Ecology and Behavior

Why do tropical songbirds lay fewer eggs?

Sometimes odd generalizations in science lead to unexpected places. Take, for example, a long obscure monograph published in 1944 by British ornithologist (bird expert) Reginald Moreau in the journal Ibis on bird eggs. Moreau had worked in Africa for many years before moving to a professorship in England in the early 1940s. He was not in England long before noting that the British songbirds seemed to lay more eggs than he was accustomed to seeing in nests in Africa. He set out to gather information on songbird clutch size (that is, the number of eggs in a nest) all over the world.

Wading through a mountain of data (his *Ibis* paper is 51 pages long!), Moreau came to one of these odd generalizations: songbirds in the tropics lay fewer eggs than their counterparts at higher latitudes (see above *right*). Tropical songbirds typically lay a clutch of 2 or 3 eggs, on average, while songbirds in temperate and subarctic regions generally lay clutches of 4 to 6 eggs, and some species as many as 10. The trend is general, affecting all groups of songbirds in all regions of the world.

What is a biologist to make of such a generalization? At first glance, we would expect natural selection to maximize evolutionary fitness—that is, songbirds the world over should have evolved to produce as many eggs as possible. Clearly, the birds living in the tropics have not read Darwin, as they are producing only half as many eggs as they are capable of doing.

A way out of this quandary was proposed by ornithologist Alexander Skutch in 1949. He argued that birds produced just enough offspring to offset deaths in the population. Any extra offspring would be wasteful of individuals, and so minimized by natural selection. An interesting idea, but it didn't hold water. Bird populations are not smaller in the tropics, or related to the size of the populations there.

A second idea, put forward a few years earlier in 1947 by a colleague of Moreau's, David Lack, was more promising. Lack, one of the twentieth-century's great biologists, argued that few if any birds ever produce as many eggs as they might under ideal conditions, for the simple reason that conditions in nature are rarely ideal. Natural selection will indeed tend to maximize reproduc-


This Kentucky warbler is tending her nest of eggs. A similar species in the tropics would lay fewer eggs. Why?

tive rate (that is, the number of eggs laid in clutches) as Darwin predicted, but only to the greatest level possible within the limits of resources. There is nothing here that would have surprised Darwin. Birds lay fewer eggs in the tropics simply because parents can gather fewer resources to provide their young there—competition is just too fierce, resources too scanty.

Lack went on to construct a general theory of clutch size in birds. He started with the sensible assumption that in a resource-limited environment birds can supply only so much food to their young. Thus, the more offspring they have, the less they can feed each nestling. As a result, Lack proposed that natural selection will favor a compromise between offspring number and investment in each offspring, which maximizes the number of offspring which are fed enough to survive to maturity.

The driving force behind Lack's theory of optimal clutch size is his idea that broods with too many offspring would be undernourished, reducing the probability that the chicks would survive. In Lack's own words:

"The average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and at the season in question, i.e. ... natural selection eliminates a disproportionately large number of young in those clutches which are higher than the average, through the inability of the parents to get enough food for their young, so that some or all of the brood die before or soon after fledging (leaving the nest), with the result that few or no descendants are left with their parent's propensity to lay a larger clutch."
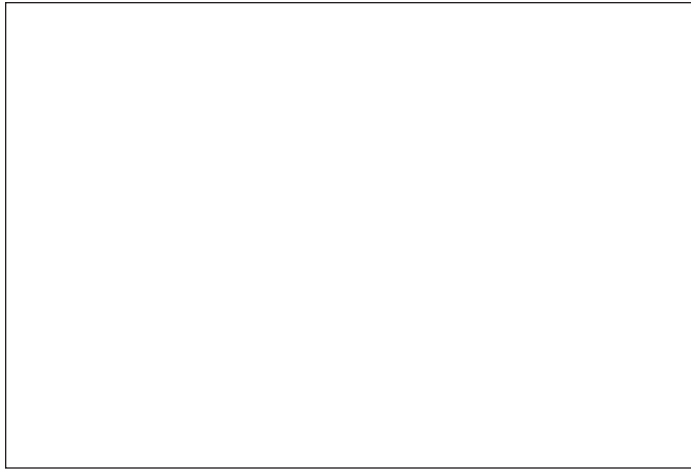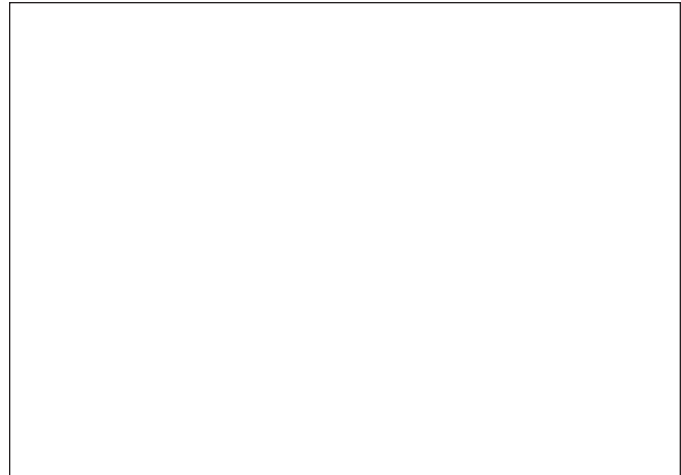
Testing Lack's theory of optimum clutch size. In this study from woods near Oxford, England, researchers found that the most common clutch size was 8, even though clutches of 12 produced the greatest number of surviving offspring. (After Boyce and Perrins, 1987.)

Two theories of optimum clutch size. David Lack's theory predicts that optimum clutch size will be where reproductive success of the clutch is greatest. George Williams's theory predicts that optimum clutch size will be where the *net* benefit is greatest—that is, where the difference between the cost of reproduction and the reproductive success of the clutch is greatest.

The Experiment

Lack's theory is attractive because of its simplicity and common sense—but is it right? Many studies have been conducted to examine this hypothesis. Typically, experimenters would remove eggs from nests, and look to see if this improved the survivorship of the remaining offspring. If Lack is right, then it should, as the remaining offspring will have access to a larger share of what the parents can provide. Usually, however, removal of eggs did not seem to make any difference. Parents just adjusted down the amount of food they provided. The situation was clearly more complicated than Lack's simple theory envisioned.

One can always argue with tests such as these, however, as they involve direct interference with the nests, potentially having a major influence on how the birds behave. It is hard to believe that a bird caring for a nest of six eggs would not notice when one turned up missing. A clear test of Lack's theory would require avoiding all intervention.

Just such a test was completed in 1987 in the woods near Oxford, England. Over many years, Oxford University researchers led by Professor Mark Boyce (now at the University of Wyoming, Laramie) carefully monitored nests of a songbird, the greater tit, very common in the English countryside. They counted the number of eggs laid in each nest (the clutch size) and then watched to see how many of the offspring survived to fly away from the nest. Nothing was done to interfere with the birds. Over 22 years, they patiently examined 4489 nests.

The Results

The Oxford researchers found that the average clutch size was 8 eggs, but that nests with the greatest number of surviving offspring had not 8 but 12 eggs in them! Clearly, Lack's theory is wrong. These birds are not producing as many offspring as natural selection to maximize fitness (that is, number of surviving offspring) would predict (see above *left*).

Lack's proposal had seemed eminently sensible. What was wrong? In 1966 the evolutionary theorist George Williams suggested the problem was that Lack's theory ignores the cost of reproduction (see above). If a bird spends too much energy feeding one brood, then it may not survive to raise another. Looking after a large clutch may extract too high a price in terms of future reproductive success of the parent. The clutch size actually favored by natural selection is adjusted for the wear-and-tear on the parents, so that it is almost always smaller than the number which would produce the most offspring in that nest—just what the Oxford researchers observed.

However, even William's "cost-of-reproduction" is not enough to completely explain Boyce's greater tit data. There were marked fluctuations in the weather over the years that the Oxford researchers gathered their data, and they observed that harsh years decreased survival of the young in large nests more than in small ones. This "bad-year" effect reduces the fitness of individuals laying larger clutches, and Boyce argues that it probably contributes at least as much as cost-of-reproduction in making it more advantageous, in the long term, for birds to lay clutches smaller than the Lack optimum.

24

Population Ecology

Concept Outline

24.1 Populations are individuals of the same species that live together.

Population Ecology. The borders of populations are determined by areas in which individuals cannot survive and reproduce. Population ranges expand and contract through time as conditions change.

Population Dispersion. The distribution of individuals in a population can be clumped, random, or even.

Metapopulations. Sometimes, populations are arranged in networks connected by the exchange of individuals.

24.2 Population dynamics depend critically upon age distribution.

Demography. The growth rate of a population is a sensitive function of its age structure; populations with many young individuals grow rapidly as these individuals enter reproductive age.

24.3 Life histories often reflect trade-offs between reproduction and survival.

The Cost of Reproduction. Evolutionary success is a trade-off between investment in current reproduction and in growth that promotes future reproduction.

24.4 Population growth is limited by the environment.

Biotic Potential. Populations grow if the birthrate exceeds the death rate until they reach the carrying capacity of their environment.

The Influence of Population Density. Some of the factors that regulate a population's growth depend upon the size of the population; others do not.

Population Growth Rates and Life History Models. Some species have adaptations for rapid, exponential population growth, whereas other species exhibit slower population growth and have intense competition for resources.

24.5 The human population has grown explosively in the last three centuries.

The Advent of Exponential Growth. Human populations have been growing exponentially since the 1700s and will continue to grow in developing countries because of the number of young people entering their reproductive years.
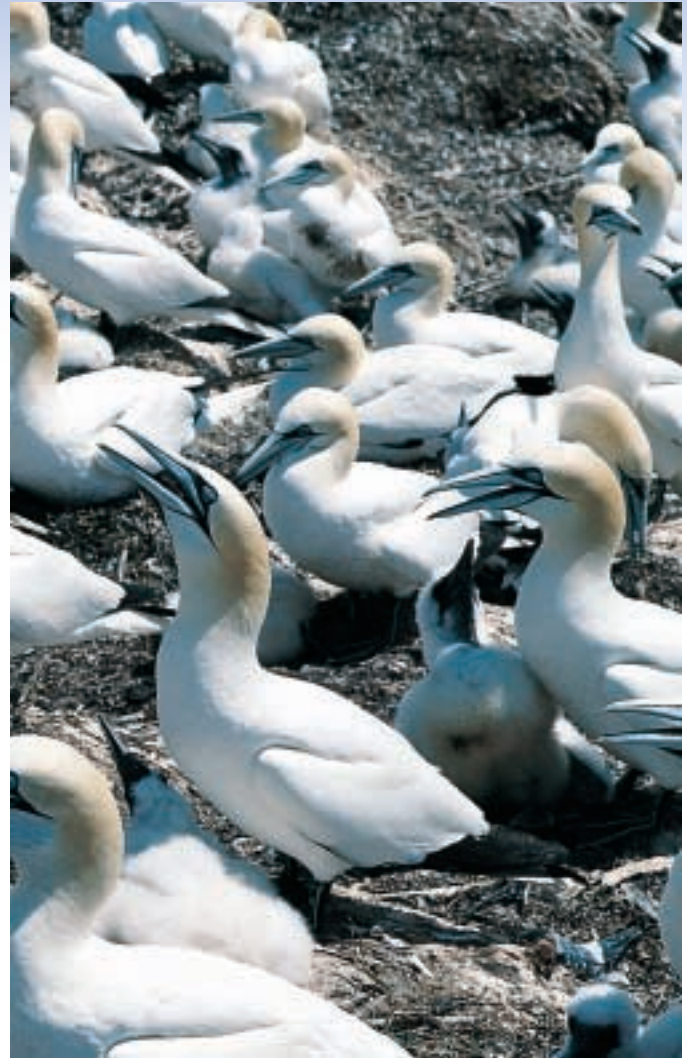

FIGURE 24.1
Life takes place in populations. This population of gannets is subject to the rigorous effects of reproductive strategy, competition, predation, and other limiting factors.

Ecology, the study of how organisms relate to one another and to their environments, is a complex and fascinating area of biology that has important implications for each of us. In our exploration of ecological principles, we will first consider the properties of populations, emphasizing population dynamics (figure 24.1). In chapter 25, we will discuss communities and the interactions that occur in them. Chapter 26 moves on to focus on animals and how and why they behave as they do. Chapter 27 then deals with behavior in an environmental context, the extent to which natural selection has molded behaviors adaptively.

Population Ecology

Organisms live as members of **populations,** groups of individuals of a species that live together. In this chapter, we will consider the properties of populations, focusing on elements that influence whether a population will grow or shrink, and at what rate. The explosive growth of the world's human population in the last few centuries provides a focus for our inquiry.

A population consists of the individuals of a given species that occur together at one place and time. This flexible definition allows us to speak in similar terms of the world's human population, the population of protozoa in the gut of an individual termite, or the population of deer that inhabit a forest. Sometimes the boundaries defining a boundary are sharp, such as the edge of an isolated mountain lake for trout, and sometimes they are more fuzzy, such as when individuals readily move back and forth between areas, like deer in two forests separated by a cornfield.

Three aspects of populations are particularly important: the range throughout which a population occurs, the dispersion of individuals within that range, and the size a population attains.
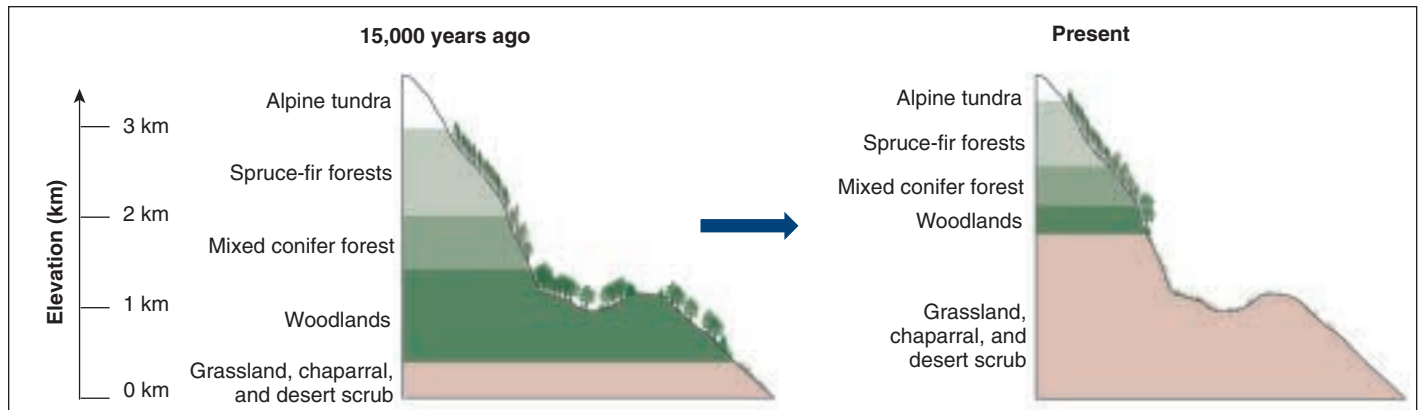
Population Distributions

No population, not even of humans, occurs in all habitats throughout the world. Most species, in fact, have relatively limited geographic ranges. The Devil's Hole pupfish, for example, lives in a single hot water spring in southern Nevada, and the Socorro isopod is known from a single spring system in Socorro, New Mexico (figure 24.2). At the other extreme, some species are widely distributed. Populations of some whales, for example, are found throughout all of the oceans of the northern or southern hemisphere.

In chapter 29 we will discuss the variety of environmental challenges facing organisms. Suffice it to say for now that no population contains individuals adapted to live in all of the different environments on the earth. Polar bears are exquisitely adapted to survive the cold of the Arctic, but you won't find them in the tropical rain forest. Certain bacteria can live in the near boiling waters of Yellowstone's geysers, but they do not occur in cooler streams that are nearby. Each population has its own requirements—temperature, humidity, certain types of food, and a host of other factors—that determine where it can live and reproduce and where it can't. In addition, in places that are otherwise suitable, the presence of predators, competitors, or parasites may prevent a population from occupying an area.
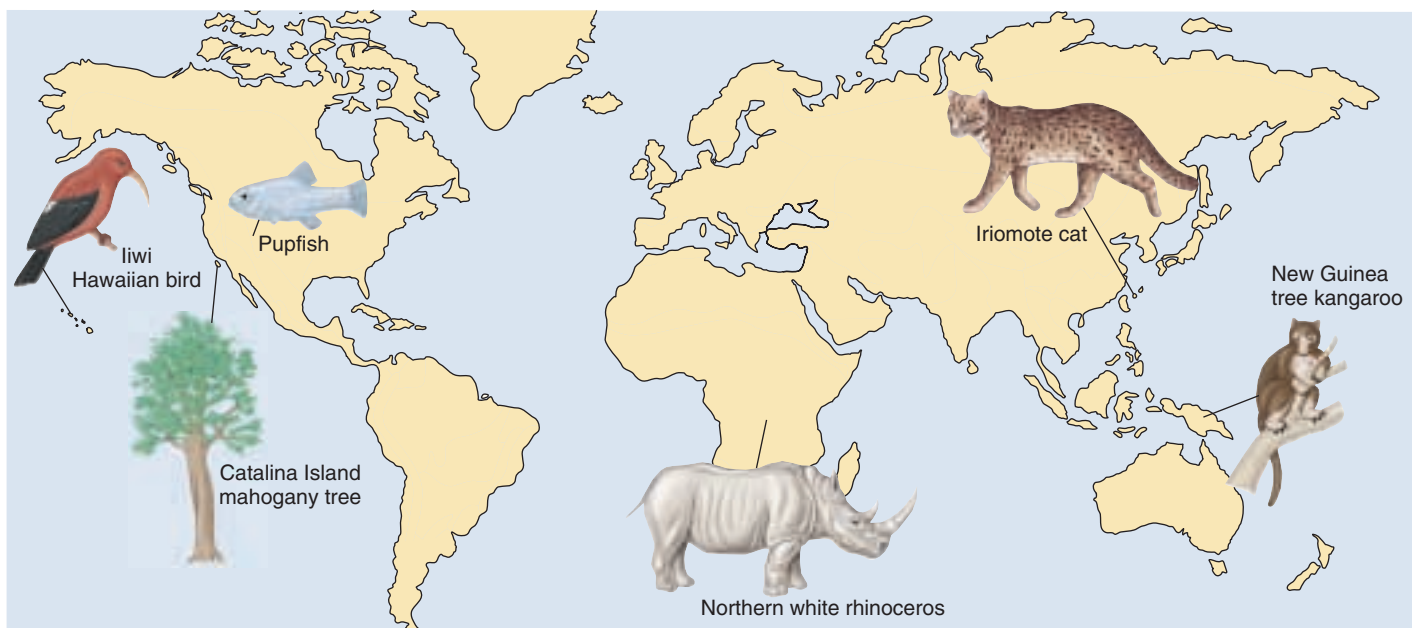
FIGURE 24.2
Species that occur in only one place. These species, and many others, are only found in a single population. All are endangered species, and should anything happen to their single habitat, the population—and the species—would go extinct.
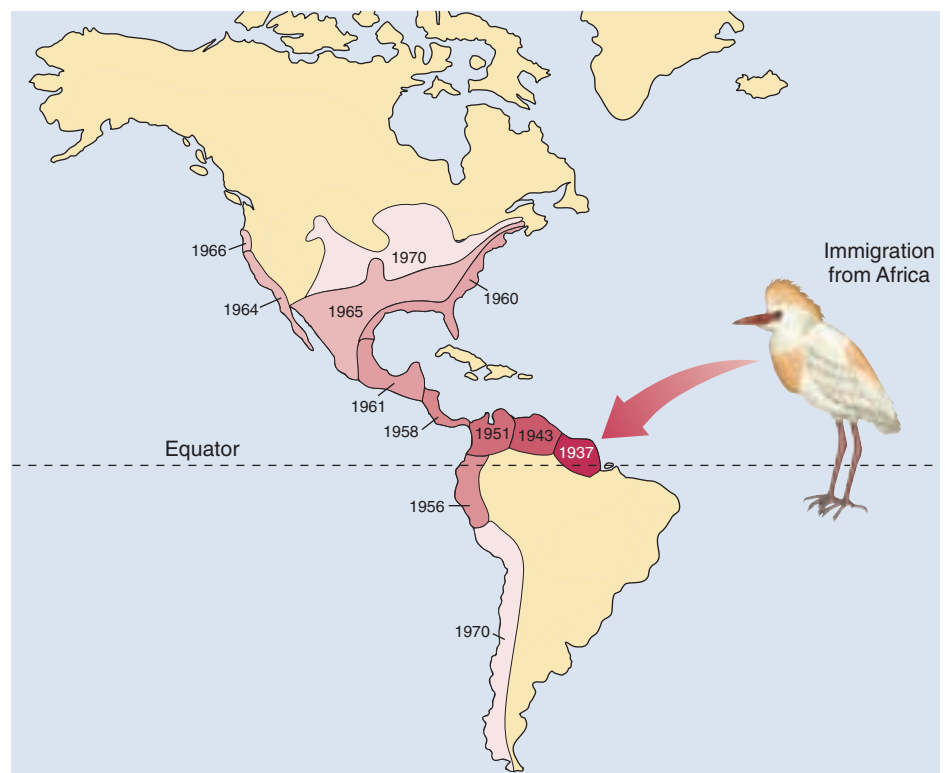
FIGURE 24.3
Altitudinal shifts in population ranges. During the glacial period 15,000 years ago, conditions were cooler than they are now. As the climate has warmed, tree species that require colder temperatures have shifted their distributional range upward in altitude so that they live in the climatic conditions to which they are adapted.

Range Expansions and Contractions

Population ranges are not static, but, rather, change through time. These changes occur for two reasons. In some cases, the environment changes. For example, as the glaciers retreated at the end of the last ice age, approximately 10,000 years ago, many North American plant and animal populations expanded northward. At the same time, as climates have warmed, species have experienced shifts in the elevation at which they are found on mountains (figure 24.3).

In addition, populations can expand their ranges when they are able to circumvent inhospitable habitat to colonize suitable, previously unoccupied areas. For example, the cattle egret is native to Africa. Some time in the late 1800s, these birds appeared in northern South America, having made the nearly 2000-mile transatlantic crossing, perhaps aided by strong winds. Since then, they have steadily expanded their range such that they now can be found throughout most of the United States (figure 24.4).

FIGURE 24.4
Range expansion of the cattle egret. Although the cattle egret—so-named because it follows cattle and other hoofed animals, catching any insects or small vertebrates that they disturb—first arrived in South America in the late 1800s, the oldest preserved specimen dates from the 1930s. Since then, the range expansion of this species has been well documented, as it has moved westward and up into much of North America, as well as down the western side of the Andes to near the southern tip of South America.

Population Dispersion

Another key characteristic of population structure is the way in which individuals of a population are arranged. They may be randomly spaced, uniformly spaced, or clumped (figure 24.5).

Randomly spaced

Individuals are randomly spaced within populations when they do not interact strongly with one another or with nonuniform aspects of their microenvironment. Random distributions are not common in nature. Some species of trees, however, appear to exhibit random distributions in Amazonian rain forests.
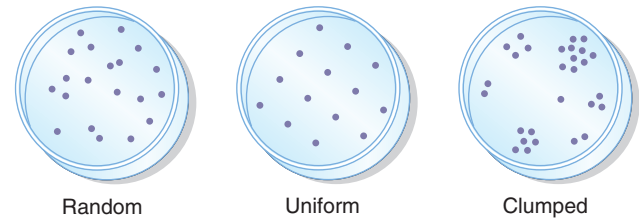
Uniformly spaced

Individuals often are uniformly spaced within a population. This spacing may often, but not always, result from competition for resources. The means by which it is accomplished, however, varies.

In animals, uniform spacing often results from behavioral interactions, which we will discuss in chapter 27. In many species, individuals of one or both sexes defend a territory from which other individuals are excluded. These territories serve to provide the owner with exclusive access to resources such as food, water, hiding refuges, or mates and tend to space individuals evenly across the habitat. Even in nonterritorial species, individuals often maintain a defended space into which other animals are not allowed to intrude.
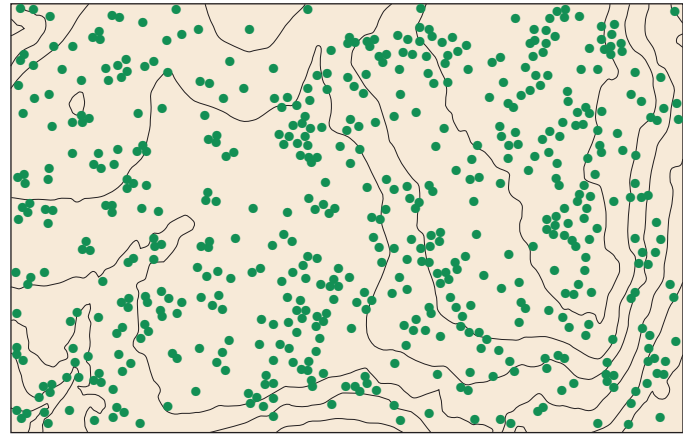
Among plants, uniform spacing also is a common result of competition for resources. In this case, however, the spacing results from direct competition for the resources. Closely spaced individual plants will contest for available sunlight, nutrients, or water. These contests can be direct, such as one plant casting a shadow over another, or indirect, such as two plants competing to see which is more efficient at extracting nutrients or water from a shared area. Only plants that are spaced an adequate distance from each other will be able to coexist, leading to uniform spacing.

Random   Uniform   Clumped

(a) Bacterial colonies

(b) Random distribution of *Brosimum alicastrum*

(c) Uniform distribution of *Coccoloba coronata*

(d) Clumped distribution of *Chamguava schippii*
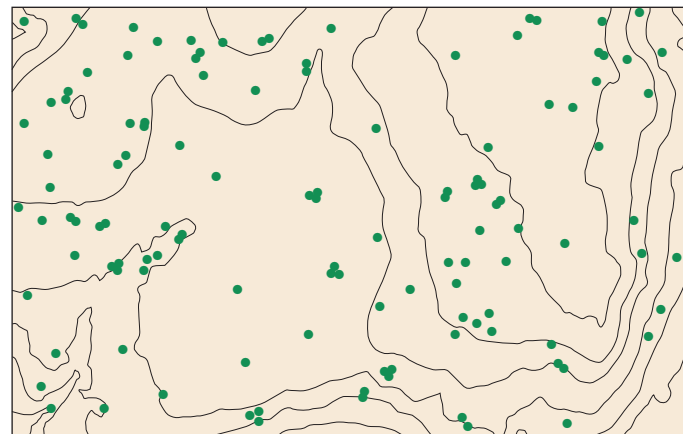
FIGURE 24.5
Population dispersion. (*a*) Different arrangements of bacterial colonies. The different patterns of dispersion are exhibited by three different species of trees from the same locality in the Amazonian rain forest. (*b*) *Brosimum alicastrum* is randomly dispersed, (*b*) *Coccoloba coronata* is uniformly dispersed, and (*d*) *Chamguava schippii* exhibits a clumped distribution.
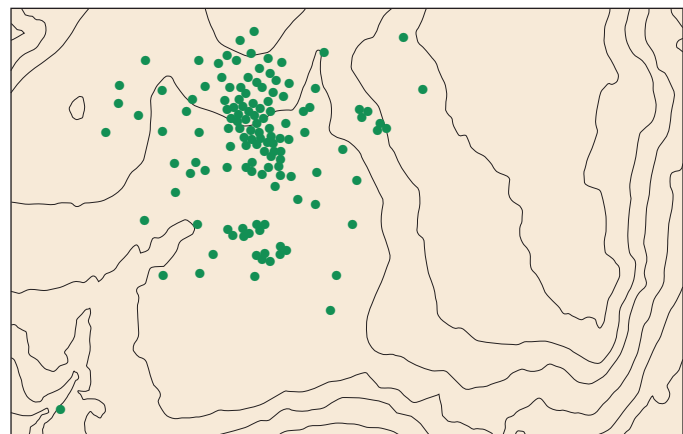
Windblown
fruits

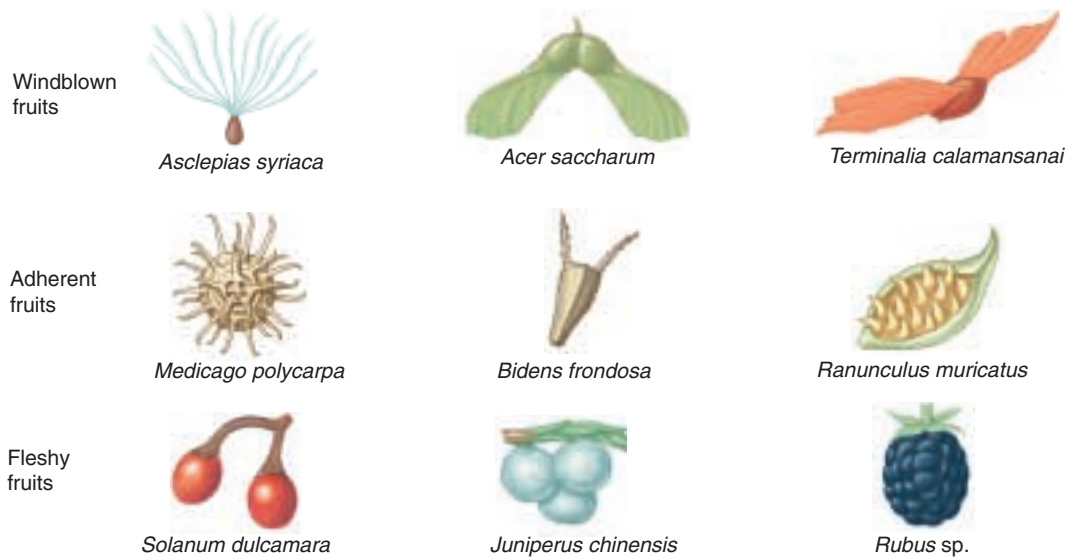*Asclepias syriaca*

Acer saccharum

Terminalia calamansanai

Adherent
fruits

Medicago polycarpa

Bidens frondosa

Ranunculus muricatus

Fleshy
fruits

Solanum dulcamara

Juniperus chinensis

Rubus sp.

FIGURE 24.6
Some of the many adaptations of seeds to facilitate dispersal. Seeds have evolved a number of different means of moving long distances from their maternal plant.

Clumped Spacing

Individuals clump into groups or clusters in response to uneven distribution of resources in their immediate environments. Clumped distributions are common in nature because individual animals, plants, and microorganisms tend to prefer microhabitats defined by soil type, moisture, or certain kinds of host trees.

Social interactions also can lead to clumped distributions. Many species live and move around in large groups, which go by a variety of names (examples include herds of antelope, flocks of birds, gaggles of geese, packs of wolves, prides of lions). Such groupings can provide many advantages, including increased awareness of and defense against predators, decreased energetic cost of moving through air and water, and access to the knowledge of all group members.

At a broader scale, populations are often most densely populated in the interior of their range and less densely distributed toward the edges. Such patterns usually result from the manner in which the environment changes in different areas. Populations are often best adapted to the conditions in the interior of their distribution. As environmental conditions change, individuals are less well adapted and thus densities decrease. Ultimately, the point is reached at which individuals cannot persist at all; this marks the edge of a population's range.

The Human Effect

By altering the environment, we have allowed some species, such as coyotes, to expand their ranges, although, sadly, for most species the effect has been detrimental. Moreover, humans have served as an agent of dispersal for many species. Some of these transplants have been widely successful. For example, 100 starlings were introduced into New York City in 1896 in a misguided attempt to establish every species of bird mentioned by Shakespeare. Their population steadily spread such that by 1980, they occurred throughout the United States. Similar stories could be told for countless numbers of plants and animals, and the list increases every year. Unfortunately, the success of these invaders often comes at the expense of native species.

Dispersal Mechanisms

Dispersal to new areas can occur in many ways. Lizards, for example, have colonized many distant islands, probably by individuals or their eggs floating or drifting on vegetation. Seeds of many plants are designed to disperse in many ways (figure 24.6). Some seeds are aerodynamically designed to be blown long distances by the wind. Others have structures that stick to the fur or feathers of animals, so that they are carried long distances before falling to the ground. Still others are enclosed in fruits. These seeds can pass through the digestive systems of mammals or birds and then germinate at the spot upon which they are defecated. Finally, seeds of *Arceuthobium* are violently propelled from the base of the fruit in an explosive discharge. Although the probability of long-distance dispersal events occurring and leading to successful establishment of new populations is slim, over millions of years, many such dispersals have occurred.

A population is a group of individuals of the same species living together at the same place and time. The range of a population is limited by ecologically inhospitable habitats, but through time, these range boundaries can change.
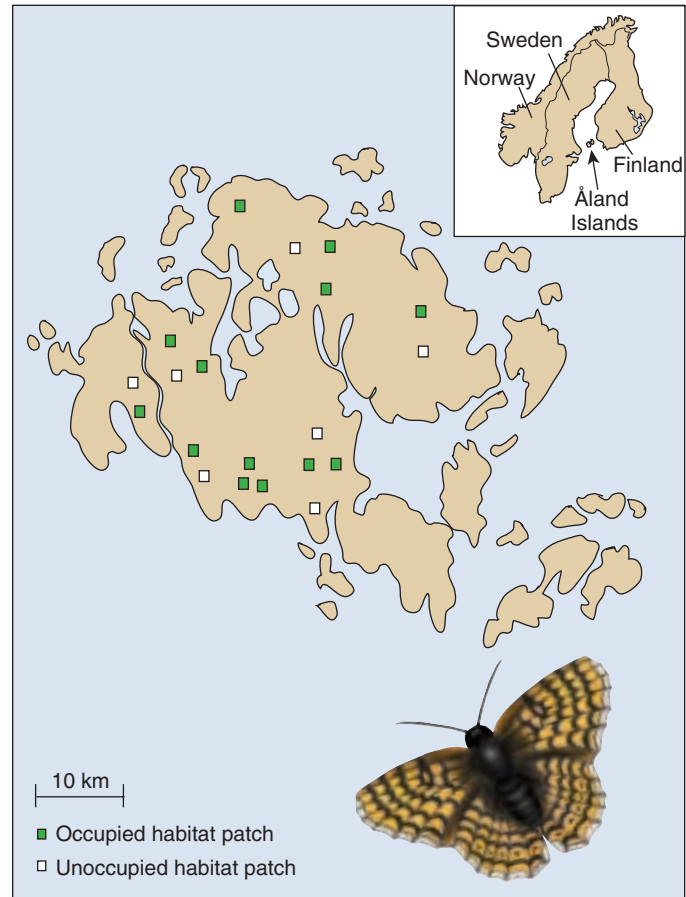
Metapopulations

Species are often composed of a network of distinct populations that interact with each other by exchanging individuals. Such networks are termed **metapopulations** and usually occur in areas in which suitable habitat is patchily distributed and separated by intervening stretches of unsuitable habitat.

To what degree populations within a metapopulation interact depends on the amount of dispersal and is often not symmetrical: populations increasing in size may tend to send out many dispersers, whereas populations at low levels will tend to receive more immigrants than they send off. In addition, relatively isolated populations will tend to receive relatively few arrivals.

Not all suitable habitats within a metapopulation's area may be occupied at any one time. For various reasons, some individual populations may go extinct, perhaps as a result of an epidemic disease, a catastrophic fire, or inbreeding depression. However, because of dispersal from other populations, such areas may eventually be recolonized. In some cases, the number of habitats occupied in a metapopulation may represent an equilibrium in which the rate of extinction of existing populations is balanced by the rate of colonization of empty habitats.

A second type of metapopulation structure occurs in areas in which some habitats are suitable for long-term population maintenance, whereas others are not. In these situations, termed **source-sink metapopulations**, the populations in the better areas (the sources) continually send out dispersers that bolster the populations in the poorer habitats (the sinks). In the absence of such continual replenishment, sink populations would have a negative growth rate and would eventually become extinct.

Metapopulations of butterflies have been studied particularly intensively (figure 24.7). In one study, Ilkka Hanski and colleagues at the University of Helsinki sampled populations of the glanville fritillary butterfly at 1600 meadows in southwestern Finland. On average, every year, 200 populations became extinct, but 114 empty meadows were colonized. A variety of factors seemed to increase the likelihood of a population's extinction, including small population size, isolation from sources of immigrants, low resource availability (as indicated by the number of flowers on a meadow), and lack of genetic variation present within the population. The researchers attribute the greater number of extinctions than colonizations to a string of very dry summers. Because none of the populations is large enough to survive on its own, continued survival of the species in southwestern Finland would appear to require the continued existence of a metapopulation network in which new populations are continually created and existing populations are supplemented by emigrants. Continued bad weather thus may doom the species, at least in this part of its range.

FIGURE 24.7
Metapopulations of butterflies. The glanville fritillary butterfly occurs in metapopulations in southwestern Finland on the Åland Islands. None of the populations is large enough to survive for long on its own, but continual emigration of individuals from other populations allows some populations to survive. In addition, continual establishment of new populations tends to offset extinction of established populations, although in recent years, extinctions have outnumbered colonizations.

Metapopulations, where they occur, can have two important implications for the range of a species. First, by continual colonization of empty patches, they prevent long-term extinction. If no such dispersal existed, then each population might eventually perish, leading to disappearance of the species from the entire area. Moreover, in source-sink metapopulations, the species as a whole occupies a larger area than it otherwise might occupy. For these reasons, the study of metapopulations has become very important in conservation biology as natural habitats become increasingly fragmented.

The distribution of individuals within a population can be random, uniform, or clumped. Across broader areas, individuals may occur in populations that are loosely interconnected, termed metapopulations.

One of the important features of any population is its size. Population size has a direct bearing on the ability of a given population to survive: for a variety of reasons discussed in chapter 31, smaller populations are at a greater risk of disappearing than large populations. In addition, the interactions that occur between members of a population also depend critically on a population's size and density.
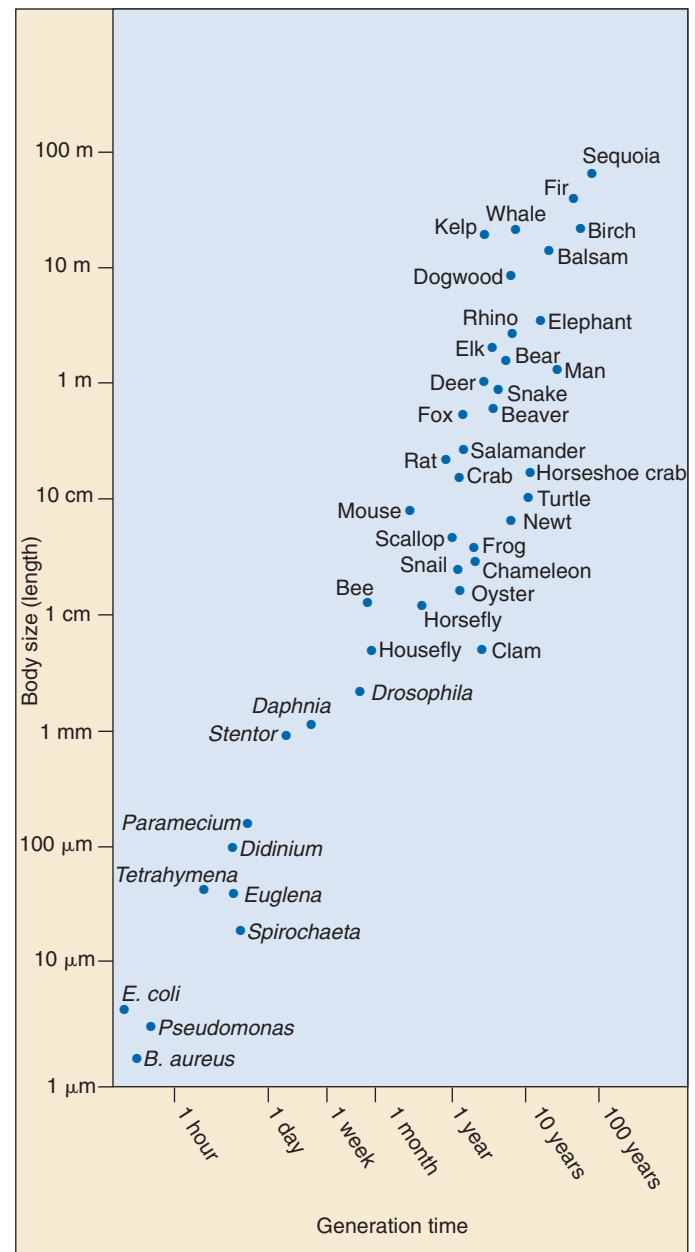
Demography

Demography (from the Greek *demos*, "the people," + *graphos*, "measurement") is the statistical study of populations. How the size of a population changes through time can be studied at two levels. At the most inclusive level, we can study the population as a whole to determine whether it is increasing, decreasing, or remaining constant. Populations grow if births outnumber deaths and shrink if deaths outnumber births. Understanding these trends is often easier if we break a population down into its constituent parts and analyze each separately.

Factors Affecting Population Growth Rates

The proportion of males and females in a population is its **sex ratio.** The number of births in a population is usually directly related to the number of females, but may not be as closely related to the number of males in species in which a single male can mate with several females. In many species, males compete for the opportunity to mate with females (a situation we discuss in chapter 27); consequently, a few males get many matings, whereas many males do not mate at all. In such species, a female-biased sex ratio would not affect population growth rates; reduction in the number of males simply changes the identities of the reproductive males without reducing the number of births. Among monogamous species like many birds, by contrast, in which pairs form long-lasting reproductive relationships, a reduction in the number of males can directly reduce the number of births.

   Generation time, defined as the average interval between the birth of an individual and the birth of its offspring, can also affect population growth rates. Species differ greatly in generation time. Differences in body size can explain much of this variation—mice go through approximately 100 generations during the course of one elephant generation—but not all of it (figure 24.8). Newts, for example, are smaller than mice, but have considerably longer generation times. Everything else equal, populations with shorter generations can increase in size more quickly than populations with long generations. Con-

versely, because generation time and life span are usually closely correlated, populations with short generation times may also diminish in size more rapidly if birthrates suddenly decrease.

FIGURE 24.8
The relationship between body size and generation time. In general, larger animals have longer generation times, although there are exceptions.

Age Structure

In most species, the probability that an individual will reproduce or die varies through its life span. A group of individuals of the same age is referred to as a **cohort.** Within a population, every cohort has a characteristic birthrate, or **fecundity,** defined as the number of offspring produced in a standard time (for example, per year), and a characteristic death rate, or **mortality,** the number of individuals that die in that period.

The relative number of individuals in each cohort defines a population's **age structure.** Because individuals of different ages have different fecundity and death rates, age structure has a critical impact on a population's growth rate. Populations with a large proportion of young individuals, for example, tend to grow rapidly because an increasing proportion of their individuals are reproductive. Populations in many underdeveloped countries are an example, as we will discuss later in the chapter. Conversely, if a large proportion of a population is relatively old, populations may decline. This phenomenon now characterizes some wealthy countries in Europe and Japan.

Life Tables and Population Change through Time

Ecologists use **life tables** to assess how populations in nature are changing. Life tables can be constructed by following the fate of a cohort from birth until death, noting the number of offspring produced and individuals that die each year. A very nice example of a life table analysis is exhibited in a study of the meadow grass *Poa annua*. This study follows the fate of 843 individuals through time, charting how many survive in each interval and how many offspring each survivor produces (table 24.1).

In table 24.1, the first column indicates the age of the cohort (that is, the number of 3-month intervals from the start of the study). The second and third columns indicate the number of survivors and the proportion of the original cohort still alive at the beginning of that interval. The fourth column presents the **mortality rate,** the proportion of individuals that started that interval alive but died by the end of it. The fifth column indicates the average number of seeds produced by each surviving individual in that interval, and the last column presents the number of seeds produced relative to the size of the original cohort.

Table 24.1 Life Table for a Cohort of the grass Poa annua					
Age (in 3-month intervals)	Number alive at beginning of time interval	Proportion of cohort surviving to beginning of time interval (survivorship)	Mortality rate during time interval	Seeds produced per surviving individual (fecundity)	Fecundity × survivorship
0	843	1.000	0.143	0.00	0.00
1	722	0.857	0.271	0.42	0.36
2	527	0.625	0.400	1.18	0.74
3	316	0.375	0.544	1.36	0.51
4	144	0.171	0.626	1.46	0.25
5	54	0.064	0.722	1.11	0.07
6	15	0.018	0.800	2.00	0.04
7	3	0.004	1.000	3.33	0.01
8	0	0.000			Total = 1.98

Modified from Ricklefs, 1997.

Much can be learned from examination of life tables. In this particular case, we see that the probability of dying increases steadily with age, whereas the number of offspring produced increases with age. By adding up the numbers in the last column, we get the total number of offspring produced per individual in the initial cohort. This number is almost 2, which means that for every original member of the cohort, on average two individuals have been produced. A figure of 1.0 would be the break-even number, the point at which the population was neither growing nor shrinking. In this case, the population appears to be growing rapidly.

In most cases, life table analysis is more complicated than this. First, except for organisms with short life spans, it is difficult to track the fate of a cohort from birth until death of the last individual. An alternative approach is to construct a cross-sectional study, examining the fate of all cohorts over a single year. In addition, many factors—such as offspring reproducing before all members of their parental generation's cohort have died—complicate the interpretation of whether populations are growing or shrinking.
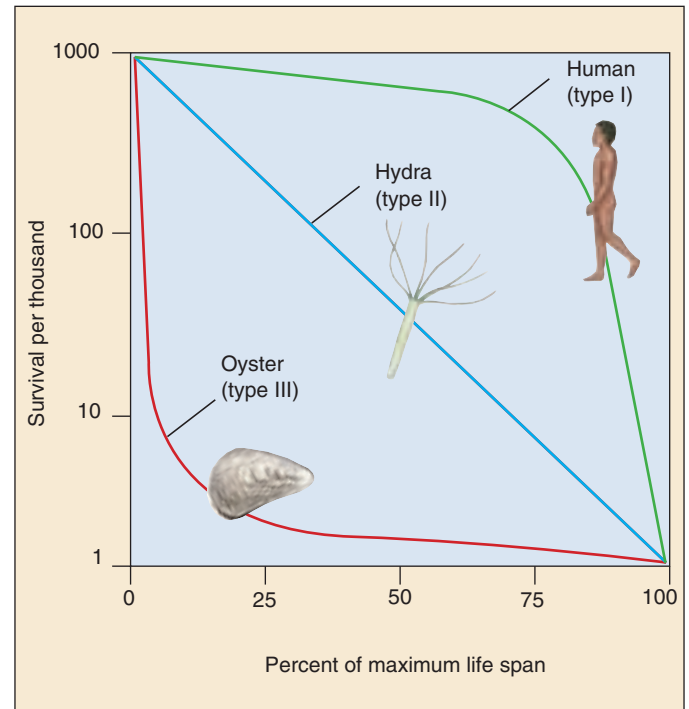
Survivorship Curves

One way to express some aspects of the age distribution characteristics of populations is through a **survivorship curve.** Survivorship is defined as the percentage of an original population that survives to a given age. Examples of different kinds of survivorship curves are shown in figure 24.9. In hydra, animals related to jellyfish, individuals are equally likely to die at any age, as indicated by the straight survivorship curve (type II). Oysters, like plants, produce vast numbers of offspring, only a few of which live to reproduce. However, once they become established and grow into reproductive individuals, their mortality rate is extremely low (type III survivorship curve). Finally, even though human babies are susceptible to death at relatively high rates, mortality rates in humans, as in many animals and protists, rise steeply in the postreproductive years (type I survivorship curve). Examination of the data for *Poa annua* reveals that it approximates a type II survivorship curve (figure 24.10).


The growth rate of a population is a sensitive function of its age structure. The age structure of a population and the manner in which mortality and birthrates vary among different age cohorts determine whether a population will increase or decrease in size.

FIGURE 24.9
Survivorship curves. By convention, survival (the vertical axis) is plotted on a log scale. Humans have a type I life cycle, the hydra (an animal related to jellyfish) type II, and oysters type III.
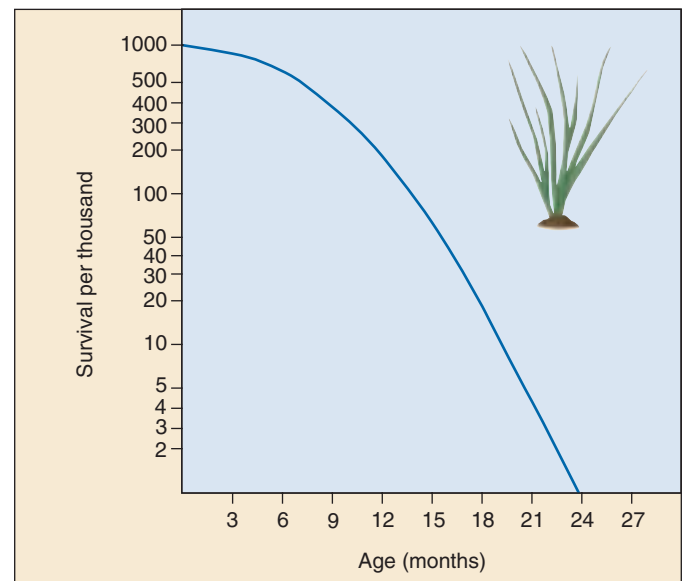
FIGURE 24.10
Survivorship curve for a cohort of the meadow grass, *Poa annua.* Mortality increases at a constant rate through time.

24.3   Life histories often reflect trade-offs between reproduction and survival.

Natural selection favors traits that maximize the number of surviving offspring left in the next generation. Two factors affect this quantity: how long an individual lives and how many young it produces each year. Why doesn't every organism reproduce immediately after its own birth, produce large families of large offspring, care for them intensively, and do this repeatedly throughout a long life, while outcompeting others, escaping predators, and capturing food with ease? The answer is that no one organism can do all of this—there are simply not enough resources available. Consequently, organisms allocate resources either to current reproduction or to increase their prospects of surviving and reproducing at later life stages.

The Cost of Reproduction

The complete life cycle of an organism constitutes its **life history**. All life histories involve significant trade-offs. Because resources are limited, a change that increases reproduction may decrease survival and reduce future reproduction. Thus, a Douglas fir tree that produces more cones increases its current reproductive success, but it also grows more slowly; because the number of cones produced is a function of how large a tree is, this diminished growth will decrease the number of cones it can produce in the future. Similarly, birds that have more offspring each year have a higher probability of dying during that year or producing smaller clutches the following year (figure 24.11). Conversely, individuals that delay reproduction may grow faster and larger, enhancing future reproduction.

In one elegant experiment, researchers changed the number of eggs in nests of a bird, the collared flycatcher (figure 24.12). Birds whose clutch size (the number of eggs produced in one breeding event) was decreased laid more eggs the next year, whereas those given more eggs produced fewer eggs the following year. Ecologists refer to the reduction in future reproductive potential resulting from current reproductive efforts as the **cost of reproduction.**

Natural selection will favor the life history that maximizes lifetime reproductive success. When the cost of reproduction is low, individuals should invest in producing as many offspring as possible because there is little cost. Low costs of reproduction may occur when resources are abundant, such that producing offspring does not impair survival or the ability to produce many offspring in subsequent years. Costs of reproduction will also be low when overall mortality rates are high. In such cases, individuals may be unlikely to survive to the next breeding season anyway, so the incremental effect of increased reproductive efforts may not make a difference in future survival.
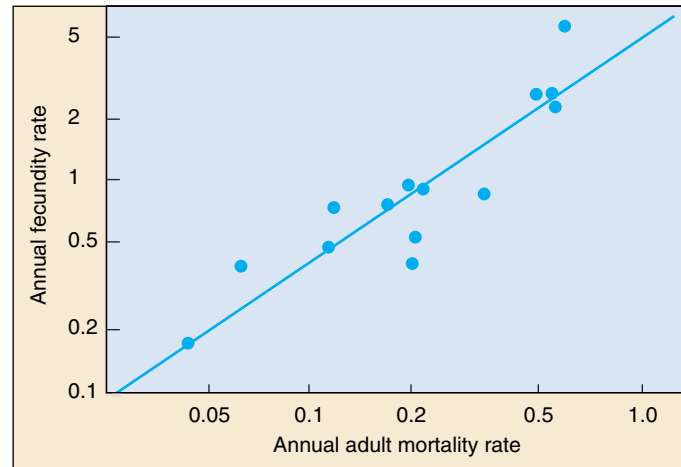
FIGURE 24.11
Reproduction has a price. Increased fecundity in birds correlates with higher mortality in several populations of birds ranging from albatross (low) to sparrow (high). Birds that raise more offspring per year have a higher probability of dying during that year.
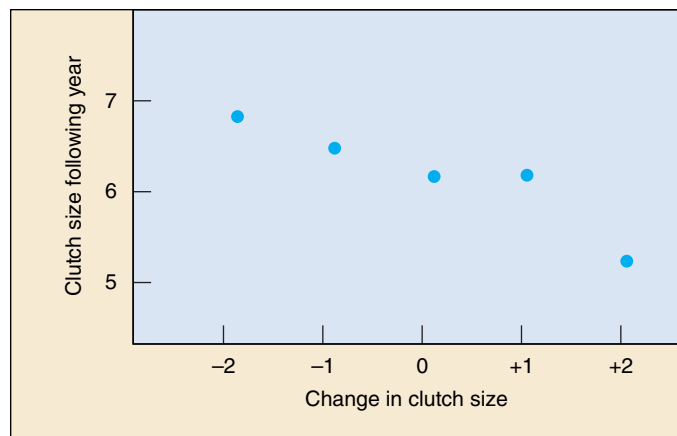
FIGURE 24.12
Reproductive events per lifetime. Adding eggs to nests of collared flycatchers (which increases the reproductive efforts of the female rearing the young) decreases clutch size the following year; removing eggs from the nest increases the next year's clutch size. This experiment demonstrates the tradeoff between current reproductive effort and future reproductive success.

Alternatively, when costs of reproduction are high, lifetime reproductive success may be maximized by deferring or minimizing current reproduction to enhance growth and survival rates. This may occur when costs of reproduction significantly affect the ability of an individual to survive or decrease the number of offspring that can be produced in the future.

Investment per Offspring

In terms of natural selection, the number of offspring produced is not as important as how many of those offspring themselves survive to reproduce.

A key reproductive trade-off concerns how many resources to invest in producing any single offspring. Assuming that the amount of energy to be invested in offspring is limited, a trade-off must exist between the number of offspring produced and the size of each offspring (figure 24.13). This trade-off has been experimentally demonstrated in the side-blotched lizard, *Uta stansburiana*, which normally lays on average four and a half eggs at a time. When some of the eggs are removed surgically early in the reproductive cycle, the female lizard produces only 1 to 3 eggs, but supplies each of these eggs with greater amounts of yolk, producing eggs that are much larger than normal.

In many species, the size of offspring critically affects their survival prospects—larger offspring have a greater chance of survival. Producing many offspring with little chance of survival might not be the best strategy, but producing only a single, extraordinarily robust offspring also would not maximize the number of surviving offspring. Rather, an intermediate situation, in which several fairly large offspring are produced, should maximize the number of surviving offspring. This example is fundamentally the same as the trade-off between clutch size and parental investment discussed above; in this case, the parental investment is simply how many resources can be invested in each offspring before they are born.

Reproductive Events per Lifetime

The trade-off between age and fecundity plays a key role in many life histories. Annual plants and most insects focus all of their reproductive resources on a single large event and then die. This life history adaptation is called **semelparity** (from the Latin *semel*, "once," + *parito*, "to beget"). Organisms that produce offspring several times over many seasons exhibit a life history adaptation called **iteroparity** (from the Latin *itero*, "to repeat"). Species that reproduce yearly must avoid overtaxing themselves in any one reproductive episode so that they will be able to survive and reproduce in the future. Semelparity, or "big bang" reproduction, is usually found in short-lived species in which the probability of staying alive between broods is low, such as plants growing in harsh climates. Semelparity is also favored when fecundity entails large reproductive cost, as when Pacific salmon migrate upriver to their spawning grounds. In these species, rather than investing some resources in an unlikely bid to survive until the next breeding season, individuals place all their resources into reproduction.
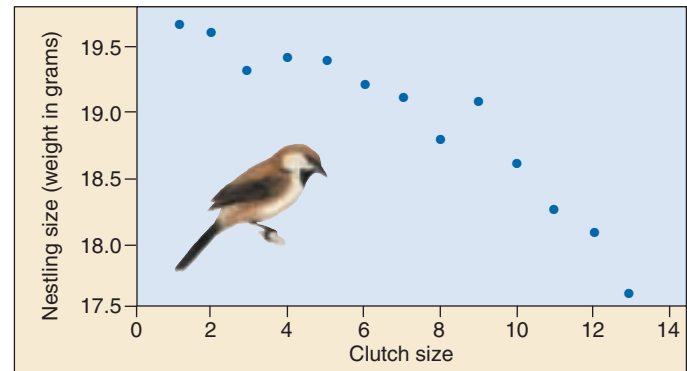
FIGURE 24.13
The relationship between clutch size and offspring size. In great tits, the size of nestlings is inversely related to the number of eggs laid. The more mouths they have to feed, the less the parents can provide to any one nestling.
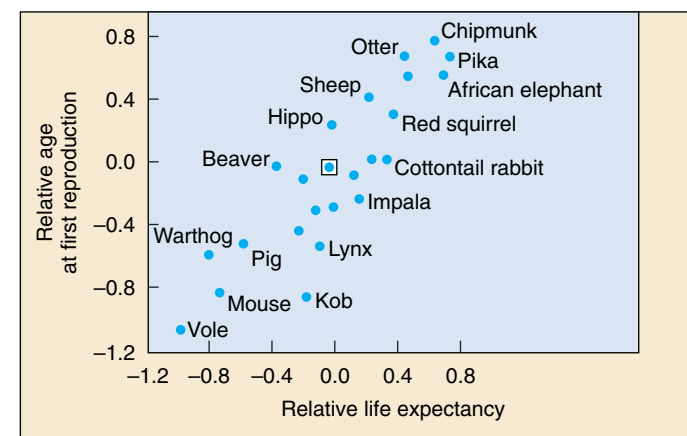
FIGURE 24.14
Age at first reproduction. Among mammals, compensating for the effects of size, age at first reproduction increases with life expectancy at birth. Each dot represents a species. Values are relative to the species symbolized □. (After Begon et al., 1996.)

Age at First Reproduction

Among mammals and many other animals, longer-lived species reproduce later (figure 24.14). Birds, for example, gain experience as juveniles before expending the high costs of reproduction. In long-lived animals, the relative advantage of juvenile experience outweighs the energy investment in survival and growth. In shorter-lived animals, on the other hand, quick reproduction is more critical than juvenile training, and reproduction tends to occur earlier.

Life history adaptations involve many trade-offs between reproductive cost and investment in survival. Different kinds of animals and plants employ quite different approaches.

24.4 Population growth is limited by the environment.

Biotic Potential

Populations often remain at a relatively constant size, regardless of how many offspring they produce. As you saw in chapter 1, Darwin based his theory of natural selection partly on this seeming contradiction. Natural selection occurs because of checks on reproduction, with some individuals reproducing less often than others. To understand populations, we must consider how they grow and what factors in nature limit population growth.

The Exponential Growth Model

The actual rate of population increase, r, is defined as the difference between the birth rate and the death rate corrected for any movement of individuals in or out of the population, whether net emigration (movement out of the area) or net immigration (movement into the area). Thus,

$$r = (b - d) + (i - e)$$

Movements of individuals can have a major impact on population growth rates. For example, the increase in human population in the United States during the closing decades of the twentieth century is mostly due to immigrants. Less than half of the increase came from the reproduction of the people already living there.

The simplest model of population growth assumes a population growing without limits at its maximal rate. This rate, called the **biotic potential,** is the rate at which a population of a given species will increase when no limits are placed on its rate of growth. In mathematical terms, this is defined by the following formula:

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

where N is the number of individuals in the population, dN/dt is the rate of change in its numbers over time, and r_i is the intrinsic rate of natural increase for that population—its innate capacity for growth.

The innate capacity for growth of any population is exponential (red line in figure 24.15). Even when the *rate* of increase remains constant, the actual increase in the *number* of individuals accelerates rapidly as the size of the population grows. The result of unchecked exponential growth is a population explosion. A single pair of houseflies, laying 120 eggs per generation, could produce more than 5 trillion descendants in a year. In 10 years, their descendants would form a swarm more than 2 meters thick over the entire surface of the earth! In practice, such patterns of unrestrained growth prevail only for short periods, usually when an organism reaches a new habitat with abundant resources (figure 24.16). Natural examples include dandelions reaching the fields, lawns, and meadows
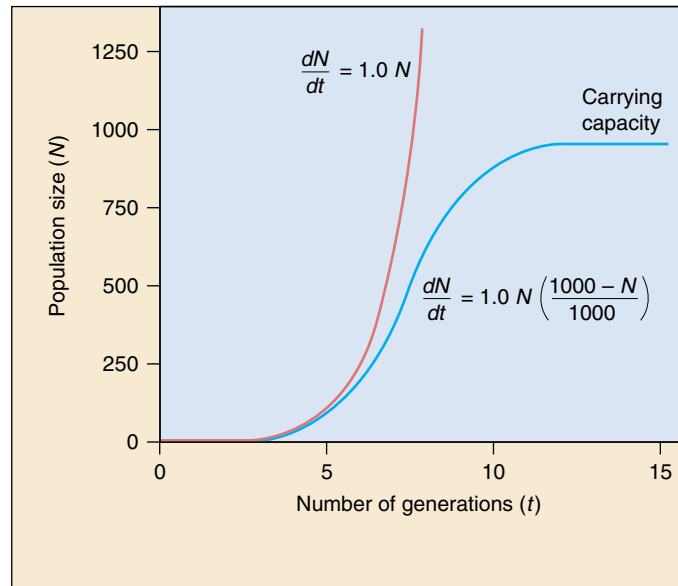

FIGURE 24.15
Two models of population growth. The red line illustrates the exponential growth model for a population with an r of 1.0. The blue line illustrates the logistic growth model in a population with $r = 1.0$ and $K = 1000$ individuals. At first, logistic growth accelerates exponentially, then, as resources become limiting, the death rate increases and growth slows. Growth ceases when the death rate equals the birthrate. The carrying capacity (K) ultimately depends on the resources available in the environment.

FIGURE 24.16
An example of a rapidly increasing population. European purple loosestrife, *Lythrum salicaria*, became naturalized over thousands of square miles of marshes and other wetlands in North America. It was introduced sometime before 1860 and has had a negative impact on many native plants and animals.

of North America from Europe for the first time; algae colonizing a newly formed pond; or the first terrestrial immigrants arriving on an island recently thrust up from the sea.

Carrying Capacity

No matter how rapidly populations grow, they eventually reach a limit imposed by shortages of important environmental factors, such as space, light, water, or nutrients. A population ultimately may stabilize at a certain size, called the **carrying capacity** of the particular place where it lives. The carrying capacity, symbolized by K, is the maximum number of individuals that a population can support.

The Logistic Growth Model

As a population approaches its carrying capacity, its rate of growth slows greatly, because fewer resources remain for each new individual to use. The growth curve of such a population, which is always limited by one or more factors in the environment, can be approximated by the following logistic growth equation:

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

In this logistic model of population growth, the growth rate of the population (dN/dt) equals its rate of increase (r multiplied by N, the number of individuals present at any one time), adjusted for the amount of resources available. The adjustment is made by multiplying rN by the fraction of K still unused (K minus N, divided by K). As N increases (the population grows in size), the fraction by which r is multiplied (the remaining resources) becomes smaller and smaller, and the rate of increase of the population declines.

In mathematical terms, as N approaches K, the *rate* of population growth (dN/dt) begins to slow, reaching 0 when $N = K$ (blue line in figure 24.18). Graphically, if you plot N versus t (time) you obtain an S-shaped **sigmoid growth curve** characteristic of many biological populations. The curve is called "sigmoid" because its shape has a double curve like the letter S. As the size of a population stabilizes at the carrying capacity, its rate of growth slows down, eventually coming to a halt (figure 24.17*a*).

In many cases, real populations display trends corresponding to a logistic growth curve. This is true not only in the laboratory, but also in natural populations (figure 24.17*b*). In some cases, however, the fit is not perfect (figure 24.17*c*) and, as we shall see shortly, many populations exhibit other patterns.
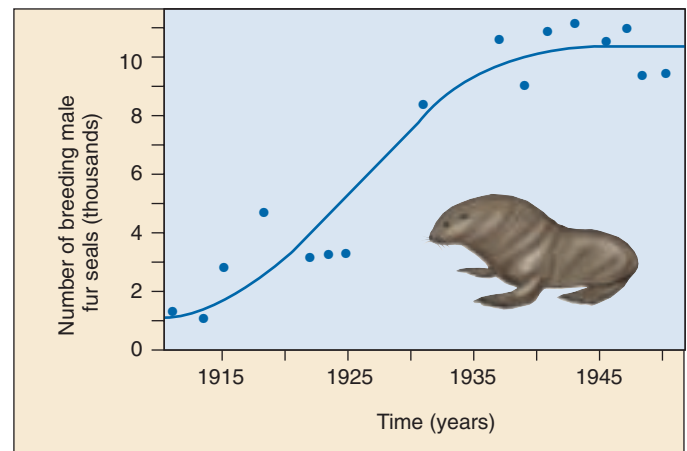

The size at which a population stabilizes in a particular place is defined as the carrying capacity of that place for that species. Populations often grow to the carrying capacity of their environment.
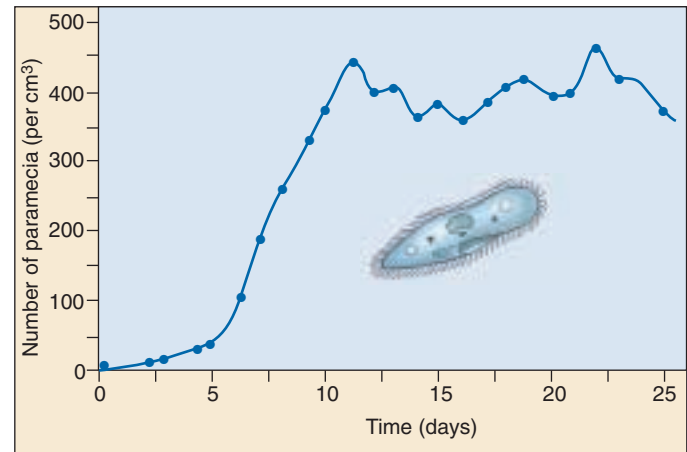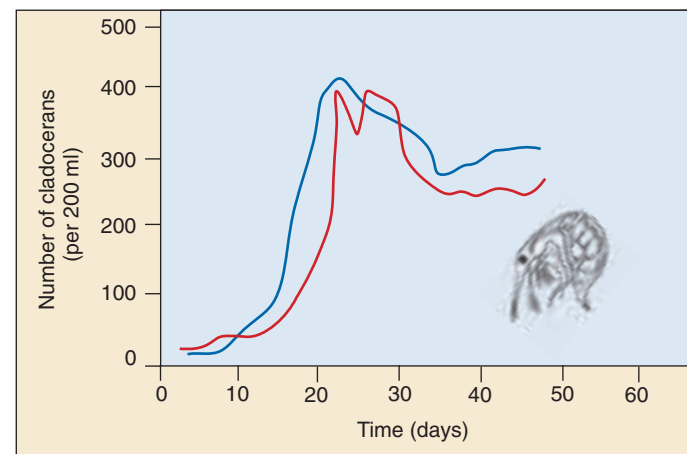

(a)

(b)

(c)

FIGURE 24.17
Most natural populations exhibit logistic growth. (*a*) *Paramecium* grown in a laboratory environment. (*b*) A fur seal (*Callorhinus ursinus*) population on St. Paul Island, Alaska. (*c*) Laboratory populations of two populations of the cladoceran *Bosmina longirsotris*. Note that the populations first exceeded the carrying capacity, before decreasing to a size which was then maintained.

The Influence of Population Density

The reason that population growth rates are affected by population size is that many important processes are **density-dependent**. When populations approach their carrying capacity, competition for resources can be severe, leading both to a decreased birthrate and an increased risk of mortality (figure 24.18). In addition, predators often focus their attention on particularly common prey, which also results in increasing rates of mortality as populations increase. High population densities can also lead to an accumulation of toxic wastes, a situation to which humans are becoming increasingly accustomed.

Behavioral changes may also affect population growth rates. Some species of rodents, for example, become antisocial, fighting more, breeding less, and generally acting stressed-out. These behavioral changes result from hormonal actions, but their ultimate cause is not yet clear; most likely, they have evolved as adaptive responses to situations in which resources are scarce. In addition, in crowded populations, the population growth rate may decrease because of an increased rate of emigration of individuals attempting to find better conditions elsewhere (figure 24.19).

However, not all density-dependent factors are negatively related to population size. In some cases, growth rates increase with population size. This phenomenon is referred to as the **Allee effect** (after Warder Allee, who first described it). The Allee effect can take several forms. Most obviously, in populations that are too sparsely distributed, individuals may have difficulty finding mates. Moreover, some species may rely on large groups to deter predators or to provide the necessary stimulation for breeding activities.
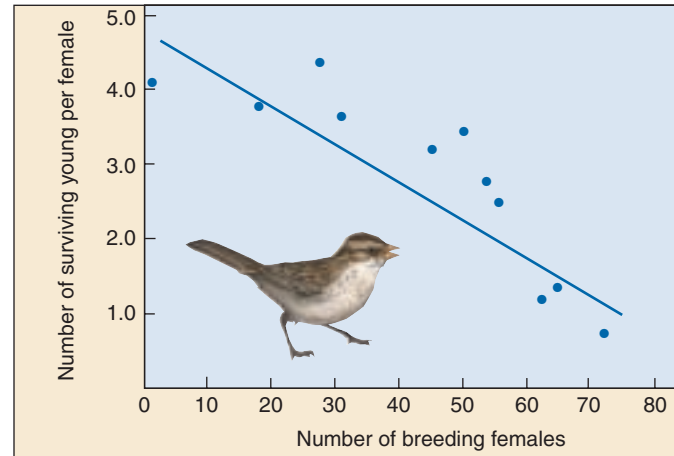
(a)
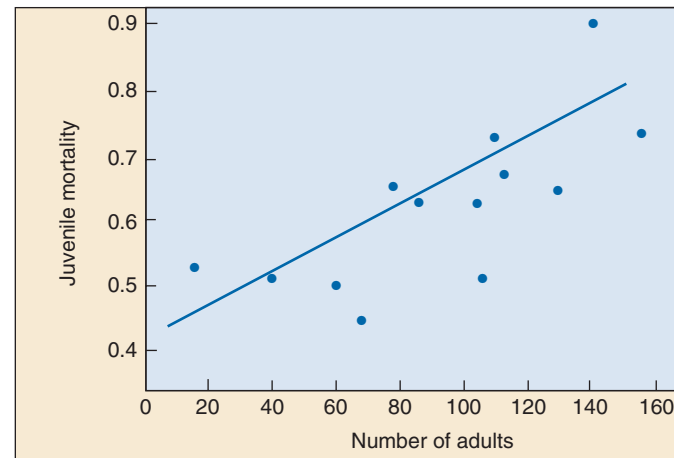
(b)

FIGURE 24.18
Density dependence in the song sparrow (*Melospiza melodia*) on Mandarte Island. Reproductive success decreases (*a*) and mortality rates increase (*b*) as population size increases.

FIGURE 24.19
Density-dependent effects. Migratory locusts, *Locusta migratoria*, are a legendary plague of large areas of Africa and Eurasia. At high population densities, the locusts have different hormonal and physical characteristics and take off as a swarm. The most serious infestation of locusts in 30 years occurred in North Africa in 1988.

Density-Independent Effects

Growth rates in populations sometimes do not correspond to the logistic growth equation. In many cases, such patterns result because growth is under the control of **density-independent effects.** In other words, the rate of growth of a population at any instant is limited by something other than the size of the population.

A variety of factors may affect populations in a density-independent manner. Most of these are aspects of the external environment. Extremely cold winters, droughts, storms, volcanic eruptions—individuals often will be affected by these activities regardless of the size of the population. Populations that occur in areas in which such events occur relatively frequently will display erratic population growth patterns in which the populations increase rapidly when conditions are benign, but suffer extreme reductions whenever the environment turns hostile.

Population Cycles

Some populations exhibit another type of pattern inconsistent with simple logistic equations: they exhibit cyclic patterns of increase and decrease. Ecologists have studied cycles in hare populations since the 1920s. They have found that the North American snowshoe hare (*Lepus americanus*) follows a "10-year cycle" (in reality, it varies from 8 to 11 years). Its numbers fall tenfold to 30-fold in a typical cycle, and 100-fold changes can occur. Two factors appear to be generating the cycle: food plants and predators.

Food plants. The preferred foods of snowshoe hares are willow and birch twigs. As hare density increases, the quantity of these twigs decreases, forcing the hares to feed on high-fiber (low-quality) food. Lower birthrates, low juvenile survivorship, and low growth rates follow. The hares also spend more time searching for food, exposing them more to predation. The result is a precipitous decline in willow and birch twig abundance, and a corresponding fall in hare abundance. It takes two to three years for the quantity of mature twigs to recover.

Predators. A key predator of the snowshoe hare is the Canada lynx (*Lynx canadensis*). The Canada lynx shows a "10-year" cycle of abundance that seems remarkably entrained to the hare abundance cycle (figure 24.20). As hare numbers increase, lynx numbers do, too, rising in response to the increased availability of lynx food. When hare numbers fall, so do lynx numbers, their food supply depleted.
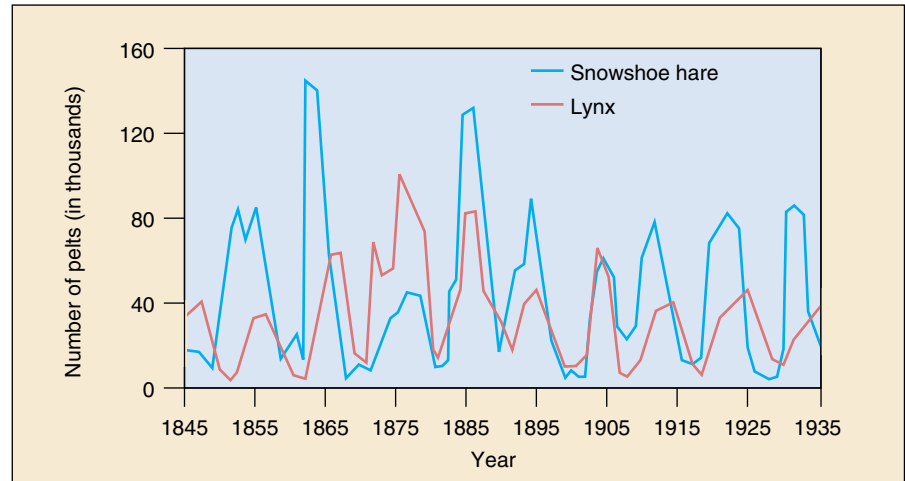
FIGURE 24.20
Linked population cycles of the snowshoe hare and the northern lynx. These data are based on records of fur returns from trappers in the Hudson Bay region of Canada. The lynx populations carefully track the snowshoe hares, but lag behind them slightly.

Which factor is responsible for the predator-prey oscillations? Do increasing numbers of hares lead to overharvesting of plants (a hare-plant cycle) or do increasing numbers of lynx lead to overharvesting of hares (a hare-lynx cycle)? Field experiments carried out by C. Krebs and coworkers in 1992 provide an answer. Krebs set up experimental plots in Canada's Yukon-containing hare populations. If food is added (no food effect) and predators excluded (no predator effect) from an experimental area, hare numbers increase tenfold and stay there—the cycle is lost. However, the cycle is retained if either of the factors is allowed to operate alone: exclude predators but don't add food (food effect alone), or add food in presence of predators (predator effect alone). Thus, both factors can affect the cycle, which, in practice, seems to be generated by the interaction between the two factors.

Population cycles traditionally have been considered to occur rarely. However, a recent review of nearly 700 long-term (25 years or more) studies of trends within populations found that cycles were not uncommon; nearly 30% of the studies—including birds, mammals, fish, and crustaceans—provided evidence of some cyclic pattern in population size through time, although most of these cycles are nowhere near as dramatic in amplitude as the snowshoe hare and lynx cycles.

Density-dependent effects are caused by factors that come into play particularly when the population size is larger; density-independent effects are controlled by factors that operate regardless of population size.

Population Growth Rates and Life History Models

As we have seen, some species usually have stable population sizes maintained near the carrying capacity, whereas the populations of other species fluctuate markedly and are often far below carrying capacity. As we saw in our discussion of life histories, the selective factors affecting such species will differ markedly. Populations near their carrying capacity may face stiff competition for limited resources. By contrast, resources are abundant in populations far below carrying capacity.

We have already seen the consequences of such differences. When resources are limited, the cost of reproduction often will be very high. Consequently, selection will favor individuals that can compete effectively and utilize resources efficiently. Such adaptations often come at the cost of lowered reproductive rates. Such populations are termed **K-selected** because they are adapted to thrive when the population is near its carrying capacity (*K*). Table 24.2 lists some of the typical features of *K*-selected populations. Examples of *K*-selected species include coconut palms, whooping cranes, whales, and humans.

By contrast, in populations far below the carrying capacity, resources may be abundant. Costs of reproduction will be low, and selection will favor those individuals that can produce the maximum number of offspring. Selection here favors individuals with the highest reproductive rates; such populations are termed **r-selected**. Examples of organisms displaying *r*-selected life history adaptations include dandelions, aphids, mice, and cockroaches (figure 24.21).

Most natural populations show life history adaptations that exist along a continuum ranging from completely *r*-selected traits to completely *K*-selected traits. Although these tendencies hold true as generalities, few populations are purely *r*- or *K*-selected and show all of the traits listed in table 24.2. These attributes should be treated as generalities, with the recognition that many exceptions do exist.

> **Some life history adaptations favor near-exponential growth, others the more competitive logistic growth. Most natural populations exhibit a combination of the two.**

Table 24.2	*r*-Selected and *K*-Selected Life History Adaptations	
Adaptation	***r*-Selected Populations**	***K*-Selected Populations**
Age at first reproduction	Early	Late
Life span	Short	Long
Maturation time	Short	Long
Mortality rate	Often high	Usually low
Number of offspring produced per reproductive episode	Many	Few
Number of reproductions per lifetime	Usually one	Often several
Parental care	None	Often extensive
Size of offspring or eggs	Small	Large

Source: Data from E. R. Pianka, *Evolutionary Ecology*, 4th edition, 1987, Harper & Row, New York.

FIGURE 24.21
The consequences of exponential growth. All organisms have the potential to produce populations larger than those that actually occur in nature. The German cockroach (*Blatella germanica*), a major household pest, produces 80 young every six months. If every cockroach that hatched survived for three generations, kitchens might look like this theoretical culinary nightmare concocted by the Smithsonian Museum of Natural History.

The Advent of Exponential Growth

Humans exhibit many *K*-selected life history traits, including small brood size, late reproduction, and a high degree of parental care. These life history traits evolved during the early history of hominids, when the limited resources available from the environment controlled population size. Throughout most of human history, our populations have been regulated by food availability, disease, and predators. Although unusual disturbances, including floods, plagues, and droughts no doubt affected the pattern of human population growth, the overall size of the human population grew only slowly during our early history. Two thousand years ago, perhaps 130 million people populated the earth. It took a thousand years for that number to double, and it was 1650 before it had doubled again, to about 500 million. For over 16 centuries, the human population was characterized by very slow growth. In this respect, human populations resembled many other species with predominantly *K*-selected life history adaptations.

Starting in the early 1700s, changes in technology have given humans more control over their food supply, enabled them to develop superior weapons to ward off predators, and led to the development of cures for many diseases. At the same time, improvements in shelter and storage capabilities have made humans less vulnerable to climatic uncertainties. These changes allowed humans to expand the carrying capacity of the habitats in which they lived, and thus to escape the confines of logistic growth and reenter the exponential phase of the sigmoidal growth curve.

Responding to the lack of environmental constraints, the human population has grown explosively over the last 300 years. While the birthrate has remained unchanged at about 30 per 1000 per year over this period, the death rate has fallen dramatically, from 20 per 1000 per year to its present level of 13 per 1000 per year. The difference between birth and death rates meant that the population grew as much as 2% per year, although the rate has now declined to 1.4% per year.

A 1.4% annual growth rate may not seem large, but it has produced a current human population of 6 billion people (figure 24.22)! At this growth rate, 77 million people are added to the world population annually, and the human population will double in 39 years. As we will discuss in chapter 30, both the current human population level and the projected growth rate have potential consequences for our future that are extremely grave.
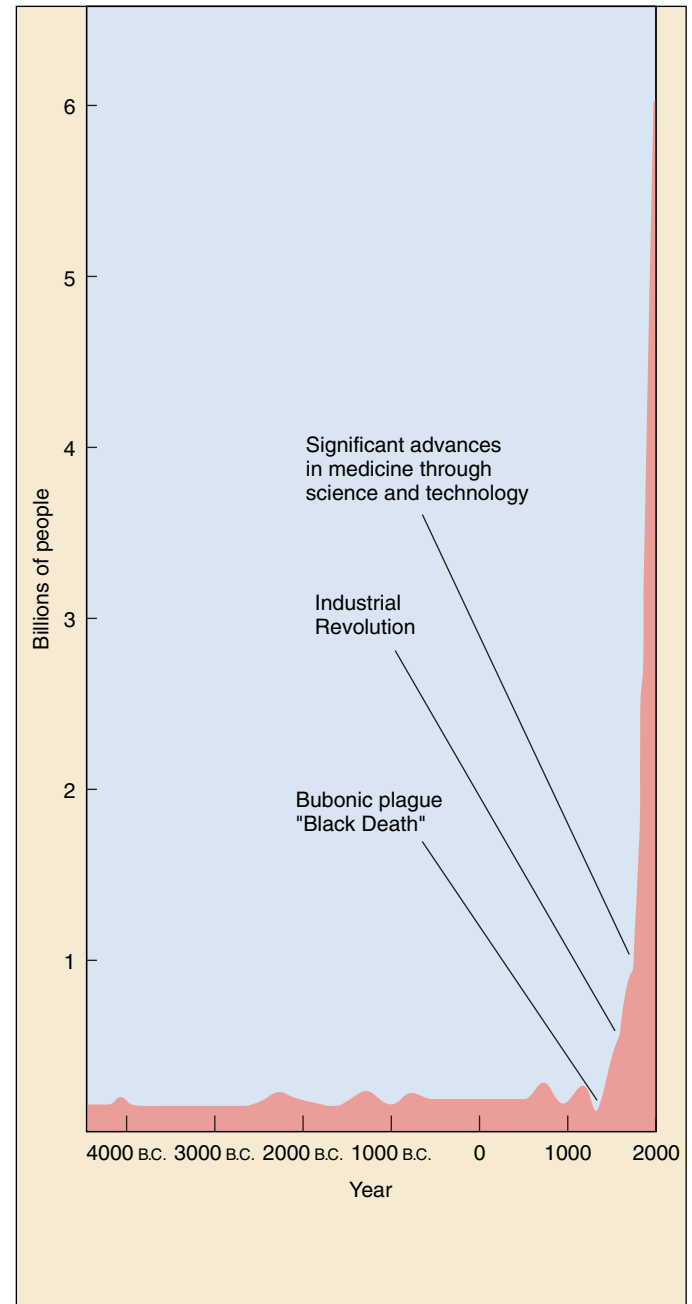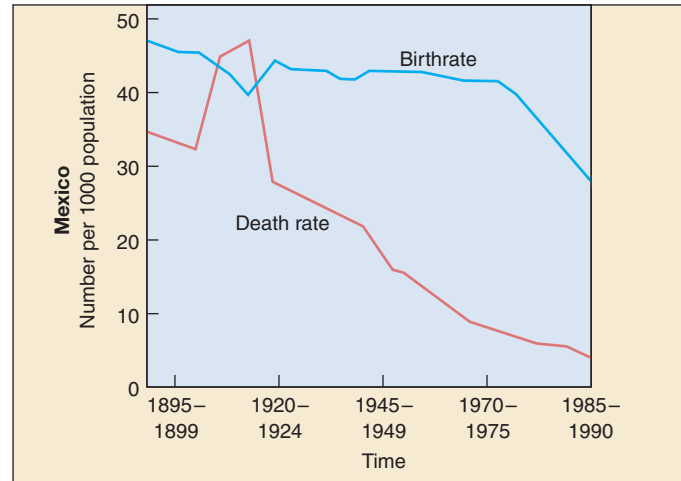

FIGURE 24.22
History of human population size. Temporary increases in death rate, even severe ones like the Black Death of the 1400s, have little lasting impact. Explosive growth began with the Industrial Revolution in the 1700s, which produced a significant long-term lowering of the death rate. The current population is 6 billion, and at the current rate will double in 39 years.

Population Pyramids

While the human population as a whole continues to grow rapidly at the close of the twentieth century, this growth is not occurring uniformly over the planet. Some countries, like Mexico, are growing rapidly, their birthrate greatly exceeding their death rate (figure 24.23). Other countries are growing much more slowly. The rate at which a population can be expected to grow in the future can be assessed graphically by means of a **population pyramid**—a bar graph displaying the numbers of people in each age category. Males are conventionally shown to the left of the vertical age axis, females to the right. A human population pyramid thus displays the age composition of a population by sex. In most human population pyramids, the number of older females is disproportionately large compared to the number of older males, because females in most regions have a longer life expectancy than males.

Viewing such a pyramid, one can predict demographic trends in births and deaths. In general, rectangular "pyramids" are characteristic of countries whose populations are stable, their numbers neither growing nor shrinking. A triangular pyramid is characteristic of a country that will exhibit rapid future growth, as most of its population has not yet entered the child-bearing years. Inverted triangles are characteristic of populations that are shrinking.

Examples of population pyramids for the United States and Kenya in 1990 are shown in figure 24.24. In the nearly rectangular population pyramid for the United States, the cohort (group of individuals) 55 to 59 years old represents people born during the Depression and is smaller in size

FIGURE 24.23
Why the population of Mexico is growing. The death rate (*red line*) in Mexico fell steadily throughout the last century, while the birthrate (*blue line*) remained fairly steady until 1970. The difference between birth and death rates has fueled a high growth rate. Efforts begun in 1970 to reduce the birthrate have been quite successful, although the growth rate remains rapid.

than the cohorts in the preceding and following years. The cohorts 25 to 44 years old represent the "baby boom." The rectangular shape of the population pyramid indicates that the population of the United States is not expanding rapidly. The very triangular pyramid of Kenya, by contrast, predicts explosive future growth. The population of Kenya is predicted to double in less than 20 years.
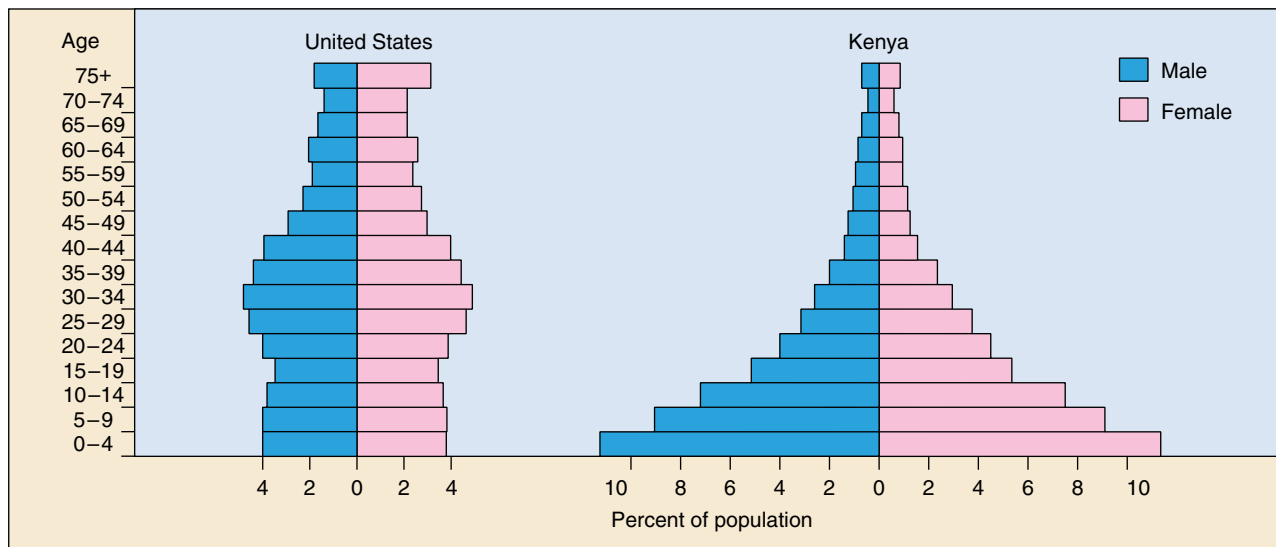
FIGURE 24.24
Population pyramids from 1990. Population pyramids are graphed according to a population's age distribution. Kenya's pyramid has a broad base because of the great number of individuals below child-bearing age. When all of the young people begin to bear children, the population will experience rapid growth. The U.S. pyramid demonstrates a larger number of individuals in the "baby boom" cohort—the pyramid bulges because of an increase in births between 1945 and 1964.

| Table 24.3 A Comparison of 1996 Population Data in Developed and Developing Countries			
	United States *(highly developed)*	Brazil *(moderately developed)*	Ethiopia *(poorly developed)*
Fertility rate	2.0	2.8	6.8
Doubling time at current rate (yr)	114	41	23
Infant mortality rate (per 1000 births)	7.5	58	120
Life expectancy at birth (yrs)	76	66	50
Per capita GNP (U.S. $; 1994)	$25,860	$3,370	$130

An Uncertain Future

The earth's rapidly growing human population constitutes perhaps the greatest challenge to the future of the biosphere, the world's interacting community of living things. Humanity is adding 77 million people a year to the earth's population—a million every five days, 150 every minute! In more rapidly growing countries, the resulting population increase is staggering (table 24.3). India, for example, had a population of 853 million in 1996; by 2020 its population will exceed 1.4 billion!

A key element in the world's population growth is its uneven distribution among countries. Of the billion people added to the world's population in the 1990s, 90% live in developing countries (figure 24.25). This is leading to a major reduction in the fraction of the world's population that lives in industrialized countries. In 1950, fully one-third of the world's population lived in industrialized countries; by 1996 that proportion had fallen to one-quarter; in 2020 the proportion will have fallen to one-sixth. Thus the world's population growth will be centered in the parts of the world least equipped to deal with the pressures of rapid growth.

Rapid population growth in developing countries has the harsh consequence of increasing the gap between rich and poor. Today 23% of the world's population lives in the industrialized world with a per capita income of $17,900, while 77% of the world's population lives in developing countries with a per capita income of only $810. The disproportionate wealth of the industrialized quarter of the world's population is evidenced by the fact that 85% of the world's capital wealth is in the industrial world, only 15% in developing countries. Eighty percent of all the energy used today is consumed by the industrial world, only 20% by developing countries. Perhaps most worrisome for the future, fully 94% of all scientists and engineers reside in the industrialized world, only 6% in developing countries. Thus the problems created by the future's explosive population growth will be faced by countries with little of the world's scientific or technological expertise.

No one knows whether the world can sustain today's population of 6 billion people, much less the far greater populations expected in the future. As chapter 30 outlines, the world ecosystem is already under considerable
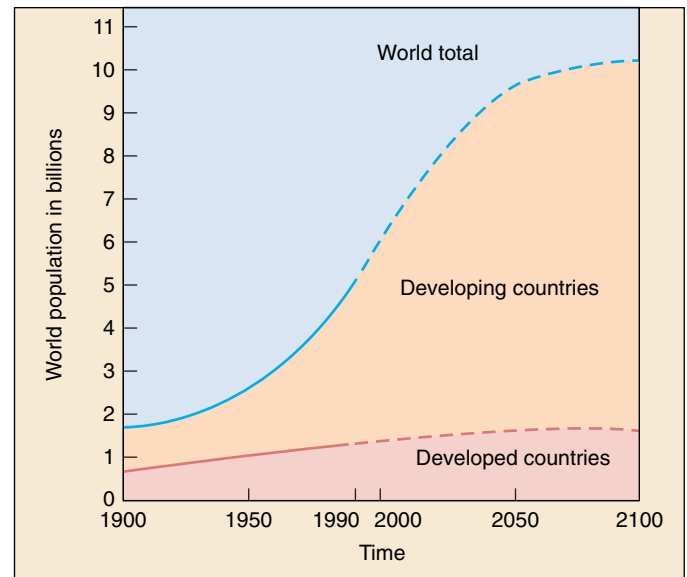
FIGURE 24.25
Most of the worldwide increase in population since 1950 has occurred in developing countries. The age structures of developing countries indicate that this trend will increase in the near future. The stabilizing of the world's population at about 10 billion (shown here) is an optimistic World Bank/United Nations prediction that assumes significant worldwide reductions in growth rate. If the world's population continues to increase at its 1996 rate, there will be over 30 billion humans by 2100!

stress. We cannot reasonably expect to continue to expand its carrying capacity indefinitely, and indeed we already seem to be stretching the limits. It seems unavoidable that to restrain the world's future population growth, birth and death rates must be equalized. If we are to avoid catastrophic increases in the death rate, the birthrates must fall dramatically. Faced with this grim dichotomy, significant efforts are underway worldwide to lower birthrates.

The human population has been growing rapidly for 300 years, since technological innovations dramatically reduced the death rate.

Summary	Questions	Media Resources

24.1 Populations are individuals of the same species that live together.

- Populations are the same species in one place; communities are populations of different species that live together in a particular place. A community and the nonliving components of its environment combine to form an ecosystem.
- Populations may be dispersed in a clumped, uniform, or random manner.

1. What are the three types of dispersion in a population? Which type is most frequently seen in nature? Why?

2. What are some causes of clumped distributions?

- Introduction to Populations
- Population Characteristics

- On Science Article: Snakes in Ireland

24.2 Population dynamics depend critically upon age distribution.

- The growth rate of a population depends on its age structure, and to a lesser degree, sex ratio.
- Survivorship curves describe the characteristics of mortality in different kinds of populations.

3. What is survivorship? Describe the three types of survivorship curves and give examples of each.

4. What is demography? How does a life table work?

- On Science Article: Deer Hunting

24.3 Life histories often reflect trade-offs between reproduction and survival.

- Organisms balance investment in current reproduction with investment in growth and future reproduction.

5. Why do some birds lay fewer than the optimal number of eggs as predicted by David Lack?

- On Science Article: Science for the Future

24.4 Population growth is limited by the environment.

- Population size will change if birth and death rates differ, or if there is net migration into or out of the population. The intrinsic rate of increase of a population is defined as its biotic potential.
- Many populations exhibit a sigmoid growth curve, with a relatively slow start in growth, a rapid increase, and then a leveling off when the carrying capacity of the environment is reached.
- Large broods and rapid rates of population growth characterize *r*-strategists. *K*-strategists are limited in population size by the carrying capacity of their environments; they tend to have fewer offspring and slower rates of population growth.
- Density-independent factors have the same impact on a population no matter what its density.

6. Define the biotic potential of a population. What is the definition for the actual rate of population increase? What other two factors affect it?

7. What is an exponential capacity for growth? When does this type of growth naturally occur? Give an example.

8. What is carrying capacity? Is this a static or dynamic measure? Why?

9. What is the difference between *r*- and *K*-selected populations?

- Stages of Population Growth

- Population Growth
- Size Regulation

- Scientists on Science: Coral Reefs Threatened
- Student Research: Prairie Habitat Fragmentation
- On Science Article: Tropical Songbirds Lay Fewer Eggs
- On Science Article: Was Malthus Mistaken?

24.5 The human population has grown explosively in the last three centuries.

- Exponential growth of the world's human population is placing severe strains on the global environment.

10. How do population pyramids predict whether a population is likely to grow or shrink?

- Human Population