53

Population Ecology

Concept Outline

53.1 Organisms must cope with a varied environment.

The Environmental Challenge. Organisms cope with environmental variation with physiological, morphological, and behavioral adaptations.

53.2 Populations are groups of individuals of the same species that live in the same place.

Population Ranges. Population borders are determined by areas in which individuals cannot survive and reproduce.

Pattern of Spacing of Individuals in a Population. The distribution of individuals in a population can be random, uniform, or clumped.

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

53.3 Population dynamics depend critically upon age distribution.

Demography. A population's growth rate is a function of its age structure and age-specific mortality rates.

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

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

53.5 Population growth is limited by the environment.

Population Growth. Populations grow if births exceed deaths until they reach the carrying capacity of their environment.

Factors that Regulate Populations. Some of the factors that regulate a population's growth depend upon the size of the population; others do not.

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

The Advent of Exponential Growth. Human populations will continue to grow in developing countries because of the number of young people entering their reproductive years.

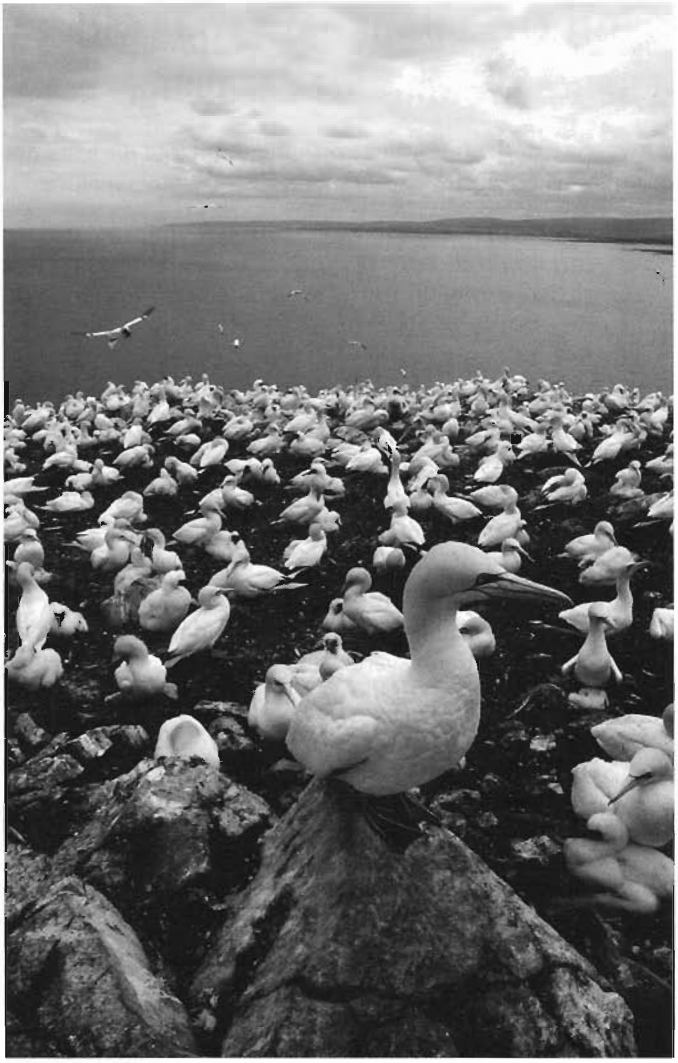


FIGURE 53.1
Life takes place in populations. This population of gannets is subject to the rigorous effects of reproductive strategy, competition, predation, and other limiting factors.

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 first consider how organisms respond to the abiotic environment in which they occur and how these responses affect the properties of populations, emphasizing population dynamics (figure 53.1). In chapter 54, we discuss communities of coexisting species and the interactions that occur among them. In subsequent chapters, we discuss the functioning of entire ecosystems and of the biosphere, concluding with a consideration of the problems facing our planet and our fellow species.

53.1 Organisms must cope with a varied environment.

The Environmental Challenge

The nature of the physical environment in large measure determines what organisms live there. Key elements include:

Temperature. Most organisms are adapted to live within a relatively narrow range of temperatures and will not thrive if temperatures are colder or warmer. The growing season of plants, for example, is importantly influenced by temperature.

Water. Plants and all other organisms require water. On land, water is often scarce, so patterns of rainfall have a major influence on life.

Sunlight. Almost all ecosystems rely on energy captured by photosynthesis; the availability of sunlight influences the amount of life an ecosystem can support, particularly below the surface in marine communities.

Soil. The physical consistency, pH, and mineral composition of soil often severely limit plant growth, particularly the availability of nitrogen and phosphorus.

Approaches to Coping with Environmental Variation

An individual encountering environmental variation may maintain a "steady-state" internal environment, a condition known as **homeostasis.** Many animals and plants actively employ physiological, morphological, or behavioral mechanisms to maintain homeostasis. The beetle in figure 53.2 is using a behavioral mechanism to cope with drastic changes in water availability. Other animals and plants are known as **conformers** because they conform to the environment in which they find themselves, their bodies adopting the temperature, salinity, and other physical aspects of their surroundings.

Responses to environmental variation can be seen over both the short and the long term. In the short term, spanning periods of a few minutes to an individual's lifetime, organisms have a variety of ways of coping with environmental change. Over longer periods, natural selection can operate to make a population better adapted to the environment.

Individual Responses to Environmental Change. *Physiology.* Many organisms are able to adapt to environmental change by making physiological adjustments. Thus, your body constricts the blood vessels on the surface of your face on a cold day, reducing heat loss (and also giving your face a "flush"). Similarly, humans who visit high altitudes initially experience altitude sickness—the symptoms of which include heart palpitations, nausea, fatigue, headache, mental impairment, and in serious cases, pulmonary edema—because of the lower atmospheric pressure and consequent lower oxygen availability in the air. After several days, however, the same people feel fine, because a number of physiological changes have increased the delivery of oxygen to their body tissues (table 53.1).

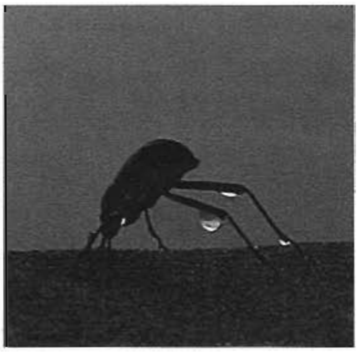


FIGURE 53.2
Meeting the challenge of obtaining moisture.
On the dry sand dunes of the Namib Desert in southwestern Africa, the beetle *Onymacris unguicularis* collects moisture from the fog by holding its abdomen up at the crest of a dune to gather condensed water.

Some insects avoid freezing in the winter by adding glycerol "antifreeze" to their blood; others tolerate freezing by converting much of their glycogen reserves into alcohols that protect their cell membranes from freeze damage.

Morphology. Animals that maintain a constant internal temperature (endotherms) in a cold environment have adaptations that tend to minimize energy expenditure. Many mammals grow thicker coats during the winter, utilizing their fur as insulation to retain body heat. In general, the thicker the fur, the greater the insulation (figure 53.3). Thus, a wolf's fur is about three times as thick in winter as in summer and insulates more than twice as well. Other mammals escape some of the costs of maintaining a constant body temperature during winter by hibernating during the coldest season, behaving, in effect, like conformers.

Behavior. Many animals deal with variation in the environment by moving from one patch of habitat to another, avoiding areas that are unsuitable. The tropical lizard in figure 53.4 manages to maintain a fairly uniform body temperature in an open habitat by basking in patches of sun and then retreating to the shade when it becomes too hot.

Table 53.1 Physiological Changes at High Altitude

Increased rate of breathing
Increased erythrocyte production, raising the amount of hemoglobin in the blood
Decreased binding capacity of hemoglobin, increasing the rate at which oxygen is unloaded in body tissues
Increased density of mitochondria, capillaries, and muscle myoglobin

By contrast, in shaded forests, the same lizard does not have the opportunity to regulate its body temperature through behavioral means. Thus, it becomes a conformer and adopts the temperature of its surroundings.

Behavioral adaptations can be extreme. Spadefoot toads (genus *Scaphiophus*), which live in the deserts of North America, can burrow nearly a meter below the surface and remain there for as long as nine months of each year, their metabolic rates greatly reduced as they live on fat reserves. When moist, cool conditions return, the toads emerge and breed. The young toads mature rapidly and burrow back underground.

Evolutionary Responses to Environmental Variation. These examples represent different ways in which organisms may adjust to changing environmental conditions. The ability of an individual to alter its physiology, morphology, or behavior is itself an evolutionary adaptation, the result of natural selection. The results of natural selection can also be detected by comparing closely related species that live in different environments. In such cases, species often have evolved striking adaptations to the particular environment in which they live.

For example, animals that live in different climates show many differences. Mammals from colder climates tend to have shorter ears and limbs—a phenomenon termed "Allen's Rule"—which reduces the surface area across which animals lose heat. Lizards that live in different climates exhibit physiological adaptations for coping with life at different temperatures. Desert lizards are unaffected by high temperatures that would kill a lizard from northern Europe, but the northern lizards are capable of running, capturing prey, and digesting food at cooler temperatures at which desert lizards would be completely immobilized.

Many species also exhibit adaptations to living in areas where water is scarce. Everyone knows of the camel and other desert animals that can go extended periods without drinking water. Another example of desert adaptation is seen in frogs. Most frogs have moist skins through which water permeates readily. Such animals could not survive in arid climates because they would rapidly dehydrate and die. However, some frogs have solved this problem by evolving a greatly reduced rate of water loss through the skin. One species, for example, secretes a waxy substance from specialized glands that waterproofs its skin and reduces rates of water loss by 95%.

Adaptation to different environments can also be studied experimentally. For example, when strains of *E. coli* were grown at high temperatures (42°C), the speed at which resources are utilized improved through time. After 2000 generations, this ability increased 30% over what it had been when the experiment started. The mechanism by which efficiency of resource use was increased is still unknown and is the focus of current research.

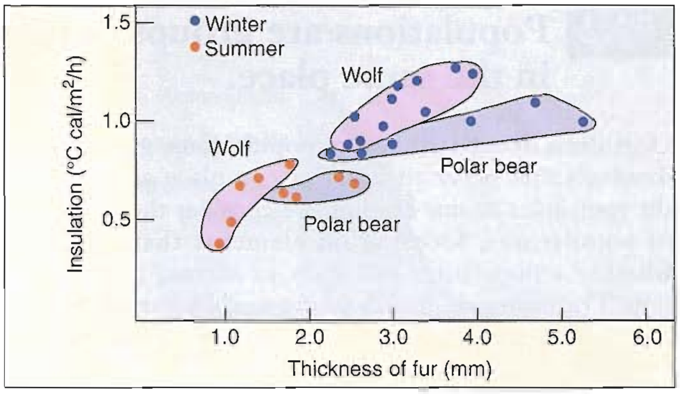


FIGURE 53.3
Morphological adaptation. Fur thickness in North American mammals has a major impact on the degree of insulation the fur provides.
Polar bears are able to live in zoos in warm climates. How thick would you expect the hair of a polar bear to be in a zoo in Miami, Florida?

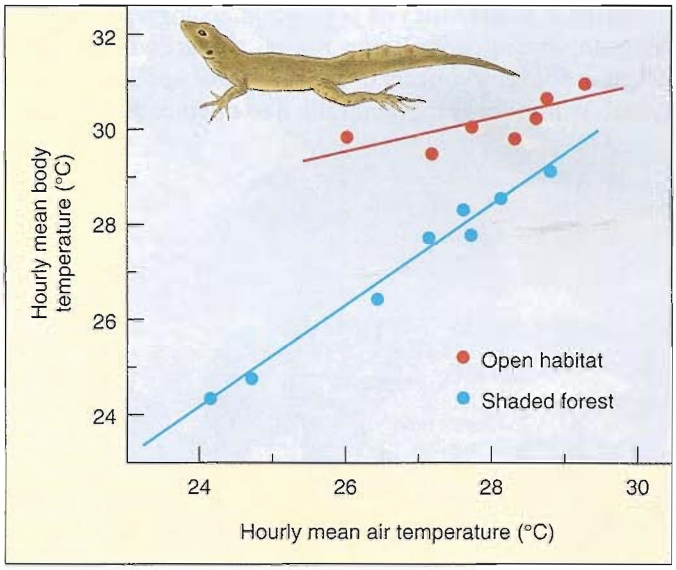


FIGURE 53.4
Behavioral adaptation. The Puerto Rican lizard *Anolis cristatellus* maintains a relatively constant temperature by seeking out and basking in patches of sunlight; in shaded forests, this behavior is not possible, and body temperature conforms to the surroundings.
When given the opportunity, lizards regulate their body temperature to maintain a temperature optimal for physiological functioning. Would lizards in open habitats exhibit different escape behaviors than lizards in shaded forest?

Organisms use a variety of physiological, morphological, and behavioral mechanisms to adjust to environmental variation. Over time, species evolve adaptations to living in different environments.

53.2 Populations are groups of individuals of the same species that live in the same place.

Organisms live as members of **populations**, groups of individuals that occur together at one place and time. In the remainder of this chapter, we 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.

The term "population" can be defined narrowly or broadly. This flexibility allows us to speak in similar terms of the world's human population, the population of protists in the gut of a termite, or the population of deer that inhabit a forest. Sometimes the boundaries defining a population are sharp, such as the edge of an isolated mountain lake for trout, and sometimes they are fuzzier, as when individual deer readily move back and forth between two forests separated by a cornfield.

Three characteristics of population ecology are particularly important: population range, the area throughout which a population occurs; the pattern of spacing of individuals within that range; and the size a population attains.

Population Ranges

No population, not even one composed of humans, occurs in all habitats throughout the world. Most species, in fact, have relatively limited geographic ranges, and the range of some species is miniscule. The Devil's Hole pupfish, for example, lives in a single hot-water spring in southern Nevada (figure 53.5), and the Socorro isopod is known from a single spring system in New Mexico. At the other extreme, some species are widely distributed. The common dolphin (*Delphinus delphis*), for example, is found throughout all the world's oceans.

As we just saw in section 53.1, organisms must be adapted for the environment in which they occur. Polar bears are exquisitely adapted to survive the cold of the Arctic, but you won't find them in the tropical rain forest. Certain prokaryotes can live in the near-boiling waters of Yellowstone's geysers, but they do not occur in cooler streams 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, a topic we will take up in chapter 54.

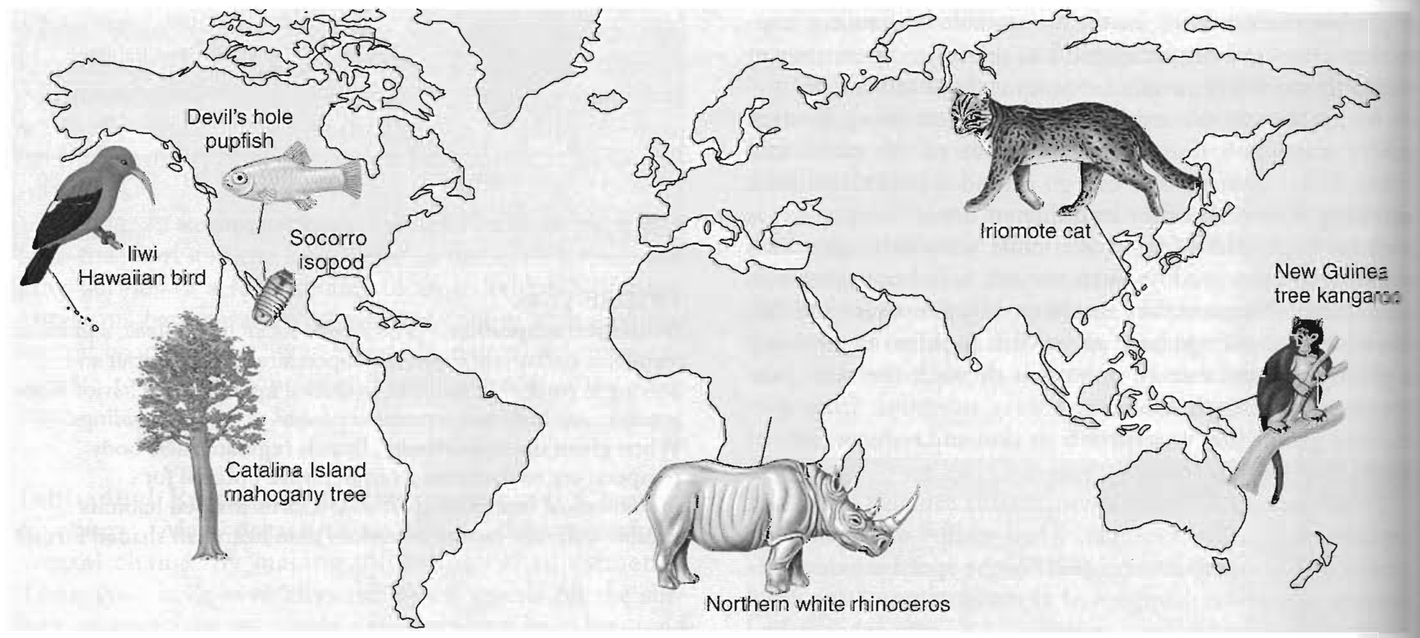


FIGURE 53.5
Species that occur in only one place. These species, and many others, are only found in a single population. All are endangered species, and should anything happen to their single habitat, the population—and the species—would become extinct.

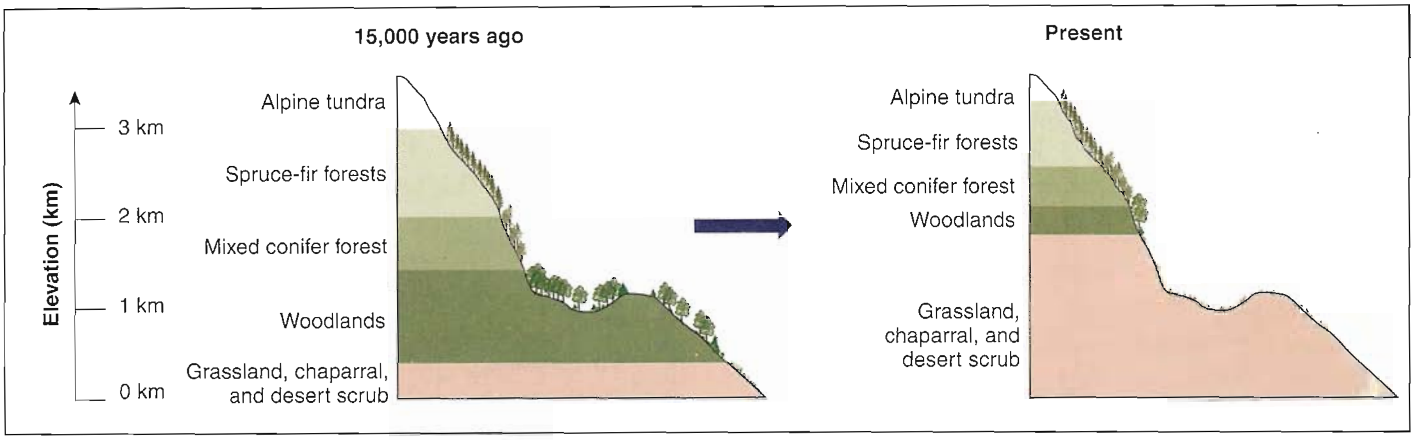


FIGURE 53.6
Altitudinal shifts in population ranges in the mountains of southwestern North America. During the glacial period 15,000 years ago, conditions were cooler than they are now. As the climate has warmed, tree species that require colder temperatures have shifted their range upward in altitude so that they live in the climatic conditions to which they are adapted.

Range Expansions and Contractions

Population ranges are not static; rather, they 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 warmed, species experienced shifts in the elevation at which they could live (figure 53.6).

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 and now can be found throughout most of the United States (figure 53.7).

A population is a group of individuals of the same species existing together in an area. Its range, the area a population occupies, changes over time.

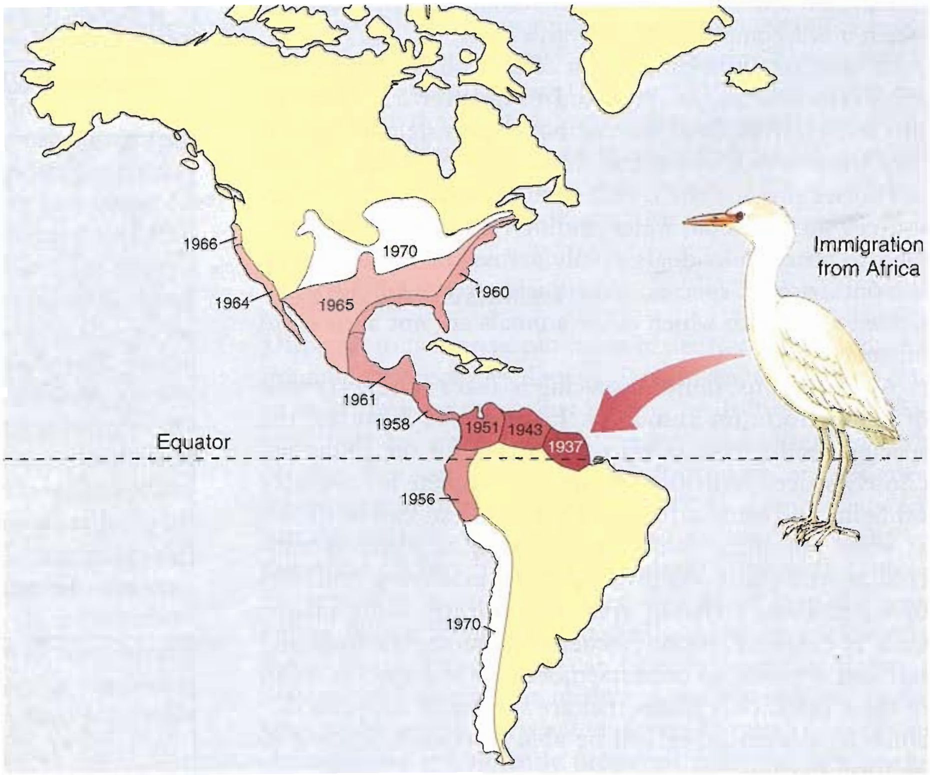


FIGURE 53.7
Range expansion of the cattle egret. The cattle egret—so named because it follows cattle and other hoofed animals, catching any insects or small vertebrates that they disturb—first arrived in South America in the late 1800s. Since the 1930s, the range expansion of this species has been well 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.

Pattern of Spacing of Individuals in a Population

Another key characteristic of population structure is the way in which individuals of a population are distributed. They may be randomly spaced, uniformly spaced, or clumped (figure 53.8).

Randomly Spaced

Individuals are randomly spaced within populations when they do not interact strongly with one another or with nonuniform aspects of their environment. Random distributions are not common in nature. Some species of trees, however, appear to exhibit random distributions in Panamanian rain forests (figure 53.8*b–d*).

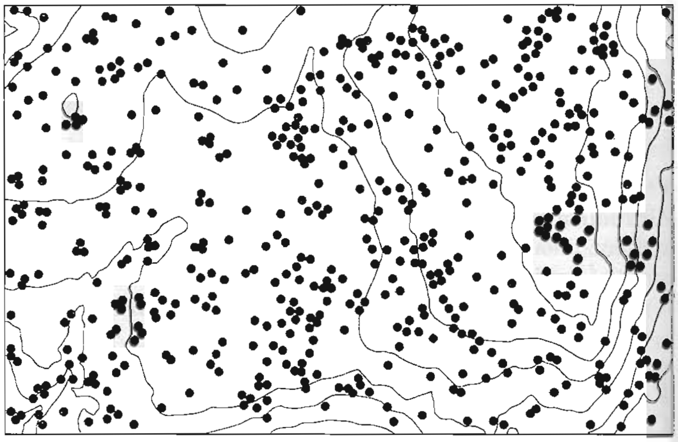
Uniformly Spaced

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

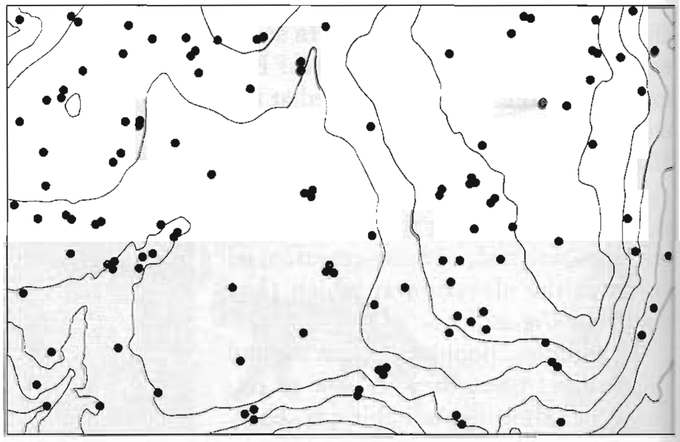
In animals, uniform spacing often results from behavioral interactions, as discussed in chapter 52. In many species, individuals of one or both sexes defend a territory from which other individuals are excluded. These territories provide the owner with exclusive access to resources such as food, water, 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 is also 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 compete for available sunlight, nutrients, or water. These contests can be direct, as when one plant casts a shadow over another, or indirect, as when two plants compete by extracting nutrients or water from a shared area. In addition, some plants, such as creosote, produce chemicals in the surrounding soil that are toxic to other members of their species. In all of these cases, only plants that are spaced an adequate distance from each other will be able to coexist, leading to uniform spacing.

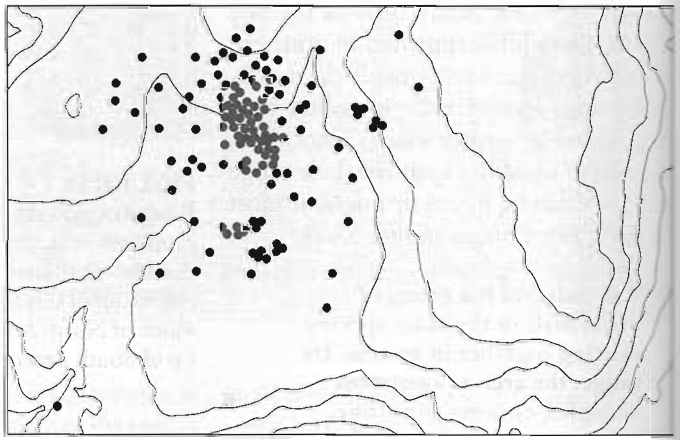
(a) Bacterial colonies



(b) Random distribution of *Brosimum alicastrum*



(c) Uniform distribution of *Coccoloba coronata*



(d) Clumped distribution of *Chamguava schippii*

FIGURE 53.8
Population dispersion. The different patterns of dispersion are exhibited by (*a*) different arrangements of bacterial colonies and (*b-d*) three different species of trees from the same locality in Panama.

Source: Data from Elizabeth Losos, Center for Tropical Forest Science, Smithsonian Tropical Research Institute.

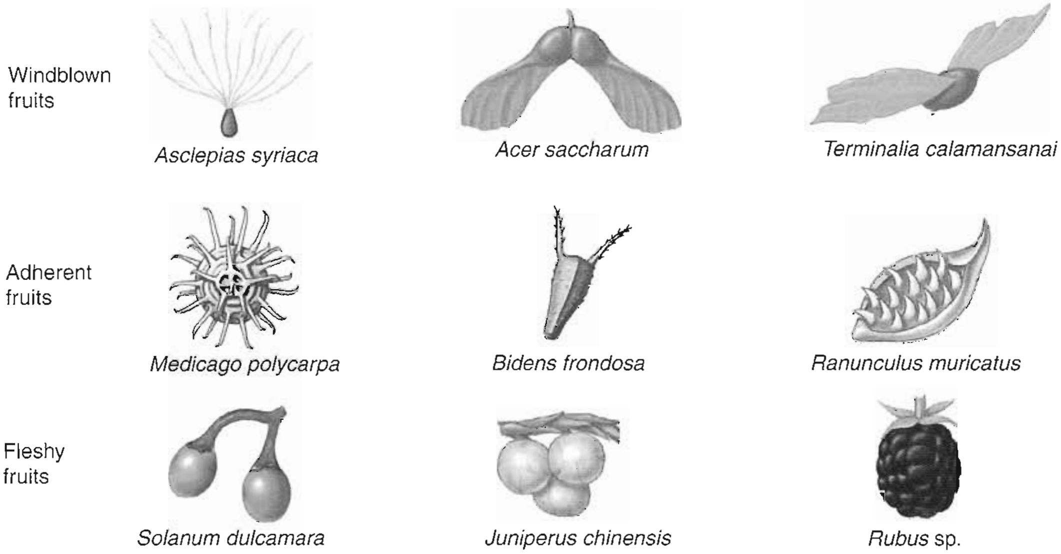


FIGURE 53.9
Some of the many adaptations of seeds. Seeds have evolved a number of different means of facilitating dispersal from their maternal plant. Some seeds can be transported great distances by the wind, whereas seeds enclosed in adherent and fleshy fruits can be transported by animals.

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 habitats defined by soil type, moisture, or other aspects of the environment to which they are best adapted.

Social interactions also can lead to clumped distributions. Many species live and move around in large groups, which go by a variety of names (for example, flock, herd, pride). 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, humans have allowed some species, such as coyotes, to expand their ranges and move into areas they previously did not occupy. Moreover, humans have served as an agent of dispersal for many species. Some of these transplants have been widely successful as is discussed in greater detail in chapter 57. 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 so that by 1980, they occurred throughout the United States. Similar stories could be told for countless 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 due to individuals or their eggs floating or drifting on vegetation. Bats are often the only mammals on distant islands because they can fly to them. Seeds of plants are designed to disperse in many ways (figure 53.9). 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 fleshy 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 leading to successful establishment of new populations is slim, over millions of years, many such dispersals have occurred.

The distribution of individuals within a population can be random, uniform, or clumped and is determined in part by the availability of resources.

Metapopulations

Species often exist as a network of distinct populations that interact with each other by exchanging individuals. Such networks, termed **metapopulations,** 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 tend to send out many dispersers, whereas populations at low levels tend to receive more immigrants than they send off. In addition, relatively isolated populations 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 become 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 species may also exhibit a metapopulation structure 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 53.10). In one study, researchers 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 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.

Metapopulations, where they occur, can have two important implications for the range of a species. First, by continually colonizing 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 occupies a larger area than it otherwise might occupy, including marginal areas that could not support a population without a continual influx of immigrants. For these reasons, the study of metapopulations has become very important in conservation biology as natural habitats become increasingly fragmented.

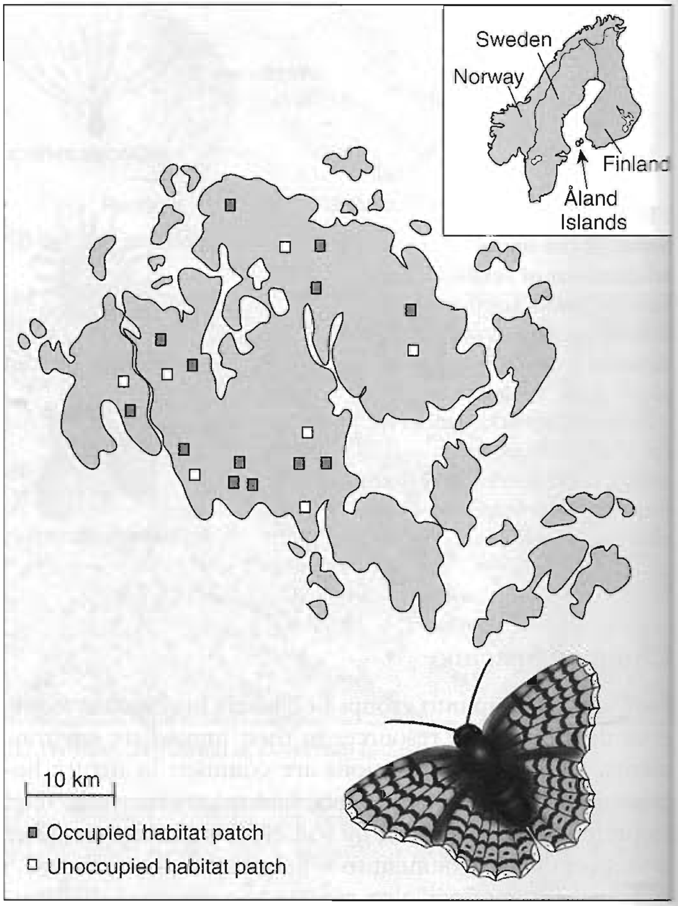


FIGURE 53.10
Metapopulations of butterflies. The glanville fritillary butterfly occurs in metapopulations in southwestern Finland on the Åland Islands. None of the populations is large enough to survive for long on its own, but continual emigration of individuals from other populations allows some populations to survive. In addition, continual establishment of new populations tends to offset extinction of established populations, although in recent years, extinctions have outnumbered colonizations.

Across broader areas, individuals may occur in populations that are loosely interconnected, termed metapopulations.

53.3 Population dynamics depend critically upon age distribution.

The dynamics of a population—how it changes through time—are affected by many factors. One important factor is the age distribution of individuals—that is, what proportion of individuals are adults, juveniles, and babies.

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: as a whole or broken down into parts. At the most inclusive level, we can study the whole population 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, however, if we break the population into smaller units composed of individuals of the same age (for example, 1-year-olds) and study the factors affecting birth and death rates for each unit separately.

Factors Affecting Population Growth Rates

Growth rates can be influenced by the population's **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 discussed in chapter 52); 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. By contrast, among monogamous species, such as many birds, in which pairs form long-lasting reproductive relationships, a reduction in the number of males can directly reduce the number of births.

Generation time, 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 53.11). Newts, for example, are smaller than mice, but have considerably longer generation times. Everything else equal, populations with short generations can increase in size more quickly than populations with long generations. Conversely, 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.

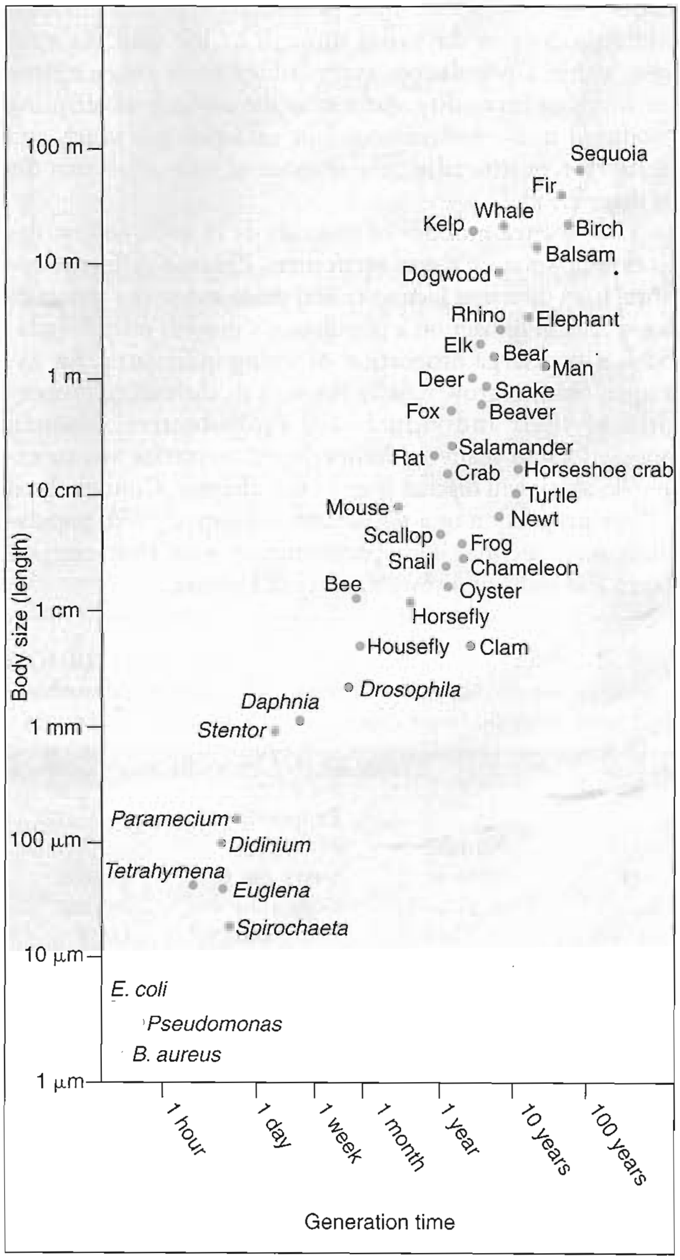


FIGURE 53.11
The relationship between body size and generation time. In general, larger animals have longer generation times, although there are exceptions.
If resources became more abundant, would you expect smaller or larger species to increase in population size more quickly?

Age Structure

A group of individuals of the same age is referred to as a **cohort.** In most species, the probability that an individual will reproduce or die varies through its life span. As a result, 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 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 different cohorts 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. Human populations in many underdeveloped countries are an example, as we will discuss later in this chapter. Conversely, if a large proportion of a population is relatively old, populations may decline. This phenomenon now characterizes Japan and some wealthy countries in Europe.

Life Tables and Population Change Through Time

To assess how populations in nature are changing, ecologists use a **life table,** which tabulates the fate of a cohort from birth until death, showing the number of offspring produced and the number of individuals that die each year. A very nice life table analysis is exhibited in a study of the meadow grass *Poa annua* (table 53.2). This study follows the fate of 843 individuals through time, charting how many survive in each interval and how many offspring each survivor produces.

In table 53.2, 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 fifth column presents the **mortality rate,** the proportion of individuals that started that interval alive but died by the end of it. The seventh 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 53.2 Life Table for a Cohort of the Grass *Poa annua*, Containing 843 Seedlings

Age (in 3-month intervals)	Number Alive at Beginning of Time Interval	Proportion of Cohort Surviving to Beginning of Time Interval (survivorship)	Deaths During Time Interval	Mortality Rate During Time Interval	Seeds Produced During Time Interval	Seeds Produced per Surviving Individual (fecundity)	Seeds Produced per Member of Cohort (fecundity × survivorship)
0	843	1.000	121	0.143	0	0.00	0.00
1	722	0.857	195	0.271	303	0.42	0.36
2	527	0.625	211	0.400	622	1.18	0.74
3	316	0.375	172	0.544	430	1.36	0.51
4	144	0.171	90	0.626	210	1.46	0.25
5	54	0.064	39	0.722	60	1.11	0.07
6	15	0.018	12	0.800	30	2.00	0.04
7	3	0.004	3	1.000	10	3.33	0.01
8	0	0.000	—		Total = 1665		Total = 1.98

Much can be learned by examining life tables. In the case of *P. annua*, we see that both the probability of dying and the number of offspring per surviving individual produced steadily 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 until the 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

The percentage of an original population that survives to a given age is called its **survivorship.** One way to express some aspects of the age distribution of populations is through a *survivorship curve.* Examples of different survivorship curves are shown in figure 53.12. 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 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 other animals and in protists, rise steeply in the postreproductive years (type I survivorship curve). Of course, these are just generalizations, and many organisms show more complicated patterns. Examination of the data for *P. annua*, for example, reveals that it is most similar to a type II survivorship curve (figure 53.13).

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.

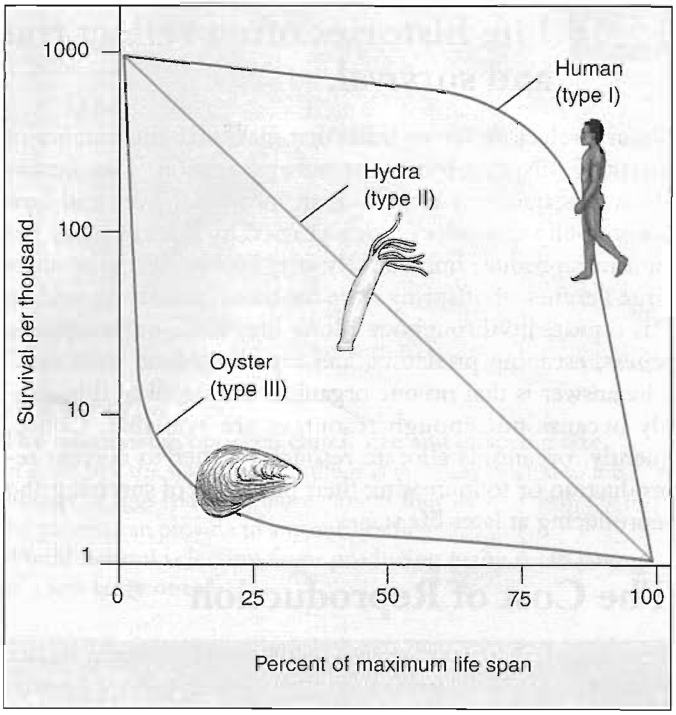


FIGURE 53.12
Survivorship curves. By convention, survival (the vertical axis) is plotted on a log scale. Humans have a type I life cycle, the hydra (an animal related to jellyfish) type II, and oysters type III.

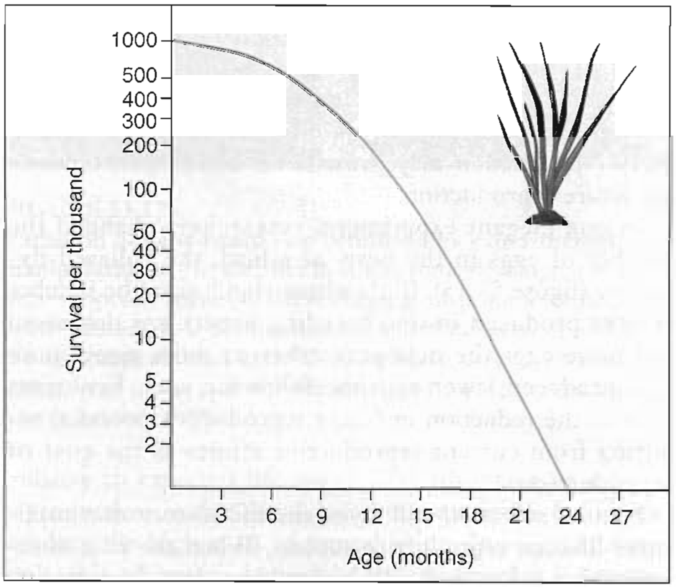


FIGURE 53.13
Survivorship curve for a cohort of the meadow grass *Poa annua*. After several months of age, mortality increases at a constant rate through time.
Suppose you wanted to keep meadow grass in your room as a houseplant. Suppose, too, that you wanted to buy a plant that was likely to live as long as possible. What age plant would you buy?

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 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, simply because not enough resources are available. Consequently, organisms allocate resources either to current reproduction or to increasing 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 53.14). Conversely, individuals that delay reproduction may grow faster and larger, enhancing future reproduction.

In one elegant experiment, researchers changed the number of eggs in the nests of a bird, the collared flycatcher (figure 53.15). 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 produce 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 are also 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.

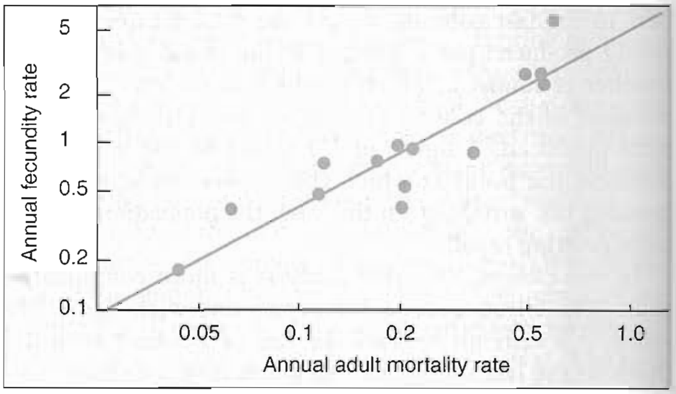


FIGURE 53.14
Reproduction has a price. Increased fecundity in birds correlates with higher mortality in several populations of birds, ranging from the albatross (lowest) to the sparrow (highest). Birds that raise more offspring per year have a higher probability of dying during that year.
Do you think that species in this graph are ordered by body size?

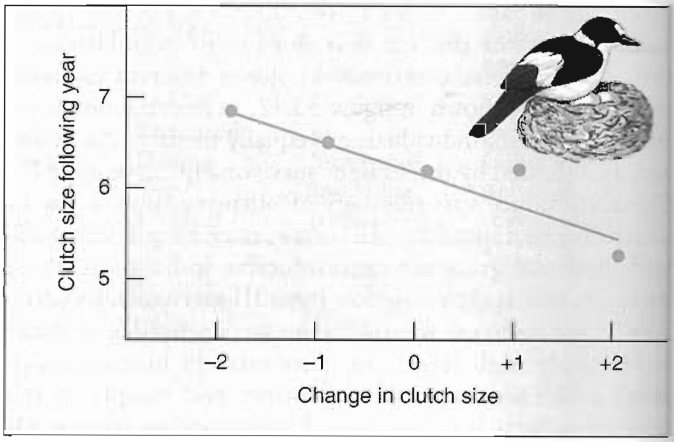


FIGURE 53.15
Reproductive events per lifetime. Adding eggs to nests of collared flycatchers (which increases the reproductive efforts of the female rearing the young) decreases clutch size the following year; removing eggs from the nest increases the next year's clutch size. This experiment demonstrates the trade-off between current reproductive effort and future reproductive success.
Why does this relationship exist?

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 occur between the number of offspring produced and the size of each offspring (figure 53.16). 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 and, subsequently, hatchlings that are much larger than normal (figure 53.17).

In the side-blotched lizard and many other 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.

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 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 that have a low probability of staying alive between broods, 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.

Age at First Reproduction

Among mammals and many other animals, longer-lived species put off reproduction longer than short-lived species (relative to expected life span). The advantage of delayed reproduction is that juveniles gain experience before expending the high costs of reproduction. In long-lived animals, this advantage outweighs the energy that is invested in survival and growth rather than reproduction. In shorter-lived animals, on the other hand, time is of the essence; thus, quick reproduction is more critical than juvenile training, and reproduction tends to occur earlier.

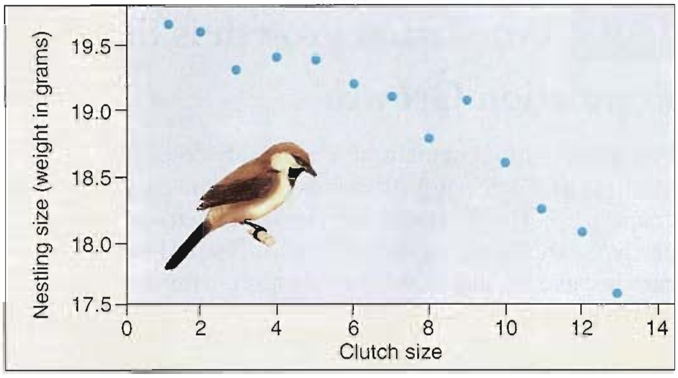


FIGURE 53.16
The relationship between clutch size and offspring size. In great tits, the size of the nestlings is inversely related to the number of eggs laid. The more mouths they have to feed, the less the parents can provide to any one nestling.
Would natural selection favor producing many small young or a few large ones?

FIGURE 53.17
Variation in baby lizard size produced by experimental manipulations. In clutches in which some developing eggs were surgically removed, the remaining offspring were larger (*center*) than lizards produced in control clutches in which all the eggs were allowed to develop (*right*). In experiments in which some of the yolk was removed from the eggs, smaller lizards hatched (*left*).

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

53.5 Population growth is limited by the environment.

Population Growth

Populations often remain at a relatively constant size, regardless of how many offspring are born. 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 producing fewer surviving offspring than others. To understand populations, we must consider how they grow and what factors in nature limit population growth.

The Exponential Growth Model

The rate of population increase, r, is defined as the difference between the birthrate (b) and the death rate (d) corrected for any movement of individuals in or out of the population, whether net emigration (e, movement out of the area) or net immigration (i, 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 was mostly due to immigration. Less than half of the increase came from the reproduction of the people already living there.

The simplest model of population growth assumes that a population grows without limits at its maximal rate and also that rates of immigration and emigration are equal. 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 biotic potential of any population is exponential (red line in figure 53.18). Even when the *rate* of increase remains constant, the actual *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. Natural examples include dandelions arriving in the fields, lawns, and meadows of North America from Europe for the first time; algae colonizing a newly formed pond; or the first terrestrial immigrants landing on an island recently thrust up from the sea.

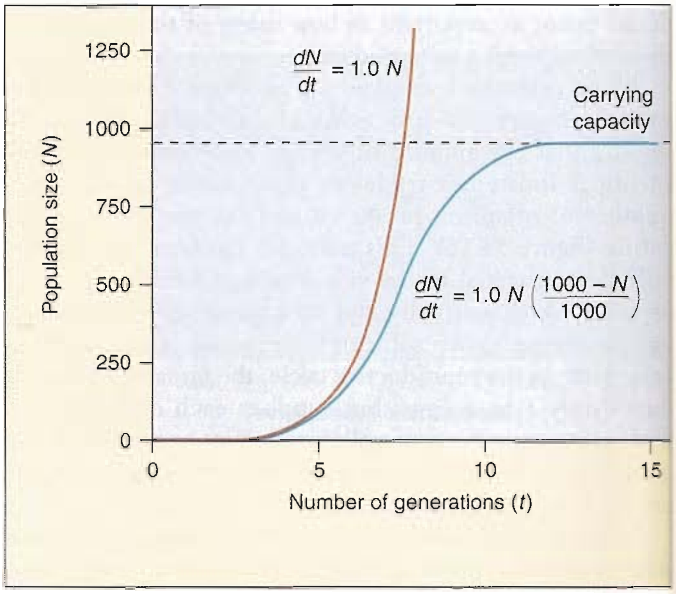


FIGURE 53.18
Two models of population growth. The red line illustrates the exponential growth model for a population with an r of 1.0. The blue line illustrates the logistic growth model in a population with $r = 1.0$ and $K = 1000$ individuals. At first, logistic growth accelerates exponentially; then, 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.

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 the environment 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

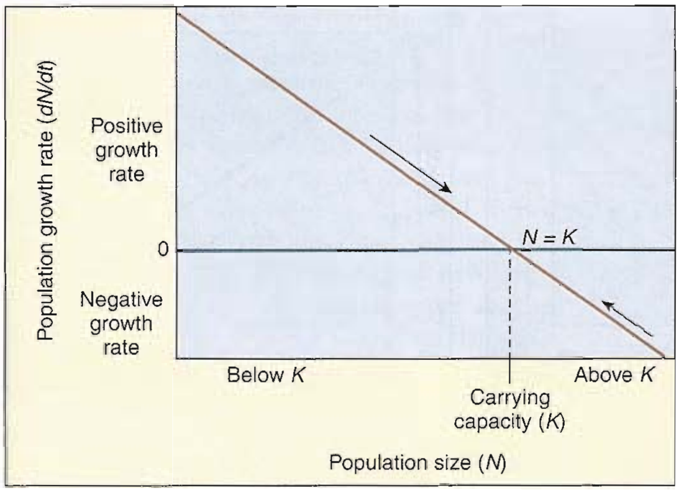


FIGURE 53.19
Relationship between population growth rate and population size. Populations far from the carrying capacity (*K*) will have high growth rates—positive if the population is below *K*, and negative if it is above *K*. As the population approaches *K*, growth rates approach zero.
Why does the growth rate converge on zero?

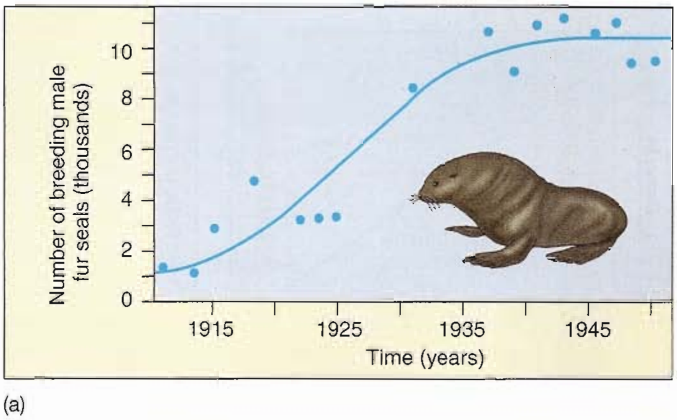
population, which is always limited by one or more factors in the environment, can be approximated by the following logistic growth equation:

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

In this model of population growth, the growth rate of the population (*dN/dt*) equals its intrinsic rate of natural 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.

Graphically, if you plot *N* versus *t* (time), you obtain a **sigmoidal growth curve** characteristic of many biological populations. The curve is called "sigmoidal" 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 (blue line in figure 53.18).

In mathematical terms, as *N* approaches *K*, the *rate* of population growth (*dN/dt*) begins to slow, reaching 0 when $N = K$ (figure 53.19). Conversely, if the population size exceeds the carrying capacity, then $K - N$ will be negative, and the population will experience a negative growth rate. As the population size declines toward the carrying capacity, the magnitude of this negative growth rate will decrease until it reaches 0 when $N = K$. Notice that the population will tend to move toward the carrying capacity regardless of whether it is initially above or below it. For this reason, logistic growth tends to return a population to the same size. In this sense, such populations are considered to be in equilibrium because they would be expected to be at or near the carrying capacity at most times.



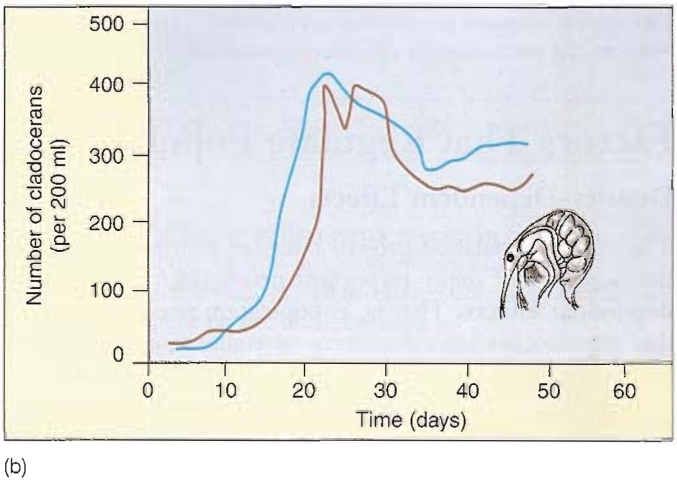


FIGURE 53.20
Many populations exhibit logistic growth. (*a*) A fur seal (*Callorhinus ursinus*) population on St. Paul Island, Alaska. (*b*) Two laboratory populations of the cladoceran *Bosmina longirostris*. Note that the populations first exceeded the carrying capacity, before decreasing to a size that was then maintained.
Why is there a hump in the population growth curve in (*b*), followed by a decline in the population?

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 53.20*a*). In some cases, however, the fit is not perfect (figure 53.20*b*), 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.

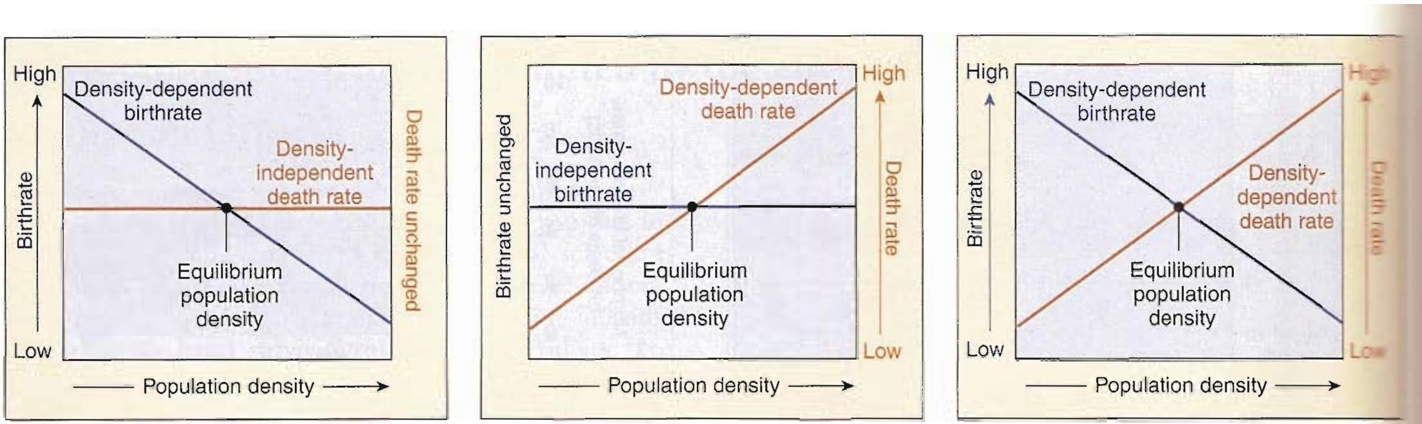


FIGURE 53.21
Density-dependent population regulation. Density-dependent factors can affect birthrates, death rates, or both.
Why might birthrates be density-dependent?

Factors That Regulate Populations

Density-Dependent Effects

The reason population growth rates are affected by population size is that many important processes have **density-dependent effects.** That is, as population size increases, either reproductive rates decline or mortality rates increase, or both, a phenomenon termed *negative feedback* (figure 53.21).

Populations can be regulated in many different ways. When populations approach their carrying capacity, competition for resources can be severe, leading both to a decreased birthrate and an increased risk of death (figure 53.22). 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 in the environment.

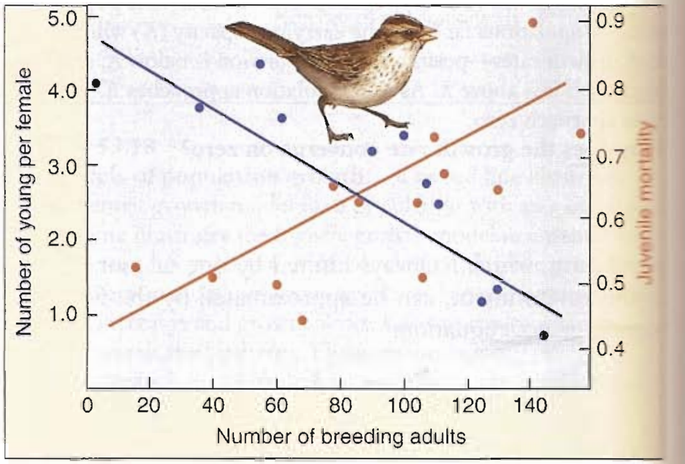


FIGURE 53.22
Density dependence in the song sparrow (*Melospiza melodia*) on Mandarte Island. Reproductive success decreases and mortality rates increase as population size increases.
What would happen if researchers supplemented the food available to the birds?

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 53.23).

FIGURE 53.23
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.

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), and is an example of *positive feedback*. 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.

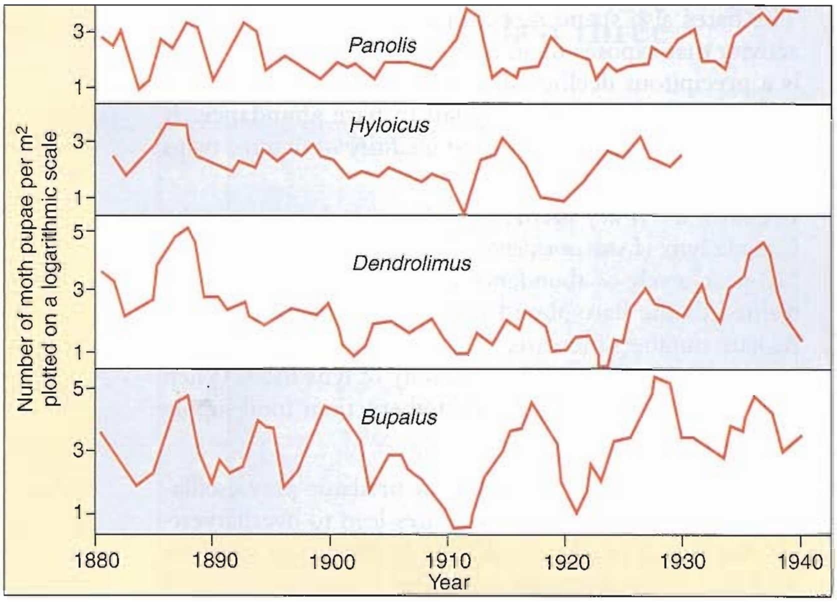


FIGURE 53.24

Fluctuations in the number of pupae of four moth species in Germany. The population fluctuations suggest that density-independent factors are regulating population size. The species concordance in trends through time suggests that the same factors are regulating population size in all species.

What might those factors be?

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 unrelated to 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, such as extremely cold winters, droughts, storms, or volcanic eruptions. Individuals often will be affected by these activities regardless of the size of the population. Populations in areas where such events occur relatively frequently will display erratic growth patterns in which the populations increase rapidly when conditions are benign, but exhibit large reductions whenever the environment turns hostile (figure 53.24). Needless to say, such populations do not produce the sigmoidal growth curves characteristic of the logistic equation.

Population Cycles

In some populations, density-dependent effects lead not to an equilibrium population size but to cyclic patterns of increase and decrease. Ecologists have studied cycles in hare populations since the 1820s. 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 10-fold to 30-fold in a typical cycle, and 100-fold changes can occur (figure 53.25). Two factors appear to be generating the cycle: food plants and predators.

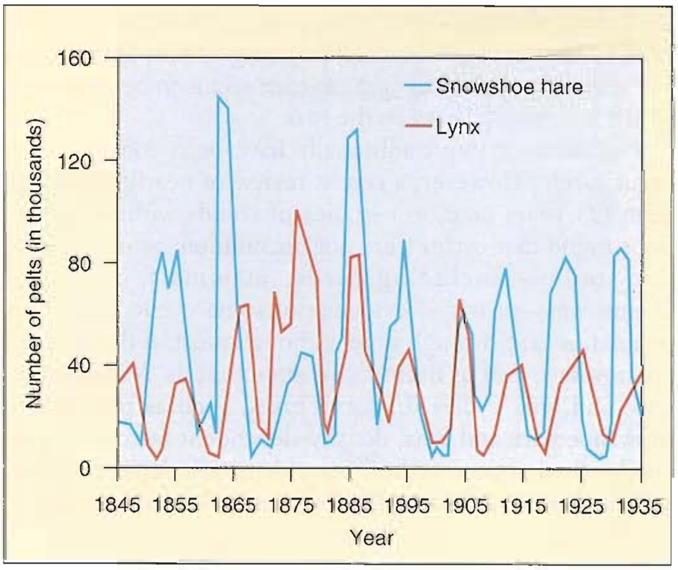


FIGURE 53.25

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 population carefully tracks that of the snowshoe hare, but lags behind it slightly.

Suppose experimenters artificially kept the hare population at a high and constant level; what would happen to the lynx population? Conversely, if experimenters artificially kept the lynx population at a high and constant level, what would happen to the hare population?

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, an activity that exposes 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 (see figure 53.25). 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.

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. In Canada's Yukon, Krebs set up experimental plots that contained hare populations. If food is added (no food shortage effect) and predators are excluded (no predator effect) in 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 shortage effect alone), or add food in the 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.

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. In some cases, such as that of the snowshoe hare and lynx, density-dependent factors may be involved, whereas in other cases, density-independent factors, such as cyclic climatic patterns, may be responsible.

Population Growth Rates and Life History Models

As we have seen, some species usually maintain stable population sizes near the carrying capacity, whereas the population sizes 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 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.

Table 53.3 *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

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 53.3 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.

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 53.3. These attributes should be treated as generalities, with the recognition that many exceptions exist.

Density-dependent effects are caused by factors that come into play particularly when the population size is larger; density-independent effects result from factors that operate regardless of population size. Some life history adaptations favor near-exponential growth; others favor the more competitive logistic growth. Most natural populations exhibit a combination of the two.

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

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 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. In other words, 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 gave 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 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 1.3% per year.

A 1.3% annual growth rate may not seem large, but it has produced a current human population of 6.3 billion people (figure 53.26)! At this growth rate, 82 million people are added to the world population annually, and the human population will double in 53 years. As we shall see, both the current human population level and the projected growth rate have potentially grave consequences for our future.

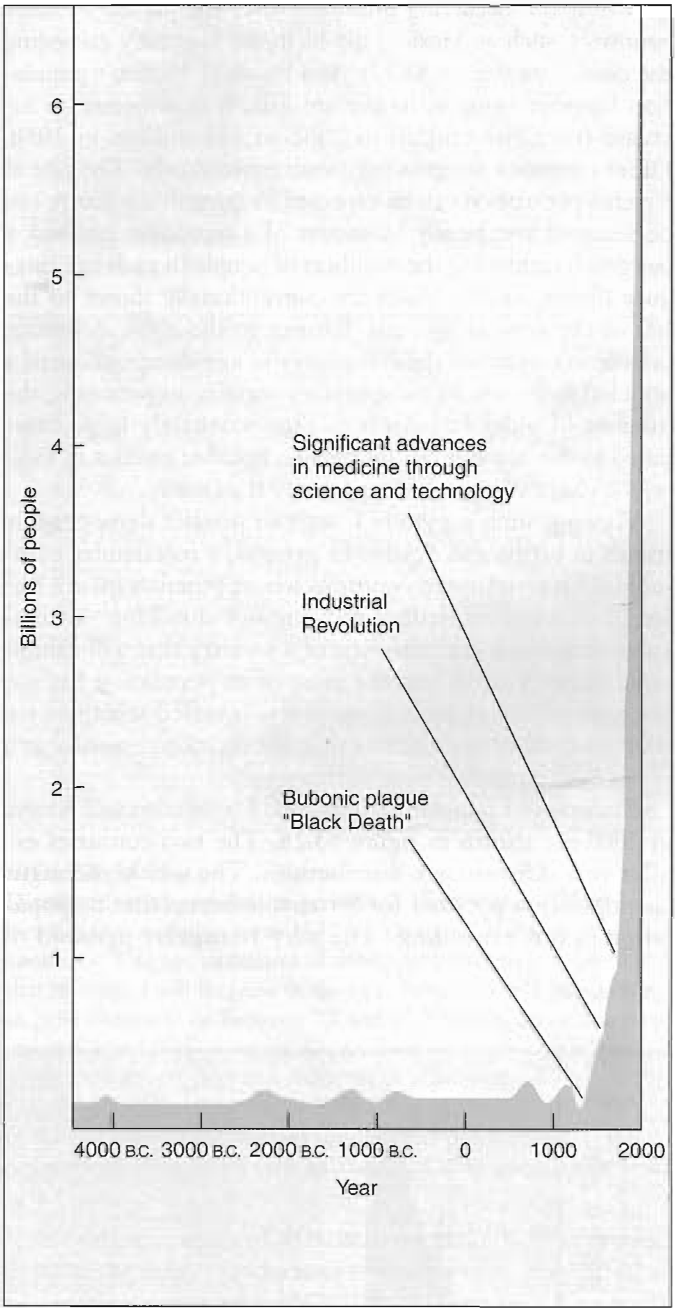


FIGURE 53.26
History of human population size. Temporary increases in death rate, even a severe one such as that occurring during the Black Death of the 1300s, have little lasting impact. Explosive growth began with the industrial revolution in the 1800s, which produced a significant, long-term lowering of the death rate. The current world population is 6.3 billion, and at the present rate, it will double in 53 years.
Based on what we have learned about population growth, what do you predict will happen to human population size?

Population Pyramids

While the human population as a whole continues to grow rapidly at the beginning of the twenty-first century, this growth is not occurring uniformly over the planet. In some countries, such as Mexico, the birthrate is greatly exceeding the death rate (figure 53.27). As a result, if Mexico's population keeps growing at its current rate, it is projected to increase from 102 million in 2002 to 151 million in 2050. 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 (figure 53.28). 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, we can predict demographic trends in births and deaths. In general, a rectangular pyramid is 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 because most of its population has not yet entered the child-bearing years. Inverted triangles are characteristic of populations that are shrinking, usually as a result of sharply declining birthrates.

Examples of population pyramids for Sweden and Kenya in 2000 are shown in figure 53.28. The two countries exhibit very different age distributions. The nearly rectangular population pyramid for Sweden indicates that its population is not expanding. The very triangular pyramid of Kenya, by contrast, predicts explosive future growth. The difference is most apparent when we consider that only 20% of Sweden's population is less than 15 years old, compared to nearly half of all Kenyans. Moreover, the fertility rate (offspring per woman) in Sweden is 1.6; in Kenya, it is 4.4. As a result, Kenya's population could double in less than 35 years, whereas Sweden's will remain stable.

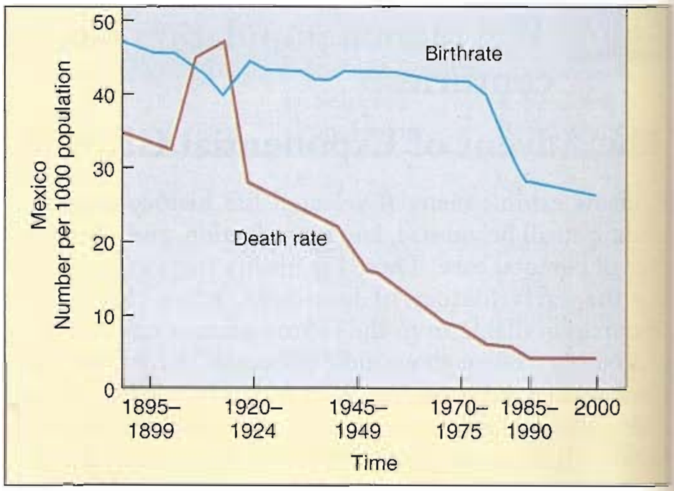


FIGURE 53.27
Why the population of Mexico is growing. The death rate (*red line*) in Mexico fell steadily throughout the last century, while the birthrate (*blue line*) remained fairly steady until 1970. The difference between birth and death rates has fueled a high growth rate. Efforts begun in 1970 to reduce the birthrate have been quite successful, but the growth rate remains high.
Is population growth rate increasing?

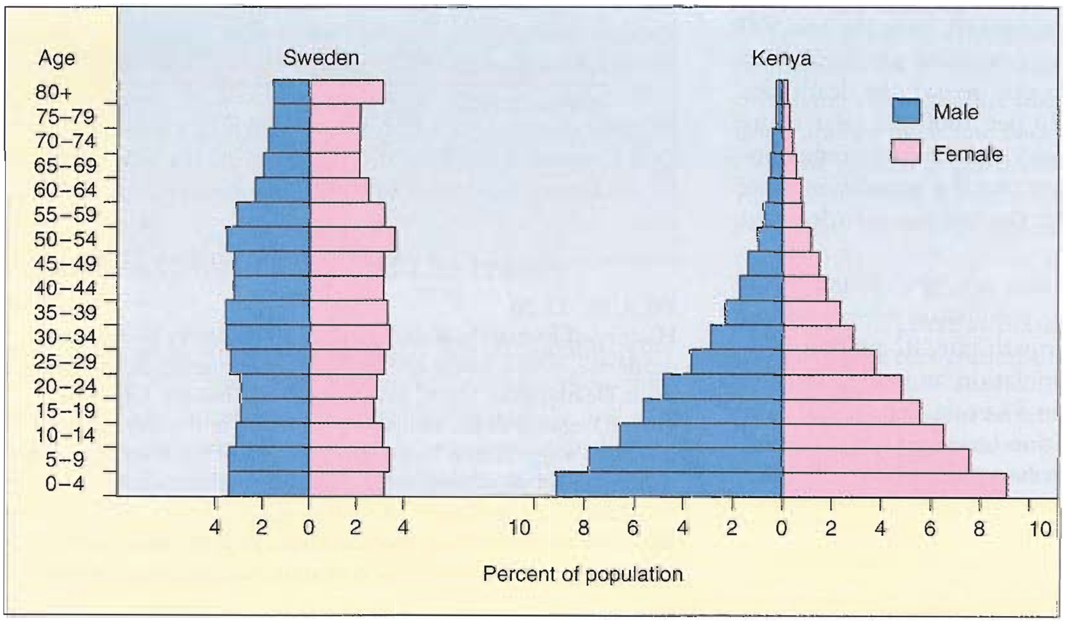


FIGURE 53.28
Population pyramids from 2000. Population pyramids are graphed according to a population's age distribution. Kenya's pyramid has a broad base because of the great number of individuals below childbearing age. When the young people begin to bear children, the population will experience rapid growth. The Swedish pyramid exhibits a slight bulge among middle-aged Swedes, the result of the "baby boom" that occurred in the middle of the twentieth century.
What will the population distributions look like in 20 years?

Table 53.4 A Comparison of 2002 Population Data in Developed and Developing Countries

	United States (highly developed)	Brazil (moderately developed)	Ethiopia (poorly developed)
Fertility rate	2.1	2.2	5.9
Doubling time at current rate (yr)	115	53	28
Infant mortality rate (per 1000 births)	6.6	33	97
Life expectancy at birth (yrs)	77	69	52
Per capita GNP (U.S. $)	$34,100	$7300	$660
Population < 15 years old (%)	21	30	44

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 82 million people a year to the earth's population—over a million every five days, 150 every minute! In more rapidly growing countries, the resulting population increase is staggering (table 53.4). India, for example, had a population of 1.05 billion in 2002; by 2050, its population will exceed 1.6 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 53.29). 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; and 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, the 19% of the world's population that lives in the industrialized world have a per capita income of $22,060, while 81% of the world's population lives in developing countries and has a per capita income of only $3,580. Further, of the people in the developing world, about one-quarter of the population gets by on $1 per day. Eighty percent of all the energy used today is consumed by the industrialized world, while only 20% is used by developing countries. Perhaps most worrisome for the future, fully 94% of all scientists and engineers reside in the industrialized world, and only 6% live 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 numbers expected in the future. As chapter 56 outlines, the world ecosystem is already under considerable stress. We cannot reasonably expect to expand its carrying capacity indefinitely, and indeed we already seem to be stretching the limits. Despite using an estimated 45% of the total biological productivity of the earth's landmasses and more than one-half of all renewable sources of fresh water, between one-fourth and one-eighth of all people in the world are malnourished. Moreover, as anticipated by Thomas Malthus in his famous 1798 *Essay on the Principle of Population,* death rates are beginning to rise in some areas. In sub-Saharan Africa, for example, population projections for the year 2025 have been scaled back from 1.33 billion to 1.05 billion (21%) because of the impact of AIDS. Similar decreases are projected for Russia as a result of higher death rates due to disease. If we are to avoid catastrophic increases in the death rate, birthrates must fall dramatically. Faced with this grim dichotomy, significant efforts are underway worldwide to lower birthrates.

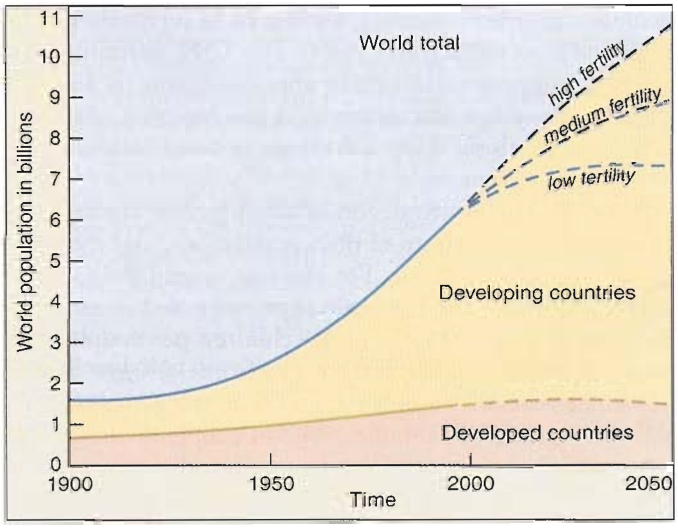


FIGURE 53.29
Distribution of population growth. Most of the worldwide increase in population since 1950 has occurred in developing countries. The age structures of developing countries indicate that this trend will increase in the near future. World population in 2050 likely will be between 7.3 and 10.7 billion, according to a recent United Nations study. Depending on fertility rates, the population at that time will either be increasing rapidly or slightly, or in the best case, declining slightly.
Is this an example of density-dependent population regulation? If so, what factors are regulating population size?

Population Growth Rate on the Decline

The world population growth rate is declining, from a high of 2.0% in the period 1965–1970 to 1.3% in 2002. Nonetheless, because of the larger population, this amounts to an increase of 82 million people per year to the world population, compared to 53 million per year in the 1960s.

The United Nations attributes the growth rate decline to increased family planning efforts and the increased economic power and social status of women. The United States has led the world in funding family planning programs abroad, but some groups oppose spending money on international family planning. The opposition states that money is better spent on improving education and the economy in other countries, leading to an increased awareness and lowered fertility rates. The U.N. certainly supports the improvement of education programs in developing countries, but interestingly, it has reported increased education levels *following* a decrease in family size as a result of family planning.

Most countries are devoting considerable attention to slowing the growth rate of their populations, and there are genuine signs of progress. For example, from 1984 to 2000, family planning programs in Kenya succeeded in reducing the fertility rate from 8.0 to 4.4 children per couple, thus lowering the population growth rate from 4.0% per year to 2.1% per year. Because of these efforts, the global population may stabilize at about 8.9 billion people by the middle of the current century. How many people the planet can support sustainably depends on the quality of life that we want to achieve; there are already more people than can be sustainably supported with current technologies.

Consumption in the Developed World Is Also a Problem

Population size is not the only factor that determines resource use; per capita consumption is also important. In this respect, we in the industrialized world need to pay more attention to lessening the impact each of us makes because, even though the vast majority of the world's population is in developing countries, the vast majority of resource consumption occurs in the industrialized countries. Indeed, the wealthiest 20% of the world's population accounts for 86% of the world's consumption of resources and produces 53% of the world's carbon dioxide emissions, whereas the poorest 20% of the world is responsible for only 1.3% of consumption and 3% of carbon dioxide emissions. Looked at another way, in terms of resource use, a child born today in the industrialized world will consume many more resources over the course of his or her life than a child born in the developing world. One way of quantifying this disparity is by calculating what has been termed the **ecological footprint,** which is the amount of productive land required to support an individual at the standard of living of a particular population through the course of his or her life. This figure estimates the acreage used for the production of food (both plant and animal), forest products, and housing, as well as the area of forest required to absorb carbon dioxide produced by the combustion of fossil fuels. As figure 53.30 illustrates, the ecological footprint of an individual in the United States is more than 10 times greater than that of someone in India. Based on these measurements, researchers have calculated that resource use by humans is now one-third greater than the amount that nature can sustainably replace. Moreover, consumption is increasing rapidly in parts of the developing world; if all humans lived at the standard of living in the industrialized world, two additional planet earths, would be needed!

Building a sustainable world is the most important task facing humanity's future. The quality of life available to our children will depend to a large extent on our success in limiting both population growth and the amount of per capita resource consumption.

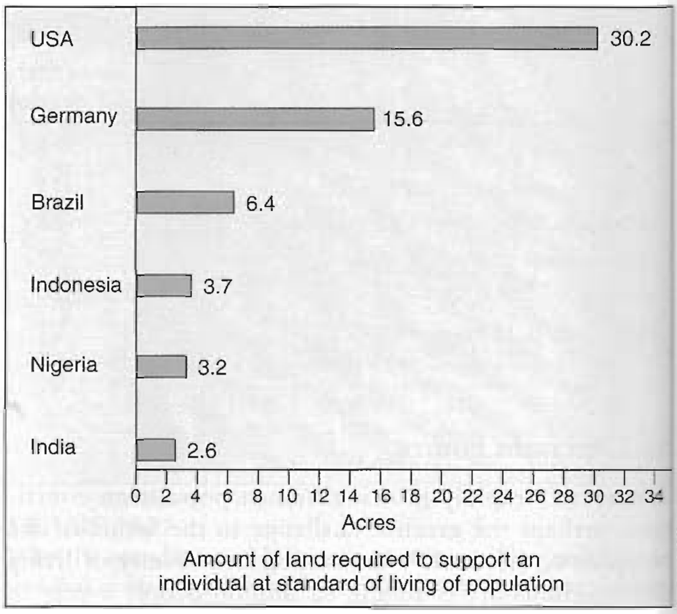


FIGURE 53.30
Ecological footprints of individuals in different countries. An ecological footprint calculates how much land is required to support a person through his or her life, including the acreage used for production of food, forest products, and housing, in addition to the forest required to absorb the carbon dioxide produced by the combustion of fossil fuels.
Which is a more important cause of resource depletion, overpopulation or overconsumption?

In 2002, the global human population of 6.3 billion people was growing at a rate of approximately 1.3% annually. At that rate, the population would double in 53 years. Growth rates, however, are declining, but consumption per capita in the developed world is also a significant drain on resources.
