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:

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

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

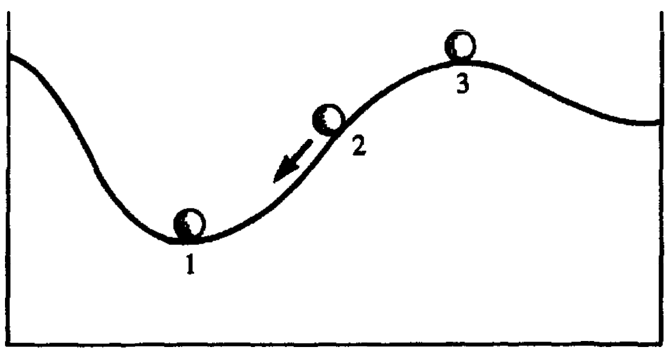


***Figure 2.1** In this landscape balls 1 and 3 are at rest and represent steady-state situations. Ball 1 is stable; if moved slightly it will return to its former position. Ball 3 is unstable. The slightest disturbance will cause it to fall into one of the adjoining valleys. Ball 2 is not in a steady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

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

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:

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

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

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

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.

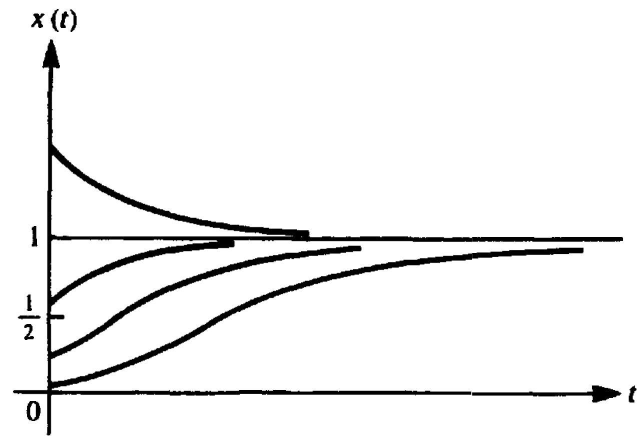


Figure 2.2 Solutions to the logistic differential *equation are characterized by a single nontrivial steady state* $\bar{x} = 1$, *which is stable regardless of the parameter value chosen for* r. *Thus* $x(t)$ *tends toward a limiting value of* $x = 1$ *for all positive starting values.*

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.

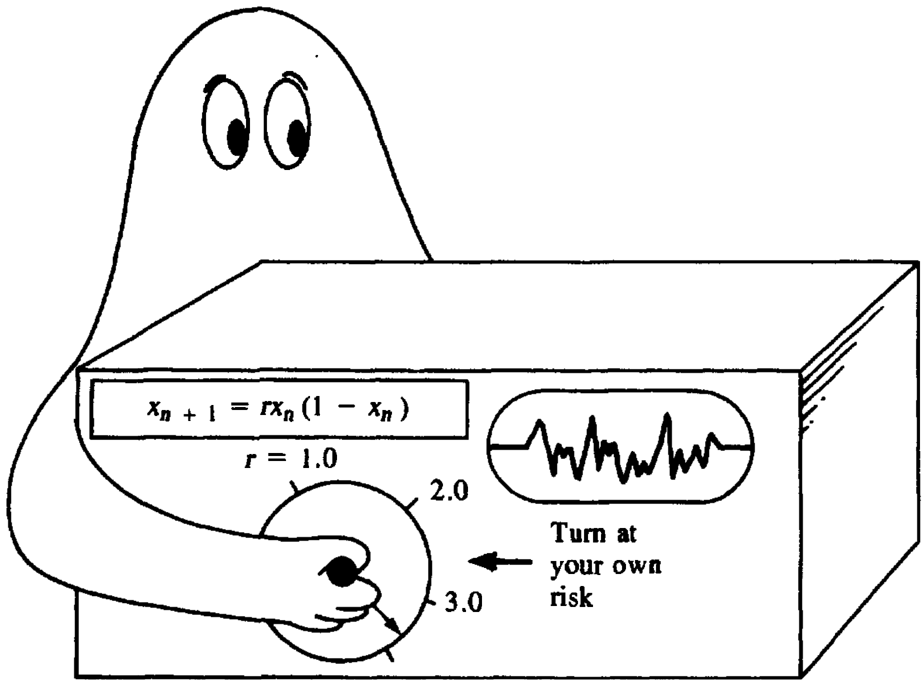


Figure 2.3

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:

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

$$x_{n+2} = x_n. \tag{13b}$$

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:

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

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.)

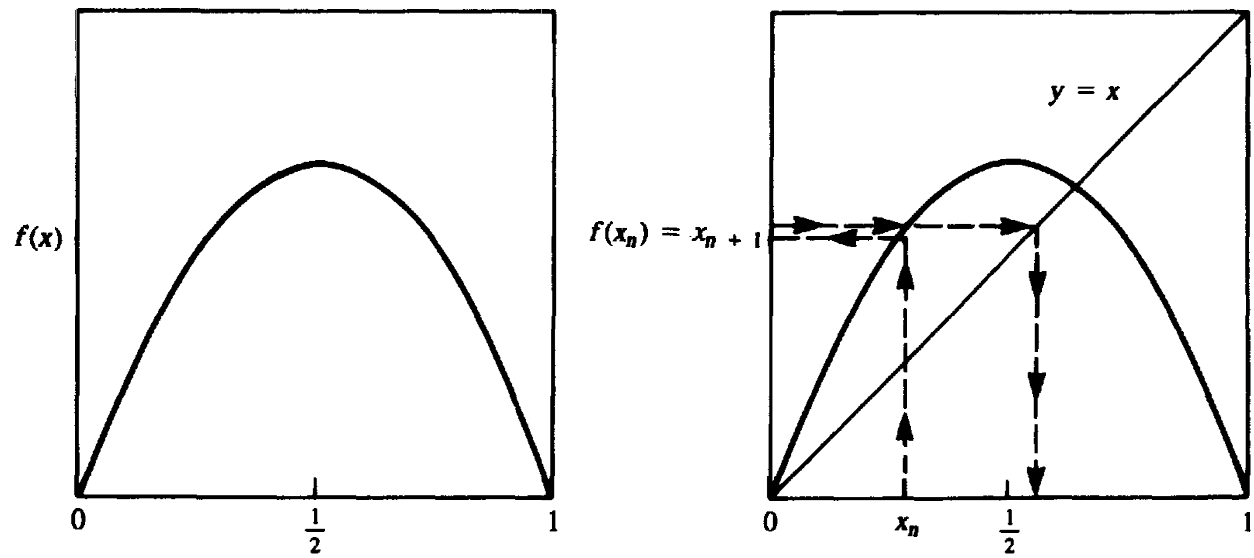
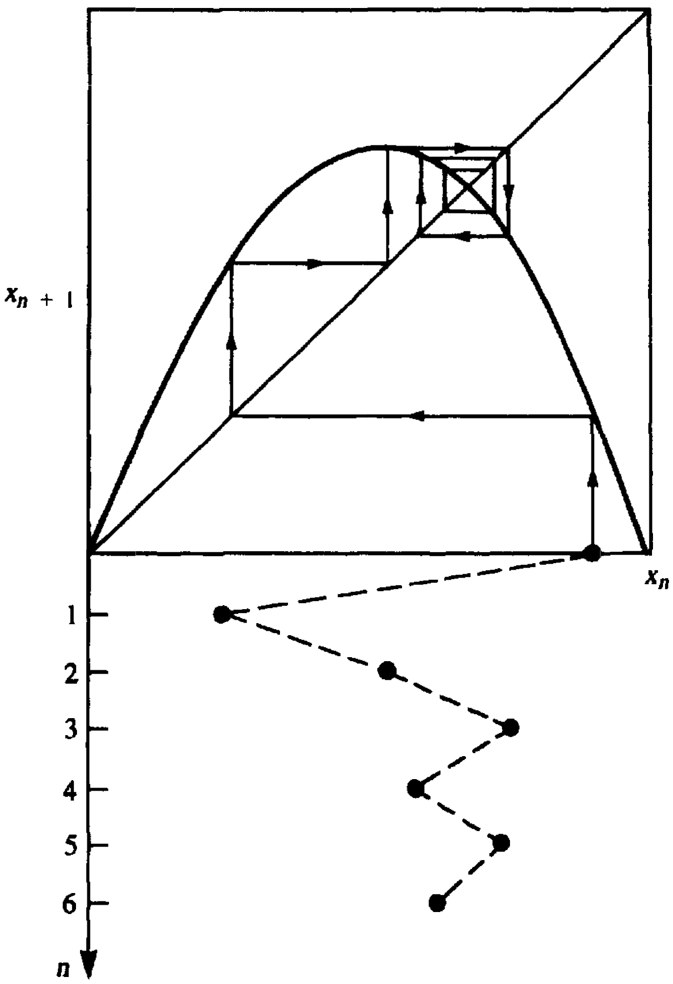


***Figure 2.4** The parabola* y = f(x) *and the line* y = x *can be used to graph the successive values of* x_n, n = 0, 1, 2, ... *This is known as the* cobwebbing method *(see Figure 2.5).*

Figure 2.5 A number of values of x_n, n = 0, 1, . . . , 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

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

Interpreted graphically, this condition means that the tangent line $\mathcal{L}$ 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

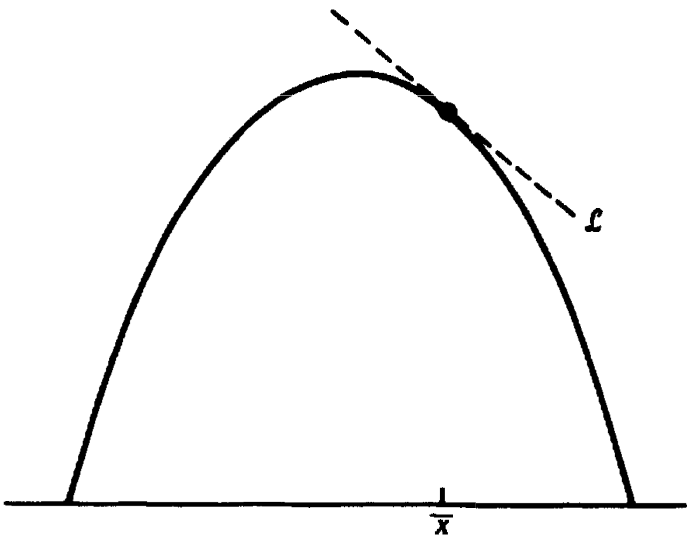


***Figure 2.6** The steady state* $\bar{x}$ *is always located at the intersection of* y = f(x) *with* y = x. $\bar{x}$ *is stable if the tangent to the curve* y = f(x) *is not too steep (a slope of magnitude less than* 1*).*

the parabola, which makes its tangent line $\mathscr{L}$ 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.

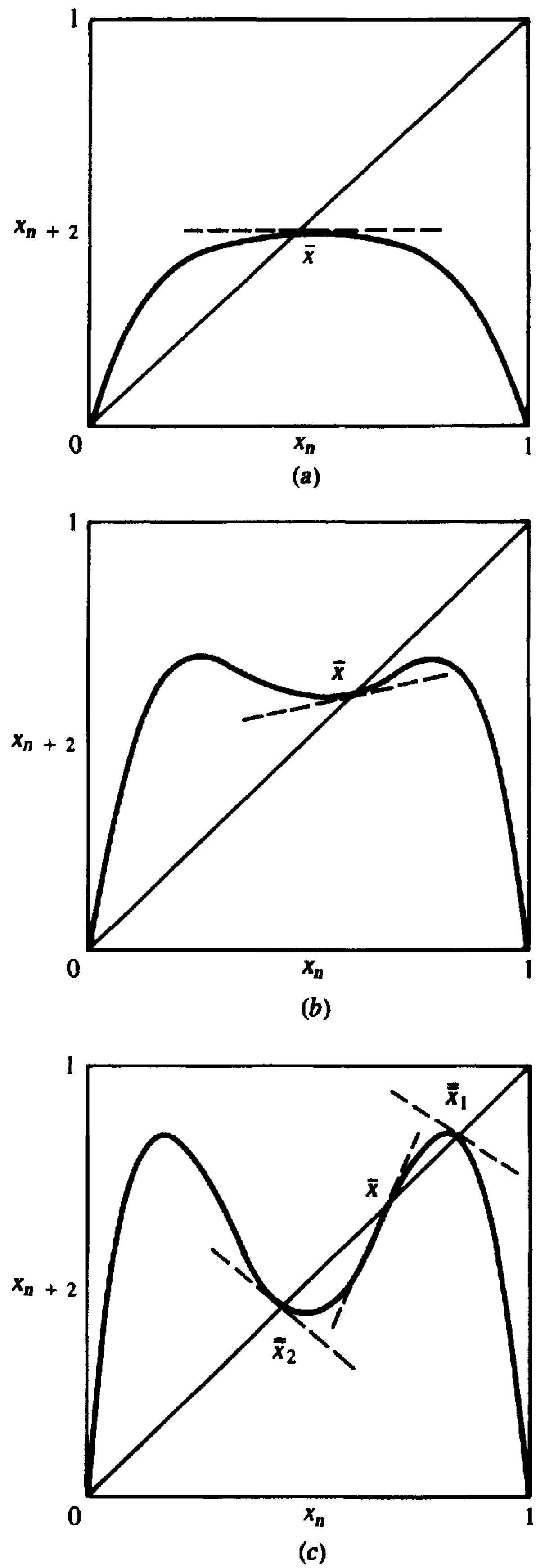


***Figure 2.7** (a) f(f(x)) initially has a flat graph with a single intersection of $x_{n+2} = x_n$ at $\bar{x}$, the steady state of $\bar{x} = f(\bar{x})$. (b) As r increases, two humps appear. As yet a single intersection is maintained. $\bar{x}$ remains stable as the slope of the tangent line is 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.*

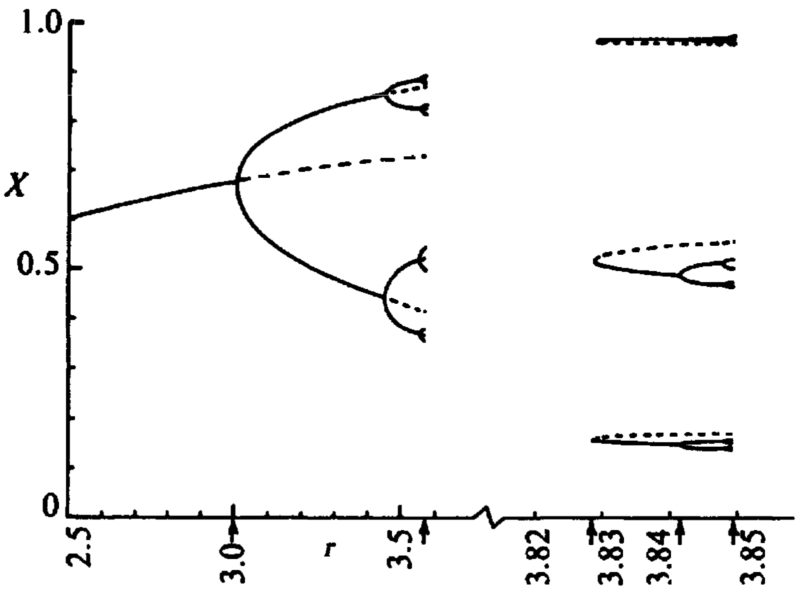


Figure 2.8 Bifurcation diagram for equation (11). [From May (1976). Reprinted by permission from Nature, 261, *pp. 459–467. Copyright © 1976 Macmillan Journals Limited.]*

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.

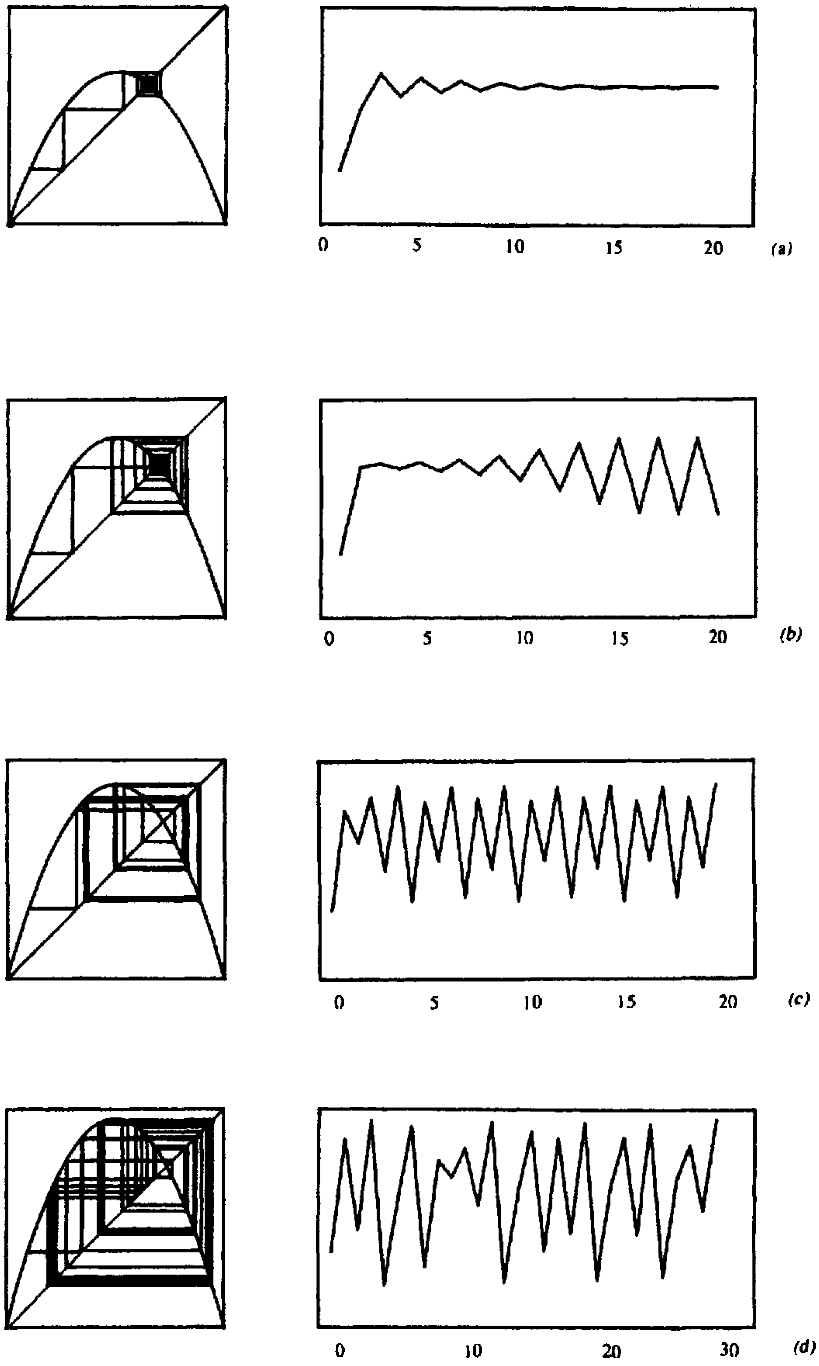


***Figure 2.9** The discrete logistic equation $x_{n+1} = rx_n(1 - x_n)$ is one of the simplest examples of a nonlinear difference equation in which complex behavior results as the single parameter r is varied. Shown here are four examples of the range of behaviors. On the left, the parabola $y = f(x) = rx(1 - x)$ 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

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

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

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

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:

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

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

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

both roots will have magnitude less than 1 if

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

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

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

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 $(-1, 1)$:

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