neurons. They received the Nobel Prize in Physiology and Medicine for this work in 1963 and, perhaps more impressively, developed a model that is still used today to study neurons and other types of cells.

In general, maintenance of biological systems depends on preserving the distinction between inside and outside while maintaining flows of necessary materials from outside to inside and vice versa. The neuron maintains itself at a different electrical potential from the surrounding tissue in order to be able to respond, while remaining ready to exchange ions with the outside to create the response. As applied mathematicians, we **quantify the basic measurements**, the concentrations of various substances inside and outside the cell. The **dynamic rules** express how concentrations change, generally as a function of properties of the cell membrane. Most commonly, the rule describes the process of **diffusion**, movement of materials from regions of high concentration to regions of low concentration.

1.1.3 Replication: Models of Genetics

Although Mendel's work on genetics from the 1860s had been rediscovered around 1900, many biologists in the following decades remained unconvinced of his proposed mechanism of genetic transmission. In particular, it was unclear whether Darwin's theory of evolution by natural selection was consistent with this, or any other, proposed mechanism.

Working independently, biologists R. A. Fisher, J.B.S. Haldane, and Sewall Wright developed mathematical models of the dynamics of evolution in natural populations. These scientists **quantified the basic measurement**, in this case the number of individuals with a particular allele (a version of a gene). Their **dynamic rules** described how many individuals in a subsequent generation would have a particular allele as a function of numerous factors, including **selection** (differential success of particular types in reproducing), and **drift** (the workings of chance). They showed that Mendel's ideas were indeed consistent with observations of evolution. This work led to the development of methods of genetic analysis used to analyze DNA sequences today. We study a simple model of selection in Section 1.10 and examine some of the consequences of Mendel's laws in Section 6.2.

1.1.4 Types of Dynamical Systems

We will study each of the three processes, growth, maintenance, and replication, with three types of dynamical system, termed **discrete-time**, **continuous time**, and **probabilistic**. The first two types are **deterministic**, meaning that the dynamics includes no chance factors. In this case, the values of the basic measurements can be predicted exactly at all future times. Probabilistic dynamical systems include chance factors and values can be predicted only on average.

Discrete-Time Dynamical Systems

Discrete-time dynamical systems describe a sequence of measurements made at equally spaced intervals (Figure 1.1.4). These dynamical systems are described mathematically by a rule that gives the value at one time as a function of the value at the previous time. For example, a discrete-time dynamical system describing population growth is a rule that gives the population in one year as a function of the population in the previous year. A discrete-time dynamical system describing the concentration of oxygen in the lung is a rule that gives the concentration of oxygen in a lung after one breath as a function of the concentration after the previous breath. A discrete-time dynamical system describing the spread of a mutant allele is a rule that gives the number of mutant alleles in one generation as a function of the number in the previous generation. Mathematical analysis of the rule can make scientific predictions, such as the maximum population size, the average concentration of oxygen in the lung, or the final number of mutant alleles. The study of these systems requires the mathematical methods of modeling (Chapter 1) and **differential calculus** (Chapters 2 and 3).

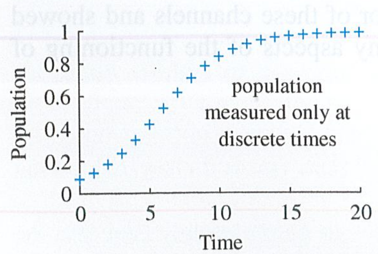


FIGURE 1.1.4
Measurements described by a discrete-time dynamical system

Continuous-Time Dynamical Systems

Continuous-time dynamical systems, usually called **differential equations**, describe measurements that are collected over an entire time interval (Figure 1.1.5). A differential equation consists of a rule that gives the **instantaneous rate of change** of a set of measurements. The miracle of differential equations is that information about a system at one time is sufficient to predict the state of a system at all future times. For example, a continuous-time dynamical system describing the growth of a population is a rule that gives the rate of change of population size as a function of the population size itself. The study of these systems requires the mathematical methods of **integral calculus** (Chapters 4 and 5).

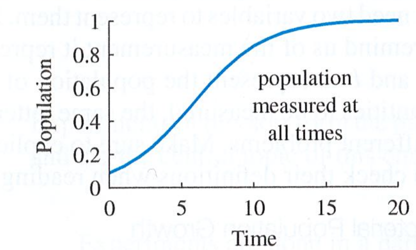


FIGURE 1.1.5
Measurements described by a continuous-time dynamical system

Probabilistic Dynamical Systems

Probabilistic dynamical systems describe measurements, in either discrete or continuous time, that are affected by random factors (Figure 1.1.6). The rule indicating how the measurements at one time depend on measurements at the previous time includes random factors. Rather than knowing with certainty the next measurements, we know only a set of possible outcomes and their associated probabilities and can therefore predict the outcome only in a probabilistic or statistical sense. For example, a probabilistic dynamical system describing population growth is a rule that gives the **probability** that a population has a particular size in one year as a function of the population in the previous year. The study of such systems requires the mathematical methods of **probability theory** (Chapters 6-7).

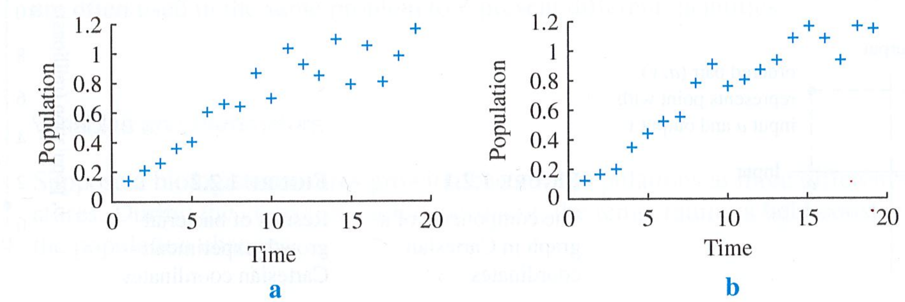


FIGURE 1.1.6
Two sets of measurements described by the same probabilistic dynamical system in discrete time. The two panels show the results of two realizations of the same mathematical model that differ only due to random factors.

1.2 Variables, Parameters, and Functions in Biology

Quantitative science is built upon measurements. Mathematics provides the notation for describing and thinking about measurements and relations between them. In fact, the development of clear notation for measurements and relations was essential for the progress of modern science. In this section, we develop the algebraic notation needed to describe measurements, introducing **variables** to describe measurements that change **during** the course of an experiment and **parameters** that remain constant during an experiment but can change **between** different experiments. The most important types of relations between measurements are described with **functions**, where the value of one can be computed from the value of the other. We will review how to graph functions, how to combine them with **addition**, **multiplication**, and **composition**, and how to recognize which functions have an **inverse** and how to compute it.

1.2.1 Describing Measurements with Variables, Parameters, and Graphs

Algebra uses letters or other symbols to represent numerical quantities.

Definition 1.1 A **variable** is a symbol that represents a measurement that can change during the course of an experiment.

A simple experiment measures how the population of bacteria in a culture changes over time. Because two changing quantities are being measured, time and bacterial population, we need two variables to represent them. In applied mathematics, we choose variables that remind us of the measurement it represents. In this case, we can use t to represent time and b to represent the population of bacteria. Because there are fewer letters than quantities to be measured, the same letter can be used to represent different quantities in different problems. Make sure to explicitly define variables when writing a model and to check their definitions when reading one.

Example 1.2.1 Describing Bacterial Population Growth

The table to the left lists measurements of bacterial population size (in millions), denoted by the variable b, at different times t after the beginning of an experiment.

t	b
0.0	1.00
1.0	1.24
2.0	1.95
3.0	3.14
4.0	4.81
5.0	6.95
6.0	9.57

Thinking about data is often easier with a graph. Graphs are drawn using **Cartesian coordinates,** which use two perpendicular number lines called the **axes** to describe two numbers (Figure 1.2.1). The argument is placed on the horizontal axis (sometimes called the x-axis), and the value on the vertical axis (sometimes called the y-axis). The crossing point of the two axes is the **origin**. The axes are labeled with the variable name, the measurement it represents, and often the units of measurement (Section 1.3). **Never draw a graph without labeling the axes.**

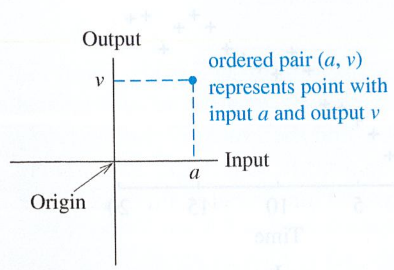


FIGURE 1.2.1
The components of a graph in Cartesian coordinates

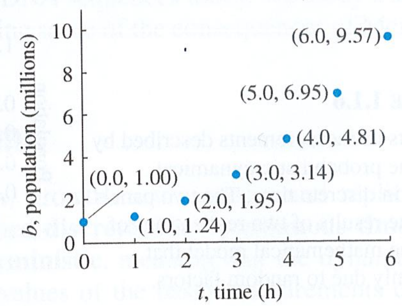


FIGURE 1.2.2
Results of bacterial growth experiment: Cartesian coordinates

Example 1.2.2 Graphing Data Describing Bacterial Population Growth

To graph the six data points in Example 1.2.1, plot each point by moving a distance t to the right of the origin along the horizontal axis and a distance b up from the origin along the vertical axis (Figure 1.2.2). For example, the data point at $t = 4.0$ is graphed by moving a distance 4.0 to the right of the origin on the horizontal axis and a distance 4.81 up from the origin on the vertical axis.

Example 1.2.3 Describing the Dynamics of a Bacterial Population

Suppose several bacterial cultures with different initial population sizes are grown in controlled conditions for one hour and then carefully counted. The population size acts as the basic measurement at both times. We must use different variables to represent these values, and choose to use **subscripts** to distinguish them. In particular, we let b_i (for the **initial** population) represent the population at the beginning of the experiment, and b_f (for the **final** population) represent the population at the end (Figure 1.2.3). The following table presents the results for six colonies.

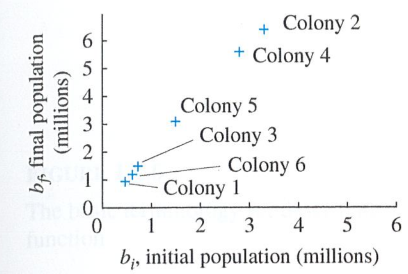


FIGURE 1.2.3
Results of alternative bacterial growth experiment

Colony	Initial Population, b_i	Final Population, b_f
1	0.47	0.94
2	3.3	6.6
3	0.73	1.46
4	2.8	5.6
5	1.5	3.0
6	0.62	1.24

Experiments of this sort form the basis of discrete-time dynamical systems (Section 1.5) and are the central topic of this chapter.

Experiments are done in a particular set of controlled conditions that remain constant during the experiment. However, these conditions might differ between experiments.

Definition 1.2 A **parameter** is a symbol that represents a measurement that does not change during the course of an experiment.

Different experiments tracking the growth of bacterial populations over time might take place at temperatures that are constant during an experiment but that differ between experiments. The temperature, in this case, is represented by a parameter. Parameters are also represented by symbols that recall the measurement. We can use T to represent temperature. In applied mathematics, capital letters (like T) and small letters (like t) are often used in the same problem to represent different quantities.

Example 1.2.4 Variables and Parameters

Suppose a biologist measures growing bacterial populations at three different temperatures. During the course of each experiment, the temperature is held constant, while the population changes.

t	b when $T = 25°$	b when $T = 35°$	b when $T = 45°$
0.0	1.00	1.00	1.00
1.0	1.14	1.45	0.93
2.0	1.30	2.10	0.87
3.0	1.48	3.03	0.81
4.0	1.68	4.39	0.76
5.0	1.92	6.36	0.70
6.0	2.18	9.21	0.66

Figure 1.2.4 compares the sizes of the three populations. The population grows most quickly at the intermediate temperature of 35°C and declines at the high temperature of 45°C.

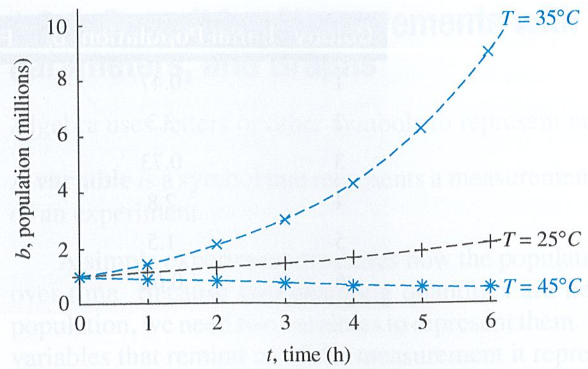


FIGURE 1.2.4
Results of bacterial growth experiment at three temperatures

1.2.2 Describing Relations Between Measurements with Functions

Numbers describe measurements, and **functions** describe **relations** between measurements. For example, bacterial population growth relates two measurements, denoted by the variables t and b. In general, a **relation** between two variables is the set of all pairs of values that are possible.

Example 1.2.5 A Relation Between Temperature and Population Size

T	P
25.0	2.18
25.0	2.45
25.0	2.10
25.0	3.03
35.0	9.21
35.0	7.39
35.0	6.36
45.0	0.66
45.0	0.93

Suppose the temperature T and final population size P are measured for nine populations, with the following results (Figure 1.2.5). These values could result from repeating the experiment in Example 1.2.4 several times and measuring the population at $t = 6.0$.

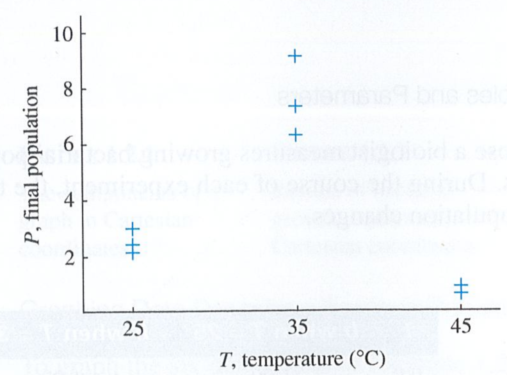


FIGURE 1.2.5
Final population size at three temperatures

Different values of the population P are related to each temperature, perhaps due to differences in experimental conditions.

A **function** describes a specific, and important, type of relation. A function is a mathematical object that takes something (like a number) as input, performs an operation on it, and returns a new object (like another number). The input is called the **argument** (or the **independent variable**), and the output is called the **value** (or the **dependent variable**) (Figure 1.2.6). The set of all possible things that a function can accept as inputs is called the **domain**; the set of all possible things a function **can** return as outputs is called the **co-domain**; and the set of all things the function **does** return as outputs is called the **range**.

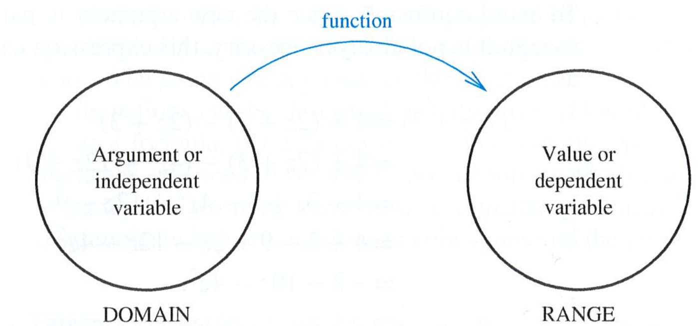


FIGURE 1.2.6
The basic terminology for describing a function

Example 1.2.6 Data That Can Be Described by a Function

The data in Example 1.2.1 can be described by a function. Each value of the input t is associated with only a single value of the output b.

Example 1.2.7 Graphing a Function from Its Formula

To graph a function from a formula, it is easiest to start by plugging in some representative arguments. Suppose we wish to graph the function $f(x) = 4 + x - x^2$ for $x \geq 0$ (a way of restricting the domain to just positive numbers and zero). Evaluating the function at the arguments 0, 1, 2 and 3, we find

$$f(0) = 4 + 0 - 0^2 = 4$$
$$f(1) = 4 + 1 - 1^2 = 4$$
$$f(2) = 4 + 2 - 2^2 = 2$$
$$f(3) = 4 + 3 - 3^2 = -2.$$

We plot the four ordered pairs $(0, 4)$, $(1, 4)$, $(2, 2)$, and $(3, -2)$, and connect them with a smooth curve (Figure 1.2.7). This is precisely the method that calculators and computers use to plot functions, except that they generally use 20 or more points to make a graph. Because the output takes on negative values, the horizontal axis is positioned at a negative value of the output. Rather than drawing axes through the origin $(0, 0)$, graphs of measurements often place the axes to cross at a value that enhances readability.

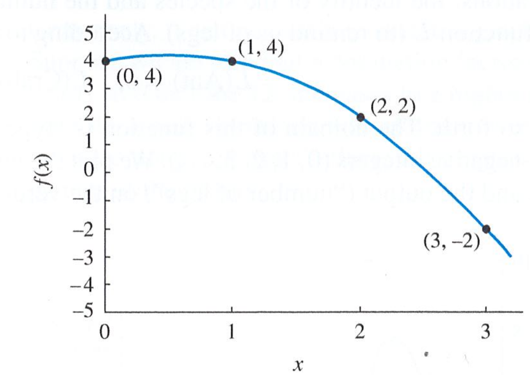


FIGURE 1.2.7
Plotting a function from its formula

One of the great advantages of functional notation is that functions can be evaluated at arguments that consist of parameters and variables (combinations of letters). To do so, replace the basic variable in the formula with the new argument, however complicated.

Example 1.2.8 Evaluating a Function at a Complicated Argument

To evaluate the function $f(x) = 4 + x - x^2$ (Example 1.2.7) at the more complicated argument $2z + 3$, replace all occurrences of x in the formula with the new argument $2z + 3$:

$$f(2z + 3) = 4 + (2z + 3) - (2z + 3)^2.$$

To avoid confusion, place the new argument in parentheses wherever it appears. Although it is not always necessary, this expression can be multiplied out and simplified as

$$\begin{aligned} f(2z+3) &= 4+(2z+3)-(2z+3)^2 && \text{original expression} \\ &= 4+(2z+3)-(4z^2+12z+9) && \text{expand the square} \\ &= 4+2z+3-4z^2-12z-9 && \text{multiply negative sign through} \\ &= 4+3-9+2z-12z-4z^2 && \text{group like terms} \\ &= -2-10z-4z^2. && \text{combine like terms} \end{aligned}$$

Example 1.2.9 A Function Describing Bacterial Population Growth

The population in Examples 1.2.1 and 1.2.2 obeys the formula

$$b(t) = \frac{t^2}{4.2} + 1.0.$$

The population size b is a function of the time t. The **argument** of the function b is t, the time after the beginning of the experiment. The **value** of the function is the population of bacteria. The formula summarizes the relation between these two measurements: the output is found by squaring the input, dividing by 4.2, and then adding 1.0.

The function b takes time after the beginning of the experiment as its input. Because negative time does not make sense in this case, the **domain** of this function consists of all positive numbers and zero. We write that

$$b \text{ is defined on the domain } t \geq 0.$$

Besides negative numbers, fruits, bacteria, and functions lie outside the domain of b. Because the function b returns population sizes as output, the **range** of b also consists of all positive numbers and zero. We write that

$$b \text{ has range } b \geq 0.$$

Example 1.2.10 A Function with Non-numeric Domain

Animal	Number of Legs
Ant	6
Crab	10
Duck	2
Fish	0
Human being	2
Mouse	4
Spider	8

Consider the following table of data. These data describe a relation between two observations: the identity of the species and the number of legs. We can express this as the function L (to remind us of legs). According to the table,

$$L(\text{Ant}) = 6, \quad L(\text{Crab}) = 10$$

and so forth. The domain of this function is "types of animals," and the range is the non-negative integers (0, 1, 2, 3, ...). We plot the input ("animal") along the horizontal axis and the output ("number of legs") on the vertical axis (Figure 1.2.8).

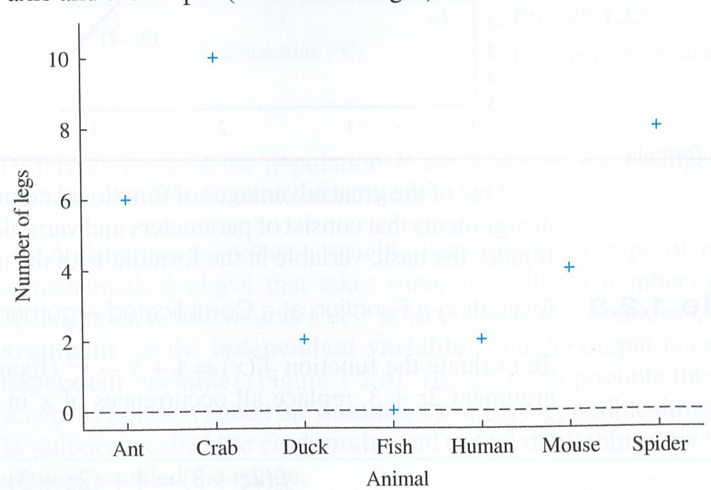


FIGURE 1.2.8
Numbers of legs on various organisms plotted on a graph

It is important to realize that the graph of a function is *not* the function, just as the spot labeled 2 on the number line is not the number 2 and a photograph of a dog is not a dog. The graph is a depiction of the function.

Functions can be described in four ways: (1) numerically (by means of a table), (2) as a formula, (3) as a graph, and (4) verbally. As biologists and applied mathematicians, we need to be able to use all four methods and to translate between them. In particular, we must know how to translate graphical information into words that communicate key observations to colleagues and the public.

Example 1.2.11 Describing Results in Graphs and Words

The following table presents a more complicated pattern of population size change.

Time	Population Size
0	0.86
2	1.69
4	2.98
6	4.49
8	5.69
10	6.17
12	5.95
14	5.29
16	4.41
18	3.50
20	2.67
22	1.96
24	1.41

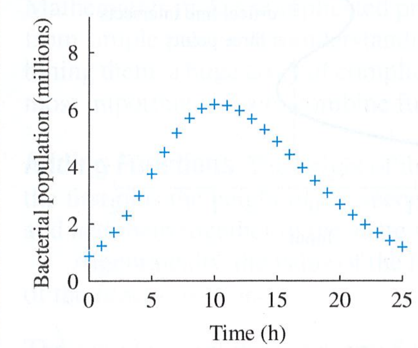


FIGURE 1.2.9
The population of bacteria in a culture

We can see (more easily from Figure 1.2.9 than from the table) that the bacterial population grew during the first ten hours and declined thereafter. The population reached a maximum at time 10. This graph and its description can be used to understand the results even without a mathematical formula.

Example 1.2.12 Sketching a Graph from a Verbal Description

Conversely, it can be useful to sketch a graph of a function from a verbal description. Suppose we are told that a population increases between time 0 and time 5, decreases nearly to 0 by time 12, increases to a higher maximum at time 20, and goes extinct at time 30. A graph translates this information into pictorial form (Figure 1.2.10). Because we were not given exact values, the graph is not exact. It instead gives a **qualitative** picture of the results.

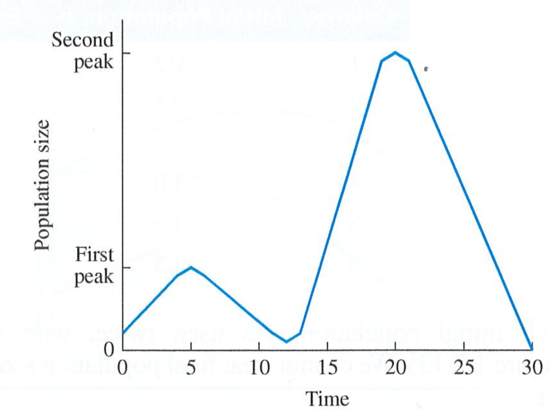


FIGURE 1.2.10
A bacterial population plotted from a verbal description

Not all relations are described by functions. A function must give a unique output for a given input. Relations between measurements can be more complicated. The **vertical line test** provides a graphical method to recognize relations that cannot be described by functions.

The Vertical Line Test A relation is not a function if some vertical line crosses the graph two or more times. In Figure 1.2.11, there are three outputs associated with the input 0.2: 1.12, 1.79, and 3.09. This relationship cannot be described with a function.

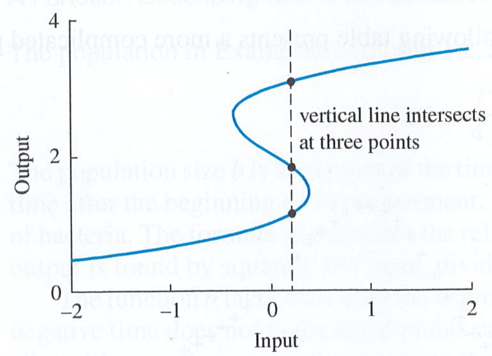


FIGURE 1.2.11
The vertical line test

There is nothing wrong with relations that cannot be described by functions. Experiments, even when performed under apparently identical conditions, rarely produce identical results. As we will see when we study statistics (Chapter 8) functions are a useful mathematical idealization of the expected or average result of an experiment.

Example 1.2.13 A Mathematical Formula That Gives a Relation That Is Not a Function

The set of solutions for x and y from the formula

$$x^2 + y^2 = 1$$

is the circle of radius 1 centered at the origin (Figure 1.2.12). Each value of x between $x = -1$ and $x = 1$ is associated with two different values of y. For example, the value $x = 0.6$ is associated with both $y = 0.8$ and $y = -0.8$.

Example 1.2.14 A Relation That Is Not a Function

Suppose several bacterial cultures with different initial population sizes are grown in controlled conditions for one hour, as in Example 1.2.3, with the following results.

Colony	Initial Population, b_i	Final Population, b_f
1	0.5	0.9
2	0.5	1.0
3	1.0	2.2
4	1.0	1.9
5	1.5	3.0
6	1.5	2.8

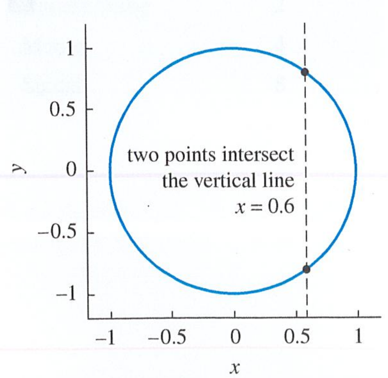


FIGURE 1.2.12
The circle describes a relation that is not a function

Each initial population was used twice, with similar but not identical results (Figure 1.2.13). We cannot treat final population size as a function of initial population size.

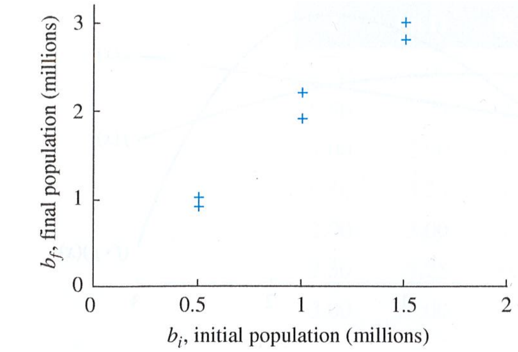


FIGURE 1.2.13
Bacterial growth experiment where results are not a function

1.2.3 Combining Functions

Mathematics makes complicated problems simpler by building complicated structures from simple pieces. By understanding each of the simple pieces and the rules for combining them, a huge array of complicated relations can be analyzed and understood. The most important ways to combine functions are as **sums**, **products**, and **compositions**.

Adding Functions The height of the graph of the sum of two functions is the height of the first plus the height of the second. Geometrically, we can graph each of the pieces and add them together in the same way.

Algebraically, the value of the function $f + g$ is computed as the sum of the values of the functions f and g.

Definition 1.3 The sum $f + g$ of the functions f and g is the function that takes on the value

$$(f + g)(x) = f(x) + g(x).$$

Multiplying Functions The value of the product $f \cdot g$ is computed as the product of the values of the functions f and g.

Definition 1.4 The product $f \cdot g$ of the functions f and g is the function that takes on the value

$$(f \cdot g)(x) = f(x) \cdot g(x).$$

We use the dot $\cdot$ rather than the times sign $\times$ to indicate multiplication to avoid confusion with the variable x.

Example 1.2.15 Adding and Multiplying Functions

Consider the functions $f(x)$ and $g(x)$ with formulas

$$f(x) = 4 + x - x^2$$
$$g(x) = 2x,$$

graphed in Figures 1.2.14 and 1.2.15. The table following the figures computes the values of $f + g$ and $f \cdot g$ at several points.

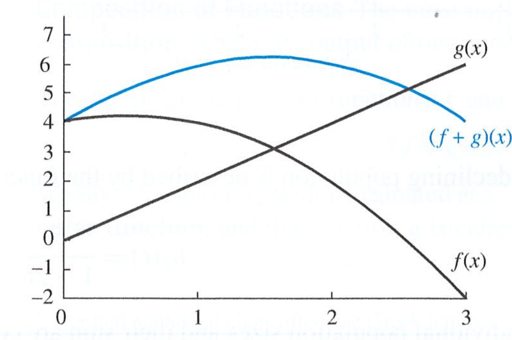


FIGURE 1.2.14
Adding functions

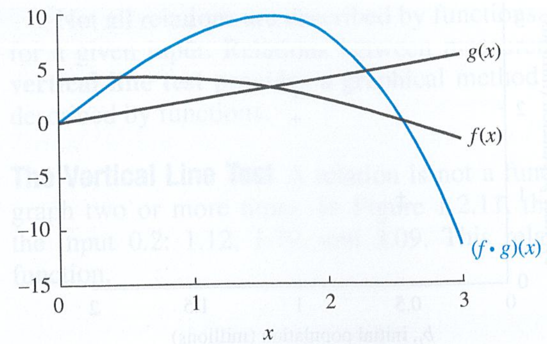


FIGURE 1.2.15
Multiplying functions

x	$f(x)$	$g(x)$	$(f+g)(x)$	$(f \cdot g)(x)$
0	4	0	4	0
0.5	4.25	1	5.25	4.25
1	4	2	6	8
1.5	3.25	3	6.25	9.75
2	2	4	6	8
2.5	0.25	5	5.25	1.25
3	−2	6	4	−12

Example 1.2.16 Adding Biological Functions

If two bacterial populations are separately counted, the total population is the sum of the two individual populations (Figure 1.2.16). Suppose a growing population is described by the function

$$b_1(t) = t^2 + 1$$

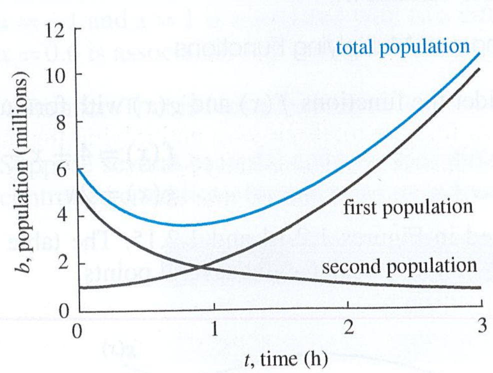


FIGURE 1.2.16
Adding biological functions

and a declining population is described by the function

$$b_1(t) = \frac{5}{1+2t}.$$

The individual population sizes and their sum are computed in the following table.

t	$b_1(t)$	$b_2(t)$	$(b_1+b_2)(t)$
0.00	1.00	5.00	6.00
0.50	1.25	2.50	3.75
1.00	2.00	1.67	3.67
1.50	3.25	1.25	4.50
2.00	5.00	1.00	6.00
2.50	7.25	0.83	8.08
3.00	10.00	0.71	10.71

Example 1.2.17 Multiplying Biological Functions

t	b	μ	$\mu \cdot b$
0.0	1.00	1.00	1.00
1.0	1.24	0.50	0.62
2.0	1.95	0.33	0.65
3.0	3.14	0.25	0.78
4.0	4.81	0.20	0.96
5.0	6.95	0.17	1.16
6.0	9.57	0.14	1.37

Many quantities in science are built as products of simpler quantities. For example, the mass of a population is the product of the mass of each individual and the number of individuals. Consider a population growing according to

$$b(t) = \frac{t^2}{4.2} + 1.0$$

(Example 1.2.9). Suppose that as the population gets larger the individuals become smaller. Let $\mu(t)$ (the Greek letter mu)[1] represent the mass of an individual at time t, and suppose that

$$\mu(t) = \frac{1}{1+t}.$$

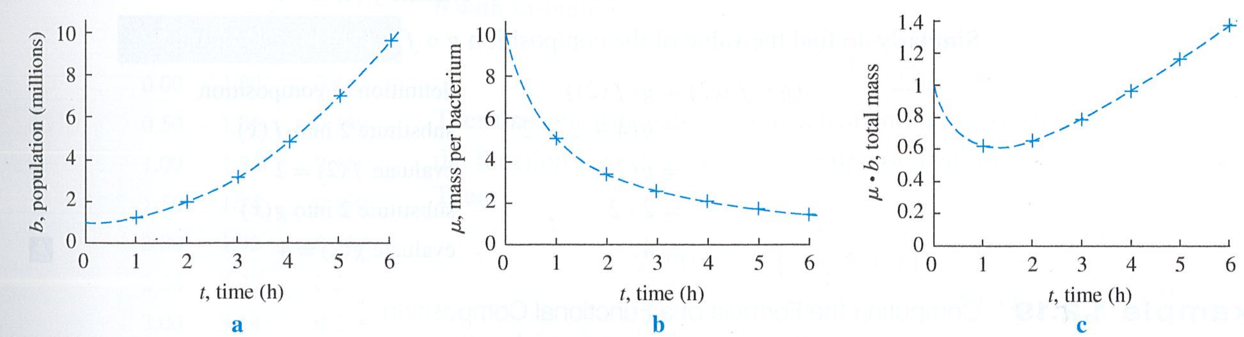


FIGURE 1.2.17
Multiplying biological functions

We can find the total mass by multiplying the mass per individual by the number of individuals, as in the table and Figure 1.2.17. The total mass of this population initially declines and then increases after about 2 hours.

Composition of Functions The most important way to combine functions is through **composition**, where the output of one function acts as the input of another.

Definition 1.5 The composition $f \circ g$ of functions f and g is a function defined by

$$(f \circ g)(x) = f(g(x)). \quad (1.2.1)$$

We say "f composed with g evaluated at x" or "f of g of x." The function f is called the **outer function**, and the function g is called the **inner function** (Figure 1.2.18).

[1] Applied mathematicians often use Greek letters to represent variables and parameters. The Greek alphabet, along with pronunciations of the letters, is given in Appendix A.

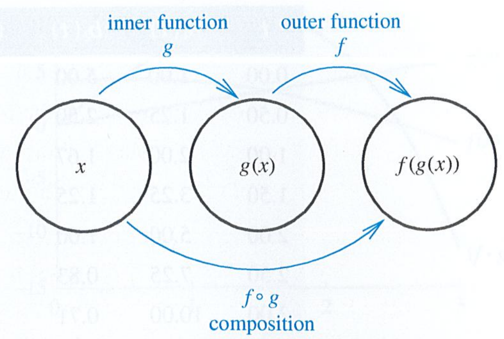


FIGURE 1.2.18
Composition of functions

Example 1.2.18 Computing the Value of a Functional Composition

Consider the functions $f(x)$ and $g(x)$ from Example 1.2.15,

$$f(x) = 4 + x - x^2$$
$$g(x) = 2x.$$

To find the value of the composition $f \circ g$ at $x = 2$, we compute

$(f \circ g)(2) = f(g(2))$	definition of composition
$= f(2 \cdot 2)$	substitute 2 into $g(x)$
$= f(4)$	evaluate $g(2) = 4$
$= 4 + 4 - 4^2$	substitute 4 into $f(x)$
$= -8.$	evaluate $f(4) = -8$

Similarly, to find the value of the composition $g \circ f$ at $x = 2$, we compute

$(g \circ f)(2) = g(f(2))$	definition of composition
$= g(4 + 2 - 2^2)$	substitute 2 into $f(x)$
$= g(2)$	evaluate $f(2) = 2$
$= 2 \cdot 2$	substitute 2 into $g(x)$
$= 4.$	evaluate $g(2) = 4$

Example 1.2.19 Computing the Formula of a Functional Composition

Consider again the functions $f(x)$ and $g(x)$ from Example 1.2.18,

$$f(x) = 4 + x - x^2$$
$$g(x) = 2x.$$

with domains consisting of all numbers. To find the composition $f \circ g$, plug the definition of the **inner function** g into the formula for the **outer function** f, or

$(f \circ g)(x) = f(g(x))$	the definition
$= f(2x)$	write out the formula for the inner function G
$= 4 + (2x) - (2x)^2$	plug the formula for G into the outer function F
$= 4 + 2x - 4x^2.$	expand the square

This is the same procedure we used to compute the value of the function $f(x)$ at a complicated argument in Example 1.2.8. In Example 1.2.18 we computed that $(f \circ g)(2) = -8$. If we evaluate by substituting into the formula $(f \circ g)(x) = 4 + 2x - 4x^2$, we find

$$(f \circ g)(2) = 4 + 2 \cdot 2 - 4 \cdot 2^2 = -8,$$

matching our earlier result.

We find the composition $g \circ f$ by following the same steps, or

$(g \circ f)(x) = g(f(x))$	the definition
$= g(4 + x - x^2)$	write out the formula for the inner function F
$= 2(4 + x - x^2)$	plug the formula for F into the outer function G
$= 8 + 2x - 2x^2.$	multiply through

The key step is substituting the output of the inner function into the outer function; the rest is algebra. In Example 1.2.18 we computed that $(g \circ f)(2) = 4$. If we evaluate by substituting into the formula $g \circ f(x) = 8 + 2x - 2x^2$, we find

$$(g \circ f)(2) = 8 + 2 \cdot 2 - 2 \cdot 2^2 = 4,$$

again matching our earlier result.

Example 1.2.19 illustrates an important point about the composition of functions: the answer is generally different when the functions are composed in a different order. If $f \circ g = g \circ f$, we say that the two functions **commute**. When the two compositions do not match, we say that the two functions do not commute. Without a good reason, never assume that two functions commute. If you think of functions as operations, this should make sense. Sterilizing the scalpel and then making an incision produces a quite different result from making an incision and then sterilizing the scalpel.

Example 1.2.20 Composition of Functions in Biology

Numbers of bacteria are usually measured indirectly, by measuring the optical density of the medium. Water allows less light to come through as the population becomes larger. Suppose that the optical density ρ is a function of the bacterial population size b with formula

$$\rho(b) = \frac{b}{2.0b + 5.0}.$$

Then the optical density as a function of time is the composition of the function $\rho(b)$ with the function $b(t)$ (Figure 1.2.19). Suppose that $b(t) = \frac{t^2}{4.2} + 1.0$ as in Example 1.2.9. Then

$$\rho(b(t)) = \rho\left(\frac{t^2}{4.2} + 1.0\right) = \frac{\frac{t^2}{4.2} + 1.0}{2\left(\frac{t^2}{4.2} + 1.0\right) + 5.0},$$

with values given in the table to the left.

t	$b(t)$	$\rho(b(t))$
0.00	1.00	0.143
0.50	1.06	0.149
1.00	1.24	0.166
1.50	1.54	0.190
2.00	1.95	0.219
2.50	2.49	0.249
3.00	3.14	0.278

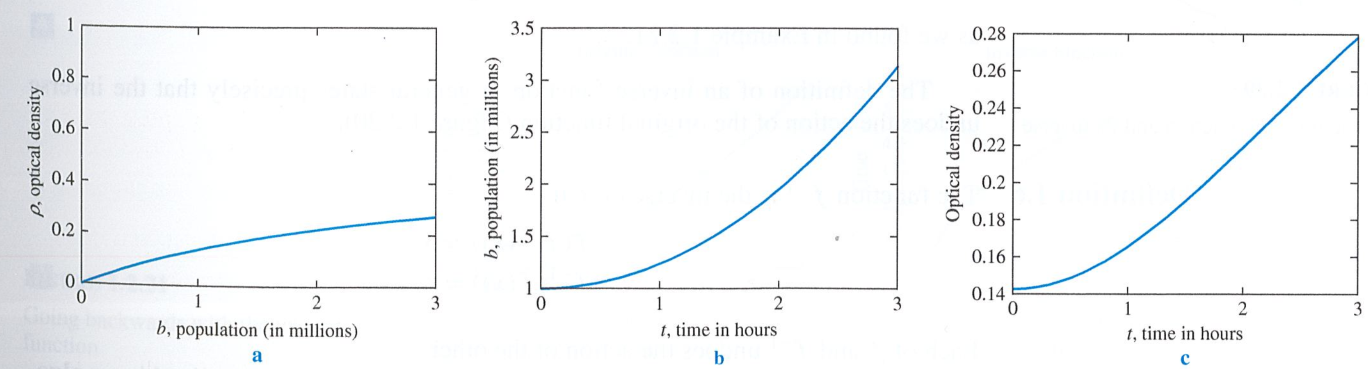


FIGURE 1.2.19
Composing biological functions

The composition $b \circ \rho$ is not merely different from the composition $\rho \circ b$; it does not even make sense. The function b accepts as input only the time t, not the optical density returned as output by the function ρ. We will study this issue more carefully in Section 1.3.

1.2.4 Finding Inverse Functions

A function describes the relation between two measurements and gives a way to compute the output from a given input. Sometimes we wish to reverse the process and figure out which input produced a given output. The **inverse function**, when it exists, provides a way to do this.

Example 1.2.21 A Simple Inverse Operation

What number, when doubled, gives 8? It is not difficult to guess that the answer is 4. However, we can formalize this process using functional notation. Let $f(x) = 2x$ be the function that doubles. Our problem is then solving

$$f(x) = 8.$$

Using the formula for $f(x)$, we find

$$2x = 8 \quad \text{the equation to be solved}$$
$$x = 4. \quad \text{divide both sides by 2}$$

Example 1.2.22 A Simple Inverse Function

Example 1.2.21 undoes the act of multiplying by 2. What function does this in general? If we set $y = f(x)$, we would like to know what value of x produces a given y in general, without picking a particular value such as $y = 8$. We follow the same steps,

$$2x = y \quad \text{the equation to be solved}$$
$$x = \frac{y}{2}. \quad \text{divide both sides by 2}$$

The function f^{-1}, read "f inverse," defined by

$$f^{-1}(y) = \frac{y}{2}$$

is the **inverse** of f; the function that undoes what f did in the first place. Whereas f takes a number as input and returns double that number population as output, f^{-1} takes the doubled number as input and returns the initial number as output.

We can use this inverse like any other function, finding that

$$f^{-1}(8) = \frac{8}{2} = 4,$$

as we found in Example 1.2.21.

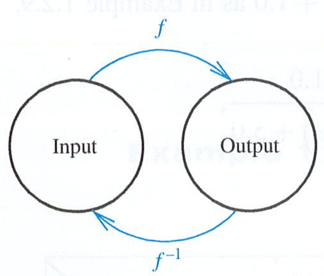


FIGURE 1.2.20
The action of a function and its inverse

The definition of an inverse function in general states precisely that the inverse undoes the action of the original function (Figure 1.2.20).

Definition 1.6 The function f^{-1} is the inverse of f if

$$f(f^{-1}(x)) = x$$
$$f^{-1}(f(x)) = x.$$

Each of f and f^{-1} undoes the action of the other.

The steps for computing the inverse of a function can be summarized in an **algorithm**, which can be thought of as a recipe. This book contains many algorithms for solving particular problems. As with a recipe, following an algorithm without thinking about and checking the steps can lead to disaster. Unlike most algorithms in this book, this one can be impossible to follow because the equation in the second step cannot be solved algebraically.

Algorithm 1.1 Finding the Inverse of a Function

1. Write the equation $y = f(x)$.
2. Solve for x in terms of y.
3. The inverse function is the operation done to y.

It may look odd to have a function defined in terms of y. Do **not** change the letters around to make it look normal. In applied mathematics different letters stand for different things and resent having their names switched as much as we do.

This algorithm may fail in two different ways: a function might not have an inverse, or the inverse might be impossible to compute. There is a useful way to recognize a function that fails to have an inverse. An operation can only be undone if you can deduce the input from the output. If any particular output is associated with more than one input, there is no way to tell where you started based solely on where you ended up.

Example 1.2.23 Finding a More Complicated Inverse

Consider the population following the equation

$$b(t) = \frac{t^2}{4.2} + 1.0$$

(Example 1.2.9, Figure 1.2.21). If we wish to find the time t from the population b, we must solve for t.

$$\frac{t^2}{4.2} + 1.0 = b \quad \text{the equation to be solved for } t$$
$$\frac{t^2}{4.2} = b - 1.0 \quad \text{subtract 1.0 from both sides}$$
$$t^2 = 4.2(b - 1.0) \quad \text{multiply both sides by 4.2}$$
$$t = \sqrt{4.2(b - 1.0)}. \quad \text{take the square root of both sides}$$

The last step requires that $b \geq 1.0$ because we cannot take the square root of a negative number.

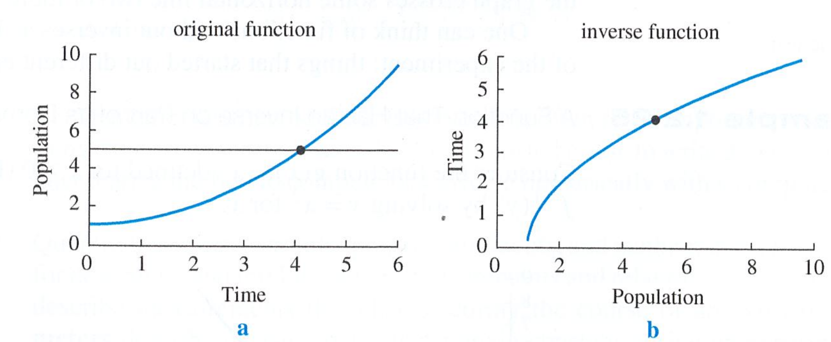


FIGURE 1.2.21
Going backwards with the inverse function

For example, to one decimal place of accuracy, the time associated with a population of 5.0 is

$$t = \sqrt{4.2(5.0 - 1.0)} = 4.099.$$

Example 1.2.24 A Relation That Cannot Be Inverted

Consider the data in the following table (Figure 1.2.22).

Initial Mass	Final Mass	Initial Mass	Final Mass
1.0	7.0	9.0	20.0
2.0	12.0	10.0	18.0
3.0	16.0	11.0	15.0
4.0	19.0	12.0	12.0
5.0	22.0	13.0	9.0
6.0	23.0	14.0	6.0
7.0	23.0	15.0	3.0
8.0	22.0	16.0	1.0

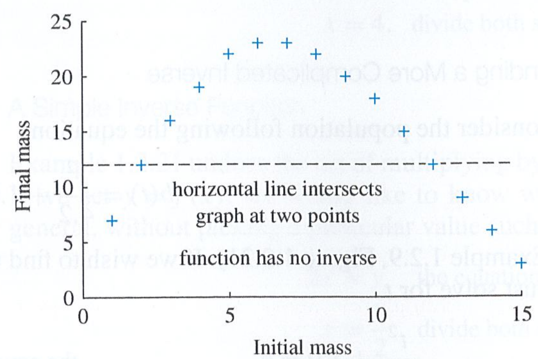


FIGURE 1.2.22
A relation with no inverse

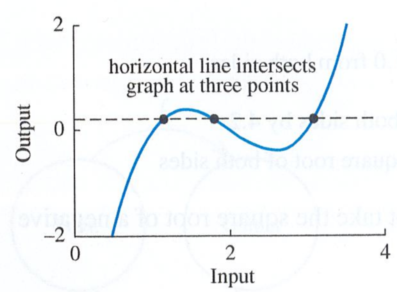


FIGURE 1.2.23
The horizontal line test

Suppose you were told that the mass at the end of experiment was 12.0 grams. Initial masses of 2.0 and 12.0 grams both produce a final mass of 12.0 grams. You cannot tell whether the input was 2.0 or 12.0. This function has no inverse. ▲

This reasoning leads to a useful graphical test for whether a function has an inverse.

The Horizontal Line Test A function has no inverse if it takes on the same value two or more times. This can be established by graphing the function and checking whether the graph crosses some horizontal line two or more times. (Figure 1.2.23)

One can think of functions without inverses as losing information over the course of the experiment: things that started out different ended up the same.

Example 1.2.25 A Function That Has an Inverse on Part of Its Domain

Consider the function $g(x) = x^2$ defined for $x \geq 0$ (Figure 1.2.24). We find the inverse $f^{-1}(y)$ by solving $y = x^2$ for x.

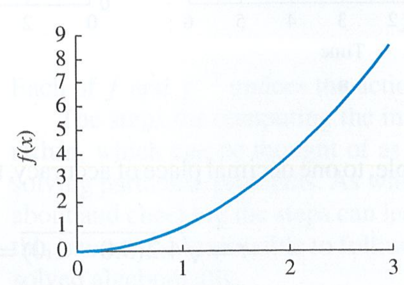


FIGURE 1.2.24
The inverse of x^2 is defined when $x \geq 0$

1. Set $y = x^2$.
2. Then $x = \sqrt{y}$.
3. $f^{-1}(y) = \sqrt{y}$. ▲

Example 1.2.26 A Function Without an Inverse

Consider the function $f(x) = 4 + x - x^2$ (used in Example 1.2.7 and graphed in Figure 1.2.25). We found that the inputs $x = 0$ and $x = 1$ both produce the same output of $f(x) = 4$. If the output is 4, it is impossible to tell which was the input. A graph shows that this function fails the horizontal line test at almost all values in its range. ▲

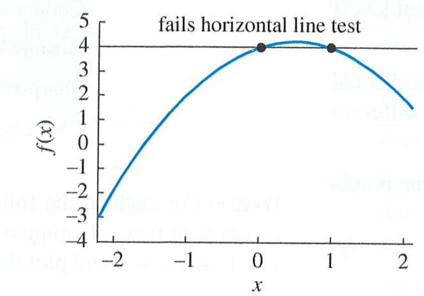


FIGURE 1.2.25
A function with no inverse

In addition, Algorithm 1.1 might fail because the algebra is impossible. Step 2 requires solving an equation. Many equations cannot be solved algebraically.

Example 1.2.27 A Function with an Inverse That Is Impossible to Compute

Consider the function

$$f(x) = x^5 + x + 1.$$

The graph satisfies the horizontal line test (Figure 1.2.26.). We try to find the inverse $f^{-1}(y)$ as follows.

1. Set $y = x^5 + x + 1$.
2. Try to solve for x. Even with the cleverest algebraic tricks, this is impossible (there is a remarkable theorem by the French mathematician Evariste Galois, proven when he was just 20 years old, that there is no formula for the solution of a polynomial with a degree greater than 4).
3. Give up.

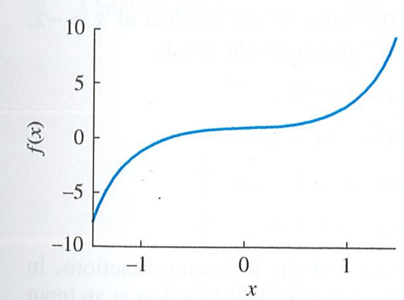


FIGURE 1.2.26
A function with an inverse that is impossible to compute

▲

In mathematical modeling, however, it is often more important to know that something exists (like the inverse in this case) than to be able to write down a formula. We will later learn a method to compute this inverse numerically with a computer (Section 3.8)

Summary Quantitative science is built upon measurements, and mathematics provides the methods for describing and thinking about measurements and relations between them. **Variables** describe measurements that change during the course of an experiment, and **parameters** describe measurements that remain constant during an experiment but might change between different experiments. **Functions** describe relations between different measurements when a single output is associated with each input, and can be recognized graphically with the **vertical line test**. New functions are built by combining functions through **addition**, **multiplication**, and **composition**. In functional composition, the output of the **inner function** is used as the input of the **outer function**. Many functions do not **commute**, meaning that composing the functions in a different order gives a different result. Finally, we used the **horizontal line test** to check whether a function has an **inverse**. If it does, the inverse can be used to compute the input from the output.

1.2 Exercises

Mathematical Techniques

1–2 ▪ Identify the variables and parameters in the following situations, give the units they might be measured in, and choose an appropriate letter or symbol to represent each.

1. A scientist measures the mass of fish over the course of 100 days, and repeats the experiment at three different levels of salinity: 0%, 2% and 5%.

2. A scientist measures the body temperature of bandicoots every day during the winter, and does so at three different altitudes: 500 m, 750 m, and 1000 m.

3–6 ▪ Compute the values of the following functions at the points indicated and sketch a graph of the function.

3. $f(x) = x + 5$ at $x = 0$, $x = 1$, and $x = 4$.

4. $g(y) = 5y$ at $y = 0$, $y = 1$, and $y = 4$.

5. $h(z) = \frac{1}{5z}$ at $z = 1$, $z = 2$, and $z = 4$.

6. $F(r) = r^2 + 5$ at $r = 0$, $r = 1$, and $r = 4$.

7–10 ▪ Graph the given points and say which point does not seem to fall on the graph of a simple function.

7. (0, −1), (1, 1), (2, 1), (3, 5), (4, 7).

8. (0, 5), (1, 10), (2, 8), (3, 6), (4, 4).

9. (0, 2), (1, 3), (2, 6), (3, 11), (4, 10).

10. (0, 45), (1, 25), (2, 12), (3, 12.5), (4, 10).

11–14 ▪ Evaluate the following functions at the given algebraic arguments.

11. $f(x) = x + 5$ at $x = a$, $x = a + 1$, and $x = 4a$.

12. $g(y) = 5y$ at $y = x^2$, $y = 2x + 1$, and $y = 2 - x$.

13. $h(z) = \frac{1}{5z}$ at $z = \frac{c}{5}$, $z = \frac{5}{c}$, and $z = c + 1$.

14. $F(r) = r^2 + 5$ at $r = x + 1$, $r = 3x$, and $r = \frac{1}{x}$.

15–16 ▪ Sketch graphs of the following relations. Is there a more convenient order for the arguments?

15. A function whose argument is the name of a state and whose value is the highest altitude in that state.

State	Highest Altitude (ft)
California	14,491
Idaho	12,662
Nevada	13,143
Oregon	11,239
Utah	13,528
Washington	14,410

16. A function whose argument is the name of a bird and whose value is the length of that bird.

Bird	Length
Cooper's hawk	50 cm
Goshawk	66 cm
Sharp-shinned hawk	35 cm

17–20 ▪ For each of the following sums of functions, graph each component piece. Compute the values at $x = -2$, $x = -1$, $x = 0$, $x = 1$, and $x = 2$ and plot the sum.

17. $f(x) = 2x + 3$ and $g(x) = 3x - 5$.

18. $f(x) = 2x + 3$ and $h(x) = -3x - 12$.

19. $F(x) = x^2 + 1$ and $G(x) = x + 1$.

20. $F(x) = x^2 + 1$ and $H(x) = -x + 1$.

21–24 ▪ For each of the following products of functions, graph each component piece. Compute the value of the product at $x = -2$, $x = -1$, $x = 0$, $x = 1$, and $x = 2$ and graph the result.

21. $f(x) = 2x + 3$ and $g(x) = 3x - 5$.

22. $f(x) = 2x + 3$ and $h(x) = -3x - 12$.

23. $F(x) = x^2 + 1$ and $G(x) = x + 1$.

24. $F(x) = x^2 + 1$ and $H(x) = -x + 1$.

25–28 ▪ Find the inverses of each of the following functions. In each case, compute the output of the original function at an input of 1.0, and show that the inverse undoes the action of the function.

25. $f(x) = 2x + 3$.

26. $g(x) = 3x - 5$.

27. $G(y) = 1/(2 + y)$ for $y \geq 0$.

28. $F(y) = y^2 + 1$ for $y \geq 0$.

29–32 ▪ Graph each of the following functions and its inverse. Mark the given point on the graph of each function.

29. $f(x) = 2x + 3$. Mark the point $(1, f(1))$ on the graphs of f and f^{-1} (based on Exercise 25).

30. $g(x) = 3x - 5$. Mark the point $(1, g(1))$ on the graphs of g and g^{-1} (based on Exercise 26).

31. $G(y) = 1/(2 + y)$. Mark the point $(1, G(1))$ on the graphs of G and G^{-1} (based on Exercise 27).

32. $F(y) = y^2 + 1$ for $y \geq 0$. Mark the point $(1, F(1))$ on the graphs of F and F^{-1} (based on Exercise 28).

33–36 ▪ Find the compositions of the given functions. Which pairs of functions commute?

33. $f(x) = 2x + 3$ and $g(x) = 3x - 5$.

34. $f(x) = 2x + 3$ and $h(x) = -3x - 12$.

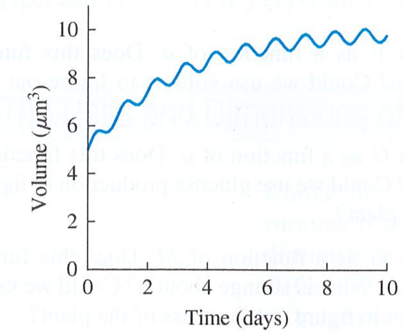
35. $F(x) = x^2 + 1$ and $G(x) = x + 1$.

36. $F(x) = x^2 + 1$ and $H(x) = -x + 1$.

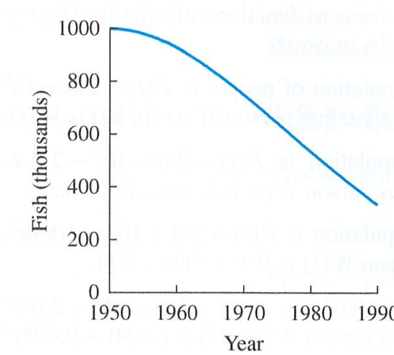
Applications

37–40 ▪ Describe what is happening in the graphs shown.

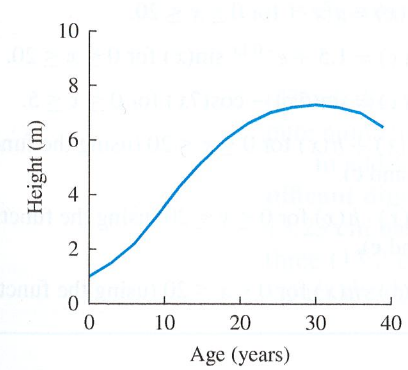
37. A plot of cell volume against time in days.



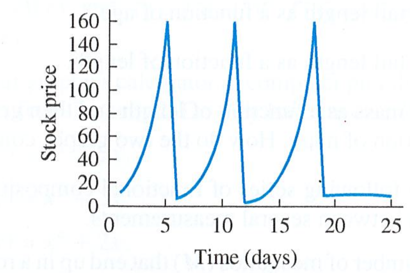
38. A plot of a Pacific salmon population against time in years.



39. A plot of the average height of a population of trees plotted against age in years.



40. A plot of an Internet stock price against time.



41–44 ▪ Draw graphs based on the following descriptions.

41. A population of birds begins at a large value, decreases to a tiny value, and then increases again to an intermediate value.

42. The amount of DNA in an experiment increases rapidly from a very small value and then levels out at a large value before declining rapidly to 0.

43. Body temperature oscillates between high values during the day and low values at night.

44. Soil is wet at dawn, quickly dries out and stays dry during the day, and then becomes gradually wetter again during the night.

45–48 ▪ Evaluate the following functions over the suggested range, sketch a graph of the function, and answer the biological question.

45. The number of bees b found on a plant is given by $b = 2f + 1$ where f is the number of flowers, ranging from 0 to about 20. Explain what might be happening when $f = 0$.

46. The number of cancerous cells c as a function of radiation dose r (measured in rads) is

$$c = r - 4$$

for r greater than or equal to 5, and is zero for r less than 5. r ranges from 0 to 10. What is happening at $r = 5$ rads?

47. Insect development time A (in days) obeys $A = 40 - \frac{T}{2}$ where T represents temperature in °C for $10 \leq T \leq 40$. Which temperature leads to the more rapid development?

48. Tree height h (in meters) follows the formula

$$h = \frac{100a}{100 + a}$$

where a represents the age of the tree in years for $0 \leq a \leq 1000$. How tall would this tree get if it lived forever?

49–52 ▪ Consider the following data describing the growth of a tadpole.

Age, a (days)	Length, L (cm)	Tail Length, T (cm)	Mass, M (g)
0.5	1.5	1.0	1.5
1.0	3.0	0.9	3.0
1.5	4.5	0.8	6.0
2.0	6.0	0.7	12.0
2.5	7.5	0.6	24.0
3.0	9.0	0.5	48.0