Finite-Difference Equations

1.1 A MYTHICAL FIELD

Imagine that a graduate student goes to a meadow on the first day of May, walks through the meadow waving a fly net, and counts the number of flies caught in the net. She repeats this ritual for several years, following up on the work of previous graduate students. The resulting measurements might look like the graph shown in Figure 1.1. The graduate student notes the variability in her measurements and wants to find out if they contain any important biological information.

Several different approaches could be taken to study the data. The student could do statistical analyses of the data to calculate the mean value or to detect long-term trends. She could also try to develop a detailed and realistic model of the ecosystem, taking into account such factors as weather, predators, and the fly populations in previous years. Or she could construct a simplified theoretical model for fly population density.

Sticking to what she knows, the student decides to model the population variability in terms of actual measurements. The number of flies in one summer

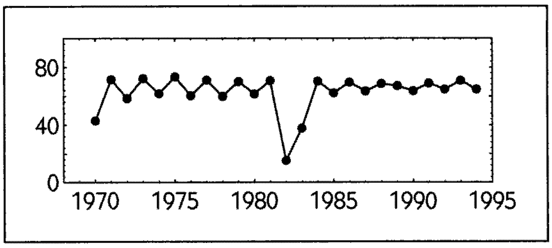

Figure 1.1 The number of flies caught during the annual fly survey.

depends on the number of eggs laid the previous year. The number of eggs laid depends on the number of flies alive during that summer. Thus, the number of flies in one summer depends on the number of flies in the previous summer. In mathematical terms, this is a relationship, or **function,**

$$N_{t+1} = f(N_t). \tag{1.1}$$

This equation says simply that the number of flies in the $t + 1$ summer is determined by (or *is a function of*) the number of flies in summer t, which is the previous summer. Equations of this form, which relate values at **discrete times** (e.g., each May), are called **finite-difference equations.** N_t is called the **state** of the system at time t. We are interested in how the state changes in time: the **dynamics** of the system.

Since the real-world ecosystem is complicated and since the measurements are imperfect, we do not expect a model like Eq. 1.1 to be able to duplicate exactly the actual fly population measurements. For example, birds eat flies, so the population of flies is influenced by the bird population, which itself depends on a complicated array of factors. The assumption behind Eq. 1.1 is that the number of flies in year $t + 1$ depends solely on the number of flies in year t. While this is not strictly true, it may serve as a working approximation. The problem now is to figure out an appropriate form for this dependence that is consistent with the data and that encapsulates the important aspects of fly population biology.

1.2 THE LINEAR FINITE-DIFFERENCE EQUATION

Let us start by making a simple assumption about the propagation of flies: For each fly in generation t there will be R flies in generation $t + 1$. The corresponding finite-difference equation is

$$N_{t+1} = RN_t. \tag{1.2}$$

Equation 1.2 is called a **linear equation** because a graph of N_{t+1} versus N_t is a straight line, with a slope of R.

The **solution** to Eq. 1.2 is a sequence of states, $N_1, N_2, N_3, \ldots$, that satisfy Eq. 1.2 for each value of t. That is, the solution satisfies $N_2 = RN_1$, and $N_3 = RN_2$, and $N_4 = RN_3$, and so on.

One way to find a solution to the equation is by the process of **iteration.** Given the number of flies N_0 in the initial generation, we can calculate the number of flies in the next generation, N_1. Then, having calculated N_1, we can apply Eq. 1.2 to find N_2. We can repeat the process for as long as we care to. The state N_0 is called the **initial condition.**

For the linear equation, it is possible to carry out the iteration process using simple algebra. By iterating Eq. 1.2 we can find N_1, N_2, N_3, and so forth.

$$N_1 = RN_0,$$
$$N_2 = RN_1 = R^2N_0,$$
$$N_3 = RN_2 = R^2N_1 = R^3N_0,$$
$$\vdots$$

There is a simple pattern here: It suggests that the solution to the equation might be written as

$$N_t = R^t N_0. \tag{1.3}$$

We can verify that Eq. 1.3 is indeed the solution to Eq. 1.2 by **substitution.** Since Eq. 1.3 is valid for all values of time t, it is also valid for time $t + 1$. By replacing the variable t in Eq. 1.3 with $t + 1$, we can see that $N_{t+1} = R^{t+1}N_0$. Expanding this, we get

$$N_{t+1} = R^{t+1}N_0 = RR^tN_0 = RN_t,$$

which shows that the solution implies the finite-difference equation in Eq. 1.2.

BEHAVIOR OF THE LINEAR EQUATION

Equation 1.3 can produce several different types of solution, depending on the value of the parameter R:

Decay When $0 < R < 1$, the number of flies in each generation is smaller than that in the previous generation. Eventually, the number falls

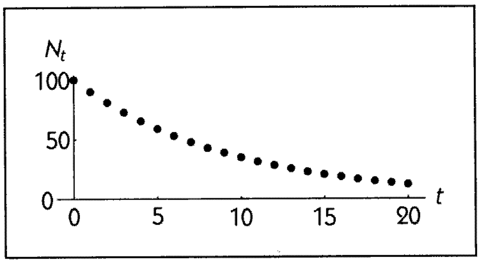

Figure 1.2
The solution to $N_{t+1} = 0.90N_t$.

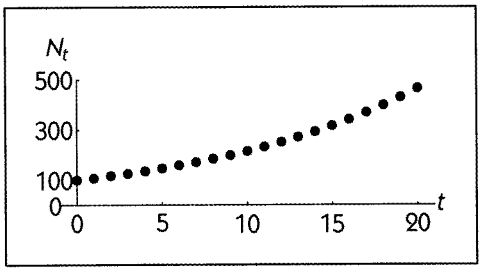

Figure 1.3
The solution to $N_{t+1} = 1.08N_t$.

to zero and the flies become extinct (see Figure 1.2). Since the solution is an exponential function of time (see Appendix A), this behavior is called **exponential decay**.

Growth When $R > 1$, the population of flies increases from generation to generation without bound. The solution is said to "explode" to ∞ (see Figure 1.3). Again the solution is an exponential function, and this behavior is thus called **exponential growth**.

Steady-state behavior When R is exactly 1, the population stays at the same level (see Figure 1.4). This is clearly an extraordinary solution, because it only happens for a single, exact value of R, whereas the other types of solutions occur for a range of R values.

The behaviors in the fly population study involve $R > 0$. It doesn't make biological sense to consider cases where $R < 0$ in Eq. 1.2. After all, how can flies

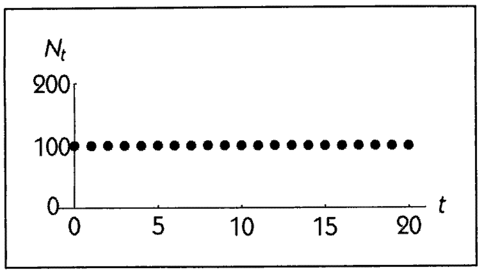

Figure 1.4
The solution to $N_{t+1} = 1.00N_t$.

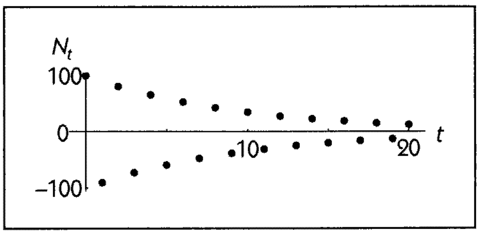

Figure 1.5
The solution to $N_{t+1} = -0.90N_t$.

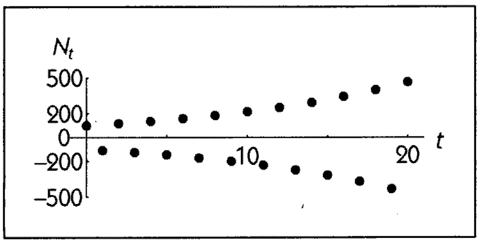

Figure 1.6
The solution to $N_{t+1} = -1.08N_t$.

lay negative eggs? Later, in Section 1.5, we shall see cases where it makes sense to talk about $R < 0$. Such cases produce different types of behavior:

Alternating decay When $-1 < R < 0$, the solution to Eq. 1.2 alternates between positive and negative values. At the same time, the amplitude of the solution decays to zero in the same exponential fashion seen for $0 < R < 1$ (see Figure 1.5).

Alternating growth When $R < -1$, the solution still alternates between positive and negative values. However, the amplitude of the solution grows exponentially and explodes to $\pm\infty$ (see Figure 1.6).

Periodic cycle When R is exactly -1, the solution alternates between N_0 and $-N_0$ and neither grows nor decays in amplitude. A periodic cycle occurs when the solution repeats itself. In this case, the solution repeats every two time steps, $\ldots, N_0, -N_0, N_0, -N_0, \ldots$, and so the duration of the period is two time steps (see Figure 1.7).

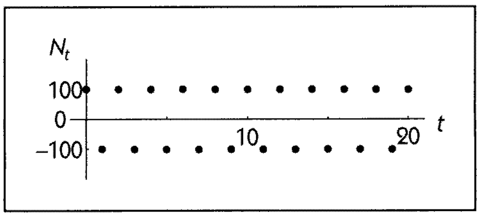

Figure 1.7
The solution to $N_{t+1} = -1.00N_t$.

1.3 METHODS OF ITERATION

We have seen how the solution to Eq. 1.2 could be found using algebra. Later we will encounter finite-difference equations in which an algebraic solution cannot be found. Here, we introduce two other methods for iterating finite-difference equations, the cobweb method and the method of numerical iteration.

THE COBWEB METHOD

The **cobweb method** is a graphical method for iterating a finite-difference equation like Eq. 1.1. No algebra is required in order to perform the iteration; one only needs to graph the function $f(N_t)$ on a piece of paper.

To illustrate the cobweb method, we will start with the linear system of Eq. 1.2. To perform the iteration using the cobweb method, we do the following:

1. Graph the function. In this case, $f(N_t) = RN_t$. In order to make a plot of the function RN_t, we need to pick a specific value for R. (Note that the algebraic method for finding solutions did not require this.) As an example, we will set $R = 1.9$ so that the finite-difference equation is $N_{t+1} = 1.9N_t$. The resulting function is shown by the dark line in Figure 1.8.

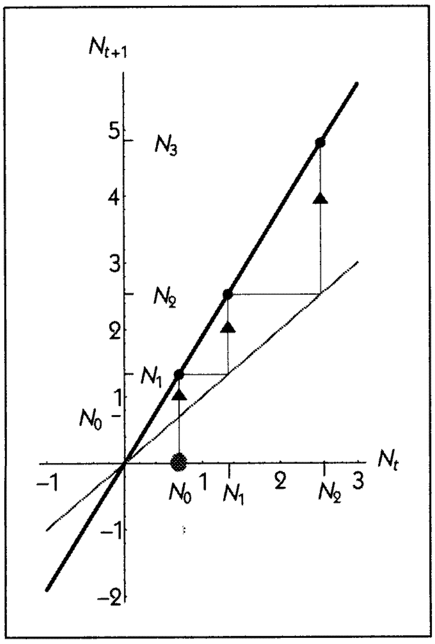

Figure 1.8
The cobweb method applied to the linear dynamical system $N_{t+1} = 1.9N_t$ with initial condition $N_0 = 0.7$.

2. Pick a numerical value for the initial condition. In this case, as an example, we will select $N_0 = 0.7$, shown as the gray dot on the x-axis in Figure 1.8. (In the algebraic method, we did not need to select a specific numerical value. Instead we were able to use the symbol N_0 to stand for any initial condition.)
3. Draw a vertical line from N_0 on the x-axis up to the function. The position where this vertical line hits the function (shown as a solid dot at the end of the arrow) tells us the value of N_1.
4. Take this value of N_1, plot it again on the x-axis, and again draw a vertical line to find the value of N_2. There is a simple shortcut in order to avoid plotting N_1 on the x-axis: Draw a horizontal line to the $N_{t+1} = N_t$ line (shown in gray—it's the 45-degree line on the plot). The place where the horizontal line intersects the 45-degree line is the point from which to draw the next vertical line to find N_2.
5. In order to find N_3, N_4, and so on, repeat the process of drawing vertical lines to the function and horizontal lines to the line of $N_{t+1} = N_t$.

As Figure 1.8 shows, the result of iterating $N_{t+1} = 1.9N_t$ is growth toward ∞. This is consistent with the algebraic solution we found in Eq. 1.3 for $R > 1$.

NUMERICAL ITERATION

Since the cobweb method is a graphical method, it may not be very precise. In order to acheive more precision, we can use **numerical iteration.** This is a simple procedure, easily implemented on a computer or even a hand calculator. To illustrate, suppose we want to find a numerical solution to $N_{t+1} = RN_t$ with $R = 0.9$ and $N_0 = 100$.

$$\begin{aligned} N_0 &= 100, \\ N_1 &= f(N_0) = 0.9 \times 100 = 90, \\ N_2 &= f(N_1) = 0.9 \times 90 = 81, \\ N_3 &= f(N_2) = 0.9 \times 81 = 72.9, \\ &\vdots \end{aligned} \tag{1.4}$$

When applied to the linear finite-difference equation in Eq. 1.2, the cobweb method and the method of numerical iteration merely allow us to confirm the existence of the types of behavior we found algebraically. Since the cobweb and numerical iteration methods require that specific numerical values be specified for the parameter R and the initial condition N_0, it might seem that they are inferior to the algebraic method. However, when we consider nonlinear equations, algebraic methods are often impossible and numerical iteration and the cobweb method may provide the only means to find solutions.

1.4 NONLINEAR FINITE-DIFFERENCE EQUATIONS

The measurements of the fly population shown in Figure 1.1 don't suggest explosion or extinction, nor do they remain steady. This suggests that the model of Eq. 1.2 is not good. It does not take much of an ecologist to see where a mistake was made in formulating Eq. 1.2. Although it is all right to have rapid growth in populations for low densities, when the fly population is high, competition for food limits growth and starvation may cause a decrease in fertility. The larger population may also increase predation, as predators focus their attention on an abundant food supply.

A simple way to modify the model is to add a new term that lowers the number of surviving offspring when the population is large. In the linear equation, R was the number of offspring of each fly in generation t. In order to make the number of offspring per fly decrease as N_t gets larger, we can make the growth rate a function of N_t. For simplicity, we will chose the function $(R - bN_t)$. The positive number b governs how the growth rate decreases as the population gets bigger. R is the growth rate when the population is very, very small.

This assumption that the number of offspring per fly is $(R - bN_t)$ gives us a new finite-difference equation,

$$N_{t+1} = (R - bN_t)N_t = RN_t - bN_t^2. \tag{1.5}$$

Equation 1.5 is a **nonlinear equation** since the rightmost side is *not* the equation of a straight line. Nonlinear equations arise commonly in mathematical models of biological systems, and the study of such equations is the focus of this book.

In Eq. 1.5 there are two parameters, R and b, that can vary independently. However, a simple change of variables shows that there is only one parameter that affects the dynamics. We define a new variable $x_t = \frac{bN_t}{R}$, which is just a way of scaling the number of flies by the number $\frac{b}{R}$. Substituting x_t and x_{t+1} in Eq. 1.5, we find the equation

$$x_{t+1} = Rx_t(1 - x_t). \tag{1.6}$$

Although Eq. 1.6 (called the **quadratic map**) may not seem much more complicated than Eq. 1.2, the solution cannot generally be found using algebra. Numerical iteration and the cobweb method, however, can be used to find solutions. In order to apply the cobweb method to Eq. 1.6, we first must draw a

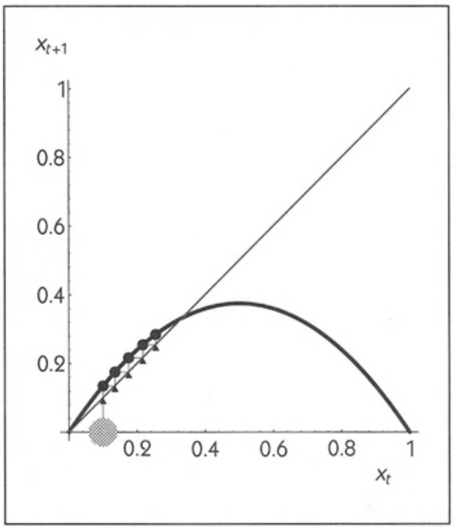

Figure 1.9
Cobweb iteration of $x_{t+1} = 1.5(1 - x_t)x_t$.

graph of the function. (Anyone who has not practiced calculus recently may find sketching the graph of an equation intimidating. If you are in this category, go over the material in Appendix A and pay particular attention to the section on quadratic functions since this is what we have here.) In this case, the graph is a parabola, with intercepts at $x_t = 0$ and $x_t = 1$, as Figure 1.9 shows.

Next, we need to pick specific values for the parameter R in Eq. 1.6. Since we don't yet know what the behavior of this equation will be, we will have to study a range of parameter values. Doing so reveals a number of different behaviors:

Steady state The nonlinear equation can have a solution that approaches a certain state and remains fixed there. This is shown in Figure 1.10 for $R = 1.5$, where the solution creeps up on the steady state from one side; this is called a **monotonic** approach.
As shown for $R = 2.9$ in Figure 1.11, the approach to a steady state can also **alternate** from one side to the other.

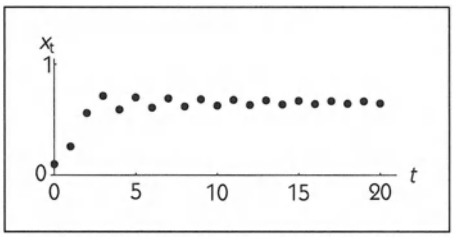

Figure 1.10
The solution to $x_{t+1} = 1.5(1 - x_t)x_t$.

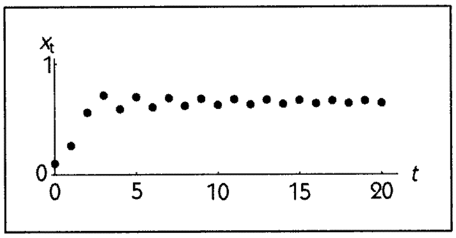

Figure 1.11
The solution to
$x_{t+1} = 2.9(1 - x_t)x_t$.

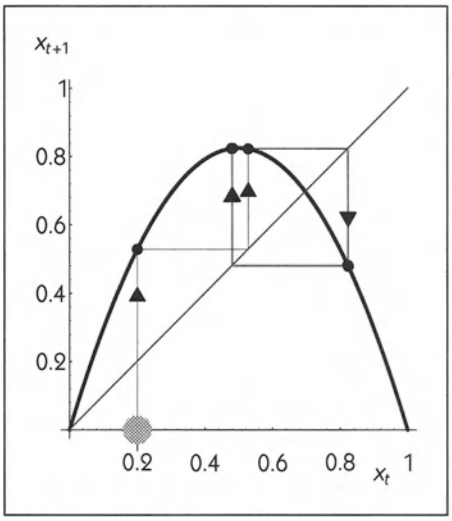

Figure 1.12
Cobweb iteration of
$x_{t+1} = 3.3(1 - x_t)x_t$.

Periodic cycles The solution to the nonlinear equation can have cycles. This is shown for $R = 3.3$ in Figures 1.12 and 1.13, where the cycle has duration 2. When carrying out the cobweb iteration, a cycle of period two looks like a square that is repeatedly traced out (see Figure 1.12). The cycle in this case follows the sequence $x_t = 0.48$, $x_{t+1} = 0.82$, $x_{t+2} = 0.48$, and so on.

For $R = b = 3.52$ (see Figure 1.14), the cycle has duration 4 and follows the sequence $x_t = 0.88$, $x_{t+1} = 0.37$, $x_{t+2} = 0.82$, $x_{t+3} = 0.51$, $x_{t+4} = 0.88$, and so forth.

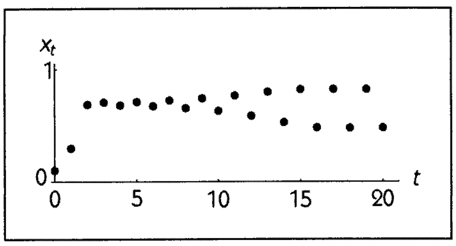

Figure 1.13
The solution to
$x_{t+1} = 3.3(1 - x_t)x_t$.

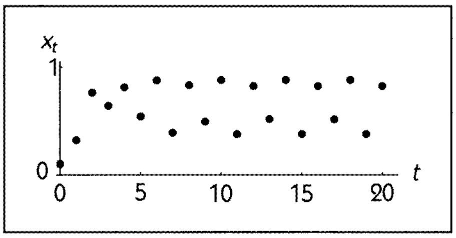

Figure 1.14
The solution to
$x_{t+1} = 3.52(1 - x_t)x_t$.

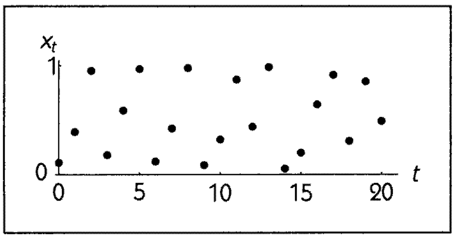

Figure 1.15
The solution to
$x_{t+1} = 4(1 - x_t)x_t$.

Aperiodic behavior The solution to the nonlinear equation may oscillate, but not in a periodic manner. Setting $R = 4$, we find the behavior shown in Figures 1.15 and 1.16—a kind of irregular oscillation that is neither exponential growth or decay, nor a steady state. The cobweb iteration shows how the irregular iteration arises from the shape of the function (see Figure 1.15). This behavior is called **chaos**, and we will investigate it in greater detail in later sections in the book.

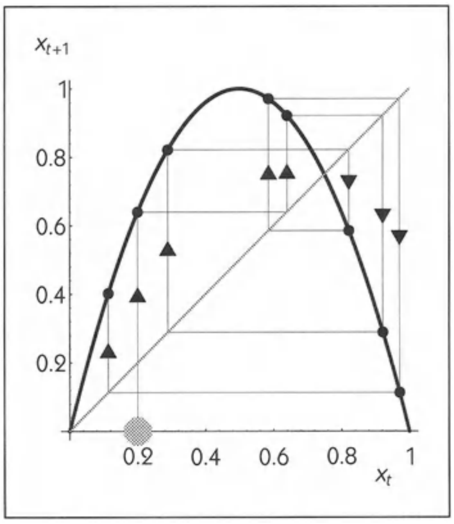

Figure 1.16
Cobweb iteration of
$x_{t+1} = 4(1 - x_t)x_t$.

1.5 STEADY STATES AND THEIR STABILITY

A simple, but important, type of dynamical behavior is when the system stays at a **steady state**. A steady state is a state of the system that remains fixed, that is, where

$$x_{t+1} = x_t.$$

Steady states in finite-difference equations are associated with the mathematical concept of a **fixed point**. A fixed point of a function $f(x_t)$ is a value $x_t^\star$ that satisfies $x_t^\star = f(x_t^\star)$. Later on, we shall see how fixed points can also be associated with periodic cycles.

There are three important questions to ask about fixed points in a finite-difference equation:

- Are there any fixed points—in other words, are there any values of $x_t^\star$ that satisfy $x_t^\star = f(x_t^\star)$?
- If the initial condition happens to be near a fixed point, will the subsequent iterates approach the fixed point? If subsequent iterates approach the fixed point, we say the fixed point is **locally stable**. (Mathematicians call this "locally asymptotic stability.")
- Will the system approach a given fixed point regardless of the initial condition? If the fixed point is approached for all initial conditions, we say that the fixed point is **globally stable**.

FINDING FIXED POINTS

From the graph of $x_{t+1} = f(x_t)$ it is easy to locate fixed points: They are simply those points where the graph intersects the line $x_{t+1} = x_t$. Or, we can use algebra to solve the equation $x_t = f(x_t)$.

For the linear finite-difference equation, $x_t^\star$ is a fixed point if it satisfies the equation $x_t^\star = Rx_t^\star$. One solution to this equation is always $x_t^\star = 0$. This means that the origin is a fixed point for a linear system. This has an obvious biological interpretation: If there are no flies in one year, there can't be any the next year (unless, of course, they migrate from distant parts or evolve again, both of which are beyond the scope of our simple model).

The solution $x_t = 0$ is the only fixed point, unless $R = 1$. If R is exactly 1, then all points are fixed points. Clearly, this is an exceptional case, because any change in R, no matter how small, will eliminate all of the fixed points except the one at the origin.

Nonlinear finite-difference equations can have more than one fixed point. Figures 1.17 and 1.18 show the location of the fixed points for Eq. 1.6 for $R = 2.9$

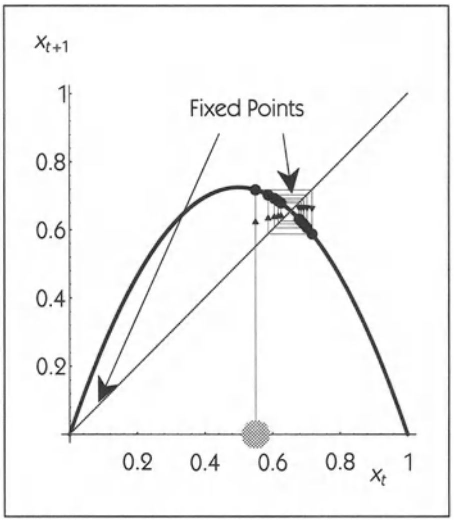

Figure 1.17
$x_{t+1} = 2.9(1 - x_t)x_t$

and $R = 3.52$, respectively. For the quadratic map of Eq. 1.6, the fixed points can also be found using algebra from the **roots** of the quadratic equation

$$x_t = Rx_t(1 - x_t) \quad \text{or,} \quad x_t(R - Rx_t - 1) = 0.$$

The roots of this equation are

$$x_t = 0 \quad \text{and} \quad x_t = \frac{R-1}{R}.$$

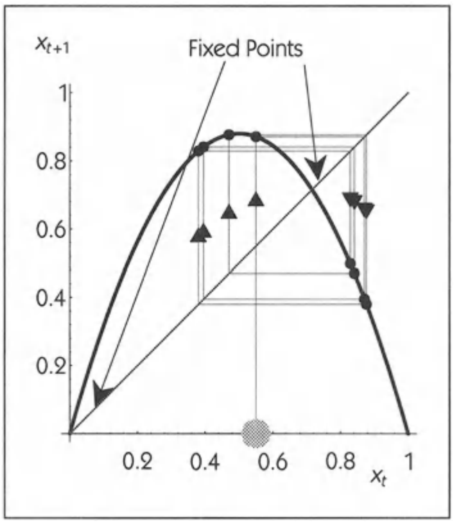

Figure 1.18
$x_{t+1} = 3.52(1 - x_t)x_t$

Again, in our model the biological meaning of the root $x_t = 0$ is that flies don't appear from nowhere. The biological interpretation of the fixed point at $x_t = \frac{R-1}{R}$ is that this is a self-sustaining level of the population, with neither a decrease nor an increase.

Clearly, it is impossible for the fly population to be at both these fixed points at the same time. So now we have to address the question of which of these fixed points will be reached by iterating from the initial condition, if indeed either of them will be.

LOCAL STABILITY OF FIXED POINTS

Figures 1.17 and 1.18 both have two fixed points, but in Figure 1.17 the iterates approach the nonzero fixed point while in Figure 1.18 the iterates do not. The difference between these cases is the *local stability* of the fixed points.

We say that a fixed point is **locally stable** if, given an initial condition sufficiently close to the fixed point, subsequent iterates eventually approach the fixed point.

How do we tell if a fixed point is locally stable? For a linear finite-difference equation, $x_{t+1} = Rx_t$, we already know the answer: The stability of the fixed point at the origin depends on the slope R of the line. If $|R| < 1$, future iterates are successively closer to the fixed point at the origin—this is exponential decay to zero. If $|R| > 1$, future iterates are successively farther away from the fixed point at the origin.

How does one determine the stability of a fixed point in a nonlinear finite-difference equation? In calculus classes, one discusses the notion that over limited regions a curve can be approximated by a straight line of the appropriate slope. In the neighborhood of the intersection of the straight line $x_{t+1} = x_t$ with the curve $x_{t+1} = f(x_t)$, it is therefore possible to approximate the curve by a straight line.

Figures 1.19 through 1.22 illustrate four separate cases that show the region of intersection. Let $x^\star$ be a fixed point of $f(\cdot)$, that is a state for which $x^\star = f(x^\star)$. The slope of the curve at the fixed point, $\frac{df}{dx_t}\big|_{x^\star}$, establishes the stability of the fixed point. We will designate this slope by m. Figures 1.19 through 1.22 plot y_{t+1} versus y_t, where $y_t = x_t - x^\star$. This means that in the figures the fixed point appears at the origin, whereas in the original variable, x_t, the fixed point is at $x^\star$. Observe that

- If $|m| < 1$, the fixed point is *stable* so that nearby points approach the fixed point under iteration.
- If $|m| > 1$, the fixed point is *unstable* and points leave the neighborhood of the fixed point.

Also, note that

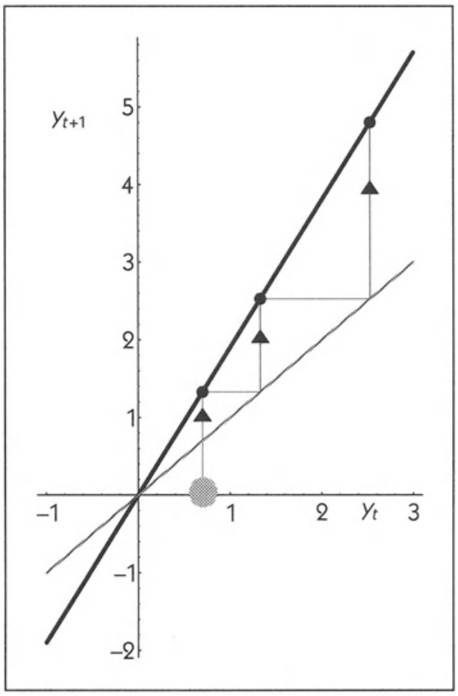

Figure 1.19
The dynamics of $y_{t+1} = my_t$. $m > 1$ produces monotonic growth as shown here with $m = 1.9$.

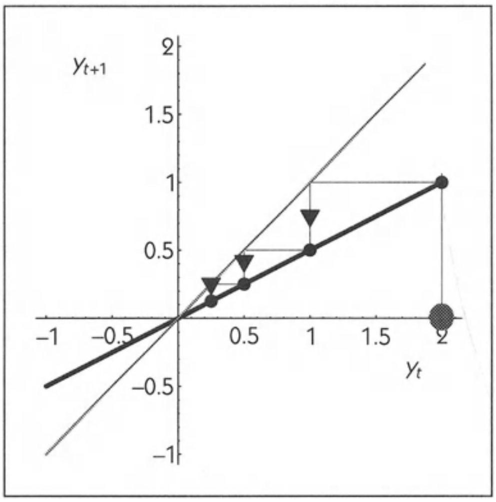

Figure 1.20
The dynamics of $y_{t+1} = my_t$. $0 < m < 1$ produces monotonic decay to $y_t = 0$. Here, $m = 0.5$.

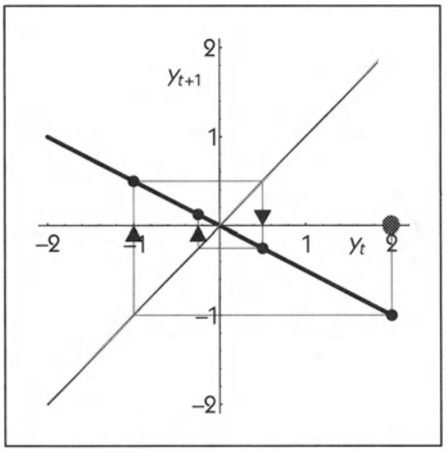

Figure 1.21
The dynamics of $y_{t+1} = my_t$. $-1 < m < 0$ produces alternating decay as shown here with $m = -0.5$.

- If $m > 0$, the points approach or leave the fixed point in a *monotonic* fashion.
- If $m < 0$, the points approach or leave the fixed point in an *oscillatory* fashion.

From the above considerations, a general method can be given for determining the stability of a fixed point in finite-difference equations with one variable. The steps are as follows:

1. Solve for the fixed points. This involves solving the equation

$$x_t = f(x_t).$$

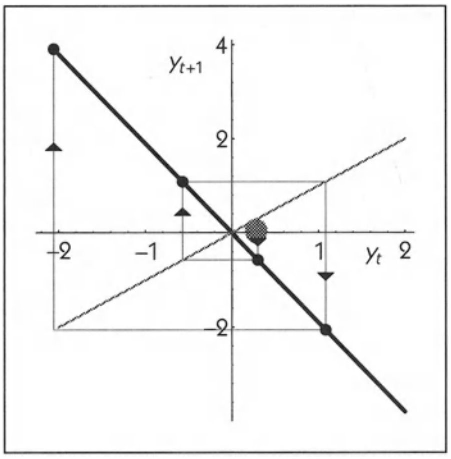

Figure 1.22
The dynamics of $y_{t+1} = my_t$. $m < -1$ produces alternating growth. Here, $m = -1.9$.

Linear equations always have only one fixed point—the one at $x_t = 0$. Nonlinear equations may have more than one fixed point. Steps 2 and 3 can be applied to each of the fixed points, one at a time. Call the fixed point we are studying x^*. Like all fixed points, this satisfies $x^* = f(x^*)$.

2. Calculate the slope m of $f(x_t)$, evaluating x_t at the fixed point x^*. That is, compute

$$m = \left.\frac{df}{dx_t}\right|_{x_t=x^*}.$$

3. The slope m at the fixed point determines its stability.

$1 < m$	Unstable, exponential growth.
$0 < m < 1$	Stable, monotonic approach to $y_t = 0$ (i.e., approach to $x_t = x^*$).
$-1 < m < 0$	Stable, oscillatory approach to $y_t = 0$ (i.e., approach to $x_t = x^*$).
$m < -1$	Unstable, oscillatory exponential growth.

TRANSIENT AND ASYMPTOTIC BEHAVIOR

If a fixed point is locally stable, then once the state is very near to the fixed point, it will stay near throughout the future. Before the state reaches the fixed point, it may show different behavior. For example, in Figure 1.10, the state is far enough away from the fixed point for the first five or six iterations that we can see it change from iteration to iteration. After that, the state appears to have reached the fixed point. In Figure 1.11, the movement toward the fixed point is visible for approximately twenty iterations. The term **asymptotic dynamics** refers to the dynamics as time goes to infinity. Behavior before the asymptotic dynamics is called **transient.**

STABILITY AND NUMERICAL ITERATION

Suppose that we want to use numerical iteration to find fixed points. One strategy would be to pick a large number of initial conditions and iterate numerically each of these initial conditions. If the iterates converge to a fixed value; then we have identified a fixed point at that value. (Figure 1.10 shows an example of this.)

If a fixed point is locally stable, then this strategy may well succeed, since the fixed point will eventually be approached if any of the initial conditions is close to the fixed point. Once the state is close to the fixed point, it will remain near the fixed point.

If a fixed point is unstable, however, then we will find it only if one of the iterates happens to land on the fixed point *exactly*, and this is extremely unlikely. In general, we can use numerical iteration only to find stable fixed points. If we want to find unstable fixed points, another approach is needed, namely solving the equation $x_t = f(x_t)$.

❑ EXAMPLE 1.1

Cells reproduce by division; the process by which the cell nucleus divides is called **mitosis**. One way to regulate the rate of reproduction of cells is by regulating mitosis. There is (controversial!) biochemical evidence that there are compounds, called **chalones**, that are tissue-specific inhibitors of mitosis (see Bullough and Laurence, 1968).

For simplicity, assume that the generations of cells are distinct and that the number of cells in each generation is given by N_t. Following the same logic as in Eq. 1.2, assume that for each cell in generation t, there are R cells in generation $t+1$. (If every cell divided in half every time step, then R would equal 2.) The finite-difference equation describing this situation is the linear equation $N_{t+1} = RN_t$, which leads either to exponential growth or to decay to zero.

A possible role of chalones is to make R depend on the number of cells. Assume that the amount of chalone produced is proportional to the number of cells. The more chalone there is, the greater the inhibitory effect on mitosis.

The biochemical action of chalones is to bind to a protein involved in mitosis, rendering the protein inactive. Binding of molecules to proteins is often modeled by a Hill function (see Section A.5), which suggests that an appropriate equation for the hypothetical chalone control mechanism is

$$N_{t+1} = f(N_t) = \frac{RN_t}{1 + \left(\frac{N_t}{\theta}\right)^n},$$

where θ and n are parameters. We will assume that $n \geq 2$. Figure 1.23 shows this finite difference equation when $R = 2, \theta = 5$, and $n = 3$.

Find the fixed points of this system and determine their stability.

1. To determine the fixed points we solve the equation

$$N^* = \frac{RN^*}{1 + \left(\frac{N^*}{\theta}\right)^n}.$$

   There are two real solutions: $N^* = 0$ and $N^* = \theta(R-1)^{\frac{1}{n}}$. These are the only fixed points. There are also imaginary solutions that can be ignored in this case because we are only concerned with biologically

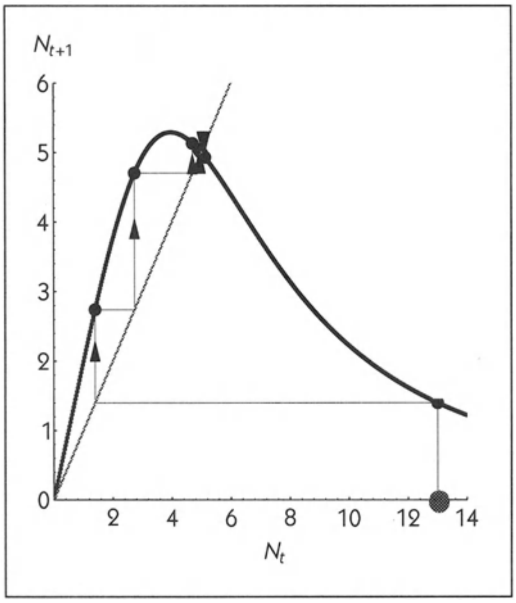

Figure 1.23 A cobweb analysis of chalone production for the parameters $R = 2$, $\theta = 5, n = 3$.

meaningful solutions, and the number of cells in each generation must be a real number.

2. To determine the stability of the fixed points it is necessary to compute the slope at the fixed points. Differentiating the right-hand side of the finite-difference equation, we find

$$\frac{df}{dN_t} = \frac{R + R\left(\frac{N_t}{\theta}\right)^n(1-n)}{\left(1 + \left(\frac{N_t}{\theta}\right)^n\right)^2}.$$

3. From the above equation we find that the slope at the fixed point $x_t = 0$ is just R. If $R > 1$, the fixed point at the origin is always unstable. (To be a plausible model of the regulation of cell reproduction, we must have $R > 1$. Otherwise, the population would always fall to zero even in the complete absence of the mitosis-inhibiting chalones.)

   The slope at the fixed point $N^* = \theta(R-1)^{\frac{1}{n}}$ is

$$\left.\frac{df}{dN_t}\right|_{N^*} = 1 + n\left(\frac{1}{R} - 1\right).$$

For $R = 2$, the fixed point will be unstable when $n > 4$ and stable otherwise. □

GLOBAL STABILITY OF FIXED POINTS

In this section we've studied local stability. Local stability tells us whether the fixed point is approached if the initial condition is sufficiently close to the fixed point. The local stability can be assessed simply by looking at the slope of the function at the fixed point.

A slightly different—and often much more difficult—question is whether a locally stable fixed point is **globally stable**.

For linear finite-difference equations, the answer is straightforward. A locally stable fixed point is also globally stable: Regardless of the initial condition, the iterates will eventually reach the locally stable point (i.e., the origin) from any initial condition.

For nonlinear finite-difference equations, there can be more than one fixed point. When multiple fixed points are present, none of the fixed points can be globally stable.

The set of initial conditions that eventually leads to a fixed point is called the **basin of attraction** of the fixed point. Often, the basin of attraction for fixed points in nonlinear systems can have a very complicated geometry (see Chapter 3). If multiple fixed are locally stable we say there is **multistability**.

1.6 CYCLES AND THEIR STABILITY

In Figures 1.7, 1.13, and 1.14 we can see that periodic cycles are one form of behavior for finite-difference equations. In everyday language, a **cycle** is a pattern that repeats itself, and the **period** of the cycle is the length of time between repetitions. In finite-difference equations like Eq. 1.1, a cycle arises when

$$x_{t+n} = x_t, \quad \text{but} \quad x_{t+j} \neq x_t \quad \text{for } j = 1, 2, \ldots, n-1. \tag{1.7}$$

There is a useful correspondence between fixed points and periodic cycles which helps in understanding how to find cycles and assess their stability. A simple case is a cycle of period 2. Consider the finite-difference equation

$$x_{t+1} = f(x_t) = 3.3(1 - x_t)x_t. \tag{1.8}$$

As shown in Figure 1.13, the solution is a cycle of period 2. The definition of a cycle of period 2 is that

$$x_{t+2} = x_t \quad \text{while } x_{t+1} \neq x_t. \tag{1.9}$$

By substitution into $x_{t+1} = f(x_t)$, we can write the value of x_{t+2} as

$$x_{t+2} = f(x_{t+1}) = f(f(x_t)). \tag{1.10}$$

If there is a cycle of period 2, then $x_t = f(f(x_t))$. For the quadratic map (Eq. 1.6), we can find $f(f(x_t))$ with a bit of algebra:

$$\begin{aligned} f(f(x_t)) = f(x_{t+1}) &= Rx_{t+1} - Rx_{t+1}^2 \\ &= R(Rx_t - Rx_t^2) - R(Rx_t - Rx_t^2)^2 \\ &= R^2x_t - (R^2 + R^3)x_t^2 + 2R^3x_t^2 - R^3x_t^4. \end{aligned} \tag{1.11}$$

The equation may seem a little formidable, but the M-shaped graph, shown in the lower graph in Figure 1.24, is quite simple.

We can see from Eq. 1.10 that there is an analogy between fixed points and cycles: If a system $x_{t+1} = f(x_t)$ has a cycle of period 2, then the function $f(f(x_t))$ has at least two fixed points. Thus, we can find the cycles of period 2 by solving the equation $x_t = f(f(x_t))$. This can be done graphically, algebraically, or numerically.

One trivial type of solution to $x_t = f(f(x_t))$ is a solution to $x_t = f(x_t)$. These solutions correspond to the fixed points of $f(x_t)$ and hence are not cycles of period 2—they are "cycles of period 1," that is, steady states. In the graph of Eq. 1.11 shown in Figure 1.24, we can see four fixed points of $f(f(x_t))$: at $x_t = 0$, at $x_t = 0.479$, at $x_t = 0.697$, and at $x_t = 0.823$. Two of these values are also fixed points of $f(x_t)$ and therefore correspond to cycles of period 1.

Longer cycles can be found in the same way. A cycle of period n is found by solving the equation

$$x_t = \underbrace{f(f(\cdots f(x_t))}_{n \text{ times}}),$$

avoiding solutions that correspond to periods less than n. In practice, this problem can be very hard to solve algebraically.

STABILITY OF CYCLES

Just as a fixed point can be locally stable or unstable, a cycle can be stable or unstable. We say that a cycle is **locally stable** if, given that the initial condition is

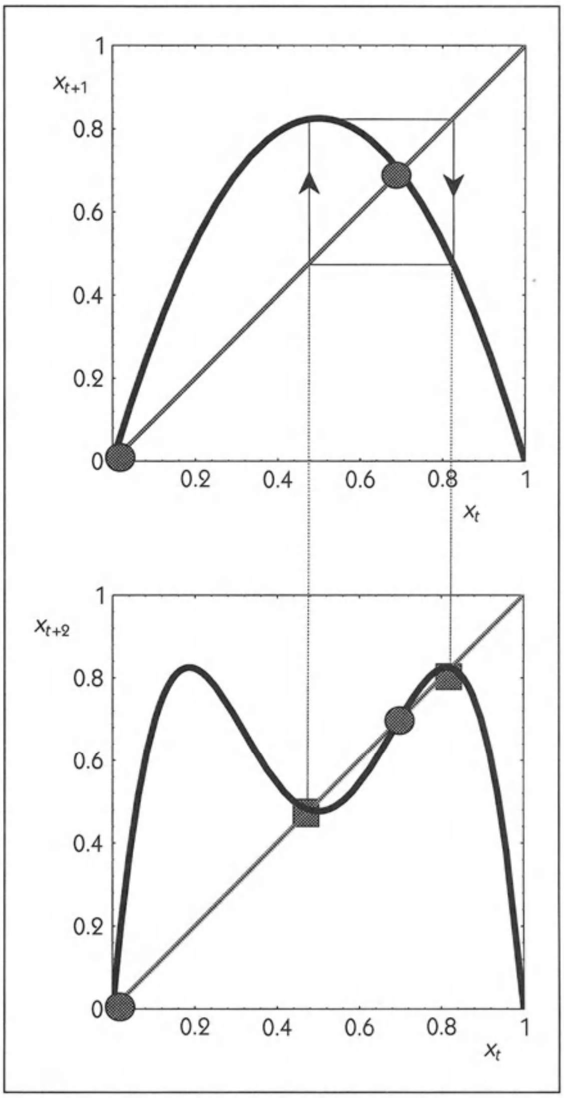

Figure 1.24 A cycle of period 2 in the system $x_{t+1} = R(1 - x_t)x_t = f(x_t)$ for $R = 3.3$. The graph of x_{t+1} versus x_t has two fixed points, marked as gray dots, but neither of them is stable. When plotted as x_{t+2} versus x_t, the cycle of period two looks like 2 fixed points in the finite-difference equation $x_{t+2} = f(f(x_t))$. Altogether, this system has four fixed points—the two corresponding to the cycle of period 2 (marked as small gray squares) and the two fixed points from the system $x_{t+1} = f(x_t)$.

close to a point on the cycle, subsequent iterates approach the cycle. (Again, this is what mathematicans call "local asymptotic stability").

We can now consider the computation of the stability of the fixed point of the finite-difference equation $x_{t+2} = f(f(x_t))$. We will use x^* to denote a solution to the equation $x_t = f(f(x_t))$ that is not also a fixed point of $x_t = f(x_t)$. Referring to Section 1.5, we can see that the stability of the fixed point of $x_{t+2} = f(f(x_t))$ depends on the value of

$$\left.\frac{df(f(x_t))}{dx_t}\right|_{x^*}.$$

Using the chain rule for derivatives, we have

$$\left.\frac{df(f(x_t))}{dx_t}\right|_{x^*} = \left.\frac{df}{dx_t}\right|_{f(x^*)} \left.\frac{df}{dx_t}\right|_{x^*}.$$

Thus, the stability of a fixed point of period 2 depends on the slope of the function $f(x_t)$ at both of the two points x^* and $f(x^*)$.

A method for finding cycles by numerical iteration is quite easy in principle: Start at some initial condition and at each iteration, see if the value has been produced previously. Once the same value is encountered twice, the intervening values will cycle over and over again.

When cycles are found by numerical iteration, it is important to realize that unstable cycles will tend not to be found. This is exactly analogous to the situation when using numerical iteration to look for fixed points. When a cycle is stable, any initial condition in the cycle's basin of attraction will eventually lead to the cycle. For unstable cycles, the cycle will not be approached unless some iterate of the initial condition lands exactly on a point on the cycle.

❑ **EXAMPLE 1.2**

Consider the finite-difference equation

$$x_{t+1} = \frac{1 - x_t}{3x_t + 1}.$$

a. Sketch x_{t+1} as a function of x_t.
b. Determine the fixed point(s), if any, and test algebraically for stability.
c. Algebraically determine x_{t+2} as a function of x_t and determine if there are any cycles of period 2. If so, are they stable? Based on the analysis above, determine the dynamics starting from any initial condition.

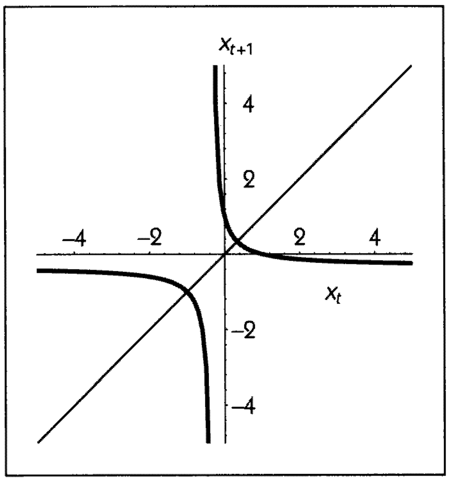

Figure 1.25
The graph of $x_{t+1} = \frac{1-x_t}{3x_t+1}$.

Solution:

a. This is the graph of a hyperbola, see Figure 1.25. There are no local maxima or minima, but there are asymptotes at $x_t = -\frac{1}{3}$ and at $x_{t+1} = -\frac{1}{3}$.

b. The fixed points are determined by setting $x_{t+1} = x_t$ to give the quadratic equation

$$3x_t^2 + 2x_t - 1 = 0.$$

This equation can be factored to yield two solutions, $x_t = \frac{1}{3}$ and $x_t = -1$. To determine stability, we compute

$$\frac{dx_{t+1}}{dx_t} = \frac{-4}{(3x_t + 1)^2}.$$

When this is evaluated at the fixed points, the slope is -1. Note that a slope of -1 does not fall into the classification scheme presented in Section 1.5—if the slope were slightly steeper than -1, the fixed point would be unstable; if the slope were slightly less steep than -1, the fixed point would be stable. We cannot determine the stability of the steady states from this computation: The steady state is neither stable nor unstable.

c. Iterating directly we find that

$$x_{t+2} = \frac{1 - x_{t+1}}{3x_{t+1} + 1}$$

$$= \frac{1 - \left(\frac{1-x_t}{3x_t+1}\right)}{3\left(\frac{1-x_t}{3x_t+1}\right) + 1}$$
$$= x_t.$$

Amazingly, all initial conditions are on a cycle of period 2. The cycles are neither locally stable nor unstable, since initial conditions neither approach nor diverge from any given cycle. □

The preceding discussion shows that if there are stable cycles, then an examination of the graph of x_{t+n} as a function of x_t will show certain definite features. If there is a stable cycle of period n, there must be at least n fixed points associated with the stable cycle, where the slope at each of the fixed points is equal and the absolute value of the slope at each of the fixed points is less than 1.

Now let's consider a specific situation, the quadratic map

$$x_{t+1} = f(x_t) = 4(1 - x_t)x_t. \tag{1.12}$$

This now-familiar parabola is plotted again in Figure 1.26. We can see that there are two fixed points, both of which are unstable because the slope of the function at these fixed points is steeper than 1.

To look for cycles of period 2, we can plot x_{t+2} versus x_t as shown in Figure 1.27. The four places where this graph intersects the line $x_{t+2} = x_t$ (i.e., the 45-degree line) are the possible points on the cycle of period 2—recall that two of the intersection points correspond to cycles of period 1. Since the slope of

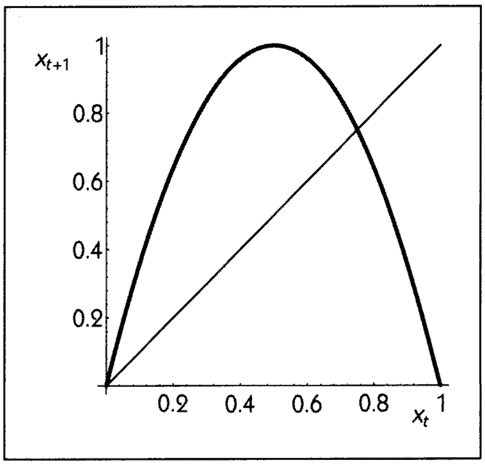

Figure 1.26
x_{t+1} versus x_t for Eq. 1.12.

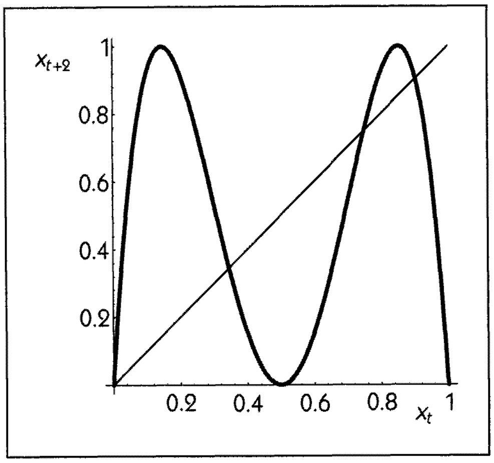

Figure 1.27
x_{t+2} versus x_t for Eq. 1.12.

the function at all these points is steeper than 1, we can conclude that there are no stable cycles of period 2 in Eq. 1.12.

We can continue looking for longer cycles. Figure 1.28 shows the graph of $x_{t+3} = f(f(f(x_t)))$. This graph intersects the line $x_{t+3} = x_t$ in eight places. (Of these, two correspond to cycles of period 1.) At all of these places the slope of the function is steeper than 1, so all of the possible cycles of period 3 are unstable. Similarly, Figure 1.29 shows that the cycles of period four are also unstable.

In fact, there are no stable cycles of *any* length, no matter how long, in Eq. 1.12, although we will not prove this here. What are the dynamics in Eq. 1.12? The next section will explore the answer to this question.

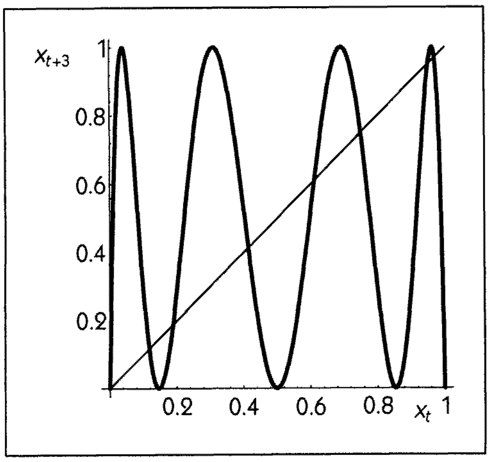

Figure 1.28
x_{t+3} versus x_t for Eq. 1.12.

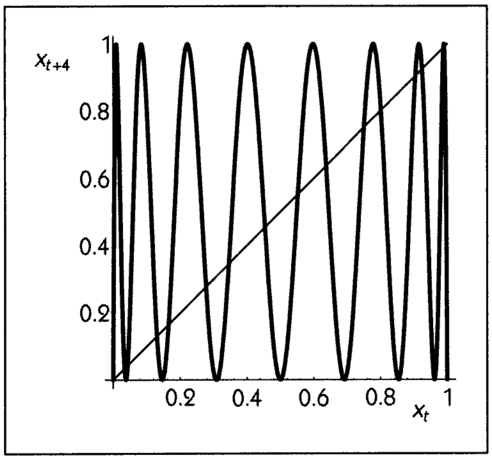

Figure 1.29
x_{t+4} versus x_t for Eq. 1.12.

1.7 CHAOS

DEFINITION OF CHAOS

Let's do a numerical experiment to investigate the properties of Eq. 1.12. Pick an initial condition, say $x_0 = 0.523423$, and iterate. Now start over, but change the initial condition by just a little bit, to $x_0 = 0.523424$. The results are shown in Figure 1.29.

There are several important features of the dynamics illustrated in Figure 1.29. In fact, based on the figure we have strong evidence that this equation displays **chaos**—which is defined to be aperiodic bounded dynamics in a deterministic system with sensitive dependence on initial conditions.

Each of these terms has a specific meaning. We define the terms and explain why each of these properties appears to be satisfied by the dynamics in Figure 1.29.

Aperiodic means that the same state is never repeated twice. Examination of the numerical values used in this graph shows this to be the case. However, in practice, by either graphically iterating or using a computer with finite precision, we eventually may return to the same value. Although a computer simulation or graphical iteration always leaves some doubt about whether behavior is periodic, the presence of very long cycles or of aperiodic dynamics in computer simulations is partial evidence for chaos.

Bounded means that on successive iterations the state stays in a finite range and does not approach $\pm\infty$. In the present case, as long as the initial condition x_0 is in the range $0 \leq x_0 \leq 1$, then all future iterates will also fall in this range. This is because for $0 \leq x_t \leq 1$, the minimum value of $4(1 - x_t)x_t$ is 0 and the maximum value is 1. Recall that in the linear

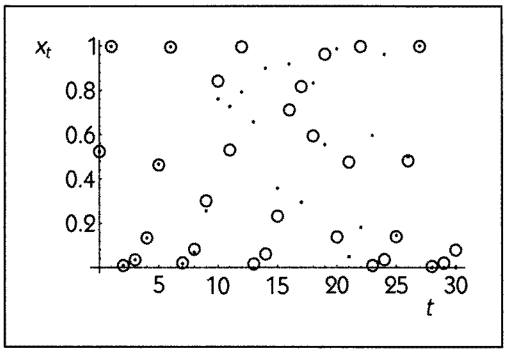

Figure 1.30 Two solutions to $x_{t+1} = (4 - 4x_t)x_t$. The solution marked with a dot has the initial condition $x_0 = 0.523423$, while the solution marked with a circle has $x_0 = 0.523424$. The solutions are almost exactly the same for the first seven iterations, and then move apart.

finite-difference equation, Eq. 1.2, we have already seen a system where the dynamics are not bounded and there is explosive growth.

Deterministic means that there is a definite rule with no random terms governing the dynamics. The finite-difference equation 1.12 is an example of a deterministic system. For one-dimensional, finite-difference equations, "deterministic" means that for each possible value of x_t, there is only a single possible value for $x_{t+1} = f(x_t)$. In principal, for a deterministic system x_0 can be used to calculate all future values of x_t.

Sensitive dependence on initial conditions means that two points that are initially close will drift apart as time proceeds. This is an essential aspect of chaos. It means that we may be able to predict what happens for short times, but that over long times prediction will be impossible since we can never be certain of the exact value of the initial condition in any realistic system. In contrast, for finite-difference equations with stable fixed points or cycles, two slightly different initial conditions may often lead to the same fixed point or cycle. (But this is not always the case; see Chapter 3.)

Although the possibility for chaos in dynamical systems was already known to the French mathematician Henri Poincaré in the nineteenth century, the concept did not gain broad recognition amongst scientists until T.-Y. Li and J. Yorke introduced the term "chaos" in 1975 in their analysis of the quadratic map, Eq. 1.12. The search for chaotic dynamics in diverse physical and biological fields, and the mathematical analysis of chaotic dynamics in nonlinear equations, have sparked research in recent years.

THE PERIOD-DOUBLING ROUTE TO CHAOS

We have seen that the simple finite-difference equation

$$x_{t+1} = R(1 - x_t)x_t$$

can display various qualitative types of behavior for different values of R: steady states, periodic cycles of different lengths, and chaos. The change from one form of qualitative behavior to another as a parameter is changed is called a **bifurcation.** An important goal in studying nonlinear finite-difference equations is to understand the bifurcations that can occur as a parameter is changed.

There are many different types of bifurcations. For example, in the linear finite-difference equation $x_{t+1} = Rx_t$, there is decay to zero when $-1 < R < 1$. For $R > 1$, however, the behavior changes to exponential growth. The bifurcation point, or the point at which a change in R causes the behavior to change, is at $R = 1$. Nonlinear systems can show many other types of bifurcations. For example, changing a parameter can cause a stable fixed point to become unstable and can lead to a change of behavior from a steady state to a periodic cycle.

The finite-difference equation in Eq. 1.6 and many other nonlinear systems displays a sequence of bifurcations in which the period of the oscillation doubles as a parameter is changed slightly. This type of behavior is called a **period-doubling bifurcation.**

We can derive an algebraic criterion for a period-doubling bifurcation. In a nonlinear finite-difference equation there are n fixed points of the function

$$x_t = \underbrace{f(f(\cdots f(x_t))}_{n \text{ times}}$$

that are associated with a period-n cycle. The slope at each of these fixed points is the same. As a parameter is changed in the system, the slope at each of these fixed points also changes. When the slope for some parameter value is equal to -1, it is typical to find that at that parameter value the periodic cycle of period n loses stability and a periodic cycle of period $2n$ gains stability. In other words, there is a period-doubling bifurcation. Unfortunately, application of this algebraic criterion can be very difficult in nonlinear equations since iteration of nonlinear equations such as Eq. 1.6 can lead to complex algebraic expressions that are not handled easily. Consequently, people have turned to numerical studies.

Using a programmable pocket calculator in a numerical investigation of period-doubling bifurcations in Eq. 1.6 led Mitchell J. Feigenbaum to one of the major discoveries in nonlinear dynamics. Feigenbaum observed that as the parameter R varies in Eq. 1.6, there are successive doublings of the period of oscillation. Numerical estimation of the values of R at the successive bifurcations lead to the following approximate values:

- For $3.0000 < R < 3.4495$, there is a stable cycle of period 2.
- For $3.4495 < R < 3.5441$, there is a stable cycle of period 4.
- For $3.5441 < R < 3.5644$, there is a stable cycle of period 8.
- For $3.5644 < R < 3.5688$, there is a stable cycle of period 16.
- As R is increased closer to 3.570, there are stable cycles of period 2^n, where the period of the cycles increases as 3.570 is approached.
- For values of $R > 3.570$, there are narrow ranges of periodic solutions as well as aperiodic behavior.

These results illustrate a sequence of period-doubling bifurcations at $R = 3.0000$, $R = 3.4495$, $R = 3.5441$, $R = 3.5644$, with additional period-doubling bifurcations as R increases. This transition from the stable periodic cycles to the chaotic behavior at $R = 3.570$ is called the **period-doubling route to chaos.**

Notice that the range of values for each successive periodic cycle gets narrower and narrower. Call Δ_n the range of R values that give a period-n cycle. For example, since $3.4495 < R < 3.5441$ gives a period-4 cycle, we have $\Delta_4 = 3.5441 - 3.4495 = 0.0946$. Similarly, $\Delta_8 = 3.5644 - 3.5441 = 0.0203$.

The ratio $\frac{\Delta_4}{\Delta_8}$ is $\frac{0.0946}{0.0203} = 4.6601$. By considering successive period doublings, Feigenbaum discovered that

$$\lim_{n \to \infty} \frac{\Delta_n}{\Delta_{2n}} = 4.6692\ldots.$$

The constant, 4.6692... is now called **Feigenbaum's number**. This number appears not only in the simple theoretical model that we have discussed here but also in other theoretical models and in experimental systems in which there is a period-doubling route to chaos.

One way to represent graphically complex bifurcations in finite-difference equations is to plot the asymptotic values of the variable as a function of a parameter that varies. This type of plot is called a **bifurcation diagram**. Figure 1.31 shows a bifurcation diagram of Eq. 1.6. This figure is constructed by scanning many values of R in the range $3 \leq R \leq 4$. For each value of R, 1.6 is iterated many times. After allowing enough time for transients to decay, several of the values x_t, x_{t+1}, x_{t+2}, and so on are plotted. For example, when $R = 3.2$, Eq. 1.6 approaches a cycle of period 2, so there are two values plotted. The period-doubling bifurcations appear as "forks" in this diagram.

A summary of the dynamic behaviors discussed in Eq. 1.6 is contained in Figure 1.32. As the parameter R changes, different behaviors are observed. If you

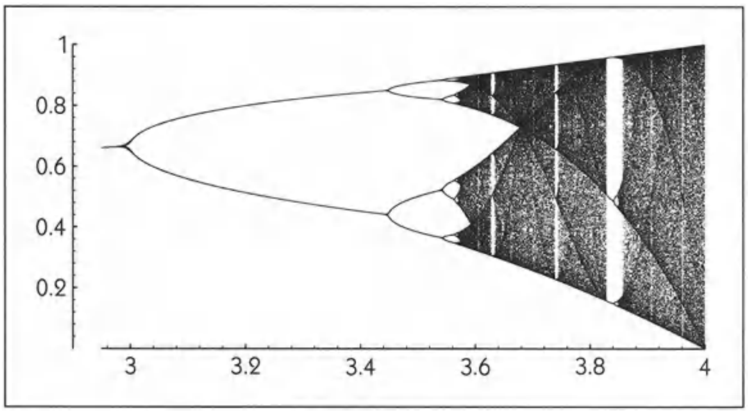

Figure 1.31 A bifurcation diagram of Eq. 1.6. The asymptotic values of x_t are plotted as a function of R using the method described in the text.

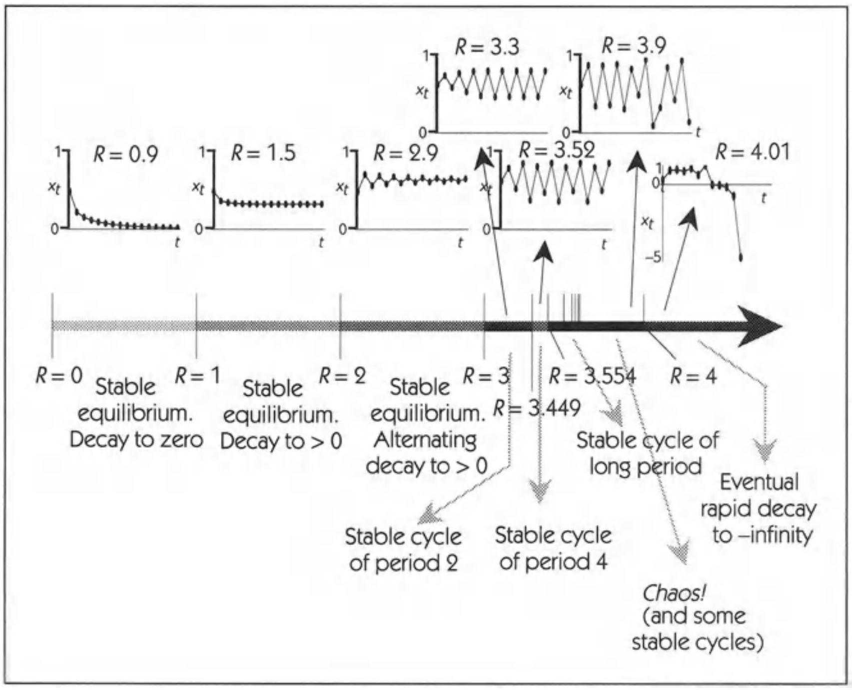

Figure 1.32 The various types of qualitative dynamics seen in $x_{t+1} = Rx_t(1 - x_t)$ for different values of the parameter R.

understand the origin of each of these behaviors, you have mastered the material in this chapter!

❑ EXAMPLE 1.3

The following equation, called the **tent map**, is often used as a very simple equation that gives chaotic dynamics.

Consider the finite-difference equation

$$x_{t+1} = f(x_t), \qquad 0 \le x_t \le 1,$$

where $f(x_t)$ is given as

$$f(x_t) = \begin{cases} 2x_t & \text{for } 0 \le x_t \le \dfrac{1}{2}, \\ 2 - 2x_t & \text{for } \dfrac{1}{2} \le x_t \le 1. \end{cases} \tag{1.13}$$

Draw a graph of x_{t+1} as a function of x_t. Graphically iterate this equation and determine if the dynamics are chaotic.

Solution: The graph of this equation looks like an old-fashioned pup tent (see Figure 1.33). Starting at two points chosen randomly near to each other we find that both points lead to aperiodic dynamics, where the distance between subsequent iterates of the points initially increases on subsequent iterations. Therefore, this system gives chaotic dynamics. This problem is tricky, however, since many people will start at a point such as 0.1, find that the subsequent iterates are 0.2, 0.4, 0.8, 0.4, 0.8, . . . , and then conclude that since they have found a cycle

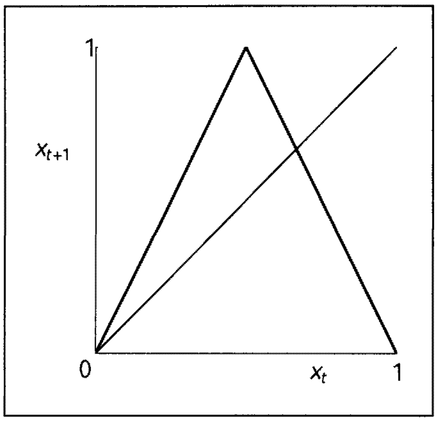

Figure 1.33
The graph of Eq. 1.13.

the dynamics in this equation are not chaotic. However, although there are many other such cycles in this equation, "almost all" values between 0 and 1 give rise to aperiodic chaotic dynamics. This is because the cycles are all unstable, as was defined in Section 1.6. Most equations that display chaotic dynamics also exhibit unstable cycles for some initial conditions, and thus this example is typical of what is found in other circumstances.

If you use a computer to iterate this map, watch out! You will probably find that the map rapidly converges to the fixed point at $x_t = 0$, even though this is an unstable fixed point. The reason involves the fact that numbers are represented in computers in base 2—all of the numbers that a computer can store in finite precision will be attracted to $x_t = 0$. To eliminate this problem, you can approximate the 2 in Eq. 1.13 by 1.9999999. □

1.8 QUASIPERIODICITY

In chaotic dynamics there is an aperiodic behavior in which two points that are initially close will diverge over time. There is another type of aperiodic behavior in which two points that are initially close will remain close over time. This type of behavior is called **quasiperiodicity**. In quasiperiodic dynamics there are no fixed points, cycles, or chaos.

To see how this type of dynamics can arise, consider the equation

$$x_{t+1} = f(x_t) = x_t + b \quad (\text{mod } 1), \tag{1.14}$$

where (mod 1) is the "modulus" operator that takes the fractional part of a number (e.g., 3.67 (mod 1) $=$ 0.67). To iterate this equation, we calculate $x_t + b$ and then take the fractional remainder. For example, if $x_t = 0.9$ and the parameter $b = 0.3$, then $x_t + b = 1.2$ and $x_t + b(\text{mod } 1) = 0.2$. Now consider the second iterate. We can do the iteration algebraically:

$$\begin{aligned} x_{t+2} &= x_{t+1} + b \quad (\text{mod } 1) = (x_t + b \quad (\text{mod } 1) + b) \quad (\text{mod } 1) \\ &= x_t + 2b \quad (\text{mod } 1). \end{aligned}$$

In similar fashion, we can find that

$$x_{t+n} = f^n(x_t) = x_t + nb \quad (\text{mod } 1).$$

Consequently, if $nb(\text{mod } 1) = 0$, then all values are on a cycle of period n; otherwise no values will be.

One way to think of this is by analogy to the odometer of a car, that shows the total mileage driven. Imagine that the odometer has a decimal point in front of it so that it shows a number between zero and one, for instance .07325. Every day the car goes b miles. After reaching .99999 the odometer resets to zero. x_t is the odometer value at the end of the trip on day t.

An example illustrates these ideas. In Figure 1.34 we show a graph of Eq. 1.14 for the particular case where $b = \frac{1}{\pi}$. This graph shows that the function has no fixed points, because there are no intersections of the function with the line $x_{t+1} = x_t$. The cobweb diagram for several iterations shows that there does not appear to be a cycle but that nearby points stay close together under subsequent iterations. Therefore, the dynamics appear to be quasiperiodic.

Can we know that there are never any periodic points no matter how many iterations we take? Here's where a bit of advanced mathematics can help. Recall the definition of a **rational number**: A number that can be written as the ratio of two integers $\frac{p}{q}$. **Irrational numbers** cannot be written as a ratio of two integers. π is an irrational number and $\frac{1}{\pi}$ is therefore also an irrational number. It follows immediately that $\frac{n}{\pi}$ (mod 1) can never be equal to 0 for any integer n. Therefore, there can never be any periodic cycles for Eq. 1.14 with $b = \frac{1}{\pi}$. Also, from the algebraic iteration, we see that the iterates of two initial conditions that are very close will remain very close. Therefore, the dynamics are quasiperiodic.

Though the concept of quasiperiodicity depends on abstract concepts in number theory, quasiperiodic dynamics can be observed in a large number of different settings. Consider the following odd sleep habits exhibited by one of our colleagues when he was in graduate school. The first day of graduate school the graduate student fell asleep exactly at midnight. Each day thereafter, the graduate student got up, worked, and went to sleep. However, this graduate student did

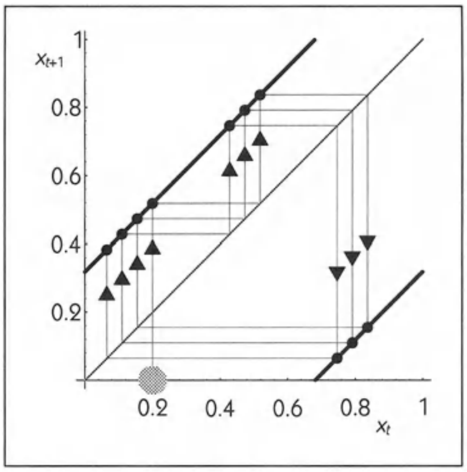

Figure 1.34
Iteration of $x_{t+1} = x_t + \frac{1}{\pi}$ (mod 1). The dynamics are an example of quasiperiodicity.

not do this at the regular rhythms but rather with a rhythm of *about* 25 hours. The graduate student came into work about an hour later each day. Eventually, after 24 days, the graduate student goes to sleep again at about midnight. If the student's sleep cycle were exactly 25 hours, then there would be a cycle: 25 calendar days would equal 24 graduate student days exactly. However, it would be very unlikely that the graduate student's day would be exactly 25 hours. For example, suppose the graduate student days were $25 + 0.001\pi$ hours. Then, using the same arguments above, the graduate student would never again go to sleep exactly at midnight (independent of the length of time needed to complete graduate school!).

Another area in which quasiperiodic dynamics are often observed is in cardiology. There can be several different pacemakers in one heart. Normally one is in charge and sets the rhythm of the entire heart by interactions with other pacemakers (we will turn to this just ahead). However, in some pathological circumstances, pacemakers carry on their own rhythm—they are not directly coupled to each other. Typically one sees variable time intervals between the firing times of one pacemaker and the other. Cardiologists generally invent esoteric names to describe reasonably simple dynamic phenomena and have classification schemes for naming rhythms that are not based on nonlinear dynamics. Thus, two different rhythms that can be considered as quasiperiodic (to a first approximation) are *parasystole* and *third-degree atrioventricular heart block*. The analysis of these cardiac arrhythmias leads naturally into problems in number theory.

❑ EXAMPLE 1.4

The finite-difference equation, sometimes called the sine map,

$$x_{t+1} = f(x_t) = x_t + b\sin(2\pi x_t),$$

where $0 \leq x_t \leq 1$, has been considered as a mathematical model for the interaction of two nonlinear oscillators (Glass and Perez, 1982). See *Dynamics in Action* 1 for a typical experiment.

This system displays period-doubling bifurcations as the parameter b is varied.

a. Find the fixed points of this equation.

b. Algebraically determine the stability of all fixed points for $0 < b \leq 1$. What are the dynamics in the neighborhood of each fixed point?

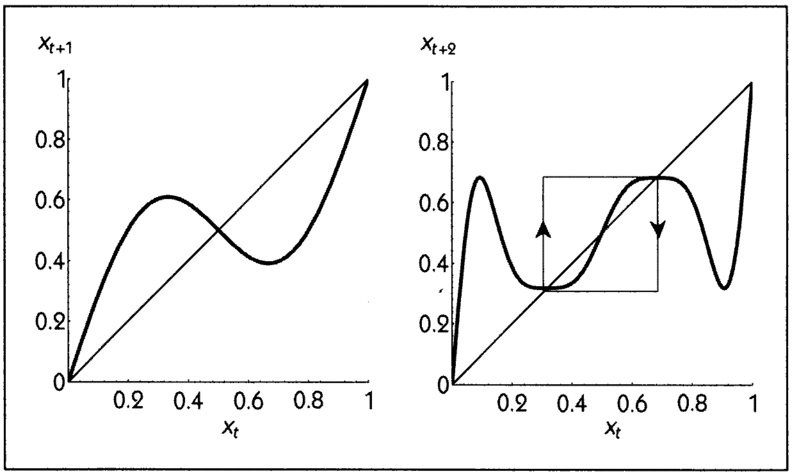

Figure 1.35 (left) The graph of $x_{t+1} = x_t + b\sin(2\pi x_t)$ for $b = 0.4$; (right) x_{t+2} versus x_t, showing the cycle of period 2 when $b = 0.4$.

Solution:

a. There are fixed points when

$$x_{t+1} = x_t + b\sin 2\pi x_t.$$

This will be true when $b\sin 2\pi x_t = 0$ which occurs when $x_t = 0, \frac{1}{2}, 1$.

b. To evaluate the stability we must first determine the slope at the steady states. The slope evaluated at the steady state is given by

$$\frac{dx_{t+1}}{dx_t} = 1 + 2\pi b\cos 2\pi x_t.$$

Therefore, when $x_t = 0$ or $x_t = 1$, the slope at the steady state is $1 + 2\pi b > 1$, which indicates that the steady state is unstable. For $x_t = \frac{1}{2}$ the slope at the steady state is $1 - 2\pi b$. For $0 < b < \frac{1}{\pi}$ this is a stable steady state, which is approached in an oscillatory fashion; and for $b > \frac{1}{\pi}$ this is an unstable steady state, which is left in an oscillatory fashion (see Figure 1.35). The slope is -1 at $b = \frac{1}{\pi}$, so this value of b gives a period-doubling bifurcation. □