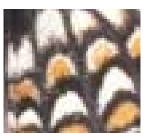
54 *Population Ecology*



The bay checkerspot butterfly lives in the hills south of San Francisco, California. If you were to travel through this region in search of butterflies, you would find checkerspots in some areas, but not in others. If you looked for butterflies in the region over a number of years, you would find more butterflies in some years than in others. In some places where you found checkerspots one year, you would go back the following year and find none, and in other places where there were previously no checkerspots, you would find them. What is the reason for these variations?

Ecologists who study populations attempt to answer this and a number of other questions: Why do the numbers of individuals of a species in a certain area fluctuate? Why do the geographic ranges of species vary so much? Why is a species abundant in some parts of its geographic range and rare in others, and why does its range change over time?

To understand how and why population sizes fluctuate, ecologists count individuals in different places and try to understand the relative importance of the processes that determine the number of individuals of a species in any particular location. These processes are influenced by individuals of the same species and by individuals of other species living in the same environment, as well as by abiotic environmental factors.

In this chapter we will discuss how and why the sizes of populations of species vary over space and time, and show how this knowledge is used to predict and manage the growth of populations of special interest to people. To set the stage for answering questions about populations, we first describe the kinds of information ecologists gather about the populations they study and how they use that information to answer the questions we just posed. Then we describe how populations of different species interact and how those interactions influence numbers of individuals and where they live. In the next chapter we will describe how interactions among populations and between populations and the physical environment influence the structure of ecological communities.

A Case Study in Subpopulations Patchy subpopulations of the rare bay checkerspot butterfly, *Euphydryas editha bayensis*, provide a well-studied example of population dynamics. This individual was photographed in Morgan Hill, a large patch of suitable habitat for this species in the San Francisco Bay area (see Figure 54.13).

Populations in Space and Time

The individuals of a species within a given area constitute a **population**. At any given moment, an individual organism occupies only one spot in space, and is of a particular age and size. The members of a population, however, are distributed over space, and they differ in age and size. The distribution of the ages of individuals in a population and the way those individuals are distributed over the environment describe **population structure**. Ecologists study population structure because the spatial distributions of individuals and their ages influence the stability of populations and affect interactions among species.

The number of individuals of a species per unit of area (or volume) is its **population density**. Ecologists are interested in population densities because dense populations often exert strong influences on their members and on populations of other species. Scientists working in agriculture, conservation, and medicine typically try to maintain high population densities of some species (crop plants, game animals, aesthetically attractive species, threatened or endangered species) and reduce the densities of others (agricultural pests, disease organisms). To manage populations, we need to know what factors cause populations to grow or decrease in size and how these factors work.

Because organisms and their environments differ, population densities may be measured in more than one way. Ecologists usually measure the densities of organisms in terrestrial environments as the number of individuals per unit of area. However, number per unit of volume is generally a more useful measure for organisms living in the water column. For species whose members differ markedly in size, as do most plants and some animals (such as mollusks, fishes, and reptiles), the percentage of ground covered or the total mass of individuals may be more useful measures of density than the number of individuals.

The structure of a population changes continually because **demographic events**—births, deaths, immigration (movement of individuals into the area), and emigration (movement of individuals out of the area)—are common occurrences. Knowledge of when individuals are born and when they die provides a surprising amount of information about a population. Let's examine how ecologists measure birth and death rates and use that information to understand **population dynamics**—the change in population density through time and space. The study of birth, death, and movement rates that give rise to population dynamics is known as **demography**.

Births, deaths, and movements drive population dynamics

Ecologists measure the *rates* (number per unit of time) at which births, deaths, and movements take place in a population, and they study how these rates are influenced by environmental factors, life histories, and population densities.

The number of individuals in a population at any given time is equal to the number present at some time in the past, plus the number born between then and now, minus the number that died, plus the number that immigrated, minus the number that emigrated. That is, the number of individuals at a given time, N_1, is given by the equation

$$N_1 = N_0 + B - D + I - E$$

where N_1 is the number of individuals at time 1; N_0 is the number of individuals at time 0; B is the number of individuals born, D the number that died, I the number that immigrated, and E the number that emigrated between time 0 and time 1. If we measure these rates over many time intervals, we can determine how a population's density changes over time.

Life tables summarize patterns of births and deaths

Life tables provide summaries of births and deaths in a population. Life tables were developed by the Romans nearly 2,000 years ago to determine how much money needed to be set aside to compensate families of soldiers that might be killed in battle. Today, life insurance companies use life tables to determine how much to charge people for insurance policies. Biologists use life tables to predict future trends in populations.

We can construct a life table by determining for a group of individuals born at the same time (called a *cohort*) the number that are still alive at later dates (*survivorship*). Some life tables also include the number of offspring produced by the cohort during each time interval. An example of a life table based on an intensive study of the cactus finch carried out on Isla Daphne in the Galápagos archipelago, is shown in Table 54.1.

The data in Table 54.1 come from 210 birds that hatched in 1978 and were followed until 1991, when only 3 individuals were still alive. The table shows that the mortality rate for these birds was high during the first year of life. It then dropped dramatically for several years, followed by a general increase in later years. Mortality rates fluctuated among years because the survival of these birds depends on seed production, which strongly correlates with rainfall. The Galápagos archipelago experiences both drought years and years of heavy rain. During drought years, plants produce few seeds, birds do not nest, and adult survival is poor. In years when rainfall is heavy, seed production is high, most birds breed several times, and adult survival is high. The survival rates in the table reflect these rainfall fluctuations. Variation in seed production resulting from the alternation of wet and dry years is a major reason why the cactus finch population fluctuates so greatly.

54.1 Life Table of the 1978 Cohort of the Cactus Finch (*Geospiza scandens*) on Isla Daphne

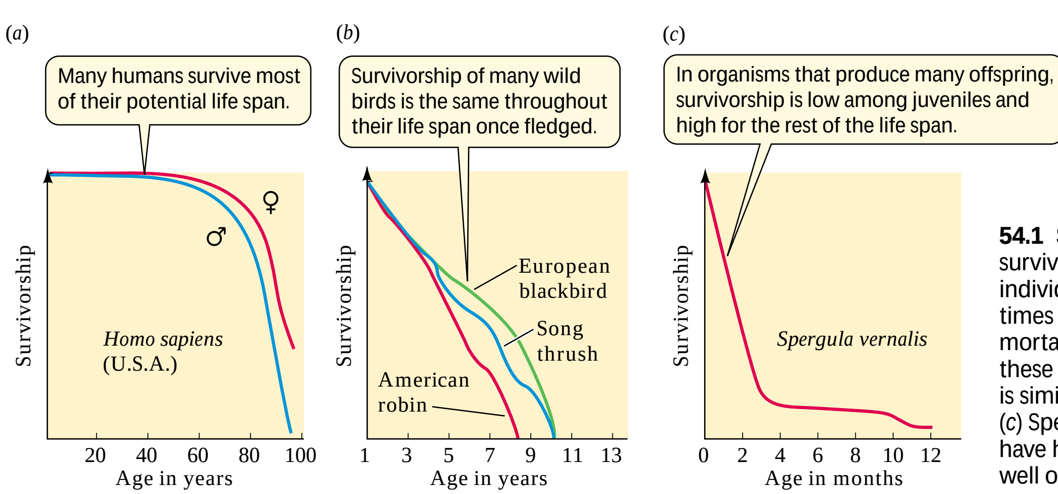
AGE IN YEARS (X)	NUMBER ALIVE	SURVIVORSHIP[a]	SURVIVAL RATE[b]	MORTALITY RATE[c]
0	210	1.000	0.434	0.566
1	91	0.434	0.857	0.143
2	78	0.371	0.898	0.102
3	70	0.333	0.928	0.072
4	65	0.309	0.955	0.045
5	62	0.295	0.678	0.322
6	42	0.200	0.548	0.452
7	23	0.109	0.652	0.348
8	15	0.071	0.933	0.067
9	14	0.067	0.786	0.214
10	11	0.052	0.909	0.091
11	10	0.048	0.400	0.600
12	4	0.019	0.750	0.250
13	3	0.014	0.996	

[a]Survivorship = the proportion of newborns who survive to age *x*.
[b]Survival rate = the proportion of individuals of age *x* who survive to age *x* + 1.
[c]Mortality rate = the proportion of individuals of age *x* who die before the age of *x* + 1.

Ecologists often use graphs to highlight the most important changes in populations. Graphs of survivorship in relation to age show when individuals survive well and when they do not. Survivorship curves in many populations fall into one of three patterns. In some populations, most individuals survive for most of their potential life span, then die at about the same age. For example, because of intensive parental care and the availability of medical services, the survivorship of humans in the United States is high for many decades, but then declines rapidly in older individuals (Figure 54.1*a*). In a second pattern, which is characteristic of many songbirds, the probability of surviving is about the same over most of the life span once individuals are a few months old (Figure 54.1*b*). A third widespread survivorship pattern is found among organisms that produce a large number of offspring, each of which receives little energy or parental care. In these species, high death rates of young individuals are followed by high survival rate during the middle part of the life span. *Spergula vernalis*, an annual plant that grows on sand dunes in Poland, illustrates this pattern (Figure 54.1*c*).

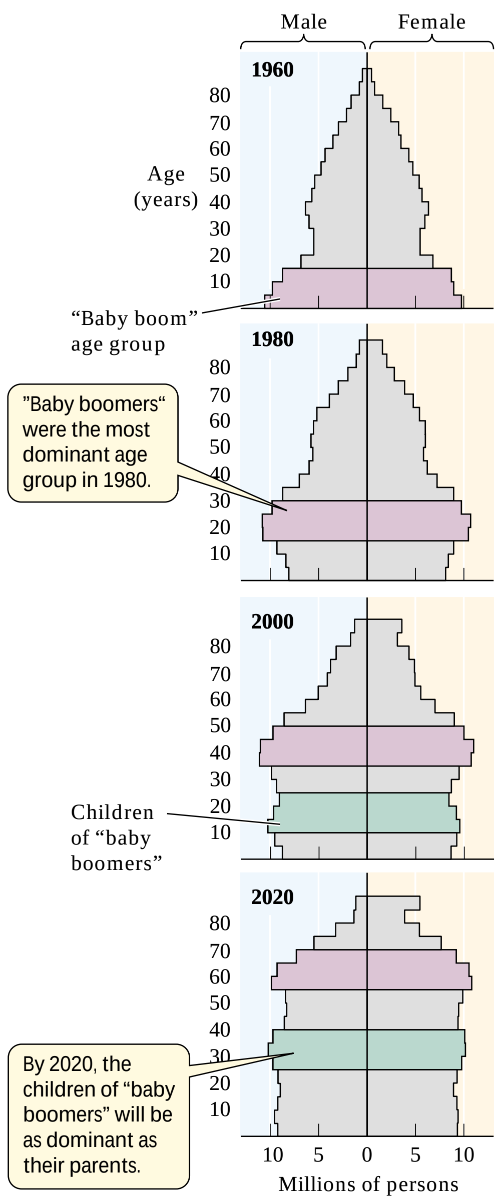
The age distribution of individuals in a population reveals much about the recent history of births and deaths in the population. The timing of births and deaths can influence age distributions for many years in populations of long-lived species. The human population of the United States is a good example. Between 1947 and 1964, the United States experienced what is known as the post-World War II baby boom. During these years, average family size grew from 2.5 to 3.8 children; an unprecedented 4.3 million babies were born in 1957. Birth rates declined during the 1960s, but Americans born during the baby boom still constitute the dominant age class in the first part of the twenty-first century (Figure 54.2). “Baby boomers” became parents in the 1980s, producing another bulge in the age distribution—a “baby boom echo”—but they had, on average, fewer children than their parents did, so the bulge is not as large.

By summarizing information on when individuals are born and die, life tables help us understand why population densities change over time. Life table data can also be used to determine how heavily a population can be harvested and which age groups should be the focus of our efforts to save rare species. We will discuss the management of populations later in this chapter, but first we'll see how interactions among species influence the dynamics of particular populations.



54.1 Survivorship Curves Three common survivorship curves show the number of individuals in a cohort still alive at different times over the life span. (*a*) For this curve, mortality is highest at advanced ages. (*b*) For these species, the probability of survivorship is similar throughout much of the life span. (*c*) Species with this survivorship pattern have high mortality at early ages, but survive well once past a critical point.

54.2 Age Distributions Change over Time The graphs shows age distributions for the human population of the United States from 1960 to 2020. The high birth rates during the "baby boom" have influenced the structure of the population over many decades.



Types of Ecological Interactions

So far, we have considered only survival and reproductive rates of single species. Before we can answer the questions we have posed about populations, we also need to look at the ways in which populations of different species interact with one another (Table 54.2) These interactions fall into five general categories:

- A **mutualism** is an interaction in which both participants benefit (+/+ interaction).
- A **commensalism** is an interaction in which one participant benefits but the other is unaffected (+/0 interaction).
- An **amensalism** is an interaction in which one participant is harmed but the other is unaffected (0/– interaction).
- A **predator–prey** or **parasite–host interaction** is one in which one participant is harmed, but the other benefits (+/– interaction).
- If two organisms use the same resources and those resources are insufficient to supply their combined needs, the organisms are called competitors, and their interactions constitute **competition** (–/– interactions).

Mutualistic interactions exist between plants and microorganisms, protists and fungi, plants and insects, among animals, and among plants. Most plants have beneficial associations with soil-inhabiting fungi, called mycorrhizae, which enhance the plant's ability to extract minerals from the soil (see Figure 31.16). Some plants have mutualistic relationships with nitrogen-fixing bacteria of the genus *Rhizobium* (see Figure 37.7).

Animals have important mutualistic interactions with protists, plants, and other animals. Corals and some tunicates gain most of their energy from photosynthetic protists living within their tissues. In exchange, they provide the protists with nutrients from the small animals they capture. Termites have nitrogen-fixing protists in their guts that help them digest the cellulose in the wood they eat. The termites provide the protists with a suitable environment in which to live and an abundant supply of cellulose.

54.2 *Types of Ecological Interactions*

		EFFECT ON ORGANISM 2		
		HARM	BENEFIT	NO EFFECT
EFFECT ON ORGANISM 1	HARM	Competition (–/–)	Predation or parasitism (–/+)	Amensalism (–/0)
	BENEFIT	Predation or parasitism (+/–)	Mutualism (+/+)	Commensalism (+/0)
	NO EFFECT	Amensalism (0/–)	Commensalism (0/+)	—

54.3 Commensalism Benefits One Partner Cattle egrets (*Bubulcus ibis*) capture more insects with less effort when they forage around large grazing mammals such as this Cape buffalo (*Syncerus caffer*). The buffaloes are neither harmed nor helped by the egrets.

An example of a commensalism is the relationship between cattle egrets and grazing mammals. Cattle egrets are found throughout the tropics and subtropics. They typically forage on the ground around cattle or other large mammals, concentrating their attention near the mammals' heads and feet, where they capture insects flushed by their hooves and mouths (Figure 54.3). Cattle egrets foraging close to grazing mammals capture more food for less effort than egrets foraging away from grazing mammals. The benefit to the egrets is clear; the mammals neither gain nor lose.

Amensalisms are widespread and important interactions. Mammals, for example, may congregate around water holes, trampling and killing many plants. The mammals benefit by drinking water, but not by trampling and killing the plants. Leaves and branches falling from trees often damage smaller plants beneath them. The trees drop their old structures regardless of whether or not they damage other plants.

Predation and competition have particularly important influences on population dynamics. For that reason, we will illustrate several examples of these interactions later in this chapter. All five types of interactions, combined with the effects of the physical environment, determine the range of environmental conditions under which a species can persist. If there were no competitors, predators, or pathogens in its environment, a species would be able to persist under a broader array of physical conditions than it can in the presence of other species that negatively affect it. On the other hand, the presence of beneficial species may increase the range of physical conditions in which a species can persist.

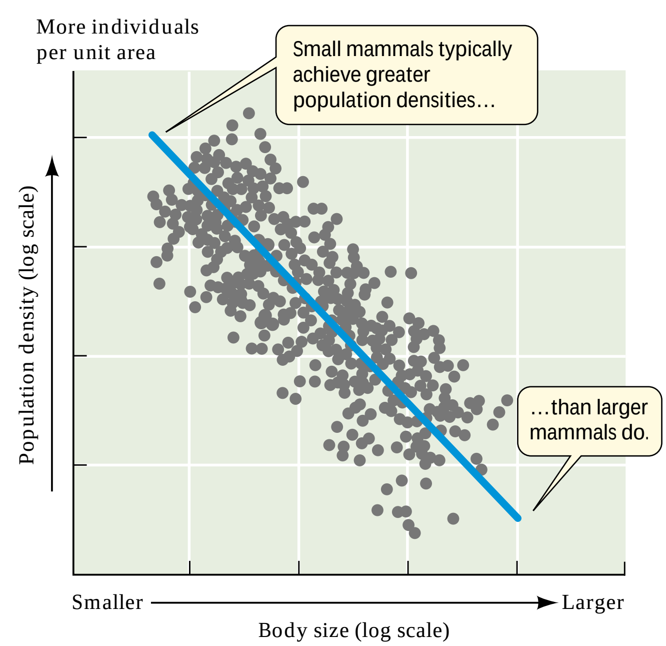
With this background information on population structure and dynamics and interactions among populations, we can now turn to the questions that we posed at the beginning of this chapter. We will begin with abundance and rarity.

Factors Influencing Population Densities

You have probably observed that in a particular area, some species are much more abundant than others. Some locally rare species may be abundant somewhere else; other species may exist at low population densities everywhere. Some species that are rare at a given time may be abundant at some later time, or vice versa. Four factors—resource abundance, the size of individuals, the length of time a species has lived in an area, and social organization—exert strong influences on population density.

- *Species that use abundant resources often reach higher population densities than species that use scarce resources.* Thus, on average, animals that eat plants are typically more common than animals that eat other animals. We will explore this pattern in greater detail in Chapter 55.
- *Species with small individuals generally reach higher population densities than species with large individuals.* In general, population density decreases as body size increases, because small individuals require less energy to survive than large individuals.

This relationship can be demonstrated by a logarithmic plot of population density against body size for a variety of mammals worldwide (Figure 54.4). Although there is a strong relationship between population density and body size, the great scatter of points on the graph shows that some small



54.4 Population Density Decreases as Body Size Increases This trend is illustrated by a logarithmic plot (that is, each tick mark is 10 times greater than the one before it) of population density against body size for mammals of different sizes; each dot represents a different species, and the resulting slope (straight line) is determined algebraically.

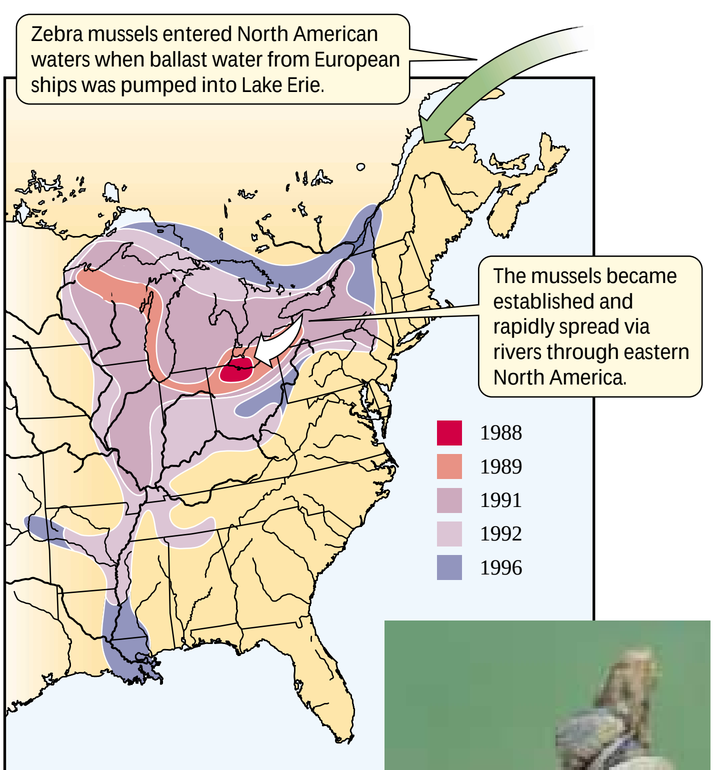
species may use scarce resources and some large species may use abundant resources.

- *Some newly introduced species reach high population densities*. Species that have recently escaped control by the factors that normally prevent them from becoming more abundant may achieve temporarily high population densities. Species that are introduced into a new region, where their normal predators and diseases are absent, sometimes reach population densities much higher than ever found in their native ranges.

The zebra mussel, *Dreissena polymorpha*, whose larvae were carried from Europe in the ballast water of commercial cargo ships, became established in the Great Lakes in about 1985. Zebra mussels spread rapidly, and today they occupy much of the Great Lakes and the Mississippi River drainage (Figure 54.5). In some places these mussels have reached densities as high as 400,000 individuals per square meter; such densities are never found in Europe. Densities of zebra mussels in North America are likely to decrease in the future as local predators and diseases begin to attack them.

- *Complex social organization may facilitate high densities*. As we saw in Chapter 53, some highly social species, including ants, termites, and humans, can achieve remarkably high population densities.

The factors that influence population density may strengthen or weaken over time. When this happens, population densities change. Let's look now at how and why population densities fluctuate.



Dreissena polymorpha

54.5 Introduced Zebra Mussels Have Spread Rapidly
Between 1989 and 1991, the range of zebra mussels in North America more than doubled.

Fluctuations in Population Densities

Although some populations fluctuate markedly in density, even the most dramatic fluctuations are much less than those that are theoretically possible. To visualize those possibilities, consider a single bacterium selected at random from the surface of this book. If all its descendants were able to grow and reproduce in an unlimited environment, explosive population growth would result. In a month, this bacterial colony would weigh more than the visible universe and would be expanding outward at the speed of light. Similarly, a single pair of Atlantic cod and their descendants, reproducing at the maximum rate of which they are capable, would fill the Atlantic Ocean basin in 6 years if none of them died. Obviously, such dramatic population growth does not occur in nature. What prevents it from happening?

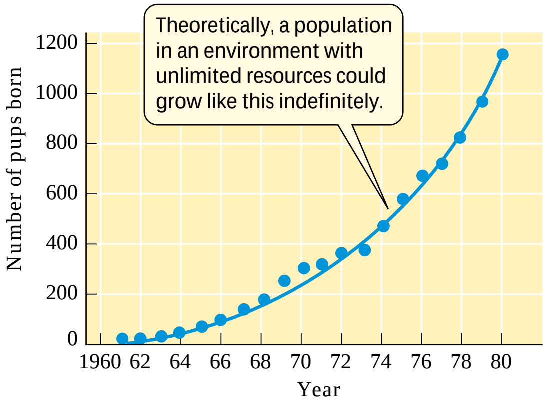
All populations have the potential for exponential growth

Bacteria and cod illustrate the fact that all populations have the potential for explosive growth. As the number of individuals in a population increases, the number of new individuals added per unit of time accelerates, even if the rate of increase expressed on a per individual basis—called the *per capita growth rate*—remains constant. If births and deaths occur continuously and at constant rates, a graph of the population size over time forms a continuous, J-shaped curve (Figure 54.6). This form of explosive increase is called **exponential growth**. It can be expressed mathematically in the following way:

$$\text{Rate of increase in number of individuals} = \begin{pmatrix} \text{Average per capita birth rate} \\ -\ \text{Average per capita death rate} \end{pmatrix} \times \text{Number of individuals}$$

or, more concisely,

$$= \frac{\Delta N}{\Delta t} = (b - d)N$$



54.6 Exponential Population Growth The growth of the elephant seal population on Año Nuevo Island, California, between 1960 and 1980 illustrates the exponential population growth curve. Theoretically, a population in a habitat with unlimited resources (including space) could continue to grow indefinitely. Since no resource on Earth is unlimited, this pattern cannot continue indefinitely for any species (including humans).

Mirounga angustirostris

where $\Delta N/\Delta t$ is the rate of change in the size of the population (ΔN = change in number of individuals; Δt = change in time).

The difference between the average per capita birth rate in a population (b) and its average per capita death rate (d) is the *net reproductive rate* (r). (In these equations, b includes both births and immigrations, and d includes both deaths and emigrations.) When conditions are optimal for the population, the net reproductive rate has its highest value, called r_{max}, or the *intrinsic rate of increase;* r_{max} has a characteristic value for each species. Therefore, the rate of growth of a population under optimal conditions is

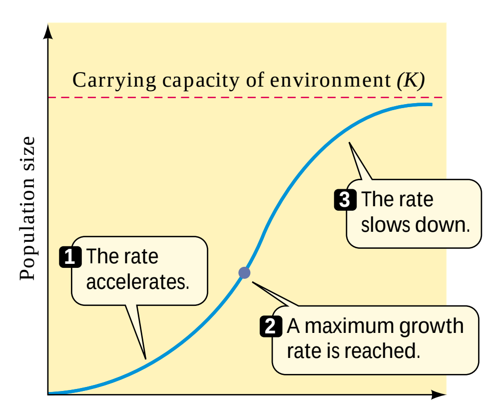
$$\frac{\Delta N}{\Delta t} = r_{max} N$$

For very short time periods, some populations may grow at rates close to the intrinsic rate of increase. For example, northern elephant seals were hunted nearly to extinction in the late nineteenth century. In 1890, only about 20 animals remained, confined to Isla Guadalupe off the northwestern coast of Mexico. Once the hunting was stopped, the population was protected from its major predator, and ample elephant seal habitat remained available, so the population began to increase rapidly. Elephant seals recolonized Año Nuevo Island near Santa Cruz, California, in 1960. In the 20 years after colonization, the population breeding on the island expanded exponentially (see Figure 54.6).

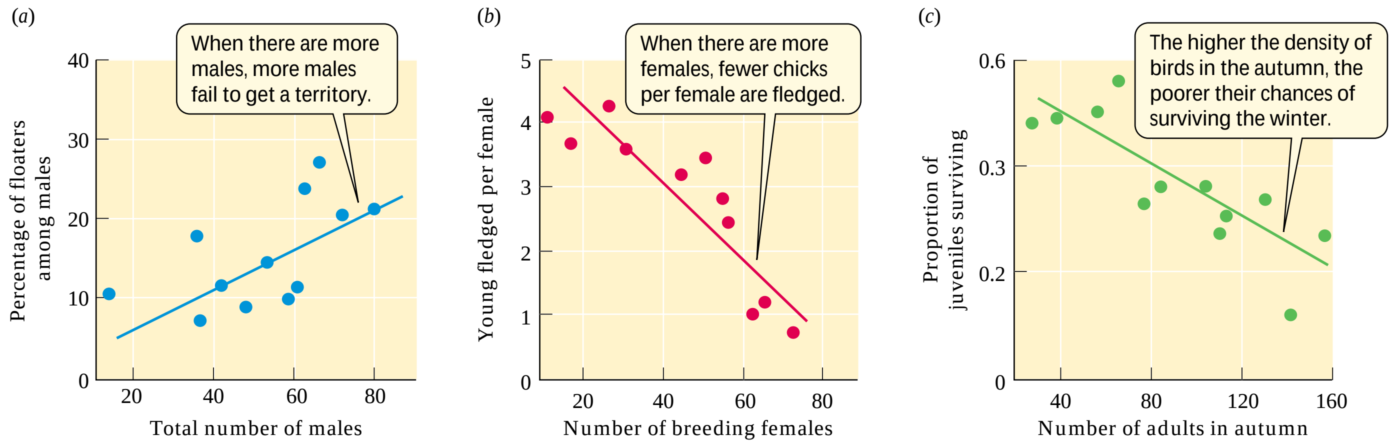
Population growth is influenced by environmental limits

No real population can maintain exponential growth for very long. As a population increases in size, environmental limits cause birth rates to drop and death rates to rise. In fact, over long time periods, the densities of most populations fluctuate around a relatively constant number. The simplest way to picture the limits imposed by the environment is to assume that an environment can support no more than a certain number of individuals of any particular species per unit of area. This number, called the **environmental carrying capacity** (K), is determined by the availability of resources—food, nest sites, shelter—as well as by disease, predators, and, in some cases, social interactions.

Because of environmental limits, the growth of a population typically slows down as its density approaches the environmental carrying capacity. A graph of the population size over time results in an S-shaped curve (Figure 54.7). This pattern is called **logistic growth**. The simplest way to generate an S-shaped growth curve is to add to the equation for exponential growth a term, $(K - N)/K$, that slows the population's growth as it approaches the carrying capacity. This



54.7 Logistic Population Growth Typically, a population in an environment with limited resources stops growing exponentially long before it reaches the environmental carrying capacity.



54.8 Regulation of an Island Population of Song Sparrows The size of the population of song sparrows (*Melospiza melodia*) on Mandarte Island, British Columbia, is determined in part by the severity of winter weather. In addition, the population is regulated by (*a*) the territorial behavior of males, (*b*) the reproductive success of females, and (*c*) the survival of juveniles in relation to population density.

term implies that each individual added to the population depresses population growth by an equal amount:

$$\frac{\Delta N}{\Delta t} = r\left(\frac{K - N}{K}\right)N$$

Population growth stops when $N = K$ because then $(K - N) = 0$, so $(K - N)/K = 0$, and thus $\Delta N/\Delta t = 0$.

Population densities influence birth and death rates

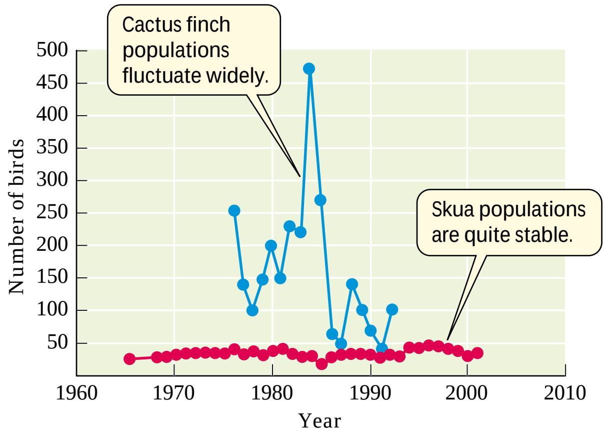
Because each additional individual typically makes things worse for other members of the population in a limited environment, per capita birth and death rates usually change in response to population density; that is, they are **density-dependent**. Birth and death rates may be density-dependent for several reasons. First, as a species increases in abundance, it may deplete its food supply, reducing the amount of food available to each individual. Poorer nutrition may increase death rates and decrease birth rates. Second, predators may be attracted to areas with high densities of their prey. If predators capture a larger proportion of the prey than they did when the prey were scarce, the per capita death rate of the prey rises. Third, diseases spread more easily in dense populations than in sparse populations.

However, not all factors affecting population size act in a density-dependent way. A cold spell in winter or a hurricane that blows down most of the trees in its path may kill a large proportion of the individuals in a population regardless of its density. Factors that change per capita birth and death rates in a population independently of its density are said to be **density-independent**.

Fluctuations in the density of a population are determined by all the density-dependent and density-independent factors acting on it. The combined action of these factors is shown by the dynamics of a population of song sparrows on Mandarte Island, off the coast of British Columbia, Canada. Over a period of 12 years, the number of song sparrows fluctuated between 4 and 72 breeding females and between 9 and 100 territorial males. Death rates are high during particularly cold, snowy winters, regardless of the density of the population. Several density-dependent factors also contribute to fluctuations in the density of the population. The number of breeding males, for example, is limited by territorial behavior: The larger the number of males, the larger the number that fail to gain territories and must live as "floaters" with little chance of reproducing (Figure 54.8*a*). Also, the larger the number of breeding females, the fewer offspring each female fledges (raises to the age when it can leave the nest) (Figure 54.8*b*). And the more birds alive in autumn, the poorer the chances of juveniles born in that year surviving the winter (Figure 54.8*c*). Thus, the number of males and females breeding each year is influenced by both density-independent and density-dependent factors.

Population Fluctuations

The cactus finch, which we met in our earlier discussion of life tables, is a small, short-lived seed-eating bird that lives only in the Galápagos archipelago. The south polar skua is a long-lived carnivorous seabird with a broad geographic range in the southern oceans. Over several decades, the number of cactus finches fluctuated widely, as we have already noted. The number of skuas fluctuated very little over an even longer time period (Figure 54.9). Why did the population of skuas fluctuate so much less than the population of cactus finches?

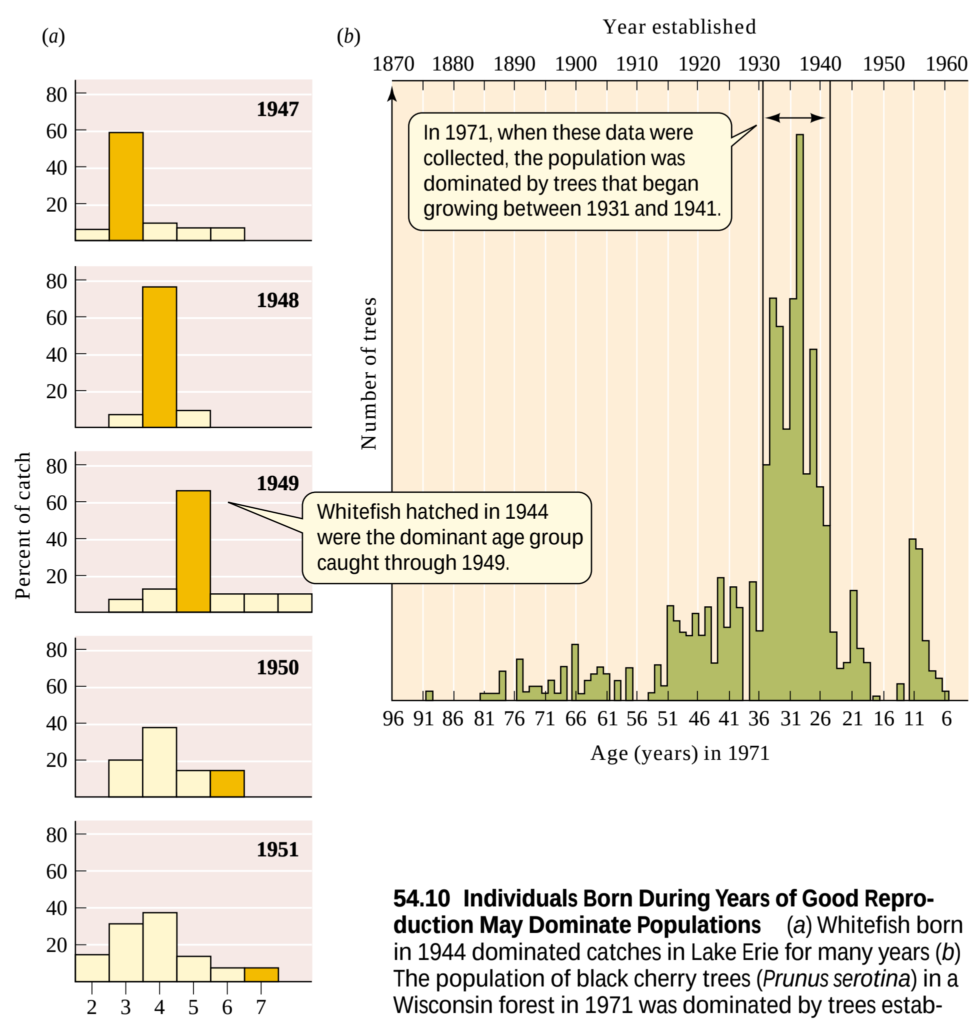


54.9 Population Sizes May Be Stable or Highly Variable Populations of small, short-lived species, such as that of cactus finches (*Geospiza scandens*) on Isla Daphne in the Galápagos Archipelago, tend to fluctuate much more than do populations of larger, longer-lived species, such as that of south polar skuas (*Catharacta maccormicki*).

All populations fluctuate less than the theoretical maximum, but the sizes of some populations fluctuate remarkably little. The comparison between south polar skuas and cactus finches illustrates one cause of such differences: Species with long-lived individuals that have low reproductive rates, such as south polar skuas, typically have more stable populations than species with short-lived individuals that have high reproductive rates, such as cactus finches. Small, short-lived individuals are generally more vulnerable to environmental changes than long-lived individuals. That is why insect population densities tend to fluctuate much more than those of birds and mammals, and population densities of annual plants fluctuate much more than those of trees.

EPISODIC REPRODUCTION GENERATES FLUCTUATIONS. For most species, some years are better for reproducing than other years. In Lake Erie, 1944 was such an excellent year for reproduction of whitefish that individuals born in that year dominated whitefish catches in the lake for several years (Figure 54.10*a*). Similarly, most of the individuals found in a population of black cherry trees in a Wisconsin forest in 1971 became established between 1931 and 1941 (Figure 54.10*b*). Population densities increase following years of good reproductive success, but they decrease following years of poor reproduction.

RESOURCE FLUCTUATIONS GENERATE CONSUMER FLUCTUATIONS. Densities of populations of species that depend on a single or just a few resources are likely to fluctuate more than those of species that use a greater variety of resources. As we have seen, cactus finch populations fluctuate with the annual production of the seeds they eat, which varies greatly. Similarly, several species of birds and mammals that live in northern coniferous forests depend on seeds in conifer cones. Most trees in northern coniferous forests reproduce synchronously and episodically; consequently, over large areas, there are years of massive seed production and years of little or no seed production. Some birds (such as crossbills) wander over large areas, looking for places where



54.10 Individuals Born During Years of Good Reproduction May Dominate Populations (*a*) Whitefish born in 1944 dominated catches in Lake Erie for many years (*b*) The population of black cherry trees (*Prunus serotina*) in a Wisconsin forest in 1971 was dominated by trees established between 1931 and 1941.

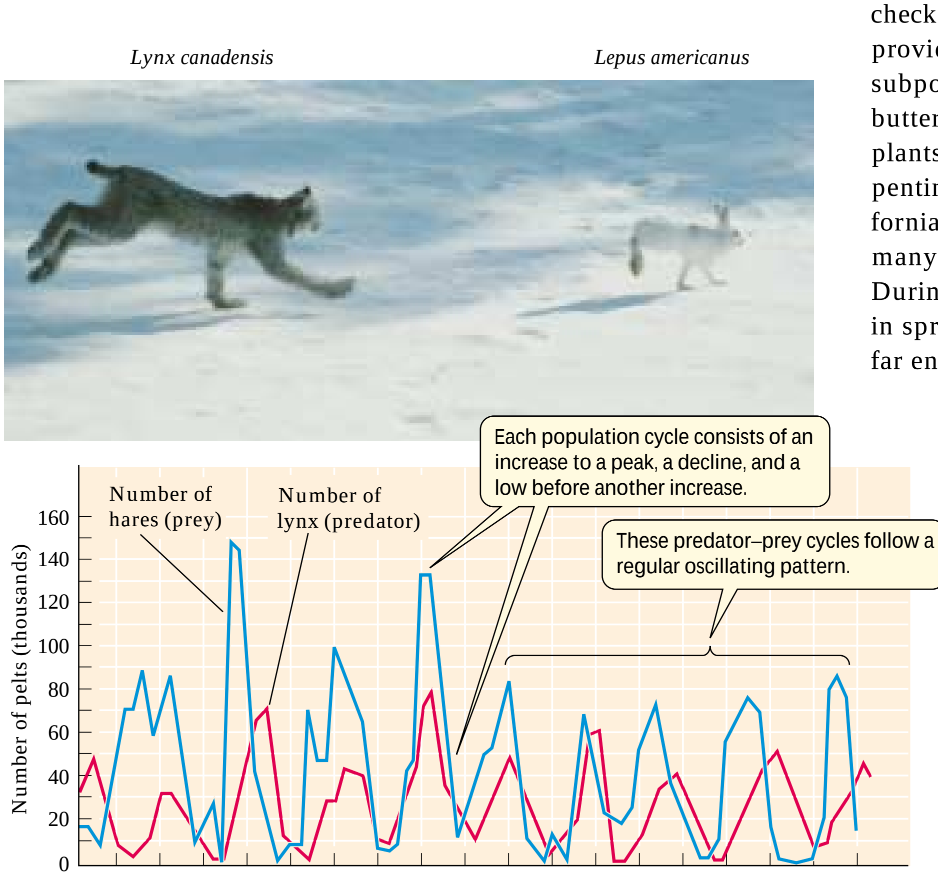
cones have been produced. Other birds (such as jays and nutcrackers) and some mammals (squirrels) store cones during years of high production, but they often suffer high mortality rates during years when the trees in their area produce few or no cones.

POPULATION INTERACTIONS GENERATE FLUCTUATIONS Predators often cause fluctuations in the densities of their prey because predator population growth nearly always lags behind growth in populations of their prey. The predator population grows and eats most of its prey population, followed by a crash in the predator population, which no longer has enough food. Population oscillations among small mammals and their predators living at high latitudes, where many predators depend on only one or a few prey species, are the best-known examples of fluctuations in population densities driven by predator–prey interactions. Populations of Arctic lemmings and their chief predators—snowy owls, jaegers, and Arctic foxes—oscillate with a 3- to 4-year periodicity. Populations of Canadian lynx and their principal prey, snowshoe hares, oscillate on a 9- to 11-year cycle (Figure 54.11).

For many years, ecologists thought that hare–lynx oscillations were caused only by interactions between hares and lynx. Recently, ecologists performed experiments in Yukon Territory, Canada, to test the hypothesis that the lynx–hare oscillations are caused by fluctuations in the hares' food supply as well as by predation by lynx. They enclosed some areas with fences through which hares, but not lynx, could pass, and they provided food in some of the enclosures. The results of the experiments show that the oscillations are driven both by predation by lynx and by interactions between hares and their food supply (Figure 54.12).

POPULATION FRAGMENTATION GENERATES FLUCTUATIONS. Populations of many species are divided into separated, discrete subpopulations living in distinct habitat patches, among which some exchange of individuals occurs. Each subpopulation has a probability of "birth" (colonization) and "death" (extinction). Within each subpopulation, growth occurs in the ways we have just described, but because the subpopulations are much smaller than the population as a whole, local disturbances and random fluctuations in numbers of individuals are more likely to cause the extinction of subpopulations than the extinction of an entire population. However, if individuals move frequently between subpopulations, immigrants may prevent declining subpopulations from becoming extinct. This process is known as the **rescue effect**.

EXAMPLES OF SUBPOPULATION DYNAMICS. The bay checkerspot butterfly (*Euphydryas editha bayensis*) provides a good illustration of the dynamics of subpopulations. The caterpillars (larvae) of this butterfly feed on only a few species of annual plants, which are restricted to outcrops of serpentine rock on hills south of San Francisco, California. The bay checkerspot has been studied for many years by Stanford University biologists. During drought years, most host plants die early in spring, before the caterpillars have developed far enough to be able to enter their summer rest-



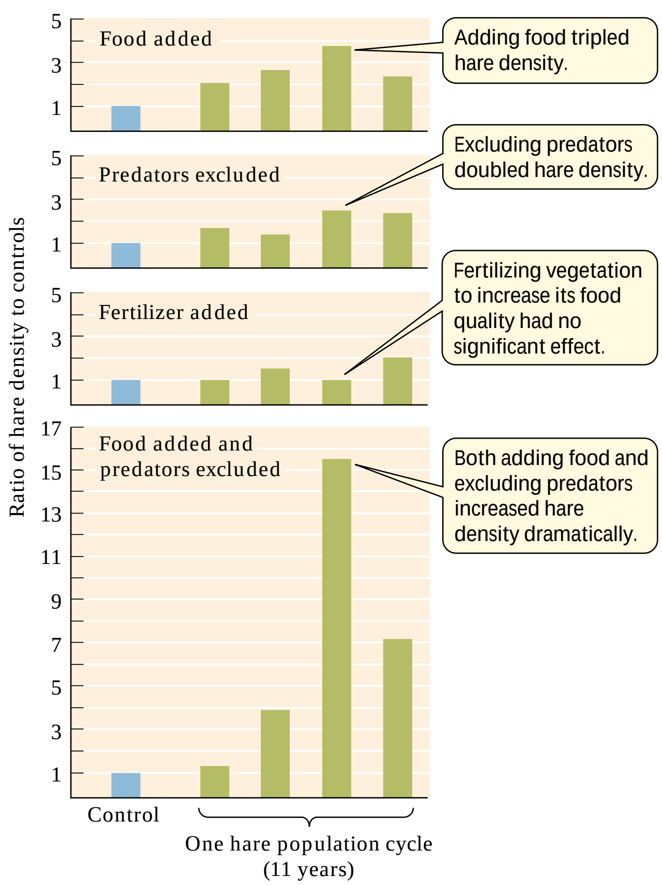
54.11 Hare and Lynx Populations Cycle in Nature The 9–11-year population cycle of the snowshoe hare and its major predator, the Canadian lynx, was revealed in records of the number of pelts that were sold to the Hudson's Bay Company by fur trappers.

EXPERIMENT

Hypothesis: Population cycles of hares are influenced by both food supply and predators.

METHOD Select 9 1-km^2 blocks of undisturbed coniferous forest. In two of the blocks give the hares supplemental food year-round. Erect an electric fence around two other blocks, with mesh large enough to allow hares, but not lynxes, to pass. Provide extra food in one of these blocks. In two other blocks add fertilizer to increase food quality. Use three other blocks as unmanipulated controls.

RESULTS



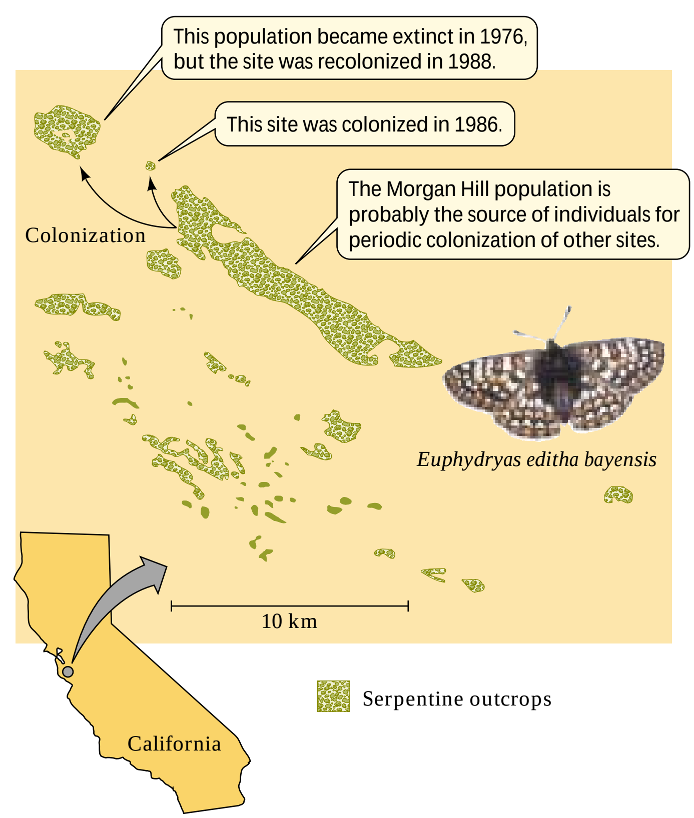
Conclusion: Population cycles of the snowshoe hare are influenced by their food supply as well as by interactions with their predators.

54.12 Prey Population Cycles May Have Multiple Causes Experiments showed that both food supply and predation (but not food quality) affect the population densities of snowshoe hares.

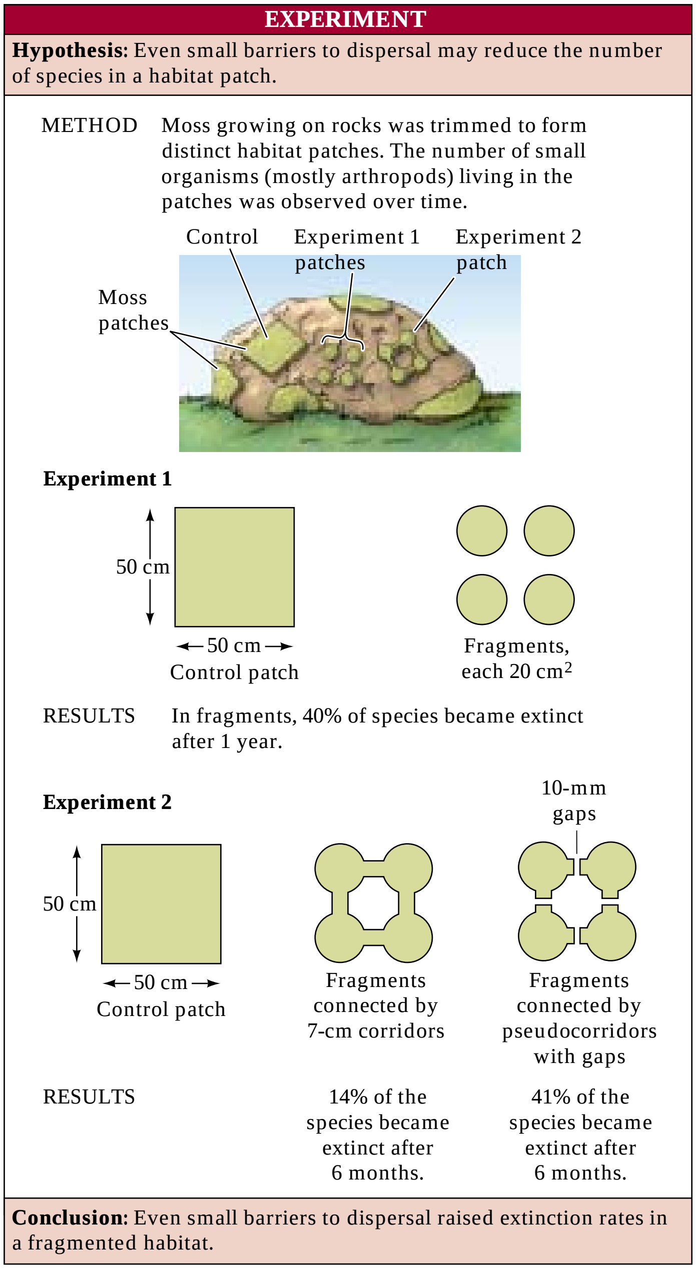
ing stage. At least three butterfly subpopulations became extinct during a severe drought in 1975–1977. The largest patch of suitable butterfly habitat, Morgan Hill, typically supports thousands of butterflies (Figure 54.13). It probably served as a source of individuals that dispersed to and recolonized small patches where the butterflies had become extinct.

In another study, ecologists manipulated the habitat of tiny arthropods (springtails—tiny insects without wings—and mites) to investigate the subpopulation dynamics of these animals. In one experiment, they created isolated patches of the animals' habitat—mosses growing on rocks—by clearing moss from parts of the rock surface (Figure 54.14, Experiment 1). The number of species present in these patches declined about 40 percent within a year, with more rare species than common species disappearing from the patches. The experiment illustrated that small, isolated populations are more likely to become extinct than large populations are.

In a second experiment, the investigators created similar patches, but these patches were connected by narrow corridors of moss that were either intact or disrupted by a barrier only 10 mm wide (Figure 54.14, Experiment 2). Moss patches connected by unbroken corridors contained more species of arthropods a year later than patches whose corridors were discontinuous. Thus, a gap of only 10 mm was sufficient to reduce the rescue effect.



54.13 Subpopulation Dynamics The bay checkerspot butterfly population is divided into a number of subpopulations confined to patches of habitat (serpentine rock) that contain the food plants of its larvae. Extinction of these subpopulations is common.



54.14 Narrow Barriers Suffice to Separate Arthropod Subpopulations Many species of small arthropods went extinct in isolated habitat patches. Recolonization of patches was prevented by barriers to dispersal as small as 10 mm.

Variations in Species' Ranges

Douglas firs are widespread in western North America, whereas giant sequoias are restricted to a few groves in the southern Sierra Nevada of California. The desert pupfish is restricted to a single spring in Death Valley, California, whereas smallmouth bass live in most of the rivers and lakes in eastern North America. Why do the geographic ranges of species vary so much? The factors contributing to this variation include speciation processes, dispersal abilities, and interactions with other species. As you might suspect, not all of the factors that influence geographic ranges are important for all species.

SPECIATION PROCESSES INFLUENCE RANGE SIZES. As we saw in Chapter 24, there are several ways in which a new species can originate. A species that arises by polyploidy inevitably begins with a very small range. Because many polyploid plant species have formed only recently and have not spread much beyond the site of their origin, many of these plants have small ranges. Similarly, species that arise through founder events begin their history with small ranges. In contrast, most species that arise via allopatric speciation begin with large ranges. Finally, as a species declines toward extinction, as may be happening to giant sequoias (Figure 54.15), its range shrinks until it vanishes when the last individual dies.

DISPERSAL ABILITIES RESTRICT GEOGRAPHIC RANGES. As we also saw in Chapter 24, the dispersal abilities of different species vary greatly. The experiments with small arthropods living in mosses on rocks show that even narrow barriers may prevent some species from reaching and colonizing an area. The solitary spring that is home to the desert pupfish is isolated from other bodies of fresh water, so the fish cannot disperse. Thus, the absence of many species from an area is simply due to a failure to get there. Zebra mussels, for

Sequoiadendron giganteum

54.15 The Last Refuge The range of giant sequoias has progressively shrunk to a few remaining groves of trees scattered in the southern Sierra Nevada mountains of California.

example, were not found in North America before 1985 because they were unable to disperse across the Atlantic Ocean from Europe. Lack of suitable habitat was not the reason for their absence, as demonstrated by their dramatic population growth in North America once they were transported there by human activities. Once they reached North America, they were able to disperse rapidly because the larvae are free-swimming and the adults can attach to moving objects, such as boat hulls.

PREDATORS MAY RESTRICT SPECIES' RANGES. Predators may eliminate their prey in some places, but not in others. For example, chorus frogs (*Pseudacris triseriata*) are found in only some of the ponds on islands in Lake Superior. Three major predators—the larvae of a salamander, the nymphs of a large dragonfly, and dytiscid beetles—eat chorus frog tadpoles. An ecologist noticed that the tadpoles were common in ponds with beetles, but rare in ponds with salamander larvae and dragonfly nymphs. In laboratory experiments, he established that the salamander larvae could eat only small tadpoles, but that dragonfly nymphs could eat tadpoles of all sizes. Therefore, he hypothesized that dragonfly nymphs were responsible for eliminating chorus frogs from many ponds. He tested his hypothesis by manipulating densities of predators and prey in ponds. The results showed that dragonfly nymphs can eliminate chorus frogs from ponds that would otherwise be suitable for them (Figure 54.16).

COMPETITION MAY RESTRICT SPECIES' RANGES. How competitive interactions may restrict the ranges of species is illustrated by interactions between two species of barnacles, *Balanus balanoides* and *Chthamalus stellatus*, on rocky North Atlantic seashores. These barnacles have planktonic larvae, which settle between high and low tide levels on the shoreline and become sessile adults. Adult *Chthamalus* generally live higher in the intertidal zone than do adult *Balanus*, and there is little overlap between the two species. What keeps their ranges so distinct?

By experimentally removing one or the other species, researchers have shown that the vertical ranges of adults of both species are greater in the absence of the other species. *Chthamalus* larvae normally settle in large numbers in the *Balanus* zone. If *Balanus* are absent, young *Chthamalus* survive and grow well in the *Balanus* zone, but if *Balanus* are present, they smother, crush, or undercut the *Chthamalus*. *Balanus* larvae also settle in the *Chthamalus* zone, but the young *Balanus* grow slowly there because they lose water rapidly when exposed to air, so *Chthamalus* outcompete *Balanus* in that zone. The result of the competitive interaction between the two species is intertidal zonation, with *Chthamalus* growing above *Balanus* (Figure 54.17).

54.16 Predators Exclude Prey from Some Habitats The speed with which dragonfly nymphs can eliminate tadpoles of the chorus frog from a pond is illustrated by the results of experiments in which populations of predators and prey were manipulated.

EXPERIMENT

Hypothesis: Dragonfly nymphs eliminate chorus frog tadpoles from otherwise suitable ponds.

METHOD Predators (dragonfly nymphs) and prey (tadpoles) were added to ponds in different combinations.

Experiment 1 Ponds 1 and 2 initially had no dragonfly nymphs and many tadpoles.

Experiment 2 Ponds 3 and 4 had many dragonfly nymphs and no tadpoles.

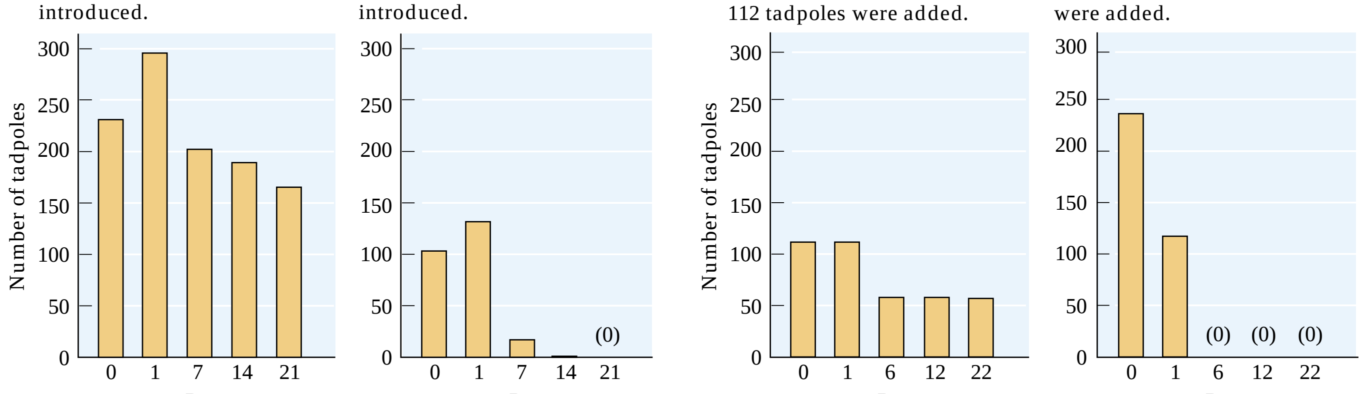
RESULTS

Pond 1: No nymphs introduced.

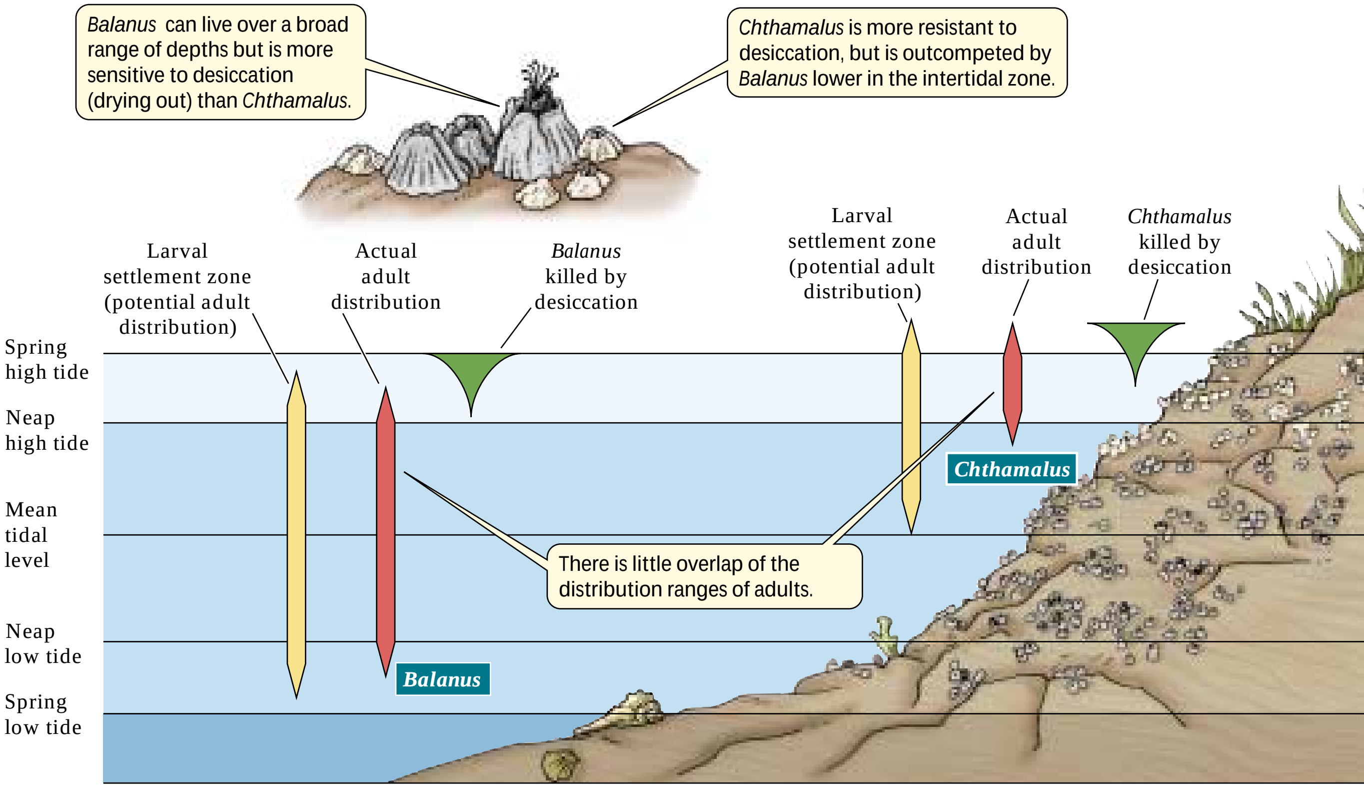
Pond 2: 33 nymphs introduced.

Pond 3: All but 7 dragonfly nymphs were removed, and 112 tadpoles were added.

Pond 4: 95 dragonfly nymphs were present, and 234 tadpoles were added.



Conclusion: Dragonfly nymphs can eliminate tadpoles from otherwise suitable ponds.



54.17 Competition Restricts the Intertidal Ranges of Barnacles Interspecific competition between *Balanus* and *Chthamalus* makes the zone each species occupies smaller than the zone it could occupy in the absence of the other species. The width of the red and gold bars is proportional to the density of the populations.

Sessile animals such as barnacles and many plants compete for space, but most mobile animals compete for food. As an example of how competition can restrict the ranges of such species, consider the distribution of two species of wasps in California. These wasps lay their eggs on scale insects, and the larvae that hatch from those eggs burrow into, eat, and kill the scale insects. Both wasps were introduced to control outbreaks of scale insects that were damaging citrus orchards. The Mediterranean wasp *Aphytis chrysomphali* was introduced to southern California around 1900, but it failed to control the scale insects. Therefore, a close relative from China, *A. lingnanensis*, was introduced in 1948. *A. lingnanensis*, which has a higher reproductive rate, increased rapidly. Within a decade it had not only reduced population densities of the scale insects, but had also displaced *A. chrysomphali* from most of its range in California.

For many centuries, people have tried to reduce populations of species they consider undesirable, such as scale insects, and maintain populations of desirable species. Efforts to control and manage populations of organisms are more likely to be successful if they are based on knowledge of how populations grow and are regulated. Let's see how such information can be used to manage populations.

Managing Populations

A general principle of population dynamics is that both the total number of births and the growth rates of individuals tend to be highest when a population is well below its carrying capacity (see Figure 54.8). Therefore, if we wish to maximize the number of individuals that can be harvested from a population, we should manage the population so that it is far enough below carrying capacity to have high birth and growth rates. Hunting seasons for game birds and mammals are established with this objective in mind.

Demographic traits determine sustainable harvest levels

Populations that have high reproductive capacities can persist even if harvest rates are high. In such populations (which include many species of fish), each female may lay thousands or millions of eggs. In these fast-reproducing populations, individual growth is often density-dependent. If prereproductive individuals are harvested at a high rate, the remaining individuals may grow faster. Some fish populations can be harvested heavily because only a modest number of females must survive to reproductive age to produce the eggs needed to maintain the population.

Fish can, of course, be overharvested. Many fish populations have been greatly reduced because so many individuals were harvested that too few reproductive adults survived to maintain the population. The Georges Bank off the coast of New England—a source of cod, halibut, and other prime food fishes—was exploited so heavily during the twentieth century that many fish stocks were reduced to levels insufficient to support a commercial fishery. The fishery has remained closed into the twenty-first century.

The whaling industry has also engaged in excessive harvests. The blue whale, Earth's largest animal, was the first whale species to be hunted nearly to extinction. The industry then turned to smaller species of whales that were still numerous enough to support commercially viable whaling operations (Figure 54.18).

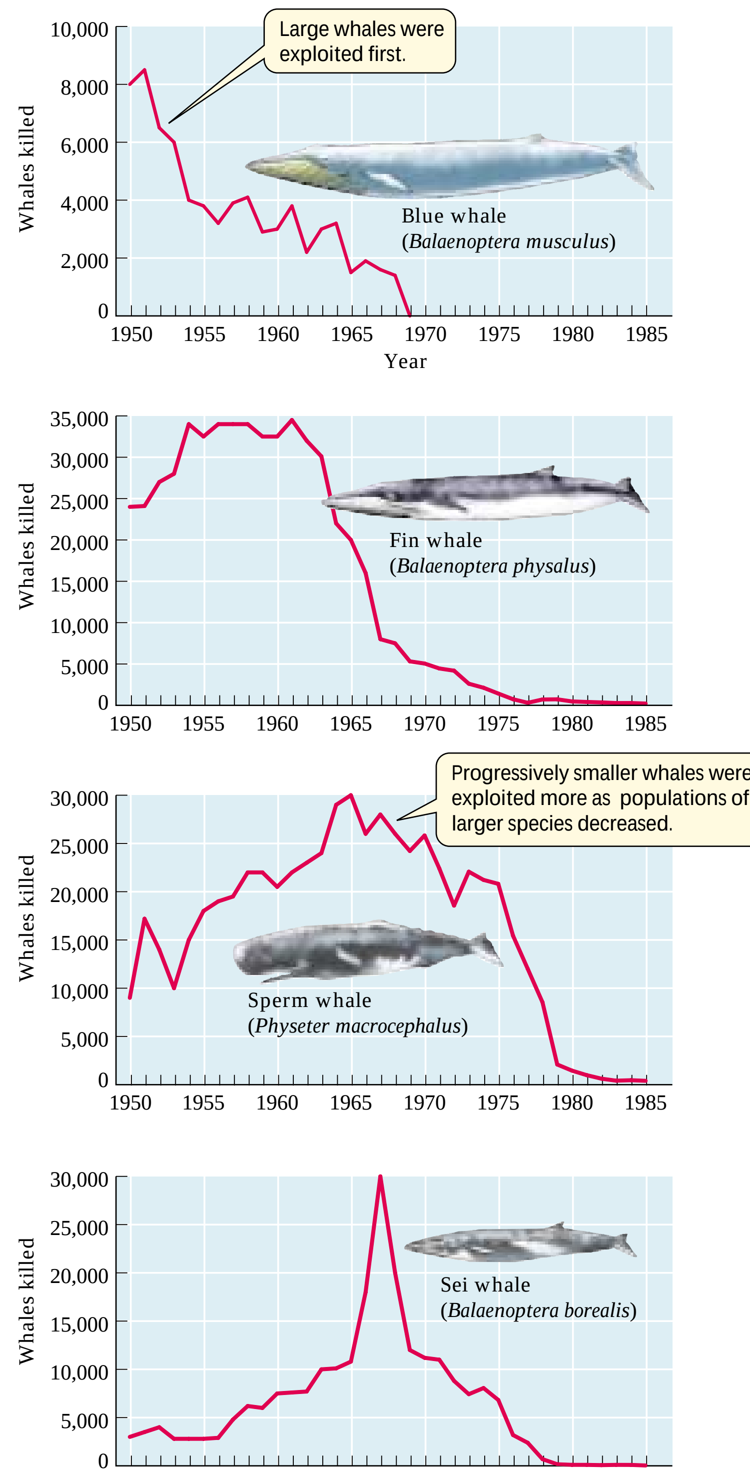
Management of whale populations is difficult for two reasons. First, unlike fish, whales reproduce at very low rates. They have long prereproductive periods before they mature, produce only one offspring at a time, and have long intervals between births. Thus, many adult whales are needed to produce even a small number of offspring. Second, because whales are distributed widely throughout Earth's oceans, they are an international resource whose conservation and wise management depends upon cooperative action by all whaling nations. This goal continues to be difficult to achieve.

Demographic information is used to control populations

The same management principles apply if we wish to reduce the size of populations of undesirable species and keep them at low densities. At densities well below carrying capacity, populations typically have high birth rates, and can therefore withstand higher death rates than they can when they are closer to carrying capacity.

When population dynamics are influenced primarily by factors that operate in a density-dependent manner, killing part of a population typically reduces it to a density at which it reproduces at a higher rate. A more effective approach to reducing such a population is to remove its resources, thereby lowering the carrying capacity of its environment. We can rid our dumps and cities of rats more easily by making garbage unavailable (reducing the carrying capacity of the rats' environment) than by poisoning rats (which only increases their reproductive rate). However, this option may not exist in agriculture, in which a high density of the crop is the management objective.

Similarly, if we wish to preserve a rare species, the most important step usually is to provide it with suitable habitat. If habitat is available, the species will usually reproduce at rates sufficient to maintain its population. If the habitat is insufficient, preserving the species usually requires expensive and continuing intervention, such as providing extra food.



54.18 Overexploitation of Whales These graphs show the numbers of whales of four species killed each year from 1950 to 1985. All four species were driven to very low population levels by sustained hunting.

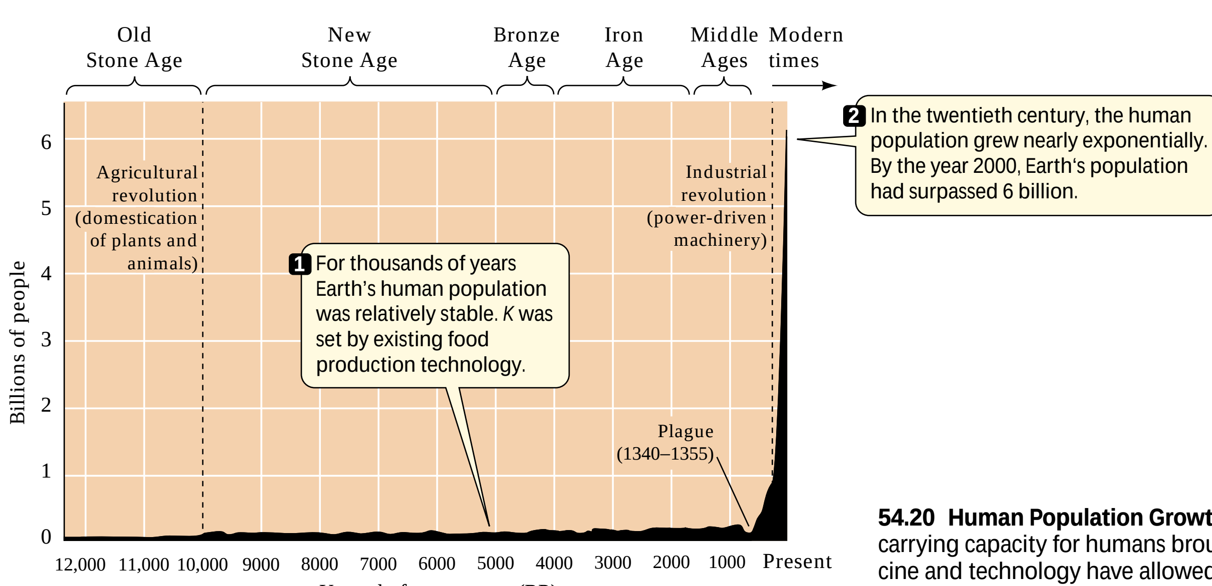
54.19 Biological Control of a Pest These *Cactoblastis* caterpillars are consuming an *Opuntia* cactus in Australia.

Humans often attempt to reduce the populations of introduced species that have dramatically increased in density by introducing their predators and parasites. For example, the cactus *Opuntia*, introduced into Australia from South America, spread rapidly and became a pest over vast expanses of valuable sheep-grazing land. *Opuntia* was controlled in Australia by the introduction of a moth (*Cactoblastis cactorum*) whose larvae eat *Opuntia*. Once female moths find a patch of cactus and lay their eggs on it, the larvae that hatch from those eggs completely destroy the patch (Figure 54.19). However, new patches of cactus arise in other places from seeds dispersed by birds. These new patches flourish until they are found and destroyed by *Cactoblastis*. Over a large region, the numbers of both *Opuntia* and *Cactoblastis* are now fairly constant and low, but in local areas, there are extreme oscillations caused by the extermination of first the cactus and then the moth. Today, both *Opuntia* and *Cactoblastis* in Australia are distributed as scattered subpopulations among which individuals occasionally disperse.

Can we manage our own population?

Managing our own population has become a matter of great concern because the size of the human population is responsible for most of the environmental problems we are facing today, from pollution to extinctions of other species. For thousands of years, Earth's carrying capacity for human populations was set at a low level by food and water supplies and disease. We saw in Chapter 53 how human social behavior and specialization has allowed us to develop technologies for increasing our resources and combating diseases. The domestication of plants and animals, improved crops and farm yields, mining and use of fossil fuels, and the development of modern medicine have all contributed to the staggering increase in Earth's human population (Figure 54.20).

What is Earth's present carrying capacity for people? Today's carrying capacity is set in part by Earth's ability to absorb the by-products, especially carbon dioxide, of our enormous consumption of fossil fuel energy; by water availability (in many areas); and by whether we are willing to cause the extinction of millions of other species to accommodate our increasing use of Earth's resources. We will explore some of the consequences of high human population densities and high per capita use of resources for the survival of other species in Chapter 57.



54.20 Human Population Growth Increases in Earth's carrying capacity for humans brought about by medicine and technology have allowed human populations to grow rapidly.

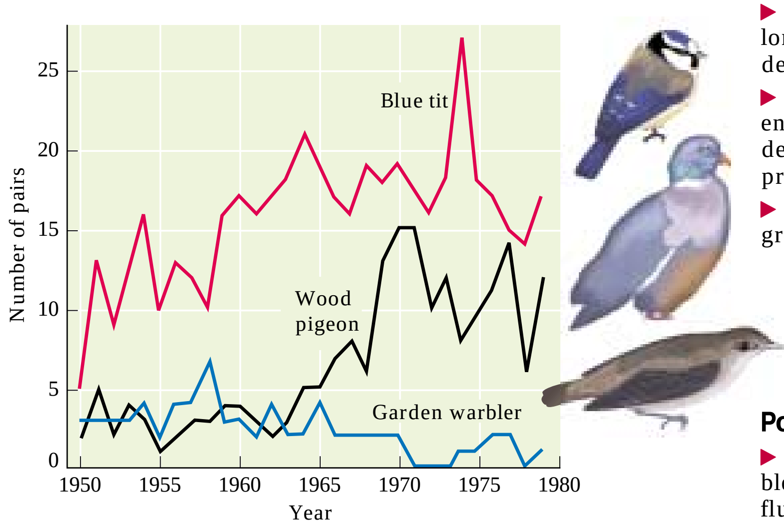
Regional and Global Processes Influence Local Population Dynamics

Between 1950 and 1980, annual counts of breeding birds were conducted in Eastern Wood, in southeastern England. During that time, populations of some species increased while others decreased (Figure 54.21). For example, the population of wood pigeons more than doubled, but the population of garden warblers decreased to zero in 1971; no more than two pairs have bred in the wood since then. The population of blue tits increased from just a few pairs to an average of more than 15 pairs. Why did these populations change so differently?

No matter how intensively ecologists might have studied the birds of Eastern Wood, they could not have answered that question, because populations of two of these three species were strongly influenced by events remote from Eastern Wood. Wood pigeons increased greatly over most of southern England during this 30-year period because of the widespread adoption of oilseed rape as an agricultural crop. Rape fields provide wood pigeons with abundant winter food. Garden warblers decreased because their overwinter survival was poor due to a severe drought on their wintering grounds in West Africa.

The population of blue tits was influenced primarily by changes within Eastern Wood itself. Until the early 1950s, trees in Eastern Wood were periodically felled and sold for timber. After the cutting stopped, more holes, in which blue tits nest, became available in mature and dead trees.

Local population dynamics are often influenced both by local interactions and by more distant or remote events, perhaps even on different continents. How processes occurring at varying spatial and temporal scales influence the structure of ecological communities is the focus of the next chapter.



54.21 Populations May Be Influenced by Remote Events Populations of some birds increased in Eastern Wood, England, while others decreased. The wood pigeon (*Columba palumbus*) and garden warbler (*Sylvia borin*) population shifts were strongly influenced by different events that took place far from Eastern Wood. Only the blue tit (*Parus caeruleus*) population was affected most strongly by events within Eastern Wood itself.

Chapter Summary

Populations in Space and Time

- A population consists of all the individuals of a species within a given area.
- The number of individuals of a species per unit of area (or volume) is its population density. Dense populations often exert strong influences on populations of other species.
- Life tables summarize information about births and deaths in populations. **Review Table 54.1**
- Graphs of survivorship in relation to age show when individuals survive well and when they do not. **Review Figure 54.1**
- The age distribution of individuals in a population reveals much about the recent history of births and deaths in the population. The timing of births and deaths may influence age distributions for many years. **Review Figure 54.2**

Types of Ecological Interactions

- Individuals of two populations may interact in ways that may benefit or harm either or both participants. **Review Table 54.2. See Web/CD Activity 54.1**

Factors Influencing Population Densities

- Species with small individuals typically achieve higher population densities than species with large individuals. **Review Figure 54.4**
- Introduced species sometimes achieve great population densities. **Review Figure 54.5**

Fluctuations in Population Densities

- All populations have the potential to grow exponentially under optimal conditions. **Review Figure 54.6. See Web/CD Tutorial 54.1**
- No population can maintain exponential growth for very long because environmental limits cause birth rates to drop and death rates to rise.
- The number of individuals of a particular species that an environment can support—called the carrying capacity (K)—is determined by the availability of resources and by disease and predators.
- A population in a limited environment shows a logistic growth pattern, in which growth rates decrease as the carrying capacity is approached. **Review Figure 54.7. See Web/CD Activity 54.2 and Tutorial 54.2**
- The density of a population is influenced by the combined effects of all density-dependent and density-independent factors affecting it. **Review Figure 54.8**

Population Fluctuations

- Populations do not fluctuate as much as theoretically possible, but some fluctuate much more than others. The amount of fluctuation is influenced by body size, reproductive rate, and range size. **Review Figure 54.9**
- Population fluctuations may be strongly influenced by years of good reproduction. **Review Figure 54.10**
- Predator–prey interactions may generate population cycles. **Review Figures 54.11, 54.12**
- Populations of many species exist as small, fragmented subpopulations. Extinction of subpopulations is common, but indi-

viduals from other fragments may recolonize them. **Review Figures 54.13, 54.14.** **See Web/CD Tutorial 54.4**

See Web/CD Tutorial 54.3

Variation in Species' Ranges

▶ Some species are restricted to very small areas, whereas others are widely distributed on Earth.

▶ Species' ranges are influenced by speciation processes, dispersal abilities, predators, and competition. **Review Figures 54.16, 54.17**

Managing Populations

▶ Humans can use the principles of population dynamics to control and manage populations of desirable and undesirable species. Nevertheless, humans have overexploited many populations. **Review Figure 54.18**

Regional and Global Processes Influence Local Population Dynamics

▶ Population densities may be influenced by both local conditions and remote events. **Review Figure 54.20**

Self-Quiz

1. The number of individuals of a species per unit of area is known as its
   a. population size.
   b. population density.
   c. population structure.
   d. subpopulation.
   e. biomass.
2. The age distribution of a population is determined by
   a. the timing of births.
   b. the timing of deaths.
   c. the timing of both births and deaths.
   d. the rate at which the population is growing.
   e. All of the above
3. Which of the following is *not* a demographic event?
   a. Growth
   b. Birth
   c. Death
   d. Immigration
   e. Emigration
4. A group of individuals born at the same time is known as a
   a. deme.
   b. subpopulation.
   c. Mendelian population.
   d. cohort.
   e. taxon.
5. Two organisms that use the same resources when those resources are in short supply are said to be
   a. predators.
   b. competitors.
   c. mutualists.
   d. commensalists.
   e. amensalists.
6. Damage caused to shrubs by branches falling from overhead trees is an example of
   a. interference competition.
   b. partial predation.
   c. amensalism.
   d. commensalism.
   e. diffuse coevolution.
7. A population grows at a rate closest to its intrinsic rate of increase when
   a. its birth rates are the highest.
   b. its death rates are the lowest.
   c. environmental conditions are optimal.
   d. it is close to the environmental carrying capacity.
   e. it is well below the environmental carrying capacity.
8. Immigrants that prevent a subpopulation from becoming extinct result in a
   a. colonization effect.
   b. rescue effect.
   c. metapopulation effect.
   d. genetic drift effect.
   e. salvage effect.
9. Density-dependent population regulation is strongest when
   a. only birth rates change in response to density.
   b. only death rates change in response to density.
   c. diseases spread in populations at all densities.
   d. both birth and death rates change in response to density.
   e. population densities fluctuate very little.
10. The best way to reduce the population of an undesirable species in the long term is to
   a. reduce the carrying capacity of the environment for the species.
   b. selectively kill reproducing adults.
   c. selectively kill pre-reproductive individuals.
   d. attempt to kill individuals of all ages.
   e. sterilize individuals.

For Discussion

1. Why are big, fierce animals rare?
2. Why do predator–prey interactions often generate cycles or great fluctuations in population densities? Would you expect lynx populations to fluctuate as much as they do if lynx had a variety of abundant prey species available to them?
3. Most organisms whose populations we wish to manage for higher densities are long-lived and have low reproductive rates, whereas most organisms whose populations we attempt to reduce are short-lived, but have high reproductive rates. What is the significance of this difference for management strategies and the effectiveness of management practices?
4. In the mid-nineteenth century, the human population of Ireland was largely dependent upon a single food crop, the potato. When a disease caused the potato crop to fail, the Irish population declined drastically for three reasons: (1) a large percentage of the population emigrated to the United States and other countries; (2) the average age of a woman at marriage increased from about 20 to about 30 years; and (3) many families starved to death rather than accept food from Britain. None of these social changes was planned at the national level, yet all contributed to adjusting the population size to the new carrying capacity. Discuss the ecological principles involved, using examples from other species. What would you have done had you been in charge of the national population policy for Ireland at that time?
5. Because some species introduced to control a pest have become pests themselves, some scientists argue that species introductions should not be used under any circumstances to control pests. Others argue that, provided they are properly researched and controlled, we should continue to use introductions as part of our set of tools for managing pest populations. Which view do you support? Why?