gain curve has the form shown in Fig. 1.5 with  $G(0) = 0$  and  $G(t) > 0$ ,  $G'(t) > 0$ , and  $G''(t) < 0$  for  $t > 0$ . Therefore, if the forager remains in the patch too long, it gets less and less energy gain per unit time. Therefore, when should the forager leave the patch and go to another patch? To complicate matters, let us impose the condition that it takes  $T$  units of time to move from one patch to another, so moving is costly because of the time lost in eating.

Again, the forager wants to maximize its rate of energy gain. Over one cycle (residing in a patch, then moving) the time is  $t + T$  and the energy gain is  $G(t)$ . Hence, the rate of energy gain over that cycle is

$$R(t) = \frac{G(t)}{t + T}.$$

See Fig. 1.5 for a typical plot of  $R$ . We can maximize  $R$  using elementary calculus. Taking the derivative and setting it to zero gives

$$R'(t) = \frac{(t + T)G'(t) - G(t)}{(t + T)^2} = 0,$$

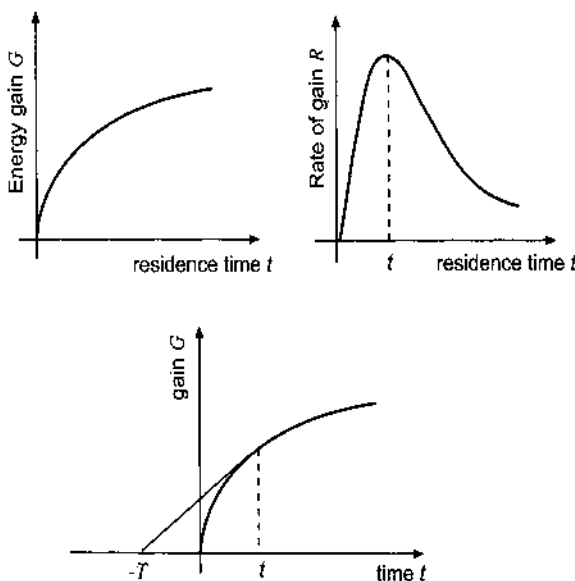
or the condition on the residence time  $t$ :

$$G'(t) = \frac{G(t)}{t + T}.$$

We can determine geometrically the value of  $t$  that solves this equation. Let us write this condition as

$$G'(t) = \frac{G(t)}{t + T} = \frac{G(t) - 0}{t - (-T)}.$$

The right side is the slope of the straight-line segment from the point  $(-T, 0)$  to  $(t, G(t))$ . So the value of the optimum residence time  $t$  is given by the value of  $t$  where the straight-line segment is tangent to the graph of  $G(t)$ . See Fig. 1.5. This construction, adapted by Charnov (1976) from economics, is often called the **marginal value theorem**.



**Figure 1.5** Plots of the energy gain and the rate of energy gain vs. residence time, and the graphical interpretation of the marginal value theorem.

## EXERCISES

- A population  $y$  is modeled by the equation  $y = f(t) = \sqrt{t}$ , where  $t$  is measured in days and  $y$  is measured in hundreds of animals. The derivative is  $f'(t) = 1/(2\sqrt{t})$ .

  - Graph  $f(t)$  and  $f'(t)$  for  $t > 0$ .
  - What are the units of  $f'(t)$ ?
  - What is the slope of the tangent line to the graph of  $f(t)$  when  $t = 4$ ? Illustrate this on the plot of  $f(t)$ , and find the equation of this tangent line.
  - Use a calculator to compute the average change of  $f$  over the interval  $[4, 4.2]$ . Indicate this quantity on the plot of  $f(t)$ .
  - Approximate the average change in the population over the interval  $[4, 4.2]$  using the derivative.
  - Find the growth rate and the per capita growth rate at time  $t = 4$ .
- A descriptive model of population growth is a logistic growth curve, which

is given by the formula

$$y = f(t) = \frac{y_0 K}{y_0 + (K - y_0)e^{-rt}},$$

where  $r$ ,  $K$ , and  $y_0$  are positive parameters, and  $y$  is the population.

- (a) Use MATLAB to plot the logistic curve when  $r = 1$ ,  $K = 10$ , and  $y_0 = 2$ .
  - (b) Use a calculator and estimate the growth rate and the per capita growth rate when  $t = 3$ . (*Hint*: You will have to approximate the derivative.)
3. A population has a constant growth rate of  $r$  per day. If the population at time  $t = 0$  is  $y_0$ , find a specific formula  $y = f(t)$  for the population as a function of time. (*Hint*: What expressions have a constant derivative?)
  4. A population  $y = f(t)$  has a per capita growth rate of  $r$  per day. Show that a population law of the form  $y = Ce^{rt}$ , where  $C$  is any constant, satisfies the condition of constant per capita growth. If the population at time  $t = 0$  is  $y_0$ , what is the formula for the population as a function of time?
  5. The length  $L$  (cm) of an organism is changing according to  $L(t) = 3(1 - e^{-0.2t})$ . One finds that  $L'(t) = 0.6e^{-0.2t}$ . Plot  $L$  and  $L'$  vs.  $t$  on the same axes. How fast is the length changing at time  $t = 10$  days?
  6. Consider the exponential function  $f(t) = e^{rt}$ , where  $r$  is a fixed constant. Near  $t = 0$ , find the Taylor polynomial approximations  $P_1(t)$ ,  $P_2(t)$ , and  $P_3(t)$ . What is  $P_n(t)$ ?
  7. The **Ricker growth law** with mortality, which models some fish populations, is

$$g(x) = bxe^{-cx} - mx, \quad b > 1,$$

where  $x$  is the population,  $b$  is the growth rate,  $m$  is the mortality rate, and  $c$  is a predation rate. Find the nonzero equilibrium population and determine the linearization of  $g(x)$  about that equilibrium. Simplify completely.

8. The **Gompertz growth law** for some tumors depends on the tumor's radius  $R$  and is given by

$$G(R) = aR(\ln R_m - \ln R),$$

where  $a$  and  $R_m$  are positive constants. Find the equilibrium radius, and determine the linearization of  $G(R)$  about that equilibrium.



9. The growth rate of a plant is dependent on the nitrogen concentration  $N$  in the soil, and it is given by **Tilman's law**:

$$f(N) = \frac{aN}{1 + bN},$$

where  $a$  and  $b$  are positive constants. What is the limiting (or, saturating) growth rate for very large nitrogen concentrations? Find a quadratic approximation for  $f(N)$  valid near  $N = 0$ .

10. Verify the Taylor series formulas (1.9), (1.10), and (1.11).
11. Find Taylor series about  $t = 0$  for the following functions:  $\cos at$ ,  $\ln(1 + t)$ , and  $1/(1 + t^2)$ .
12. The survival of a fish egg through its critical period is a function of its mass  $x$ . The larger the egg, the more nutrients are present and the more likely it is to hatch successfully. This survivorship is often modeled by a function of the form

$$s(x) = 1 - cx^{-b}, \quad x \geq c,$$

where  $c$  and  $b$  are positive parameters. If  $G$  is the total gonadal mass of the female, the number of eggs laid by the female is  $G/x$ , and the number of eggs that survive through the critical period is

$$E(x) = \frac{G}{x}(1 - cx^{-b}).$$

Show that the egg size that optimizes the female's number of eggs is

$$x^* = (c + bc)^{1/b}.$$

Sketch generic plots of  $s(x)$  and  $E(x)$ .

13. In the optimum residence-time problem (Section 1.2.2), take the energy gain function to be

$$G(t) = \frac{t}{t + 3}$$

and the travel time between patches to be  $T = 3$ . Use calculus to find the optimum residence time and illustrate your result by the Charnov construction.

### 1.3 Balance Laws

Many models in ecology come from a simple bookkeeping or accounting for a given quantity—where it comes from and where it goes. This bookkeeping, or balancing, gives a law which is often expressed as a differential equation.

In terms of setting up models, this section may be the most important in the book! It is based on a very simple idea that is used in all of science and engineering: that of a balance law. To explain what we mean, let  $Q$  be any quantity whatsoever in a fixed, well-defined domain. To list a few examples,  $Q$  could be:

- The number of animals in a fixed area
- The number of milligrams of a medicine in a person's blood
- The mass (kilograms) of a toxic chemical pollutant in a lake
- The amount of heat energy (calories) in a small animal's body
- The number of individuals in a community infected with a communicable disease

To determine how fast a quantity  $Q$  changes in a fixed domain all we have to do is keep track of where it comes from and where it goes. There are four possibilities.  $Q$  can enter the domain from outside; it can leave the domain and go outside; it can be created inside the domain; or it can be destroyed inside. Figure 1.6 shows how we represent these four notions pictorially in the case of animals in a fixed region. They can immigrate into the region or emigrate out of the region. Inside the region they can be born or they can die, which we represent by appropriate arrows. For the scenario of a toxin in a lake, the chemical can be pumped into the lake by a factory, and it can flow out of the lake through estuaries; while in the lake, the chemical can degrade or be consumed by reactions.

We can write the balance, or accounting law, in symbols. The rate of change of the total quantity  $Q$  in the domain is, by definition, the derivative  $dQ/dt$ . We give each of the four cases a name:

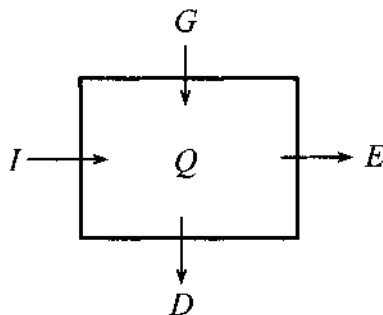
$I$  = rate  $Q$  flows into the domain from outside

$E$  = rate  $Q$  flows out of the domain

$G$  = rate that  $Q$  is created inside the domain

$D$  = rate that  $Q$  is destroyed inside the domain

Notice that  $I$ ,  $E$ ,  $G$ , and  $D$  are rates, measured in quantity per time. For the population scenario,  $I$  is the immigration rate,  $E$  is the emigration rate,  $G$  is



**Figure 1.6** Net rate of change of  $Q$  is  $I - E + G - D$ . The rates are added or subtracted according to whether they increase or decrease  $Q$ .

the birth rate (gain), and  $D$  is the death rate (loss). For the lake,  $I$  is the rate at which toxins are pumped into the lake,  $E$  is the rate at which they flow out into the estuaries, and  $D$  is the degradation rate; in this example,  $G = 0$ . The **balance law** states that

$$\frac{dQ}{dt} = I - E + G - D. \quad (1.12)$$

In other words, all the rates have to balance; the right side of (1.12) accounts for how fast  $Q$  can change. This is a fundamental law of science.

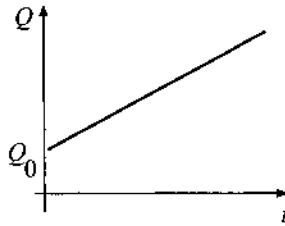
Now, here is how this helps us. Once we determine expressions for each of the rates on the right side of (1.12), we will have a specific equation for  $Q$ . Because some of these rates may depend on  $Q$  itself (e.g., the emigration rate  $E$  of a population may depend on the population  $Q$ ), the balance law (1.12) becomes a differential equation for the *unknown* function  $Q = Q(t)$ . Often, our goal is to solve the differential equation: that is, to find  $Q(t)$  or to understand qualitatively how  $Q(t)$  behaves.

### Example 1.7

If all the rates on the right side of (1.12) are constant,  $r = I - E + G - D$  is constant and the balance law is

$$\frac{dQ}{dt} = r.$$

This is a simple differential equation: It says that the derivative of  $Q$  is constant. So  $Q$  must be changing as a linear function of  $t$ , or  $Q = rt + c$ , where  $c$  is *any* constant. In different words,  $Q$  is the antiderivative of  $r$ . If we have an initial



**Figure 1.7** The linear function  $Q = rt + Q_0$  with slope  $r > 0$  and intercept  $Q_0$ .

condition on  $Q$ , say  $Q(0) = Q_0$ , then  $c = Q_0$  and

$$Q = rt + Q_0.$$

A generic plot is shown in Fig. 1.7.  $\square$

### Example 1.8

The equation

$$\frac{dy}{dt} = ry,$$

where  $r$  is a fixed, constant parameter, is a differential equation for an unknown function  $y = y(t)$ ; it relates the rate that  $y$  is changing to the quantity  $y$  itself. We want to find a  $y = y(t)$  that works to make the equation true; such a  $y$  is called a *solution*. It is easily checked that a solution is

$$y(t) = Ce^{rt},$$

where  $C$  is any constant, called an *arbitrary constant*. If  $y(0) = y_0$  is imposed, where  $y_0$  is a given, fixed initial value, then  $C = y_0$  and the solution is

$$y(t) = y_0e^{rt}.$$

Typically, a differential equation has infinitely many solutions containing an arbitrary constant (here,  $C$ ). But specifying an initial condition at  $t = 0$  picks out one of these many solutions by fixing a value of  $C$ . Then we get a unique solution, as we expect in scientific problems. The differential equation in this example models exponential growth when  $r > 0$  and exponential decay when  $r < 0$ .  $\square$

### Example 1.9

Here is a more difficult example. Let  $V$  be the volume of blood in the body and let  $C = C(t)$  be the concentration (milligrams per deciliter) of a cancer-fighting chemical in the blood. Through chemotherapy, a patient is injected with the chemical at the rate of  $I$  milligrams per hour. At the same time, the body tissues absorb the chemical at a rate proportional to its concentration, or at rate  $kC$ , where  $k$  is the constant of proportionality, given in units of  $\text{hours}^{-1}$ . If the initial concentration is zero, or  $C(0) = 0$ , what is the concentration  $C(t)$  in the blood at any time  $t$ ? We set up a differential equation for the *mass* of the chemical. (A rule: *Masses are always balanced; concentrations never.*) Let  $M = M(t)$  be the mass of the chemical in the blood. Mass and concentration are related by

$$\text{mass} = \text{concentration} \times \text{volume},$$

so that  $M = CV$ . Then, by the balance law,

$$\frac{dM}{dt} = \text{rate mass flows in} - \text{rate mass is absorbed}.$$

We always have to be careful about units; each term must be in mass per time. The rate at which mass flows in is given to be  $I$ ; the rate at which mass is absorbed is  $kC$ , which is mass per volume per unit of time. So the rate that mass is absorbed is  $kVC = kM$ , which is mass per unit of time. Thus, the balance law is

$$\frac{dM}{dt} = I - kM,$$

which is a differential equation for  $M = M(t)$ . We can write the balance equation in terms of concentration (which is what we would measure) as

$$\frac{d(VC)}{dt} = I - kVC,$$

or, using the fact that  $d(VC)/dt = V(dC/dt)$ , we have

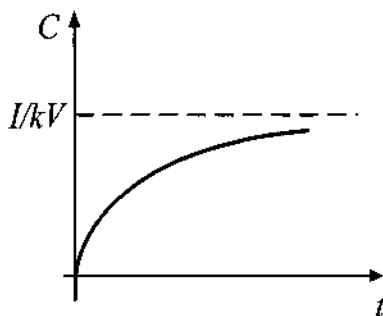
$$\frac{dC}{dt} = \frac{I}{V} - kC. \quad (1.13)$$

We know, initially, that  $C(0) = 0$ , which is the *initial condition*. We can now use a computer software program, for example, to find a formula for the solution  $C(t)$  to this equation. But here is how we can do it ourselves. We choose a new dependent variable  $y = y(t)$ , defined by

$$y = \frac{I}{V} - kC.$$

Then  $dy/dt = -k(dC/dt)$ , and (1.13) can be written

$$-\frac{1}{k} \frac{dy}{dt} = y$$



**Figure 1.8** Concentration of the medicine in the blood.

or

$$\frac{dy}{dt} = -ky.$$

This is the exponential decay equation, and from the last example we know that its solution is

$$y = Ae^{-kt},$$

where  $A$  is an arbitrary constant. But this means going back to the variable  $C$ ,

$$\frac{I}{V} - kC = Ae^{-kt}.$$

Solving for  $C$  then yields

$$C(t) = \frac{I}{kV} - \frac{A}{k}e^{-kt}.$$

We can find the value of the arbitrary constant  $A$  using the initial condition. We have  $C(0) = I/(kV) - A/k = 0$ , which gives

$$A = \frac{I}{V}.$$

Therefore, the concentration of the medicine in the blood is

$$C(t) = \frac{I}{kV} - \frac{I}{kV}e^{-kt}.$$

This formula gives the solution to the model (1.13) with initial condition  $C(0) = 0$ . We can draw a generic graph of  $C$  vs.  $t$ . Notice that  $C(0) = 0$ , and, from calculus, the limiting value of the concentration  $C$  as  $t \rightarrow \infty$  is  $I/(kV)$ , which means that the graph is approaching the line  $C = I/(kV)$ . The plot is shown in Fig. 1.8.  $\square$

**Remark 1.10**

The method we used in Example 1.9 is applicable to any differential equation of the form

$$\frac{dQ}{dt} = a + bQ,$$

where  $Q = Q(t)$  is the unknown quantity and  $a$  and  $b$  are fixed parameters. This equation occurs very frequently in biological applications. The change of dependent variable

$$y = a + bQ$$

transforms the differential equation for  $Q$  into

$$\frac{dy}{dt} = by,$$

which is solved by  $y = Ae^{bt}$ , where  $A$  is an arbitrary constant. Then  $a + bQ = Ae^{bt}$ , which can be solved algebraically for  $Q$ . The value of  $A$  is determined by an initial condition  $Q(0) = Q_0$ , where  $Q_0$  is a fixed number.  $\square$

**Example 1.11**

A population has  $N$  individuals, and initially  $I_0$  of them are infected with a communicable illness, while the remaining  $S_0$  are susceptible to the illness. Let us set up a model that tracks the number  $I = I(t)$  of infective individuals over time. Let  $S(t) = N - I(t)$  be the total number susceptible to the illness. By the balance law, the rate of change of the number of infectives,  $dI/dt$ , is equal to the rate that susceptible individuals become infected. We will assume no deaths, no births, and that no individuals get over the illness. If there are  $I$  infectives and  $S$  susceptibles, we can argue that the rate that individuals become infected is proportional to the number of encounters between susceptibles and infectives. For example, if there were 200 susceptibles and 8 infectives, there would be 1600 possible encounters; a fraction of those, say  $a$ , will result in an infection. The constant  $a$  is the **transmission rate**. In general, the rate of infection is

$$\text{infection rate} = aSI = a(N - I)I.$$

Therefore the balance law is

$$\frac{dI}{dt} = a(N - I)I,$$

which is a differential equation for  $I = I(t)$ . This is called an *SI model*. The solution to this equation (which is derived in an exercise) is

$$I(t) = \frac{N}{1 - Ce^{-aNt}},$$

where  $C$  is an arbitrary constant. It may be determined by the condition  $I(0) = I_0$ , to get  $C = 1 - N/I_0$ .  $\square$

## EXERCISES

- Find and plot a function  $y = y(t)$  that solves the problem  $dy/dt = -2$ ,  $y(0) = 5$ .
- Find and plot the function  $y = y(t)$  that solves the problem  $dy/dt = -2y$ ,  $y(0) = 5$ .
- Find and plot the function  $y = y(t)$  that solves the problem  $dy/dt = 20 - 2y$ ,  $y(0) = 5$ .
- This exercise leads to the solution  $I = I(t)$  of the disease model in Example 1.11:

$$\frac{dI}{dt} = a(N - I)I.$$

- (a) Rewrite the equation in terms of the dependent variable  $w$  defined by  $w = 1/I$ , or  $I = 1/w$ . You should get

$$\frac{dw}{dt} = a - aNw.$$

[*Hint:* The chain rule for derivatives requires that  $dI/dt = -(1/w^2)(dw/dt)$ . Why?]

- (b) Next observe that the equation in part (a) has the form of that in Remark 1.10. Make the appropriate transformation and solve, and then rewrite the solution in terms of the original variable  $I$ .
- (c) Sketch a generic graph of  $I$  vs.  $t$  for different initial conditions.
- A nonreactive chemical toxin of concentration  $C = C(t)$  grams per volume is dissolved uniformly in a pond of volume  $V$  gallons. Initially, the concentration is  $C_0$ . The toxin flows into the pond from a stream at a volumetric flow rate of  $q$  gallons per day at concentration  $\gamma$ . It is perfectly mixed and flows out in another stream at the same rate  $q$ .
    - Write down a differential equation and an initial condition whose solution would give the concentration in the pond at any time  $t$ .
    - Find a formula for the concentration and show a generic plot. What is the eventual concentration of the toxin in the pond?
    - Set up the differential equation for  $C(t)$  if the volumetric flow rate is  $q_i$  and the flow rate out is  $q_o$ , with  $q_i > q_o$ . (Note that the volume changes in this case.)



## 1.4 Temperature in the Environment

How does an animal's body temperature depend on its environment? In this section we present a model for calculating an animal's equilibrium temperature based on the environmental temperature, solar radiation, and the heating characteristics of the animal.

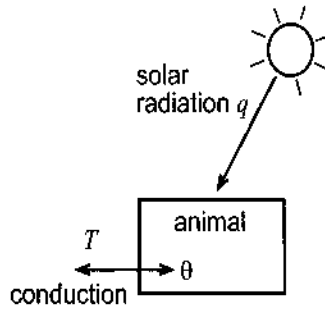
All life forms have to deal with their environment. That is partly what ecology is about. The environment consists of **biotic** influences (other organisms, competition, availability of food resources, etc.) and **abiotic** influences (weather, temperature, etc.). Here we discuss temperature effects and how we can model those effects on certain organisms. Questions such as this are crucial in times of global climate change.

### 1.4.1 Heat Transfer

For survival, an animal typically has to maintain its body temperature within a certain range. Either it generates its own heat, as a mammal does, or it does not, as in the case of an insect or reptile. Animals that generate their own heat are called **homeothermic**, and those that do not are **poikilothermic**. To fix the idea, we consider a small reptile, such as a lizard with body temperature  $\theta$ . (We always measure temperature in degrees Celsius.) In the interest of formulating a simple model of how an animal's temperature may be determined, we consider only two effects: heat transfer with its microhabitat and radiative heating from the sun. We let the microhabitat temperature be  $T$ , and we assume that the solar radiation has value  $q$ , measured in calories per hour. See Fig. 1.9. We are avoiding the effects of both convective cooling caused by the wind and the complex behavior of many poikilothermic animals, who thermoregulate by exposing themselves to direct or indirect sunlight, or orient their bodies to receive more, or less, sunlight.

First we ignore solar heating. If the ambient temperature  $T$  is larger than the body temperature  $\theta$  (i.e.,  $\theta - T < 0$ ), the body temperature increases, and if  $T$  is smaller than  $\theta$  (i.e.,  $\theta - T > 0$ ), the body temperature decreases. We are assuming that heat flows from hotter objects to colder objects, which is the second law of thermodynamics; so the reptile exchanges heat with its environment. It is a common assumption in science and engineering to assume that the rate heat flows between two adjacent regions of different temperatures (here, the body and the air) is proportional to the difference between the two temperatures,  $\theta - T$ . Therefore, the rate at which heat is exchanged is

$$k(\theta - T),$$



**Figure 1.9** An animal at temperature  $\theta$  receiving solar energy  $q$  and exchanging heat energy with its environment at a rate proportional to  $\theta - T$ , where  $T$  is the environmental temperature.

where  $k$  is the constant of proportionality. We call  $k$  the **heat transfer coefficient** and its units are calories/(time-deg). This constant is characteristic of the animal, and it measures how fast the animal conducts and transfers heat.

Therefore, the net rate  $f$  at which the animal receives heat, in calories per hour, is

$$f = q - k(\theta - T).$$

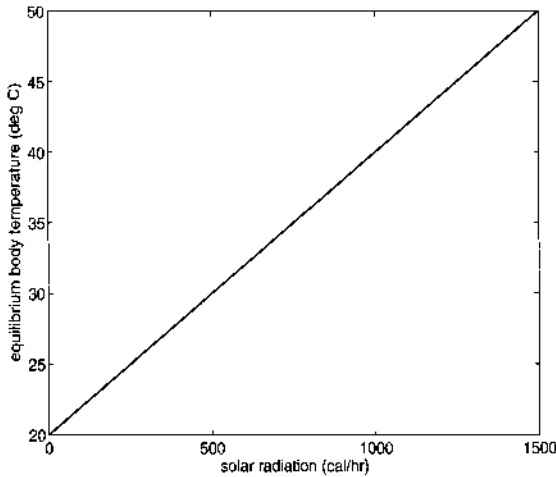
The quantity  $f$  is called the **heat flux**; the right side of this equation is the rate at which heat flows in minus the rate at which heat flows out. To fix the idea, reasonable values for  $k$  and  $q$  might be 1000 cal/(hours-deg) and 50 cal/h, respectively.

The animal's body temperature is in equilibrium when  $f = 0$ , or  $q = k(\theta - T)$ . Equilibrium occurs when the rate at which heat flows in equals the rate at which heat flows out. Consequently, the animal's equilibrium temperature is given by the formula

$$\theta_e = T + \frac{q}{k},$$

which occurs when the solar radiation balances the heat loss due to conduction. For example, if the environmental temperature were 20° C, then  $\theta_e = 40^\circ$  C, which may be near a lethal temperature for the animal. In this case the animal would have to seek shade or thermoregulate to lower its temperature.

We can plot the equilibrium temperature  $\theta_e$  vs.  $q$ , which is a linear relationship, using MATLAB commands in the command window (see Fig. 1.10):



**Figure 1.10** MATLAB plot of the equilibrium body temperature as a function of solar radiation when  $k = 50$  and  $T = 20$ .

```
k=50; T=20;  
q=0:1500;  
theta=T+q/k;  
plot(q,theta)  
xlabel('solar radiation (cal/h)')  
ylabel('equilibrium body temperature (deg C)')
```

## 1.4.2 Dynamic Temperatures

To understand how changing environmental temperatures affect the body temperature of an animal, we must develop a dynamic model, or a differential equation. In this section we develop such models and present two MATLAB procedures to calculate how an animal heats up.

In the preceding section we considered only steady states (equilibria). All the quantities were constant. We ignored the fact that the solar radiation  $q$  and the environmental temperature  $T$  may change during the day. If we include time-dependent parameters [e.g.,  $q = q(t)$  and  $T = T(t)$ ], we have a *dynamic* problem, and the body temperature  $\theta$  changes with time, or  $\theta = \theta(t)$ . If we knew formulas for  $q(t)$  and  $T(t)$ , how can we find  $\theta(t)$ ? In these cases we cannot use the equilibrium formulas from Section 1.4.1; they were derived under constant conditions, and now we are considering dynamical conditions.

Even if the parameters  $q$  and  $T$  are constant, we can still have a dynamical problem if the animal begins the day at a temperature different from its equilibrium temperature. For example, if its temperature is lower than the equilibrium value, we expect its temperature to increase in time up to that value. The reader should compare this heating problem to the problem of putting a turkey at room temperature in a hot oven and asking how fast it will heat up; that is, what is the temperature history?

To create a dynamical model, we first need to determine how time progresses. Does it progress continuously, or do we want it to tick off in discrete steps, say hourly? This question arises in every dynamic model. The answer often depends on when we take data, census a population, and so on. In the present problem, temperature is changing continuously in time.

To fix the idea, let us ask how we can obtain an expression for the rate of change of body temperature,  $d\theta/dt$ . From elementary science we know that the total amount of heat energy  $E$ , in calories, in a object of mass  $m$  is  $E = mc\theta$ , where  $c$  is the **specific heat** (cal/(g·deg)) of the object, or the amount of heat energy required to raise the temperature of a 1-g mass exactly 1 degree.<sup>1</sup> Therefore, the time rate of change of energy (cal/h) is

$$\frac{dE}{dt} = \frac{d}{dt}(mc\theta) = mc \frac{d\theta}{dt}. \quad (1.14)$$

We reason that this rate of change must equal the net energy flux into the animal,  $q - k(\theta - T)$ , because of the balance law. Hence,

$$mc \frac{d\theta}{dt} = q - k(\theta - T),$$

or

$$\frac{d\theta}{dt} = \frac{q}{mc} - \frac{k}{mc}(\theta - T). \quad (1.15)$$

This dynamical equation, which is called **Newton's law of cooling**, provides a relation between the unknown temperature  $\theta = \theta(t)$  and its derivative  $d\theta/dt$ , which is also unknown. Equation (1.15) is another example of a **differential equation**. To review our earlier comments, a differential equation is an equation that relates an unknown function to some of its derivatives. If we know the initial temperature  $\theta(0) = \theta_0$  of the animal, we fully expect that there should be a temperature function  $\theta(t)$  that describes its temperature at any time  $t > 0$ . The problem of finding the specific function  $\theta(t)$  that solves (1.15) with the initial condition  $\theta(0) = \theta_0$  is called in mathematics an **initial value problem**. By *solve* we mean that (1.15) is satisfied identically for all

<sup>1</sup> Note that the mass  $m$  of an object is related to its volume  $V$  and its density  $\rho$  by the formula  $\rho = m/V$ . So  $E = \rho V c \theta$ .

times  $t$  when the formulas for  $\theta = \theta(t)$  and its derivative  $d\theta/dt$  are substituted into the equation.

How can we discover the formula for the temperature function  $\theta = \theta(t)$ ? Well, there are techniques, taught in elementary courses in differential equations, for determining the unknown function that solves a simple differential equation. In Section 1.3 we learned a general method to solve this equation. Software packages (e.g., Maple, Mathematica, and the Symbolic Toolbox in MATLAB), and even calculators (e.g., the TI-89, or the TI Voyage 200), can find solution formulas for simple equations with an initial condition. In the next example we present a script MATLAB m-file that uses commands from the symbolic toolbox to solve and plot the solution to (1.15) with  $\theta(0) = \theta_0$ . The reader should enter this code in MATLAB and run it. The solution to (1.15) with  $\theta(0) = \theta_0$ , which is found by the first line of the code below, is

$$\theta(t) = \frac{q}{k} + T - e^{-kt/(mc)} (q + kT - k\theta_0) k^{-1}.$$

### Example 1.12

```
theta=dsolve('Dtheta=q/(m*c)-(k/(m*c))*(theta-T)','theta(0)=theta0');
theta=vectorize(theta);
k=50; q=1000; m=1; c=1; T=38; theta0=15;
t=0:.005:0.2;
theta=eval(theta);
plot(t,theta,'r')
ylim([0 60])
title('How an Animal Heats Up','FontSize',14)
xlabel('time (hrs)','FontSize',14)
ylabel('body temp (deg C)','FontSize',14)  □
```

Now comes a big caveat! For the most part, differential equations in ecology cannot be solved with a formula; another type of solution must be determined. One type is a numerical solution, which is only an approximate solution. We explain this next.

A **numerical solution** is an approximation to the actual solution  $\theta = \theta(t)$ . A numerical solution leads to approximate values of  $\theta = \theta(t)$  at a set of discrete times as well as an approximate graph of the actual solution. The idea is to select a discrete set of equally spaced times  $t_0 = 0$ ,  $t_1 = h$ ,  $t_2 = 2h$ ,  $t_3 = 3h$ , ..., where  $h$  is the **step size**. Note that  $t_{n+1} = t_n + h$  for  $n = 0, 1, 2, \dots$ . If we evaluate the differential equation at the discrete time  $t_n$ , we have

$$\theta'(t_n) = \frac{q}{mc} - \frac{k}{mc} (\theta(t_n) - T). \quad (1.16)$$

Now, if  $h$  is reasonably small, the derivative on the left side can be approximated by its difference quotient, or

$$\frac{\theta(t_{n+1}) - \theta(t_n)}{h} \approx \frac{q}{mc} - \frac{k}{mc} (\theta(t_n) - T). \quad (1.17)$$

This equation is approximate, but it allows us to solve for  $\theta(t_{n+1})$  in terms of  $\theta(t_n)$ . To this end, we have

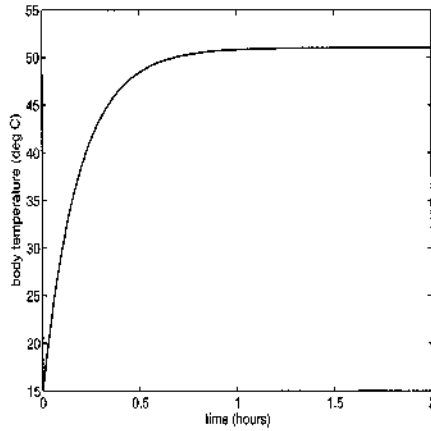
$$\theta(t_{n+1}) \approx \theta(t_n) + h \left( \frac{q}{mc} - \frac{k}{mc} (\theta(t_n) - T) \right). \quad (1.18)$$

We can use this approximate equation as a recursive algorithm to obtain approximate values of  $\theta(t)$  at the discrete times  $t_1, t_2, t_3, \dots$ . We simply take  $\theta(t_0)$ , which is given, and find  $\theta(t_1)$  from the formula. Then we take this computed value of  $\theta(t_1)$  and use the formula to compute  $\theta(t_2)$ , and so on, until we cover the range of times that we desire. This is easily accomplished using a recursive *for-end* loop on a computer. This numerical method is called the **Euler algorithm** for solving a differential equation and initial condition.

### Example 1.13

Let us fix the parameter values  $k = 50$ ,  $T = 35$ ,  $q = 800$ ,  $m = 10$ , and  $c = 1$ , and assume that the initial temperature of the animal is  $\theta(0) = 15$ . Next we create in MATLAB an m-file titled `NewtonHeating.m`, and we simulate time for 2 hours with 100 time steps, giving  $h = 0.02$ . Using a *for-end* loop we recursively calculate the temperatures `theta`, saving them in a list `thetahistory`, which we then plot. The program listing is given below and the temperature history is given in Fig. 1.11.

```
function NewtonHeating
clear all
theta=15; thetahistory=15;
k=50; T=35; c=1; q=800; m=10;
Time=2; N=100; h=Time/N;
for n=1:N
theta=theta+(h/(m*c))*(q-k*(theta-T));
thetahistory=[thetahistory theta];
end
t=0:h:Time;
plot(t,thetahistory)
xlabel('time'),
ylabel('body temperature')
axis([0 Time]) □
```



**Figure 1.11** Temperature vs. time of an animal.

### Example 1.14

Next we ask how to include variable environmental temperatures and variable sunlight. The same initial value problem holds, but now  $T$  and  $q$  are functions of  $t$ . Let us specify

$$T(t) = 26 - 11 \cos(\pi \times t/12)$$

$$q(t) = \frac{1000}{64}(1 - \cos(\pi \times t/12))^6.$$

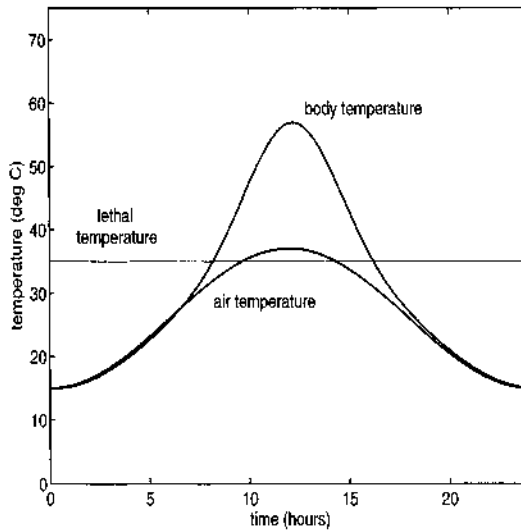
The preceding m-file is modified by including two function definitions (the last four lines) as follows:

```
function variabletemp
clear all
theta=15; thetahistory=15; k=50;
T=35; c=1; q=800; m=10; Time=24; N=10000; h=Time/N;
t=0;
for n=1:N
theta:=theta+(h/(m*c))*(sunlight(t)-k*(theta-ambient(t)));
thetahistory=[thetahistory,theta];
t=t+h;
end
hrs=0:h:Time;
plot(hrs,thetahistory,hrs,26-11*cos(pi*hrs/12),hrs,35)
xlabel('time (hours)'), ylabel('temperature (deg C)')
```

```

axis([0 Time0 75])
function que=sunlight(t)
que=(1000/64)*(1-cos(pi*t/12))^6;
function tee=ambient(t)
tee=26-11*cos(pi*t/12);

```



**Figure 1.12** Hourly body temperature of an animal.

Figure 1.12 shows the body temperature, the air temperature, and an upper lethal temperature for the animal over the period of a day. We can infer that the animal is active only when the body temperature is under the lethal value; during the period of higher body temperatures the animal would seek refuge in a cooler environment. Activity times are those times when a predator may be seeking prey, or when prey may be foraging. Changing temperature levels, such as those associated with global climate change, can affect the interactions of predators and prey; we discuss this issue in a later section.  $\square$

### 1.4.3 Development Rate

Temperature is a key factor in the rate at which many plants and poikilothermic animals develop and mature. Development is usually measured in degree-days, and the development rate is measured in degree-days per day. An organism accumulates 1 degree-day if its body temperature  $\theta(t)$  is maintained at exactly



1 degree above some minimal, threshold temperature  $\theta_h$  for one 24-hour period, 1 day. Of course, body temperature fluctuates throughout the day, so the total degree-days  $D(t)$  accumulated from time  $t = 0$  to time  $t$  is the integrated value

$$D(t) = \int_0^t [\theta(\tau) - \theta_h]^+ d\tau,$$

where  $\theta(t)$  is the body temperature and

$$[\theta(t) - \theta_h]^+ = \begin{cases} 0, & \theta(t) \leq \theta_h, \\ \theta(t) - \theta_h, & \theta(t) > \theta_h, \end{cases}$$

denotes the positive part of the difference between  $\theta(t)$  and  $\theta_h$ . Geometrically, the number of degree-days accumulated is the area from  $t = 0$  to  $t$  under the temperature curve  $\theta(t)$  and above the constant threshold temperature  $\theta_h$ . The development rate  $r$  is the derivative of  $D(t)$  and is given by

$$r(\theta(t)) = \frac{dD}{dt} = [\theta(t) - \theta_h]^+. \quad (1.19)$$

Full development, or maturity, occurs at a time  $T$  when the organism accumulates a certain number of degree-days  $D_0$ . Thus,

$$D_0 = D(T) = \int_0^T [\theta(\tau) - \theta_h]^+ d\tau = \int_0^T r(\theta(t)) dt.$$

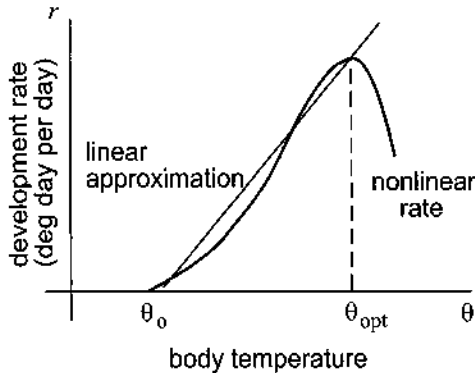
Therefore,  $D(t)$  satisfies the initial value problem

$$\frac{dD}{dt} = r(\theta(t)), \quad t > 0; \quad D(0) = 0. \quad (1.20)$$

The reader should take care going through these definitions and formulas, which are just restatements of the fundamental theorems of calculus.

We observe that the body temperature of a poikilothermic animal is typically a function of its microhabitat temperature, which in turn is related to the ambient air temperature. However, because poikilothermic animals thermoregulate, their actual body temperature remains in a fairly narrow range.

Equation (1.19) states that the development rate is a linear function of temperature. This, however, is just a commonly used approximation that holds for limited temperature ranges. In fact, most plants and animals have a nonlinear development rate curve that has the shape shown in Fig. 1.13. There is a minimal temperature below which no development occurs ( $\theta_h$ ), and there is an optimum temperature value  $\theta_m$  where the maximum rate occurs. Beyond  $\theta_m$  temperatures are often lethal and there is a rapid drop-off in development rate. Equation (1.20) also holds for any rate function  $r = r(\theta)$ .



**Figure 1.13** Nonlinear development rate (degree-days per day) as a function of body temperature  $\theta$ . Also shown is a linear approximation that many researchers use.

Often, the development is normalized such that full development occurs when  $D = 1$ . We can carry out this normalization by defining a new development variable  $x$  by

$$x = \frac{D}{D_0}.$$

Then  $x$  is dimensionless and

$$\frac{dx}{dt} = R(\theta(t)), \quad x(0) = 0,$$

where  $R(\theta) = (1/D_0)r(\theta)$  is the normalized development rate. Then the development time  $T$  is defined by  $x(T) = 1$ .

### Example 1.15

A grasshopper beginning its third instar (stage) has a development rate  $R(\theta) = 0.004[\theta - 15]^+$  during that instar. If its body temperature is a constant  $35^\circ\text{C}$  degrees throughout, how many days will it take the insect to reach the end of the instar? We have  $R(\theta) = 0.004[35 - 15] = 0.08$ . Then

$$1 = \int_0^T 0.08 dt = 0.08T.$$

Therefore,  $T = 12.5$  days.  $\square$

**Example 1.16**

Suppose that the body temperature varies periodically over a day from  $23^\circ\text{C}$  to  $33^\circ\text{C}$  deg via

$$\theta(t) = 28 + 5 \cos 2\pi t,$$

where  $t$  is given in days, and suppose that its development rate  $R(\theta)$  is given as in Example 1.15. To determine the time of development  $T$ , we must solve the differential equation

$$\frac{dx}{dt} = 28 + 5 \cos 2\pi t - 15, \quad x(0) = 0,$$

and stop the calculation when  $x = 1$ . Although this differential equation can be solved by direct integration, it is easier to write MATLAB code using the Euler method to solve the equation.

```
function degreeday
clear all
x=0; maxtime=30; numsteps=100000; h=0.01;
for n=1:numsteps
    if x<1
        x=x+h*0.004*(28+5*cos(2*pi*(n-1)*h)-15);
    else
        break
    end
end
x
days=n*h
```

The output is “days = 19.2.”  $\square$

**EXERCISES**

1. Suppose that the nonlethal body temperature range for an animal is  $22 \leq \theta_e \leq 38$ . If the animal's heat conduction coefficient is  $k = 50$ , find and sketch the region in *climate space*, the  $qT$  plane, where the animal's body temperature is in the nonlethal range.
2. Use the MATLAB program `NewtonHeating.m` to examine how animals of different sizes heat up. For example, use  $m = 5, 10, 25,$  and  $50$ . Can you make a general conclusion? Make similar calculations and conclusions for different values of  $k$ .

3. Suppose that the upper lethal temperature of the animal studied in Example 1.13 is  $35^\circ\text{C}$ . How long can the animal safely survive before having to seek shade? Draw the plot in Fig. 1.12 with the lethal temperature  $\theta = 35$  superimposed on the graph.
4. Sketch plots of the air temperature function  $T = T(t)$  and the solar flux  $q = q(t)$  in Example 1.14.
5. Referring to Exercise 3 in Section 1.1, state why changes in the number of species  $S$  on an island satisfies the differential equation

$$\frac{dS}{dt} = I \left( 1 - \frac{S}{P} \right) - \frac{ES}{P}.$$

- (a) Find a formula for the solution  $S = S(t)$  of the equation if  $S(0) = S_0$ .
  - (b) Plot the solution to the problem if the parameters are given by  $I = 8$  per year,  $E = 3$  per year,  $P = 48$  species, and  $S_0 = 11$  species.
  - (c) On your plot in part (b), graph the number of species vs. time when the island has an equilibrium number of species.
  - (d) Referring to part (b), graph the solution to the differential equation if the immigration rate is a periodic function given by  $I(t) = 8 - 5 \cos 4t$ .
6. In Exercise 2 in Section 1.1 we assumed that the growth rate of a spherical marine animal of radius  $r$  is the rate at which it consumes nutrients minus the rate at which it uses the nutrients. These two rates are proportional to the animal's surface area ( $4\pi r^2$ ) and to its volume ( $\frac{4}{3}\pi r^3$ ), respectively. Therefore, if we use mass  $m$  as a measure of growth, we can write the rate of increase in its mass as

$$\frac{dm}{dt} = 4a\pi r^2 - \frac{4b}{3}\pi r^3,$$

where  $a$  and  $b$  are constants of proportionality. But mass can be written as density times volume, or  $m = \rho \frac{4}{3}\pi r^3$ .

- (a) Using the chain rule of calculus to calculate  $dm/dt$  in terms of  $dr/dt$ , show that the radius of the animal is governed by the differential equation

$$\frac{dr}{dt} = \frac{a}{\rho} - \frac{b}{3\rho}r. \quad (1.21)$$

- (b) Use the MATLAB symbolic toolbox commands as in Example 1.12 to find a formula for the solution  $r(t)$  to equation (1.21) if  $r(0) = 0$ .
- (c) Take  $a = 200$ ,  $b = 100$ , and  $\rho = 10$ , and plot  $r$  vs.  $t$  from part (b).

7. An insect with a temperature threshold of  $12^\circ\text{C}$  has a linear development rate function with a maximum development rate occurring at  $40^\circ\text{C}$ . If it develops fully in 8 days at a constant temperature of  $40^\circ\text{C}$ , what is its normalized development rate  $R(\theta)$ ? How many days will it take to develop at a constant body temperature of  $35^\circ\text{C}$ ? How many days will it take to develop if its body temperature is

$$\theta = 30 + 10 \cos 2\pi t?$$

## 1.5 Dimensionless Variables

When we formulate models involving differential equations, the variables and the parameters have dimensions (such as time or distance), and they are given by specific units (such as minutes and meters). It is often a good idea to reformulate the model in a form where all the variables and parameters have no dimensions; that is, they are dimensionless. Usually, there is considerable economy associated with the dimensionless form of a problem because the number of parameters is reduced.

Consider the dynamic temperature model we derived in Section 1.4:

$$\frac{d\theta}{dt} = \frac{q}{mc} - \frac{k}{mc}(\theta - T), \quad (1.22)$$

$$\theta(0) = \theta_0. \quad (1.23)$$

The variables  $\theta$  and  $t$  have dimensions (degrees and time), and all the parameters have dimensions as well— $m$  is mass,  $q$  is energy per time,  $k$  is energy/(deg·time), and  $T$  and  $\theta_0$  are in degrees. Instead of measuring the temperature  $\theta$  of the animal, we can opt to measure the temperature relative to the ambient air temperature  $T$ . This leads to the introduction of a new dependent variable  $y$ , defined by

$$y = \frac{\theta}{T}, \quad (1.24)$$

which is dimensionless (degrees  $\div$  degrees). We say that  $y$  is a *dimensionless temperature*. Similarly, we can measure time  $t$  relative to the value  $mc/k$ , which has units of time. So we introduce a new *dimensionless* time  $\tau$  by defining

$$\tau = \frac{t}{mc/k}. \quad (1.25)$$

Now we can rewrite the model (1.22)–(1.23) in terms of the new dimensionless quantities. First, note that the derivative becomes

$$\frac{d\theta}{dt} = \frac{d(Ty)}{d((mc/k)\tau)} = \frac{kT}{mc} \frac{dy}{d\tau}.$$

Then (1.22) and (1.23) become

$$\begin{aligned}\frac{kT}{mc} \frac{dy}{d\tau} &= \frac{q}{mc} - \frac{k}{mc} (Ty - T), \\ Ty(0) &= \theta_0.\end{aligned}$$

This simplifies to

$$\frac{dy}{d\tau} = Q - (y - 1), \quad (1.26)$$

$$y(0) = B, \quad (1.27)$$

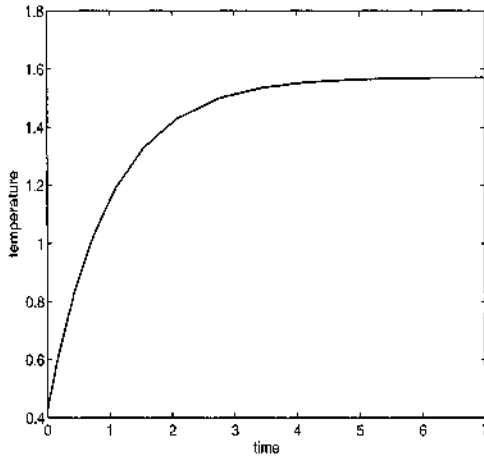
where  $Q$  and  $B$  are dimensionless constants given by

$$Q = \frac{q}{kT}, \quad B = \frac{\theta_0}{T}. \quad (1.28)$$

Let us review what we accomplished. By introducing dimensionless dependent and independent variables  $y$  and  $\tau$ , respectively, the dimensioned problem (1.22)–(1.23) has been replaced by the dimensionless problem (1.26)–(1.27). The dimensioned problem has six parameters, whereas the dimensionless form of the problem has only two! Therefore, if we were going to perform a parameter study, it would be much simpler to work in a two-dimensional  $Q, B$  parameter space than in a six-dimensional parameter space. Our analysis actually shows that there are only two independent parameters in this problem.

The value  $T$  against which we measure temperature is called a *temperature scale* for the problem; we say that the temperature has been *scaled* by  $T$ . Similarly,  $mc/k$  is a *time scale*, and we say that we have *scaled* time by  $mc/k$ . The time scale, which is often not unique, is roughly the order in which time processes occur in the problem; time scales should be chosen so that the dimensionless time  $\tau = t/T$  is neither large nor small. [A thorough discussion of dimensionless variables and how to select them may be found in Logan (2006); it is also shown that every consistent physical law can be reformulated in terms of dimensionless variables; the latter result is called the *Buckingham Pi Theorem*.]

In the last section we showed two ways in which an initial value problem for a differential equation could be solved using MATLAB: either with the symbolic toolbox, which gives an exact formula for the solution (when it works), or approximately, by discretizing time and writing a simple MATLAB m-file to perform the recursion required (the Euler algorithm). But there is another method that uses highly accurate, built-in MATLAB routines that solve differential equations automatically, with much greater accuracy than the Euler algorithm.



**Figure 1.14** Plot of the dimensionless temperature vs. dimensionless time.

### Example 1.17

Consider the dimensionless problem (1.26)–(1.27) with  $B = 0.4286$  and  $Q = 0.5714$ . [The values of  $B$  and  $Q$  are computed from (1.28) with  $q = 1000$ ,  $k = 50$ ,  $T = 35$ , and  $\theta_0 = 15$ .] The third line in the code uses the package `ode23`, which calls the differential equation `newton`, defined in the last three lines.

```
function heateqn
global B Q
B=0.4286; Q=0.5714;
[time,temp]=ode23(@newton,0,2,B);
plot(time,temp)
function yprime=newton(t,y)
global B Q
yprime=Q-(y-1);
```

A plot of the dimensionless solution is shown in Fig. 1.14.  $\square$

### EXERCISES

- Use the MATLAB routine `ode23` to find graphical solutions of the following initial value problems:

(a)  $dy/dt = -0.1y$ ,  $y(0) = 6$ .

$$(b) \quad dY/dt = 1.5Y(1 - Y/20), \quad Y(0) = 2.$$

$$(c) \quad dS/dt = 3(1 - S/30) - S/15, \quad S(0) = 6.$$

$$(d) \quad dy/dt = -0.1y + 5e^{-t}, \quad y(0) = 6.$$

2. In the biogeography model for the number of species on an island,

$$\frac{dS}{dt} = I \left( 1 - \frac{S}{P} \right) - \frac{ES}{P}.$$

find the dimensions of all the parameters and variables, and nondimensionalize the equation, scaling time by  $I^{-1}$  and species by  $P$ .

3. Nondimensionalize the problem (see Exercise 6 in Section 1.4)

$$\frac{dr}{dt} = \frac{a}{\rho} - \frac{b}{3\rho}r. \quad (1.29)$$

Use the MATLAB symbolic toolbox to find the solution to the dimensionless form of the differential equation with the initial condition  $r(0) = 0$ .

4. The logistic law for population growth is the differential equation

$$\frac{dP}{dt} = rP \left( 1 - \frac{P}{K} \right),$$

where  $t$  is time in days,  $P$  is the number of animals,  $r$  is the growth rate in days<sup>-1</sup>, and  $K$  is the carrying capacity in number of animals. Replace  $P$  and  $t$  by dimensionless variables and rewrite the logistics law in dimensionless form. (You will find that all of the parameters disappear!)

## 1.6 Descriptive Statistics

Researchers in all areas generate and collect data. Elementary techniques used to organize and understand the data sets are called *descriptive statistics*. In Chapter 6 we take a more advanced approach to data analysis.

Ecologists collect experimental data of all types. Statistics is the mathematical science of analyzing the data. Notwithstanding the classical quotes, “You can prove anything with statistics” (unknown) and “There are three kinds of lies: lies, damned lies, and statistics” (Disraeli), statistics offers well-defined mathematical methods to describe and understand the overall features of data and how the data might be used to predict future events and develop valid models. In this module we discuss how data can be described in simple terms that are familiar to most people.



There are three common characteristics of a data set that describe its nature: its *central tendency*, its *spread*, and its *shape*. The central tendency is a single value that is representative of the set. The usual measures of central tendency are the arithmetic mean, geometric mean, median, and mode. Each has advantages, depending on the intended purpose. (This is where statistics can lie!) If the data set is  $x_1, x_2, x_3, \dots, x_N$ , the **arithmetic mean** is

$$\bar{x} = \frac{x_1 + x_2 + x_3 + \dots + x_N}{N}.$$

We usually call the arithmetic mean the *average*, or just the *mean*. The **geometric mean** is

$$x_{\text{geom}} = (x_1 x_2 x_3 \dots x_N)^{1/N}.$$

One can show that  $\bar{x} > x_{\text{geom}}$ . The *median* is the value  $M$  for which half the values are lower and half the values are higher, and the *mode* is the value in the data set that occurs most often, or the most probable value; there may be more than one value of the mode.

Now consider the two data sets 2, 2, 2, 2, 2, 2, 2 and 0, 0, 0, 2, 2, 4, 4, 4. Both have mean  $\bar{x} = 2$ , but they are clearly different. In the first there is no spread; in the second there is spread. To determine the spread of the data, or its dispersion, we use the variance, which measures how the data spread about the mean. The **sample variance** is defined by

$$s^2 = \frac{(x_1 - \bar{x})^2 + (x_2 - \bar{x})^2 + \dots + (x_N - \bar{x})^2}{N - 1}.$$

The positive square root  $s$  of  $s^2$  is the **sample standard deviation**. The numerator is the sum of the squares of the deviations from the mean. There are other ways to define deviations from the center (mean) rather than the square of the difference, but we do not consider them in this book. In our simple illustration, the variance of the first data set is zero, whereas in the second data set the variance is  $24/7$ . There are reasons that we divide by  $N - 1$  rather than  $N$ .

Consider the two data sets 21, 28, 30, 33, 33, 35 and 881, 888, 890, 893, 893, 895. Most people would say that the first data set has more variability. The means are 30 and 890, but both have the same variance (5.0596) because the second data set is just the first data set with 860 added to each datum! Our intuitive answer is based on the size of the numbers involved. The **coefficient of variation** is defined by

$$\text{CV} = \frac{s_x}{\bar{x}}.$$

For these two data sets,  $\text{CV} = 0.0750$  and  $\text{CV} = 0.0025$ . We are comparing the variation with the size of the numbers—the standard deviation relative to the mean. The coefficient of variation is a dimensionless quantity that serves our intuition in measuring variability.

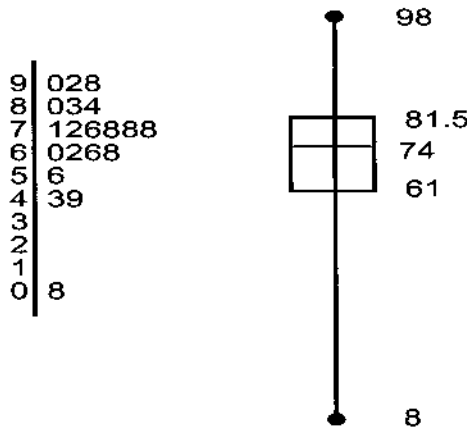


Figure 1.15 Stem plot of the data.

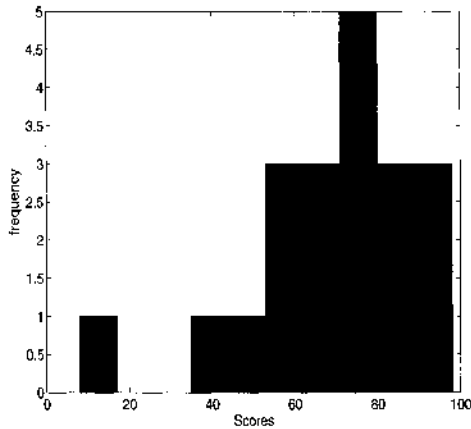
### Example 1.18

During an 8-year period from 1950 through 1957 data were collected on the number of Canadian lynx furs sold in various provinces. Ecologists use this information to estimate population sizes. The data are given in the vector  $\text{furs}=[9592\ 6653\ 12636\ 10876\ 13876\ 9660\ 8397\ 8958]$ . Then MATLAB can compute the basic statistics as follows:

MATLAB command	MATLAB response
<code>length(furs)</code>	8
<code>sum(furs)</code>	80648
<code>mean(furs)</code>	10081
<code>std(furs)</code>	2324.6
<code>max(furs)</code>	13386
<code>min(furs)</code>	6653
<code>median(furs)</code>	9626

If  $\text{year}=[1950\ 1951\ 1952\ 1953\ 1954\ 1955\ 1956\ 1957]$ , the commands `bar(year,furs)`, `plot(year,furs)`, and `scatter(year,furs)` plot a bar graph, a line graph, and a scatter diagram, respectively. The command `sort(furs)` sorts the data vector. The z-scores can be computed via  $z=(\text{furs}-\text{mean}(\text{furs}))/\text{std}$ . MATLAB responds  $z = [-0.2104\ -1.4747\ 1.0991\ 0.3420\ 1.6325\ -0.1811\ -0.7244\ -0.4831]$ . The coefficient of variation is  $CV=\text{std}(\text{furs})/\text{mean}(\text{furs})=0.2036$ , or about 20% variability.  $\square$

If the data set is large, we are interested in its shape, or distribution. Usually we draw a picture of the data, either a box plot or a stem-and-leaf plot.



**Figure 1.16** Histogram.

### Example 1.19

Figure 1.15 (left) shows a stem plot of 20 scores on a recent examination. The scores are 98, 92, 90, and so on, down to 8. To obtain a box plot we find the minimum  $L$  and maximum  $H$  of the scores:  $L = 8$  and  $H = 98$ . The median score is  $M = 74$ . The first quartile,  $Q_1$ , is the median of the numbers below the median  $M$ , and the third quartile,  $Q_3$ , is the median of the numbers above  $M$ . Here  $Q_1 = 61$  and  $Q_3 = 81.5$ . A box plot displays the numbers  $L$ ,  $Q_1$ ,  $M$ ,  $Q_3$ ,  $H$ , as shown in Fig. 1.16 (right). A histogram is a frequency diagram that displays the number of data values in certain bins. The MATLAB command `hist(scores,10)` creates a histogram (Fig. 1.16) of the scores that has 10 bins, where `scores` is a vector of the scores, or `scores=[98 92 90 84 83 ... 49 43 8]`. In place of the frequency on the vertical axis, we often plot the relative frequency, or percentage of the whole.  $\square$

### EXERCISE

1. In a medical study, 50 small rodents were infected with a virus, and the number of days they survived was recorded. The results are as follows:

40	47	53	57	57	60	68	68	75	76
80	80	87	89	95	95	97	98	99	101
108	110	120	121	123	123	125	128	129	130
133	135	136	139	140	144	150	154	165	171
190	202	221	251	280	305	330	362	380	402

- (a) Find the mean, sum, product, standard deviation, median, and coefficient of variation.
- (b) Sketch a stem plot with multiples of 10's in the left column.
- (c) Sketch a box plot.
- (d) Plot a histogram with eight bins.

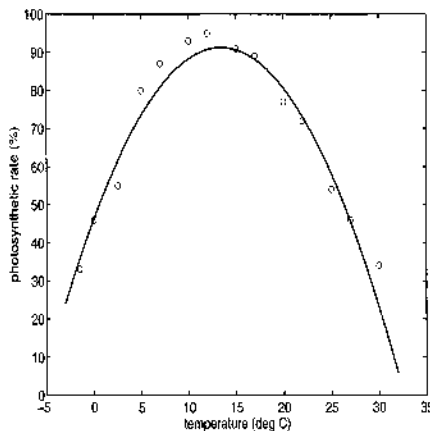
## 1.7 Regression and Curve Fitting

Fitting a curve to a data set is a good way of extracting the main features of data and discovering important patterns and trends. This process, called *regression*, is carried out by the method of least squares, and it is fundamental in developing descriptive models of ecological phenomena.

In this section we show how to set up a descriptive model of a relationship between two variables for which data have been collected. The process of constructing the model is called **regression**, or curve fitting. We begin with an example that illustrates the process.

The table shows data collected that relate the photosynthetic rate  $P$  of a certain species of grass to the temperature  $T$  of the environment.

$T$	-1.5	0	2.5	5	7	10	12	15	17	20	22	25	27	30
$P$	33	46	55	80	87	93	95	91	89	77	72	54	46	34



**Figure 1.17** Data with a parabolic trend.

$T$  is given in degrees Celsius and  $P$  is given as a percentage. Figure 1.17 [use `scatter(T,P)`] shows a scatter diagram of the data, and it appears that the shape, or trend, of the data is parabolic, as shown. This suggests a quadratic, descriptive model of the form

$$P = P(T) = a + bT + cT^2 \quad (1.30)$$

for some constants  $a$ ,  $b$ , and  $c$  to be selected. In this context, we sometimes call the independent variable  $T$  the *explanatory variable* and the dependent variable  $P$  the *response variable*. We want to find the constants for which the parabolic curve best fits the data. So this brings up the issue of what we mean by *best fit*. Imagine for a moment that we have values of  $a$ ,  $b$ , and  $c$ . There are many ways to measure the error we would make in approximating the data by (1.30), but the most successful way is to minimize the sum of squares of the errors at each data point. This is called the **method of least squares**. To be precise, at each temperature  $T_i$  the *error* in the approximation is  $d_i = P(T_i) - P_i$ . That is, the error at the  $i$ th data point is the computed value  $P(T_i)$  (found using the model) minus the observed value  $P_i$ . See Fig. 1.18. Then we define the total error

$$S = \sum_{i=1}^N (P(T_i) - P_i)^2 = \sum_{i=1}^N (a + bT_i + cT_i^2 - P_i)^2, \quad (1.31)$$

which is the sum of the squares of the errors over the  $N = 14$  data points. Notice that  $S$  depends on the choice of the constants  $a$ ,  $b$ , and  $c$ , or  $S = S(a, b, c)$ . The method of least squares is, simply:

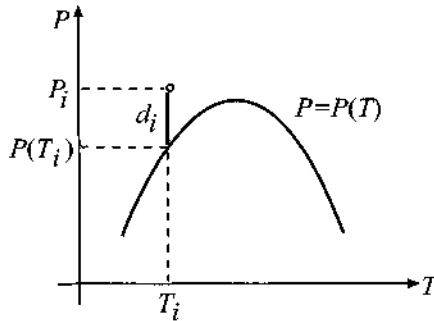
Find  $a$ ,  $b$ ,  $c$  such that  $S = S(a, b, c)$  is minimum.

This is a calculus problem. We recall that to minimize a function we take the derivative and set it equal to zero. Here there are three derivatives of  $S$ , one with respect to each variable. So if the values  $a$ ,  $b$ , and  $c$  provide a local minimum, then

$$S_a = 0, \quad S_b = 0, \quad S_c = 0,$$

where the subscripts on  $S$  mean to take the derivative with respect to that variable while holding the other variables fixed. Using the chain rule, and dropping the understood indices on the summation, we have

$$\begin{aligned} S_a &= 2 \sum (a + bT_i + cT_i^2 - P_i) = 0, \\ S_b &= 2 \sum (a + bT_i + cT_i^2 - P_i)T_i = 0, \\ S_c &= 2 \sum (a + bT_i + cT_i^2 - P_i)T_i^2 = 0. \end{aligned}$$



**Figure 1.18** The error at  $T_i$  is  $d_i = P(T_i) - P_i$ . The quantity  $d_i^2$  is the square of the error at that temperature. The total error is the sum of the  $d_i^2$  over all the points.

These equations can be written in the form of three linear equations in three unknowns,  $a$ ,  $b$ , and  $c$ . We write

$$\begin{aligned} Na + \left(\sum T\right)b + \left(\sum T^2\right)c &= \left(\sum P\right), \\ \left(\sum T\right)a + \left(\sum T^2\right)b + \left(\sum T^3\right)c &= \left(\sum PT\right), \\ \left(\sum T^2\right)a + \left(\sum T^3\right)b + \left(\sum T^4\right)c &= \left(\sum PT^2\right), \end{aligned} \quad (1.32)$$

where we are using the simplified notation

$$\sum T_i = \sum T, \quad \sum T_i^2 = \sum T^2, \dots$$

The system (1.32) can be solved by elementary methods to obtain  $a$ ,  $b$ , and  $c$ , and therefore the quadratic (1.30) that best fits the data.

We can easily set up the system (1.32) in MATLAB by defining vectors  $\mathbf{T}$  and  $\mathbf{P}$  containing the 14 data points, and then compute the sums that give the coefficients. For example,  $\sum T = \text{sum}(\mathbf{T})$ ,  $\sum T^2 = \text{sum}(\mathbf{T}.\wedge 2)$ , ...,  $\sum PT = \text{sum}(\mathbf{P}.*\mathbf{T})$ , and so on. In matrix notation, (1.32) has the form

$$A\mathbf{x} = \mathbf{f},$$

where the matrix  $A$  and the vector  $\mathbf{f}$  are given by

$$A = \begin{pmatrix} N & \sum T & \sum T^2 \\ \sum T & \sum T^2 & \sum T^3 \\ \sum T^2 & \sum T^3 & \sum T^4 \end{pmatrix}, \quad \mathbf{f} = \begin{pmatrix} \sum P \\ \sum PT \\ \sum PT^2 \end{pmatrix},$$

and  $\mathbf{x}$  is the vector of unknowns

$$\mathbf{x} = \begin{pmatrix} a \\ b \\ c \end{pmatrix}.$$

Once  $A$  and  $\mathbf{f}$  are entered into MATLAB as  $A$  and  $\mathbf{f}$ , the vector  $\mathbf{x}$  of coefficients can be found from the command  $A \setminus \mathbf{f}$ .

In practice, we do not always choose to solve the system (1.32). Rather, we use MATLAB to minimize (1.31) directly using a search method that is shown in the following m-file. We make a guess  $[1 \ 1 \ 1]$  and use the built-in command `fminsearch`.

```
function quadraticfit
global T P T=[-1.5 0 2.5 5 7 10 12 15 17 20 22 25 27 30];
P=[33 4655 80 87 93 95 91 89 77 72 54 46 34];
[x,fval]=fminsearch(quadSQ,[1 1 1])
function S=quadfitQ(x)
global T P
S=sum((x(1)+x(2)*T+x(3)*T.^2 -P).^2);
```

MATLAB returns  $\mathbf{x} = 46.3705 \quad 6.7671 \quad -0.2488$ ,  $\text{fval} = 292.1180$ . So the quadratic of best fit is

$$P(T) = 46.3705 + 6.7671T - 0.2488T^2.$$

Figure 1.17 is a plot of the data and the parabolic curve of best fit.

This process of least squares can be carried out to fit data with any function we choose—a linear function, a polynomial function, exponential functions, trigonometric functions, and so on. The idea is the same. Let  $x_1, \dots, x_N$  and  $y_1, \dots, y_N$  be two data sets. A scatter plot of all the points  $(x_i, y_i)$  usually suggests a function  $y = f(x, a_1, a_2, \dots, a_r)$ , depending on  $r$  parameters  $a_1, a_2, \dots, a_r$ , that may fit the data. The sum of the errors squared is a function  $S$  of the  $r$  parameters,

$$S(a_1, a_2, \dots, a_r) = \sum_{i=1}^N (f(x_i, a_1, a_2, \dots, a_r) - y_i)^2.$$

The least squares criterion is to determine the values  $a_1, a_2, \dots, a_r$  that minimize  $S$ .

If the  $r$  parameters  $a_1, a_2, \dots, a_r$  occur linearly in the model  $y = f(x, a_1, a_2, \dots, a_r)$ , the system of  $r$  equations

$$S_{a_1} = 0, \dots, S_{a_r} = 0$$

that we have to solve is a linear system. If the parameters occur nonlinearly, then the model is called a **nonlinear regression model** and the system of equations for the parameters is a nonlinear system. Typical nonlinear models are

$$y = a_1 + a_2 e^{a_3 x} \quad (\text{exponential})$$

$$y = \frac{a_1 e^{a_2 x}}{1 + a_1 e^{a_2 x}} \quad (\text{logistics}).$$

How do we measure the goodness of the fit when we obtain a regression formula? Let us answer this question for linear regression, where  $y = f(x) = a_1 + a_2 x$ . Then the least squares error is

$$S(a_1, a_2) = \sum_{i=1}^N (a_1 + a_2 x_i - y_i)^2.$$

We leave it to the reader (Exercise 1) to show that

$$a_1 = \frac{\sum X^2 \cdot \sum Y - \sum X \cdot \sum XY}{N \sum X^2 - (\sum X)^2}, \quad a_2 = \frac{N \sum XY - \sum X \cdot \sum Y}{N \sum X^2 - (\sum X)^2}, \quad (1.33)$$

with the obvious notation for the sums. Here  $a_1$  and  $a_2$  represent the  $y$ -intercept and the slope of the line of best fit, respectively. This straight line is called the **regression line**. The reader may be familiar with this idea from elementary algebra courses. At this point the calculation is strictly formal. What do the coefficients  $a_1$  and  $a_2$  have to do with the actual goodness of fit? With a little algebra we can show that

$$a_2 = r \frac{s_y}{s_x}, \quad a_1 = \bar{y} - a_2 \bar{x},$$

where  $\bar{x}$  and  $\bar{y}$  are the mean values of the  $x$  and  $y$  data sets and  $s_x$  and  $s_y$  are their sample standard deviations. The constant  $r$  is given by

$$r = \frac{1}{N-1} \sum \left( \frac{x_i - \bar{x}}{s_x} \right) \left( \frac{y_i - \bar{y}}{s_y} \right), \quad (1.34)$$

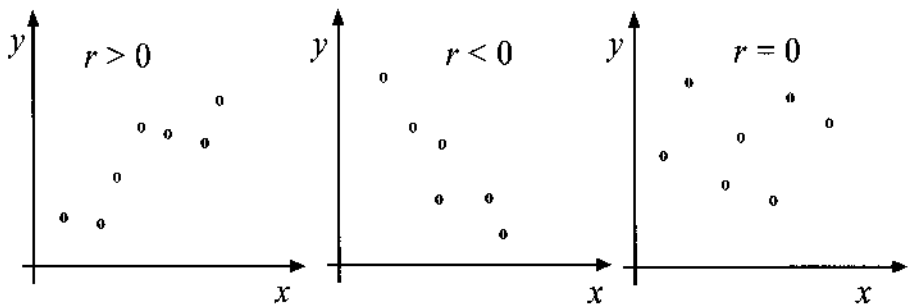
and it is a measure of how well the  $x$  and  $y$  data sets *correlate*; it is called the **correlation coefficient**. Note that  $r$  is an average of the product of  $z$ -scores for the two data sets. It is a dimensionless quantity with

$$-1 \leq r \leq 1.$$

(Can you show this?) We say that the data sets are *positively correlated* if the  $x_i$  values above the mean match up with the  $y_i$  values above the mean, and the values of  $x_i$  below the mean match up with the values of  $y_i$  below the mean. If they match up mostly in this way, the product of the  $z$ -scores will be positive



and  $r$  will be near its maximum value of 1, and the line of best fit will have a positive slope. If the  $x_i$  values above the mean match up with the  $y_i$  values below the mean, and conversely, the products of the  $z$ -scores are mostly negative and we say that the data sets are *negatively correlated*. In this case,  $r$  is near its minimum value of  $-1$  and the line of best fit has a negative slope. In the third case there may be little matching of the  $z$ -scores, and some terms in (1.34) will be positive and some will be negative. Thus, they will add and subtract and  $r$  will be near zero; in this case we say that there is no correlation. Figure 1.19 illustrates the three cases. If we find the regression line, we can ask how well it

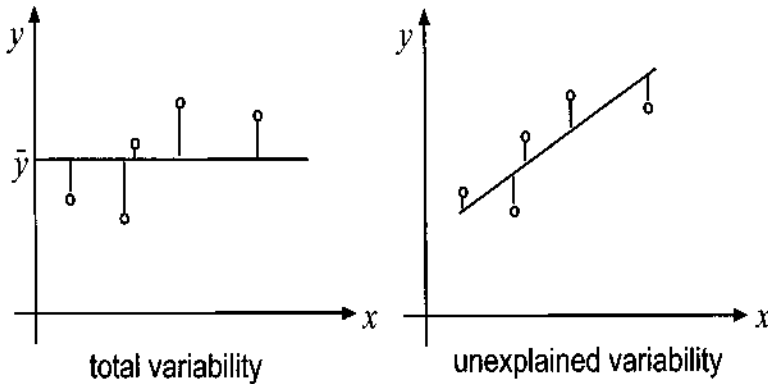


**Figure 1.19** Three sets of data, showing positive, negative, and no correlation.

explains the data. The original variability of the response variable is measured with respect to the mean value of the  $y_i$  by  $\sum(y_i - \bar{y})^2$ . After the regression line is fit in, there is still unexplained variability measured by how much the regression line deviates from the data, or  $\sum(y_i - Y_i)^2$ , where  $Y_i = a_1 + a_2x_i$  is the estimated value on the regression line. The original variation minus the unexplained variability is the explained variability. See Fig. 1.20. Measured relative to the original amount of variability, we have

$$\text{explained variability} = R^2 = \frac{\sum(y_i - \bar{y})^2 - \sum(y_i - Y_i)^2}{\sum(y_i - \bar{y})^2}.$$

With algebra one can show that this value is equal to the square of the correlation coefficient,  $R^2 = r^2$ . Thus,  $100 \times r^2$  is interpreted as the *percentage of the total variability that is explained by the linear fit*. So a value, for example,  $r^2 = 0.91$ , would mean that 91% of the data is explained by the linear model. Despite the high values of  $r^2$ , we have to be careful in remembering that *correlation does not imply causation*. Although there are other measures of fit, the value  $R^2$  is common and it is in the output for most statistical packages. Moreover, the  $R^2$  value computed in (1.7) does not require that the model be linear, so it may be extended to nonlinear regression.



**Figure 1.20** Total variability and unexplained variability.

### Remark 1.20

There is another MATLAB routine that determines the best least squares *polynomial*

$$p(x) = b_0x^n + b_1x^{n-1} + \cdots + b_{n-1}x + b_n$$

that fits the data  $x_1, \dots, x_N$  and  $y_1, \dots, y_N$ . If the data are typed in as vectors  $x$  and  $y$ , then `polyfit(x,y,n)` returns the coefficients  $b_0, b_1, \dots, b_n$ . (Note the order of the coefficients.) This routine may be used to find the regression line when  $n = 1$ .

### Example 1.21

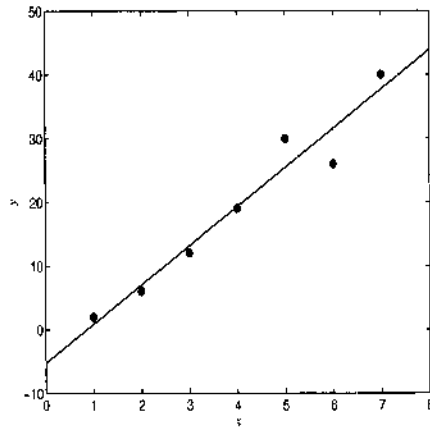
The following m-file plots the data and the regression line. The result is shown in Fig. 1.21.

```
function polynomialfit
x=[1 2 3 4 5 6 7]; y=[2 6 12 19 30 26 40];
p=polyfit(x,y,1);
xx=0:1:8;
plot(x,y,'o',xx,polyval(p,xx),'-','MarkerSize',25,'LineWidth',1.5)
```

Many calculators also perform simple regression.  $\square$

## EXERCISES

1. (Linear regression) For linear regression, derive the formulas (1.33) for the constants  $a_1$  and  $a_2$ . [Hint: Multivariable calculus is required for this problem; set the partial derivatives of  $S(a_1, a_2)$  equal to zero and solve for  $a_1$  and  $a_2$ .]



**Figure 1.21** Regression line and data.

- The average weights (in kilograms) of female black bears in age classes 1 through 15 years were found to be 35, 55, 68, 70, 71, 75, 79, 82, 81, 80, 78, 99, 99, 82. Fit the data with a straight line and determine the goodness of the fit.
- In Exercise 2 fit the data with a logistics curve. Compute the  $R^2$  value and compare to the linear fit.
- The population of insects in a hostile environment over days  $t = 0, 1, 3, 4$  was found to be  $y = 200, 129, 58,$  and  $33,$  respectively. Find the curve of the form  $y = ae^{-bt}$  that best fits the data in the least squares sense.
- The pesticide DDT was one reason for the decline of the bald eagle population. In 1972 the pesticide was banned and eagle populations began to rise. From 1973 to 1979 the number of young eagles per unit area were counted to be 0.78, 0.86, 0.96, 0.82, 0.98, 1.12, and 0.82. Find the regression line and the  $R^2$  value, and then use the regression line to predict the number of young eagles for 1982 through 1985.

## 1.8 Reference Notes

There is an extensive list of broadly based textbooks below, all covering aspects of mathematical ecology and biology. These are the texts on our shelves, and all of them have something to offer a reader; some are elementary, some are advanced, and some are more mathematically than biologically oriented. We

recognize the omission of many other excellent books, but we wanted to list the books with which we are extremely familiar. We have found success using several of these in courses in mathematical biology (in both mathematics and biology departments) over the last seven years. We have not listed specialty books, which is an even longer list.

Three books are listed that focus on modeling issues. Mooney & Smith (1999) is an excellent elementary introduction. The classic text in applied mathematics is Lin & Segel (1974), and Logan (2006) has a beginning chapter devoted to modeling issues. An outstanding instruction manual for MATLAB, with examples, is Higham & Higham (2005).

Some of the texts fall into the elementary class in that they require limited mathematics skills at the beginning. Allman & Rhodes (2004), Vandermeer & Goldberg (2003), Gotelli (2008), Berryman (1999), Hastings (1997), and Otto & Day (2007) fit into this category, and are all excellent. Each requires grasping at the mathematics as the exposition proceeds. Neuhauser's beginning (2004) calculus text for biology students is an outstanding resource and it includes material on linear algebra, matrices, differential equations, and probability.

The remaining books on the list fit into the category of mathematical modeling in biology, and they introduce a substantial amount of mathematical ideas and symbolism. Some are penned by biologists, and some by mathematicians, but both lie in that intersection that brings the ideas of mathematical modeling and formalism to some of the central questions in biology.

A notable book is that of Roughgarden (1998), who incorporates MATLAB programs and techniques thoroughly into an exposition of ecological principles. Two excellent mathematical resources for optimal control in biology settings are Clark (2005) and Lenhart & Workman (2007). Wodarz (2007) is a very readable introduction to mathematical modeling of the virus-immune system dynamics and it shows the close similarities to ecosystem models.

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