

5

Density Dependent Population Growth

Using the analogy of Newton's first law of motion (a body in motion tends to stay in motion), we can ask: What forces might act like friction to prevent populations from growing ever larger or declining inevitably to extinction? What forces might allow populations to eventually come "to rest" at some intermediate level of abundance? As we have shown, temporal and spatial variation alone cannot explain when and where numbers stabilize. Several more deterministic biological factors, however, can act to produce a negative feedback between population size and population growth rate.

1. Available food may decrease as more individuals have to share the same food base.
2. The foraging success of the average individual may decrease because other foragers scare prey or interfere with each other's ability to find and successfully capture prey.
3. Available living space may become filled (this applies particularly to sessile species like plants, barnacles, or even mobile territorial animals if they have a fixed lower limit to how small their territories can become).
4. Aggression may increase, leading to detrimental effects on birth and survival rates.
5. Enemies of a species may numerically increase, leading to eventual declines in birth and survival rates.
6. As a prey species increases, its enemies will have more learning opportunities with the prey and thus perfect their hunting and handling abilities with the result that a greater proportion of prey are eaten or parasitized.
7. Emigration rates may increase with population density as individuals search for less occupied territories.
8. Fewer individuals may move into an overcrowded population (immigration rates decline).

The ecological literature is filled with examples of each of these mechanisms, all of which lead to qualitative decreases in population growth rate. The consequence is that the rate of population expansion will often slow down as population size increases. In the next section we examine this tendency in detail.

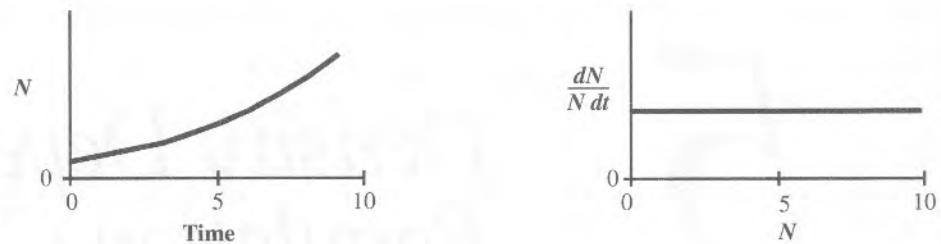
A GRAPHICAL MODEL FOR DENSITY DEPENDENCE

Density dependent growth is contrasted with exponential growth in Figures 5.1 and 5.2.

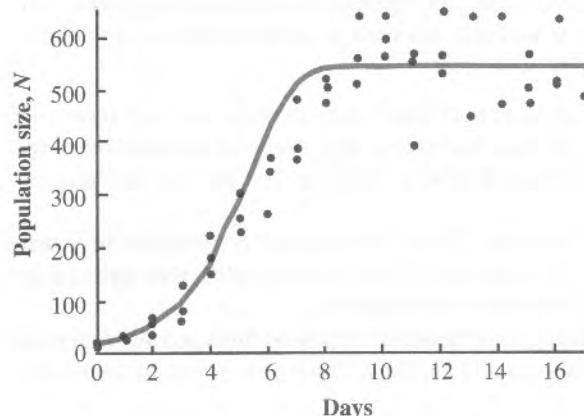
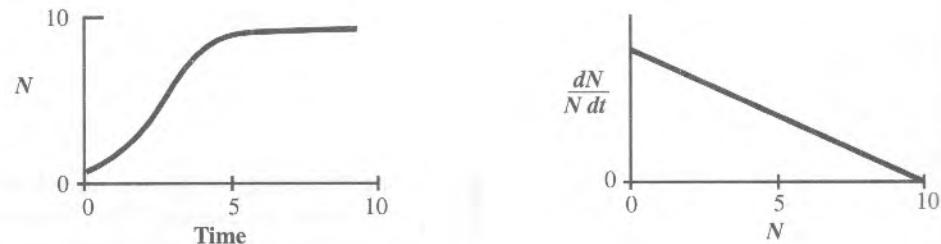
In Figure 5.2 the per capita growth rate declines with increasing population size, finally reaching zero at some relatively high population size where the population size becomes asymptotic. At this asymptotic population size, the population growth rate must equal zero since the population size is no longer changing. This in turn implies that for a closed population, birth rates must equal death rates at this asymptotic population size. Symbolically, then, the per capita birth rate and death rate are functions of N and at the equilibrium population size $b(N) - d(N) = 0$.

Figure 5.1

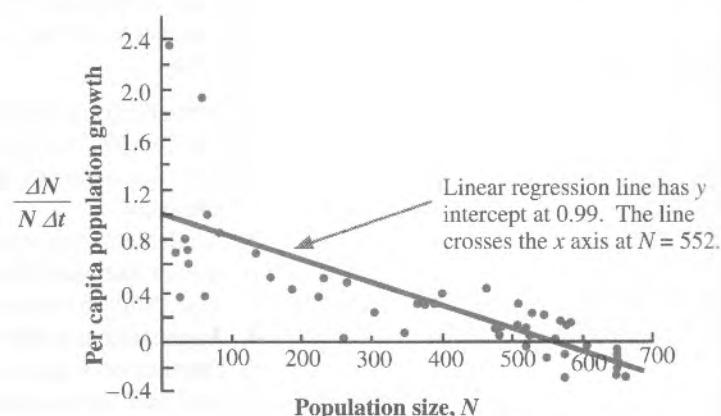
For exponential growth, population size, N , increases exponentially over time. The per capita rate of growth does not decline with population size.

**Figure 5.2**

With density dependent growth the population size reaches an equilibrium. The per capita rate of growth declines as population size increases.



(a)



(b)

Figure 5.3

(a) The growth of *Paramecium aurelia* in test tubes containing Osterhaut culture medium with bacteria as food (after Gause 1934, as plotted by Roughgarden 1971). Population size is number per 0.5 ml. (b) The same data replotted to show the relationship between per capita growth rate and population size.

The population growth of the protozoan *Paramecium* in test tubes provides a match to this expectation as illustrated in Figure 5.3 (data from Gause 1934). Under the conditions of the experiment, the population stopped growing when there were about 552 individuals per 0.5 ml. The time points show some scatter, which is caused both by the difficulty in accurately measuring population size (only a subsample of the population is counted) and by environmental variation over time and between replicate test tubes.

Species colonizing new areas often exhibit a decrease in growth rate as their population size increases, as shown in Figure 5.4.

Of course, there is no strong reason why the decline in the per capita growth rate should necessarily be linear as population size increases. It could conceivably decline like any of the alternatives shown in Figure 5.5. All three populations have the same maximal per capita growth rate at very low N , and all three curves decline to zero per capita growth rate at about the same density but the shape of the decline differs. Above this density the per capita growth rate becomes negative as the average individual's likelihood of death at these high densities exceeds its birth rate.

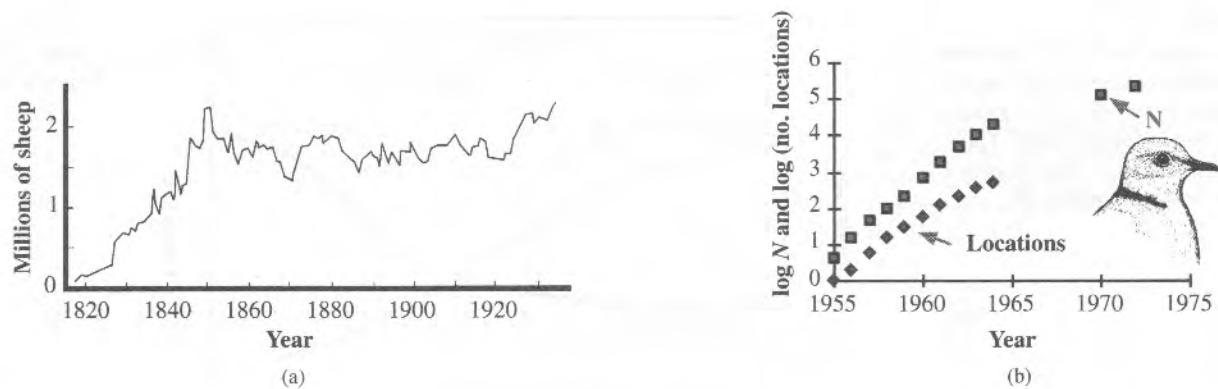
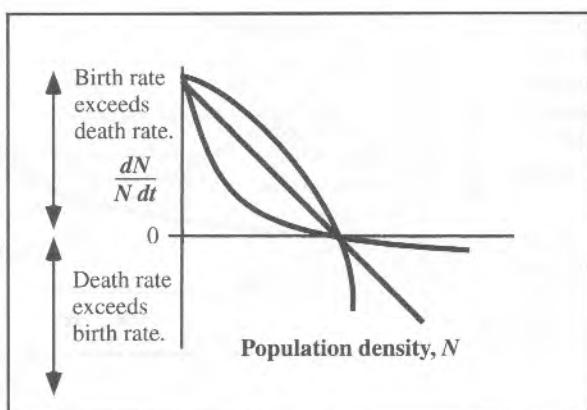


Figure 5.4

Two populations whose rate of growth slows as population size increases. (a) Sheep after being introduced into Tasmania (Davidson 1938). The variation in numbers around the asymptote is partly due to errors in estimating the yearly sheep population and partly due to variation in numbers due to climatic differences between years. (b) Collared doves (*Streptopelia decaocto*) after expanding their range into Great Britain (Hengeveld 1989). Total population size, N , and the number of locations with doves present increased over time but at a diminishing rate.

Figure 5.5
Some possible modes of decline in the per capita growth rate with population density.



The reason that the per capita growth rate declines in a closed population could be because birth rates decrease with density or because death rates increase with density or some combination of both, as depicted in Figure 5.6.

The per capita birth rate equals the per capita death rate at the population density N^* . This state of affairs means that N^* is an **equilibrium** population size, since if births equal deaths, the population size will not change over time. Note too in Figure 5.6 that both the birth and death rate axes are scaled identically from 0 to 1. More typically the range for birth rates may be greater than that for death rates. Discrete death rates cannot exceed 1 (a single mother can die at most once), but a mother can give birth to several young per time period. If the axes were scaled differently, then the N^* at which births just equal deaths would, of course, not be the place where the two curves intersect, but it still would be the density at which birth rates equal death rates.

Note also that, when the population is below N^* —for example, at N_{low} —the birth rate exceeds the death rate, and thus the population density will increase in the next generation as illustrated in Figure 5.7. On the other hand, when the density is greater than N^* —for example, at N_{high} —the death rate exceeds the birth rate, and thus the population size will decrease in the next generation. In this way the population density will move toward N^* from sizes above or below it.

Consequently N^* is not only an equilibrium point but it is a stable equilibrium point. The concept of stability is different from the concept of equilibrium. Equilibrium

Figure 5.6
The per capita birth rate decreases with density while the per capita death rate increases in this example of density dependent growth. The density where these two rates are equal is an equilibrium, N^* .

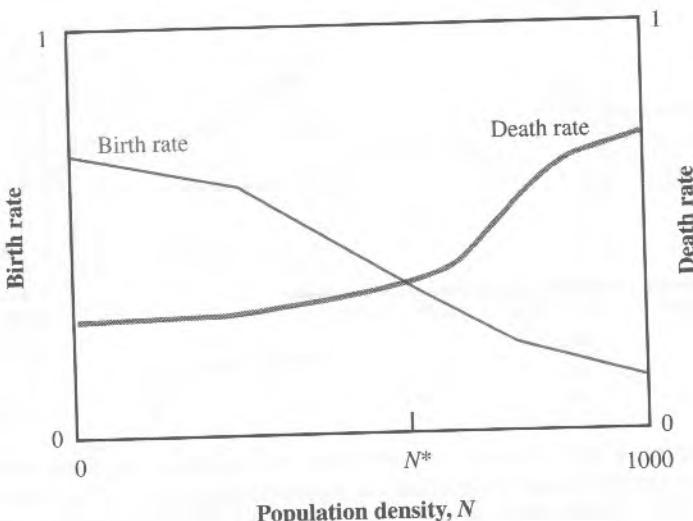
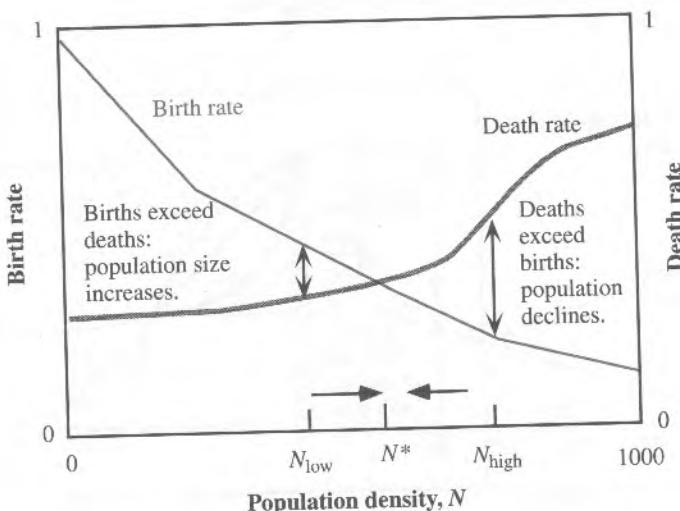


Figure 5.7
A hypothetical population experiencing density dependence in both per capita birth rates and death rates; N^* is the equilibrium population size. Perturbations of numbers above or below N^* lead to changes in the population growth rate that return the population to N^* .

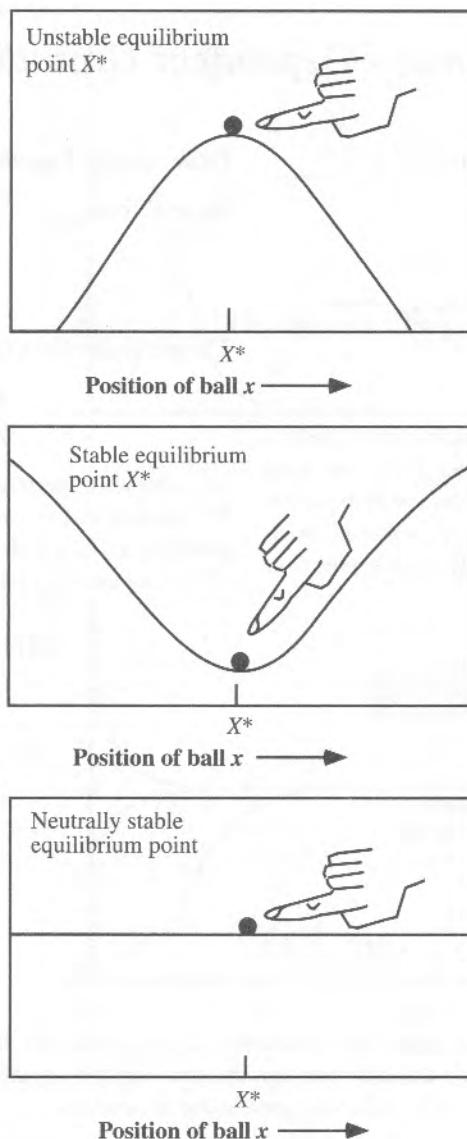


means an absence of change. **Stability** means that the system tends to return to its equilibrium state following perturbations away from that state. Consider the thought experiment suggested by Figure 5.7. Suppose that we have a population at size N^* and that we perturb the population size by the one-time addition of some additional individuals. Now we step aside and see what happens. At this new higher density (above N^*) the death rate exceeds the birth rate, leading to a population decline. In this way the population size or density tends to return to N^* following the perturbation. Similarly a perturbation in the opposite direction, by removing individuals from an equilibrium population, would result in a new lower density. At this lower density the birth rate exceeds the death rate and the population will climb back up to N^* over time. Thus N^* is a **stable equilibrium point**.

The diagrams in Figure 5.8 illustrate the concept of the stability of an equilibrium point, using an analogy with gravity. A ball placed on a landscape is subject to the force of gravity, which acts on the ball's mass. Of course, with population dynamics it is not the force of gravity operating on the system but the force of population growth, the inherent tendency of life to reproduce, and the influence of population density acting on birth and death rates. Consider a population at equilibrium at N^* . It is then perturbed by a one-time “nudge” (i.e., by the addition or subtraction of some additional individuals). Does population size tend to return to equilibrium following the perturbation (indicating a stable equilibrium), or does it grow or shrink even more (indicating an unstable

Figure 5.8

A gravity analogy to illustrate the concept of stability.



equilibrium)? The simple graphical model presented yields a stable equilibrium point by this criterion. At the end of this chapter we develop some mathematical tools for the evaluation of stability. For now, however, let's explore the surprising behavior of one general model with density-dependence, the logistic equation.

THE LOGISTIC EQUATION: A PARTICULAR MODEL OF DENSITY DEPENDENCE

Perhaps the simplest expression that produces a stable equilibrium population size is the logistic equation. It is presented in both continuous and discrete forms in Box 5.1.

We explain the discrete logistic and Ricker diagrams a bit later; for now, let's begin with the continuous logistic equation,

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right).$$

Note that without the term in parentheses, the population growth rate is exponential with intrinsic rate r . Also, if $N = K$, the term in parentheses becomes zero so population growth becomes zero when the population size hits K , regardless of the initial

Box 5.1 Models of Density Dependent Growth: Logistic Equations

Difference Equations, Discrete Time

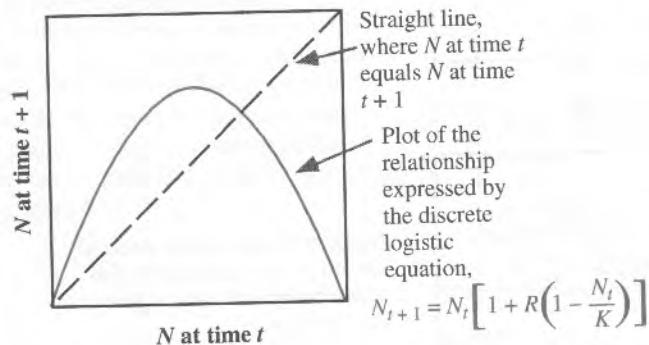
General form:

$$N_{t+1} = F(N_t).$$

The particular form for the discrete logistic equation:

$$N_{t+1} = N_t \left(1 + R \left(1 - \frac{N_t}{K} \right) \right). \quad (\text{a})$$

To solve, the object is to try to find an expression for population size, N_{t+T} , after an arbitrary number T of time steps into the future. Unfortunately, unlike the case with exponential growth (Box 1.1), no neat closed form solution exists and the easiest method is to follow the dynamics over time by plotting **Ricker Diagrams**:



For exponential growth it was possible to make the substitution $\lambda = e^r$ so that the discrete and continuous models yielded identical results. **There is no such simple substitution for the two logistic equations (a) and (b). Although they look very similar they can produce qualitatively different population dynamics.**

Differential Equations, Continuous Time

General form:

$$\frac{dN}{dt} = f(N).$$

The particular form for the continuous logistic equation:

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right). \quad (\text{b})$$

To solve a differential equation we find an expression for $N(t)$ (not dN/dt) as a function of t . To find it we integrate the differential equation and plug in the initial conditions $N(0) = N_0$ and $t(0) = 0$. After several steps, the solution is

$$N(t) = \frac{K}{1 + \left(\frac{K - N_0}{N_0} \right) e^{-rt}}. \quad (\text{c})$$

population size. The population growth rate is also zero when $N = 0$. In words, the logistic equation says

$$\left[\begin{array}{l} \text{The rate of} \\ \text{increase of the} \\ \text{population} \end{array} \right] = \left[\begin{array}{l} \text{the maximum rate of} \\ \text{population growth} \\ \text{per capita, } r \end{array} \right] \left[\begin{array}{l} \text{the number of} \\ \text{individuals, } N \end{array} \right] \left[\begin{array}{l} \text{the unutilized} \\ \text{opportunity for} \\ \text{population growth} \end{array} \right].$$

A typical time course of logistic growth is illustrated in Figure 5.9.

Figure 5.10 illustrates the approach to K from three different initial N_0 .

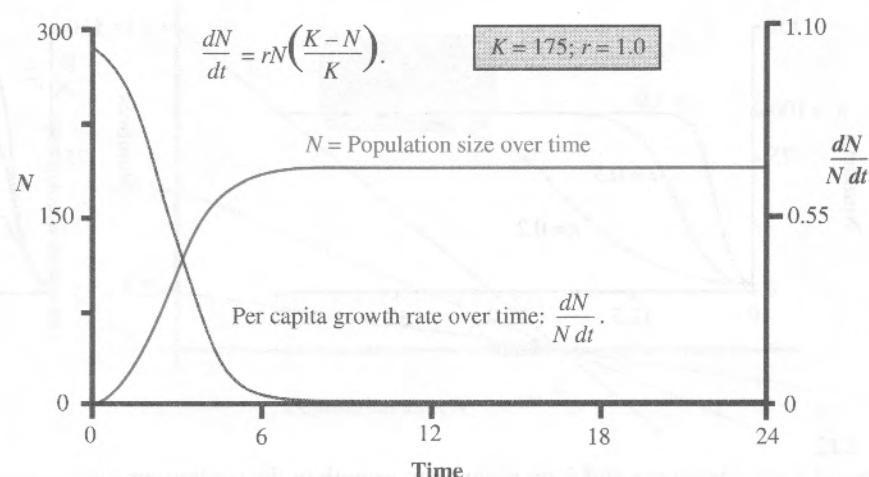
Now let us explore the logistic equation algebraically. Multiplying through the parentheses of the logistic equation and simplifying gives

$$\frac{dN}{dt} = rN - \frac{rN^2}{K}. \quad (5.1)$$

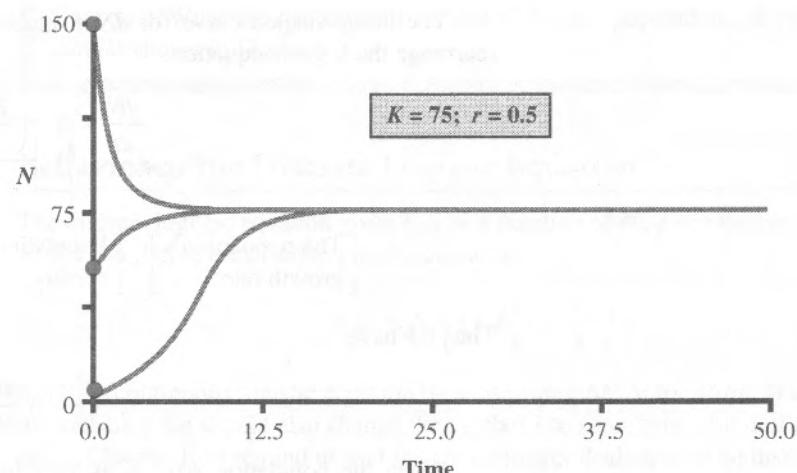
Note that the expression on the right of the equals sign contains both a term in N and a term in N^2 ; thus a plot of dN/dt versus N must look like a parabola (see Appendix 1, Visualizing Equations). An example of population growth, dN/dt , plotted versus population size, N , for the case where the carrying capacity K is 200 is shown in Figure 5.11 for three different values of r .

Figure 5.9

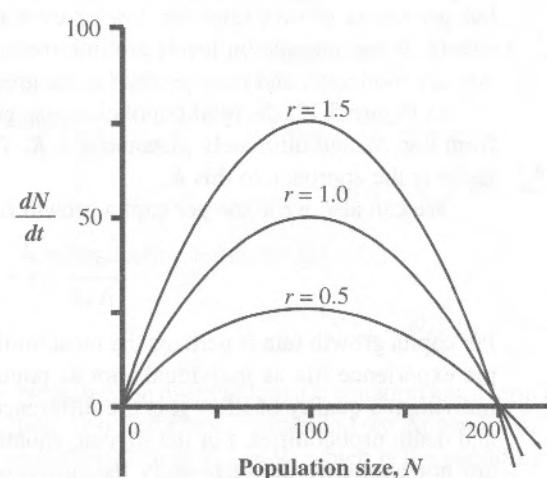
Time course of a population growing according to the continuous logistic equation.

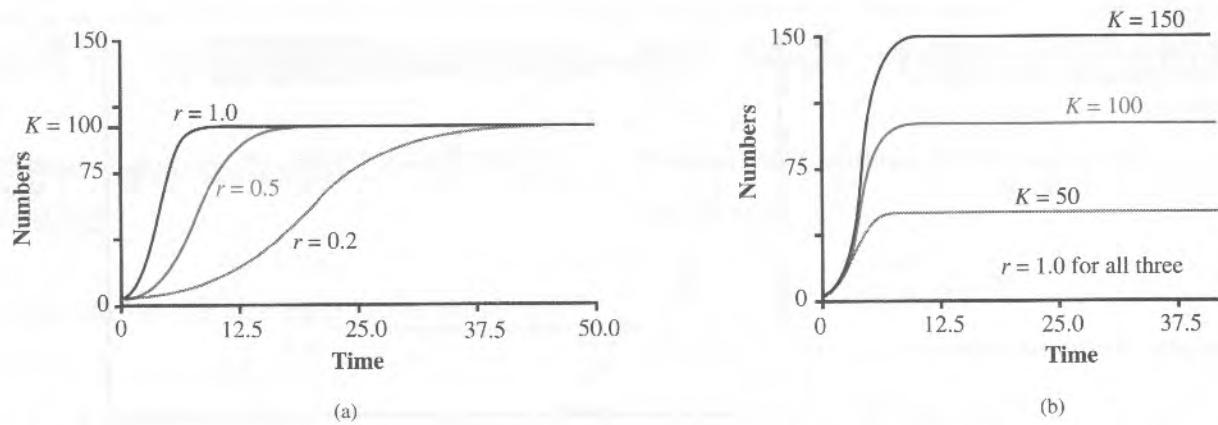
**Figure 5.10**

Logistic with three different initial population sizes. The time course of population size based on the logistic equation, with initial density, N , of 150, 50, or 10.

**Figure 5.11**

Logistic growth with different values of r . The relationship between population growth rate, dN/dt , and population size, N , for three different values of the intrinsic growth rate, r . $K = 200$ for all three values.



**Figure 5.12**

The effect of the parameters r and K on population growth in the continuous logistic equation. (a) Same K 's but different r 's. (b) Same r 's but different K 's.

The hump-shaped curve for dN/dt makes intuitive sense. To see this easily we rearrange the logistic equation:

$$\frac{dN}{dt} = N \left[r \left(\frac{K - N}{K} \right) \right].$$

[The population's growth rate] = [Population density] $\left[\begin{array}{c} \text{Per capita growth rate,} \\ \frac{dN}{N dt} \end{array} \right]$

Thus we have

$$\frac{dN}{dt} = N \frac{dN}{N dt}.$$

When the population size, N , is very low (near 0), the per capita growth rate, $dN/N dt$ is high because there is little competition, but few individuals are present to reproduce so the growth rate of the total population is low ($dN/dt = N(dN/N dt)$). At the other extreme, when the population is very high (near K), there are many individuals but per capita growth rates are low or even negative, so again the population grows slowly. When population levels are intermediate, both per capita rates and population size are moderate, and their product is the greatest; thus the population grows faster.

In Figure 5.12, the total population size grows with an S-shaped curve, beginning from low N_0 and ultimately plateauing at K . The larger the intrinsic growth rate, r , the faster is the approach to this K .

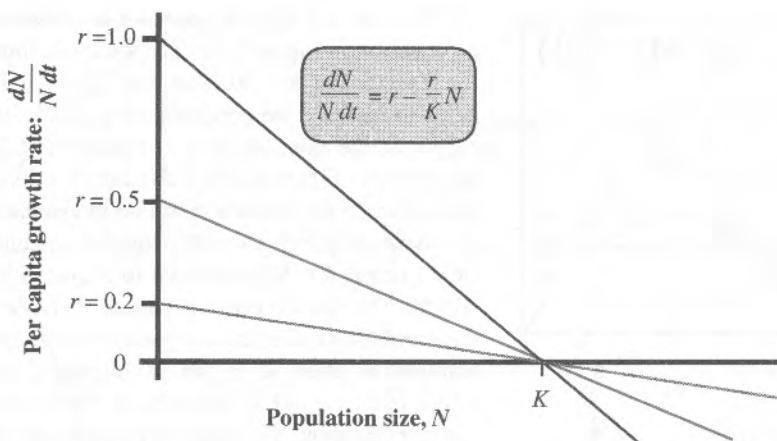
We can also write the per capita growth rate as

$$\frac{dN}{N dt} = r - \frac{rN}{K}. \quad (5.2)$$

Per capita growth rate is perhaps the most intuitive measure we can think of, since people experience life as individuals not as populations. Per capita growth expresses an individual's quality of life—it is the difference between the average individual's birth and death probabilities. For the logistic equation, the birth and death rates themselves are not explicitly defined—only the difference between them is. This difference is $dN/N dt$ and follows the equation of a straight line, Eq. (5.2), as a function of N . The growth rate declines linearly from a maximum of r (the y intercept) when the population size is zero to zero when the population size is at **carrying capacity**, K . Increases in population size N beyond K lead to negative per capita growth rates (the death rate exceeds the birth rate). The slope of the line is $-r/K$, as shown in Figure 5.13.

Figure 5.13

In the logistic equation, per capita population growth declines linearly with population size—illustrated here for three values of r .



Exercise: What are the values of r and K for the populations of *Paramecium aurelia* shown in Figure 5.3?

Behavior of the Discrete Logistic Equation

The discrete logistic equation gives N_{t+1} as a function of N_t , given the parameters R and K . We can derive the discrete logistic equation,

$$N_{t+1} = N_t \left(1 + R \left(1 - \frac{N_t}{K} \right) \right),$$

from the continuous logistic equation by substituting $\Delta N/\Delta t$ for dN/dt . When shifting to discrete time we should also change the symbol r to something else. Let's use R , as we did in Chapter 1, to remind us that we are no longer dealing with an instantaneous rate of population change but a discrete rate. Thus we write

$$\begin{aligned} \frac{\Delta N}{\Delta t} &= RN_t \frac{(K - N_t)}{K} \\ \Delta N &= N_{t+1} - N_t = RN_t \frac{(K - N_t)}{K} \Delta t, \end{aligned}$$

and since $\Delta t = (t + 1) - t = 1$,

$$N_{t+1} = N_t + RN_t \frac{(K - N_t)}{K}.$$

After collecting terms we get

$$N_{t+1} = N_t \left(1 + R \left(1 - \frac{N_t}{K} \right) \right).$$

Note that the discrete logistic equation has a term in N_t and a term in N_t^2 ; thus this equation also describes a parabola (see Appendix 1, Visualizing Equations). When $N_t = 0$ and $N_t = K$, then $N_{t+1} = N_t$, which is the condition for an equilibrium point.

Exercise: Use the discrete logistic equation to determine the values of N_t , such that $N_{t+1} = 0$.

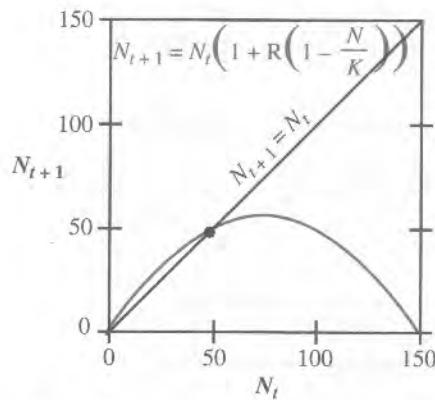


Figure 5.14

The discrete logistic equation is plotted in red, and the line $N_{t+1} = N_t$ is plotted in black. Where the two lines intersect, the population is at equilibrium since $N_{t+1} = N_t$.

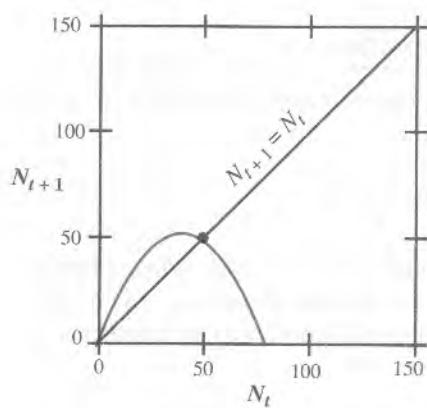


Figure 5.15

An example of a discrete logistic equation with a higher value of R but the same K as in Figure 5.14.

We take a graphical approach to understanding the dynamics of the discrete logistic equation in Figure 5.14. The parabola shown is simply the discrete logistic equation for $R = 0.5$ and $K = 50$. The line $N_{t+1} = N_t$ is simply a construction line—a line that helps to identify the condition of equality between the two axes. By definition, when $N_{t+1} = N_t$, the population is at equilibrium. There are two values of N that represent equilibria in Figure 5.14: $N = 0$ and $N = 50$. These two N 's are easily seen as the only points where the construction line intersects the population growth parabola.

An example of a discrete logistic equation with a higher value of R but the same K ($R = 1.6$ and $K = 50$) is shown in Figure 5.15. The nonzero population equilibrium is still 50. The growth curve is shifted to the left compared to the one in Figure 5.14, and the parabola is shorter and somewhat steeper. This change in shape now causes the equilibrium point, K , to fall on the right-hand side of the peak of the parabola instead of the left, as it did in Figure 5.14. Now, let's trace the growth of a population following this equation. We arbitrarily begin with an initial density at time 0 of 20 individuals. We follow the approach taken in Chapter 1, Figure 1.7, except that now the population growth is logistic not geometric, as depicted in Figure 5.16.

First look at Figure 5.16(a). From the initial population size of $N = 20$, the population increases to about $N = 39$ at the next time step. By moving a line horizontally across to the construction line, we can begin the next iteration, which results in a population size of about 53, overshooting the carrying capacity of $N = 50$. The numbers along the vertical axis in Figure 5.16(b) indicate the various time steps (starting at 0); a running chart of population size over the first few time periods results. Note how the numbers line up in the two parts of the figure.

This diagram is known as a **Ricker diagram** (Ricker 1952); it is a convenient way to graphically follow the growth of a population in discrete time steps. The diagonal construction line (slope = 45°) allows us to simply convert the last N_{t+1} to the starting density, N_t , for the next iteration. In this example, the population initially overshoots its carrying capacity at time step 2 and then it undershot the carrying capacity at time step 3. As time goes on these oscillations damp out and population size zeros in on its equilibrium of $N = 50$.

We increase R still more in Figure 5.17. The Ricker diagram and the corresponding time series plot are shown.

The dynamics in Figure 5.17 illustrate a stable two-point **limit cycle**. The cycles do not converge to the equilibrium point, K , which apparently is now an *unstable* equilibrium point. Instead the population oscillates between the same two levels of N —one above K , the other below.

In summary, as R increases, the discrete logistic equation parabola of N_{t+1} versus N_t becomes steeper. This in turn implies that the slope of the parabola is steeper at the equilibrium point, K . If steep enough, trajectories that begin near this equilibrium point wind outward instead of inward to the equilibrium point. In the next section, we provide a more formal description of this process so that we can precisely define “steep enough.”

The two-point limit cycle obtained with $R = 2.1$ is a *stable cycle*, since alternative initial conditions converge on this same cycle, though not necessarily in phase, as the time series in Figure 5.18 shows.

For ectothermic animals, increasing ambient temperature increases their metabolic rate and growth rate, shortening generation times and thus increasing R . This can have the result in some laboratory populations of shifting population dynamics from a stable equilibrium point to apparently stable oscillations. Two examples are shown in Figure 5.19.

Increasing R still more in this model produces increasingly larger amplitudes for the two-point cycle, but something qualitatively different happens when R exceeds 2.449. An example of the time series for $R = 2.5$ ($K = 100$) is shown in Figure 5.20. The asymptotic behavior of this population is a four-point limit cycle. It takes a little while, but eventually the population oscillates continually over the same four values of N . We labeled these values points 1, 2, 3, and 4.

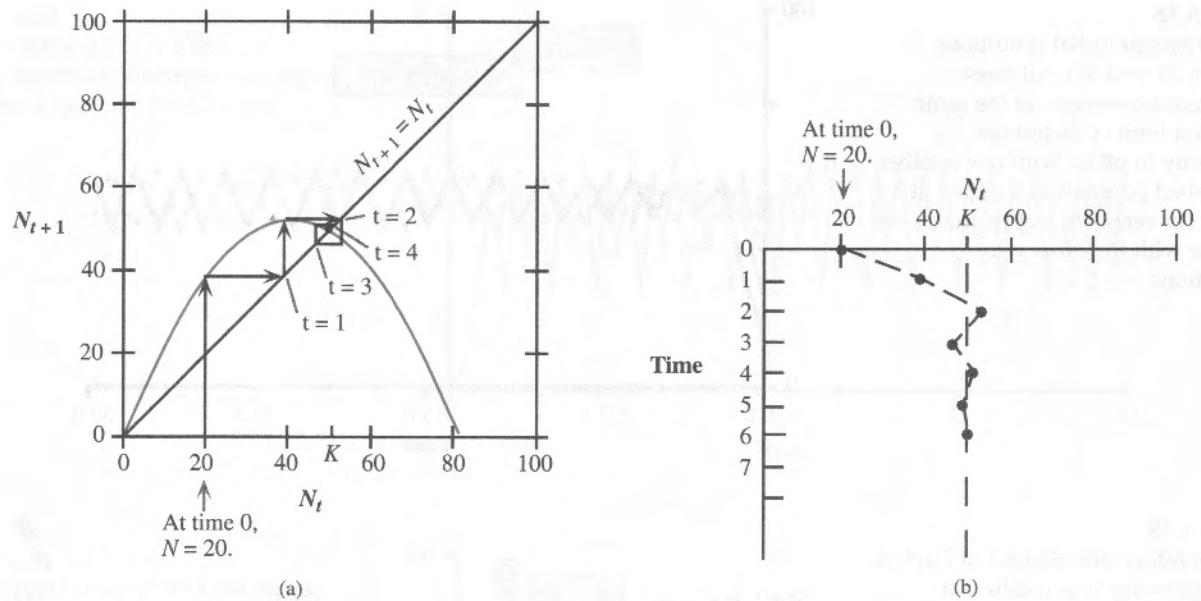


Figure 5.16

(a) The curve for the discrete logistic equation and an initial population size of 20. The black lines and arrows depict how the population grows over successive time steps. (b) Transcription of these population sizes to a time-step plot.

Figure 5.17

(a) A Ricker diagram and (b) a time series plot for $R = 2.1$. A two-point limit cycle is reached.

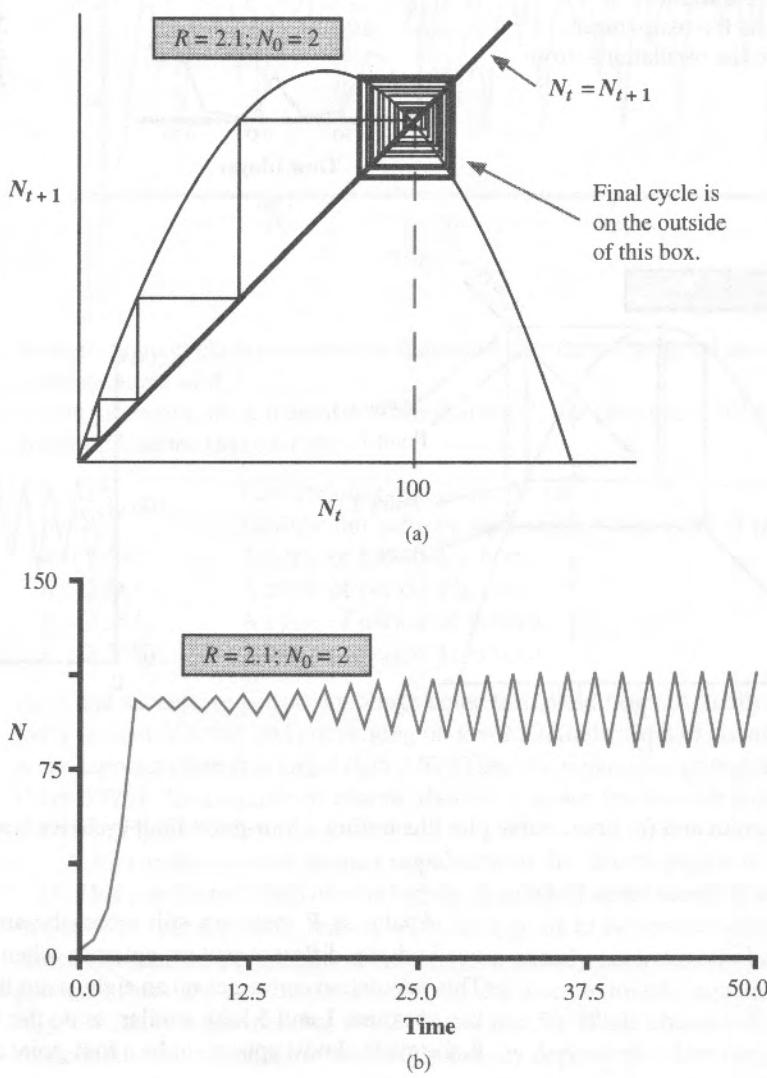
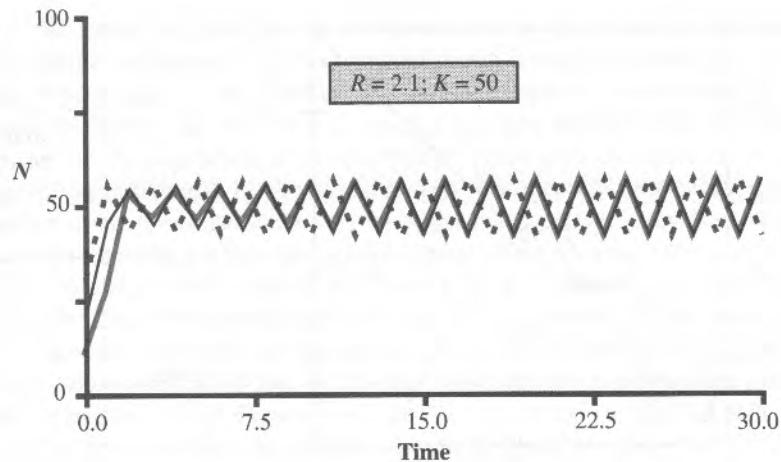
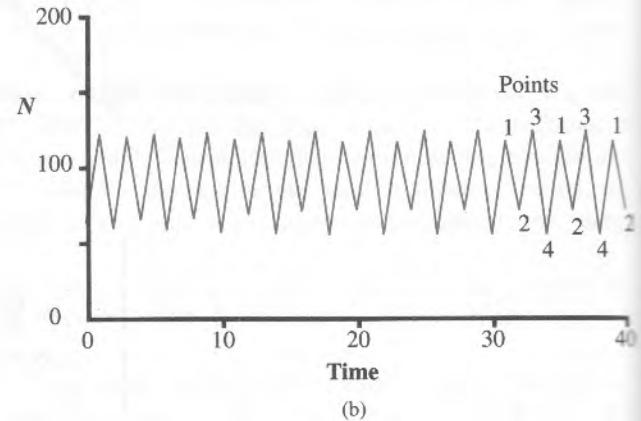
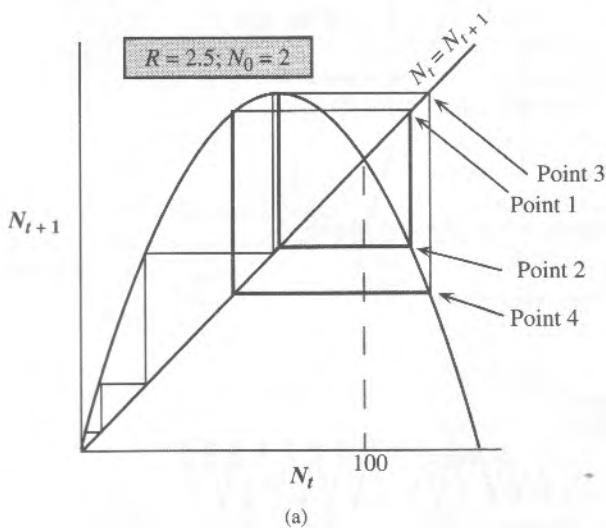
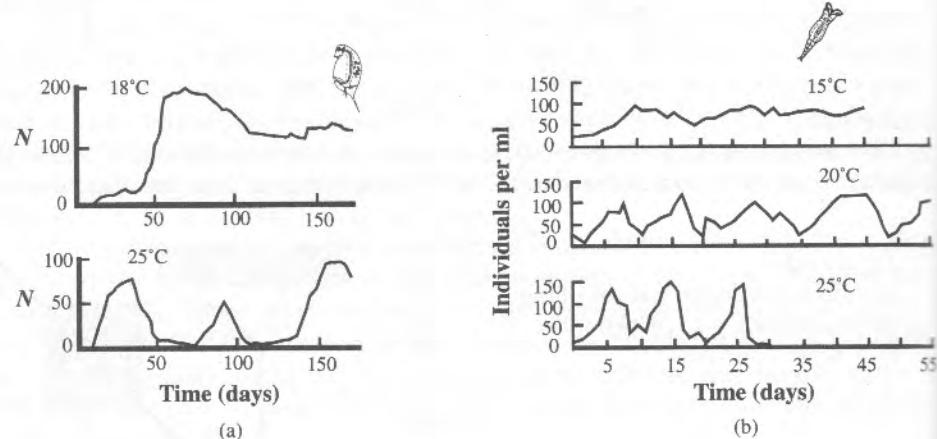


Figure 5.18

Three different initial conditions ($N_0 = 10, 20, and 30). All three populations converge on the same two-point limit cycle but not necessarily in phase with one another. The dashed population initiated at $N_0 = 30$ converges to a cycle that is out of phase with the other two populations.$

**Figure 5.19**

(a) Laboratory populations of *Daphnia magna* growing at two different temperatures (from Pratt 1943). The population at 25°C has a higher growth rate and oscillates. (b) Laboratory populations of rotifers growing at three different temperatures. As the temperature increases, so do the oscillations (from Halbach 1979).

**Figure 5.20**

(a) A Ricker diagram and (b) time course plot illustrating a four-point limit cycle for $R = 2.5$.

Again, as R increases still more, the amplitude of these cycles increases until a qualitatively different pattern emerges when $R > 2.544$, as illustrated in Figure 5.21. This population converges on an eight-point limit cycle. At first glance, because the values of points 1 and 5 look similar, as do the values of points 2 and 6 and points 4 and 8, the cycle almost appears to be a four-point cycle. The range of R values that produce

Figure 5.21
A time course plot for a discrete logistic equation, illustrating an eight-point limit cycle for $R = 2.55$ and $K = 50$.

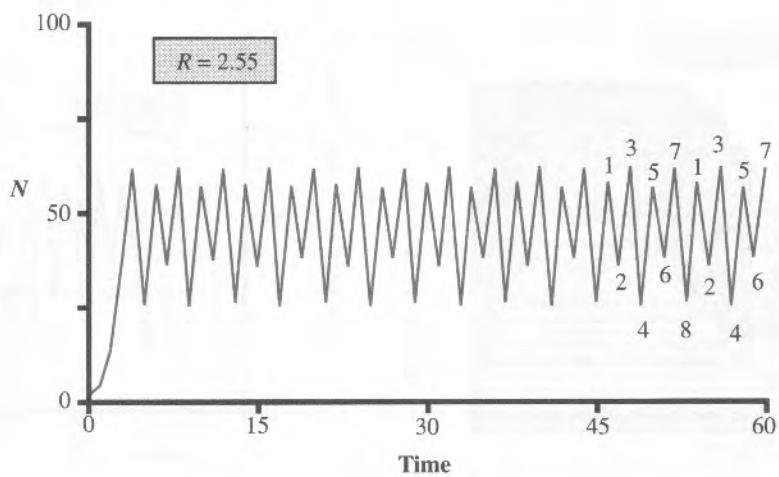
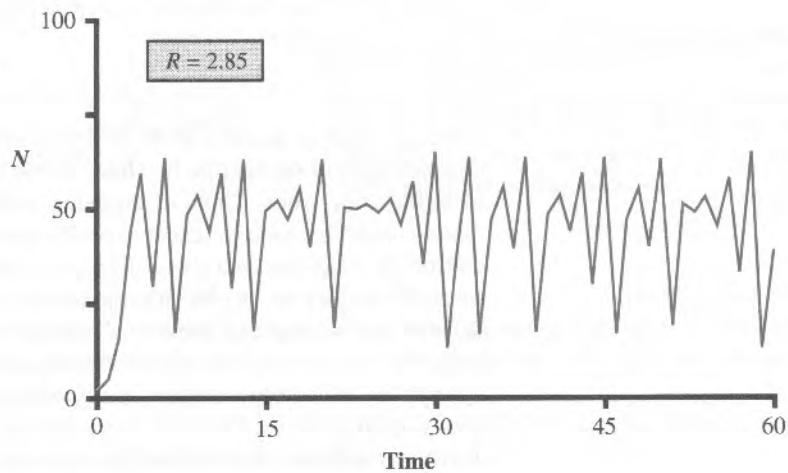


Figure 5.22
A time course plot of the discrete logistic equation for $R = 2.85$.



an eight-point cycle is even smaller than the range for a four-point cycle and, as before, is independent of K .

In summary, as R increases from 0 upward, the population behaves as a period-doubling scheme (May 1976):

$R < 2$	Equilibrium point is locally stable.
$R = 2.0$	Equilibrium point becomes unstable; a cycle of period 2 is born.
$R = 2.449\dots$	A cycle of period 4 is born.
$R = 2.544\dots$	A cycle of period 8 is born.
$R = 2.564\dots$	A cycle of period 16 is born.
$R = 2.5687\dots$	A cycle of period 32 is born.

Note that successive period doublings come faster and faster. Actually they are following a geometric series and converging on $R = 2.57$, in the limit of an infinite period. But what happens when R is larger than 2.57? Then the population growth becomes **chaotic** (May 1976). An example of chaotic dynamics under the discrete logistic equation is shown in Figure 5.22.

A Ricker diagram for another population in the chaotic region is shown in Figure 5.23. This population's behavior is highly irregular; it never seems to settle into exactly the same temporal pattern, and its behavior appears to be erratic—almost random. But remember that the population is following an exactly deterministic behavior specified precisely from one time step to the next by the discrete logistic equation. In the case of Figure 5.22, this equation has $R = 2.85$ and $K = 50$. While chaotic, the behavior is not random since the population is strongly density dependent; when the population's size

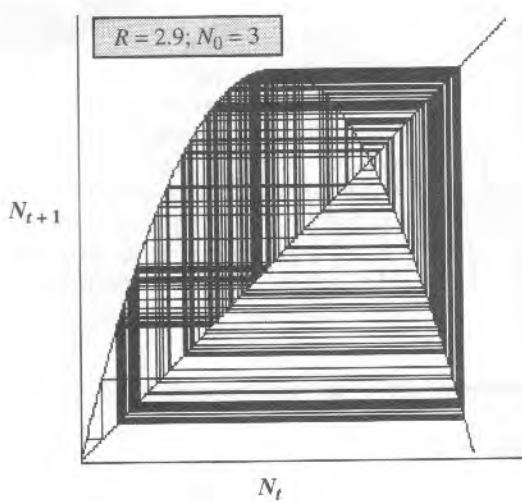


Figure 5.23
A Ricker diagram for $R = 2.9$.

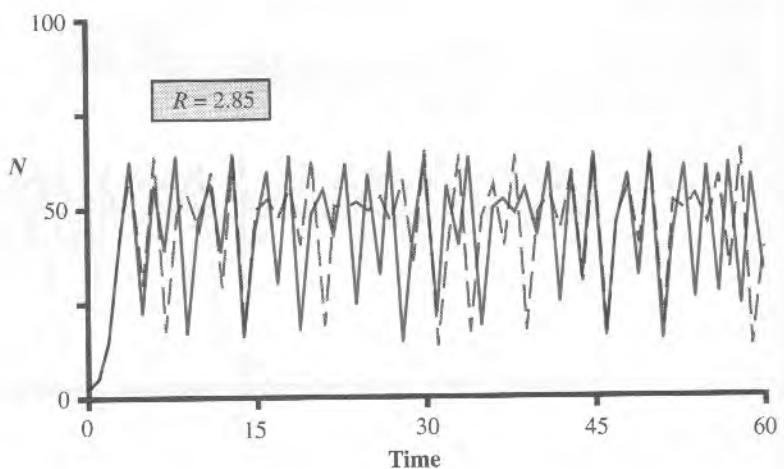


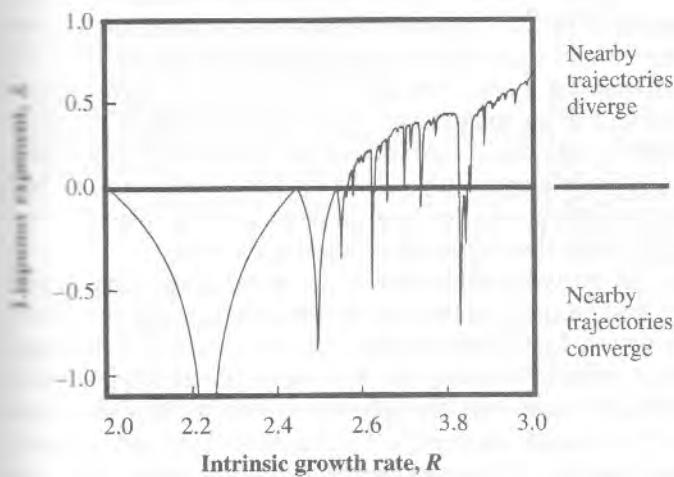
Figure 5.24
Time series for two populations that start at nearly identical points but quickly diverge.

is high, it tends to decrease at the next time step, and, when it is low, it tends to increase. One hallmark of **deterministic chaos** is that the dynamics show **sensitive dependence to initial conditions**. Think of throwing a die—we consider the face that comes up a random event because we cannot specify exactly all the variables that influence its roll and initial trajectory. All these difficult to specify initial conditions interact with the sharp 90° angles on the die to make the roll unpredictable. The slightest difference in the toss can produce an entirely different face up. Similarly, for chaotic population behavior, sensitivity to initial conditions means that the time course of the population appears unpredictable and that slightly different initial conditions produce increasingly divergent time series. The time series for two populations initiated at $N_0 = 1.0$ and 1.1 are shown in Figure 5.24. While the trajectories for the two populations are nearly identical over about the first five time steps, they rapidly diverge after that. In fact, as time goes on the probability of the two populations sharing the same size at the same time becomes vanishingly small.

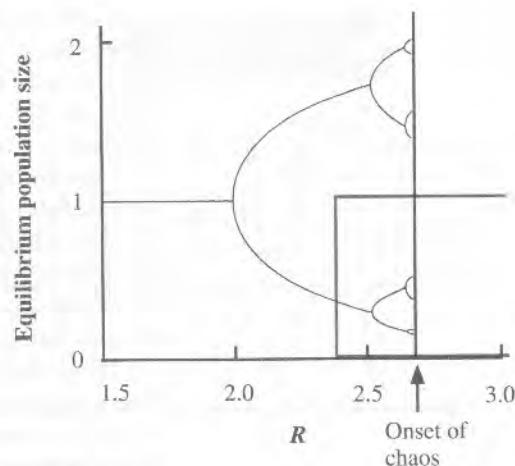
It is this sensitivity to initial conditions that is the signature of deterministic chaos. Much current research is devoted to analyzing time series to assess the degree of density dependence and sensitivity to initial conditions. To quantify this degree of sensitivity, theoreticians have introduced a measure called the **Liapunov exponent**. Here's the intuition behind its definition. Imagine an initial population at size N_0 and consider a nearby point at $N_0 + \Delta_0$, where Δ_0 is very small. After n time steps we measure the sizes of the two populations, one starting at N_0 and the other at $N_0 + \Delta_0$. Let $|\Delta_n|$ be the absolute value of their difference. We do this again and again for different time periods, n , and then fit this data to an exponential model with elapsed time n as the independent variable:

$$|\Delta_n| = |\Delta_0| e^{n\lambda}. \quad (5.3)$$

This model has one parameter, the **Liapunov exponent**, λ . Note use of the same symbol that was used earlier for both the discrete growth rate and eigenvalues (Chapter 3). This is because there is a functional relationship between these concepts. If λ is negative, then populations are converging on the same temporal pattern as time goes by (either a stable equilibrium point or a limit cycle), while if λ is positive the deviation between populations initialized at slightly different numbers is growing over time; this is the signature of deterministic chaos. There are more computationally useful formulas for calculating Liapunov exponents directly from time series data, but they are less intuitive than Eq. (5.3); in general they require a computer. Figure 5.25 shows the relationship between the Liapunov exponent and the magnitude of R in the discrete logistic equation (Olsen and Degn 1985).

**Figure 5.25**

The Liapunov exponent, λ , as a function of R for the discrete logistic equation. When the Liapunov exponent is positive, then nearby trajectories diverge over time—the signature of deterministic chaos.

**Figure 5.26**

Equilibrium population size for the discrete logistic equation as a function of R ; K is set to 1. The first bifurcation (to a two-point limit cycle) occurs at $R = 2.0$. The curve traces the magnitude of the two-cycle points as R increases. Each of these points, in turn, bifurcates to produce a four-point cycle at $R = 2.449$. A blowup of the red box is shown in Figure 5.27(a).

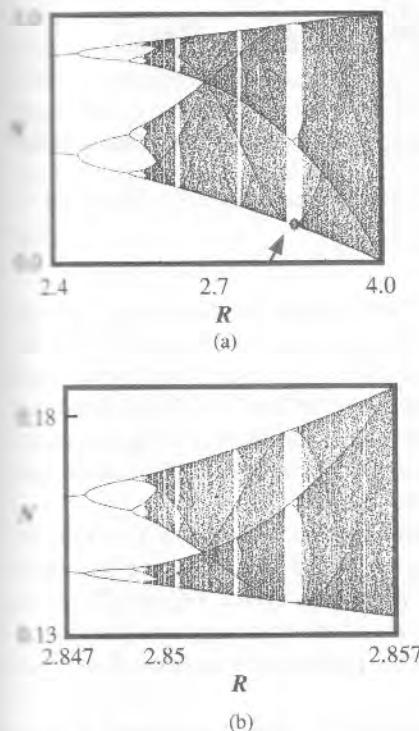
Note that the first time λ becomes positive is at 2.57. For R greater than 2.57, the Liapunov exponent increases with sudden dips and spurts below 0. These dips are associated with regions of periodic cycles. The large dip at $R = 2.83$ is a window of R where cycles of period 3 emerge and later disappear.

Figures 5.26 and 5.27 show the relationship between the ultimate population size and the magnitude of the growth parameter R .

In Figure 5.27, even for R 's beyond the onset of chaos, we see an unexpected mixture of intervals where chaos is interrupted with orderly cycles, mostly with odd numbers (e.g., cycles of period 3 at $R = 2.83$). When we blow up a portion of Figure 5.27(a), in the bottom part of the period 3 cycle region in the vicinity of $R = 2.83$, Figure 5.27(b), we see that the bifurcation diagram appears to reappear in miniature. The pattern of behavior is **fractal**, in the sense that the same geometric pattern is reproduced at successively larger or smaller scales.

The important lesson from this is that the discrete logistic equation, simple as it is, has a rich and surprising variety of behaviors compared to the continuous logistic equation, which was quite boring in comparison. **In discrete time a population has an implicit lag time of one time unit in its response to N . No such lag time exists with differential equations.**

Which model is the most realistic? The answer depends on the population being modeled. The fundamental difference between the two models is the inherent time lag in the discrete logistic equation caused by the form of the difference equations. The population responds in jerks. Imagine if your stereo had a short in the electronics such that there was a time lag between the time you adjusted the volume knob and the time that the volume in the speakers actually changed. If the sound was too low to hear, you would turn the volume up—but nothing would happen immediately, so you might keep turning the volume up more. After some time, the adjusted volume would finally click in, but now the volume would be higher than you had intended, so you would turn the volume down—again the time lag would prevent an immediate response between your adjustment of the knob and the volume coming out of the speaker, so you might overadjust before the new volume emerged from the speaker: this time too low. In this way, the volume would oscillate as you overadjust, then underadjust. The faster you turn the volume knob, the greater will be the amplitude of the volume cycle (higher highs and

**Figure 5.27**

Blowups of equilibrium population size as a function of R . (a) The red box region of Figure 5.26. The very small region circled in red in (a).

lower lows) emerging from the speaker—just as the greater the R , the larger are the population cycles. Ultimately, since humans are intelligent, you would catch on to the problem and adjust the knob slowly. But animal populations are sometimes kept from compensating for time lags by enforced features of their environment (e.g., strict seasonality) and the constraints set by the lengths of their generation times.

Consider the case of lemmings living in the tundra zone of the far north. Populations of these rodents cycle with an approximate 3-year period. What is the actual mechanism behind the density dependence and the creation of a time lag? Experiments have shown that the cycles are not apparently caused by delayed responses to food exploitation nor by a delayed response by predators to these lemming numbers—two obvious choices. Instead, current views suggest the following scenario.

The winter is actually a pretty favorable time for lemmings. They make tunnels underneath the snow and feed on frozen shoots and lichens. The snow insulates them from the cold and helps protect them from predators, so females continue breeding. When the snow melts in the summer, lemmings move on the surface and their numbers during an increase year will be large—but aggression now becomes important since individuals encounter each other more frequently. This aggression leads to much scarring, young don't mature quickly, and females eventually stop breeding. Next year when the snow melts—strangely, even though lemming numbers are now lower—lemmings still “act” like they are crowded. It's not known if this response is due to some long-term hormonal change in the surviving individuals or due to short-term genetic changes in the composition of the population. In any event, the cycle starts over again in the third year (Krebs 1988).

The Continuous Time-Lagged Logistic Equation

In later chapters on predation, we show that population cycles can also be generated by the interaction of predators and their prey. The numerical increase in predator numbers as prey increase leads to increased predator birth, but this takes some finite time to effect. Consequently oscillations frequently emerge in both theoretical and empirical predator-prey interactions. The important role of time lags in causing population cycles can be shown in another way. We can start with the continuous (differential equation) density dependent model and insert a time lag T . There are several ways to do this, however. Hutchinson (1948) introduced a model where the time lag occurred only in the density dependent term:

$$\frac{dN}{dt} = rN \left(\frac{K - N(t-T)}{K} \right). \quad (5.4)$$

How might this time lag arise? Let's think of this species as a herbivore. The vegetation may take τ time units to regrow to full size after being consumed. Even if the limitation to herbivore population growth is proportional to present food levels, these plant levels are related to not just the present number of grazers but also to those that lived (and consumed food) between now and τ time steps earlier. It is often then possible to approximate this integral of consumption by the numbers $N(t-T)$ at some specific earlier time T (where $0 < T < \tau$) (May 1973).

This model behaves like the continuous logistic equation when r (or T) is low, but it is more like the discrete logistic equation when r (or T) is high. However, instead of giving the sawtoothed behavior, it yields smooth population cycles. Figure 5.28 shows the behavior of this model for three different values of the time lag T and the same r . When the lag time is 2.8 (or nearly three times r), the population overshoots K so much that it comes crashing down to extinction.

This behavior is not unlike the population dynamics of reindeer introduced to some of the Alaskan Pribilof Islands as illustrated in Figure 5.29. The reindeer lack predators on these islands, so their population growth responds primarily to food availability. Their food is lichens, short willows, and other plants in the tundra. The climate is generally cold with a short growing season. Thus these plants grow very slowly. The lag

Figure 5.28

An illustration of the time-lagged continuous logistic equation for three different values of the time lag, T . For the purposes of this simulation, this population becomes extinct if its numbers fall below a single individual, as is the case for a time lag of 2.8. Here $r = 1.0$ and $K = 50$.

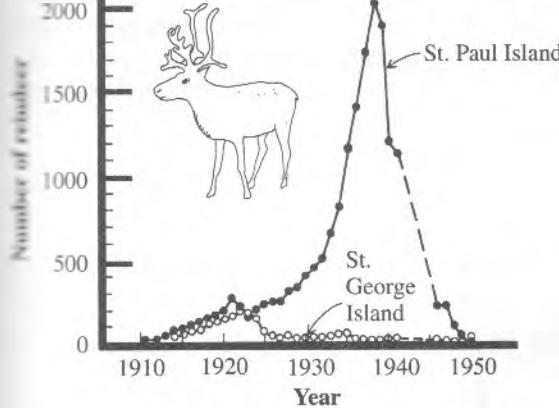
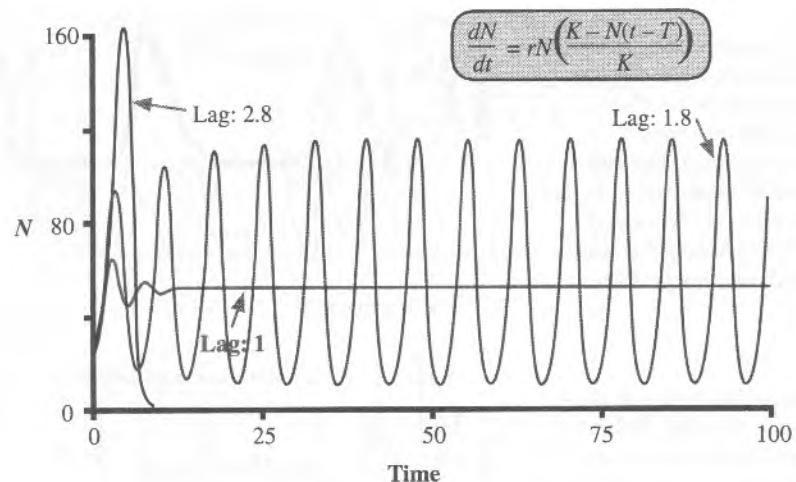


Figure 5.29

Introduced reindeer populations on two small islands in the Alaskan Pribiloff Islands. After Scheffer (1951).

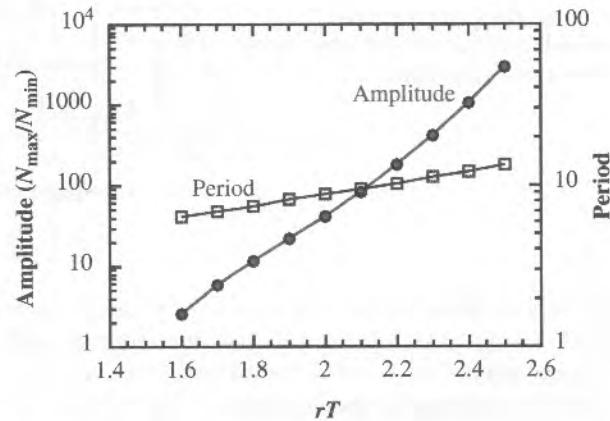


Figure 5.30

The amplitude and period of cycles for the time delayed continuous logistic as a function of the product rT , where r is the intrinsic growth rate and T is the time lag. Note the log scale on both vertical axes.

time between plant consumption and subsequent plant recruitment is large, consistent with a large lag time. Why these two reindeer populations behaved so differently, however, is not known. The model would predict that either the reindeer on St. George Island has a lower R for some reason or that the plants there had a faster recruitment rate, reducing the lag time.

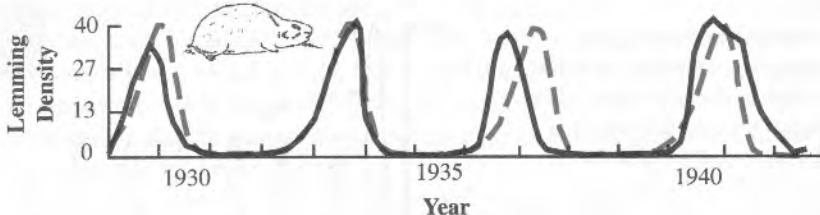
The same progression of dynamic behaviors seen in Figure 5.28 can be reproduced by keeping the lag time, T , constant and instead increasing the intrinsic growth rate, r . This is because the behavior of this model is controlled only by the product rT . When $rT < \pi/2$, the carrying capacity is stable, but when $rT > \pi/2$, it is unstable and a stable limit cycle emerges (Wangersky and Cunningham 1957). As rT increases, the amplitude of the population cycle grows, as shown in Figure 5.30. The period also grows but much more slowly. If N_{\max}/N_{\min} exceeds K , then the population will crash to extinction before completion of one full cycle.

Lemming population cycles in the arctic north are nicely described by a time delay logistic equation, as shown in Figure 5.31.

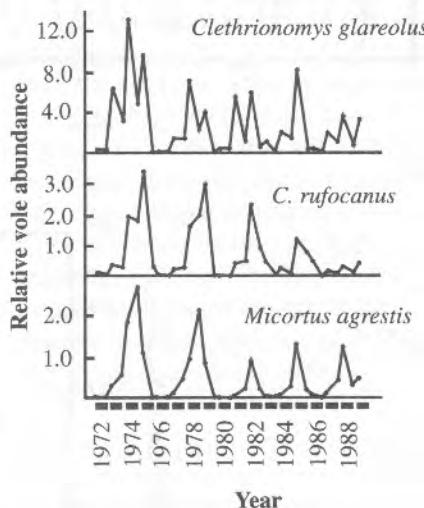
Voles are small rodents in the same family as lemmings, and they again display roughly 3-year cycles at northern latitudes (Figure 5.32). Hornfeldt (1994) found a strong correlation between their growth rate and their numbers delayed about 9 months.

Figure 5.31

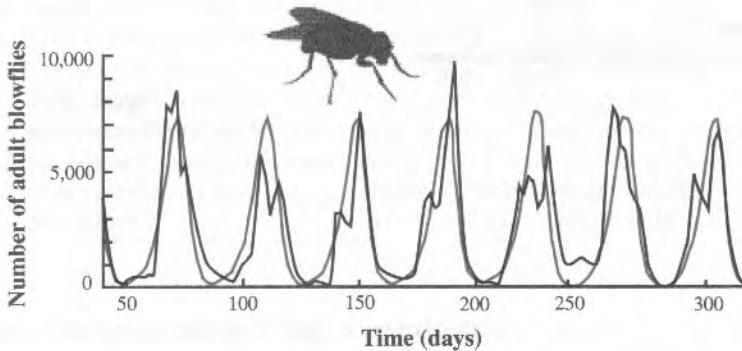
The black curve shows the density of lemmings (*Dicrostonyx groenlandicus*) in the Churchill area of northern Manitoba, Canada (number of individuals per hectare). The red dashed curve is the time delay logistic equation with $r = 3.333/\text{year}$ and $T = 0.72 \text{ year}$. After May (1981) and based on data of Shelford (1943).

**Figure 5.32**

Approximately 3-year cycles in three species of voles in Sweden. Relative vole abundance is determined by trapping success (the number of voles trapped per 100 trap nights). The black bars on the x axis show the winter months. Trapping occurred immediately before and after winter. After Hornfeldt (1994).

**Figure 5.33**

Blowfly numbers are shown as the black line. These are fit with the time delay continuous logistic equation, with $rT = 2.1$, shown as the red line. After Nicholson (1958) and May (1975).

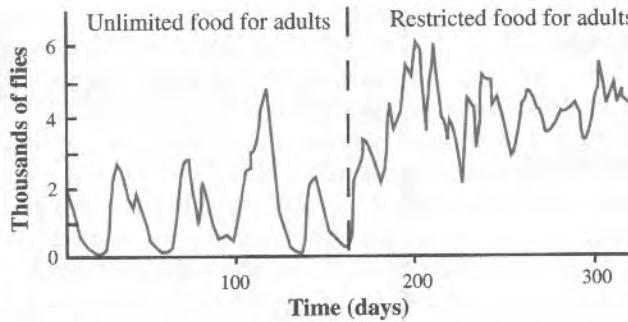


Another classic example of delayed density dependence comes from the experiments of the Australian population ecologist Nicholson, using laboratory cages of sheep blowflies, which can be a serious pest of sheep in Australia. Nicholson (1958) arranged a two-tiered cage to rear the blowfly adults separate from the eggs and larvae. In one experiment, adults were given an unlimited supply of liver, but larvae were provided with only 50 g of liver per day. In this experiment, the adult blowfly population exhibits regular fluctuations, as illustrated in Figure 5.33. Presumably the density dependence felt by the larvae—with a limited food supply—leads to a reduced survival to adulthood, but since each adult has unlimited food and can lay hundreds of eggs, the population tends to overshoot and oscillate. These dynamics can be fit quite well by the time delay logistic equation.

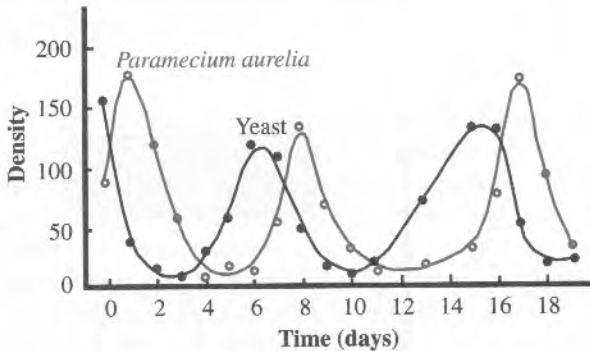
A clever test of the time delay hypothesis is to eliminate experimentally the lag time in the density dependent response by making the deleterious effects of competition at high fly densities felt more immediately by the adults. Nicholson (1958) was able to do this by restricting food to adults (only 1 g of liver per day) as well as to larvae. Figure 5.34 shows the results.

Figure 5.34

Fluctuations in laboratory populations of blowflies when the amount of food available for adults is limited to 1 g per day at the point of the dashed line (from Nicholson 1958).

**Figure 5.35**

Roughly periodic oscillations in the density of *Paramecium aurelia* (per 15 cc) and the yeast *Saccharomyces exiguum* (per 0.001 cc). Lag time is longer with *Paramecium* feeding on yeast instead of bacteria. The r of *Paramecium* is $\approx 1/\text{day}$; the r of yeast is $\approx 4/\text{day}$; the r of bacteria is $\approx 20/\text{day}$. Compare these dynamics to those in Figure 5.3.



Regular cycles were eliminated with the restriction of food for adults, and the age structure became more even. Note also the surprising increase in the average number of adults over time. For unknown reasons, less food for adults led to higher average adult numbers. This last component is unexplained by our model since the equilibrium point, K , which is in the center of the cycles does not vary with changes in r and T . Clearly, there is more going on here than the time delay logistic can describe.

Still another example is provided by Gause's work with *Paramecium aurelia*, shown previously in Figure 5.3. This logisticlike curve was produced by *Paramecium* feeding on bacteria in laboratory test tubes. The r for these *Paramecium* is about 1/day compared to a much higher r of about 20/day for their bacteria prey. If we substitute a food organism that has a slower intrinsic growth rate, closer to that of the *Paramecium* themselves, we can introduce a lag time into this interaction. The results of such an experiment conducted by Gause (1936) are shown in Figure 5.35 and confirm the theoretical expectation of cycles. In addition to the reduction in prey, r , the switch to yeast also induces a lag time because yeast excretes toxic waste products that accumulate in the medium, ultimately reducing survival and reproduction in both *Paramecium* and yeast.

The behavior of time-lagged density dependent models can become still more complicated than the simple sinelike function shown in Figure 5.28, as we now demonstrate. Another way of deriving a biological meaning for the lag time is as a crude approximation to the maturation time for young in an age-structured population. Suppose that the birth function is logistic and that young require T_1 time units to mature into adults. Then we would have

$$\frac{dN}{dt} = rN(t - T_1) \left(\frac{K - N(t - T_1)}{K} \right),$$

where N now is just the adult population of herbivores. Note that the lag time occurs in both N terms. In addition, suppose that there is also a density independent adult death rate d that is instantaneous (i.e., not lagged), which gives,

$$\frac{dN}{dt} = rN(t - T_1) \left(\frac{K - N(t - T_1)}{K} \right) - dN(t).$$

Figure 5.36
Two illustrations of the double time-lagged logistic equation. (a) The parameters yield “shoulders” on the front edge of each cycle. (b) The dynamics are much more complicated.

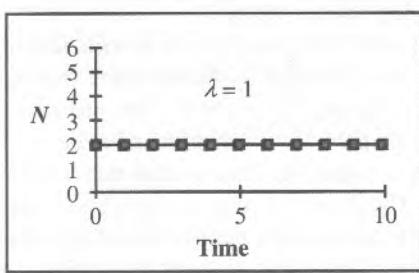
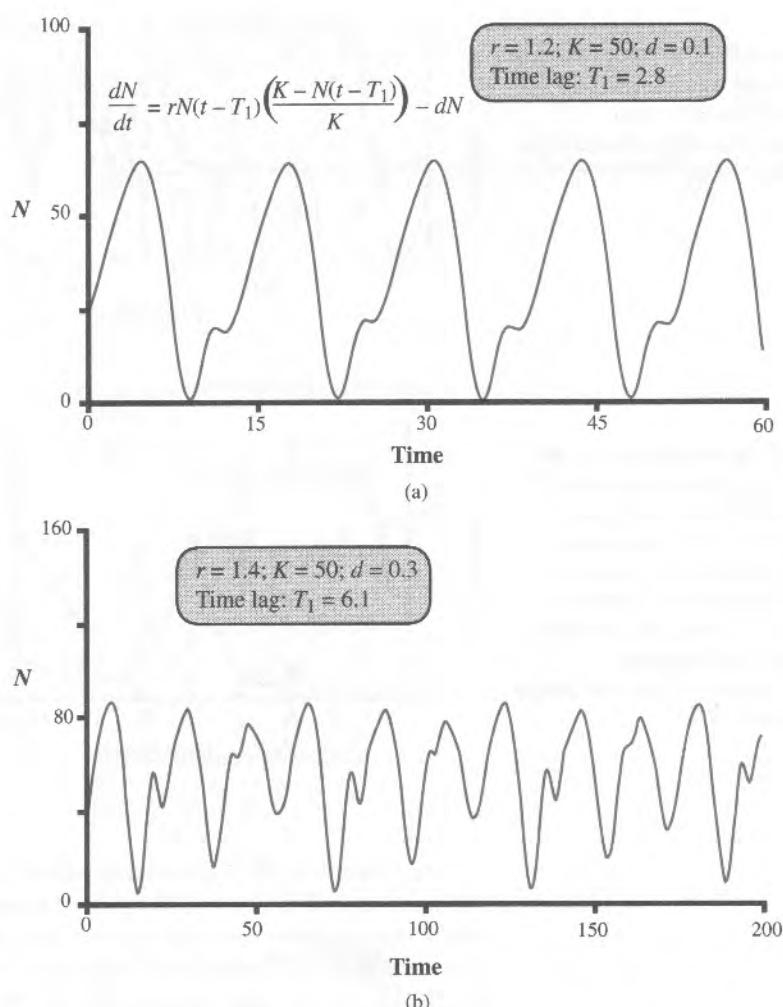


Figure 5.37

Geometric growth when $\lambda = 1$. The initial population size is 2.

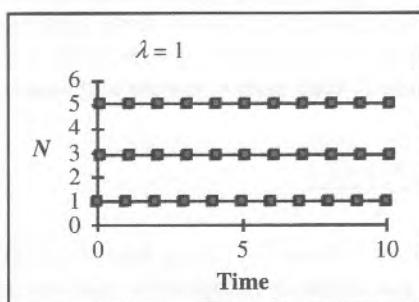


Figure 5.38

Geometric growth for three values of N_0 when $\lambda = 1$.

An example of the dynamics of this equation, the double time-lagged logistic equation is shown in Figure 5.36.

More complicated differential delay equations for density dependence like these can even produce chaotic behavior (May 1981, Nisbet 1997).

Stability Analysis of Discrete Density Dependent Population Growth

For unlimited geometric population growth, the qualitative behavior of a population falls into three categories according to the magnitude of λ (or the sign of R).

1. If $\lambda = 1.0$ ($R = 0$), then a population will remain through time at its initial size (Figure 5.37).

When $\lambda = 1.0$, there is an equilibrium, but it is determined solely by the initial conditions, N_0 . In category 1 the initial population size, N_0 , is 2.0, and the population remains at $N = 2$ over time. Whatever the value of N_0 , that is where the population remains (Figure 5.38).

2. If $\lambda > 1.0$ ($R > 0$), then the population grows geometrically to infinity (Figure 5.39).
3. If $\lambda < 1.0$ ($R < 0$), then the population declines asymptotically to 0 (Figure 5.40).

Only if $\lambda < 1.0$ can the geometric model yield an equilibrium point ($N^* = 0$) that is stable. The zero point is a stable equilibrium point since trajectories from different nonzero population sizes all converge at 0, as in Figure 5.41 for $\lambda = 0.8$. This zero equilibrium point is often called the *trivial equilibrium*, since it's not very interesting. Obviously we

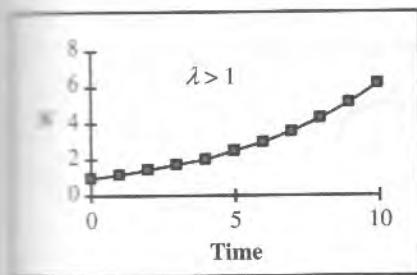


Figure 5.39
Geometric growth when $\lambda > 1$.

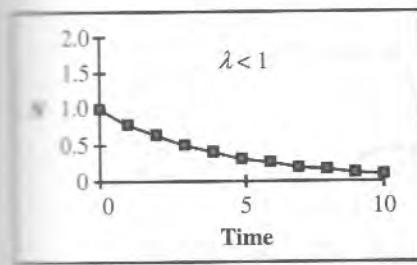


Figure 5.40
Geometric growth when $\lambda < 1$.

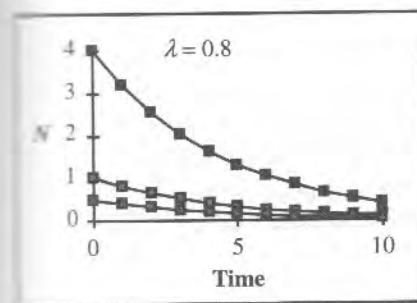


Figure 5.41
Geometric growth for three values of $\lambda < 1$.

can't get a population to exist from zero individuals. However, this concept of exponential decline toward an equilibrium will prove useful later when we evaluate the stability of nontrivial equilibrium points (i.e., $N^* \neq 0$).

For both discrete or continuous time models of density dependent growth, the population has an equilibrium carrying capacity, K , which represents a nontrivial equilibrium point, $N^* = K$. This point can be reached from a wide variety of different initial conditions and for many different R 's. However, in discrete time models for low R 's the equilibrium, K , is stable, while for higher R 's the same equilibrium point becomes unstable, becoming effectively unreachable. In this section, we develop the mathematics to evaluate the stability of an equilibrium point. We keep things as general as possible so that the conclusions apply not just to the discrete logistic equation but also to many possible density dependent population growth equations. Consequently, the details of the particular growth equation will be left unspecified; let's call it F and let F be a function of N_t . Then

$$N_{t+1} = F(N_t). \quad (5.5)$$

The function F converts (or maps) the present value of N , which is N_t , to a new value of N one time step later, N_{t+1} . The discrete logistic equation is one example of a possible $F(N_t)$ function, which involves N_t , N_t^2 and two parameters, R and K . We could easily imagine much more complex functional forms for F that might include higher-order or even transcendental terms involving N_t and many parameters. This is all permissible for what follows. However, we are not allowing F to be a function of still earlier population densities such as N_{t-1} or N_{t-2} , and so on. In this sense the population dynamics have no memory of former size but respond solely to present size and the parameters of growth.

To evaluate the stability of an equilibrium point we perform the mathematical equivalent of nudging the ball at equilibrium (see Figure 5.8). After the nudge, or perturbation, does the ball tend to move back to the original equilibrium position (the stable case), or does it tend to move even farther away in the next time step (the unstable case)? Figure 5.42 conveys this same idea in terms of population size.

A **local stability analysis** performs the mathematical equivalent of nudging the ball. Figure 5.43 shows how it operates.

Figure 5.44 shows a blowup of a portion of Figure 5.43 in the vicinity of the equilibrium point, N^* . At time t , the population density is perturbed very slightly away from N^* to a new point $N^* + n_t$. The number of individuals added to the population by this perturbation is n (or the number subtracted, if n is negative), so

$$N_t = N^* + n_t. \quad (5.6)$$

At time t the equilibrium population size, N^* , is perturbed to a slightly higher level by the addition of n individuals.

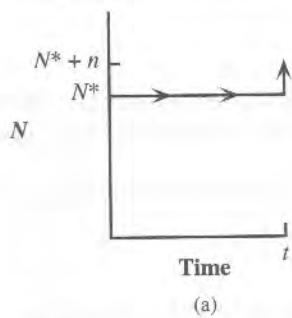
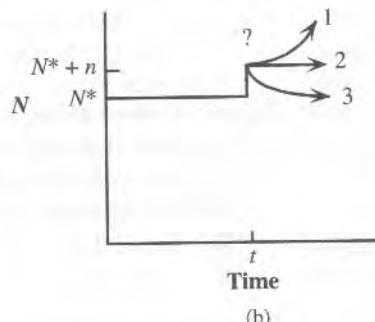


Figure 5.42

(a) The force of population growth—the nature of the density dependence—determines (b) behavior following a perturbation in numbers.

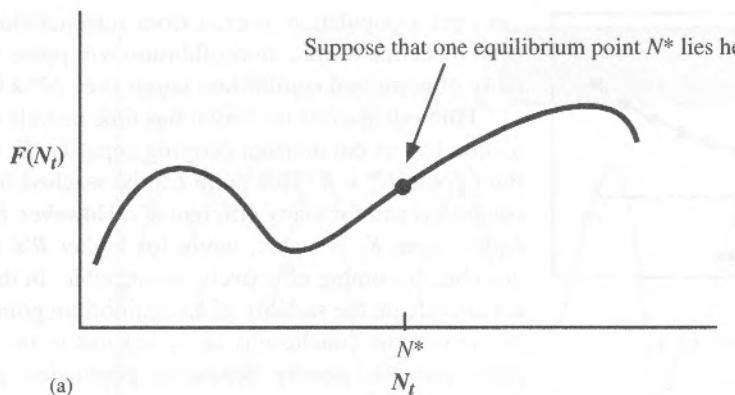
Possible dynamics following this perturbation:



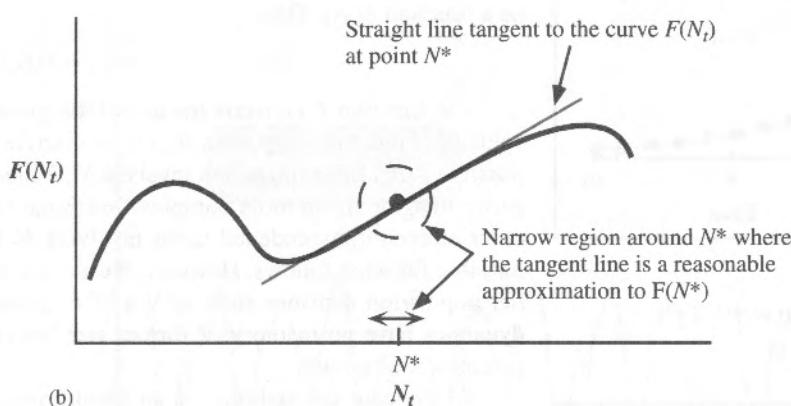
1. Numbers may tend to move farther away from N^* ; therefore N^* is locally unstable.
2. Numbers may stay exactly at new position $N^* + n$; therefore N^* is neutrally stable.
3. Numbers may tend to come back to N^* ; therefore N^* is locally stable.

Figure 5.43

A local stability analysis around the point N^* .



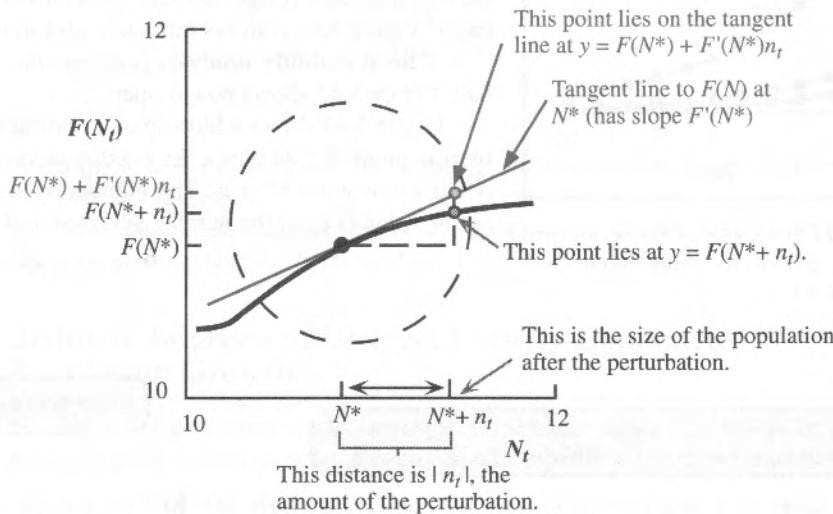
(a)



(b)

Figure 5.44

A blowup of a portion of Figure 5.43.



To proceed, we want to understand how this small difference in population size changes in subsequent time steps. Does it grow larger or smaller? This is equivalent to asking if the ball rolls back to equilibrium or runs off in Figure 5.8.

We now rearrange Eq. (5.6) to produce an expression for just the perturbation component, n_t :

$$n_t = N_t - N^*. \quad (5.7)$$

Based on our general growth equation Eq. (5.5), the population will change in the next time step as

$$N_{t+1} = F(N_t),$$

and since following the perturbation $N_t = N^* + n_t$, we have

$$N_{t+1} = F(N^* + n_t). \quad (5.8)$$

Rewriting Eq. (5.7) in terms of n_{t+1} instead of n_t yields

$$n_{t+1} = N_{t+1} - N^*. \quad (5.9)$$

Substituting Eq. (5.8) into Eq. (5.9) gives

$$n_{t+1} = F(N^* + n_t) - N^*.$$

This is the height on the y axis at $F(N^*)$ and, at equilibrium, $F(N^*) = N^*$.

This is the height on the y axis after the perturbation to $N_t = N^* + n_t$.

The difference represents the part of $y = F(N_t)$ due to the perturbation amount, n_t .

(5.10)

The motivation for Eq. (5.10) is important. We have reduced our original dynamical equation, Eq. (5.5), which specified changes in N over time, to a new related model, Eq. (5.10), that predicts changes in just the perturbation component, n , which, after all, is the component we are primarily concerned with when evaluating stability. Does n shrink or grow larger over time?

Since, as we've shown, F may be a complicated function, Eq. (5.10) may not be easy to evaluate. To make further headway we'd like to simplify the F function of Eq. (5.10). To do so we approximate F with a simple linear function. This linearization is shown graphically in Figures 5.43 and on Figure 5.44 as the tangent line to $F(N)$ at point N^* . (Don't confuse the tangent line in Figure 5.44 at N^* with the construction line $N_{t+1} = N_t$ in the Ricker diagrams—they are very different lines.)

How can we justify this simplification by which we convert a curved function F to a straight line? As you can see in Figures 5.43 and 5.44, in a narrow region around N^* the tangent line to the curve $F(N_t)$ at N^* is a reasonable approximation to the actual curve $F(N_t)$ around N^* , although it deviates wildly when n is large and thus $N^* + n$ is far from N^* . Since the perturbation n is a small quantity (just a nudge), this limitation is acceptable. As long as the region is narrow enough, any function can be approximated by a straight line. For wider regions, however, we could find better approximating functions than a straight line. A simple way is to decompose $F(N_t)$ into a polynomial. The more higher-order terms included in the polynomial, the greater is the similarity to the $F(N_t)$ function being approximated. A straight line (the tangent line) is this polynomial with all the terms except the first two (the slope and the y intercept) lopped off.

What are these additional terms? We want the polynomial to follow all the bends and curves of the real function F . Consequently, these additional terms are successive derivatives of F evaluated at the equilibrium point in question, in our case $F(N_t)$ evaluated at N^* . The inclusion of more terms corresponding to these successively higher derivatives would, in the limit (as the number of terms grows very large), match $F(N_t)$ everywhere, not just narrowly around N^* . (This assumes that $F(N_t)$ is a smooth continuous function so that these derivatives exist and that the derivatives are continuous.) The approximation of a function by a polynomial, which is the sum of terms containing successively higher derivatives of the original function, is called a **Taylor's expansion**. The general formula for a Taylor's expansion evaluated around a point x^* is

$$F(x) \approx F(x^*) + \frac{F'(x^*)(x - x^*)}{1!} + \frac{F''(x^*)(x - x^*)^2}{2!} + \frac{F'''(x^*)(x - x^*)^3}{3!} + \dots, \quad (5.11)$$

where F' means the first derivative of F with respect to x ; F'' indicates the second derivative, and so on. Note that, for small perturbations where $x - x^*$ is much less than 1.0, $(x - x^*)^2$ is smaller than $(x - x^*)$ and $(x - x^*)^3$ is smaller yet. In other words, the higher-order terms of $(x - x^*)$ add successively smaller corrections; this provides the justification for ignoring them if the perturbation is small.

Now let's return to the simplest case where all the higher-order terms in Eq. (5.11) are ignored. Using Eq. (5.11), we write Eq. (5.10) as

$$\begin{aligned} n_{t+1} &= F(N^* + n_t) - N^* \\ &\approx F(N^*) + F'(N^*)n_t - N^*, \end{aligned} \quad (5.12)$$

and, since by definition for an equilibrium, $F(N^*) = N^*$, Eq. (5.12) becomes

$$n_{t+1} \approx F'(N^*)n_t. \quad (5.13)$$

The value of $F'(N^*)$ is simply the slope of the tangent line in Figure 5.44 at the equilibrium point N^* . If we assume that n_t is positive (i.e., we did an addition perturbation), then according to Eq. (5.13) the magnitude of the distance from equilibrium after one time step (i.e., n_{t+1}) will be smaller at $t + 1$ than it was at time t (i.e., n_t), as long as the slope $F'(N^*)$ is less than 1. But since $F'(N^*)$ is simply the slope of the tangent line, the condition for the stability of the equilibrium point reduces to a condition on the slope of $F(N)$ at point N^* ; it must be less than 1. On the other hand, if this slope is greater than 1, then the deviation will increase at $t + 1$ (i.e., now $n_{t+1} > n_t$). More generally, since the perturbations may be either additions (n_t is positive) or subtractions (n_t is negative), we can write the condition for stability, using the absolute value of the slope, as

$$|F'(N^*)| < 1. \quad (5.14)$$

Equation (5.14) is the central result: In words: **For a single species density dependent equilibrium point to be stable, the line tangent to $F(N)$ at this equilibrium point must have a slope whose absolute value is less than 1.**

Now you see why increases in R destabilized the equilibrium K in the discrete logistic equation. Increases in R increased the steepness of the parabola, $F(N_t)$, and this steepened the slope (made it more negative than -1) at point $N^* = K$. In Box 5.2, we solve for the value of R that just destabilizes $N^* = K$. In Box 5.3 we perform a stability analysis for an equilibrium point of a continuous time differential equation.

Because of the assumption of linearizing the dynamics, which is only a good approximation to the real population dynamics in a narrow vicinity around an equilibrium point, this method for evaluating stability is strictly valid only for relatively small

Box 5.2 Solving for the Value of R That Just Destabilizes the Equilibrium Point

The discrete logistic equation is

$$\begin{aligned} N_{t+1} &= F(N_t) = N_t \left(1 + R \left(1 - \frac{N_t}{K} \right) \right) \\ &= N_t + RN_t - \frac{RN_t^2}{K}. \end{aligned}$$

The slope of this equation at K is the first derivative with respect to N_t ,

$$F'(N_t) = 1 + R - \left(\frac{2RN_t}{K} \right).$$

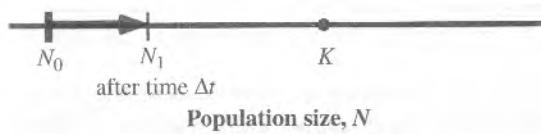
We evaluate this derivative at point $N_t = K$:

$$1 + R - \left(\frac{2RK}{K} \right) = 1 - R.$$

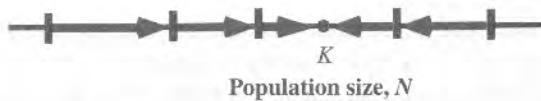
For stability of K this derivative must have absolute value < 1 , and since R is a positive number, $|1 - R| < 1$, means that $R < 2$ is necessary for stability of the equilibrium point K .

Box 5.3 Stability Analysis for the Continuous Logistic Equation

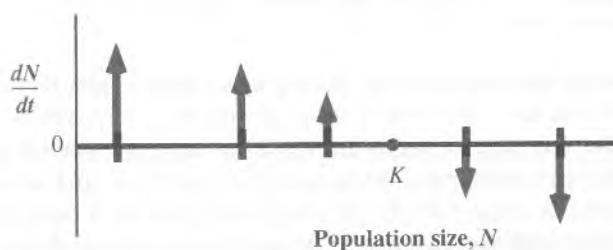
In Box 5.2 we performed a local stability analysis on an equilibrium point of a difference equation in one variable: $N_{t+1} = F(N_t)$. Now we repeat this process but consider a differential equation $dN/dt = f(N)$. We have already shown that, for the continuous time logistic equation, the equilibrium point is always stable, regardless of the value of r , but here we bring this observation into line with the analytical methods that we just developed for a difference equation. Again let's consider a situation where $N(t)$ changes over time and eventually reaches a stable equilibrium point K . Assume that we begin at some initial population size N_0 , and, after an elapsed time period Δt , we again measure the population size to produce the red arrow shown in the following diagram.



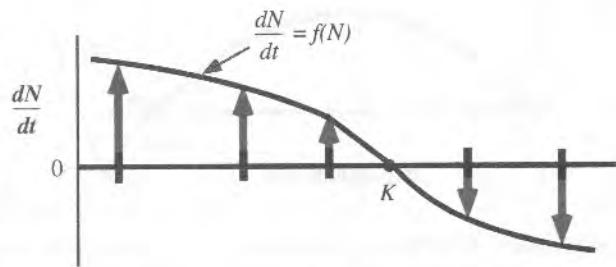
If N starts far below K , then its initial growth rate will be rapid; if N starts very close to K , then its growth rate will be slower, or



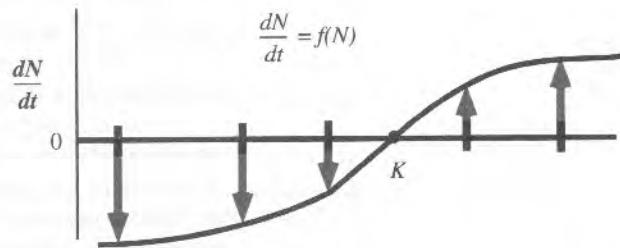
The tail of each red vector is at the beginning N , and the tip of arrowhead is the population size after some one time period. Thus the length of each vector equals the magnitude of growth from point N_0 , and the direction of the vector indicates the sign of that growth rate. Now by flipping these vectors up on their tails, and assuming that Δt is a fairly small time interval, we have a direct measure of the magnitude and sign of dN/dt at each of the starting population sizes:



By repeating this process from many different additional starting points, we could determine the rate of growth from other N and, by interpolation, fill in the whole $f(N)$ curve:



Thus the $f(N)$ function can be experimentally derived by such a procedure. The preceding diagram clearly shows that small perturbations in N below the equilibrium point K (e.g., $K - n$, where n is the perturbation amount) lead to increases in population size (upward pointing arrows). Similarly, small perturbations in N above K ($K + n$) lead to negative dN/dt and thus decreases in population size. Thus the equilibrium population size, K , tends to be restored, implying that K is a locally stable equilibrium point. Contrast this situation with the following:



Now, K plus a small perturbation n , leads to a positive growth rate and therefore to an increasing population size; the population size escapes from K after the perturbation. In this diagram K is an unstable equilibrium point. Comparing the last two figures you can see that the condition for stability is simply that the slope of $f(N)$ evaluated at the equilibrium point, K , be negative. For the logistic equation this yields

$$f(N) = \frac{dN}{dt} = rN \left(\frac{K-N}{K} \right) = rN - \frac{rN^2}{K}$$

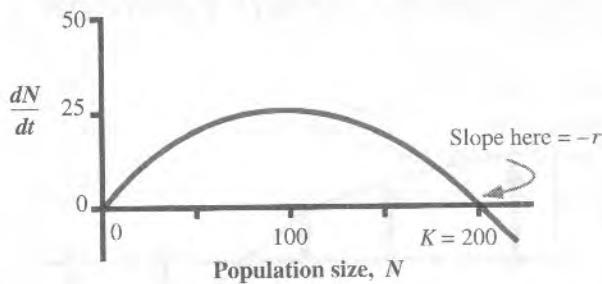
and

$$\text{Slope of } f(N) = \frac{\partial f(N)}{\partial N} = r - \frac{2rN}{K}.$$

At $N = K$,

$$\text{Slope} = r - \frac{2rK}{K} = r - 2r = -r,$$

as illustrated in the following diagram.

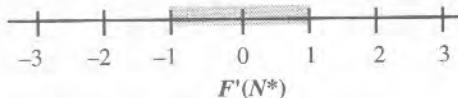


We conclude that the equilibrium point $N^* = K$ in the continuous logistic equation is stable as long as r is positive. From this same argument you can see that the equilibrium point $N^* = 0$ is not locally stable since the slope of $f(N)$ at $N = 0$ is positive.

In summary, for stability we have (a) for the discrete logistic equation, $| \text{slope at } N^* | < 1$; and (b) for the continuous logistic equation, slope at equilibrium point $N^* < 0$.

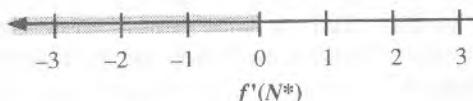
Discrete Logistic Equation

N^* will be locally stable when the slope of $F(N)$ at N^* falls in this region:



Continuous Logistic Equation

N^* will be locally stable when the slope of $f(N)$ at N^* falls in this region:



perturbations, n , from equilibrium. Consequently, this method is referred to as an evaluation of **local stability**. An equilibrium point that is locally stable (i.e., stable to small perturbations) might still be unstable to much larger perturbations. A metaphoric example of this is illustrated Figure 5.45. Local stability does not necessarily imply **global stability**, although if an equilibrium point is globally stable it surely must be locally stable. We explore an example of a modified density dependent model with two locally stable equilibria in the next section.

Also, although we have developed a method to evaluate the stability or instability of an equilibrium point, we have *not* developed an analytical method to determine the dynamics of the population if that equilibrium point is unstable. Will the population decline to extinction? Will it display a limit cycle? If so, what period and amplitude will the cycle have? Will chaos emerge? While mathematical methods do exist to determine the presence or absence of these more complicated dynamical behaviors for one-, two-, and sometimes even three-species systems, they are limited and general analytical predictions are much more difficult and often impossible to make for larger numbers of interacting species. In practice, then, we are often left to simulate the dynamics on a computer.

Modifications to the Logistic Equation

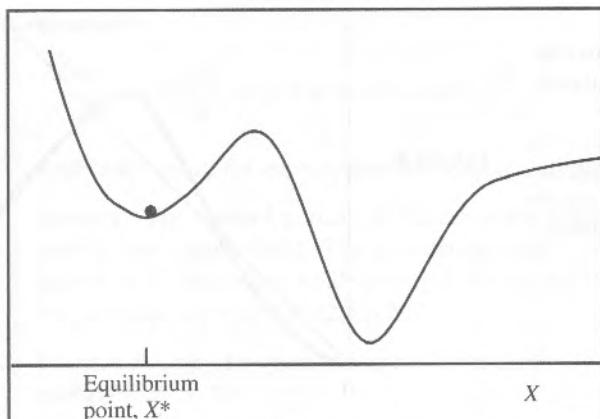
An Allee Effect

The logistic equations are not the only way that density dependence might be manifested. The techniques that you have just learned are applicable to other possible density dependent functions. In particular, the *linear* decline in per capita growth rate with increasing density is not biologically general. Most species do not show such a linear decline (Pomerantz et al. 1980, Fowler 1988). In some cases there is a continuous decline, but it is curved, not straight (see Figure 5.5). There is a simple fix to this problem: an additional parameter may be added to the logistic model to produce the so-called theta (θ) model. By adjusting the value of θ , you can create convex and concave per capita growth curves of infinite variety. This model is left as an exercise at the end of this chapter (Problem 3).

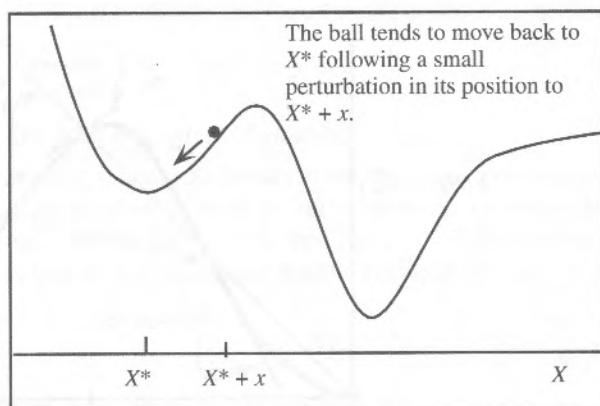
More fundamentally, some animal and plant species do not show a monotonic decline in per capita growth with increasing density. Instead per capita growth rates may *increase* with population density at low population levels and decline only at much

Figure 5.45

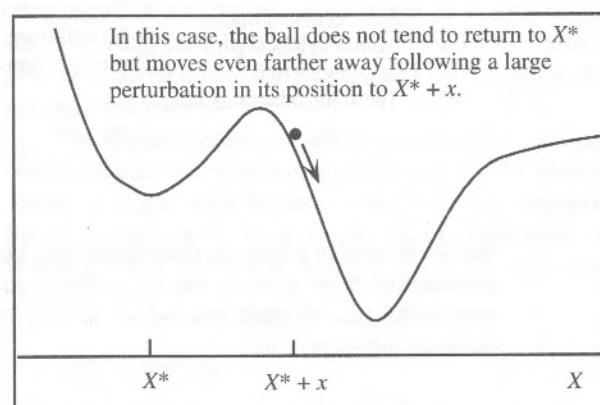
Gravity metaphors for local and global stability. (a) The equilibrium point X^* is (b) locally stable but (c) not globally stable.



(a)



(b)

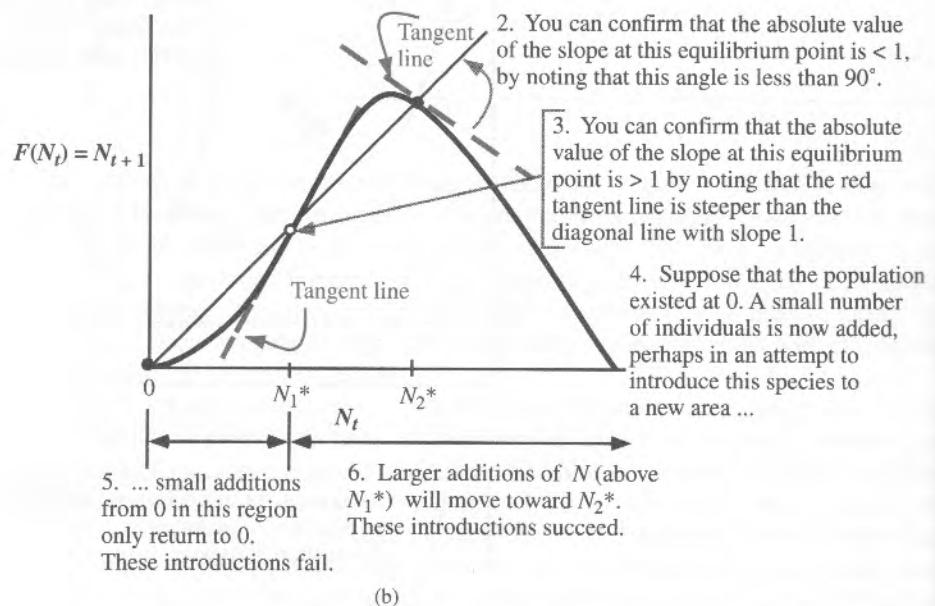
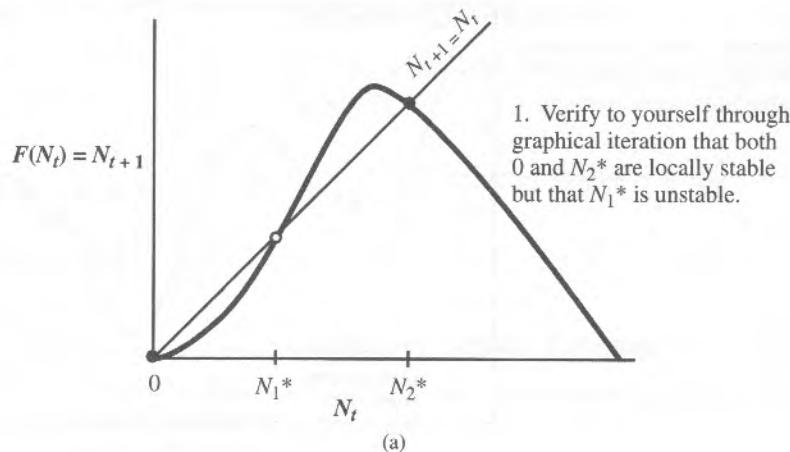


(c)

higher population levels. One biological reason for the ascending part of the curve at low density is that species may require conspecifics for protection from predators or from climatic extremes; other species may forage more effectively in groups than alone. In sexual species, individuals may have a difficult time finding mates at low densities, so mating rates increase with population density. The result of these types of effects is that positive per capita growth rates might not even be possible until the population reaches some threshold size and per capita growth rates then increase with population density—at least up to a point. Only when population densities are far above this size might the negative effects of crowding become evident. This population response is often referred to as an **Allee effect** (Allee 1931). Figure 5.46 incorporates these

Figure 5.46

An Allee effect added to the discrete logistic equation. (a) This population displays an **Allee effect** at low densities. Note that three equilibrium points exist, at $N = 0$, N_1^* , and N_2^* . (b) Conclusion: 0 and N_2^* are both locally stable, but neither is globally stable.



considerations in a discrete time model and explores the stability consequences. This is accomplished by skewing the $N_{t+1} = F(N_t)$ curve so that, for low levels of N_t , N_{t+1} is even lower than N_t (and thus below the diagonal line). The population cannot begin to increase unless $N_t > N_1^*$.

Problem: Consider a modified logistic differential equation that incorporates an Allee effect in the following way. The *per capita* growth rate begins at $-r$ when $N = 0$ and then rises linearly to a value of $+r$ at the point where N equals M . From $N = M$ onward, however, the per capita growth rate declines with a slope equal but opposite in sign to the first part of the curve. Below M , increases in density result in higher individual birth rates, while above M , crowding results in progressively lower birth rates with N . Figure 5.47 shows this curve for the values of $r = 0.5$ and $M = 15$.

Express these per capita growths in differential equations.

Answer:

$$\frac{dN}{N dt} = -r + \frac{2rN}{M} \text{ (for } 0 \leq N < M) \text{ and } \frac{dN}{N dt} = r - \frac{2r(N-M)}{M} \text{ (for } N \geq M).$$

Problem: Solve for the carrying capacity, K , in Figure 5.47.

Answer: The upward portion of the curve has slope $= 2r/M$, and the downward portion has slope $-2r/M$. The population stops growing when the per capita growth is 0, which can be determined by solving $0 = 0.5 - (2)(0.5)(N - 15)/15$. The solution for N is $N = 22.5 = K$.

Problem: Using the parameters $r = 0.5$ and $M = 15$, plot the population growth curve dN/dt .

Answer: We multiply the per capita equations by N to get the curve plotted in Figure 5.48.

The Ricker Logistic Equation

Another unrealistic feature of the discrete logistic equation is that $N(t+1)$ can become negative when $N_t \gg K$. In our simulations, we stopped this from happening by enforcing a rule: if $N(t+1) < 0$, then $N(t+1) = 0$. A different and more continuous approach is followed in the Ricker logistic equation (Ricker 1952):

$$N_{t+1} = N_t \exp\left(R\left(1 - \frac{N_t}{K}\right)\right). \quad (5.15)$$

Note that, when $N_t = K$, the exponent in parentheses becomes 0 and thus $N_{t+1} = N_t$, yielding an equilibrium point at $N^* = K$, as before for the discrete logistic equation. For $N_t > K$, the exponent is negative, but e raised to a negative number is still positive. As N_t approaches infinity, N_{t+1} approaches zero. Two examples of Ricker curves with different R 's and sample trajectories are shown in Figure 5.49. Figure 5.49(a) shows the case of a stable equilibrium point; in Figure 5.49(b) R is larger, and the dynamics are complex cycles.

The Ricker logistic equation has dynamics that go through the same sequence of behaviors that we have already explored for the discrete logistic equation. The exact values of R that mark the transitions from one dynamical phase to another are similar but not always exact. For example, the onset of chaos with the Ricker logistic equation is at $R > 2.692$, rather than at $R > 2.570$ as for the logistic equation.

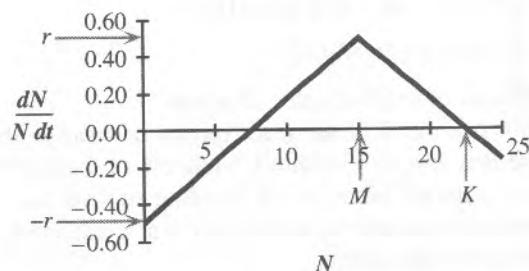


Figure 5.47

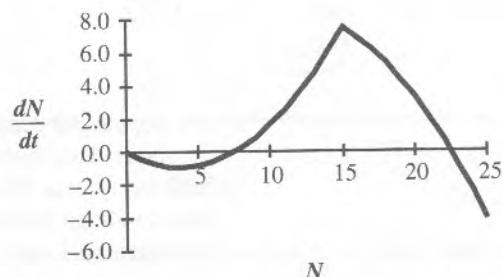


Figure 5.48

Population growth rate as a function of population size for the per capita growth shown in Figure 5.47.

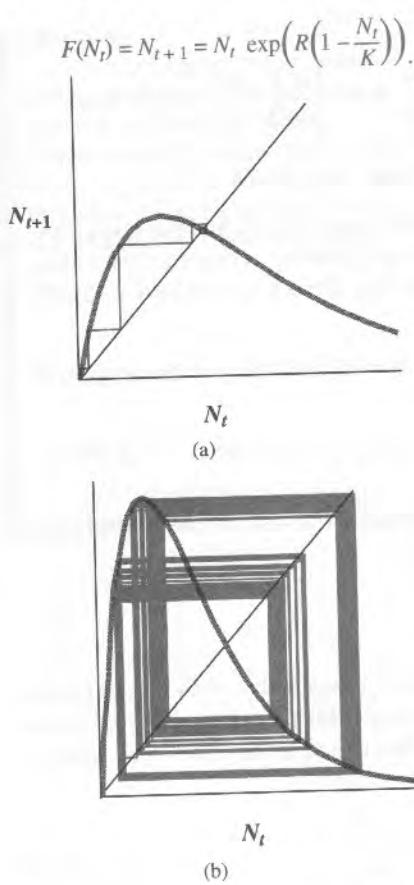


Figure 5.49
Ricker diagrams based on the Ricker equation: (a) $R = 1.5$ and (b) $R = 2.7$.

Exercise: For the Ricker logistic equation, at what value of R will the equilibrium point at K become unstable?

Solution: From the stability analysis of the previous section, we know that this will occur when the absolute value of the slope of $F(K) > 1.0$. For the Ricker logistic equation,

$$F(N_t) = N_{t+1} = N_t \exp\left(R\left(1 - \frac{N_t}{K}\right)\right).$$

We take the first derivative of $F(N)$ to find the slope of $F(N)$:

$$\begin{aligned} F' &= N_t \exp\left(R\left(1 - \frac{N_t}{K}\right)\right) \left(\frac{-R}{K}\right) + \exp\left(R\left(1 - \frac{N_t}{K}\right)\right) \\ &= \exp\left(R\left(1 - \frac{N_t}{K}\right)\right) \left(1 - \frac{RN_t}{K}\right). \end{aligned}$$

At point $N_t = K$, this reduces to

$$F' = 1 - R.$$

The slope F' will become steeper than -1 when $R > 2$. This result turns out to be identical to that for the discrete logistic equation.

Density Dependence in Stage-Structured Models. Annual bluegrass, *Poa annua*, is a widespread weed and a good colonizer of open habitats. Figure 5.50(a) presents the fecundity (seed production) rates, and Figure 5.50(b) presents the survival rates for different age groups over a typical year. Law (1975) found that some of these vital rates were density dependent. He divided the life history into five stages (seeds, seedlings, young adults, A_1 , medium adults, A_2 , and old adults, A_3 , with the transitions illustrated in Figure 5.51. Further, Law found that seedling survival rates, s_{seedling} , and seed production rates of adults B_i decreased with increasing density, N . Thus he was able to form the following transition matrix:

$$\begin{bmatrix} \text{Seed} \\ \text{Seedlings} \\ \text{Adults 1} \\ \text{Adults 2} \\ \text{Adults 3} \end{bmatrix}_{t+1} = \begin{bmatrix} 0.2 & 0 & B_1(N) & B_2(N) & B_3(N) \\ 0.05 & 0 & 0 & 0 & 0 \\ 0 & s_{\text{seedling}}(N) & 0 & 0 & 0 \\ 0 & 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0 & 0.75 & 0 \end{bmatrix} \begin{bmatrix} \text{Seeds} \\ \text{Seedlings} \\ \text{Adults 1} \\ \text{Adults 2} \\ \text{Adults 3} \end{bmatrix}_t, \quad (5.16)$$

where the density dependent terms, determined from his field data, were

$$s_{\text{seedling}} = 1 - 0.25 \exp(-0.0005N)$$

$$B_1(N) = B_3(N) = 100 \exp(-0.0001N)$$

$$B_2(N) = 200 \exp(-0.0001N)$$

and population density, N , is the sum of seedlings plus all adults.

Note that, in the transition matrix, 20% of the seeds remain dormant in the seed bank every year (the term in the first row, first column), while 5% of them germinate into seedlings (second row, first column). When $N = 0$, seedling survival rate is at a maximum of $1 - 0.25 = 0.75$ (since $e^0 = 1$), and adult fecundity is at a maximum of 100 in young and old adults and 200 in medium adults.

By iterating the transition matrix, we can trace the expected course of population growth from year to year, as depicted in Figure 5.52. This simulation is based on the density dependence as measured in the field.

The population initially fluctuates but eventually reaches an asymptotic density. On the other hand, as we demonstrated earlier with density dependence in discrete time,

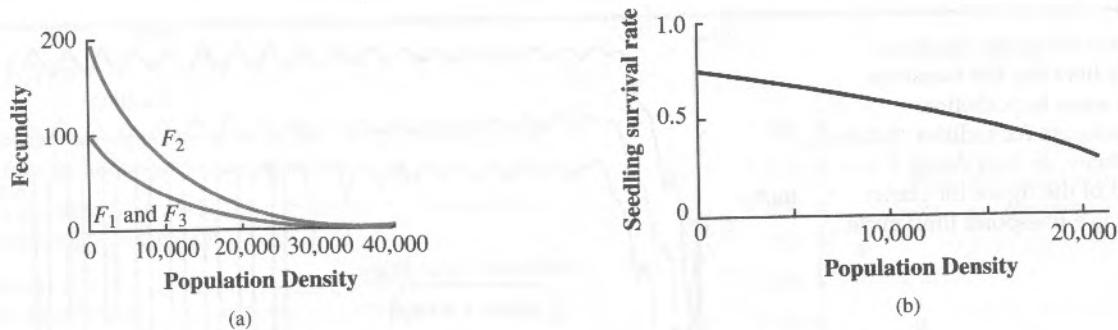


Figure 5.50
Density dependence in (a) adult seed production and (b) seedling survival in *Poa annua* (from Law 1975).

Figure 5.51
Stage transitions in the annual grass,
Poa annua.

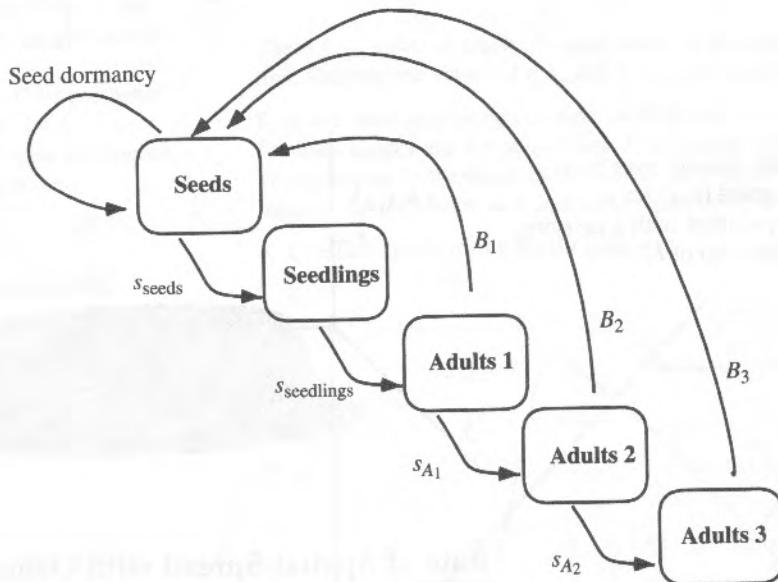
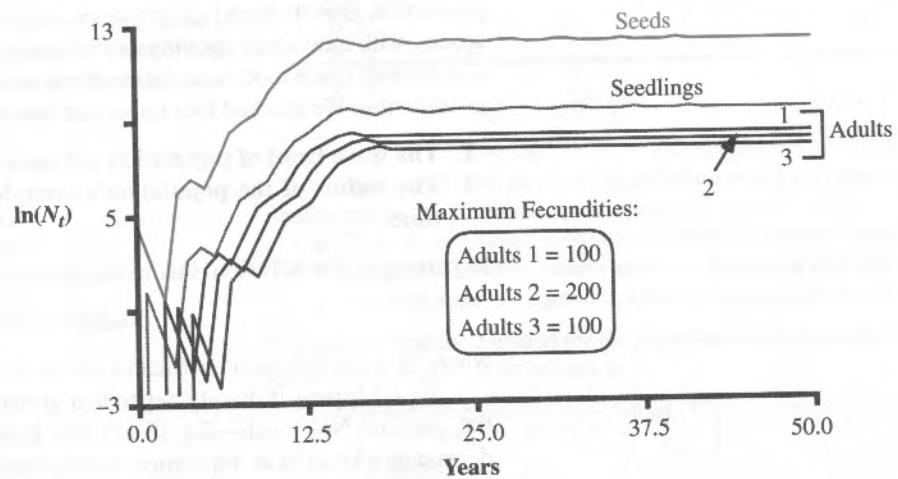


Figure 5.52
Time series for the grass *Poa annua*,
produced by iterating the transition
matrix of Eq. (5.16).

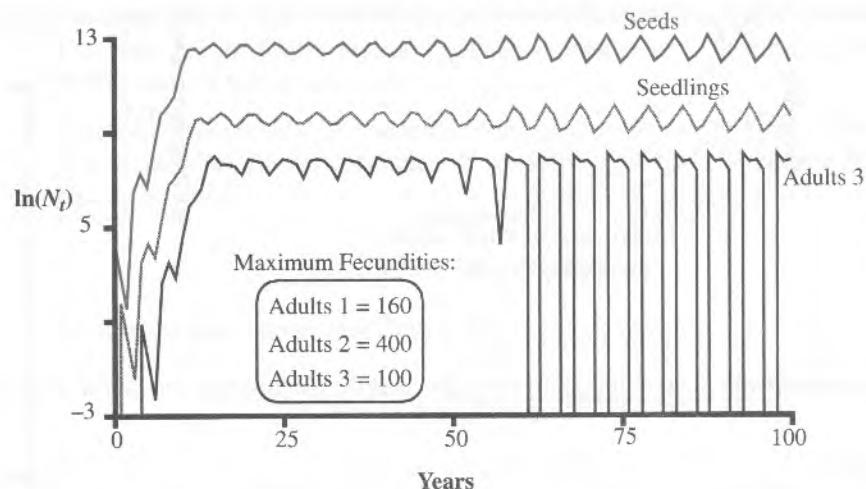


increases in the age-specific fecundities can produce unstable equilibrium points, oscillations, and chaos. Figure 5.53 shows a time series based on some elevated seed production rates. This simulation examines the effect of increasing the maximum seed production rates.

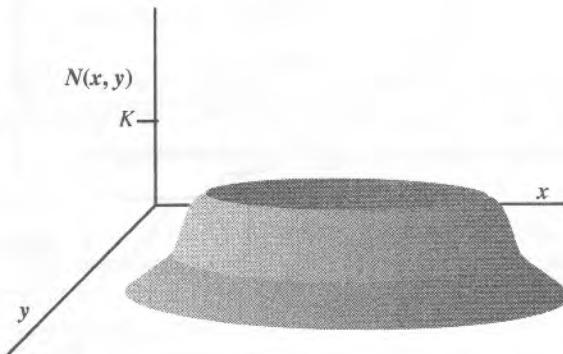
Each age group in this population settles into a five-point limit cycle during which each of the adult age classes crashes to zero at each cycle. Further increases in maximum fecundity can lead to even more erratic population behavior.

Figure 5.53

Time series for the grass *Poa annua*, produced by iterating the transition matrix with some hypothetical elevated maximum fecundities. Adults 1 and 2 fluctuate, as does Adult 3, but were left out of the figure for clarity. This pattern is a five-point limit cycle.

**Figure 5.54**

The population density over two-dimensional space (x, y) for a spreading population with a carrying capacity (in density) of K .



Rate of Spatial Spread with Density Dependent Growth

In Chapter 2, we added random walk movements of individuals across space to the local population growth model of geometric growth. We imagined a gridded space (discrete space), with individuals moving each time step only to adjacent cells. This discrete time and discrete space model can be modified to continuous time and continuous space, that is, diffusion. We reached two important results earlier.

1. The wave front of population advance quickly reaches a constant velocity.
2. The radius of the population's occupied area grows with the square root of time.

In particular, for diffusion, this radius increases at the rate

$$\text{Radius} = 2(\ln(\lambda)D)^{0.5}, \quad (5.17)$$

where D is the diffusion coefficient and $\ln \lambda = r$ is the rate of exponential growth.

What happens if density dependent growth occurs in each cell instead of exponential growth? Not much—Eq. (5.17) still holds, but only approximately. The density dependence kicks in as population density builds up in a local area. But, by the time that happens, some individuals have already immigrated to adjacent vacant areas. Consequently, it is primarily the rate of growth, λ , not K , that dominates the rate of spatial spread. The spreading population looks like that shown in Figure 5.54, where the rate of advance in each direction is given by Eq. (5.17).

However, if the density dependence had an Allee effect, then on the leading edge of the front, where the population is at low density, the individuals there would be at a disadvantage. This would retard the rate of population spread and lead to a “clumpiness” of populations at the edge of the wave of population advance.

PROBLEMS

1. Prove mathematically that the peak of the dN/dt versus N plot occurs at $K/2$ for the continuous logistic equation.

2. Under each example on the left enter the number(s) of the most appropriate answer(s) from the right.

a. Example(s) of a neutrally stable equilibrium point ____.

b. Example(s) of a locally and globally stable equilibrium point ____.

c. Example(s) of an unstable equilibrium point ____.

d. System(s) that lacks any stable equilibrium points ____.

e. Example(s) of a smooth limit cycle ____.

f. System(s) that lacks any stable asymptotic behavior (points or cycles) ____.

3. Consider the three-parameter density dependent model,

$$\frac{dN}{dt} = rN \left(1 - \left(\frac{N}{K} \right)^\theta \right).$$

It is called the "theta logistic" equation because of the introduction of the new parameter, θ . For $\theta = 0.5, 1$, and 2 draw the following plots (set $r = 1$ and $K = 1$).

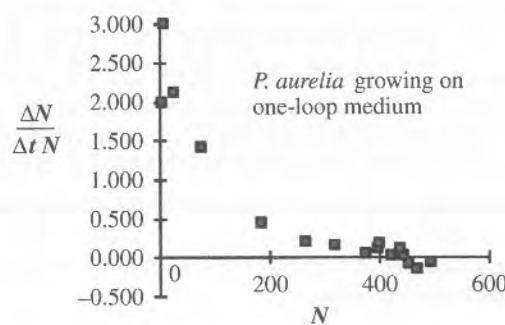
a. dN/dt versus N

b. $dN/N dt$ versus N

c. Under what biological circumstances might θ be less than 1? Greater than 1?

4. In one set of Gause's (1934) experiments with *Paramecium* growing in his "one-loop medium," he produced the following results, which we have plotted in terms of per capita growth as a function of population size. The relationship deviates substantially from the linear relationship expected for the discrete logistic equation.

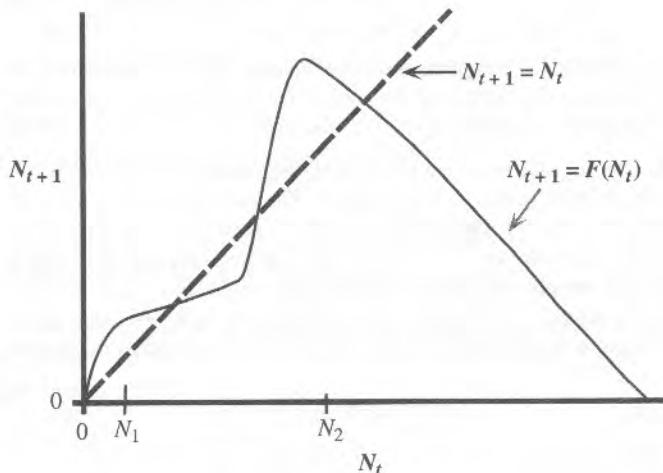
Day	N	Per capita growth rate
0	2	2.000
1	6	3.000
2	24	2.125
3	75	1.427
4	182	0.451
5	264	0.205
6	318	0.173
7	373	0.062
8	396	0.119
9	443	0.025
10	454	-0.075
11	420	0.043
12	438	0.123
13	492	-0.049
14	468	-0.145
15	400	0.180
16	472	



These data, however, can be fit quite nicely by the theta logistic equation. Estimate the values of r , K , and θ that provide reasonable fits.

5. In the discrete logistic equation, as R increases the growth curve becomes steeper and the equilibrium K eventually becomes unstable. What happens to the shape of the growth curve and the dynamic stability of the population as K instead of r gets larger and larger?

6. Consider the following Ricker diagram.



a. Draw small dots on all the equilibrium points and label each equilibrium point with a letter (a , b , etc.).

b. For each equilibrium point, state whether it is stable or unstable.

c. Trace the population growth trajectory, beginning at density N_1 .

d. Trace the population growth trajectory, beginning at density N_2 .

7. A discrete logistic equation for the population growth rate of some hypothetical lizards can be written as

$$N_{t+1} = (R+1)N_t - \left(\frac{RN_t^2}{100} \right).$$

a. What is the equilibrium population size? _____

b. If $R = 2.7$, is this equilibrium stable? _____

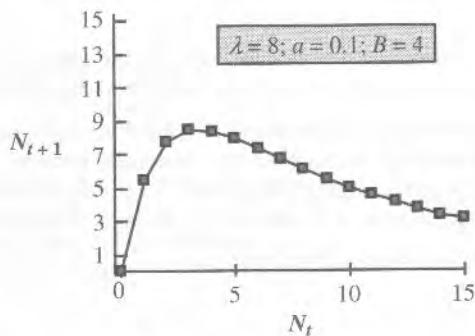
c. If $R = 1.9$, is this equilibrium stable? _____

8. For the discrete time logistic equation, what two different values of population size N_t at time t will produce exactly the value 0 for the population size one time step later? Let the growth rate parameter $R = 1$.

9. A species grows according to the discrete time logistic equation. A plot of N_{t+1}/N_t versus N_t for several populations of this species at different densities N_t reveals a linear relationship described by $N_{t+1}/N_t = 3.04 - 0.01N_t$. What are the values of R and K for this species? Is the equilibrium point, K , stable?

10. Another species grows according to the Ricker logistic equation. A plot of N_{t+1}/N_t versus N_t for several populations of this species at different densities N_t reveals a linear relationship described by $\ln(N_{t+1}/N_t) = 1 - 0.01N_t$. What are the values of R and K for this species?

11. Another discrete density dependent model that is sometimes applied to insect populations is $F(N_t) = \lambda N_t(1 + aN_t)^{-B}$, with three parameters, λ , a , and B . A graph of this function for one set of parameter values is the following.



Is $N = 0$ a stable equilibrium for this model? What is the solution, in terms of the parameters of the model, for the nontrivial equilibrium point N^* ?

12. The bobcat population in Wyoming was studied by Crowe (1975). Bobcats reach sexual maturity at age 1. The average litter size for adult females is $B = 2.8$ kittens/litter and the sex ratio is 1:1. All females breed once each year. The survival rate of kittens to year 1 is s_0 and is strongly density dependent. The survival rate of adults, which includes natural mortality and deaths due to trapping, is $s_a = 0.67$. This information can be combined into a Leslie matrix (census taken just before reproduction):

$$\mathbf{L} = \begin{bmatrix} s_0 B & s_0 B \\ s_1 & s_1 \end{bmatrix}$$

Find s_0 so that the population is stationary (i.e., $\lambda = 1.0$). If trapping is curtailed, adult survival jumps to 0.98. Now what s_0 is necessary for the population to be stationary?

13. A population grows according the equation

$$\frac{dN}{dt} = rN(t-T)\left(\frac{K-N(t-T)}{K}\right),$$

where $T = 5$ years, $r = 1/\text{year}$, and $K = 1000$. In 1990 the population size N is 30. What will be the population size 2000 years later?

14. Krebs (1986) reported the following data on the yearly discrete growth rate ($\lambda_t = N_{t+1}/N_t$) of snowshoe hare populations at different natural densities in the Yukon.

No. per acre	N_{t+1}/N_t	No. per acre	N_{t+1}/N_t
10	0.1	370	0.25
10	0.6	290	0.9
3	2.5	280	0.2
2	4	255	1.2
6	3.8	70	2.8

No. per acre	N_{t+1}/N_t	No. per acre	N_{t+1}/N_t
2	6.2	109	1.1
2	6.1	110	0.1
7	8.2	115	0.3
8	8.9	120	0.1
15	0.2	150	1.8
30	1.3	148	2.1
40	1.5	200	3.1
30	3.1	220	0.7
60	0.2	250	0.5
60	2.9		

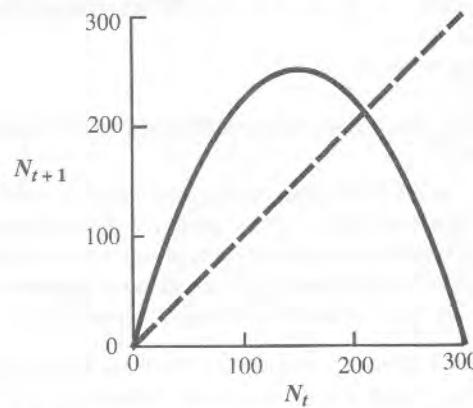
We wish to determine if these data are consistent with a population that overshoots its carrying capacity, cycles, or experiences chaos—or, alternatively, a population that should have a stable equilibrium point. Make a determination by fitting these data to the discrete logistic equation.

Answer:

We plot these yearly growth rates on the y axis against population density and determine the regression line $\lambda = 3.34 - 0.011N$ (correlation coefficient, $r = 0.476$). Based on the form of the discrete logistic equation we may now make some parameter estimates:

$$\frac{N_{t+1}}{N_t} = 1 + R\left(1 - \frac{N_t}{K}\right) = 1 + R - \frac{RN_t}{K}.$$

Therefore the y intercept $= 1 + R = 3.34$, which implies that $R = 3.34 - 1 = 2.34$. The slope $= -R/K = -0.011$; therefore $K = 2.34/0.011 = 213$. The plot of the equation is shown in the following diagram.



This high R implies population cycles. But a question remains: Is the discrete logistic equation the correct model for this species? Would we reach a different conclusion if we fit these data to a different model?

15. We've been using population numbers and population density interchangeably because we've been assuming a closed population in some circumscribed area; as numbers increase, so must density. However, it would be possible to decouple density and numbers, at least experimentally, by changing the physical dimensions of the area holding the population. Suppose that we did such an experiment, say, with flour beetles, in which in one set of vials we hold density the same, but vary absolute numbers and thus the sizes of the vials and the amounts of flour that they hold. In another set of experiments we keep absolute numbers the same but vary density by changing vial size. Will density dependence and population size dependence necessarily be equivalent? What biological functions might depend more on absolute numbers than density? What biological properties might depend more on density than absolute numbers?