

A population of Caribbean flamingos (*Phaenicopterus ruber*). Each pair of flamingos in this breeding colony incubates a single egg in a mud nest.

STUDY PLAN

49.1 The Science of Ecology

Ecologists study levels of organization ranging from individual organisms to the biosphere

Ecologists test hypotheses with observational and experimental data

49.2 Population Characteristics

A population's size and density determine the amount of resources it uses

Populations differ in how they are distributed in space

A population's age structure, generation time, and sex ratio influence how quickly it will grow

49.3 Demography

Life tables summarize a population's survival and reproductive rates

Survivorship curves depict changes in survival rate over the life span

49.4 The Evolution of Life Histories

Organisms face trade-offs in their allocation of resources

Life history patterns vary dramatically among species

Ecologists analyze the individual components of life histories

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The logistic model describes population growth when resources are limited

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Interacting environmental factors often limit population sizes

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Some species exhibit regular cycles in population size

49.7 Human Population Growth

Human populations have sidestepped the usual density-dependent controls

Age structure and economic development may now control our population growth



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49 Population Ecology

WHY IT MATTERS

When humans immigrate to new places, they often transport familiar plants and animals from home, introducing them into their new gardens, fields, and forests. Some organisms fail to survive in the new environments. But other species—like the European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) that are now so common in North America—flourish and sometimes become pests.

In 1859, an Australian rancher released a few pairs of European rabbits (*Oryctolagus cuniculus*) for sport hunting in the state of Victoria. The rabbits bred rapidly, sometimes producing litters of four or five offspring every month. They had no natural predators in Australia, and by 1900, an estimated 20 million rabbits had overrun much of the continent; their advance was limited only by extreme climates, clay soil, and lack of food or water. The rabbits destroyed natural vegetation and the pastures that supported a large sheep industry. The government tried in vain to poison the rabbits. Ranchers introduced predators, hoping that they would eat rabbits faster than the rabbits could reproduce. But the rabbits continued to multiply. Eventually, the government built a “rabbit-proof fence” that stretched more than



Figure 49.1
Introduced organisms. European rabbits multiplied so rapidly and destroyed so much vegetation in Australia that the government built a fence across the country to prevent their spread.

3200 km (2000 miles) to keep the rabbits out of the rich pasture lands in Western Australia (**Figure 49.1**).

In 1950, scientists tackled the devastating problems caused by the introduced rabbits. Biologists collected myxoma virus (a relative of smallpox) from infected rabbits in South America

and released it among the European rabbits in Australia. The virus was lethal to European rabbits, which had never evolved resistance to it. The first epidemic of myxomatosis killed more than 99% of infected rabbits. But in the following season, the virus killed only 90% of infected rabbits, and within a few years, the virus was killing only half the rabbits it infected. Clearly, some rabbits were becoming more resistant to the virus. Resistant rabbits survived and reproduced, comprising a larger percentage of the population over time (see Section 20.3 to review natural selection). Subsequent research showed that the virus had also become less virulent. Today, wildlife-control agents develop and release more deadly viruses to control the rabbit population.

This brief history of an environmental disruption introduces our unit on **ecology**, the study of interactions between organisms and their environments. All environments have both **abiotic** (nonbiological) and **biotic** (biological) components. The abiotic environment includes temperature, moisture, soil chemistry, and other physical factors; the biotic environment includes all the organisms found in a particular place.

This story also identifies several ecological phenomena that we consider in this chapter. For example, some species produce large numbers of young at frequent intervals; their numbers may increase rapidly for a period of time and then drop precipitously. Moreover, a species' abundance is often governed by the presence of other species—its food, predators, parasites, and disease-causing microorganisms. Finally, over time, ecological interactions foster adaptation and evolutionary change.

49.1 The Science of Ecology

The subject matter of ecology is so vast and so diverse that research in ecology is often linked to work in genetics, physiology, anatomy, behavior, paleontology, and evolution as well as in geology, geography, and environmental science. Many ecological phenomena occur over huge areas and long time spans. Ecologists

must devise ways to determine how environments influence organisms and how organisms change the environments in which they live. Today, the science of ecology encompasses two related disciplines. The major research questions of *basic ecology* relate to the distribution and abundance of species and how they interact with each other and the physical environment. Using these data as a baseline, workers in *applied ecology* develop conservation plans and amelioration programs to limit, repair, and mitigate ecological damage caused by human activities.

Ecologists Study Levels of Organization Ranging from Individual Organisms to the Biosphere

Ecology can be divided into five increasingly complex and inclusive levels of organization. In **organismal ecology** researchers study the genetic, biochemical, physiological, morphological, and behavioral adaptations of organisms to the abiotic environment. We have described many such adaptations in Units V and VI; we describe the evolution of animal behavior in Chapter 55.

Population ecology, the subject of this chapter, focuses on **populations**, groups of individuals of the same species that live together. Population ecologists study how the size and other characteristics of populations change in space and time. Research in **community ecology** examines groups of populations that occur together in one area. Community ecologists study interactions between species, analyzing how predation, competition, and environmental disturbances influence a community's development, organization, and structure. We address major issues in community ecology in Chapter 50. Ecologists studying **ecosystem ecology** explore the cycling of nutrients and the flow of energy between the biotic components of an ecological community and the abiotic environment. We consider this topic in Chapter 51. Finally, some ecological studies focus on the **biosphere**, the total of all ecosystems on Earth. In Chapter 52, we examine global patterns in abiotic factors and their effects on populations, communities, and ecosystems. We discuss biodiversity and conservation biology in Chapter 53.

Ecologists Test Hypotheses with Observational and Experimental Data

Ecology has its roots in descriptive natural-history studies that date back to the ancient Greeks. Modern ecology was born in 1870 when the German biologist Ernst Haeckel coined the term (*oikos* = house). Contemporary researchers still gather descriptive information about ecological relationships, but these observations are only a starting point for more rigorous studies.

Most ecologists create hypotheses about ecological relationships and how they change through time or differ from place to place. Like other scientists, some ecologists formalize these ideas in mathematical models that express clearly defined, but hypothetical, relationships among important variables in a system. Manipulation of a model, usually with the help of a computer, can allow researchers to ask what would happen if some of the variables or their relationships change. Thus, researchers can simulate natural events and large-scale experiments before investing time, energy, and money in field and laboratory work. Bear in mind, however, that mathematical models are no better than the ideas and assumptions they embody, and useful models are constructed only after basic observations define the relevant variables.

Ecologists often conduct field or laboratory studies to test the predictions of their hypotheses. In controlled experiments, researchers compare data from an experimental treatment (in which one or more variables are artificially manipulated) with data from a control (in which nothing is changed). Sometimes the distributions of species create “natural experiments,” eliminating the need to manipulate variables. For example, two species of fishes, cutthroat trout (*Oncorhynchus clarki*) and Dolly Varden char (*Salvelinus malma*), live in coastal lakes of British Columbia, Canada. Some lakes have either trout or char, but other lakes contain both species. The natural distributions of these fishes allowed researchers to measure the effect of each species on the other. In lakes where both species live, each restricts its activities to fewer areas and feeds on a smaller variety of prey than it does in lakes where it occurs alone.

STUDY BREAK

1. Why are studies of ecosystems more “inclusive” than studies of populations?
2. In what ways are mathematical models useful in ecological research?

49.2 Population Characteristics

Populations have characteristics that transcend those of the individuals they comprise. For example, every population has a **geographical range**, the overall spatial boundaries within which it lives. Geographical ranges vary enormously. A population of snails might inhabit a small tidepool, whereas a population of marine phytoplankton might occupy an area orders of magnitude larger. Every population also occupies a **habitat**, the specific environment in which it lives, as characterized by its biotic and abiotic features. Ecologists also mea-

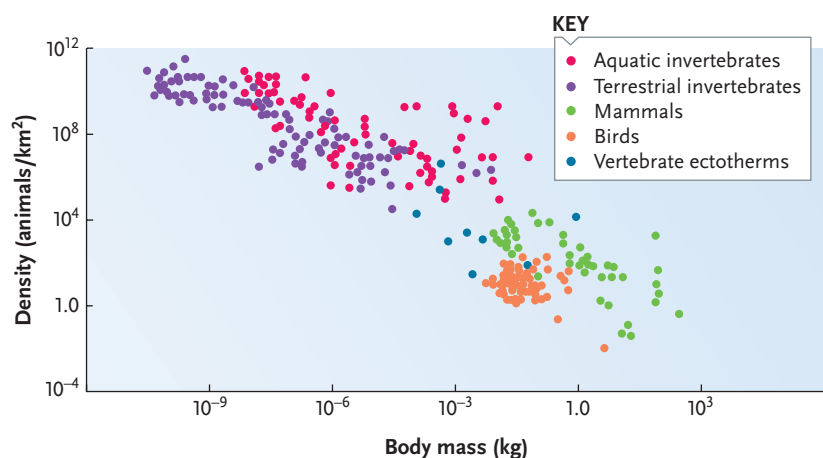


Figure 49.2
Population density and body size. Population density generally declines with increasing body size among animal species. Similar trends exist for other types of organisms.

sure other population characteristics, such as size, distribution in space, and age structure.

A Population’s Size and Density Determine the Amount of Resources It Uses

Population size is simply the number of individuals in a population at a specified time. **Population density** is the number of individuals per unit area or per unit volume of habitat. Species with large body size generally have lower population densities than those with small body size (**Figure 49.2**). Although population size and density are related measures, knowing a population’s density provides more information about its relationship to the resources it uses. For example, if a population of 200 oak trees occupies 1 hectare (10,000 m²), its population density is 200/10,000 m² or one tree per 50 m². But if a population of 200 oaks is spread over 5 hectares, its density is one tree per 250 m². Clearly, the second population is less dense than the first, and its members will have greater access to sunlight, water, and other resources.

Ecologists measure population size and density to monitor and manage populations of endangered species, economically important species, and agricultural pests. For large-bodied species, a simple head count provides accurate information. For example, ecologists survey the size and density of African elephant (*Loxodonta africana*) populations by flying over herds and counting individuals. Researchers use a variation on that technique to estimate population size in tiny organisms that live at high population densities. To estimate the density of aquatic phytoplankton, for example, you might collect water samples of known volume from representative areas in a lake and use a microscope to count the organisms; you could then extrapolate their population size and density based on the estimated volume of the entire lake. In other cases, researchers use the mark-release-recapture sampling technique (**Figure 49.3**).

Figure 49.3 Research Method

Using Mark-Release-Recapture to Estimate Population Size

PURPOSE: Ecologists use the mark-release-recapture technique to estimate the population size of mobile animals that live within a restricted geographic range.

PROTOCOL: A sample of organisms is captured, marked in some permanent but harmless way, and released. Insects and reptiles are marked with ink or paint, birds with rings on their legs, and mammals with ear tags or collars. Some time later, a second sample of organisms is captured, and the researcher notes what proportion of the second sample carries the mark. That proportion tells us what percentage of the total population was captured and marked at the first sampling. The total population size is estimated as $(\text{number marked}) \times (\text{number in the second sample} / \text{number of marked recaptures})$.

INTERPRETING THE RESULTS: Imagine that you capture 120 butterflies, mark each with a black spot on its wing, and release them. A week later, you capture a second sample of 150 butterflies and find that 30 of them have the black mark. Thus, you had marked one out of every five butterflies (30/150) on your first field trip. Because you captured 120 individuals on that first excursion, you would estimate that the total population size is $120 \times (150/30) = 600$ butterflies.

The technique is based on several assumptions that are critical to its accuracy: (1) that being marked has no effect on survival; (2) that marked and unmarked animals mix randomly in the population; (3) that no migration into or out of the population takes place during the estimating period; and (4) that marked individuals are just as likely to be captured as unmarked individuals. (Sometimes animals become “trap shy” or “trap happy,” a violation of the fourth assumption.)



Michael C. Singer, University of Texas

Populations Differ in How They Are Distributed in Space

Populations also vary in their **dispersion**, the spatial distribution of individuals within the geographical range. Ecologists define three theoretical patterns of dispersion: *clumped*, *uniform*, and *random* (Figure 49.4).

Three reasons explain why a **clumped dispersion**—with individuals grouped together—is extremely common in nature. First, suitable conditions often have a patchy distribution. For example, certain pasture plants may be clumped in small, scattered areas where cowpats fell months before, locally enriching the soil. Second, some animals live in social groups (see Section 55.5). Mates are easy to locate within groups, and individuals may cooperate in rearing offspring, feeding, or defending themselves from predators. Third, some organisms are clumped because of their reproductive pattern. Plants and animals that produce asexual clones, such as aspen trees and sea anemones, often occur in large aggregations (see Chapters 34 and 47).

In other species, seeds, eggs, or larvae lack dispersal mechanisms, and offspring grow near their parents.

Organisms are evenly spaced in their habitat, a pattern called **uniform dispersion**, when individuals repel each other because resources are in short supply. For example, creosote bushes (*Larrea tridentata*) are uniformly distributed in the dry scrub deserts of the American Southwest. Mature bushes deplete the surrounding soil of water and secrete toxic chemicals, making it impossible for seedlings to grow. Moreover, seed-eating ants and rodents that live at the base of mature bushes consume any seeds that fall nearby. Territorial behavior, the defense of an area and its resources, produces uniform dispersion in animals (see Section 55.2).

For some populations, environmental conditions don't vary much within a habitat, and individuals are neither attracted to nor repelled by others of their species. These populations exhibit **random dispersion**, which has a formal statistical definition that serves as a theoretical baseline for assessing whether organisms are clumped or uniformly distributed. In cases of random dispersion, individuals are distributed unpredictably. Some spiders, burrowing clams, and rainforest trees exhibit random dispersion.

Whether the spatial distribution of a population appears to be clumped, uniform, or random depends partly on how large an area an ecologist studies. Oak seedlings may be randomly dispersed on a spatial scale of a few square meters, but over an entire mixed hardwood forest, they are clumped under the parent trees.

In addition, the dispersion of animal populations often varies through time in response to natural environmental rhythms. Few habitats provide a constant supply of resources throughout the year, and many animals move from one habitat to another on a seasonal cycle. For example, tropical birds and mammals are often widely dispersed in deciduous forests during the wet season. But during the dry season, they crowd into narrow “gallery forests” along watercourses where evergreen trees provide food and shelter.

A Population's Age Structure, Generation Time, and Sex Ratio Influence How Quickly It Will Grow

All populations have an **age structure**, a statistical description of the relative numbers of individuals in each age class (see Section 49.7). Individuals can be roughly categorized as prereproductive (younger than the age of sexual maturity), reproductive, or postreproductive (older than the maximum age of reproduction). A population's age structure reflects its recent growth history and predicts its future growth potential. Populations that include many prereproductive individuals grew rapidly in the recent past and will

continue to grow larger as the young individuals mature and reproduce.

Another characteristic that influences a population's growth is its **generation time**, the average time between the birth of an organism and the birth of its offspring. Generation time is usually short in species that reach sexual maturity at a small body size (**Figure 49.5**). Their populations often grow rapidly because of the speedy accumulation of reproductive individuals.

Populations also vary in their **sex ratio**, the relative proportions of males and females. In general, the number of females in a population has a bigger impact on population growth than the number of males because only females actually produce offspring. Moreover, in many species, one male can mate with several females, and the number of males may have little effect on the population's reproductive output. In northern elephant seals (*Mirounga angustirostris*), for example, mature bulls fight for dominance on the beaches where the seals mate, and only a few males may ultimately inseminate a hundred or more females. Thus, the presence of other males in the group has little effect on the size of future generations. In animals that form lifelong pair bonds, such as geese and swans, the number of males does influence reproduction in the population.

Population ecologists often try to determine the proportion of individuals in a population that are reproducing. This issue is particularly relevant to the conservation of any species in which individuals are rare or widely dispersed in the habitat (see Section 53.4). As *Insights from the Molecular Revolution* describes, ecologists now use DNA analysis to address this question. In the next section we consider factors that influence the age structure of a population and its potential for future growth.

STUDY BREAK

1. What is the difference between a population's size and its density?
2. What do the three patterns of dispersion imply about the relationships between individuals in a population?

49.3 Demography

Populations grow larger through the birth of individuals and the **immigration** (movement into the population) of organisms from neighboring populations. Conversely, death and **emigration** (movement out of the population) reduce population size. **Demography** is the statistical study of the processes that change a population's size and density through time.

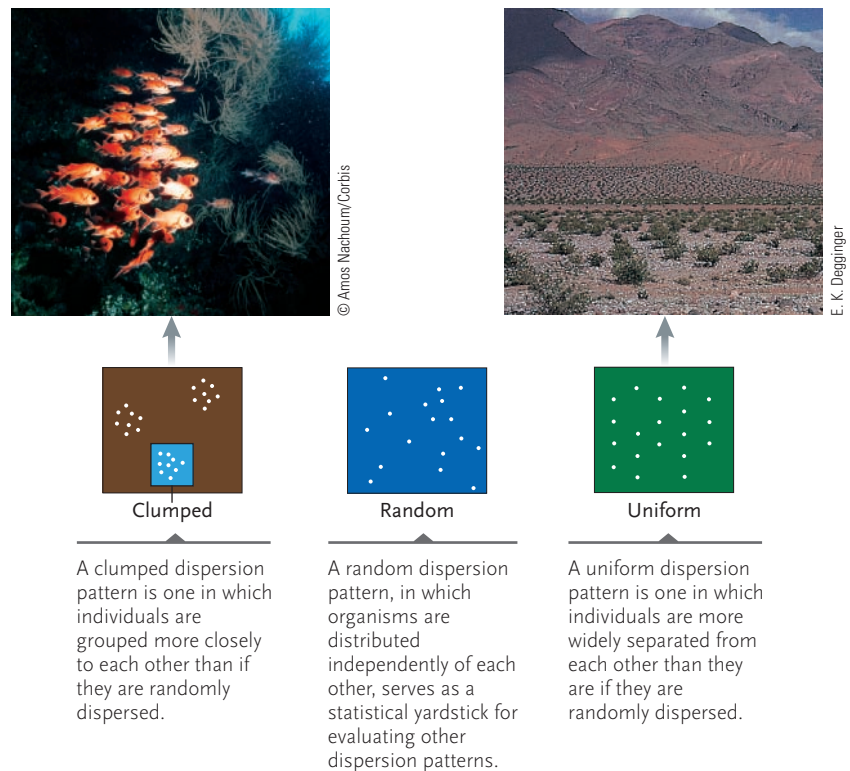


Figure 49.4

Dispersion patterns. Schooling fishes, like these sabre squirrelfish (*Sargocentron spiniferum*) from the Maldives in the Indian Ocean, exhibit a clumped pattern of dispersion. A random pattern of dispersion, which is fairly rare in nature, occurs in organisms that are neither attracted to nor repelled by each other. Creosote bushes (*Larrea tridentata*) near Death Valley, California, exhibit uniform dispersion.

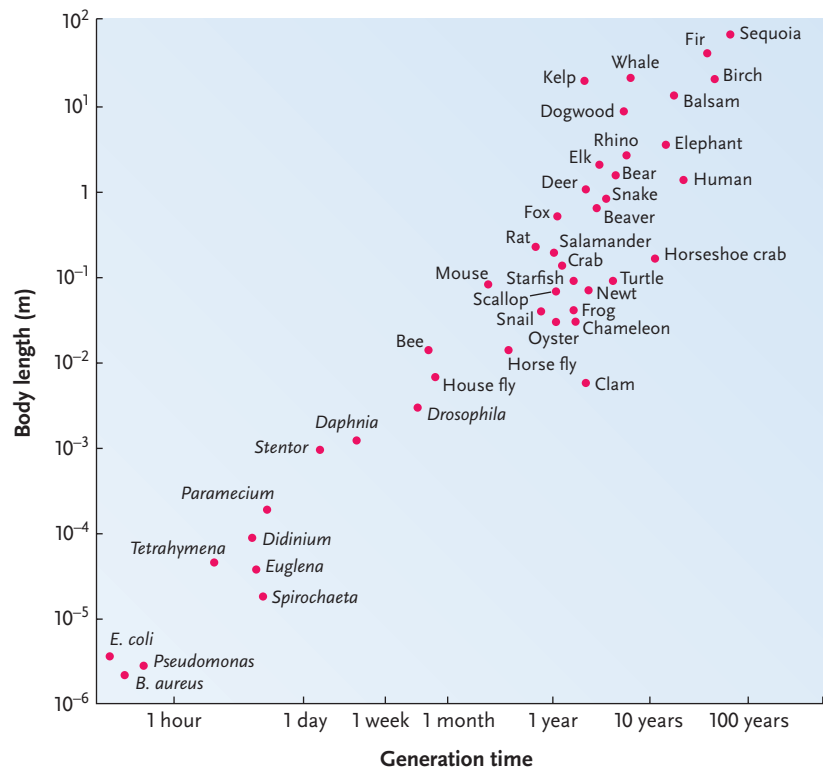


Figure 49.5

Generation time and body size. Generation time increases with body size among bacteria, protists, plants, and animals. The logarithmic scale on both axes compresses the data into a straight line.



INSIGHTS FROM THE MOLECULAR REVOLUTION

Tracing Armadillo Paternity and Migration

Nine-banded armadillos (*Dasypos novemcinctus*) are slow moving and solitary animals. Given their almost completely asocial behavior, what proportion of an armadillo population successfully mates? And, given their slow movements, how have they spread from Mexico and southern Texas through most of the southern United States in only 100 years?

Paulo A. Prodöhl and his colleagues at the University of Georgia, University of Washington, and Valdosta State University used molecular techniques to answer these questions. Their previous work had identified seven short tandem repeat (STR) loci in the armadillo genome. An STR locus consists of a segment of a chromosome with a short sequence repeated in series (see Section 18.2). Here the loci are approximately 200 bp long with 2- and 4-bp tandemly repeated sequences. Alleles of each locus vary in the number of copies of the repeated sequences, resulting in variable lengths for the locus. Because alleles of STR loci are inherited in the same way as alleles of genes, the allelic variations of the

STR loci made it possible for the researchers to trace parentage and migration patterns, in a manner analogous to human DNA fingerprinting.

Prodöhl and his coworkers collected tissue samples by clipping small pieces of tissue from the ears of 290 armadillos living in the Tall Timbers Research Station near Tallahassee, Florida. They extracted genomic DNA from the tissue sample and used the polymerase chain reaction (PCR) to amplify alleles for each of the seven STR loci. They determined the sizes of the fragments amplified by PCR using gel electrophoresis. (These molecular techniques are discussed in Chapter 18.)

The investigators used statistical methods to compare the gel patterns produced by DNA from adults with those from juveniles to determine their relatedness. Adult males and females with gel patterns most similar to those of a given juvenile were considered to be its parents. When the data identified more than two possible parents, the male and female living closest to a juvenile were scored as the most likely candidates. These techniques allowed

the investigators to assign parents to 69 sets of juveniles. Only seven juveniles could not be assigned parents, possibly because the parents had died, avoided capture, or emigrated from the population.

The results from 4 years of study suggest that 36% to 46% of adult armadillos reproduced at least once, despite their asocial habits—a moderately successful reproductive rate. In general, parents and offspring lived between 800 and 1500 m of each other, and individuals were usually captured within a 200-m radius of the same spot from season to season and from one year to the next. Thus, migration appears to be very limited, leaving the basis of their rapid spread unexplained.



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Ecologists use demographic analysis to predict a population's future population growth. For human populations, these data help governments anticipate the need for social services such as schools and hospitals. Demographic data also allow conservation ecologists to develop plans to protect endangered species. For example, demographic data on the northern spotted owl (*Strix occidentalis caurina*) helped convince the courts to restrict logging in the owl's primary habitat, the old growth forests of the Pacific Northwest. *Life tables* and *survivorship curves* are among the tools ecologists use to analyze demographic data.

Life Tables Summarize a Population's Survival and Reproductive Rates

Although every species has a characteristic life span, few individuals survive to the maximum age possible. Mortality results from starvation, disease, accidents, predation, or the inability to find a suitable habitat. Life insurance companies first developed techniques for measuring mortality rates, but ecologists adapted these approaches to the study of nonhuman populations.

A **life table** summarizes the demographic characteristics of a population (**Table 49.1**). To collect life-table data for short-lived organisms, demographers typically mark a **cohort**, a group of individuals of similar age, at birth and monitor their survival until all members of the cohort die. For organisms that live more than a few years, a researcher might sample the population for 1 or 2 years, recording the ages at which individuals die, and then extrapolate those results over the species' life span.

In any life table, the life span of the organisms is divided into age intervals of convenient length: days, weeks, or months for short-lived species; years or groups of years for longer-lived organisms. Mortality can be expressed in two complementary ways. **Age-specific mortality** is the proportion of individuals alive at the start of an age interval that died during that age interval. Its more cheerful reflection, **age-specific survivorship**, is the proportion of individuals alive at the start of an age interval that survived until the start of the next age interval. Thus, for the data shown in Table 49.1, the age-specific mortality rate during the 3-to-6-month age interval is $195/722 = 0.270$, and the

Table 49.1 Life Table for a Cohort of 843 Individuals of the Grass *Poa annua* (Annual Bluegrass)

Age Interval (in months)	Number Alive at Start of Age Interval	Number Dying During Age Interval	Age-Specific Mortality Rate	Age-Specific Survivorship Rate	Proportion of Original Cohort Alive at Start of Age Interval	Age-Specific Fecundity (Seed Production)
0–3	843	121	0.144	0.856	1.000	0
3–6	722	195	0.270	0.730	0.856	300
6–9	527	211	0.400	0.600	0.625	620
9–12	316	172	0.544	0.456	0.375	430
12–15	144	90	0.625	0.375	0.171	210
15–18	54	39	0.722	0.278	0.064	60
18–21	15	12	0.800	0.200	0.018	30
21–24	3	3	1.000	0.000	0.004	10
24–	0	—	—	—	—	—

Source: Begon, M., and M. Mortimer. *Population Ecology*. Sunderland, MA: Sinauer Associates, 1981. Adapted from R. Law. 1975.

age-specific survivorship rate is $527/722 = 0.730$. For any age interval, the sum of age-specific mortality and age-specific survivorship always equals 1. Life tables also summarize the proportion of the cohort that survived to a particular age, a statistic that identifies the probability that any randomly selected newborn will still be alive at that age. For the 3-to-6-month age interval in Table 49.1, this probability is $722/843 = 0.856$.

Life tables also include data on **age-specific fecundity**, the average number of offspring produced by surviving females during each age interval. Table 49.1 shows, for example, that plants in the 3-to-6-month age interval each produced an average of 300 seeds. In some species, including humans, fecundity is highest in individuals of intermediate age. Younger individuals have not yet reached sexual matu-

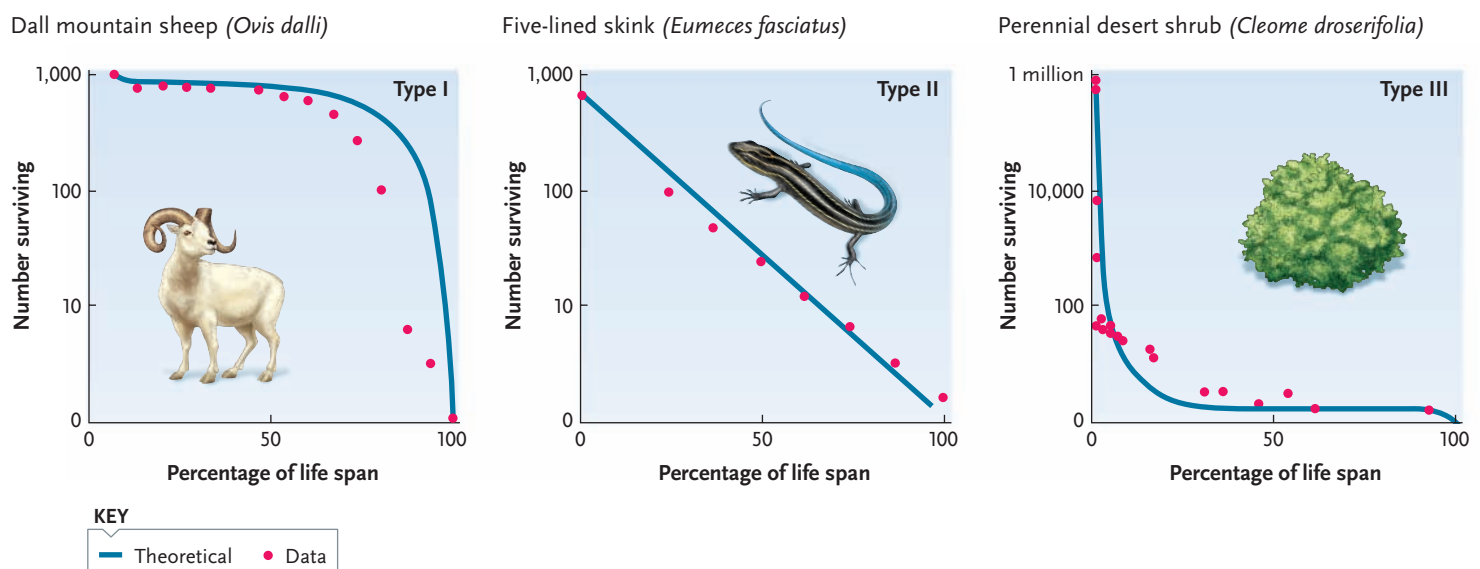
riety, and older individuals are past their reproductive prime. However, in some plants and animals fecundity increases steadily with age.

Survivorship Curves Depict Changes in Survival Rate over the Life Span

Survivorship data are depicted graphically in a **survivorship curve**, which displays the rate of survival for individuals over the species' average life span. Ecologists have identified three generalized survivorship curves (blue lines in Figure 49.6), although most organisms exhibit survivorship patterns that fall between these idealized patterns.

Type I curves reflect high survivorship until late in life, when mortality takes a great toll. Type I curves are

Figure 49.6 Survivorship curves. The survivorship curves of many organisms (pink data points) roughly match one of three idealized patterns (blue curves).



typical of large animals that produce few young and provide them with extended care, which reduces juvenile mortality. For example, large mammals, such as the Dall mountain sheep (*Ovis dalli*), produce only one or two offspring at a time and nurture them through their vulnerable first year.

Type II curves reflect a relatively constant rate of mortality in all age classes, a pattern that produces steadily declining survivorship. Many lizards, such as the five-lined skink (*Eumeces fasciatus*), as well as songbirds and small mammals, face a constant probability of mortality from predation, disease, and starvation.

Type III curves reflect high juvenile mortality, followed by a period of low mortality once the offspring reach a critical age and size. For example, *Cleome droserifolia*, a desert shrub from the Middle East, experiences extraordinarily high mortality in its seed and seedling stages. Researchers estimate that for every 1 million seeds produced, fewer than 1000 germinate, and only about 40 individuals survive their first year. Once a plant becomes established, however, its likelihood of future survival is higher, and the survivorship curve flattens out. Many plants, insects, marine invertebrates, and fishes exhibit type III survivorship.

STUDY BREAK

1. What statistics are usually included in a life table?
2. Which type of survivorship curve is characteristic of humans in industrialized countries? Explain your answer.

49.4 The Evolution of Life Histories

The analysis of life tables reveals how natural selection affects the **life histories**—the lifetime patterns of growth, maturation, and reproduction—that characterize different species. Ecologists study life histories to understand how trade-offs in the allocation of resources influence the evolution of specific traits. The results of their research suggest that natural selection adjusts the allocation of resources to maximize an individual's number of surviving offspring.

Organisms Face Trade-Offs in Their Allocation of Resources

Every organism is constrained by a finite **energy budget**, the total amount of energy that it can accumulate and use to fuel its activities. An organism's energy budget is like a savings account. When the individual accumulates more energy than it needs, it makes deposits to this account—energy is stored as starch, glycogen, or fat. When it expends more energy than it

harvests, it makes withdrawals from its energy stores. But unlike a bank account, an organism's energy budget cannot be overdrawn, and no loans against future "earnings" are possible.

Organisms use the energy they harvest for three broadly defined functions: maintenance (the preservation of good physiological condition), growth, and reproduction. And when an organism devotes energy to any one of these functions, the balance in its energy budget is reduced, leaving less energy for the other functions.

Life History Patterns Vary Dramatically among Species

A fish, a deciduous tree, and a mammal illustrate the dramatic variations that exist in life history patterns. Larval coho salmon (*Oncorhynchus kisutch*) hatch in the headwaters of a stream, where they feed and grow for about a year before assuming their adult body form. After swimming downstream to the ocean, they remain at sea for a year or two, feeding voraciously and growing rapidly. Eventually, salmon use sun-compass, geomagnetic, and chemical cues to return to the rivers and streams where they hatched. The fishes swim upstream, and each female lays hundreds or thousands of relatively small eggs. After spending all of their energy reserves on the upstream journey and reproduction, their condition deteriorates and they die.

Most deciduous trees in the temperate zone, such as oaks (genus *Quercus*) and maples (genus *Acer*), begin their lives as seeds in late summer. The seeds remain metabolically inactive until the following spring or a later year. After germinating, trees collect nutrients and energy and continue to grow throughout their lives. Once they achieve a critical size, they may produce thousands of seeds annually for many years. Thus, growth and reproduction occur simultaneously through much of the trees' life.

European red deer (*Cervus elaphus*) are born in spring, and young remain with their mothers for an extended period, nursing and growing rapidly. After weaning, they feed on their own. Female red deer begin to breed after reaching adult size in their third year, producing one or two offspring annually until they are about 16 years old, when they reach their maximum life span and die.

How can we summarize the similarities and differences in the life histories of these organisms? All three species harvest energy throughout their lives. Salmon and deciduous trees continue to grow until old age, whereas deer reach adult size fairly early in life. Salmon produce many offspring in a single reproductive episode, whereas deciduous trees and deer reproduce repeatedly. However, most trees produce thousands of seeds annually, whereas deer produce only one or two young each spring.

What factors have produced these variations in life history patterns? Life history traits—like all population characteristics—are modified by natural selection. Thus, organisms exhibit evolutionary adaptations that increase the fitness of individuals. Each species' life history is, in fact, a highly integrated “strategy”—not in the human sense of planning ahead, but as a suite of selection-driven adaptations.

Ecologists Analyze the Individual Components of Life Histories

In analyzing life histories, ecologists compare the number of offspring with the amount of care provided to each by the parents; they look at the number of reproductive episodes in the organism's lifetime; and they look at the timing of first reproduction. Because these characteristics evolve together, a change in one trait is likely to influence the success of the others.

Fecundity versus Parental Care. If a female has a fixed amount of energy for reproduction, she can package that energy in various ways. By way of illustration, a female duck with 1000 units of energy for reproduction might lay 10 eggs that each contain 100 units of energy per egg. A salmon, which has higher fecundity, might lay 1000 eggs, each endowed with 1 unit of energy. The amount of energy invested in each offspring *before* it is born represents the **passive parental care** that the female provides. Passive parental care is provided through yolk in an egg, endosperm in a seed, or, in mammals, nutrients that cross the placenta.

Many animals, especially birds and mammals, also provide **active parental care** to offspring *after* their birth. In general, species that produce many offspring in a reproductive episode—such as the coho salmon—provide relatively little active parental care *to each offspring*. In fact, female coho salmon, which produce 2400 to 4500 eggs, die before their eggs even hatch. Conversely, species that produce only a few offspring at a time—such as the European red deer—provide a lot of care to each. A red deer doe nurses its single fawn for up to 8 months before weaning it.

One Reproductive Episode versus Several. A second life history characteristic adjusted by natural selection is the number of reproductive episodes in an organism's lifetime. Some organisms, like the coho salmon, devote all of their stored energy to a single reproductive event. Any adult that survives the upstream migration is likely to leave some surviving offspring. Other species, like deciduous trees and red deer, reproduce multiple times. In contrast to salmon, individuals of these species devote only some of their energy budget to reproduction at any time, with the balance allocated to maintenance and growth. Moreover, in some plants, invertebrates, fishes, and reptiles, larger individuals produce more offspring than small ones do. Thus, one advantage of

using only part of the energy budget for reproduction is that continued growth may result in greater fecundity at a later age. However, if an organism does not survive until the next breeding season, the potential advantage of putting energy into maintenance and growth is lost.

Early Reproduction versus Late Reproduction. Individuals that first reproduce at the earliest possible age may stand a good chance of leaving some surviving offspring. But the energy devoted to reproduction is no longer available for maintenance and growth. Thus, early reproducers may be smaller and less healthy than individuals that delay reproduction in favor of these other functions. Conversely, an individual that delays reproduction may increase its chance of survival and its future fecundity by becoming larger or more experienced. But there is always some chance that it will die before the next breeding season, leaving no offspring at all. Thus, a finite energy budget and the risk of mortality establish a trade-off in the timing of first reproduction. Mathematical models suggest that delayed reproduction will be favored by natural selection if a sexually mature individual has a good chance of surviving to an older age, if organisms grow larger as they age, and if larger organisms have higher fecundity. Early reproduction will be favored if adult survival rates are low, if animals don't grow larger as they age, or if larger size does not increase fecundity.

Life history characteristics not only vary from one species to another, but they also vary among populations of a single species. *Focus on Research* describes how predation influences life history characteristics in natural populations of guppies (*Poecilia reticulata*) in Trinidad.

STUDY BREAK

1. To what two broad categories of activities do children devote their energy budget?
2. Why do fecundity and the amount of parental care devoted to each offspring exhibit an inverse relationship?

49.5 Models of Population Growth

We now examine mathematical models of population growth that describe very different responses to changes in a population's density. *Exponential* models apply when populations experience unlimited growth. The *logistic* model applies when population growth is limited, often because available resources are finite. These simple models are tools that help ecologists refine their hypotheses, but neither provides entirely accurate predictions of population growth in nature. In the simplest versions of these models, ecologists define births as the production of offspring by any form

FOCUS ON RESEARCH

Basic Research: The Evolution of Life History Traits in Guppies

Some years ago, drenched with sweat and with fishnets in hand, two ecologists were engaged in fieldwork on the Caribbean island of Trinidad. They were after guppies (*Poecilia reticulata*)—small fish that bear live young in shallow mountain streams (**Figure a**). John Endler and David Reznick, then of the University of California at Santa Barbara, were studying the environmental variables that influence the evolution of life history patterns in guppies.

Male guppies are easy to distinguish from females. Males, which stop growing at sexual maturity, are smaller, and their scales have bright colors that serve as visual signals in intricate courtship displays. The drably colored females continue to grow larger throughout their lives.



Figure a
David Reznick surveys a shallow stream in the mountains of Trinidad.

David Reznick/University of California, Riverside

In the mountains of Trinidad, guppies living in different streams—and even in different parts of the same stream—are eaten by one of two other fish species (**Figure b**). In some streams, a large pike-cichlid (*Crenicichla alta*) prefers mature guppies and tends not to spend time hunting small, immature ones. In other streams, a small killifish (*Rivulus hartii*) preys on immature guppies but does not have much success with the larger adults.

Reznick and Endler found that the life history patterns of guppies vary among streams with different preda-

tors. In streams with pike-cichlids, both male and female guppies mature faster and begin to reproduce at a smaller size and a younger age than their counterparts in streams where killifish live (**Figure c**). In addition, female guppies from pike-cichlid streams reproduce more often and produce smaller and more numerous young (**Figure d**). These differences allow guppies to avoid some predation. Those in pike-cichlid streams begin to reproduce when they are smaller than the size preferred by that predator. And those from killifish streams grow

Male guppy (right) that shared a stream with pike-cichlids (below)



Male guppy (right) that shared a stream with killifish (below)



Figure b

Male guppies from streams where pike-cichlids live (top) are smaller, more stream-lined, and have duller colors than those from streams where killifish live (bottom). The pike-cichlid prefers to eat large guppies, and the killifish feeds on small guppies. Guppies are shown approximately life-size, adult pike-cichlids grow to 16 cm in length, and adult killifish grow to 10 cm. (Guppy photos: David Reznick/University of California, Riverside; computer enhanced by Lisa Starr; predator photos: Hippocampus Bildarchiv.)

of reproduction, and ignore the effects of immigration and emigration.

Models of Exponential Population Growth Describe Growth without Limitation

Sometimes populations increase in size for a period of time with no apparent limits on their growth. In models of exponential growth, population size increases steadily by a constant ratio. Bacterial populations provide the most obvious examples, but multicellular organisms also sometimes exhibit exponential population growth.

Bacterial Population Growth. Bacteria reproduce by binary fission. A parent cell divides in half, producing two daughter cells, which each divide to produce two

granddaughter cells. Generation time in a bacterial population is simply the time between successive cell divisions. And if no bacteria in the population die, the population doubles in size each generation.

Bacterial populations grow quickly under ideal temperatures and with unlimited space and food. Consider a population of the human intestinal bacterium *Escherichia coli*, for which the generation time can be as short as 20 minutes. If we start with a population of one bacterium, the population doubles to two cells after one generation, to four cells after two generations, and to eight cells after three generations (**Figure 49.7**). After only 8 hours, or 24 generations, the population will number more than 16 million. And after a single day, or 72 generations, the population will number nearly 5×10^{21} cells. Although other bacteria grow more slowly than *E. coli*, it is no wonder that patho-

quickly to a size that is too large to be consumed by killifish.

Although these life history differences were correlated with the distributions of the two predatory fishes, they might result from some other, unknown differences between the streams. Endler and Reznick investigated this possibility with controlled laboratory experiments. They shipped groups of guppies to California, where they bred guppies from each kind of stream for two generations. Both types of experimental populations were raised under identical conditions in the absence of predation. Even when predators were absent, the two types of experimental populations retained their life history differences. These results provided evidence of a heritable genetic basis for the observed life history differences.

Endler and Reznick also examined the role of predators in the *evolution* of the size differences. They raised guppies for many generations in the laboratory under three experimental conditions—some alone, some with killifish, and some with pike-cichlids. As predicted, the guppy lineage that was subjected to predation by killifish became larger at maturity. Individuals that were small at maturity were frequently eaten, and their reproduction was limited. The lineage that was

raised with pike-cichlids showed a trend toward earlier maturity. Individuals that matured at a larger size faced a greater likelihood of being eaten before they had reproduced.

Finally, when they first visited Trinidad, Endler and Reznick had introduced guppies from a pike-cichlid stream to another stream that contained killifish but no pike-cichlids or guppies. Eleven years later, the guppy populations had changed. As the researchers predicted, the guppies had become larger in size and reproduced more slowly, characteristics that are typical of natural guppy populations that live and die with killifish.

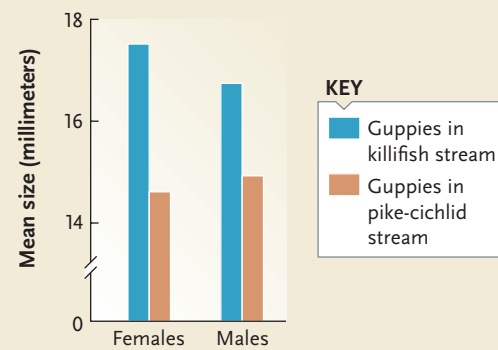


Figure c
Guppies in streams occupied by pike-cichlids are smaller than those in streams occupied by killifish.

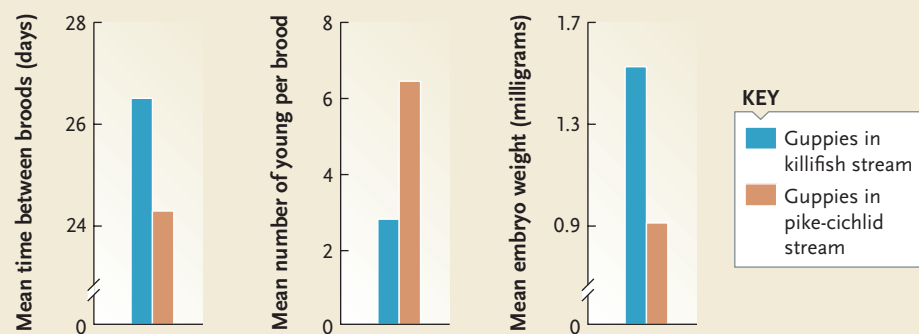


Figure d
Female guppies from streams occupied by pike-cichlids reproduce more often (shorter time between broods) and produce more young per brood and smaller young (lower embryo weight) than females living in streams occupied by killifish.

genic bacteria, such as those causing cholera or plague, can quickly overtake the defenses of an infected animal.

Exponential Population Growth in Other Organisms.

By contrast to bacteria, many plants and animals live side-by-side with their offspring. In these populations, births increase a population's size and deaths decrease it. Over a given time period:

$$\text{change in population size} = \text{number of births} - \text{number of deaths}$$

We express this relationship mathematically by defining N as the population size; ΔN (pronounced "delta N") as the change in population size; Δt as the time period during which the change occurs; and B and D as the numbers of births and deaths, respectively, dur-

ing that time period. Thus, $\Delta N/\Delta t$ symbolizes the change in population size over time, and

$$\Delta N/\Delta t = B - D$$

The preceding equation applies to any population for which we know the exact numbers of births and deaths.

Ecologists usually express births and deaths as *per capita* (per individual) rates, allowing them to apply the model to a population of any size. The per capita birth rate, symbolized b , is simply the number of births in the population during the specified time period divided by the population size: $b = (B/N)$. Similarly, the per capita death rate, d , is the number of deaths divided by the population size: $d = (D/N)$. If, for example, in a population of 2000 field mice, 1000 mice are born and 200 mice die during 1 month's time, $b = 1000/2000 =$

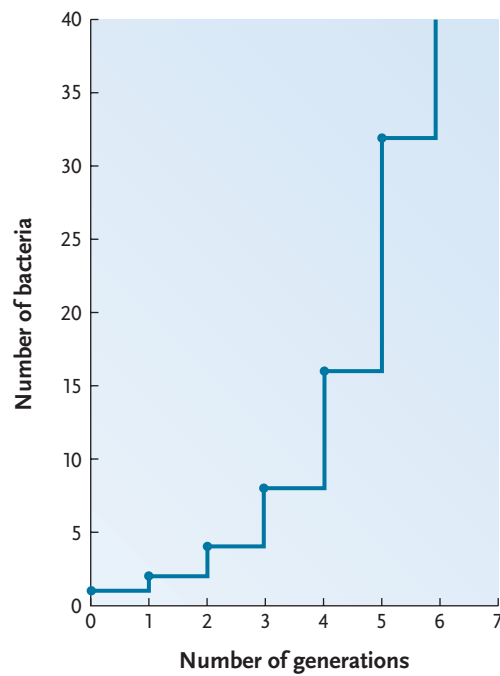


Figure 49.7 Bacterial population growth. If all members of a bacterial population divide simultaneously, a plot of population size over time forms a stair-stepped curve in which the steps get larger as the number of dividing cells increases.

0.5 births per individual per month, and $d = 200/2000 = 0.1$ deaths per individual per month. Of course, no mouse can give birth to half an offspring, and no individual can die one-tenth of a death. But these rates tell us the per capita birth and death rates *averaged over all mice in the population*. Per capita birth and death rates are always expressed over a specified time period. For long-lived organisms, such as humans, time is measured in years; for short-lived organisms, such as fruit

flies, time is measured in days. We can calculate per capita birth and death rates from data in a life table.

We can now revise the population growth equation to use per capita birth and death rates instead of the actual numbers of births and deaths. The change in a population's size during a given time period ($\Delta N/\Delta t$) depends on the per capita birth and death rates, as well as on the number of individuals in the population. Mathematically, we can write

$$\Delta N/\Delta t = B - D = bN - dN = (b - d)N$$

or, in the notation of calculus,

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

This equation describes the **exponential model of population growth**. (Note that in calculus, dN/dt is the notation for the population growth rate; the “d” in dN/dt is *not* the same “d” that we use to symbolize the per capita death rate.)

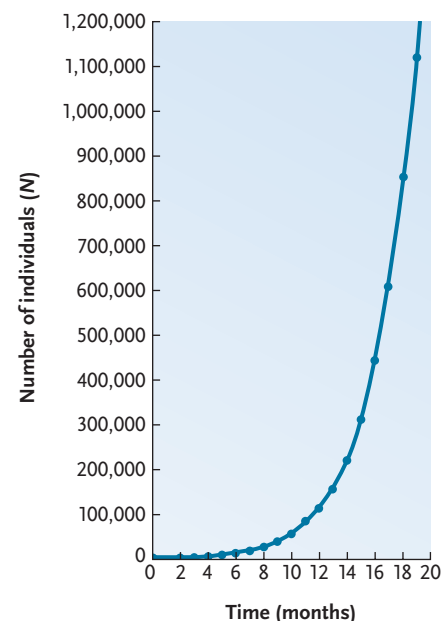
The difference between the per capita birth rate and the per capita death rate, $b - d$, is the **per capita growth rate** of the population, symbolized by r . Like b and d , r is always expressed per individual per unit time. Using the per capita growth rate, r , in place of $(b - d)$, the exponential growth equation is written

$$dN/dt = rN$$

If the birth rate exceeds the death rate, r has a positive value ($r > 0$), and the population is growing. In our example with field mice, $r = 0.5 - 0.1 = 0.4$ mice per mouse per month. If, on the other hand, the birth rate is lower than the death rate, r has a negative value ($r < 0$), and the population is getting smaller. In populations where the birth rate equals the death rate, r is exactly zero, and the population's size is not changing—a situation known as **zero population**

Figure 49.8 Exponential population growth. Exponential population growth produces a J-shaped curve of population size plotted against time. Although the per capita growth rate (r) remains constant, the increase in population size gets larger every month, because more individuals are reproducing.

Month	Old Population Size		Net Monthly Increase		New Population Size
1	2,000	+	800	=	2,800
2	2,800	+	1,120	=	3,920
3	3,920	+	1,568	=	5,488
4	5,488	+	2,195	=	7,683
5	7,683	+	3,073	=	10,756
6	10,756	+	4,302	=	15,058
7	15,058	+	6,023	=	21,081
8	21,081	+	8,432	=	29,513
9	29,513	+	11,805	=	41,318
10	41,318	+	16,527	=	57,845
11	57,845	+	23,138	=	80,983
12	80,983	+	32,393	=	113,376
13	113,376	+	45,350	=	158,726
14	158,726	+	63,490	=	222,216
15	222,216	+	88,887	=	311,103
16	311,103	+	124,441	=	435,544
17	435,544	+	174,218	=	609,762
18	609,762	+	243,905	=	853,667
19	853,677	+	341,467	=	1,195,134



growth, or ZPG. Even under conditions of ZPG, births and deaths still occur, but the numbers of births and deaths cancel out.

As long as a population's per capita growth rate is positive ($r > 0$), the population will increase in size. In our hypothetical population of field mice, we started with $N = 2000$ mice, and calculated a per capita growth rate of 0.4 mice per individual per month. In the first month, the population grows by $0.4 \times 2000 = 800$ mice (**Figure 49.8**). At the start of the second month, $N = 2800$ and r still = 0.4. Thus, in the second month, the population grows by $0.4 \times 2800 = 1120$ mice. Notice that even though r remains constant, the *increase* in population size gets larger each month simply because more individuals are reproducing. In less than 2 years, the mouse population will grow to more than 1 million! A graph of exponential population growth has a characteristic J shape, getting steeper through time. The population grows at an ever-increasing pace because the change in a population's size depends on the number of individuals in the population as well as its per capita growth rate.

Population Growth under Ideal Conditions. Imagine a hypothetical population living in an ideal environment—one with unlimited food and shelter; no predators, parasites, or disease; and a comfortable abiotic environment. Under such circumstances, which are admittedly unrealistic, the per capita birth rate is very high, the per capita death rate is very low, and the per capita growth rate, r , is as high as it can possibly be. This maximum per capita growth rate, symbolized r_{max} , is the population's **intrinsic rate of increase**. Under these ideal conditions, our exponential growth equation is

$$dN/dt = r_{max}N$$

When populations are growing at their intrinsic rate of increase, population size increases very rapidly. Across a wide variety of protists and animals r_{max} varies inversely with generation time: species with short generation time have higher intrinsic rates of increase than those with long generation time (**Figure 49.9**).

The Logistic Model Describes Population Growth When Resources Are Limited

The exponential model predicts unlimited population growth. But we know from even casual observations that the population sizes of most species are somehow limited—we are not knee-deep in bacteria, rosebushes, or garter snakes. What factors limit the growth of populations? As a population gets larger, it uses more vital resources, and a shortage of resources may eventually develop. As a result, individuals may have less energy available for maintenance and reproduction, causing per capita birth rates to decrease and per capita death rates to increase. Changes in these rates reduce the

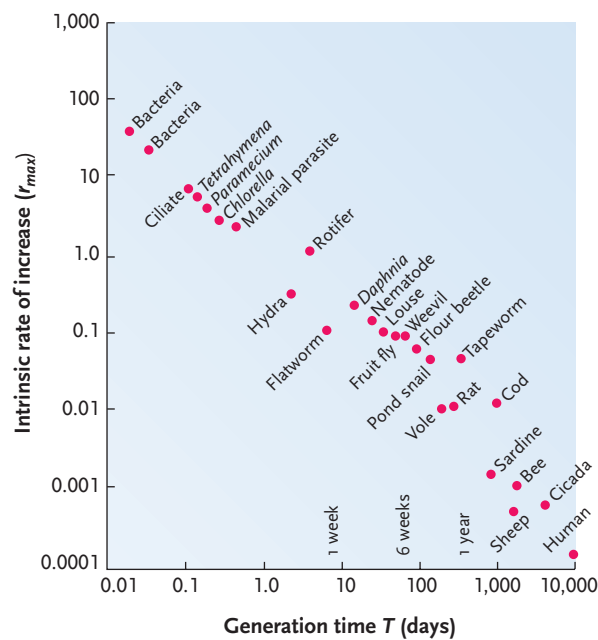


Figure 49.9 Generation time and r_{max} . The intrinsic rate of increase (r_{max}) is high for protists and animals with short generation time and low for those with long generation time. The logarithmic scale on both axes compresses the data into a straight line.

population's per capita growth rate, causing population growth to slow down or to stop altogether.

The Logistic Model. Environments provide enough resources to sustain only a finite population of any species. The maximum number of individuals that an environment can support indefinitely is termed its **carrying capacity**, symbolized K . The carrying capacity, which is defined for each population, is a property of the environment, and it varies from one habitat to another and in a single habitat through time. For example, the spring and summer flush of insects in temperate habitats supports large populations of insectivorous birds. But fewer insects are available in autumn and winter, causing a seasonal decline in the carrying capacity *for birds*. Many birds then migrate to habitats that provide more food and better weather.

The **logistic model of population growth** assumes that a population's per capita growth rate, r , decreases as the population gets larger (**Figure 49.10a**). In other words, population growth slows as the population size approaches the carrying capacity. The mathematical expression $(K - N)$ tells us how many individuals can be added to a population before it reaches carrying capacity. And the expression $(K - N)/K$ indicates what *percentage* of the carrying capacity is still available.

To create the logistic model, we factor the impact of carrying capacity into the exponential model by letting $r = r_{max}(K - N)/K$. This calculation reduces the per capita growth rate (r) from its maximum value (r_{max}) as N increases:

$$dN/dt = r_{max}N(K - N)/K$$

The calculation of how r varies with population size is straightforward (**Table 49.2**). In a very small population (N much smaller than K), plenty of resources are still

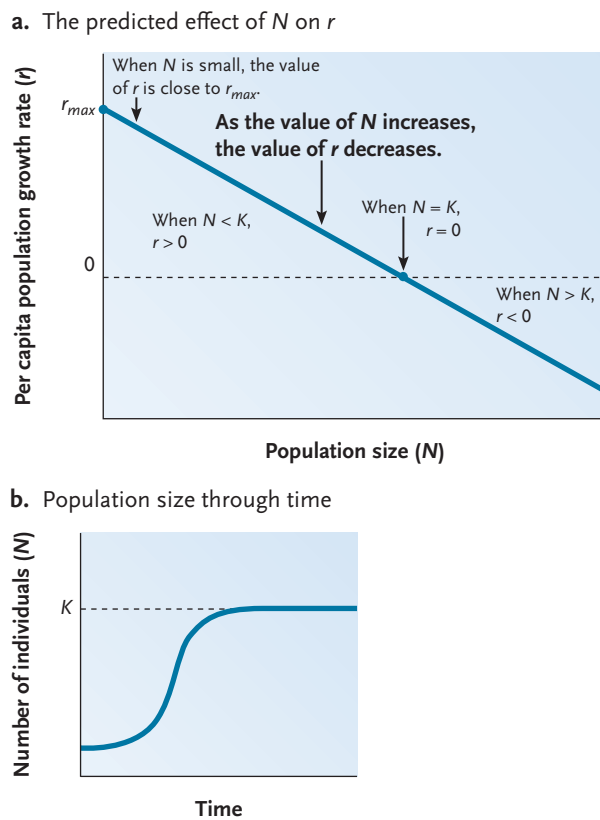


Figure 49.10 The logistic model of population growth. (a) The logistic model assumes that the per capita population growth rate (r) decreases linearly as population size (N) increases. (b) The logistic model predicts that population size increases quickly at first, but then slowly approaches the carrying capacity (K).

Table 49.2 The Effect of N on r and ΔN^* in a Hypothetical Population Exhibiting Logistic Growth in which $K = 2000$ and $r_{\max} = 0.04$ per capita per year

N (population size)	$(K - N)/K$ (% of K available)	$r = r_{\max}(K - N)/K$ (per capita growth rate)	$\Delta N = rN$ (change in N)
50	0.990	0.0396	2
100	0.950	0.0380	4
250	0.875	0.0350	9
500	0.750	0.0300	15
750	0.625	0.0250	19
1000	0.500	0.0200	20
1250	0.375	0.0150	19
1500	0.250	0.0100	15
1750	0.125	0.0050	9
1900	0.050	0.0020	4
1950	0.025	0.0010	2
2000	0.000	0.0000	0

* ΔN rounded to the nearest whole number.

available; the value of $(K - N)/K$ is close to 1, and the per capita growth rate (r) is therefore close to the maximum possible (r_{\max}). Under these conditions, population growth is close to exponential. If a population is large (N close to K), few additional resources are available; the value of $(K - N)/K$ is small, and the per capita growth rate (r) is very low. When the size of the population exactly equals the carrying capacity, $(K - N)/K$ becomes zero, and so does the population growth rate—the situation defined as ZPG.

The logistic model of population growth predicts an S-shaped graph of population size over time, with the population slowly approaching its carrying capacity and remaining at that level (Figure 49.10b). According to this model, the population grows slowly when the population size is small, because there are few individuals reproducing. It also grows slowly when the population size is large because the per capita population growth rate is low. The population grows quickly (dN/dt is highest) at intermediate population sizes, when a sizable number of individuals are breeding and the per capita population growth rate (r) is still fairly high (see Table 49.2).

Intraspecific Competition. The logistic model assumes that vital resources become increasingly limited as a population grows larger. Thus, the model is a mathematical portrait of **intraspecific** (within species) **competition**, the dependence of two or more individuals in a population on the same limiting resource. For animals, limiting resources can be food, water, nesting sites, refuges from predators, and, for sessile species (those permanently attached to a surface), space. For plants, sunlight, water, inorganic nutrients, and growing space can be limiting. The pattern of uniform dispersion described earlier often reflects intraspecific competition for limited resources.

In some very dense populations, the accumulation of poisonous waste products may also reduce survivorship and reproduction. Most natural populations live in open systems where wastes are consumed by other organisms or flushed away. But the buildup of toxic wastes is common in laboratory cultures of microorganisms. For example, yeast cells ferment sugar and produce ethanol as a waste product. Thus, the alcohol content of wine rarely exceeds 13% by volume, the ethanol concentration that poisons winemaking yeasts.

Logistic Growth in the Laboratory and in Nature. How well do species conform to the predictions of the logistic model? In simple laboratory cultures, relatively small organisms, such as *Paramecium*, some crustaceans, and flour beetles, often show an S-shaped pattern of population growth (Figure 49.11). Moreover, large animals that have been introduced into new environments sometimes exhibit a pattern of population

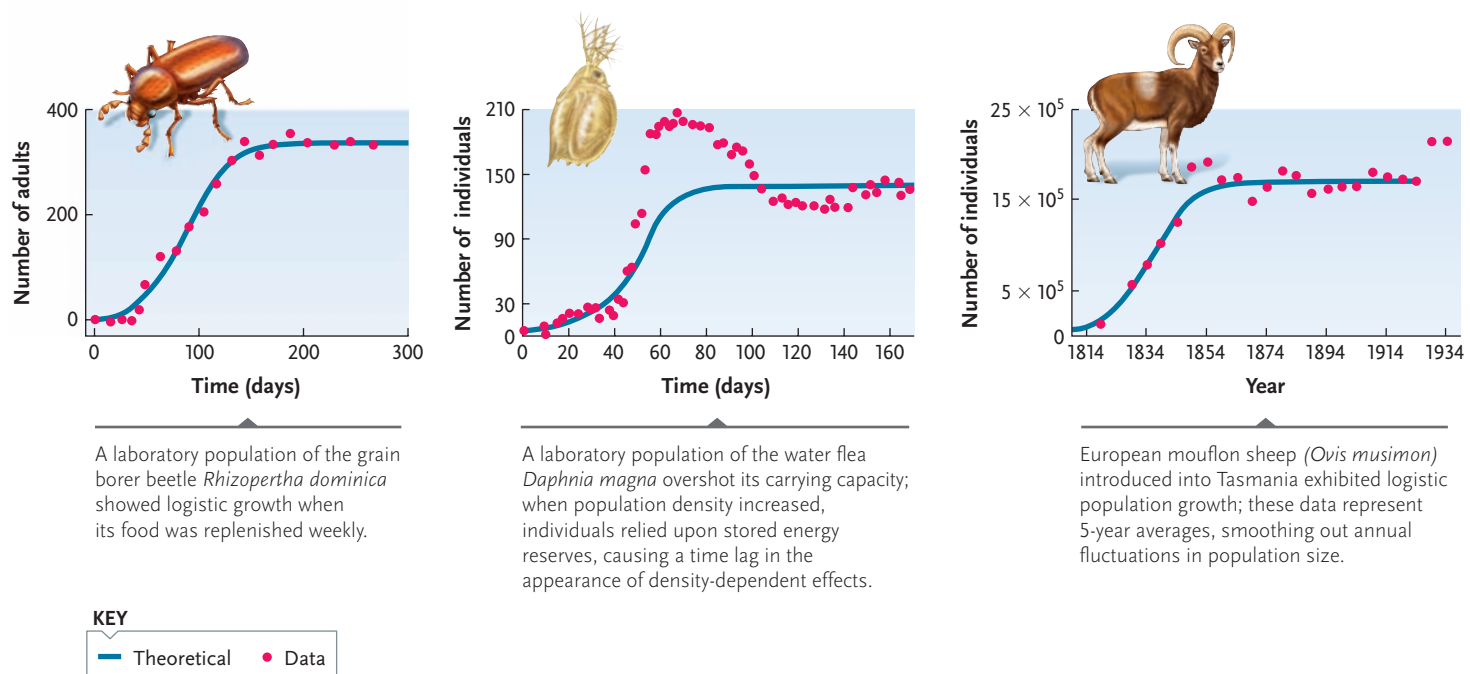


Figure 49.11
Examples of logistic population growth.

growth that matches the predictions of the logistic model (see Figure 49.11).

Nevertheless, some assumptions of the logistic model are unrealistic. For example, the model predicts that survivorship and fecundity respond immediately to changes in a population's density. But many organisms exhibit a delayed response, called a **time lag**. Some time lags occur because fecundity is usually determined by the availability of resources at some time in the past, when individuals were adding yolk to eggs or endosperm to seeds. Moreover, when food resources become scarce, individuals may use stored energy reserves to survive and reproduce, and the effects of crowding may not be felt until those reserves are depleted. As a result, the population size may temporarily overshoot its carrying capacity (see Figure 49.11b). Deaths may then outnumber births, causing the population size to drop below the carrying capacity, at least temporarily. Time lags often cause a population to oscillate around its carrying capacity.

Another unrealistic assumption of the logistic model is that the addition of new individuals to a population always decreases survivorship and fecundity, no matter how small the population is. But in small populations, modest population growth probably doesn't have much effect on these processes. In fact, most organisms probably require a minimum population density to survive and reproduce. For example, some plants flourish in small clumps that buffer them from physical stresses, whereas a single individual living in the open would suffer adverse effects. And in some animal populations, a minimum population density is necessary for individuals to find mates—an important issue in conservation biology (see Chapter 53).

STUDY BREAK

1. How does the prediction of the exponential model of population growth differ from that of the logistic model?
2. What is carrying capacity? Is it a property of a habitat or of a population?
3. What is a time lag?

49.6 Population Regulation

As you have seen, the population sizes of some species change from month to month or from year to year, whereas others remain fairly stable. What environmental factors influence population growth rates and control fluctuations in population size?

Density-Dependent Factors Often Regulate Population Size

Some factors that affect population size are **density-dependent**: their influence increases or decreases with the density of the population. Examples of density-dependent environmental factors include intraspecific competition and predation. The logistic model includes the effects of density-dependence in its assumption that per capita birth and death rates change with a population's density.

The Effects of Crowding. Numerous laboratory and field studies show that crowding (high population density) decreases the individual growth rate, adult size,

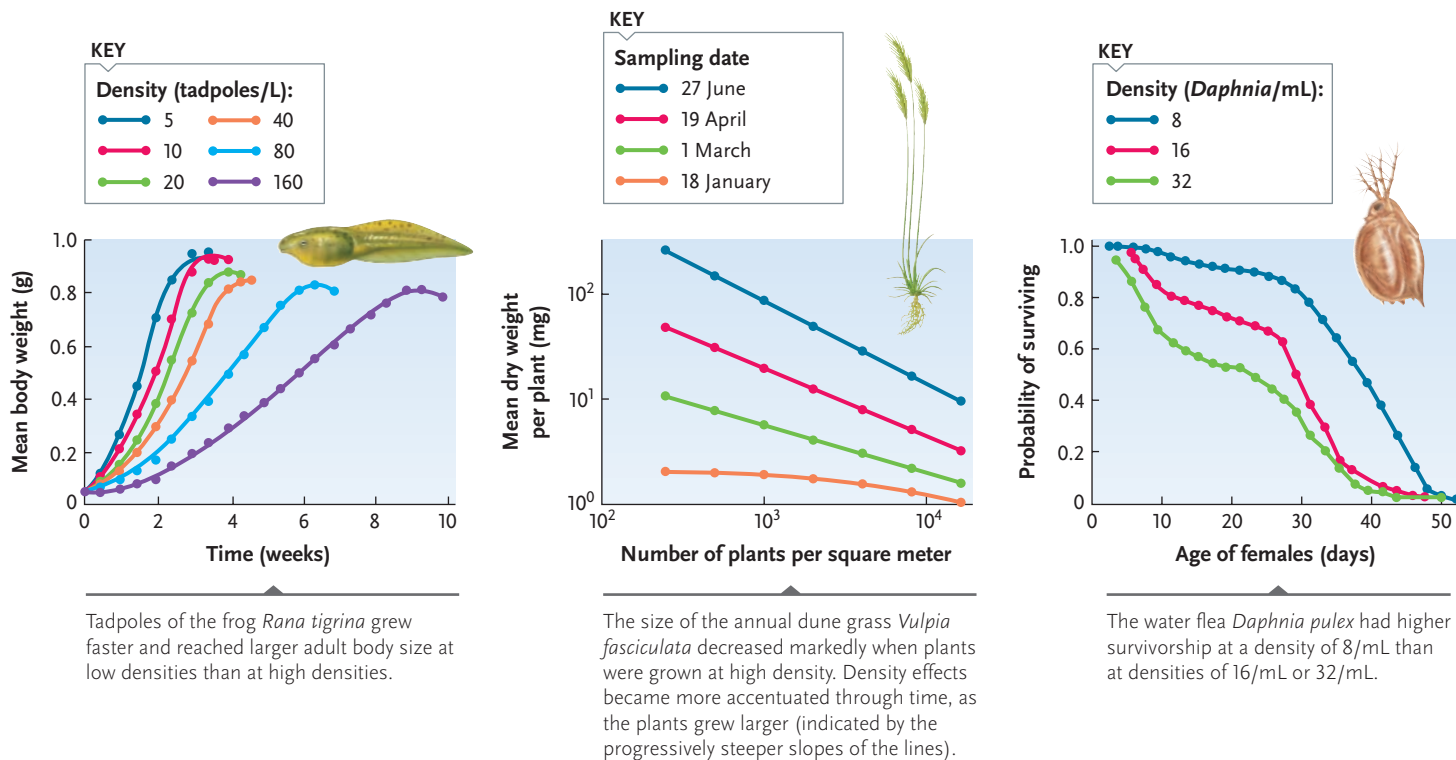
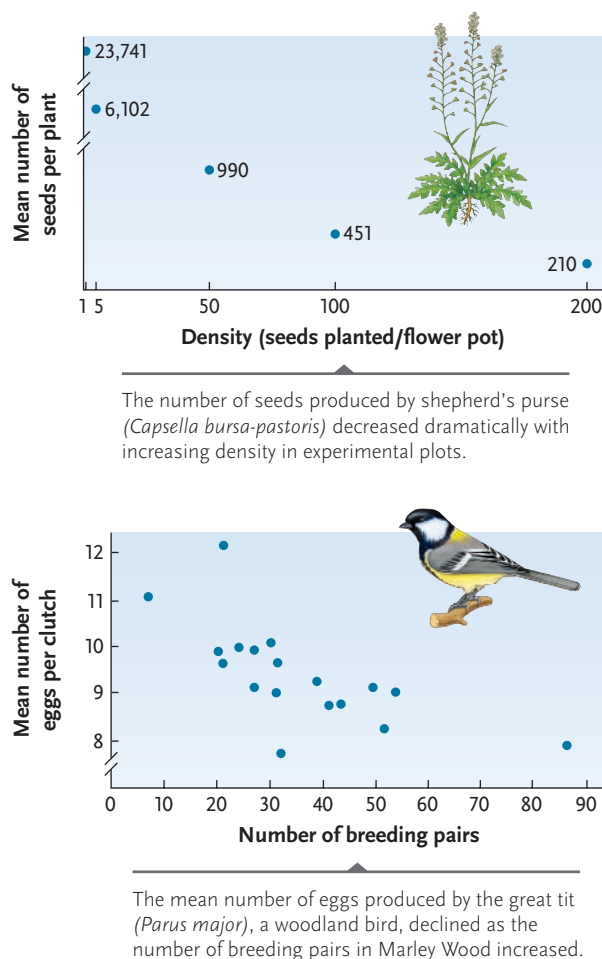


Figure 49.12
Effects of crowding on individual growth, size, and survival.

Figure 49.13
Effects of crowding on fecundity.



and survival of plants and animals (Figure 49.12). Organisms living in extremely dense populations are unable to harvest enough resources; they grow slowly and tend to be small, weak, and less likely to survive. Gardeners understand this relationship, thinning their plants to a density that maximizes the number of vigorous individuals.

Crowding also has a negative effect on reproduction (Figure 49.13). When resources are in short supply, each individual has less energy available for reproduction after meeting its basic maintenance needs. Hence, females in crowded populations produce either fewer offspring or smaller offspring that are less likely to survive.

In some species, crowding stimulates developmental and behavioral changes that may influence the density of a population. For example, migratory locusts (*Locusta migratoria*) can develop into either solitary or migratory forms in the same population. Migratory individuals have longer wings and more body fat, characteristics that allow them to disperse great distances. High population density increases the frequency of the migratory form, and huge numbers of locusts move away from the area of high density (Figure 49.14), reducing the size of the original population.

These studies confirm the assumptions of the logistic equation, but they don't prove that natural populations are regulated by density-dependent factors. A convincing demonstration requires experimental evi-



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Figure 49.14

A swarm of locusts. Migratory locusts (*Locusta migratoria*), moving across an African landscape, can devour their own weight in plant material every day.

dence that an increase in population density causes population size to decrease, and that a decrease in density causes it to increase. In one study conducted in the 1960s, Robert Eisenberg of the University of Michigan experimentally increased the numbers of aquatic snails in some ponds, decreased them in others, and maintained natural densities in control ponds. Although adult survivorship did not differ between experimental and control treatments, snails in the high-density ponds produced fewer eggs, and those in the low-density ponds produced more eggs, than those living at the control density. In addition, the survival rates of young snails declined as density increased. After 4 months, the densities in the two experimental groups converged on those in the control, providing strong evidence of density-dependent population regulation.

Other Density-Dependent Factors. Our discussion of the logistic equation described intraspecific competition as the primary density-dependent factor regulating population size. Competition between populations of different species also exerts density-dependent effects on population growth, a topic we consider in Section 50.1.

Predation can also cause density-dependent population regulation. As a particular prey species becomes more numerous, predators may consume more of it because it is easier to find and catch. Once a prey species has exceeded a threshold density, predators may consume a *larger percentage* of the prey population, which is a density-dependent effect (see Figure 20.16). For example, on rocky shores in California, sea stars concentrate their feeding on the most abundant of several invertebrate species. When one prey species becomes common, predators feed on it disproportionately, drastically reducing its numbers.

Like predation, parasitism and disease cause density-dependent regulation of plant and animal populations. Infectious microorganisms spread quickly

in a crowded population. In addition, if crowded individuals are weak or malnourished, they are more susceptible to infection and may die from diseases that healthy organisms would survive.

Density-Independent Factors Can Limit Population Size

Some populations are affected by **density-independent** factors that reduce population size regardless of its density. If an insect population is not physiologically adapted to high temperature, a sudden hot spell may kill 80% of the insects whether they number 100 or 100,000. Fires, earthquakes, storms, and other natural disturbances may contribute directly or indirectly to density-independent mortality. But because such factors do not cause a population to fluctuate around its carrying capacity, density-independent factors do not *regulate* population size, although they may reduce it.

Density-independent factors have a particularly strong effect on populations of small-bodied species that cannot buffer themselves against environmental change. Their populations grow exponentially for a time, but shifts in climate or random events cause high mortality before populations reach a size at which density-dependent factors regulate their numbers. When conditions improve, populations grow exponentially—at least until another density-independent factor causes them to crash again. For example, a small Australian insect, *Thrips imaginis*, feeds on pollen and flowers of plants in the rose family; they are frequently abundant enough to damage the blooms. *Thrips* populations grow exponentially in spring, when many flowers are available and the weather is warm and moist (**Figure 49.15**). But populations crash predictably during summer because *Thrips* do not tolerate extremely hot

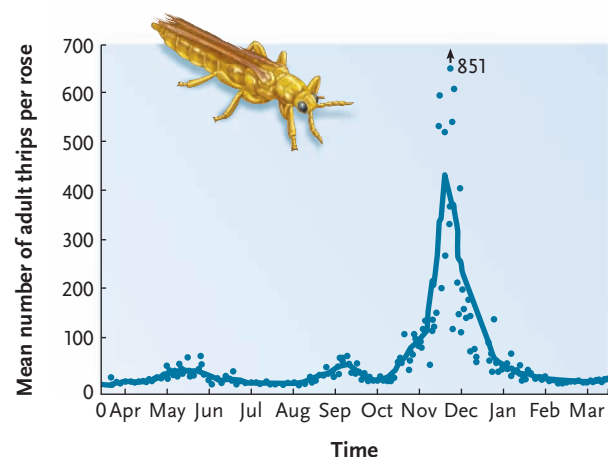


Figure 49.15

Booms and busts in a *Thrips* population. Populations of the Australian insect *Thrips imaginis* grow exponentially when conditions are favorable during spring (which begins in September in the southern hemisphere). The populations crash in summer, however, when hot and dry conditions cause high mortality.

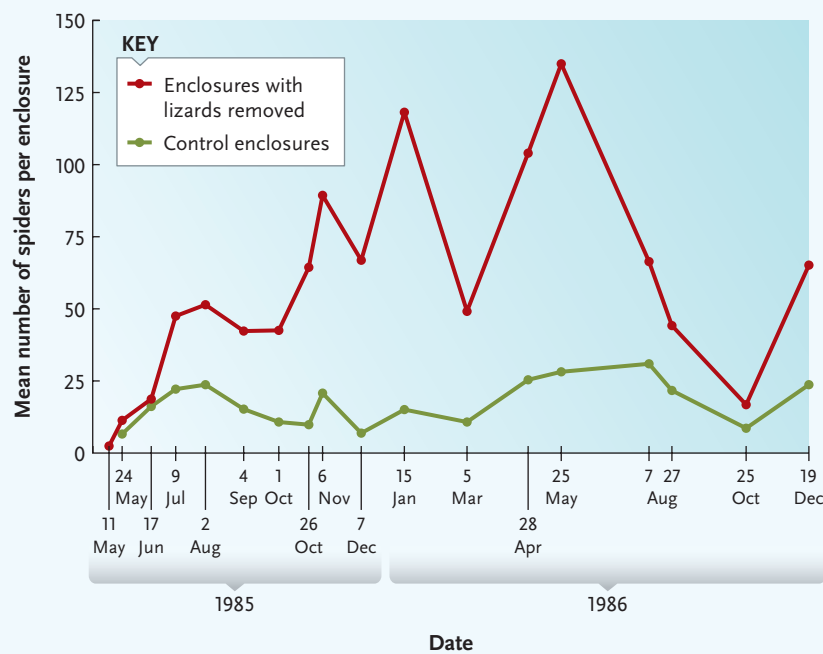
Figure 49.16 Experimental Research

Evaluating Density-Dependent Interactions between Species

QUESTION: Does the population density of lizards on Caribbean islands have any effect on the population density of spiders?

EXPERIMENT: Spiller and Schoener built fences around a series of study plots on a small island in the Bahamas. They excluded all individuals of three lizard species from the experimental plots, but left resident lizards undisturbed in the control plots. They then made monthly measurements of population densities of the web-building spider *Metepeira datona* in both experimental plots and control plots.

RESULTS: Over the 20-month course of the experiment, spider densities were as much as five times higher in the experimental plots than in the control plots.



CONCLUSION: Spiller and Schoener concluded that the presence of lizards has a large impact on spider populations. The lizards not only compete with the spiders for insect food, but they also appear to prey on the spiders.

and dry conditions. After the crash, a few individuals survive in remaining flowers, forming the stock from which the population grows exponentially the following spring.

Interacting Environmental Factors Often Limit Population Sizes

Sometimes several density-dependent factors influence a population at the same time. For example, on small islands in the West Indies, the spider *Metepeira datona* is rare wherever lizards (*Ameiva festiva*, *Anolis*

carolinensis, and *Anolis sagrei*) are abundant, but common where the lizards are rare or absent. To test whether the presence of lizards limits the abundance of spiders, David Spiller and Tom Schoener of the University of California, Davis, built fences around plots on islands where these species occur. They eliminated lizards from experimental plots, but left them in control plots. After 2 years, spider populations in some experimental plots were five times denser than those in control plots (Figure 49.16). In this case, lizards had two density-dependent effects on spider populations: they preyed upon spiders, and they competed with them for food.

Density-dependent factors can also interact with density-independent factors, limiting population growth. For example, food shortage caused by high population density (a density-dependent factor) may lead to malnourishment; in turn, malnourished individuals may be more likely to succumb to the stress of extreme weather (a density-independent factor).

Populations can also be affected by density-independent factors in a density-dependent manner. For example, animals often retreat into shelters to escape environmental stresses, such as floods or severe heat. If a population is small, most individuals can fit into a limited number of available refuges. But if a population is large, only a small proportion will find suitable shelter; and the larger the population is, the greater the percentage of individuals that will experience the stress. Thus, although the density-independent effects of weather limit *Thrips* populations, it is the availability of flowers in summer—clearly a density-dependent factor—that regulates the size of the *Thrips* starting stock the following spring. Hence, both types of factors influence the size of *Thrips* populations.

The Life History Characteristics of a Species Govern Fluctuations in Its Population Size through Time

Even casual observation reveals tremendous variation in how rapidly population size changes in different species. For example, new weeds often appear in a vegetable garden overnight, whereas the number of oak trees in a forest may remain relatively stable for years. Why do some species have the potential for explosive population growth, but others do not? The answer lies in how natural selection has molded life history strategies that are adapted to different ecological conditions. Ecologists describe two divergent life history patterns—*r*-selected species and *K*-selected species—with very different characteristics (Table 49.3, Figure 49.17). These strategies represent extremes on a continuum of possible patterns, and the life histories of most species actually fall somewhere between them.

Species with an *r*-selected life history are adapted to function well in rapidly changing environments. They are generally small, have short generation times,

and produce numerous, tiny offspring, often in a single reproductive event. The offspring receive little or no parental care of any kind. Because species with short generation times tend to have high r_{max} (see Figure 49.9), their populations grow exponentially when environmental conditions are favorable—hence the name *r*-selected. Although their numerous offspring disperse and rapidly colonize available habitats, most die before reaching sexual maturity (Type III survivorship). Thus, the success of an *r*-selected life history depends on flooding the environment with a *large quantity* of young, only a few of which may be successful.

Because they have small body size, *r*-selected species lack physiological mechanisms to buffer them from environmental variation. Thus, as described earlier for the Australian thrips living in roses, survivorship and fecundity are often greatly influenced by density-independent factors, and population size fluctuates markedly. In good years, survivorship and fecundity may be high, and the population explodes. In bad years, survivorship and reproduction may be low, and the population crashes. Populations of *r*-selected species are often so greatly reduced by changes in abiotic environmental factors, such as temperature or moisture, that they never grow large enough to face a shortage of limiting resources; thus, their carrying capacity cannot be estimated, and changes in their population size cannot be described by the logistic model of population growth.

By contrast, *K*-selected species thrive in more stable environments. They are generally large, have long generation times, and produce offspring repeatedly during their lifetimes. Their offspring receive substantial parental care, either as energy reserves in an egg or seed or as active care, ensuring that most survive the early stages of life (Type I or Type II survivorship). Because *K*-selected species typically have a low r_{max} , their populations often grow slowly. The success of a *K*-selected life history therefore depends on the production of a relatively small number of *high quality* offspring that join an already well-established population.

The large body size of *K*-selected species allows them to use behavioral and physiological mechanisms to buffer themselves against environmental change, so that survivorship and fecundity do not fluctuate wildly in response to environmental variations. Instead, their populations are often affected by density-dependent factors, which regulate population size near their carrying capacity—hence the name *K*-selected. For these species, natural selection has favored life history characteristics that result in stable population sizes: the production of relatively few offspring, extensive parental care, good competitive ability, a long life span, and repeated reproductions. Many large terrestrial vertebrates are examples of *K*-selected species.

Table 49.3

Characteristics of *r*-Selected and *K*-Selected Species

Characteristic	<i>r</i> -Selected Species	<i>K</i> -Selected Species
Maturation time	Short	Long
Life span	Short	Long
Mortality rate	Usually high	Usually low
Reproductive episodes	Usually one	Usually several
Time of first reproduction	Early	Late
Clutch or brood size	Usually large	Usually small
Size of offspring	Small	Large
Active parental care	Little or none	Often extensive
Population size	Fluctuating	Relatively stable
Tolerance of environmental change	Generally poor	Generally good

Some Species Exhibit Regular Cycles in Population Size

The population densities of many insects, birds, and mammals in the northern hemisphere fluctuate between species-specific lows and highs in a multiyear cycle. Arctic populations of small rodents vary in size over a 4-year cycle, whereas snowshoe hares, ruffed grouse, and lynxes have 10-year cycles. Ecologists documented such cyclic fluctuations more than a century ago, but none of the general hypotheses so far proposed explains the cycles in all species. The availability and quality of food, the abundance of predators, the prevalence of disease-causing microorganisms, and variations in weather may influence population growth. Furthermore, a cycling population's food supply and

a. An *r*-selected species



b. A *K*-selected species



Figure 49.17

Life history differences. (a) An *r*-selected species, like quinoa (*Chenopodium quinoa*), matures in one growing season and produces many tiny seeds, which were a traditional food staple for the indigenous people of North and South America. (b) A *K*-selected species, like the coconut palm (*Cocos nucifera*), grows slowly and produces a few large seeds repeatedly during its long life.

predators are themselves influenced by the population's size.

Theories of *intrinsic control* suggest that as an animal population grows, individuals undergo hormonal changes that increase aggressiveness, reduce reproduction, and foster dispersal to other areas. The dispersal phase of the cycle may be dramatic. For example, when populations of the Norway lemming (*Lemmus lemmus*), a rodent that lives in the Scandinavian arctic, reach their peak density, aggressive interactions drive younger and weaker individuals away from their place of birth. The exodus of many thousands of lemmings, scrambling over rocks and even cliffs, is sometimes incorrectly portrayed in nature films as a suicidal mass migration. Researchers do not yet know how widespread these hormonal and behavioral changes are among different species or exactly what regulates them.

Other explanations focus on *extrinsic control*, such as the relationship between a cycling species and its food or predators. A dense population may exhaust its food supply, increasing mortality and decreasing reproduction. But experimental food sup-

plementation does not always prevent the decline in mammal populations, indicating that other factors are also at work.

Some researchers have suggested that the cycles of predators and their prey are induced by time lags in each population's response to changes in density of the other (**Figure 49.18**). The 10-year cycles of snowshoe hares (*Lepus americanus*) and their feline predators, Canada lynxes (*Lynx canadensis*), were often cited as a classic example of such an interaction. But recent research has cast doubt on this straightforward explanation. Hare populations exhibit a 10-year fluctuation even on islands where lynxes are absent. Thus, the lynx cannot be solely responsible for the hare's cycle, although cycles in the hare populations may trigger cycles in populations of their predators.

Charles Krebs and his colleagues at the University of British Columbia studied hare and lynx interactions with a large-scale, multiyear experiment in the southern Yukon. They fenced experimental areas where they added food for the hares, excluded mammalian predators, or applied both experimental treatments; unmanipulated plots served as controls. Where mammalian

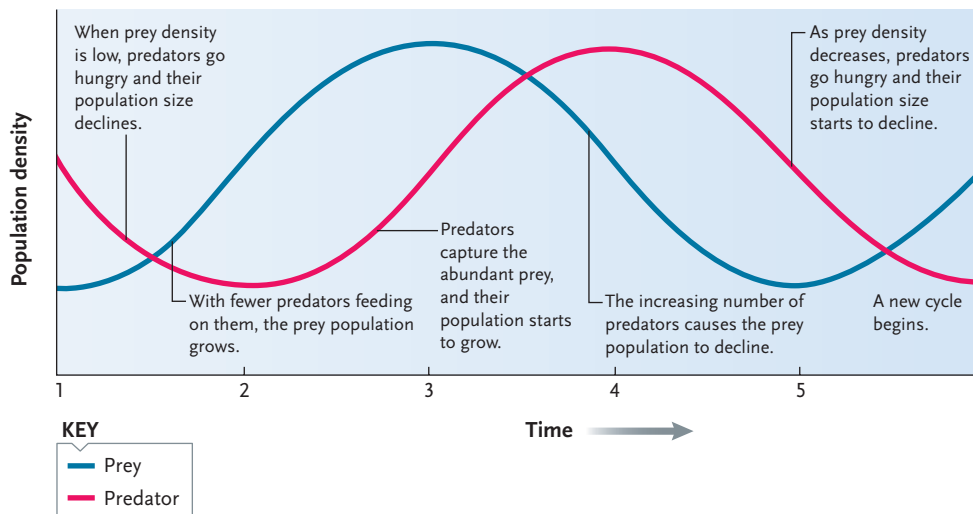


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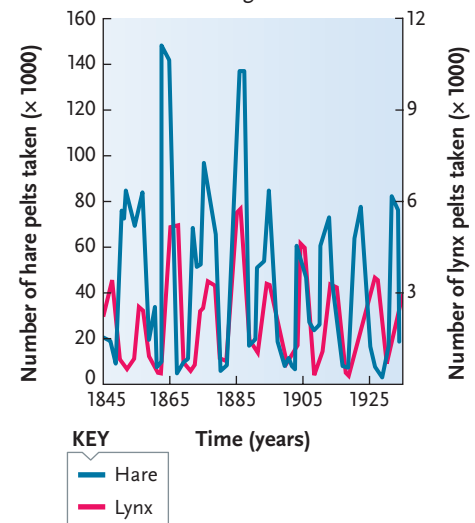
Figure 49.18

The predator-prey model. Predator-prey interactions may contribute to density-dependent regulation of both populations. (a) A mathematical model predicts cycles in the numbers of predators and prey because of time lags in each species' responses to changes in the density of the other. (Predator population size is exaggerated in this graph: predators are usually less common than prey.) (b) The interaction between the Canada lynx (*Lynx canadensis*) and the snowshoe hare (*Lepus americanus*) was often described as a cyclic predator-prey interaction. The abundances of lynx and hare are based on counts of pelts that trappers sold to Hudson's Bay Company over a 90-year period. Recent research has shown that population cycles in snowshoe hares are caused by complex interactions between the hare, its food plants, and its predators.

a. Predictions of a predator-prey model



b. Lynx and hare population sizes through time



predators were excluded, hare densities approximately doubled relative to the controls. Where food was added, hare densities tripled. But in plots where food was added *and* predators were excluded, the hare densities increased 11-fold. Krebs and his colleagues concluded that neither food availability nor predation alone is solely responsible for arctic hare population cycles; instead, complex interactions between the hares, their food plants, and their predators create the cyclic fluctuations in hare population size.

STUDY BREAK

1. How can you tell whether an environmental factor causes density-dependent or density-independent effects on a population?
2. Are the effects of infectious diseases on populations more likely to be density-dependent or density-independent?

49.7 Human Population Growth

How do human populations compare with those of other species we have studied? The worldwide human population surpassed 6 billion on October 12, 1999. Like many other species, humans live in somewhat isolated populations, which vary in their demographic traits and access to resources. Although many of us live comfortably, at least a billion people are malnourished or starving, lack clean drinking water, and live without adequate shelter or health care. Even if it were possible to double the food supply, increased agricultural production would inevitably increase pollution and contribute to spoiled croplands, deforestation, and desertification, which are described in Chapter 53.

Human Populations Have Sidestepped the Usual Density-Dependent Controls

For most of human history, our population grew slowly; but over the past two centuries, the worldwide human population has grown exponentially (**Figure 49.19**). Demographers have identified three ways in which humans have avoided the effects of density-dependent regulating factors.

First, humans have expanded their geographical range into virtually every terrestrial habitat. Our early ancestors lived in tropical and subtropical grasslands, but by 40,000 years ago, they had dispersed through much of the world (see Section 30.13). Their success resulted from their ability to solve ecological problems by building fires, assembling shelters, making clothing and tools, and planning community hunts. Vital survival skills spread from generation to generation and from one population to another because language allowed the communication of complex ideas and knowledge.

Second, humans have increased the carrying capacities of habitats they occupy. About 11,000 years ago, many populations shifted from hunting and gathering to agriculture. They cultivated wild grasses, diverted water to irrigate crops, and used domesticated animals for food and labor. Such innovations increased the availability of food, raising both the carrying capacity and the population growth rates. In the mid-eighteenth century, people harnessed the energy in fossil fuels, and industrialization began in Western Europe and North America. Food supplies and the carrying capacity increased again, at least in the industrialized countries, through the use of synthetic fertilizers, pesticides, and efficient methods of transportation and food distribution.

Third, advances in public health have reduced the effects of critical population-limiting factors such as malnutrition, contagious diseases, and poor hygiene. Over the past 300 years, modern plumbing and sewage

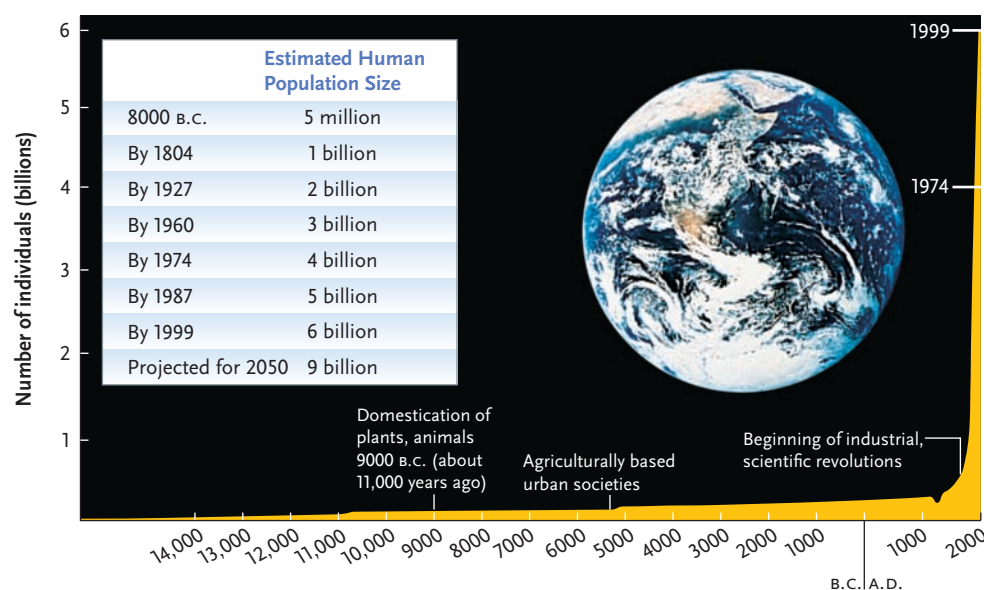


Figure 49.19

Human population growth. The worldwide human population grew slowly until 200 years ago, when it began to increase explosively. The dip in the mid-fourteenth century represents the death of 60 million Asians and Europeans from the bubonic plague. The table shows the years when the human population reached each additional billion people. (Photo: NASA.)

treatment, improvements in food handling and processing, and medical discoveries have reduced death rates sharply. Births now greatly exceed deaths, especially in less industrialized countries, resulting in rapid population growth.

Age Structure and Economic Development May Now Control Our Population Growth

Where have our migrations and technological developments taken us? It took about 2.5 million years for the human population to reach 1 billion, 123 years to reach the second billion, and only 13 years to jump from 5 billion to 6 billion (see the inset table in Figure 49.19). Rapid population growth may now be an inevitable consequence of our age structure and economic development.

Population Growth and Age Structure. On a worldwide scale, the annual growth rate for the human population averaged nearly 1.2% ($r = 0.012$ new individuals per individual per year) between 2000 and 2005. Population experts expect that rate to decline, but even so, the human population will probably exceed 9 billion by 2050.

The population growth rates of individual nations vary widely, however, ranging from much less than 1% to more than 3% in 2001 (Figure 49.20a). The industrialized countries of Western Europe have achieved nearly zero population growth, but other countries—notably those in Africa, Latin America, and Asia—will experience huge increases over the next 20 or 25 years (Figure 49.20b).

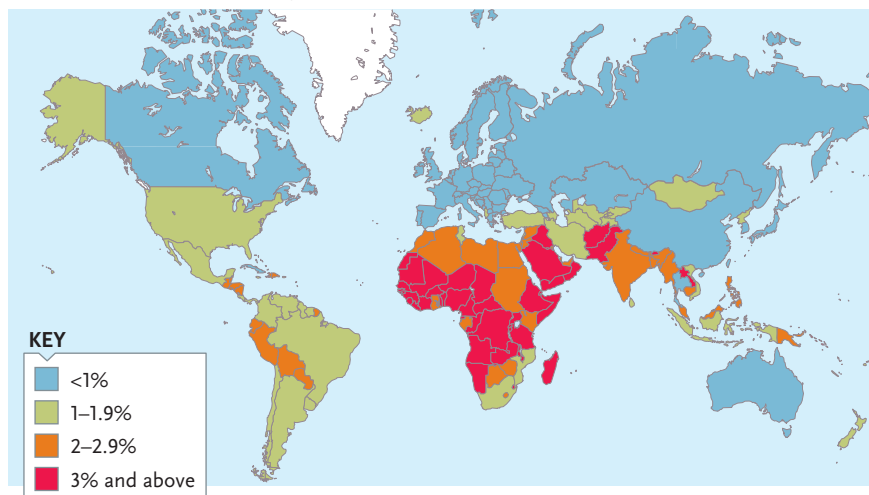
For all long-lived species, differences in age structure are a major determinant of differences in population growth rates (Figure 49.21). The uniform age struc-

ture of countries with zero growth—with approximately equal numbers of people of reproductive and prereproductive ages—suggests that individuals have just been replacing themselves and that these populations will not experience a growth spurt when today’s children mature. By contrast, the narrow-based age structure of countries with negative growth illustrates a continuing decrease in population size. Reproductives have been producing very few offspring, and the small group of prereproductives may not even replace themselves. Countries with rapid growth have a broad-based age structure, with many youngsters born during the previous 15 years. Worldwide, more than one-third of the human population falls within this prereproductive base. This age class will soon reach sexual maturity. Even if each woman produces only two offspring, populations will continue to grow rapidly because so many individuals are reproducing.

The age structure of the United States falls between those for countries with zero growth and countries with rapid growth. The average number of children per family has declined to the two that are necessary to replace their parents in the population. Nevertheless, the U.S. population will continue to grow slowly for the next couple of generations largely because of continued immigration.

Population Growth and Economic Development. The relationship between a country’s population growth and its economic development can be depicted by the **demographic transition model** (Figure 49.22). This model describes historical changes in demographic patterns in the industrialized countries of Western Europe; we do not know if it accurately predicts the future for developing nations today.

a. Mean annual population growth rates



b. Projected population sizes for 2025

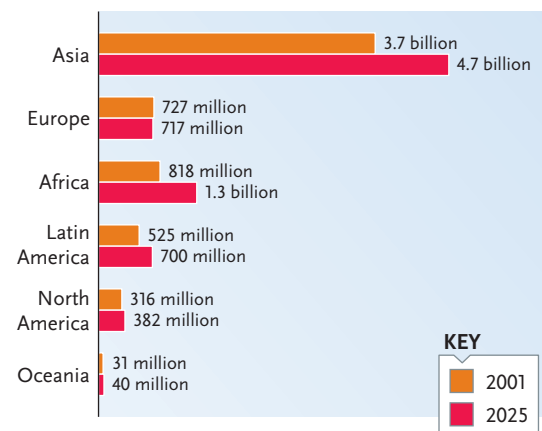
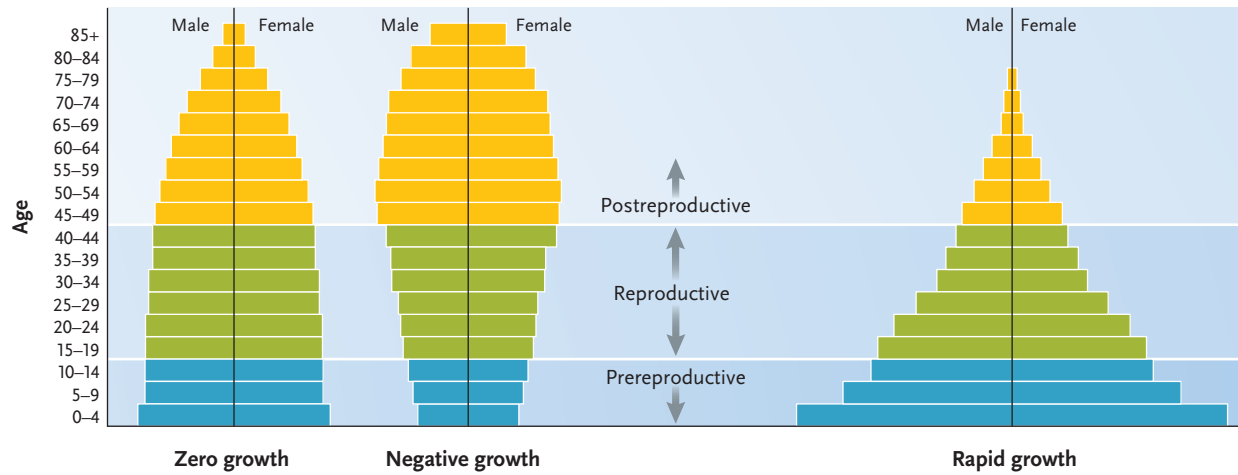


Figure 49.20

Local variation in human population growth rates. (a) Average annual population growth rates varied among countries and continents in 2001. (b) In some regions, the population is projected to increase greatly by 2025 (red) as compared with the population size in 2001 (orange); the population of Europe will likely decline.

a. Hypothetical age distributions for populations with different growth rates



b. Age pyramids for the United States and Mexico in 2000

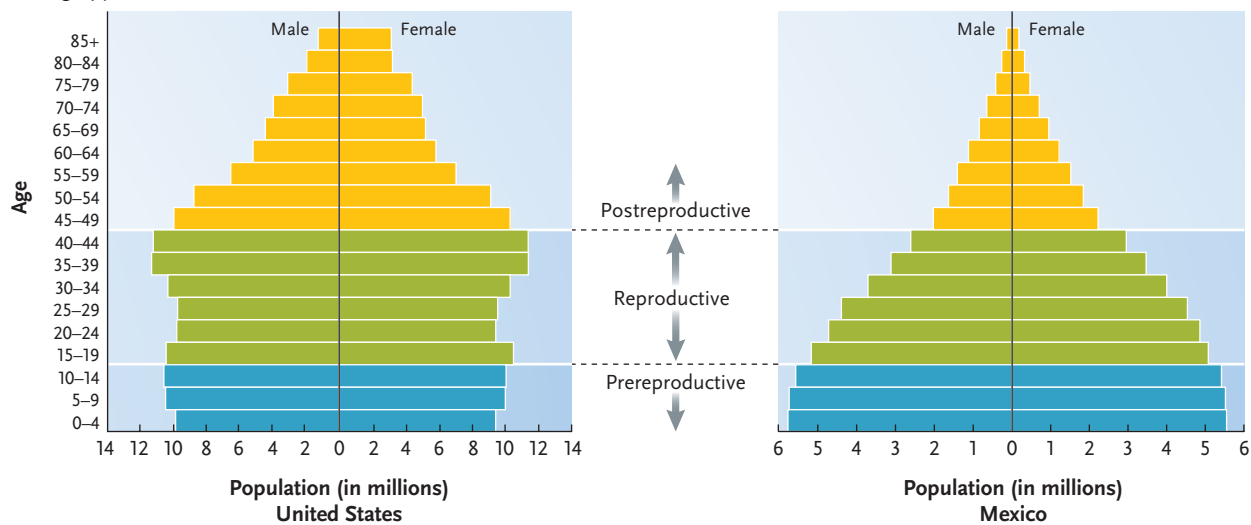


Figure 49.21

Age-structure diagrams. (a) Age-structure diagrams differ for countries with zero, negative, and rapid population growth rates. The width of each bar represents the proportion of the population in each age class. (b) Age-structure diagrams for the United States and Mexico in 2000 (measured in millions of people) suggest that these countries would experience different population growth rates.

According to this model, during a country's *preindustrial* stage, birth and death rates are high, and the population grows slowly. Industrialization begins a *transitional* stage, when food production rises, and health care and sanitation improve. The death rate declines, resulting in an increased rate of population growth. Later, as living conditions improve, the birth rate also declines, causing the population growth rate to drop. When the *industrial* stage is in full swing, population growth slows dramatically. People move from the countryside to cities, and urban couples often choose to accumulate material goods instead of having large families. Zero population growth is reached in the *postindustrial* stage. Eventually, the birth rate falls below the death rate, r falls below zero, and population size begins to decrease.

Today, the United States, Canada, Australia, Japan, Russia, and most of Western Europe are in the industrial stage. Their growth rates are slowly decreasing. In

Bulgaria, Germany, Hungary, and Sweden, birth rates are lower than death rates, and populations are getting smaller, indicating their entry into the postindustrial stage. Kenya and other less industrialized countries are in the transitional stage, but they may not have enough skilled workers or enough capital to make the transition to an industrialized economy. Thus, many poorer nations may be stuck in the transitional stage.

Limiting Population Growth. Most governments realize that increased population size is now the major factor causing resource depletion, excessive pollution, and an overall decline in the quality of life. The principles of population ecology demonstrate that a slowing of population growth—or an actual decline in population size—can be achieved only by decreasing the birth rate or increasing the death rate. And because increasing mortality is neither a rational nor humane means

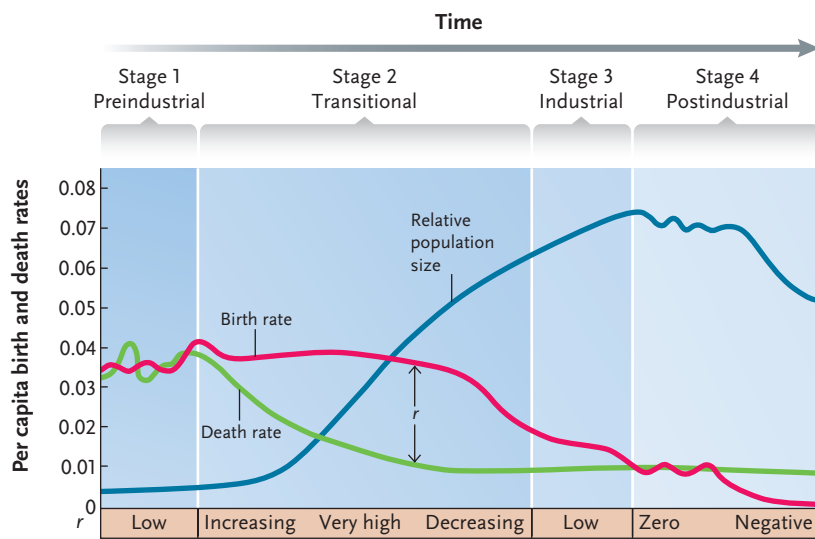


Figure 49.22

The demographic transition. The demographic transition model describes changes in the birth and death rates and relative population size as a country passes through four stages of economic development. The bottom bar describes the net population growth rate, r .

of population control, most governments are attempting to lower birth rates with **family planning programs**. These programs educate people about ways to produce an optimal family size on an economically feasible schedule. Programs vary in their details, but all provide information on methods of birth control (see Section 47.6). When thoughtfully developed and carefully administered, family planning programs cause birth rates to decline significantly.

All species face limits to their population growth. We have postponed the action of most factors that limit

UNANSWERED QUESTIONS

Are there universal governing principles in population ecology, similar to the laws of physical sciences? Or is the natural world so complex that each population must be considered individually, leaving us with just a series of case studies?

These types of broad questions motivated the founders of modern ecological studies, such as G. Evelyn Hutchinson and Robert MacArthur. Many ecologists have attempted to codify aspects of population ecology in terms of specific principles, sometimes imposing artificial dichotomies in the process. For example, this chapter considered whether or not natural populations are subject to either density-dependent or density-independent regulation. Ecologists have also attempted to uncover basic patterns in community ecology, which are described in the next chapter. We do know that some general principles are often important in governing the structure of populations or natural communities but, as yet, we cannot apply any of them to a specific system without also including a detailed study of that system.

What is the importance of scale in ecology?

Although an individual population can be a meaningful object of study, ecologists often collect data from multiple populations of the same species to compare results among the “replicates.” However, although the separate populations may appear to be replicates, they are often quite different in appearance, age structure, life history, or other characteristics. Ecologists confronted with such variation might seek explanations in the differences between the populations’ environments, including both abiotic and biotic factors. However, such local variation may also be attributable to the larger context, such as the landscape or surrounding communities.

One important manifestation of this question applies to how the populations of a species are distributed in space. In many cases, discrete populations are widely separated from one another. Such separation is easy to imagine in terms of fish that live in lakes or organisms that live on islands, but it also applies in a diversity of other organisms. For example, many plants and animals are found only on chemically distinct patches of soil that are distributed like islands across a terrestrial environment. Many

lizards prefer to live in rock outcrops that dot the landscape. Other organisms live on cool, wet mountaintops surrounded by desert. Such isolation is often exaggerated by human modification of the landscape, which progressively fragments and isolates habitable environments from one another. How does such subdivision change the dynamics of the individual populations? How does it change the way they evolve? These are questions that have challenged population and evolutionary biologists for decades. The effects of humans on the environment are making the answers to these questions more than a theoretical concern.

What is the importance of evolution in ecological interactions?

Most research in ecology, ranging from formal models of population growth and regulation to empirical studies, treats populations as if they were unchanging—as if they were not evolving. This implicit perspective does not deny that evolution is happening, but treats it as if it happens on such a long time scale that it need not be considered in contemporary studies. However, many recent studies have shown that populations may evolve quickly, often on a year-to-year basis. If this observation is generally true, then ecological studies that do not include evolutionary change may be compromised. For example, the monitoring and management of commercially exploited fish populations are based entirely on models of population growth, demography, and life histories similar to those considered in this chapter. Commercial fisheries often capture a large proportion of a population every year, focusing on the largest adults. Although research has clearly shown that these practices are likely to select for earlier maturity at a smaller size, these findings have not yet been incorporated into fisheries-management policy. More generally, ecologists have not yet included sufficient emphasis on the interaction between evolution as it occurs on the scale of our day-to-day existence and the modeling and empirical study of ecological processes.



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population growth, but no amount of invention can expand the ultimate limits set by resource depletion and a damaged environment. We now face two options for limiting human population growth: we can make a global effort to limit our population growth, or we can wait until the environment does it for us.

STUDY BREAK

1. How have humans sidestepped the controls that regulate populations of other organisms?
2. How does the age structure of a population influence its future population growth?

Review

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[Animation: Life history patterns](#)

[Animation: Guppy characteristics](#)

49.1 The Science of Ecology

- Ecology is the study of the interactions between organisms and their environments. Basic ecology focuses on undisturbed natural systems, whereas applied ecology considers the effects of human disturbance (Figure 49.1).
- Ecologists do research at five levels of organization: organisms, populations, communities, ecosystems, and the biosphere.
- Ecologists test hypotheses about ecological relationships with experimental or observational data. They sometimes frame hypotheses in mathematical models.

49.2 Population Characteristics

- A population's size and density can be measured directly or with sampling techniques (Figures 49.2 and 49.3).
- Organisms within a population may be clumped, uniformly distributed, or randomly distributed within their habitat (Figure 49.4). Clumped dispersion is the most common, but animals may change their dispersion pattern seasonally.
- The relative numbers of individuals of different ages determines a population's age structure. Generation time is the average time between an individual's birth and the birth of its offspring (Figure 49.5). A population's sex ratio is the relative proportion of males and females.

[Animation: Distribution patterns](#)

[Animation: Mark-recapture method](#)

[Animation: Age structure diagrams](#)

49.3 Demography

- Demography is the study of the survivorship, reproduction, immigration, and emigration patterns that influence population characteristics.
- Life tables summarize age-specific mortality, survivorship, and age-specific fecundity of surviving individuals (Table 49.1).
- Survivorship curves depict a population's survival pattern over its life span. Ecologists define three general patterns of survivorship: high survivorship until late in life, a constant mortality level at all ages, and high juvenile mortality (Figure 49.6).

49.4 The Evolution of Life Histories

- An organism's energy budget mandates trade-offs in the allocation of energy to maintenance, growth, and reproduction.
- Natural selection has molded several interacting components of life history variation based upon the allocation of resources to growth, maintenance, and reproduction: the trade-off between fecundity and parental care; whether to reproduce once versus multiple times; and the age of first reproduction.

49.5 Models of Population Growth

- Bacteria reproduce by binary fission, and their populations double in size each generation (Figure 49.7).
- The exponential growth model, $dN/dt = rN$, describes unlimited population growth. A graph of exponential growth is J-shaped (Figure 49.8).
- The logistic model, $dN/dt = r_{max}N(K - N/K)$, includes the effects of resource limitation. The carrying capacity, K , is the maximum population size that an environment can sustain. The per capita population growth rate, r , decreases as N approaches K . A graph of logistic growth is S-shaped (Figures 49.9 and 49.10, Table 49.2).
- Some populations exhibit logistic growth in the laboratory and in nature, but time lags in responses to increased density may cause N to oscillate around K (Figure 49.11).

[Animation: Exponential growth](#)

[Animation: Effect of death on growth](#)

[Practice: Comparison of exponential and logistic population growth](#)

49.6 Population Regulation

- Density-dependent factors regulate population size by reducing individual growth rates, adult size, survivorship, and fecundity (Figures 49.12 and 49.13). Competition within populations or between species, predator-prey interactions, parasites, and infectious diseases can cause density-dependent population regulation (Figure 49.14).
- Abiotic environmental factors, which affect a population regardless of its size, cause density-independent limitation of population size (Figure 49.15).
- Interactions between density-dependent and density-independent factors often influence population size (Figure 49.16).
- The life history patterns of most organisms fall between two extremes: r -selected species and K -selected species (Figure 49.17). They differ in many life history characteristics (Table 49.3).
- Some animal populations exhibit cyclic fluctuations in size (Figure 49.18). No general model has successfully explained all population cycles.

49.7 Human Population Growth

- Human populations have sidestepped density-dependent population regulation by expanding into most terrestrial habitats, increasing carrying capacity, and reducing death rates with improved medical care and sanitation (Figures 49.19 and 49.20).
- Age structure may now control human population growth rates (Figure 49.21). In countries with large numbers of young people, populations will continue to grow rapidly as they reach sex-

ual maturity. The populations of countries with a uniform age structure will not experience much growth in the foreseeable future.

- The demographic transition model describes the influence of economic development on population growth (Figure 49.22).

- Many governments encourage population control through family planning programs.

Animation: Current and projected population sizes by region

Animation: U.S. age structure

Animation: Demographic transition model

Questions

Self-Test Questions

1. Ecologists sometimes use mathematical models to:
 - a. avoid conducting laboratory studies or field work.
 - b. simulate natural events before conducting detailed field studies.
 - c. make basic observations about ecological relationships in nature.
 - d. collect survivorship and fecundity data to construct life tables.
 - e. determine the geographical ranges of populations.
2. The number of individuals per unit area or volume of habitat is called the population's:
 - a. geographical range.
 - b. dispersion pattern.
 - c. density.
 - d. size.
 - e. age structure.
3. One day you caught and marked 90 butterflies in a population. A week later, you returned to the population and caught 80 butterflies, including 16 that had been marked previously. What is the size of the butterfly population?
 - a. 170
 - b. 450
 - c. 154
 - d. 186
 - e. 106
4. A uniform dispersion pattern implies that members of a population:
 - a. cooperate in rearing their offspring.
 - b. work together to escape from predators.
 - c. use resources that are patchily distributed.
 - d. may experience intraspecific competition for vital resources.
 - e. have no ecological interactions with each other.
5. The model of exponential population growth predicts that the per capita population growth rate (r):
 - a. does not change as a population gets larger.
 - b. gets larger as a population gets larger.
 - c. gets smaller as a population gets larger.
 - d. is always at its maximum level (r_{max}).
 - e. fluctuates on a regular cycle.
6. A population of 1000 individuals experiences 462 births and 380 deaths in 1 year. What is the value of r for this population?
 - a. 0.842/individual/year
 - b. 0.462/individual/year
 - c. 0.380/individual/year
 - d. 0.820/individual/year
 - e. 0.082/individual/year
7. According to the logistic model of population growth, the absolute number of individuals by which a population grows during a given time period:
 - a. gets steadily larger as the population size increases.
 - b. gets steadily smaller as the population size increases.
 - c. remains constant as the population size increases.
 - d. is highest when the population is at an intermediate size.
 - e. fluctuates on a regular cycle.
8. Which example might reflect density-dependent regulation of population size?
 - a. An exterminator uses a pesticide to eliminate carpenter ants from a home.
 - b. Mosquitoes disappear from an area after the first frost.
 - c. The lawn dies after a month-long drought.
 - d. Storms blow over and kill all willow trees along a lake.
 - e. The size of a clam population declines as the number of predatory herring gulls explodes.

9. A K -selected species is likely to exhibit:
 - a. a Type I survivorship curve and a short generation time.
 - b. a Type II survivorship curve and a short generation time.
 - c. a Type III survivorship curve and a short generation time.
 - d. a Type I survivorship curve and a long generation time.
 - e. a Type II survivorship curve and a long generation time.
10. One reason that human populations have sidestepped factors that usually control population growth is:
 - a. The carrying capacity for humans has remained constant since humans first evolved.
 - b. Agriculture and industrialization have increased the carrying capacity for our species.
 - c. The population growth rate (r) for the human population has always been small.
 - d. The age structure of human populations has no impact on its population growth.
 - e. Plagues have killed off large numbers of humans at certain times in the past.

Questions for Discussion

1. Choose an animal or plant species that lives in your environment and identify the density-dependent and density-independent factors that might influence its population size. How could you demonstrate conclusively that the factors work in either a density-dependent or density-independent fashion?
2. Many city-dwellers have noted that the density of cockroaches in apartment kitchens appears to vary with the habits of the occupants: people who wrap food carefully and clean their kitchen frequently tend to have fewer arthropod roommates than those who leave food on kitchen counters and clean less often. Interpret these observations from the viewpoint of a population ecologist.
3. How could you define the worldwide carrying capacity for humans? What factors would you have to take into account?

Experimental Analysis

Design an experiment using fruit flies or some other small laboratory animal to test the hypothesis that delaying the age of first reproduction will decrease a population's per capita birth rate. Your experimental design should include experimental and control groups as well as details about your experimental methods and the data you would collect.

Evolution Link

Many animals, including humans and other primates, live long beyond their reproductive years. Develop an evolutionary hypothesis to explain this observation, and design a study that might test it.

How Would You Vote?

Some people oppose any deer hunting, whereas others see hunters as a logical substitute for an absence of natural predators. Do you support encouraging hunting in areas where the presence of too many deer is harming the habitat? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.