2 Nonlinear Difference Equations

. . . It could be argued that a study of very simple nonlinear difference equations . . . should be part of high school or elementary college mathematics courses. They would enrich the intuition of students who are currently nurtured on a diet of almost exclusively linear problems.

R. M. May and G. F. Oster (1976)

Before reading through this chapter, you are invited to do some exploration using a calculator and some graph paper. The problem is to understand the behavior of the rather innocent-looking difference equation shown below:

$$x_{n+1} = rx_n(1 - x_n). \qquad (1)$$

Set $r = 2.5$, let $x_0 = 0.1$, and find $x_1, x_2, \ldots, x_{20}$ using equation (1). Now repeat the process for $r = 3.3$, 3.55, and 3.9. As r is increased from 3 to 4, you should notice some changes in the sort of solutions you get.

In this chapter we will devote some time to understanding this equation while developing some concepts and techniques of more general applicability.

The first thing to notice about equation (1) is that it is *nonlinear*, since it involves a term x_n^2. Attempting to "solve" (1) by setting $x_n = \lambda^n$ as for linear problems leads nowhere. Clearly this problem cannot be understood directly by methods used in Chapter 1. Indeed, nonlinear difference equations must be handled with special methods, and many of them, despite their apparent simplicity, to this day puzzle mathematicians.

Why then should we study nonlinear difference equations? Mainly because almost all biological processes are truly nonlinear. In Chapter 3 many examples of difference equation models drawn from population biology illustrate the fact that self-regulation of a population or interactions of competing species lead to nonlinearity. For example, the per capita growth rate of a population often depends on its size, so that as density increases, the birth rate or survivorship declines. As a second example, the proportion of a prey population killed by predators varies depending on the predator population. Even the problem of annual plants is much more complicated than implied in Chapter 1 since seed germination and plant survival may be regulated by the competition for available resources.

On the other hand, transcending the immediate application of difference equation models are some rather deep philosophical issues. For example, an important discovery in the last decade is that what may appear to be totally random fluctuations in a population with discrete (nonoverlapping) generations could in fact arise from a purely deterministic rule such as equation (1) (May, 1976). At least one example of this effect is recognized in real populations (see Section 3.1), though broader application is regarded with some doubt. Before delving more deeply into these exotic results, some of the methods of tackling equations such as (1) analytically deserve consideration.

2.1 RECOGNIZING A NONLINEAR DIFFERENCE EQUATION

A nonlinear difference equation is any equation of the form

$$x_{n+1} = f(x_n, x_{n-1}, \ldots), \tag{2}$$

where x_n is the value of x in generation n and where the recursion function f depends on nonlinear combinations of its arguments (f may involve quadratics, exponentials, reciprocals, or powers of the x_n's, and so forth). A solution is again a general formula relating x_n to the generation n and to some initially specified values, e.g., x_0, x_1, and so on. In relatively few cases can an analytic solution be obtained directly when equation (2) is nonlinear. Thus we must generally be satisfied with determining something about the nature of solutions or with exploring solutions with the help of the computer.

While the methods of Chapter 1 cannot be applied directly to solving nonlinear difference equations, we shall soon see their usefulness in understanding the characteristics of special classes of solutions. Before proceeding to demonstrate these *linear techniques,* certain key concepts must be established to prepare the way. In the following section we discuss specifically the case of *first-order difference equations,* which take the form

$$x_{n+1} = f(x_n). \tag{3}$$

Properties of solutions of equation (3) will be encountered again in many related situations.

2.2 STEADY STATES, STABILITY, AND CRITICAL PARAMETERS

The concepts of *homeostasis, equilibrium,* and *steady state* relate to the absence of changes in a system. An important question stemming from many problems in the natural sciences is whether constant solutions representing these static situations exist.

In some cases steady-state solutions are of intrinsic interest: for example, most living organisms function well in rather narrow ranges of temperature, acidity, or salinity. (More highly evolved organisms have developed intricate internal mechanisms for maintaining body temperatures and other factors at their appropriate constant levels.) On the other hand, steady-state solutions may seem of marginal interest in problems involving dynamic events such as growth, propagation, or reproduction of a population. Nevertheless, it is often true that by examining carefully what happens in a steady state, we can better understand the behavior of a system, as will be demonstrated shortly.

In the context of difference equations, a *steady-state solution* $\bar{x}$ is defined to be the value that satisfies the relations

$$x_{n+1} = x_n = \bar{x}, \tag{4}$$

so that no change occurs from generation n to generation $n + 1$. From equation (3) it follows that $\bar{x}$ also satisfies the relation

$$\bar{x} = f(\bar{x}) \tag{5}$$

and is thus frequently referred to as a *fixed point* of the function f (a value that f leaves unchanged). While not always the case, it is often true that solving an equation such as (5) for the steady-state value is simpler than finding a general solution to a full nonlinear difference equation problem such as equation (3).

We now distinguish between two types of steady-state solutions. Here the concept of *stability* must be introduced. Since this is best described by analogy, see Figure 2.1, which exemplifies three situations, two of which are steady states; one steady state is stable, the other unstable.

A steady state is termed stable if neighboring states are attracted to it and unstable if the converse is true. As shown in Figure 2.1, while an object balanced precariously on a hill may be in steady state, it will not return to this position if disturbed slightly. Rather, it may proceed on some lengthy excursion leading possibly to a second, more stable situation.

Such distinctions are of interest in biology. When steady states are unstable, great changes may be about to happen: a population may crash, homeostasis may be disrupted, or else the balance in a number of competing groups may shift in favor of

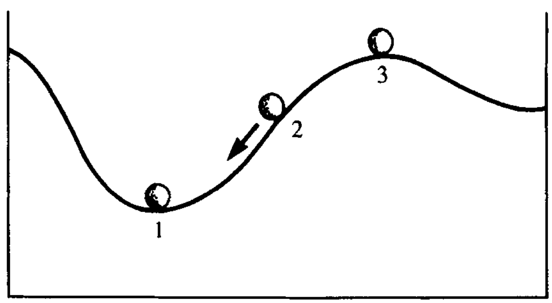


***Figure 2.1** In this landscape balls 1 and 3 are at rest and represent steady-state situations. Ball 1 is stable; if moved slightly it will return to its former position. Ball 3 is unstable. The slightest disturbance will cause it to fall into one of the adjoining valleys. Ball 2 is not in a steady state, since its position and speed are continually changing.*

the few. Thus, even if an exact mathematical solution is not easy to come by, qualitative information about whether change is imminent is of potential importance. With this motivation behind us, we turn to the analysis that permits us to make such predictions.

Let us assume that, given equation (3), we have already determined $\bar{x}$, a steady-state solution according to equation (5). We now proceed to explore its stability by asking the following key question: Given some value x_n *close* to $\bar{x}$, will x_n tend toward or away from this steady state? To address this question we start with a solution

$$x_n = \bar{x} + x'_n, \tag{6}$$

where x'_n is a small quantity termed a *perturbation* of the steady state $\bar{x}$. We then determine whether x'_n gets smaller or bigger. As we will show presently, these steps reduce the problem to a linear difference equation, so that we can apply methods developed in the previous section.

From equations (5) and (6) it follows that the perturbation x'_n satisfies

$$x'_{n+1} = x_{n+1} - \bar{x} = f(x_n) - \bar{x} = f(\bar{x} + x'_n) - \bar{x}. \tag{7}$$

Equation (7) is still not in a form from which direct information can be gleaned because the RHS involves the function f evaluated at $\bar{x} + x'_n$, a value that often is not known. Now we resort to a classic step that will be used again in many nonlinear problems; the value of f will be *approximated* by exploiting the fact that x'_n is a small quantity. That is, in writing a Taylor series expansion, we note that for a suitable function f,

$$f(\bar{x} + x'_n) = f(\bar{x}) + \left(\frac{df}{dx}\bigg|_{\bar{x}}\right)x'_n + \underbrace{O(x'^2_n)}_{\text{very small terms}}.$$

The "very small terms" can be neglected, at least close to the steady state. This approximation results in some cancellation of terms in (7) because $f(\bar{x}) = \bar{x}$ according to equation (5). Thus the approximation

$$x'_{n+1} \simeq f(\bar{x}) - \bar{x} + \left(\frac{df}{dx}\bigg|_{\bar{x}}\right)x'_n$$

can be written as

$$x'_{n+1} = ax'_n, \tag{8}$$

where

$$a = \left(\frac{df}{dx}\bigg|_{\bar{x}}\right).$$

The nonlinear problems in equations (3) or (7) have led to a linear equation (8) that describes what happens close to some steady state. Note that the constant a is a known quantity, obtained by computing the derivative of f and evaluating it at $\bar{x}$. Thus to understand whether small deviations from steady state increase or decrease, we can now apply the methods of linear difference equations. From Chapter 1 we know that the solution of equation (8) will be decreasing whenever $|a| < 1$. We conclude that

Condition for Stability

$$\bar{x} \text{ is a stable steady state of (3)} \Leftrightarrow \left| \frac{df}{dx}\bigg|_{\bar{x}} \right| < 1. \tag{9}$$

Example 1

Consider the following nonlinear difference equation for population growth:

$$x_{n+1} = \frac{kx_n}{b + x_n}, \qquad b, k > 0. \tag{10}$$

(1) Does equation (10) have a steady state? (2) If so, is that steady state stable?

Solutions: (1) To compute a steady-state value, let

$$\bar{x} = x_{n+1} = x_n.$$

Then

$$\bar{x} = \frac{k\bar{x}}{b + \bar{x}}, \qquad \bar{x}(b + \bar{x}) = k\bar{x}, \qquad \bar{x}(\bar{x} + b - k) = 0.$$

So

$$\bar{x} = k - b \qquad \text{or} \qquad \bar{x} = 0.$$

The steady state makes sense only if $k > b$, since a negative population $\bar{x}$ would be biologically meaningless.

(2) As previously mentioned, any small deviation must satisfy

$$x'_{n+1} = ax'_n, \tag{8}$$

where now

$$a = \frac{df}{dx}\bigg|_{\bar{x}} = \frac{d}{dx}\left(\frac{kx}{b + x}\right)\bigg|_{\bar{x}} = \frac{kb}{(b + \bar{x})^2} = \frac{b}{k}.$$

Thus, by the stability condition, the steady state is stable if and only if $|b/k| < 1$. Since both b and k are positive, this implies that

$$k > b.$$

Thus, the nontrivial steady state is stable whenever it exists. Stability of $\bar{x} = 0$ is left as an exercise.

In example 2, stability of one of the steady states is conditional on a *parameter* r. If r is greater or smaller than certain critical values (here 1 or 3), the steady state $\bar{x}_2$ is not stable. Such critical parameter values, often called *bifurcation values*, are points of demarcation for abrupt changes in qualitative behavior of the equation or of the system that it models. There may be a multitude of such transitions, so that as increasing values of the parameter are used, one encounters different behaviors.

Example 2

Now consider the following equation:

$$x_{n+1} = rx_n(1 - x_n), \qquad (11)$$

and determine stability properties of its steady state(s).

Solution:

Again, steady states are computed by setting

$$\bar{x} = r\bar{x}(1 - \bar{x}),$$

so that

$$r\bar{x}^2 - \bar{x}(r - 1) = 0.$$

This time two steady states are possible:

$$\bar{x}_1 = 0 \quad \text{and} \quad \bar{x}_2 = 1 - 1/r.$$

Perturbations about $\bar{x}_2$ satisfy

$$x'_{n+1} = ax'_n,$$

where here

$$a = \left.\frac{df}{dx}\right|_{\bar{x}_2} = r(1 - 2x)\Big|_{\bar{x}_2} = (2 - r).$$

Thus x_2 will be stable whenever $|a| < 1$ according to our linear theory. For stability of this steady state we conclude that the parameter r must satisfy the condition that $1 < r < 3$.

Equation (11), which will be the subject of some scrutiny in Section 2.3, provides a striking example of bifurcations.

One of the particularly important underlying ideas here is that we can think of a particular difference equation as a rule that governs the behavior of many classes of systems (e.g., different populations, distinct species, or one species at different stages of evolution or at different developmental stages). The rules can have shades of meaning depending on critical parameters that appear in the equation. This point, which we will amply illustrate and exploit in a variety of settings, will reappear in discussions of almost all models.

2.3 THE LOGISTIC DIFFERENCE EQUATION

Equation (11) encountered in example 2 has been known for some time to possess interesting behavior, but it first received public attention as an outcome of a classic paper by May (1976) which provided an exposition to some of the perhaps unexpected properties of simple difference equations. Sometimes known as the *discrete logistic equation,* (11) is an equivalent version of

$$y_{n+1} = y_n(r - dy_n), \qquad (12)$$

where r and d are constants. To see this, we redefine variables as follows. Let

$$x_n = \left(\frac{d}{r}\right) y_n.$$

This just means that quantities are measured in units of d/r. This results in a reduction of parameters based on consideration of scale, which we will discuss at great length in later chapters. This type of first step proves an aid in both formulating and analyzing complicated models.

The resulting equation,

$$x_{n+1} = rx_n(1 - x_n), \tag{11}$$

is one of the simplest nonlinear difference equations, containing just one parameter, r, and a single quadratic nonlinearity. While (11) could be a description of a population whose reproductive rate is density-regulated, there are practical problems with this interpretation. (In particular, it is necessary to restrict x and r to the intervals $0 < x < 1$, $1 < r < 4$ since otherwise the population becomes extinct; see May, 1976.)

Comparison with a Continuous Equation

Consider the following ordinary differential equation:

$$\frac{dx}{dt} = rx(1 - x), \qquad x \geq 0.$$

Sometimes called the *Pearl-Verhulst* or logistic equation, the above is often used to describe continuous density-dependent growth rates of populations. Its solutions are shown in Figure 2.2.

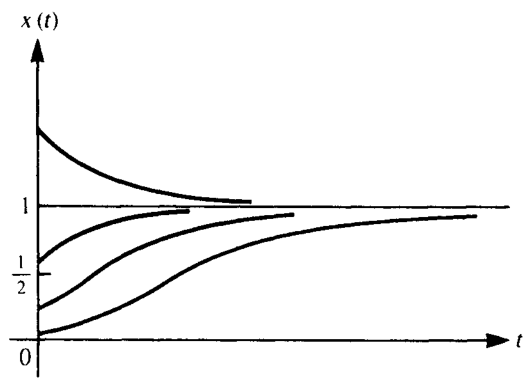


Figure 2.2 *Solutions to the* logistic differential *equation are characterized by a single nontrivial steady state* $\bar{x} = 1$, *which is stable regardless of the parameter value chosen for* r. *Thus* x(t) *tends toward a limiting value of* x = 1 *for all positive starting values.*

In example 2 of Section 2.2 we showed that equation (11) has two possible steady states, only one of which is *nontrivial* (nonzero): $\bar{x}_2 = 1 - 1/r$. The steady state is stable only when the parameter r satisfies $1 < r < 3$. (Notice that the parameter d in equation (12) only influences scaling of the qualitative behavior.)

What happens beyond the value of $r = 3$ and up to the permitted maximal value of r? Let us cautiously turn the knob on our metaphorical dial (Figure 2.3) and find out.

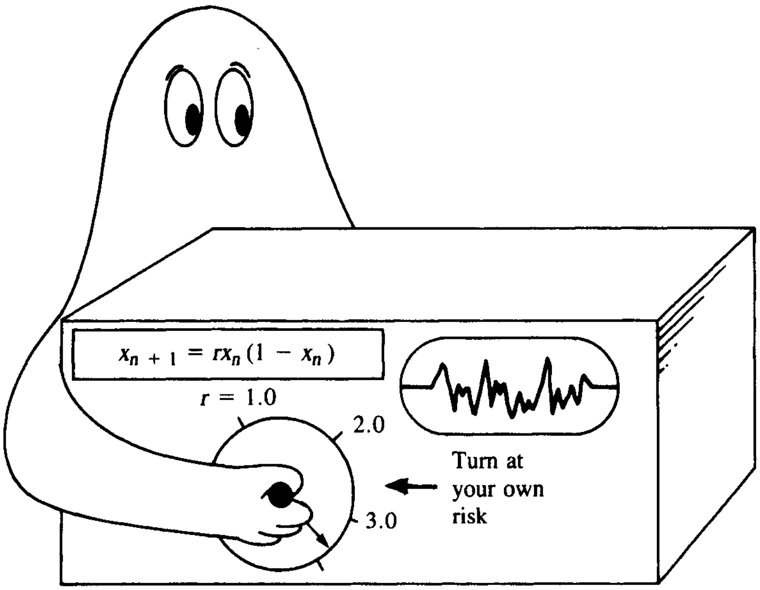


Figure 2.3

2.4 BEYOND $r = 3$

We shall resort to a clever trick (May, 1976) to prove that as r increases slightly beyond 3 in equation (11) *stable oscillations* of period 2 appear. A stable oscillation is a periodic behavior that is maintained despite small disturbances. Period 2 implies that successive generations alternate between two fixed values of x, which we will call $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$. Thus period 2 oscillations (sometimes called *two-point cycles*) simultaneously satisfy two equations:

$$x_{n+1} = f(x_n), \qquad (13a)$$

$$x_{n+2} = x_n. \qquad (13b)$$

Now observe that these can be combined,

$$f(x_{n+1}) = f(f(x_n)),$$

so that

$$x_{n+2} = f(f(x_n)). \tag{14}$$

Let us call the composite function by the new name g,

$$g(x) = f(f(x)),$$

and let k be a new index that skips every other generation:

$$k = n/2, \qquad n \text{ even}.$$

Then equation (14) becomes

$$x_{k+1} = g(x_k), \tag{15}$$

and a steady state of equation (15), $\bar{\bar{x}}$ (or a fixed point of g), is really a period 2 solution of (13a). Note that there must be two such values, $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$ since by assumption $\bar{\bar{x}}$ oscillates between two fixed values.

By this trick we have reduced the new problem to one with which we are familiar. That is, stability of a period 2 oscillation can be determined by using the methods of Section 2.2 on equation (15). Briefly, suppose an initial situation is created whereby $x_0 = \bar{\bar{x}}_1 + \epsilon_0$, where ϵ_0 is a small quantity. Stability of $\bar{\bar{x}}_1$ implies that periodic behavior will be reestablished, i.e., that the deviation ϵ_0 from this behavior will grow small. This happens whenever

$$\left| \left(\frac{dg}{dx} \right) \bigg|_{\bar{\bar{x}}_i} \right| < 1. \tag{16}$$

It is a straightforward calculation (see problem 5) to prove that this condition is equivalent to stating the following:

$$x_i \text{ is a stable 2-point cycle} \Leftrightarrow \left| \left(\frac{df}{dx} \bigg|_{\bar{\bar{x}}_1} \right) \left(\frac{df}{dx} \bigg|_{\bar{\bar{x}}_2} \right) \right| < 1 \tag{17}$$

From equation (17) we conclude that the stability of period 2 oscillations depends on the size of df/dx at $\bar{\bar{x}}_i$. The results will now be applied to further exploration of equation (11). Steps will include (1) determining $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$, the steady two-period oscillation values, and (2) exploring their stability.[1]

1. *To the instructor:* This section may be skipped without loss of continuity in the discussion.

Example 3
Find $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$ for the two-point cycles of equation (11).

Solution
To do so, first determine the composite map $g(x) = f(f(x))$:

$$\begin{aligned} g(x) &= r[rx(1-x)](1-[rx(1-x)]) \\ &= r^2x(1-x)[1-rx(1-x)]. \end{aligned} \tag{18}$$

Next, in equation (18) set $\bar{\bar{x}}$ equal to $g(\bar{\bar{x}})$ to obtain

$$1 = r^2(1-\bar{\bar{x}})[1-r\bar{\bar{x}}(1-\bar{\bar{x}})]. \tag{19}$$

Here it is necessary to be slightly resourceful, for the expression obtained is a third-order polynomial. We look back at the information at hand and use an important fact in solving this problem.

We notice that any steady-state values of the equation $x_{n+1} = f(x_n)$ are automatically steady states also of $x_{n+1} = f(f(x_n))$ or of any higher composition of f with itself. (In other words, $\bar{x}$ is also a periodic solution in the trivial sense.) This means that $\bar{x}$ satisfies the equation $\bar{x} = g(\bar{x})$. To see this, note that

$$\bar{x} = x_n = x_{n+1} = x_{n+2},$$

so

$$\bar{x} = f(\bar{x}) = f(f(\bar{x})) = g(\bar{x}).$$

Continuing the analysis of example 3, we now exploit the fact that $x = 1 - 1/r$ must be one solution to equation (19). This enables us to factor the polynomial so that the problem is reduced to solving a quadratic equation. To do this, we expand equation (19):

$$p(x) = x^3 - 2x^2 + \left(1 + \frac{1}{r}\right)x + \left(\frac{1}{r^3} - \frac{1}{r}\right) = 0. \tag{20}$$

Now divide by the factor $\{x - [1 - (1/r)]\}$, to get

$$\left[x - \left(1 - \frac{1}{r}\right)\right]\left[x^2 - \left(1 + \frac{1}{r}\right)x + \left(\frac{1}{r} + \frac{1}{r^2}\right)\right] = p(x) = 0. \tag{21}$$

This can be done by standard long division of polynomials.

The second factor is a quadratic expression whose roots are solutions to the equation

$$x^2 - \left(\frac{r+1}{r}\right)x + \left(\frac{r+1}{r^2}\right) = 0.$$

Hence

$$\bar{\bar{x}} = \frac{1}{2}\left[\left(\frac{r+1}{r}\right) \pm \sqrt{\left(\frac{r+1}{r}\right)^2 - \frac{4(r+1)}{r^2}}\right],$$

$$\bar{\bar{x}}_1, \bar{\bar{x}}_2 = \frac{r + 1 \pm \sqrt{(r-3)(r+1)}}{2r}. \tag{22}$$

The two possible roots, denoted $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$, are real if $r < -1$ or $r > 3$. Thus for positive r, steady states of the two-generation map $f(f(x_n))$ exist only when $r > 3$. Note that this occurs when $\bar{x} = 1 - 1/r$ ceases to be stable.

With $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$ computed, it is a straightforward (albeit algebraically messy) task to test their stability. To do so, it is necessary to compute (df/dx) and evaluate at the values $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$. When this is done, we obtain a second range of behavior: stability of the two-point cycles for $3 < r < r_2$ with $r_2 \simeq 3.3$. Again we could pose the question, What happens beyond $r = r_2$?

It should be emphasized that the trick used in exploring period 2 oscillations could be used for any higher period n: $n = 3, 4, \ldots$. Because the analysis becomes increasingly cumbersome, this method will not be further applied. Instead, we will explore some underlying geometric ideas that make the process of "tuning" a parameter more immediately significant.

2.5 GRAPHICAL METHODS FOR FIRST-ORDER EQUATIONS

In this section we examine a simple technique for visualizing the solutions of first-order difference equations that can be used for gaining insight into the stability of steady states and the effects of parameter variations. As an example, consider equation (11). Let us draw a graph of $f(x)$, the next-generation function (Figure 2.4). In this case $f(x) = rx(1 - x)$, so that f describes a parabola passing through zero at $x = 1$ and $x = 0$ and with a maximum at $x = \frac{1}{2}$.

Choosing an initial value x_0, we can read off $x_1 = f(x_0)$ directly from the parabolic curve. To continue finding $x_2 = f(x_1)$, $x_3 = f(x_2)$ and so on, we need to similarly evaluate f at each succeeding value of x_n. One way of achieving this is to use the line $y = x$ to reflect each value of x_{n+1} back to the x_n axis (Figure 2.4). This process, which is equivalent to bouncing between the curves $y = x$ and $y = f(x)$ (Figure 2.5) is a recursive graphical method for determining the population level. In Figure 2.5, a time sequence of x_n values is also shown. (This method should be compared to the one outlined in problem 13.)

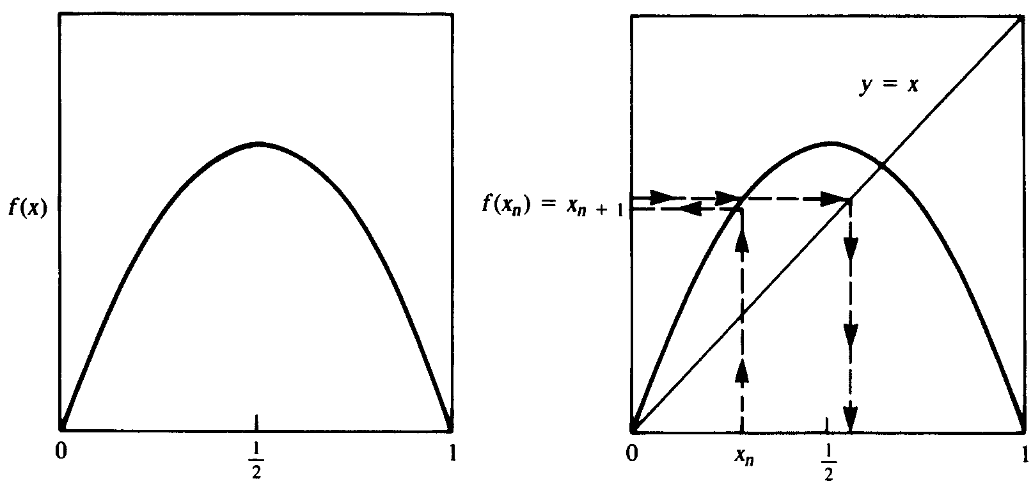
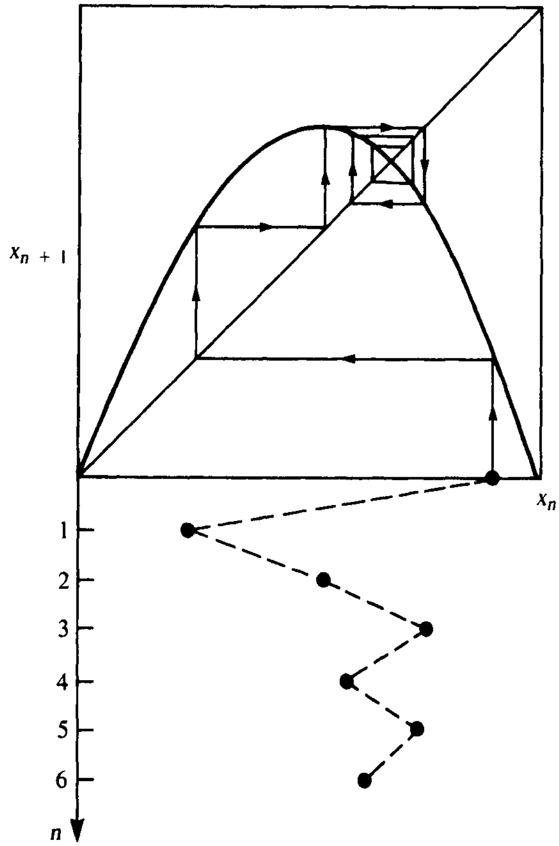


Figure 2.4 *The parabola* y = f(x) *and the line* y = x *can be used to graph the successive values of* x_n, n = 0, 1, 2, ... *This is known as the* cobwebbing method *(see Figure 2.5).*

***Figure 2.5** A number of values of* x_n, $n = 0, 1, \ldots, 7$ *are shown. Below is the corresponding time sequence, where the vertical axis shows time* n.



In Figure 2.5 the sequence of points converges to a single point at the intersection of the curve with the line $y = x$. This point of intersection satisfies

$$x_{n+1} = x_n \qquad \text{and} \qquad x_{n+1} = f(x_n).$$

It is by definition a steady state of the equation. The present example illustrates a particular regime for which this steady state is stable. Recall that the condition for stability is that

$$|a| = \left| \left. \frac{df}{dx} \right|_{\bar{x}} \right| < 1.$$

Interpreted graphically, this condition means that the tangent line $\mathscr{L}$ to $f(x)$ at the steady state value $\bar{x}$ has a slope not steeper than 1 (see Figure 2.6). Notice what happens when the parameter r is increased. This effectively increases the steepness of

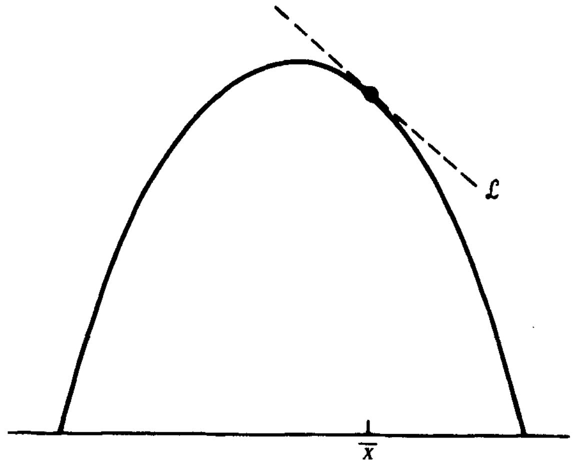


***Figure 2.6** The steady state $\bar{x}$ is always located at the intersection of* $y = f(x)$ *with* $y = x$. *$\bar{x}$ is stable if the tangent to the curve* $y = f(x)$ *is not too steep (a slope of magnitude less than* 1*).*

the parabola, which makes its tangent line $\mathcal{L}$ at $\bar{x}$ steeper, so that eventually the stability condition is violated (see Figure 2.7).

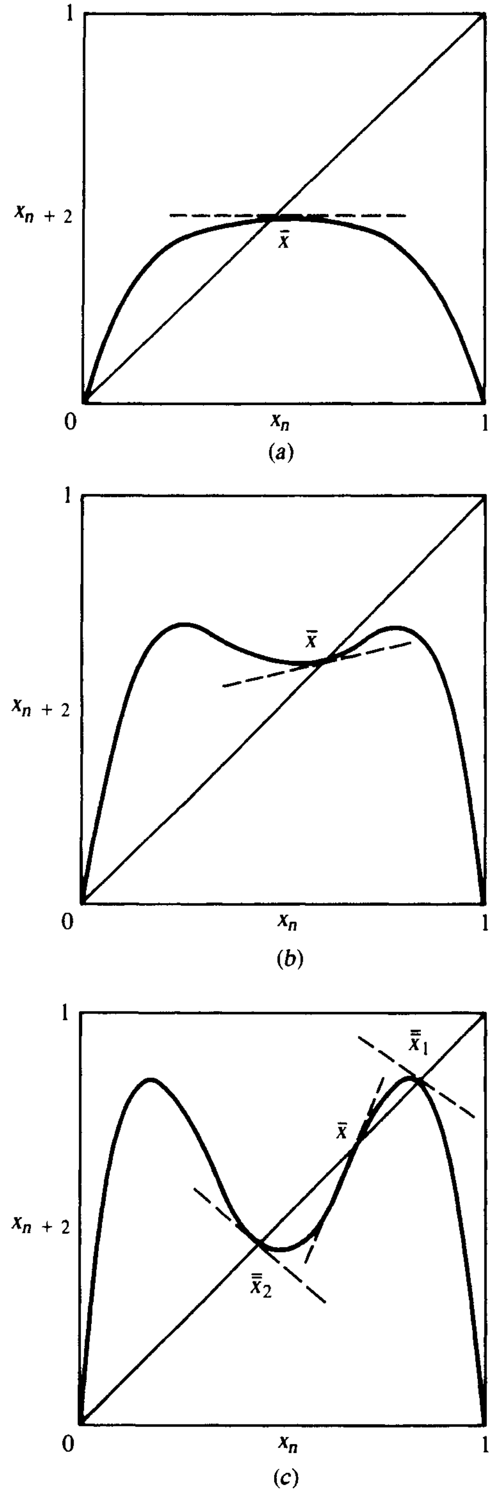
A similar procedure can be applied to the case of period 2 solutions discussed analytically in example 3, or indeed solutions of higher period. Here one is required to construct a graph of $f(f(x))$ [or $f^n(x)$]. This task can be accomplished once the maxima and minima of these composed functions are identified, for instance by setting their derivatives equal to zero. (It can also be done computationally.) One can verify that the function $f(f(x))$ given in example 3 undergoes the following sequence of shape changes as the parameter r is increased. Initially, $g(x) = f(f(x))$ has a flat graph, but as r increases, two humps appear and grow in size. Eventually these are big enough to intersect the line $y = x$ at three locations: $\bar{x}$ (as before) and $\bar{\bar{x}}_1$, $\bar{\bar{x}}_2$. At this point $\bar{x}$ loses its stability to the two-point cycle consisting of $\bar{\bar{x}}_1$, $\bar{\bar{x}}_2$.

As r is increased even further, $\bar{\bar{x}}_1$ and $\bar{\bar{x}}_2$ in turn lose their property of stability to other periodic states (with periods 4, 8, etc.). Each time a transition point of bifurcation value is reached, some new qualitative behavior is established. One can see these effects graphically or by using the simple pocket calculator computations, as suggested in the introduction to this chapter.

One way of summarizing the range of behaviors is shown in Figure 2.8, a *bifurcation diagram,* which depicts the locations and stability properties of periodic states. In the case of the logistic difference equation (11), since all of the relevant cases must fall within the interval $1 < r < 4$ (see May, 1976), the intervals of stability of any of the 2^n periodic solutions become increasingly smaller.

The first significantly new thing that happens (when $r \simeq 3.83$) is that a solution of period 3 suddenly appears. Li and Yorke (1975) proved that period 3 orbits were harbingers of a somewhat perplexing phenomenon they called *chaos*. This is a solution that appears to undergo large random fluctuations with no inherent periodicity or order whatsoever. An example of this type of behavior is given in Figure 2.9.

Figure 2.7 *(a)* f(f(x)) *initially has a flat graph with a single intersection of* $x_{n+2} = x_n$ *at* $\bar{x}$*, the steady state of* $\bar{x} = f(\bar{x})$. *(b) As* r *increases, two humps appear. As yet a single intersection is maintained.* $\bar{x}$ *remains stable as the slope of the tangent line is still less than* 1. *(c) As the two humps grow and as* r *increases beyond* 3, *two new intersections appear. Simultaneously,* $\bar{x}$ *becomes unstable.* $\bar{\bar{x}}_1$ *and* $\bar{\bar{x}}_2$ *are now stable as fixed points of* f(f(x)). *They thus form the period* 2 *orbit of this system.*



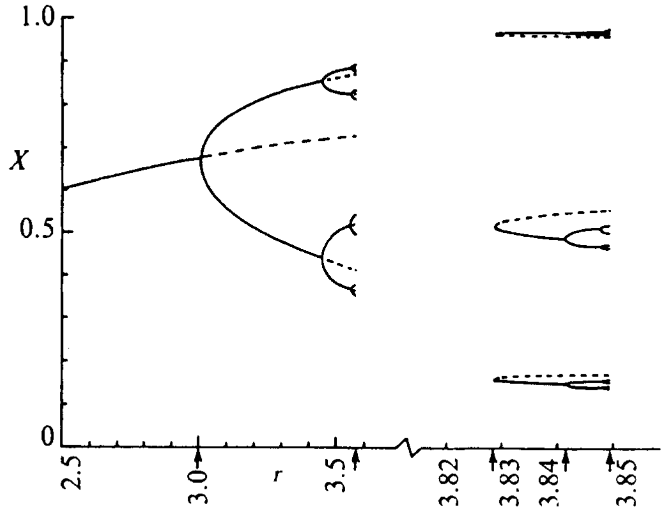


Figure 2.8 Bifurcation diagram for equation (11). [From May (1976). Reprinted by permission from Nature, 261, *pp. 459–467. Copyright © 1976 Macmillan Journals Limited.]*

A disturbing aspect of this type of solution is that two very close initial values x_0 and y_0 will in general grow very dissimilar in a few iterations. May (1976) remarked that it may be visually impossible to distinguish between a totally random sequence of events and the chaotic solution of a deterministic equation such as (11).

Does the chaotic regime of a difference equation have any biological relevance? In Chapter 3 one example of a chaotically fluctuating population, the blowflies, will be discussed. The majority of biologists feel, however, that most biological systems operate well within the range of stability of the low order periodic solutions. Thus the rather bizarre chaos remains largely a mathematical curiosity.

Bifurcation Diagrams

The effect of a parameter variation on existence and stability properties of steady states in equations such as (11) are often represented on a bifurcation diagram, such as the one in Figure 2.8. The horizontal axis gives the parameter value (e.g., r in equation (11)). The vertical axis represents the magnitudes of steady state(s) of the equation. A branch of the diagram (shown in solid lines) represents the dependence of the steady state level on the parameter. At points of bifurcation (e.g., at $r = 3.0$, $r = 3.5$, . . .) new steady states come into existence and old ones lose their stability (henceforth shown dotted). Two stable branches imply that a stable period 2 orbit exists; four stable branches imply that a period 4 orbit exists; and so on. Note that the succession of bifurcations may occur at ever closer intervals. The values of r at which such transitions occur are called bifurcation values.

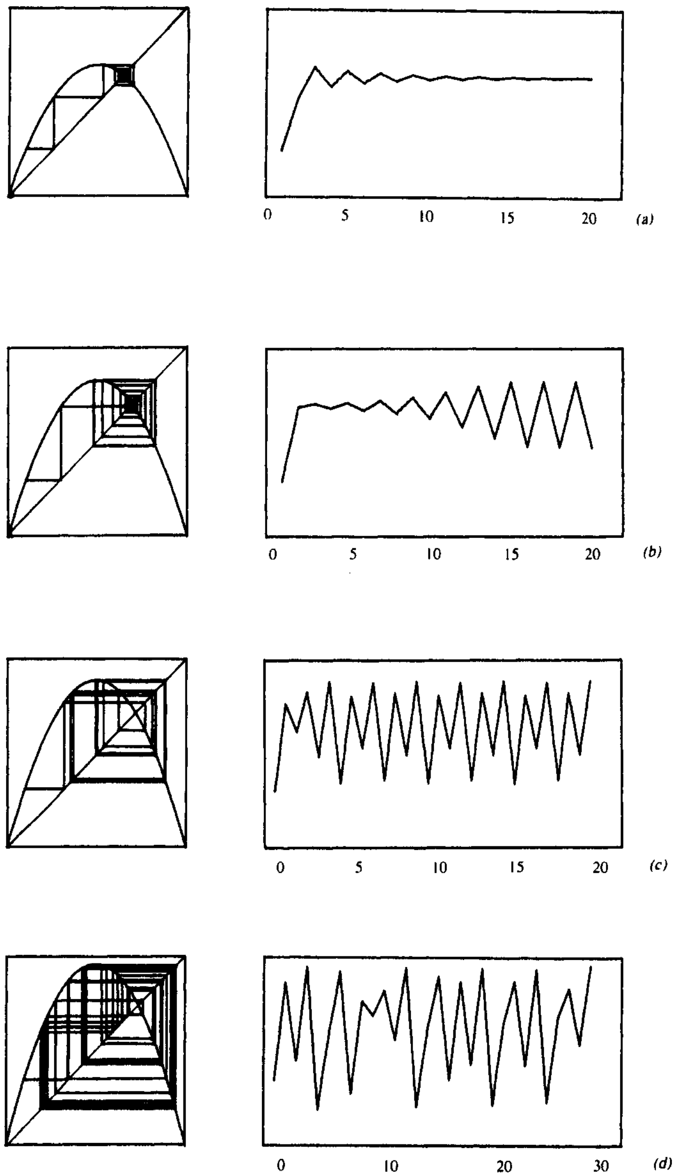


Figure 2.9 *The discrete logistic equation* $x_{n+1} = rx_n(1 - x_n)$ *is one of the simplest examples of a nonlinear difference equation in which complex behavior results as the single parameter* r *is varied. Shown here are four examples of the range of behaviors. On the left, the parabola* $y = f(x) = rx(1 - x)$ *and the line* $y = x$ *provide a graphical method for following successive iterates* $x_1, x_2, \ldots, x_n$ *by the cobwebbing method. On the right, successive values of* x_n *are displayed.* r *values are (a)* 2.8, *(b)* 3.3, *(c)* 3.55, *and (d)* 3.829. *Note that as* r *increases, the parabola steepens. There are transitions from a stable steady state (a), to a two-point (b), four-point (c) cycle, and eventually to chaos (d). See text for explanation. These figures were produced by a FORTRAN program on an IBM 360 digital computer.*

Summary and Applications of the Logistic Difference Equation (11)

Equation (11) has been used as a convenient example for illustrating a number of key ideas. First, we saw that the number of parameters affecting the qualitative features of a model may be smaller than the number that initially appear. Further, we observed that existence and stability of steady states and periodic solutions changed as the critical parameter was varied (or "tuned"). Finally, we had a brief exposure to the fact that difference equations can produce somewhat unusual solutions quite unlike their "tame" continuous counterparts.

Equation (11) is seldom used as an honest-to-goodness biological model. However, it serves as a useful pedagogical example of calculations and results that also hold for other, more realistic models, some of which will be described in Chapter 3. For a more detailed and thorough analysis of this equation, turn to the lucid review by May (1976).

2.6 A WORD ABOUT THE COMPUTER

Perhaps one of the most pleasing properties of difference equations is that they readily yield to numerical exploration, whether by calculator or with a digital computer. This property is not shared with the continuous differential equations. Solutions to difference equations are obtainable by sequential arithmetic operations, a task for which the computer is precisely suited. Indeed, the key strategy in tackling the more problematic differential equations by numerical computations is to find a reliable approximating difference equation to solve instead. This makes it particularly important to appreciate the properties and eccentricities of these equations.

2.7 SYSTEMS OF NONLINEAR DIFFERENCE EQUATIONS

To conclude this chapter, we will extend the methods developed for single equations to systems of n difference equations for arbitrary n. For simplicity of notation we will discuss here the case where $n = 2$. Assume therefore that two independent variables x and y are related by the system of equations

$$\begin{aligned} x_{n+1} &= f(x_n, y_n), \\ y_{n+1} &= g(x_n, y_n), \end{aligned} \tag{23}$$

where f and g are nonlinear functions. Steady-state values $\bar{x}$ and $\bar{y}$ satisfy

$$\begin{aligned} \bar{x} &= f(\bar{x}, \bar{y}), \\ \bar{y} &= g(\bar{x}, \bar{y}). \end{aligned} \tag{24}$$

We now explore the stability of these steady states by analyzing the fate of small deviations. As before, this will result in a linearized system of equations for the small perturbations x' and y'. To achieve this we must now use Taylor series expansions of the functions of two variables, f and g (see Appendix at end of chapter). That is, we approximate $f(\bar{x} + x', \bar{y} + y')$ by the expression

$$f(\bar{x} + x', \bar{y} + y') = f(\bar{x}, \bar{y}) + \left.\frac{\partial f}{\partial x}\right|_{\bar{x},\bar{y}} x' + \left.\frac{\partial f}{\partial y}\right|_{\bar{x},\bar{y}} y' + \ldots, \tag{25}$$

and do the same for g. You should verify that when other steps identical to those made in the one-variable case are carried out, the result is

$$\begin{aligned} x'_{n+1} &= a_{11}x'_n + a_{12}y'_n, \\ y'_{n+1} &= a_{21}x'_n + a_{22}y'_n, \end{aligned} \tag{26}$$

where now

$$\begin{aligned} a_{11} &= \left.\frac{\partial f}{\partial x}\right|_{\bar{x},\bar{y}}, \qquad a_{12} = \left.\frac{\partial f}{\partial y}\right|_{\bar{x},\bar{y}}, \\ a_{21} &= \left.\frac{\partial g}{\partial x}\right|_{\bar{x},\bar{y}}, \qquad a_{22} = \left.\frac{\partial g}{\partial y}\right|_{\bar{x},\bar{y}}. \end{aligned} \tag{27}$$

The matrix consisting of these four coefficients, i.e.,

$$\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \tag{28}$$

is called the *Jacobian* of the system of equations (23). One often encounters the matrix notation

$$\mathbf{x}'_{n+1} = \mathbf{A}\mathbf{x}'_n, \tag{29}$$

as a shorthand representation of equations (26), where

$$\mathbf{x}'_n = \begin{pmatrix} x'_n \\ y'_n \end{pmatrix}. \tag{30}$$

The problem has again been reduced to a linear system of equations for states that are in proximity to the steady state $(\bar{x}, \bar{y})$. Thus we can determine the stability of $(\bar{x}, \bar{y})$ by methods given in Chapter 1. To briefly review, this would entail the following:

1. Finding the characteristic equation of (26) by setting

   $$\det(\mathbf{A} - \lambda\mathbf{I}) = 0.$$

   The result is always the quadratic equation

   $$\lambda^2 - \beta\lambda + \gamma = 0,$$

   where

   $$\begin{aligned} \beta &= a_{11} + a_{22}, \\ \gamma &= a_{11}a_{22} - a_{12}a_{21}. \end{aligned}$$

2. Determining whether the roots of this equation (the eigenvalues) are of magnitude smaller than 1.

If the answer to (2) is affirmative, we can conclude that small deviations from the steady state will decay, i.e., that the equilibrium is stable. In the next section we show that it is not always necessary to compute the eigenvalues explicitly in order to determine their magnitudes. Rather, as we will demonstrate, it is sufficient to test whether the following condition is satisfied:

$$2 > 1 + \gamma > |\beta| \rightarrow \begin{cases} \text{both eigenvalues } |\lambda_i| < 1 \\ \text{steady state } (\bar{x}, \bar{y}) \text{ is stable} \end{cases}$$

2.8 STABILITY CRITERIA FOR SECOND-ORDER EQUATIONS

It is possible to formulate stability criteria for systems of difference equations in terms of the coefficients in the corresponding characteristic equation. May, et al. (1974) were among the first to derive explicitly a necessary and sufficient condition for second-order systems:

Given the characteristic equation

$$\lambda^2 - \beta\lambda + \gamma = 0, \tag{31}$$

both roots will have magnitude less than 1 if

$$2 > 1 + \gamma > |\beta|. \tag{32}$$

Now we examine how this condition is derived.

Derivation of Condition (32)

Recall that roots of equation (31) are

$$\lambda_{1,2} = \frac{\beta \pm \sqrt{\beta^2 - 4\gamma}}{2}. \tag{33}$$

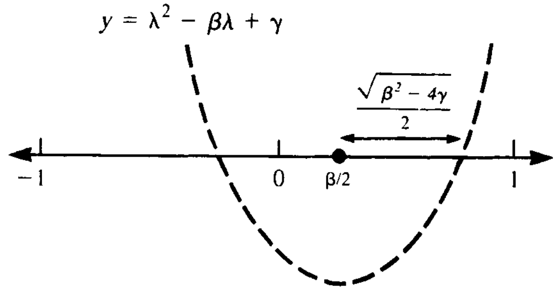
For stability it is necessary that

$$|\lambda_1| < 1 \quad \text{and} \quad |\lambda_2| < 1. \tag{34}$$

Figure 2.10 shows the desired result geometrically when equation (31) has real roots. Notice that roots of equation (31) are equidistant from the value $\beta/2$. Thus it is first necessary that this midpoint should be within the interval $(-1, 1)$:

$$-1 < \beta/2 < 1, \quad \text{or} \quad \left|\frac{\beta}{2}\right| < 1. \tag{35}$$

Figure 2.10 For stability of a second-order system such as (23), both eigenvalues corresponding to roots of the characteristic equation $y = \lambda^2 - \beta\lambda + \gamma$ *must lie within the interval* $(-1, 1)$.



Furthermore, it is necessary that the distance from $\beta/2$ to either root be *smaller* than the distance to an endpoint of the interval. In the situation graphed shown in Figure 2.10 this implies that

$$1 - \left|\frac{\beta}{2}\right| > \frac{\sqrt{\beta^2 - 4\gamma}}{2}.$$

Squaring both sides does not change the inequality since each side is positive.

$$\left(1 - \left|\frac{\beta}{2}\right|\right)^2 > \frac{\beta^2 - 4\gamma}{4},$$

$$1 - |\beta| + \frac{\beta^2}{4} > \frac{\beta^2}{4} - \gamma.$$

Cancelling $\beta^2/4$ and rearranging terms gives

$$1 + \gamma > |\beta|. \qquad (36)$$

The final step of combining the inequalities in equations (35) and (36) is left as a problem.

2.9 STABILITY CRITERIA FOR HIGHER-ORDER SYSTEMS

Thus far we have examined only the relatively straightforward case of two coupled difference equations. In theory the techniques of analyzing stability of steady-state solutions are similar for bigger systems, e.g., a set of k equations. However, computationally one can encounter problems in estimating magnitudes of eigenvalues because the characteristic equation associated with this system is a polynomial of degree k. In general it is then impossible to actually determine the eigenvalues, and it is necessary to use certain criteria to obtain information about their magnitudes.

One such criterion, called *the Jury test* as developed by Jury (1971), is described in this section. See Lewis (1977), for a broader discussion.

Consider the polynomial

$$P(\lambda) = \lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + \cdots + a_{n-1}\lambda + a_n.$$

Define the following combinations of parameters:

$$
\begin{array}{lll}
b_n = 1 - a_n^2, & c_n = b_n^2 - b_1^2, & d_n = c_n^2 - c_2^2, \\
b_{n-1} = a_1 - a_n a_{n-1}, & c_{n-1} = b_n b_{n-1} - b_1 b_2, & d_{n-1} = c_n c_{n-1} - c_2 c_3, \\
\vdots & \vdots & \vdots \\
b_{n-k} = a_k - a_n a_{n-k}, & c_{n-k} = b_n b_{n-k} - b_1 b_{k+1}, & d_{n-k} = c_n c_{n-k} - c_2 c_{k+2}, \\
\vdots & \vdots & \vdots \\
b_1 = a_{n-1} - a_n a_1, & c_2 = b_n b_2 - b_1 b_{n-1}, & d_3 = c_n c_3 - c_2 c_{n-1}.
\end{array}
$$

The list grows shorter at each stage until there are just three quantities that relate to their predecessors by the rule

$$q_n = p_n^2 - p_{n-3}^2,$$

$$q_{n-1} = p_n p_{n-1} - p_{n-3} p_{n-2},$$

$$q_{n-2} = p_n p_{n-2} - p_{n-3} p_{n-1}.$$

Now we formulate the criterion as follows:

Jury Test

Necessary and sufficient conditions for all roots of $P(\lambda)$ to satisfy the condition that $|\lambda| < 1$ are the following:

1. $P(1) = 1 + a_1 + \cdots + a_{n-1} + a_n > 0.$
2. $(-1)^n P(-1) = (-1)^n[(-1)^n + a_1(-1)^{n-1} + \cdots + a_{n-1}(-1) + a_n] > 0,$
3. (a) $|a_n| < 1,$
   $|b_n| > |b_1|,$
   $|c_n| > |c_2|,$
   $|d_n| > |d_3|,$
   $\vdots$
3. (q) $|q_n| > |q_{n-2}|.$

Example
Apply the Jury test to

$$\lambda^4 + \lambda^3 + \lambda^2 + \lambda + 1 = 0.$$

Solution
We note that $n = 4$ and examine conditions 1 and 2:

1. $P(1) = 1 + 1 + 1 + 1 + 1 > 0$
2. $(-1)^4 P(1) = 1(1 - 1 + 1 - 1 + 1) > 0$

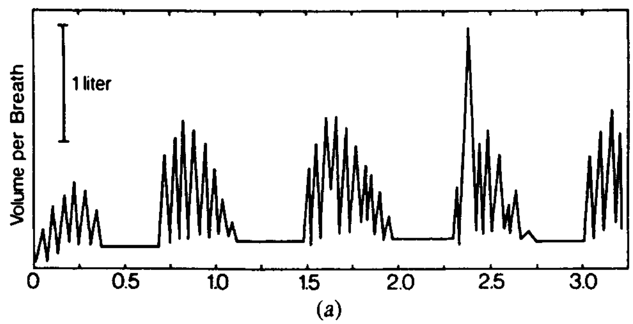
Since these are both satisfied, we go on to the first part of condition 3, namely that $|a_n| < 1$. We see that this condition is not satisfied since $a_4 = 1$. Thus the polynomial will have at least one root whose magnitude is not smaller than 1.

2.10 FOR FURTHER STUDY: PHYSIOLOGICAL APPLICATIONS

In recent years several problems in physiology have been modeled by the use of difference equations or by a combination of difference-differential equations (called *delay equations*) that share certain properties. One of the earliest review articles on this subject, entitled "Oscillation and Chaos in Physiological Control Systems," dates back to 1977 (see Mackey and Glass, 1977). Students who are interested in such applications should consult the references provided. Two of these are briefly highlighted here.

1. In their 1978 article, Glass and Mackey describe several respiratory disorders in which the pattern of breathing is irregular. In normal resting humans, ventilation volume is approximately constant from one breath to another. *Cheyne-Stokes breathing* consists of a repeated waxing and waning of the depth of breathing, with an amplitude of ventilation volume that oscillates over intervals of 0.5 to 1 min. Other disorders (such as *biot breathing* and *infant apnea*) also seem to indicate a problem in the control system governing ventilation.

A simple linear model for ventilation volumes and chemoreceptor sensitivity to CO_2 in the blood was described in Section 1.9 and outlined in problem 18 of Chapter



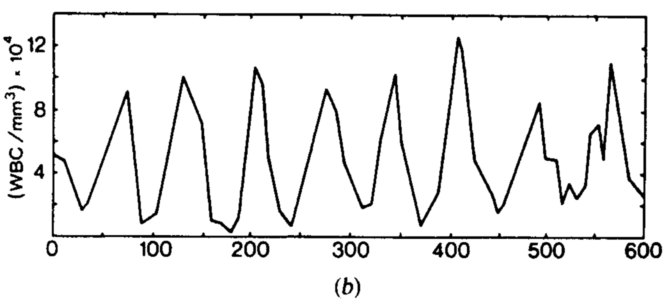


Figure 2.11 Two dynamical diseases: (a) In Cheyne-Stokes respiration, the volume per breath undergoes periodic cycles of deep breathing interspersed by intervals of apnea (no breathing). (b) Chronic granulocyclic leukemia is associated with characteristic oscillations in the level of circulating white blood cells (WBCs) over periods of several months. [From Mackey and Glass (1977), "Oscillations and Chaos in Physiological Control Systems," Science, *197, 287–289. Reprinted by permission. Copyright 1977 by the AAAS.]*

1. We continue to develop the model in problem 17 of this chapter. The articles by Glass and Mackey are recommended for good summaries of the phenomena and for a more sophisticated approach using delay equations. The authors apply similar models to *hematopoiesis* (the control and formation of circulating blood components). This makes for a more detailed model of a process described rather crudely in Section 1.9.

2. Cardiac and neurological disorders have also been modeled with discrete equations. These processes too are characterized by events that recur at some regular time intervals. The beating pattern of the heart is regular in normal resting humans. Specialized tissues at sites called the sinoatrial (SA) node and the atrioventricular (AV) node act as pacemakers to set the rhythm of contraction of the atria and ventricles. When one of these nodes is not functioning properly, *arrhythmia* (irregular rhythms) may result. The papers by Keener (1981) and Ikeda et al. (1983) outline models for arrhythmia based on the interaction of the SA node with some secondary pacemaker in the ventricle.

Collectively, physiological disorders in which a generally adequate control system becomes unstable have been called *dynamical diseases* (Figure 2.11). Some of the very simple abstract models given in this chapter have revealed that such phenomena can arise spontaneously when one or several parameters of a system have values slightly beyond certain threshold bifurcation points.

PROBLEMS*

1. Indicate whether each of the following equations is linear or nonlinear. If linear, determine the solution; if nonlinear, find any steady states of the equation.

(a) $x_n = (1 - \alpha)x_{n-1} + \beta x_n$, α and β are constants

(b) $x_{n+1} = \dfrac{x_n}{1 + x_n}$

(c) $x_{n+1} = x_n\, e^{-ax_n}$, a is a constant

(d) $(x_{n+1} - \alpha)^2 = \alpha^2(x_n^2 - 2x_n + 1)$, α is a constant

(e) $x_{n+1} = \dfrac{K}{k_1 + k_2/x_n}$, k_1, k_2 and K are constants

2. Determine when the following steady states are stable:

(a) $x_{n+1} = rx_n(1 - x_n)$, $\bar{x} = 0$

(b) $x_{n+1} = -x_n^2(1 - x_n)$, $\bar{x} = (1 + \sqrt{5})/2$

(c) $x_{n+1} = 1/(2 + x_n)$, $\bar{x} = \sqrt{2} - 1$

(d) $x_{n+1} = x_n \ln x_n^2$, $\bar{x} = e^{1/2}$

Sketch the functions $f(x)$ given in this problem. Use the cobwebbing method to sketch the approximate behavior of solutions to the equations from some initial starting value of x_0.

*Problems preceded by an asterisk (*) are especially challenging.

3. In population dynamics a frequently encountered model for fish populations is based on an empirical equation called the *Ricker equation* (see Greenwell, 1984):

$$N_{n+1} = \alpha N_n e^{-\beta N_n}.$$

In this equation, α represents the maximal growth rate of the organism and β is the inhibition of growth caused by overpopulation.

(a) Show that this equation has a steady state

$$\bar{N} = \frac{\ln \alpha}{\beta}.$$

(b) Show that the steady state in (a) is stable provided that

$$|1 - \ln \alpha| < 1.$$

4. Consider the equation

$$N_{t+1} = N_t \exp[r(1 - N_t/K)].$$

This equation is sometimes called an analog of the logistic differential equation (May, 1975). The equation models a single-species population growing in an environment that has a *carrying capacity* K. By this we mean that the environment can only sustain a maximal population level $N = K$. The expression

$$\lambda = \exp[r(1 - N_t/K)]$$

reflects a density dependence in the reproductive rate. To verify this observation, consider the following steps:

(a) Sketch λ as a function of N. Show that the population continues to grow and reproduce only if $N < K$.

(b) Show that $\bar{N} = K$ is a steady state of the equation.

(c) Show that the steady state is stable. (Are there restrictions on parameters r and K?)

(d) Using a hand calculator or simple computer program, plot successive population values N_t for some choice of parameters r and K.

***5.** Show that a first-order difference equation

$$x_{n+1} = f(x_n)$$

has stable two-point cycles if condition (17) is satisfied.

6. Show that by using a Taylor series expansion for the functions f and g in equations (23) one obtains the linearized equations (26) for perturbations (x', y') about the steady state $(\bar{x}, \bar{y})$.

7. In Section 2.8 we demonstrated that conditions (35) and (36) are necessary for both roots of $\lambda^2 - \beta\lambda + \gamma = 0$ to be negative.

(a) Derive an additional constraint that $\gamma < 1$ and hence show that condition (32) must be satisfied.

(b) Show that the same result is obtained when $\beta/2$ is negative.

(c) Equation (31) admits complex conjugate roots $\lambda_{1,2} = a \pm bi$ when $\beta^2 < 4\gamma$. In this situation it is necessary that the modulus $(a^2 + b^2)^{1/2}$ be smaller than 1 for the quantities λ_i^n to decay with increasing n (see

Figure 2.2). Show that this will be true whenever condition (32) is satisfied.

8. The equation

$$N_{t+1} = \lambda N_t(1 + aN_t)^{-b},$$

where λ, a, $b > 0$ is often encountered in the biological literature as an empirical description of density-limited population growth. For example, see M. P. Hassell (1975). λ is a growth rate, and a and b are parameters related to the density feedback rate.

(a) Show that by rescaling the equation one can reduce the number of parameters.

(b) Find the steady states of the equation $N_{t+1} = \lambda N_t(1 + aN_t)^{-b}$ and determine the conditions for stability of each steady state.

(c) Draw the function $f(x) = \lambda x(1 + ax)^{-b}$ and use it to graph $N_1, \ldots, N_{10}$ for some starting value N_0.

9. The difference equation

$$N_{t+1} = \left[\lambda_1 + \frac{\lambda_2}{1 + \exp A(N_t - B)}\right] N_t$$

is discussed by C. Pennycuik, R. Compton, and L. Beckingham (1968). A computer model for simulating the growth of two interacting populations. *J. Theor. Biol. 18,* 316–329; and by M. B. Usher (1972). Developments in the Leslie Matrix Model, in J. N. R. Jeffers, ed., *Mathematical Models in Ecology,* Blackwells, Oxford. Determine the behavior of solutions to this equation. (Assume λ_1, λ_2, A, $B > 0$.)

10. Graph the function

$$f(x) = \frac{\lambda x}{1 + (ax)^b},$$

for λ, a, $b > 0$ and use this to deduce the properties of the equation

$$N_{t+1} = \frac{\lambda N_t}{1 + (aN_t)^b}.$$

This is one example of a class of equations discussed by Maynard Smith (1974). What happens when $b = 1$?

11. In May (1978), Host-parasitoid systems in patchy environments: a phenomenological model. *J. Anim. Ecol.*, *47*, 833–843, the following system of equations appear:

$$H_{t+1} = FH_t(1 + aP_t/k)^{-k},$$
$$P_{t+1} = H_t - H_{t+1}/F.$$

Determine the steady states and their stability for this system. (The parameters F, a, k are positive.)

12. In Chapter 1 a problem for annual plant propagation led to a set of linear difference equations whose eigenvalues were given by equation (34). Using the criteria in Section 2.8, determine a general condition that ensures growth of the plant population.

13. In Levine (1975), a single species population is assumed to be governed by the difference equation

$$n_{k+1} = F(n_k),$$

where the function F has the shape shown in part (*a*) of the figure.

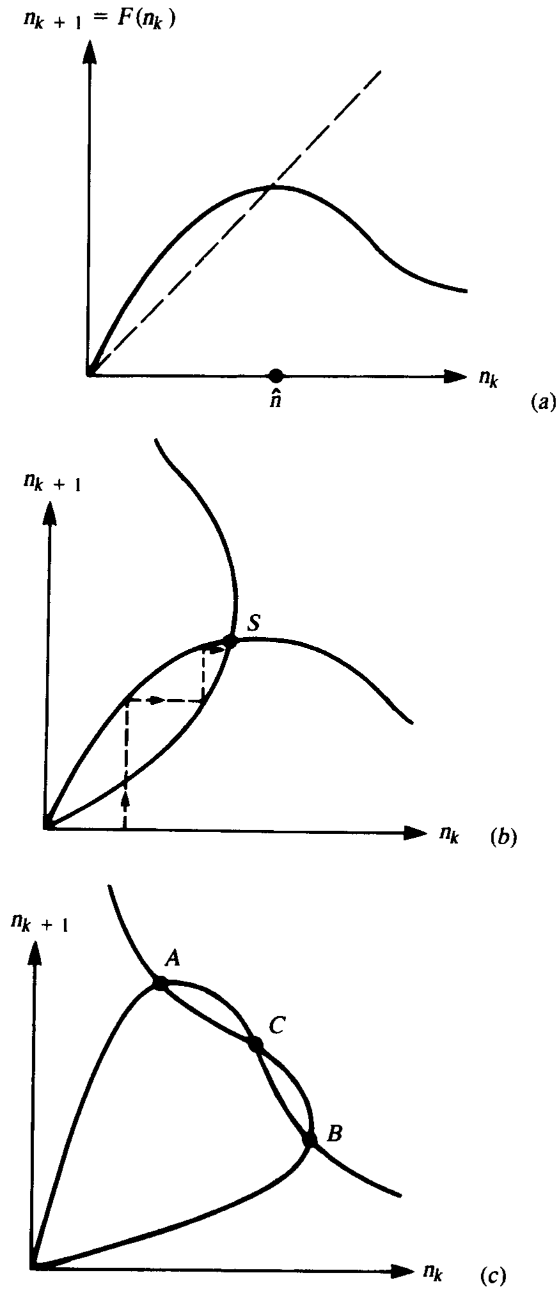


Figure for problem 13.

(a) Levine shows a variant of the cobwebbing method discussed in this chapter, in which a graph of $F(n)$ and its reflection $\bar{F}(n)$ are used to produce successive iterates n_k (see part (*b*) of the figure). What is the point marked S in this figure? A somewhat different situation is shown in part (*c*) of the figure. Interpret the points A, B, C, and discuss what happens to the population n_k.

(b) Levine describes the problem of stability in enriched ecosystems by suggesting that "enrichment should tend to elevate the curve $F(n_k)$ though not necessarily in a simple fashion." Explain this statement. Illustrate how a sequence of ecosystems enriched to different degrees might correspond to functions $F(n_k)$, which yield changes in stability of the steady state, $\hat{n}$.

14. Show that the steady state $\bar{x} = 0$ of equation (10) is unstable whenever the nontrivial steady state is stable.

15. *Advanced exercise or project.* Analyze the model

$$x_{n+1} = ax_n^2(1 - x_n)$$

for $a > 0$. See Marotta (1982).

16. *Waves of disease.* In a popular article that appeared in the *New Scientist,* Anderson and May (1982)[2] suggest a simple discrete model for the spread of disease that demonstrates how regular cycles of infection may arise in a population. Taking the average period of infection as the unit of time, they write equations for the number of disease cases C_t and the number of susceptible individuals S_t in the tth time interval. They make the following assumptions: (i) The number of new cases at time $t + 1$ is some fraction f of the product of current cases C_t and current susceptibles S_t; (ii) a case lasts only for a single time period; (iii) the current number of susceptibles is increased at each time period by a fixed number, $B(B \neq 0)$ and decreased by the number of new cases. (iv) Individuals who have recovered from the disease are immune.

(a) Explain assumption (i).

(b) Write the equations for C_{t+1} and S_{t+1} based on the above information.

(c) Show that $\hat{S} = 1/f$, $\hat{C} = B$ is a steady state of the equations.

(d) Use stability analysis to show that a small deviation away from steady state may result in oscillatory behavior.

(e) What happens when $f = 2/B$?

(f) Using a hand calculator or a simple computer program, show how solutions to the equations depict waves of incidence of the disease. Typical parameter values given by Anderson and May (1982) are

B = 12 births per 1000 people for the U.K.,
or 36 births per 1000 in a third-world country.
$f = 0.3 \times 10^{-4}$.

2. *Note to the instructor:* The article by Anderson and May (1982), which deals with the control of disease by vaccination, is accessible to students at this stage and may be considered as a topic for class presentation. More advanced models for epidemics will be discussed in Chapter 6.

Typical population data are

$$S_0 = 2000, \qquad C_0 = 20.$$

17. This problem pursues further the topic of blood CO_2 and ventilation volume first described in Section 1.9 and problem 16 of Chapter 1. There we studied a *linear* model for the process; we now examine a nonlinear extension.

(a) Whereas in problem 1.16 we assumed that the amount of CO_2 lost, $\mathcal{L}(V_n, C_n)$, was simply proportional to V_n and independent of C_n, let us now consider the case in which

$$\mathcal{L}(V_n, C_n) = \beta V_n C_n.$$

Explain the biological difference between these distinct hypotheses.

(b) Further assume that the ventilation volume V_{n+1} is simply proportional to C_n, so that

$$V_{n+1} = \alpha C_n$$

as before. Write down the system of (nonlinear) equations for C_n and V_n.

(c) Show that the steady state of this system is

$$C_n = V_n/\alpha = (m/\beta\alpha)^{1/2}$$

and determine its stability.

(d) Are oscillations in V_n and C_n possible for certain ranges of the parameters?

(e) Now consider a more realistic model (based on Mackey and Glass, 1977, 1978). Assume that the sensitivity of chemoreceptors to CO_2 is not linear but rather *sigmoidal,* i.e.,

$$\mathcal{S}(C) = \frac{C^\ell}{K^\ell + C^\ell}$$

where

ℓ = an integer,
K = some real number.

Further suppose that

$$V_{n+1} = V_{\max} \mathcal{S}(C_n),$$

with $\mathcal{L}(V_n, C_n)$ as before. Write down the system of equations, and show that it can be reduced to the following single equation for C_n:

$$C_{n+1} = C_n - \beta V_{\max} C_{n-1}^\ell C_n/(K^\ell + C_{n-1}^\ell) + m.$$

(f) Sketch $\mathcal{S}(C)$ as a function of C for $\ell = 0, 1, 2$. The integer ℓ can be described as a *cooperativity parameter*. (For $\ell > 1$ the binding of a single CO_2 molecule to its chemoreceptor *enhances* additional binding; this type of kinetic assumption is described in Chapter 7.)

(g) Determine what equation is satisfied by the steady states C_n and V_n.

(h) For $\ell = 1$ find the value of the physiological steady state(s). Give a condition for their stability.

(i) Investigate the model by writing a computer simulation or by further analysis. Are oscillations possible for $\ell = 1$ or for higher ℓ values?

Comment: After thinking about this problem, you may wish to refer to the articles by Mackey and Glass. Their model combines differential and difference equations so that the details of the analysis are different. See references in Chapter 1.

REFERENCES

Stability, Oscillations, and Chaos in Difference Equations

Frauenthal, J. C. (1979). *Introduction to Population Modelling* (UMAP Monograph Series). Birkhauser, Boston, 59–73.

Frauenthal, J. C. (1983). Difference and differential equation population growth models. Chap. 3 in (M. Braun, C. S. Coleman, and D. A. Drew, eds.), *Differential Equation Models*. Springer-Verlag, New York.

Guckenheimer, J.; Oster, G.; and Ipaktchi, A. (1977). The dynamics of density-dependent population models. *J. Math. Biol., 4,* 101–147.

Hofstadter, D. (1981). Strange attractors: Mathematical patterns delicately poised between order and chaos. *Sci. Am.*, November 1981 vol. 245, pp. 22–43.

Kloeden, P. E., and Mees, A. I. (1985). Chaotic phenomena. *Bull. Math. Biol., 47,* 697–738.

Li, T. Y., and Yorke, J. A. (1975). Period three implies chaos. *Amer. Math. Monthly, 82,* 985–992.

May, R. M. (1975). Biological populations obeying difference equations: Stable points, stable cycles, and chaos. *J. Theor. Biol., 51,* 511–524.

May, R. M. (1976). Simple mathematical models with very complicated dynamics. *Nature, 261,* 459–467.

May, R. M., and Oster, G. (1976). Bifurcations and dynamic complexity in simple ecological models. *Am. Nat., 110,* 573–599.

Perelson, A. (1980). Chaos. In L. A. Segel, ed., *Mathematical Models in Molecular and Cellular Biology*. Cambridge University Press, Cambridge.

Rogers, T. D. (1981). Chaos in Systems in Population Biology, in R. Rosen ed., *Progress in Theoretical Biology, 6,* 91–146. Academic Press, New York.

Physiological Applications

Glass, L., and Mackey, M. C. (1978). Pathological conditions resulting from instabilities in physiological control systems. *Ann. N. Y. Acad. Sci., 316,* 214–235, published 1979.

Ikeda, N., Yoshizawa, S., and Sato, T. (1983). Difference equation model of ventricular parasystole as an interaction between cardiac pacemakers based on the phase response curve. *J. Theor. Biol., 103,* 439–465.

Keener, J. P. (1981). Chaotic cardiac dynamics. Pp. 299–325 in F. C. Hoppenstaedt, ed. in *Mathematical Aspects of Physiology*. American Mathematical Society, Providence, R.I.

Mackey, M. C., and Glass, L. (1977). Oscillation and chaos in physiological control systems. *Science, 197,* 287–289.

Mackey, M. C., and Milton, J. (1986). Dynamical Diseases, *Ann, N.Y. Acad. Sci.*, in press.

May, R. M. (1978). Dynamical Diseases. *Nature, 272,* 673–674.

(See also miscellaneous papers in New York Academy of Sciences (1986). *Perspectives on Biological Dynamics and Theoretical Medicine;* and in *Ann. N.Y. Acad. Sci.*, vol. 316.)

Miscellaneous

Anderson, R., and May, R. (1982). The logic of vaccination. *New Scientist*, November 1982.

Greenwell, R. (1984). The Ricker salmon model. UMAP Unit 653. Reprinted in *UMAP Journal*, *5*(3), 337–359.

Hassell, M. P. (1975). Density dependence in single-species populations. *J. Anim. Ecol.*, *44*, 283–295.

Jury, E. I. (1971). The inners approach to some problems of system theory. *IEEE Trans. Automatic Contr.*, *AC–16*, 233–240.

Levine, S. H. (1975). Discrete time modeling of ecosystems with applications in environmental enrichment. *Math. Biosci.*, *24*, 307–317.

Lewis, E. R. (1977). *Network Models in Population Biology* (*Biomath.*, vol. 7). Springer-Verlag, New York.

Marotta, F. R. (1982). The dynamics of a discrete population model with threshold. *Math. Biosci.*, *58*, 123–128.

May, R. M., Conway, G. R., Hassell, M. P., and Southwood, T. R. E. (1974). Time delays, density dependence and single species oscillations. *J. Anim. Ecol.*, *43*, 747–770.

Maynard Smith, J. (1974). *Models in Ecology*. Cambridge University Press, Cambridge, Eng.

APPENDIX TO CHAPTER 2: TAYLOR SERIES

PART 1: FUNCTIONS OF ONE VARIABLE

Technical Matters

In order for a function $F(x)$ to have a Taylor series at some point x_0, it must have derivatives of all orders at that point. (The function $F(x) = |x|$ at $x = 0$ does not qualify because of the sharp corner it makes at $x = 0$.)

A Taylor series about x_0 is an expression involving powers of $(x - x_0)$, where x_0 is a point at which F and all its derivatives are known. Written in the form

$$T(x) = \sum_{n=0}^{\infty} a_n(x - x_0)^n, \tag{37}$$

this expression is called a *power series* and may be thought of as a polynomial with infinitely many terms. Equation (37) makes sense only for values of x for which the infinite sum is some finite number (i.e., when the series *converges*). There are precise tests (e.g., the *ratio test*) that determine whether a given power series converges.

Suppose $T(x)$ is a power series that converges whenever $|x - x_0| < r$ (r is then called the *radius of convergence*). It can be shown that

$$F(x) = T(x) = \sum_{n=0}^{\infty} a_n(x - x_0)^n$$

provided the coefficients a_n are of the following form:

$$a_0 = F(x_0),$$

$$a_1 = \left.\frac{dF}{dx}\right|_{x_0},$$

$$a_2 = \frac{1}{2}\frac{d^2F}{dx^2}\bigg|_{x_0},$$

$$\vdots$$

$$a_n = \frac{1}{n!}\frac{d^nF}{dx^n}\bigg|_{x_0}, \qquad (38)$$

$$\vdots$$

where these expressions are derivatives of F evaluated at the point x_0. A technical question is whether the sum (37) with the coefficients in (38) actually equals the value of F at points x other than x_0. Below we assume this to be the case.

Practical Matters

The Taylor series of a function of one variable can be written as follows:

$$F(x) = F(x_0) + \frac{dF}{dx}\bigg|_{x_0}(x - x_0) + \frac{1}{2}\frac{d^2F}{dx^2}\bigg|_{x_0}(x - x_0)^2 + \frac{1}{3!}\frac{d^3F}{dx^3}\bigg|_{x_0}(x - x_0)^3$$
$$+ \cdots + \frac{1}{n!}\frac{d^nF}{dx^n}\bigg|_{x_0}(x - x_0)^n + \cdots.$$

When $x - x_0$ is a very small quantity, the terms $(x - x_0)^k$ for $k > 1$ can usually be neglected (provided the derivative coefficients are not very large; i.e., the function does not make abrupt changes). In this case

$$F(x) \approx F(x_0) + \frac{dF}{dx}\bigg|_{x_0}(x - x_0) + \cdots + \text{(neglected terms)}.$$

Figure 2.12 demonstrates how this expression approximates the actual function.

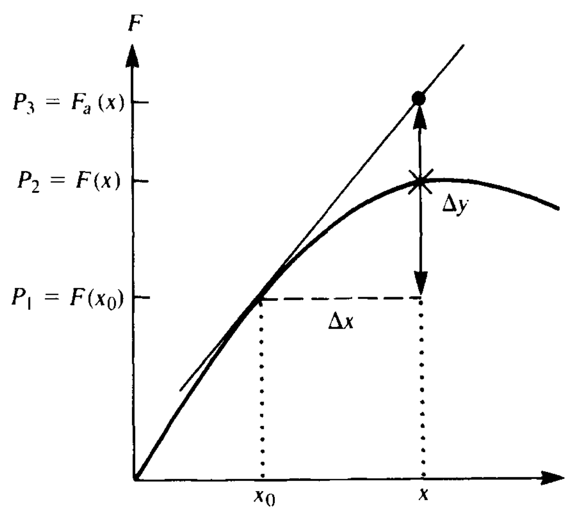


***Figure 2.12** By retaining the first two terms in a Taylor series expansion for a function, the value of the function at a point* x, $P_2 = F(x)$, *is approximated by the expression*

$$P_3 = F_a(x) = F(x_0) + \Delta y = F(x_0) + (\text{slope})\,\Delta x.$$

The quantity $\frac{dF}{dx}\Big|_{x_0}$ *is the slope of the tangent line, and* $\Delta x = x - x_0$. *Using these terms one arrives at an approximation that is accurate only when* x_0 *and* x *are close.*

PART 2: FUNCTIONS OF TWO VARIABLES

Technical Matters

Consider the function of two variables $F(x, y)$ that has partial derivatives of all orders with respect to x and y at some point (x_0, y_0) such that $P_1 = F(x_0, y_0)$. Then the value of F at a neighboring point $P_2 = F(x, y)$ can be calculated using a Taylor series expansion for F, provided this expansion converges to the value of the function. Since variation in both x and y must be taken into account, the series involves partial derivatives. It proves convenient to define the following quantity:

$$\hat{\Delta}F = \left(h\frac{\partial}{\partial x} + k\frac{\partial}{\partial y}\right)F(x, y) \stackrel{\text{def}}{\equiv} (x - x_0)\frac{\partial F}{\partial x} + (y - y_0)\frac{\partial F}{\partial y}.$$

By nth power of the above expression we mean the following:

$$\hat{\Delta}^n F = \left(h\frac{\partial}{\partial x} + k\frac{\partial}{\partial y}\right)^n F(x, y) \equiv (x - x_0)^n\frac{\partial^n F}{\partial x^n} + n(x - x_0)^{n-1}(y - y_0)\frac{\partial^n F}{\partial x^{n-1}\partial y}$$
$$+ \cdots + n(x - x_0)(y - y_0)^{n-1}\frac{\partial^n F}{\partial x \partial y^{n-1}}$$
$$+ (y - y_0)^n\frac{\partial^n F}{\partial y^n}.$$

Using this notation, we can now express the Taylor series of F as follows:

$$F(x, y) = F(x_0, y_0) + \hat{\Delta}F(x_0, y_0) + \frac{1}{2!}\hat{\Delta}^2 F(x_0, y_0) + \cdots + \frac{1}{n!}\hat{\Delta}^n F(x_0, y_0) + \cdots$$

In this shorthand, the similarity to functions of one variable is apparent. Note that the expressions $\hat{\Delta}^n F$ are binomial expansions involving mixed partial derivatives of F that are evaluated at (x_0, y_0).

Practical Matters

When (x, y) is close to (x_0, y_0), the function F can be approximated by retaining the first two terms of a Taylor series expansion, as follows:

$$F(x, y) \simeq F(x_0, y_0) + \hat{\Delta}F(x_0, y_0)$$
$$= F(x_0, y_0) + (x - x_0)\left.\frac{\partial F}{\partial x}\right|_{x_0, y_0} + (y - y_0)\left.\frac{\partial F}{\partial y}\right|_{x_0, y_0}.$$

Figure 2.13 illustrates how this expression approximates the value of the function. The geometric ideas underlining this expression are best understood by readers who have had some exposure to vector calculus. For others it suffices to remark that this is a natural extension of the one-variable case to a higher dimension.

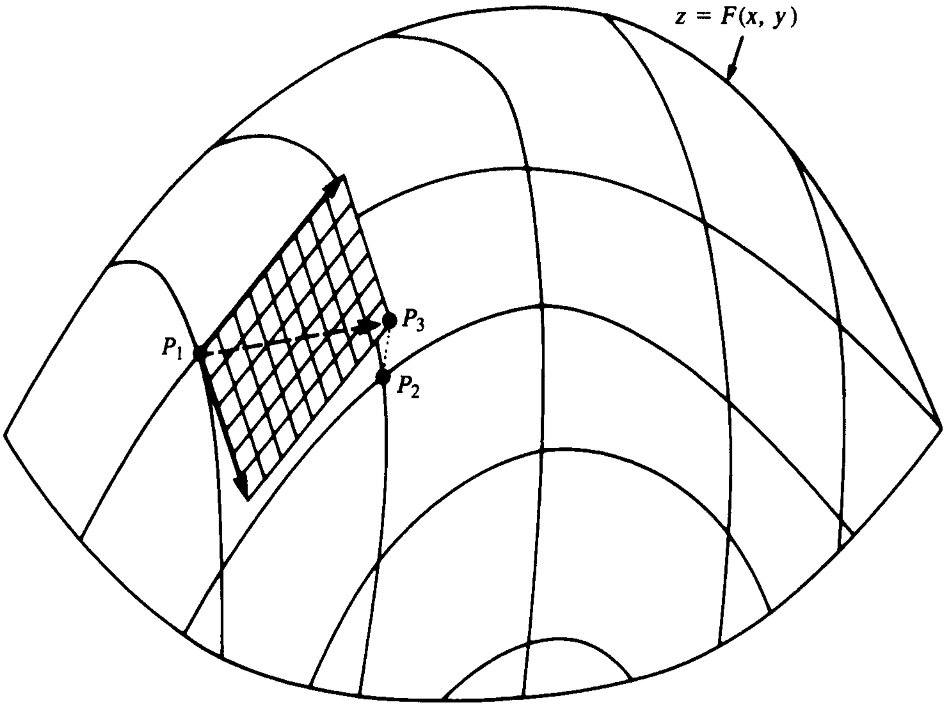


Figure 2.13 *Shown is the surface* z = F(x, y), *where* F *is a function of two variables. Assuming that the value of* F *at* (x_0, y_0), $P_1 = F(x_0, y_0)$, *is known, we approximate the value of* F *at some neighboring point* (x, y), $P_2 = F(x, y)$ *by a Taylor series expansion. If only terms up to* order 1 *are taken, the expression yields*

$$P_3 = F(x_0, y_0) + \left.\frac{\partial F}{\partial x}\right|_{x_0, y_0}(x - x_0) + \left.\frac{\partial F}{\partial y}\right|_{x_0, y_0}(y - y_0).$$

The value $P_3 \neq P_2$ *can be interpreted geometrically.* P_3 *is actually the height* [*at* (x_0, y_0)] *of a tangent plane (shaded) that approximates the surface* z = F(x, y). *The partial derivatives of* F *are slopes of the vectors that are shown as bold arrows.*