Populations are dynamic. Depending on the nature of the organism, population numbers may change from hour to hour, day to day, season to season, year to year. In some years certain organism are abundant; in other years they are scarce. Local populations appear, expand, decline, or become extinct. Eventually the area may be recolonized by individuals moving in from other populations. Such changes come about as the interaction of organisms and their environment affects birth rates, death rates, and the movement of individuals.

RATE OF INCREASE

Possessing a sufficiently large sample of individuals of all ages in the population to construct a life table and knowing the age-specific fecundity (discussed in Chapter 10), we can determine some characteristics of population growth. We will begin by constructing a life/fecundity table for the hypothetical squirrel population in Table 11.1. It provides the survivorship schedule, l_x, fecundity schedule, m_x, and an additional parameter p_x, the proportion of animals surviving in each age class; the parameter p_x is the complement of q_x and is equal to $1 - q_x$. With this data we can chart the growth of a population by constructing a **population projection table.**

We will illustrate the construction of a population projection table by using a hypothetical population of 10 female squirrels, all age 1, introduced into an empty oak forest. The year of establishment will be designated as year 0. For this population we will use a hypothetical life table (Table 11.1) to provide schedules of survivorship, fecundity, and the probability of survival. These 10 females in the year of introduction (year 0) will give birth to 40 young, half of which, 20, will be female. Because females form the reproductive units of the population, we follow only the females in the construction of the table (Table 11.2). The total population of the female squirrels for the year 0 stands at 30 squirrels, 10 of which are age 1 and 20 of which are age 0. Not all of these squirrels will survive into the next year. The survival of these two age groups is obtained by multiplying the number of each by the p_x value. Because the p_x of the females of age 1 is 0.5, we know that 5 individuals ($10 \times 0.5 = 5$) survive to year 1 (age 2). The p_x value of age 0 is 0.3, so that only 6 of the 20 in this age class in year 0 survive ($20 \times 0.3 = 6$) to year 1 (age 1). In year 1 we now have 6 one-year-olds and the 5 two-year-olds, with both age classes reproducing. The m_x value of the 6 one-year-olds is 2.0, and so they produce 12 offspring. The 5 two-year-olds have an m_x value of 3.0, and so they produce 15 offspring. Together the two age classes produce 27 young, which now make up age class 0. The total population for year 1 is 38. Survivorship and fecundity are determined in a similar manner for each succeeding year. Survivorship is tabulated year by year diagonally down the table to the right through the years, while new individuals are being adding each year to age class 0.

The steps for determining the number of offspring in year t (N_t) are given by the equation

$$N_{tx} = \sum_{x=1}^{\infty} N_{tx} m_x$$

where N_{t0} is the number in age class 0 at the given year t and N_{tx} is the number of age x at year t. For year 0 the calculation is

$$N_0 = (10)(2) = 20$$

and for succeeding years

$$N_1 = (6)(2) + (5)(3) = 27$$
$$N_2 = (8.1)(2) + (3)(3) + (3)(3) = 34.2$$

TABLE 11.1 Life Table for a Hypothetical Squirrel Population

x	l_x	q_x	p_x	e_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.0	0.7	0.3	1.09	0	0	
1	0.3	0.5	0.5	1.47	2.0	0.60	0.60
2	0.15	0.4	0.6	1.43	3.0	0.45	0.90
3	0.09	0.55	0.45	1.05	3.0	0.27	0.81
4	0.04	0.75	0.25	0.75	2.0	0.08	0.32
5	0.01	1.0	0.00	0.5	0.00	0.00	0.00
Σ						1.40	2.63

TABLE 11.2 Population Projection Table, Hypothetical Squirrel Population

Age	YEAR										
	0	1	2	3	4	5	6	7	8	9	10
0	20	27	34.1	40.71	48.21	58.37	70.31	84.8	101.86	122.88	148.06
1	10	6	8.1	10.23	12.05	14.46	17.51	21.0	25.44	30.56	36.86
2	0	5	3.0	4.05	5.1	6.03	7.23	8.7	10.50	12.72	15.28
3	0	0	3.0	1.8	2.43	3.06	3.62	4.4	5.22	6.30	7.63
4	0	0	0	1.35	0.81	1.09	1.38	1.6	1.94	2.35	2.83
5	0	0	0	0	0.33	0.20	0.27	0.35	0.40	0.49	0.59
Total	30	38	48.2	58.14	68.93	83.21	100.32	120.85	145.36	175.30	211.25
Lambda	λ	1.27	1.27	1.21	1.19	1.21	1.20	1.20	1.20	1.20	1.20

and so on. Thus *the number of offspring added to age 0 each year is obtained by multiplying the number in each age group by the m_x value for that age and summing these values over all ages.*

From such a population projection table we can calculate **age distribution** (see Chapter 10), the proportion of individuals in the various age classes for any one year, by dividing the number in each age group by the total population size for that year. The general equation is

$$C_{tx} = \frac{N_{tx}}{\sum_{y=0}^{\infty} N_{ty}}$$

where C_{tx} is the proportion of age group x at year t, N_{tx} is the number in each age group x at year t, and N_{ty} is the number in age group y at year t.

Comparing the age distribution of the hypothetical squirrel population in year 3 with that of the population in year 7, we observe that the population attains a stable or unchanging age distribution by year 7 (Table 11.3). From that year on, the proportions of each age group in the population and the rate of growth remain the same year after year, even though the population is steadily increasing.

The population projection table demonstrates an important concept of population growth. The constant rate of increase of the population from year to year and stable age distribution depend on survivorship (l_x) from each age class to the next and on fecundities of each age class (m_x). Both factors were used in the development of the population projection table. By dividing the total number of individuals in year $x + 1$ by the total number of individuals in the previous year x, one can arrive at the finite multiplication rate, λ (lambda), for each time period.

Lambda can be used as a multiplier to project but not predict population size some time in the future:

$$N_t = N_0 \lambda^t$$

For our hypothetical population, we can multiply the population size, 30, at time (year) 0 by $\lambda = 1.20$, the value derived from the population projection table, to obtain a population size of 36 for year 1. If we multiply 36 again by 1.20, or the initial population size 30 by λ^2 (1.20^2), we get a population

size of 43 for year 2; and if we multiply the population at $N_0 = 30$ by λ^{10}, we arrive at a projected population size of 186 for year 10. These population sizes do not correspond to the population sizes early in the population projection table, because in the lower years λ is higher and the population has not reached a stable age distribution. Only after the population achieves a stable age distribution does the λ value of 1.20 project future population size. For example, if population size N in year 7 is used as N_0, then 121×1.20^3 projects a population size of 209 in the year 10. This example emphasizes that population projections using λ assume a stable age distribution.

We will use the information in Table 11.1 to obtain another measure of population increase. By multiplying age-specific survivorship (l_x) by age-specific fecundity (m_x) and summing all the $l_x m_x$ values for the entire lifetime, as we did in Table 10.3, we obtain the **net reproductive rate** R_0, defined as

$$\sum_{x=0}^{\infty} l_x m_x$$

If R_0 equals 1, the birth rate equals the death rate; individuals are replacing themselves and the population remains stable. If the value is greater than 1, the population is increasing; if it is less than 1, it is decreasing. R_0 for our hypothetical population is 1.40, and so our population is increasing.

In contrast to λ, which projects population growth from one point in time to another and is always positive, R_0 measures the finite rate of increase in terms of discrete generation time ~~and can be negative.~~ If generations are discrete, as they are in many insects, then the unit of time (t) and generation time (T) are the same. But what about populations with overlapping generation times for which growth does not take place in discrete generation time? To calculate growth in populations with overlapping generations, such as our squirrel population, the value of T has to be changed to a **mean cohort generation time** (T_c). T_c is the mean period of time elapsing between the birth of the parents and the birth of the offspring. Mean cohort generation time is computed from the fecundity schedule by multiplying each $l_x m_x$ by its corresponding age x. All values are summed and divided by the sum of the $l_x m_x$ or R_0 to obtain T_c.

This parameter enables us to calculate r, the **per capita rate of increase** per unit time. r is a measure of the instantaneous rate of change of population size per individual. It is

TABLE 11.3 Approximation of Stable Age Distribution, Hypothetical Squirrel Population

| Age | PROPORTION IN EACH AGE CLASS FOR YEAR | | | | | | | | | | |
	0	1	2	3	4	5	6	7	8	9	10
0	.67	.71	.71	.71	.69	.70	.70	.70	.70	.70	.70
1	.33	.16	.17	.17	.20	.17	.17	.18	.18	.18	.18
2		.13	.06	.07	.06	.07	.07	.07	.07	.07	.07
3			.06	.03	.03	.04	.04	.03	.03	.03	.03
4				.02	.01	.01	.01	.01	.01	.01	.01
5					.01	.01	.01	.01	.01	.01	.01

the difference between instantaneous birth rates, b, and instantaneous death rate, d, or $r = b - d$. In a closed population, one in which no individual enters or leaves the population, r is known as the intrinsic rate of increase.

The relationship between the per capita growth rate r and per generation growth rate (R_0) is approximately

$$r = \frac{\ln R_0}{T_c}$$

For the squirrel population in Table 11.1 the cohort generation time is $\Sigma x l_x m_x / R_0 = 2.63/1.40 = 1.87$. The per capita rate of increase can be approximated by $\log_e 1.40/1.87 = 0.336/1.87 = 0.1797$.

The per capita rate of increase (or decrease) can be converted to the finite rate of increase by the formula $\lambda = e^r$, where e is the base of natural logarithms ($e = 2.71828...$). By determining e^r with an r value of 0.1797 or 0.180 we obtain $\lambda = 1.198$ or 1.20. This value agrees with that obtained from the population projection after stable age distribution was achieved.

The per capita rate of increase can be obtained more precisely from the Euler equation:

$$\sum_1^\infty e^{-rx} l_x m_x = 1$$

This equation can be solved only by using a trial and error method (iteration, see Appendix B). **Iteration** is accomplished by introducing different values of r and rx above and below the estimated value of r until the sum on the left-hand side approximates the given value of 1 on the right. The iterated value of r for the squirrel population is 0.186, which gives λ a value of 1.203.

POPULATION GROWTH

Exponential Growth

If a population were suddenly presented with an unlimited environment, as can happen when a small number of bacteria, plants, or animals are introduced into a suitable but unoccupied habitat, it would tend to expand exponentially. Knowing λ, you can project population growth by the equation

$$N_t = N_0 \lambda^t$$

where N_0 is the population size at some given time, N_t is the projected population at some later time t, and λ^t is value of λ raised to the power t, the number of projected years. Such a calculation has been done earlier in this chapter. Calculating change in population size in this manner provides an assessment of geometric rate of increase involving discrete time units or discrete generations.
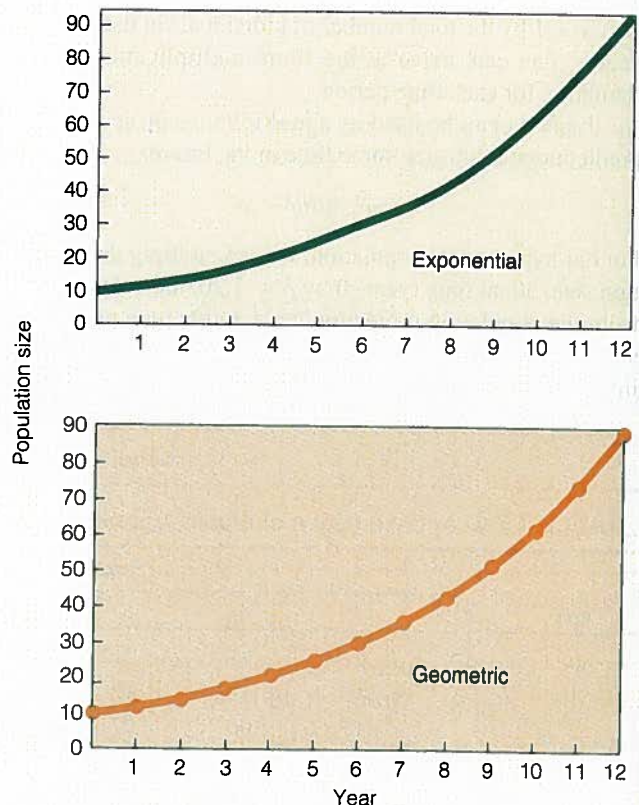
Assuming there were no movement in or out of the population and no mortality, then the excess of births would account for changes in population numbers. Under this condition population would increase like compound interest, a continual increase called **exponential growth.** But the growth rate of populations is tempered by death, and so a death rate is factored in with the birth rate in values for λ, R_0, and r.

Changes in population size can be projected by using the exponential equation

$$N_t = N_0 e^{rt}$$

where e is the base of natural logarithms 2.71828..., r is the per capita rate of increase, and t is the unit of time. This equation is similar to the geometric growth projected by $N_t = N_0 \lambda^t$. The term e^{rt} takes the place of λ^t. Provided that the geometric growth rate and the exponential growth rate are the same, species with discrete and overlapping generations will produce similar growth curves, except that geometric growth rate of species with discrete generations will have discrete points (Figure 11.1), whereas species with continuous growth will exhibit continuous or instantaneous change. Comparisons of changes in population sizes projected by the two equations are:

	Population Size	
Year	Exponential ($r = 0.180$)	Geometric ($\lambda = 1.20$)
0	10	10
1	12	12
3	17	17
5	25	25
7	35	36
9	52	52
12	87	89

FIGURE 11.1   Geometric growth curve plotted for $\lambda = 1.20$ and exponential growth curve plotted for $r=0.186$. The curves are similar except that the geometric curve has discrete points.

The population growth described and graphed is for a specific value of $r = 0.187$. Different values of r describe different exponential curves, as illustrated in Figure 11.2.

The equations just discussed project the number of individuals added to the population. Exponential growth can also be expressed as the rate of change in numbers over time:

$$dN/dt = (b - d)N$$

or

$$dN/dt = rN$$

This equation states that the rate of change dN/dt is directly proportional to the size of the population (N); dN/dt is equal to N times the per capita rate of increase, r. With instantaneous change in population growth, the time interval increments approach zero (Figure 11.3).

An example of exponential growth is the rise of a reindeer herd on St. Paul, one of the Pribilof Islands in Alaska (Figure 11.4). Introduced in 1910, reindeer expanded from 4 males and 22 females to a herd of 2000 in only 30 years. Exceeding the ability of the range to support it, the population crashed in an exponential fashion. Such curves are typical of populations that grow rapidly and exceed available resources.

Knowing the value of r for a population allows the calculation of doubling time of that population's growth. The doubling of a population occurs at the time t when $N_t/N_0 = 2$. Therefore $N_0e^{rt}/N_0 = 2$. Thus $e^{rt} = 2$, and $rt = \log_e 2 = 0.693$; then $t = 0.693/r$. The doubling time of the hypothetical squirrel population in Table 11.1 is $0.693/0.180 = 3.85$ years.

Logistic Growth

Exponential growth is not biologically realistic: no population can grow indefinitely. The environment is not constant,

and resources such as food and space are limited. As population density increases, competition for available resources among its members also increases. Eventually the detrimental effects of increased density—increased mortality from disease, starvation, and predation; decreased fecundity; and
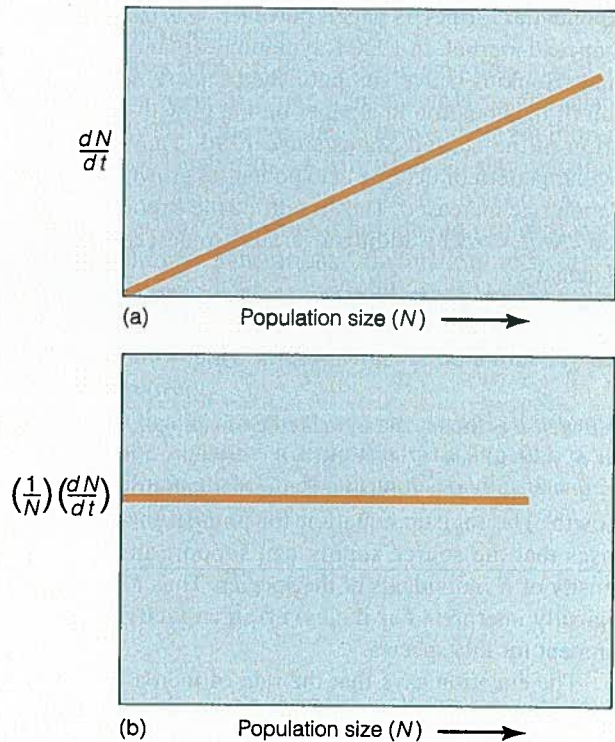
FIGURE 11.3 (a) Exponential population growth rate (dN/dt) as a function of population size. (b) Per capita exponential growth rate r, $(1/N)(dN/dt)$, as a function of population size. (After Gotelli 1995.)
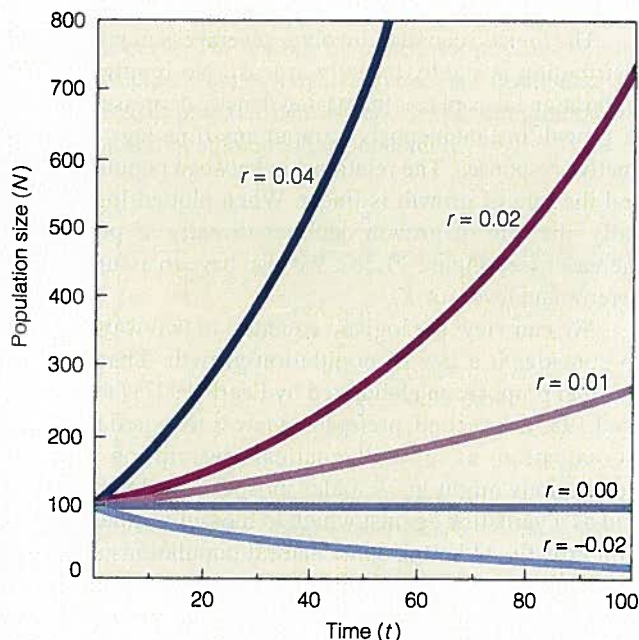
FIGURE 11.2 Trajectories of exponential population growth calculated from a starting population of 100 individuals for several values of r.
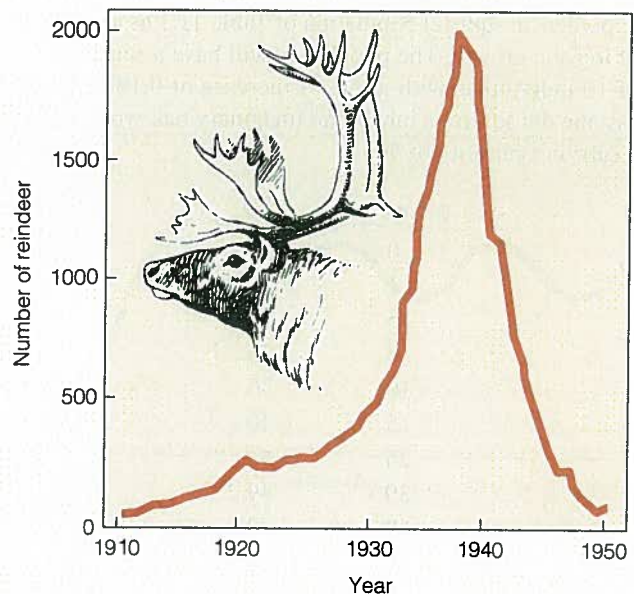
FIGURE 11.4 Exponential growth of the St. Paul reindeer herd is illustrated by the left side of the graph. When the herd outstripped its resources, the population crashed. (From Scheffer 1951.)

emigration—begin to slow population growth until it ceases, the population reaching a level at which theoretically it is in equilibrium with its environment.

This concept of the decline of the exponential growth rate as the size of the population increases was described by the mathematician Pierre-Francois Verhulst in 1838. He called this equation logistic because of its logarithmic-exponential form. His paper, however, was buried in a seldom-read journal. In 1920 Raymond Pearl and I. J. Reed of Johns Hopkins University published a nearly identical version of the equation in a paper on the growth of the population of the United States since 1790. They predicted a regular pattern of decline in exponential growth as the population size increased. They modified the exponential equation $dN/dt = rN$ by adding a variable to describe the effect of density:

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

Here dN/dt is the instantaneous rate of change, N is the number of individuals, K is the carrying capacity, and $(K-N)/K$ or $1 - N/K$ is the unutilized opportunity for population growth. The logistic equation for population growth supposes that the source supply can support an equilibrium density of K individuals of the species. Thus K is often biologically interpreted as the **carrying capacity** of the environment for this species.

The equation says that the rate of increase of a population over a unit of time is equal to the potential increase of a population times the unutilized portion of the resources. When N is low, $(K-N)/N \approx 1$ (thus most of the resources are unutilized). When $N \approx K$, $(K-N)/K \approx 0$ (thus most of the resources are utilized) and the population grows little or none at all. If $N > K$, then dN/dt is negative and N declines toward K (Figure 11.5).

Let us use the rate of increase of 0.180 derived from the hypothetical squirrel population of Table 11.1 as an example of logistic growth. The population will have a starting value of 10 individuals with a rate of increase of 0.180. We will assume the squirrels inhabit an imaginary oak woodlot with a carrying capacity of 50:

Year	Size
0	10
1	11
5	19
8	26
10	30
15	40
25	48
30	49.2
40	49.8
50	49.98
70	49.99

[handwritten margin note: note the earlier model and data did not have a carrying capacity]

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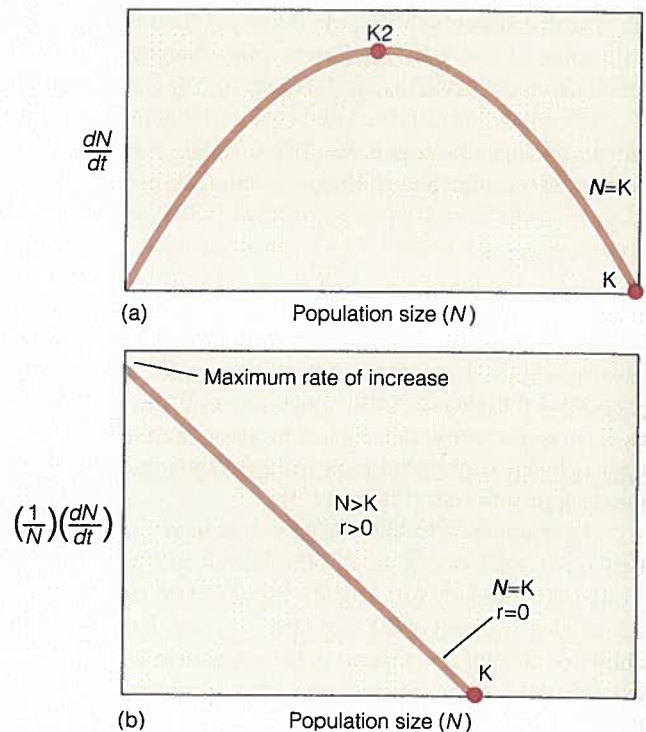
FIGURE 11.5   (a) Logistic population growth (dN/dt) as a function of population size. (b) Per capita logistic growth rate, $r[(1/N)(dN/dt)]$, as a function of population size. (After Gotelli 1995.)

Note how the population grows slowly at first, accelerates, and then slows (Figure 11.6). The point in the logistic growth curve where population growth is maximal, known as the **inflection point,** is $K/2$ (in this example, 27). From this point on, population growth slows as each individual added to the population causes an incremental decrease in the per capita rate of increase.

The logistic equation involves several assumptions. Age distribution is stable, initially at least. No immigration or emigration takes place. Increasing density depresses the rate of growth instantaneously without any time lags in reproductive responses. The relationship between population size and the rate of growth is linear. When plotted logarithmically, the rate of growth declines directly as population increases (see Figure 11.5b). We also have to assume a predetermined level for K.

We can view the logistic equation in two ways. One is to consider it a law of population growth. That was the original proposition elaborated by Pearl (1927) (see Kingsland 1985). A second, preferable view is to regard the logistic equation as a mathematical description of how populations might grow under most favorable conditions and as a yardstick against which to measure actual population growth. Although some natural populations appear to grow logistically, rarely, if ever, does their growth curve match the predicted logistic curve, because the assumptions are too simplistic.
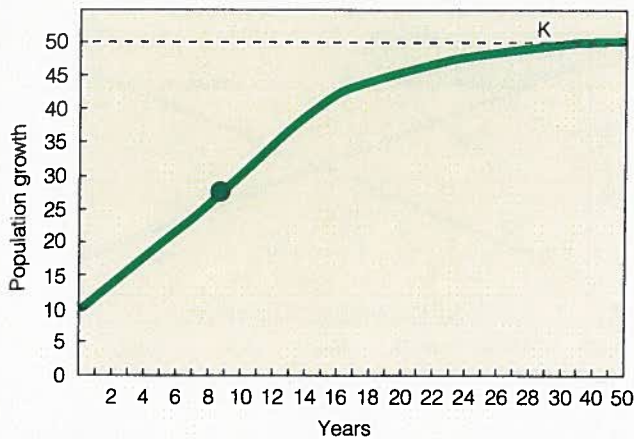
FIGURE 11.6 The logistic growth curve for a hypothetical squirrel population, from Table 11.1, with an r value of 0.180. The curve is sigmoidal. Its upper limit, K, is termed the carrying capacity. The inflection point, at which density begins to slow population growth, is located at $K/2$. In this example the inflection point stands at population size 27.

For example, consider the growth of the human population in Monroe County, West Virginia, whose economic base has been agriculture and small industry. It was settled by Europeans in the early 1700s, and the population was well established in 1800, the year for which U.S. Census data are first available. The population reached 13,200 in 1900 and has fluctuated about that number since then. The population grew most rapidly from 1800 to 1850, so growth during that period provides the data to estimate r, the rate of increase, as 0.074. K, based on the population levels since the year 1900, is 13,200. With these values of r and K the logistic equation predicts that the population would reach the asymptote around 1870, 30 years before it actually did. The predicted growth curve rises much more steeply than the actual growth curve (Figure 11.7). The human growth curve approaches but does not conform to the logistic curve. The reasons for nonconformity are obvious. The age structure was not stable; birth rates and death rates varied from census period to census period; and immigration and emigration were common to the population.
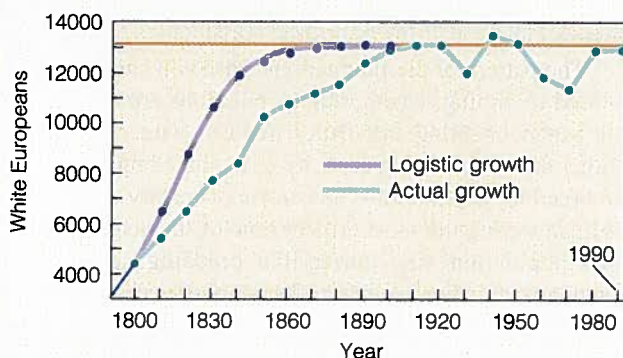
FIGURE 11.7 Actual and logistically predicted population growth of the white European population in Monroe County, West Virginia. (Data from U.S. Census Bureau.)
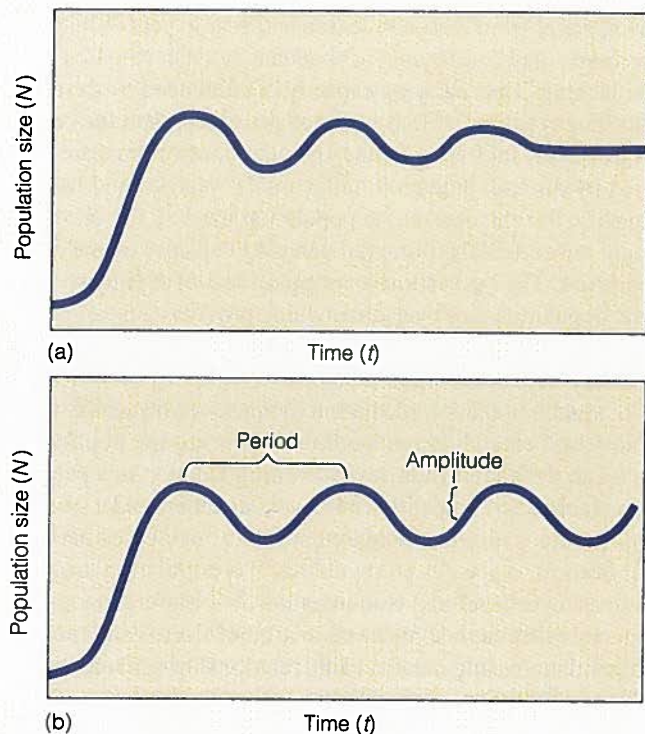
Time Lags

The logistic equation suggests that populations function as systems, regulated by positive and negative feedback. Growth is stimulated by positive feedback (as illustrated by the exponential growth curve), then slowed by the negative feedback of competition and dwindling resources. As N approaches K, the population theoretically responds instantaneously as density-dependent reactions set in.

Rarely does such feedback work as smoothly in real life as the equation suggests. Often adjustments lag, and available resources may allow the population to overshoot equilibrium (Figure 11.8). Unable to sustain itself on the remaining resources, the population declines to some point below carrying capacity, but not before it has altered resource availability for future generations. Population recovery as determined by reproductive rates is influenced by the density of the previous generation and the recovery of the resources, especially food supply. These factors build a time lag into population recovery.

To make the logistic equation more realistic, we need to factor into the equation a **reaction time lag** (w), a lag between environmental change and corresponding change in the rate of population growth:

$$\frac{dN}{dt} = rN\left(\frac{K - N_{t-w}}{K}\right)$$

(a)   Time (t)

(b)   Time (t)

FIGURE 11.8 Logistic growth curves with a time lag. (a) A medium time lag generates damped oscillations and a convergence on K. (b) A large time lag generates cycles that rise and fall but do not converge on K. (After Gotelli 1995: 36, Figure 2.5).

Another factor is a **reproductive time lag (g)**, a lag between environmental change and change in the length of gestation or its equivalent:

$$\frac{dN}{dt} = rN_{t-g}\left(\frac{K - N_{t-w}}{K}\right)$$

Means of incorporating time lags into the logistic equation are detailed by Krebs (1985) and Berryman (1981).

Time lags result in population fluctuations (Figure 11.8). The population may fluctuate widely without any reference to equilibrium size. Such populations may be influenced by some powerful outside, or extrinsic, force such as weather. A population may fluctuate about the equilibrium level, K, rising and falling between some upper and lower limits.

FIGURE 11.9   Density-dependent per capita birth rates and death rates change as a function of density. The population reaches stability at $N=K$.

DENSITY-DEPENDENT RESPONSES TO GROWTH

Sooner or later all populations have to confront the carrying capacity of the environment in which they live. Although explicitly defined in the logistic equation, a constant equilibrium level rarely exists. Because the environment is variable, K, the number of individuals the environment can support at any one time, is also variable. Carrying capacity is the level at which available resources can sustain individuals in a population at survival level. The availability of resources, however, varies from season to season and year to year. While one resource may be adequate or abundant, another resource may be lacking. Thus carrying capacity is influenced by the most limiting resource. If that resource increases, then the carrying capacity increases. Further, populations over time are limited by disease, predation, unfavorable weather, and habitat quality. For this reason the population level at any one time may not reflect the potential carrying capacity of the environment. The best estimate we can obtain of K is to average the population size over time, which provides a mean population size. Populations tend toward this equilibrium through density-dependent regulation.

Such population regulation increases or decreases mortality and reproduction. Both tend to bring the population back to the equilibrium set by limiting factors. As a population increases, competition among its members and a scarcity of resources result in increased mortality, decreased natality, or both for a species so regulated. If a population drops to some lower level and resources become more abundant, it increases through some combination of decreasing mortality and increasing natality. This relationship is illustrated in Figure 11.9. For population regulation the birth rate, death rate, or both must be density-dependent.

Through most of the sigmoid growth curve, both positive and negative feedback operate, with a change in the relative importance of each. In the early stages of population growth, positive feedback dominates. As population reaches
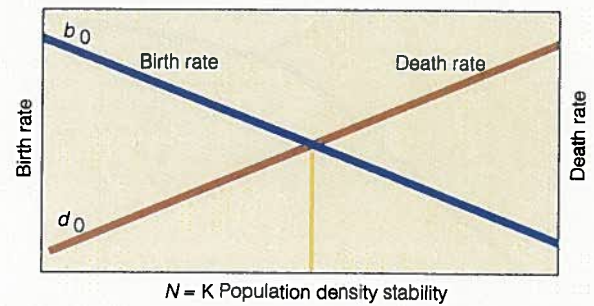
$K/2$, negative feedback overcomes positive feedback. How rapidly these two responses function relates to the population's impact on resources and future growth. If individuals remove a resource faster than it is replaced, then the present population impoverishes the environment for the next generation, slowing population growth.

POPULATION FLUCTUATIONS AND CYCLES

As you may have observed, the abundance of some species of insects, birds, and mammals seems to remain about the same from one year to the next. Other species may be noticeably abundant some years and noticeably scarce in others. Why the difference?

Population fluctuations are mostly local phenomena. A species may show stability over the whole of its range, but be highly variable locally. Populations fluctuate because time lags in density-dependent mechanisms, particularly birth rates and death rates, tend to either undercompensate or overcompensate for population size. In addition, populations are affected by changes in carrying capacity and other extrinsic influences, especially weather, predation, and competition (Figure 11.10).

The pattern of the fluctuations, based on census data, is colored by timing, whether the populations are censused in fall, winter, or spring. Population trends in winter may reflect neither the true carrying capacity of the breeding habitat nor the breeding population. The carrying capacity of the environment during the most critical time of the year can influence population size during the breeding season. Fall populations of some species, reflecting the success of recruitment, may be larger or more variable from year to year than spring populations (Figure 11.11).

The nature of the fluctuation reflects the population's **resilience.** Resilience is the rate at which a population returns to equilibrium after a disturbance takes it away from balance
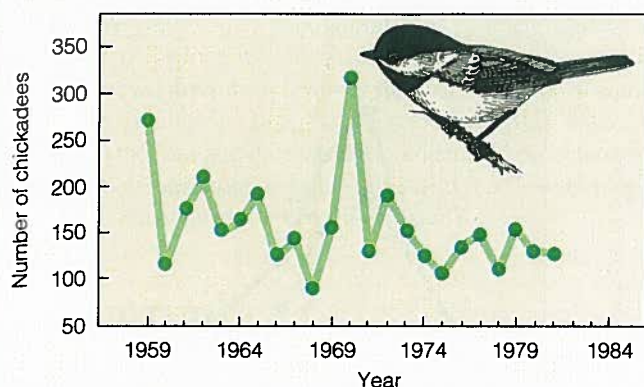
FIGURE 11.10 Fluctuation in a wintering population of black-capped chickadees (*Parus atrieapillos*) in northwestern Connecticut about a mean long-term density of 160 birds. The short-term decline in the population in 1968–1969 was attributed to an influx of competitive tufted titmice (*Parus bicolor*). In spite of fluctuations the population exhibited no sustained increase or decrease. (Data from Loery and Nichols 1985.)
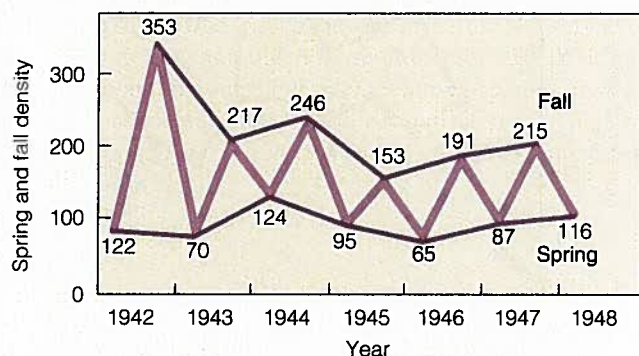
FIGURE 11.11 Trends of spring and fall populations in the northern bobwhite (*Colinus virginianus*) in Wisconsin. Note the seasonal fluctuations of population density. Fall densities fluctuate more than spring densities. (After Kabat and Thompson 1963:78.)

with its environment (Pimm 1991). In other words, resilience is a measure of how fast the population declines from above and how quickly it increases from below equilibrium. The resilience of a population is strongly influenced, if not determined, by its reproductive rate.

Size provides a clue. Small-bodied animals, such as meadow mice, fluctuate more widely than large-bodied ones, such as deer. Small animals have shorter lives, die more quickly, and thus decrease more dramatically from year to year. However, they reproduce fast, and can recover from their losses quickly. Such species have a high resilience. Large-bodied animals possess more stability about an equilibrium level because they live longer and are less subject to environmental vagaries. Very long-lived animals reproduce slowly and may require a substantial period of time to return to equilibrium. Consider, for example, the slow population growth of whales. Such species possess low resilience. The

measure of resilience, then, is the time required for the population to return toward equilibrium. The longer the time, the less the resilience.

The return time can be influenced by interactions with other species. A population of a given species does not live alone. If you disturb one species, you affect others as well. If species A depends on species B for food, both have experienced disturbance. Species A cannot return to equilibrium until species B has done so (for a good discussion, see Pimm 1991). This point will be emphasized throughout later chapters.

Population fluctuations that are more regular than we would expect by chance are called **oscillations** or **cycles**. In natural populations the two most common intervals between peaks are three to four years, typified by voles (Figure 11.12), and nine to ten years, typified by the snowshoe hare. These cyclic fluctuations are largely confined to simpler ecosystems, such as the boreal forest and tundra. Usually only local or regional populations are affected, although there is some evidence to suggest broader synchronies.

A number of theories have been advanced to explain cycles. A general theory among biologists holds that something in the physical environment, in the ecosystem, or in the population itself causes cycles. Predation has been singled out as a cause (see Chapter 15) (Keith et al. 1984, Korpimäki and Krebs 1996). Malfunction of the animal's endocrine system has been cited, as well as changes in the frequencies of genes that make much of the population less resistant to environmental changes, aggressive behavior (Krebs 1985), dispersal (Stenseth 1983), parasites (Hodson et al. 1985, 1992), and food shortages. Food shortages have been implicated in snowshoe hare decline (Keith 1974) (see Chapter 12) and in cycles of lemmings in the arctic tundra (Pitelka 1973, Batzli et al. 1980).
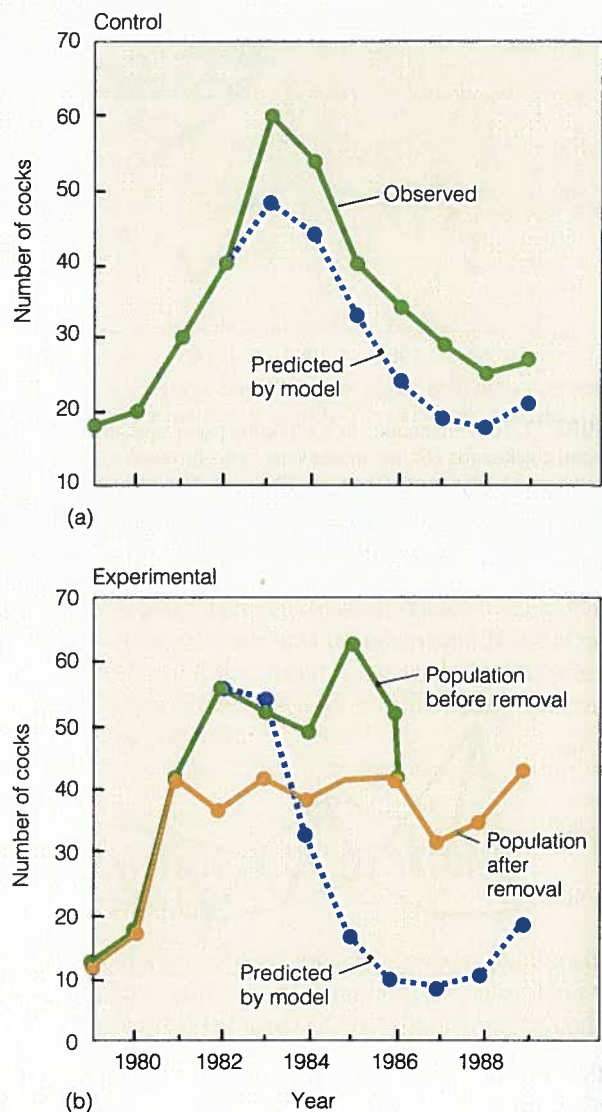
Experimental studies by Moss et al. (1996) suggest that causes of cycles may rest within the population itself, particularly for the red grouse (*Lagopus lagopus scoticus*). Their studies, which refute the prevailing theories, at least for the territorial and monogamous red grouse, point to changes in age structure and associated behavior. The social structure of red grouse is kin-oriented (see Chapter 13) with fathers and sons occupying clusters of territories, characterized by less aggressive territorial behavior (see Chapter 12) toward kin than non-kin. The population attains peak density when it reaches minimum territorial size. High density results in smaller clutches and limits the recruitment of young cocks into the spring population. The lack of recruitment reduces the number of kin cocks as well as the ratio of young cocks to old in the population. In the spring for five successive years during the increase phase of the six- to seven-year cycle, the experimenters removed enough territorial cocks to prevent the population from attaining peak population densities (Figure 11.13). The removal of the cocks resulted in a similar loss of hens from the breeding population, induced by the lack of territorial males. The combined loss of cocks and hens held the population below peak densities that trigger a cycling decline. Because of the
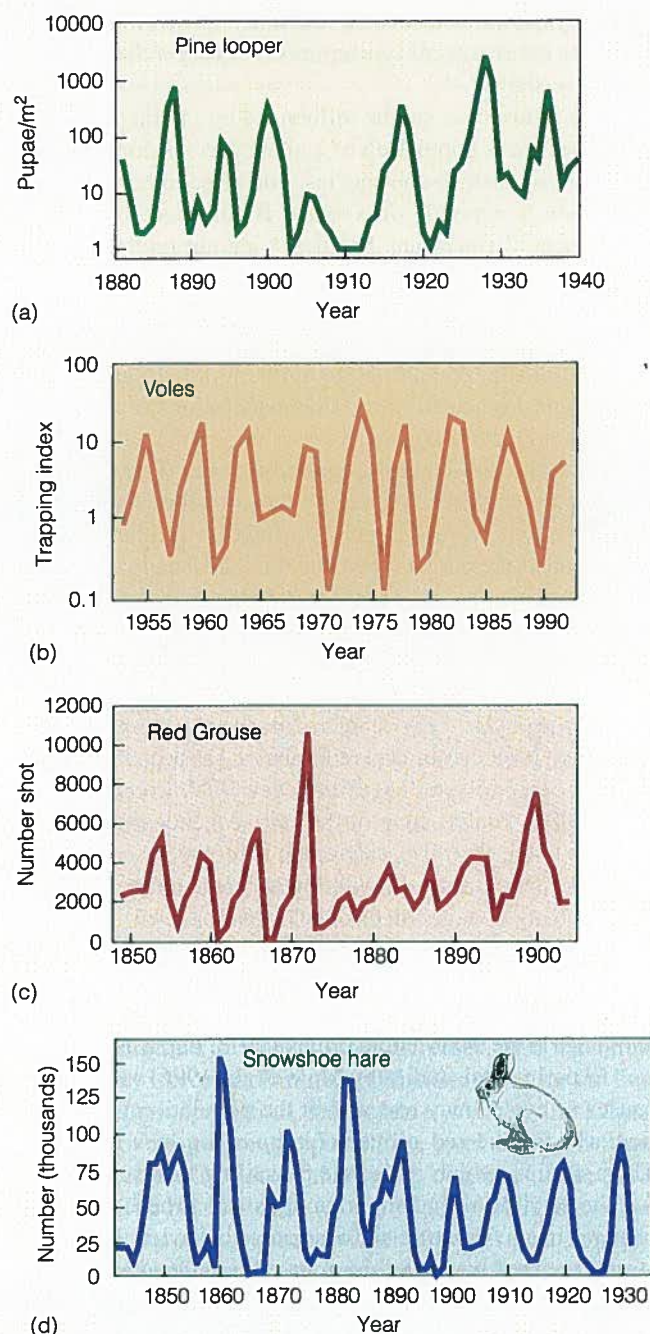
FIGURE 11.12 Examples of cyclic populations. (a) Pine looper (*Bupalus piniarius*) in Germany (Kendall et al. 1999 after Schwerdtfeger 1941). (b) Voles (*Microtus* and *Cleithrionomys*) at Kilpisjarvi, northern Finland (Kendall et al. 1999 after Hanski et al. 1993). (c) Red grouse (*Lagopus lagopus scoticus*) in Scotland (Middleton 1934). (d) Snowshoe hare (*Lepus americanus*). (From MacCulich 1937.)

FIGURE 11.13 Spring numbers of red grouse cocks in the control (a) and experimental removal (b) areas. See text for description of the experiment. The upper points and graph in the experimental area show the number of cocks in spring prior to removal. The lower points and graph show the number of cocks in the spring population after removal. Vertical lines indicate the number of cocks removed. Hens followed a similar pattern in both areas. The control populations exhibited cyclic behavior. Removal of cocks damped the cycle. (Moss et al. 1996:1517).

resulting low density and large territories, recruitment of young becomes easier and population density increases. By reducing population density over the five years, the experimenters were able to manipulate the age structure so as to favor recruitment of young cocks and thus prevent the population cycle from occurring.

Cycling populations exhibit certain demographic characteristics. L. Keith and his associates (Meslow and Keith 1968; Keith and Windberg 1978; Keith et al. 1984) followed snowshoe hare populations through two periods of increase and three of decline in the Rochester district of central Alberta. These studies provide insights into the demographic features of the ten-year snowshoe hare cycle. The decline, which set in

prior to the peak winter populations, was characterized by a high winter-to-spring weight loss, decrease in juvenile growth rate, decreased juvenile overwinter survival, reduction of adult survival beginning one year after the population peak and continuing to the low, and decreased reproduction (characterized by reductions in ovulation rates, third- and fourth-litter pregnancy rates, and length of breeding season).

EXTINCTION

When deaths exceed births and emigration exceeds immigration, populations decline. R becomes less than 1; r becomes negative. Unless the population can reverse the trend, it at worst faces extinction or at best an increased probability of becoming extinct.

Vulnerability to extinction varies widely among species (Table 11.4). Some species are common—widely distributed across their range and occupying a variety of habitats. Most species are relatively rare. Some occupy a wide natural range, but within it they are restricted to certain habitats. Others have a narrow range within which they are restricted to a very narrow habitat. They are much more vulnerable to extinction than the common ones; but even common species are not immune, as exemplified by the extinct passenger pigeon (*Ectopistes migratorius*) and the endangered black rhinoceros (*Diceros bicornus*).

There are several causes of declines in small populations. When only a few individuals are present, females of reproductive age may have little chance of meeting a fertile male. Many females remain unfertilized, reducing average fecundity. A small population suffers more from predation and sudden environmental changes, because there are fewer individuals to survive. They are also vulnerable to hybridization with related species. An example is the hybridization of sharp-tailed grouse (*Pedioecetes phasianellus*) with prairie chickens (*Tympanuchus cupido*). Losses feed upon losses until the population disappears.

Extinction is a natural process. Through millions of years of Earth's history, species have appeared and disappeared, leaving a record of their existence as fossils and trails in sedimentary rock. Some species could not adapt to geological and climatic changes. Others diverged into new species while the parent stock disappeared. Massive extinctions have occurred at several points in Earth's history: the late Ordovician; the late Devonian; the late Permian, which witnessed the extinction of up to 96 percent of species; and the Cretaceous-Tertiary, which saw the end of the dinosaurs (Figure 11.14).

Mass extinction is happening today at an accelerated pace. Some estimates place current extinction rates at 100 species a day, many of which are not yet known to science. The greatest number of extinctions has taken place since A.D. 1600. Well over 75 percent of modern-day extinctions have been caused by humans through the alteration and destruction of habitat,

TABLE 11.4 A Classification of Rare Species Based on Three Characteristics: Geographic Range, Habitat Specificity, and Local Population Size

Geographic Range	Habitat Specificity	Local Population Size	Examples
Extensive	Wide	Large	Commonly abundant in range of habitats (robin, *Turdus migratorius;* pigweed, *Chenopodium album*)
Large	Wide	Small	Constantly sparse over a large range and in several habitats (bald eagle, *Haliaeetus leucocephalus;* bristle grass, *Setaria geniculata*)
Large	Narrow	Large; dominant somewhere	Locally abundant over a large range in a specific habitat (California sea lion, *Zalophus californianus;* red mangrove *Rhizophora mangle*)
Large	Narrow	Small, nondominant	Constantly sparse in a specific habitat but over a large range (red-cockaded woodpecker, *Picoides borealis;* Pacific yew, *Taxus brevifolia*)
Small	Wide	Large; dominant somewhere	Locally abundant in several habitats but restricted geographically (orangebelly darter, *etheostoma radiosum;* Mountain pine, *Pinus mugo*)
Small	Wide	Small; nondominant	Constantly sparse and geographically restricted in several habitats (pigmy hippo, *Choeropsis liberiensis;* yellowwood, *Cladrastis kentukea*)
Small	Narrow	Large; dominant somewhere	Locally abundant in a specific habitat but restricted geographically (Kirtlandt's warbler, *Dendroica kirtlandii;* shale barren rockcress *Arabis serotina*)
Small	Narrow	Small; dominant	Constantly sparse and geographically restricted in a specific habitat) gaur, *Bos gauris;* Furbish's lousewort, *Pedicularis burbishiae*)

With the exception of the first set of characteristics, which describes a common species, combinations of the reduced states of any two of the three characteristics describe a form of rarity.

Source: After Rabinowitz 1981.
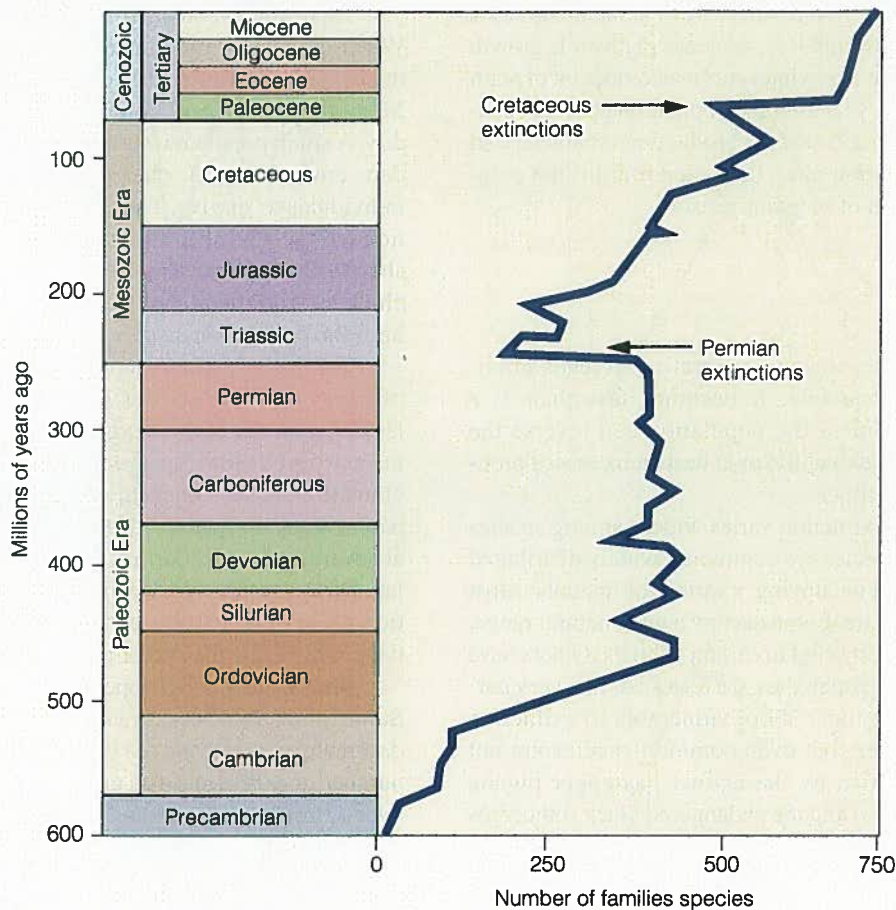
FIGURE 11.14   The Permian mass extinction event resulted in the loss of 96 percent of all marine species, and perhaps as many as 50 percent of the total species on Earth.

introduced predators and parasites, predator and pest control, competition for resources, and hunting of various types.

Despite popular impressions, extinction does not take place simultaneously over the full range of a species. It begins with isolated local extinctions when environmental conditions deteriorate or the population is unable to replace itself. Local extinctions often begin when habitats are destroyed and the dispossessed find remaining habitats filled. Restricted to marginal habitats, the individuals may persist for a while as nonreproducing members of a population or succumb to predation and starvation. As the habitat becomes more and more fragmented, the species is broken down into small isolated or "island" populations out of contact with other populations of its species. As a result the population is subject to inbreeding and genetic drift, reducing the ability of the small population to withstand environmental changes (see Chapter 19).

The maintenance of local populations often depends heavily on the immigration of new individuals of the same species. As the distance between local populations of "islands" (metapopulations) increases and as the size of the local population declines, their continued existence becomes more precarious. As the number falls below some minimum level (see Chapter 18), the local population may become extinct simply through random fluctuations. Although we equate such situations mostly with rarer species, even the more common species experience local extinctions. These often go unnoticed because the loss is masked by the influx of immigrants from surrounding areas. One study of a suburban population of robins showed that because of the losses of nests and young through predation by cats and interference by humans, the robins were not replacing themselves. Robins sang each spring only because new birds moved into the area. Thus suburbia became a population sink rather than a population source.

In fact, most local populations do not thrive for long. They are revived fast enough by new immigrants that replace the losses and keep the population going. As one local population slides down the slope toward extinction, a local population somewhere else is experiencing over-

crowding and supplies new recruits for depleted habitats (see Chapters 10 and 12).

Extinctions are of two sorts: deterministic and stochastic. **Deterministic extinction** comes about through some force or change from which there is no escape. The Cretaceous-Tertiary extinctions are an example. So is destruction of habitat on a local or regional scale. Habitat destruction rarely causes the extinction of a species except when a species is endemic or it is already on the verge of extinction. Examples are the recently extinct dusky seaside sparrow (*Ammodramus maritimus nigrescens*) of the Merritt Island and St. Johns River marshes of southern Florida and the thicktail chub (*Gila crassicauda*) of the Central Valley of California, whose habitat was destroyed by drainage, dam building, and water diversion.

Small localized populations of a species are more often subject to **stochastic extinction,** which comes about from normal random changes within the population or environment. Such changes normally do not destroy a population but merely thin it out; a smaller population, though, faces an increased risk of extinction from some decimating event.

Stochastic events may be demographic or environmental. Demographic stochasticity is chance variations in individual births and deaths. Demographic stochasticity results from habitat deterioration and loss through normal successional processes, reducing population size and restricting individuals to local patches of habitat. In a small population, a high death rate or low birth rate can lead to a random or accidental extinction. When a population falls below a minimal viable size, it faces very great risk of going extinct. Environmental stochasticity is a random series of adverse environmental changes, which comes about mostly through deterioration in environmental quality. If all members of a local population are affected equally by an adverse environmental change, the population may be reduced to a level at which demographic stochasticity takes over. How long a population can exist at a low level depends on the size of individuals, longevity, mode of reproduction, and seed banks in plants.

A classic example of an extinction is that of the heath hen (*Tympanuchus cupido cupido*). Formerly abundant in New England, the heath hen, an eastern form of the prairie chicken, was driven by excessive hunting and habitat destruction to the island of Martha's Vineyard off the Massachusetts coast and to the pine barrens of New Jersey. By 1880 it was restricted to Martha's Vineyard. At this point the population was subjected to deterministic extinction over most of its range. The small population, confined to a small island, was highly vulnerable to stochastic events. At first the population prospered, growing from a population of 200 birds in 1890 to more than 2000 in 1920. Then a major stochastic event, a combination of fire, winter gales, and cold weather, reduced the population to 50. The heath hen never recovered, and the last bird died in 1932.

Summary

1. Populations increase when births and immigration exceed deaths and emigration. The difference between the two (when measured as an instantaneous rate) is the population's per capita rate of increase, *r.*
2. In an unlimited environment a population expands geometrically, a phenomenon that may occur when a small population is released in a unfilled habitat. Geometric increase is characterized by a constant schedule of birth and death rates, an increase in numbers equal to the per capita rate of increase, and the assumption of a fixed or stable age distribution, which is maintained indefinitely.
3. Because the environment is limited, geometric growth is not maintained indefinitely. Population growth eventually slows and arrives at a point of equilibrium, *K,* the number of the species the environment can support. Biologically this number, which varies with environmental conditions, is often interpreted as the environmental carrying capacity.
4. However, natural populations rarely achieve such equilibrium levels; instead a population fluctuates in numbers, above and below *K,* because of time lags in density-dependent mechanisms, particularly birth and death rates and environmental influences.
5. Population fluctuations more regular than expected by chance are called cycles. The two most common intervals between peaks are three to four years, typified by lemmings, and nine to ten years, typified by the snowshoe hare. Many theories have been advanced to explain cycles, but the true nature of cycles still needs to be solved.
6. When populations become quite small, they become vulnerable to extinction. Extinctions are of two sorts: deterministic and stochastic. Deterministic extinctions come about through some force or change from which there is no escape, such as destruction of habitat or changes in environment. Stochastic extinctions result from random changes within the population or the environment, to which small populations are very vulnerable.

Review Questions

1. What is the difference between lambda λ, R_0, and r? What is the relationship among them?
2. Distinguish between exponential growth and logistic growth. Give the equations for each.
3. What are the weaknesses and limitations of the logistic equation? Why is the equation useful?
4. What is carrying capacity (K)? Why do populations fluctuate about some estimated value of K?
5. What are some of the hypotheses regarding the causes of cycles? Consult the cited papers and discuss the evidence and arguments for each of the hypotheses.
6. Why do species go extinct?
7. Distinguish between deterministic and stochastic causes of extinction.
8. Has the human population in some parts of the world reached or exceeded carrying capacity (economic as well as ecological)? Consider some of the African countries and India. What evidence do you have?
9. What are some signs of stress in human populations? (See Brown et al. 1998.)