45 POPULATION ECOLOGY

The Numbers Game

In 1944 Allied forces invaded Normandy, which marked the beginning of the end of Hitler's "Fortress Europe." On the other side of the world, the United States Coast Guard stationed nineteen men on a remote island in the Bering Sea. The enlisted men set up long-range navigational aids for ships and aircraft. They barged in twenty-nine reindeer (*Rangifer tarandus*) as an emergency food source.

Remember, reindeer preferentially eat lichens (Chapter 24). Thick mats of lichens carpeted St. Matthew, an island where winds howl across tundra and tall cliffs above the sea. The island, which is 320 kilometers from Alaska, is only 6.4 kilometers (about 4 miles) wide and 51 kilometers long.

World War II started to wind down before any reindeer were shot. The Coast Guard pulled out, leaving behind some seabirds, arctic foxes, and voles—and a herd of healthy reindeer with nothing big enough to hunt them down.

In 1957 a biologist with the U.S. Fish and Wildlife Service, who later became a University of Alaska professor, visited St. Matthew. On a hike from one end of the island to the other, David Klein counted 1,350 well-fed reindeer. He noticed lichens that had been overgrazed and trampled.

Six years after that, Klein and three other biologists returned to the small island. They counted 6,000 reindeer. They could not help but notice the profusion of reindeer tracks and feces, and a lot of pummeled lichens.

Klein did not return to St. Matthew until the summer of 1966. Bleached-out reindeer bones littered the island. Forty-two reindeer were still alive. Only one was a male, and it had abnormally shaped antlers. There were no fawns. The population had plummeted to 1 percent of the founding herd! Apparently, thousands had starved to death during the winter of Klein's previous visit. By the time the 1980s rolled around, there were no reindeer at all.

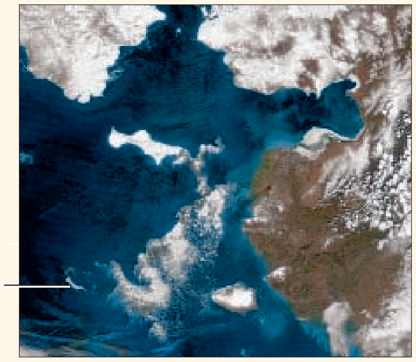
St. Matthew Island is small, with clear boundaries, so it is easy to draw a lesson from this unintended experiment in population ecology: *A population's growth depends on environmental resources, few of which are unlimited.*

Does the lesson apply to other populations, in other places? Another case, on another isolated island, suggests that it does. Remember the Chapter 27 introduction? That human population, too, plummeted in size after growing beyond the capacity of the environment to sustain it.

What if the environment for a population is as big as a continent or a sea? Do resources still run out? Consider this: There are more whitetail deer (*Odocoileus virginianus*) in North America than there were five centuries ago. There are an estimated 20 million to 33 million. The nation's forests no longer can sustain them. Deer now overbrowse ground vegetation. They strip trees of leaves and bark. By eating so many acorns and seedlings, they have stopped the self-renewal of many oak forests. Forests remain in good shape only when there are no more than twenty deer per square mile. Today, densities are often greater than seventy deer per square mile.

Figure 45.1 What happens when you import a small herd of herbivores to a remote island where there are no natural predators and then forget about them?

IMPACTS, ISSUES



The rampant browsing of the whitetail deer population also is endangering nesting birds, wildflowers, and other species. Deer spill into human habitats as well. They cause highway accidents that kill 200 or so people and cost about a billion dollars' worth of property damage annually. Each year, farmers lose about 400 million dollars' worth of crops to deer. Many of us know firsthand what even a few hungry deer can do to gardens.

Fewer people are hunting deer for sport, and hunting for the commercial market is banned. Animal rights groups are pleased. They want to control local populations with birth control or other nonlethal methods. However, it is difficult and expensive to track down and treat deer with injectable birth control drugs. Efforts to introduce birth control drugs into the deer's food sources could harm other herbivores.

The point is, *certain principles govern the growth and sustainability of all populations over time*. These principles are the bedrock of **ecology**—the systematic study of how organisms interact with one another and with the physical and chemical environment. Ecological interactions start within and between populations and extend on through communities, ecosystems, and the biosphere. They are the focus of this last unit of the book. After presenting the basic principles, this chapter invites you to apply them to the past, present, and future of the human species.

How Would You Vote?

Some people oppose any deer hunting, while 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? See BiologyNow for details, then vote online.

Key Concepts

WHAT ARE THE DEMOGRAPHICS?

Ecological principles govern the growth and sustainability of all populations. Genetic factors and a population's size, density, distribution, and the number of individuals in its various age categories influence patterns of growth. Sections 45.1, 45.2

EXPONENTIAL RATES OF GROWTH

Any population that is growing at a rate proportional to its size is showing exponential growth. Depending on the size of the population's reproductive base, exponential growth may be slow or fast. Section 45.3

LIMITS ON INCREASES IN SIZE

In time, exponential growth typically overshoots the carrying capacity, which is the maximum number of individuals of a population that environmental resources can sustain indefinitely. Some populations stabilize after a crash. Others never do recover. Section 45.4

PATTERNS OF SURVIVAL AND REPRODUCTION

Competition, disease, predation, and other factors that control population growth vary among species and help shape their life history patterns. Sections 45.5, 45.6

THE HUMAN POPULATION

Historically, expansion into new habitats around the world, cultural interventions, and technological innovations have allowed human populations to postpone abiotic and biotic limits to growth. However, the operative word is "postpone." Sections 45.7–45.10

Links to Earlier Concepts

Earlier chapters defined the population, a unit of biological organization that undergoes evolution (Sections 1.4, 17.3, 19.1–19.3). They introduced you to certain morphological, physiological, and behavioral traits that help characterize populations in general (17.3, 18.1, 18.8). With this chapter we turn to demographics—population size and other vital statistics—and the factors that limit increases in size.

WHAT ARE THE DEMOGRAPHICS?

45.1 Characteristics of Populations

LINKS TO SECTIONS 17.3, 18.1, 18.8

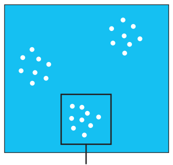
By this point in the book, you know that a population is a group of individuals of the same species. Ecological interactions begin with characteristics of populations. We call these vital statistics ***demographics****.*

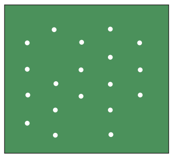
Each population has a gene pool and an evolutionary history, as explained in Chapters 17 and 18. It also has a characteristic size, density, distribution, and number of individuals in its various age categories.

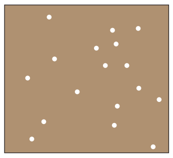
Population size is the number of individuals that actually or potentially contribute to the gene pool. The **age structure** is the number of individuals in each of several age categories. For instance, individuals often are grouped by *pre-reproductive*, *reproductive*, and *post-reproductive* ages. Those in the first category have the capacity to produce offspring when mature. Together with individuals in the second category, they make up the population's **reproductive base**.

Population density is the number of individuals in some specified area or volume of a habitat. A *habitat*, remember, is the type of place where a species lives. We characterize a habitat by its physical and chemical features and its particular array of species. **Population distribution** is the pattern in which the individuals are dispersed in a specified area.

Crude density is a measured number of individuals in a specified area. It does not reveal how much of the habitat is actually being used for living space. Even areas that seem rather uniform, such as a long, sandy shoreline, are more like tapestries of light, moisture, temperature, composition, and many other variables. Only one portion of the habitat might be suitable for a given population. It might be suitable all of the time or only some of the time, as in summer versus winter.


clumped


nearly uniform


random

Different species occupying the same area typically compete for energy, nutrients, living space, and other resources. Such *interspecific* interactions influence each population's density and dispersion through a habitat.

Theoretically, populations show a clumped, nearly uniform, or random distribution pattern (Figure 45.2). Clumping is the most common, for several reasons. First, each species is adapted to particular conditions and resources, which often are not uniform through a habitat. Some animals cluster by a water hole, seeds sprout only in moist soil, and so on. Second, animals may live in social groups, which offer more protection and mating opportunities. A school of fish is like this. Third, many plant seedlings and the offspring of many animals cannot disperse far from their parents.

With nearly uniform distribution, individuals are more evenly spaced than we would expect on the basis of chance alone. Uniform distribution is relatively rare in nature. It sometimes occurs when competition for resources or territory is fierce, as in a nesting colony of seabirds. Figures 45.2 and 49.16 show examples.

We observe random dispersion only when habitat conditions are nearly uniform, resource availability is fairly steady, and individuals of a population or pairs of them neither attract nor avoid one another. Each wolf spider does not hunt far from its burrow, which can be almost anywhere in forest soil (Figure 45.2).

Each population has characteristic demographics, such as size, density, distribution pattern, and age structure.

Environmental conditions and species interactions shape these characteristics, which may change over time.

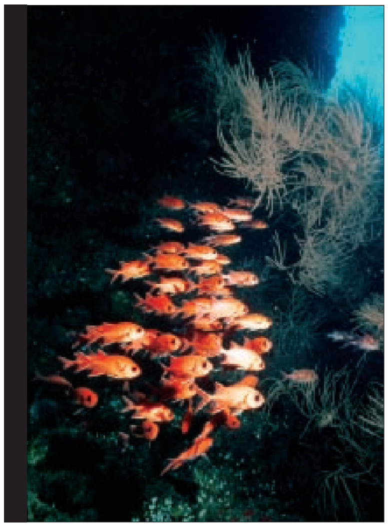


Figure 45.2 Three patterns of population distribution: clumped, as in squirrelfish schools; more or less uniform, as in a royal penguin nesting colony; and random, as when wolf spiders live in randomly located burrows in forest soil.

FOCUS ON SCIENCE

45.2 Elusive Heads to Count

Ecologists go into the field to test theories about species interactions and population dynamics, and to monitor the health of threatened or endangered populations.

As the chapter introduction indicated, deer are all around us in forests, grasslands, golf courses, and gardens. How would you go about counting the ones living near you?

A full count would be a measure of absolute population density. Census takers supposedly make such a count of human populations every ten years, although not everyone answers the door. Ecologists make counts of large species in small areas, such as birds in a forest, northern fur seals at their breeding grounds, and sea stars in a tidepool. More often, however, a full count is impractical, so ecologists sample part of a population and estimate its total density.

For instance, you could divide a map of your county into small plots, or quadrats. **Quadrats** are sampling areas of the same size and shape, such as rectangles, squares, and hexagons. You could count individual deer in several plots and, from that, extrapolate the average number for the county as a whole. Ecologists often conduct such counts for plants and other species that stay put (Figure 45.3). Some counts in small areas also help them estimate the population sizes of migrating animals.

Deer are among the animals that do not stay put. How can ecologists be sure that the individuals being counted in a given plot are not the same ones counted earlier in a different plot? **Capture–recapture methods** are one way to sample a population of mobile animals. Such individuals are captured and marked in some way. Deer get collars, squirrels get tattoos, salmon get tags, birds get leg rings, butterflies get wing markers, and so on (Figure 45.4). The marked animals are released at time 1. At time 2, traps are reset. When all goes well, the proportion of marked animals in the second sample is representative of the proportion marked in the whole population:

$$\frac{\text{Marked individuals in sampling at time 2}}{\text{Total captured in sampling 2}} = \frac{\text{Marked individuals in sampling at time 1}}{\text{Total population size}}$$

Ideally, both marked and unmarked individuals of the population are captured at random, none of the marked animals is overlooked, and none dies or otherwise departs during the study interval.

In the real world, recapturing marked individuals might not be random. For example, squirrels that were marked after being attracted to bait in boxes might now be trap-happy or trap-shy. Such individuals may overrepresent or underrepresent their population. Other examples: Instead of mailing tags of marked fish to ecologists, a fisherman may keep them as good-luck charms. Birds lose leg rings.

Your estimate also depends on the time of year when you make a sampling. Population distribution varies with time, as during migrations in response to environmental rhythms. Few places yield abundant resources all year long, so many populations move between habitats as seasons change. Canada geese are like this. So are deer. In such cases, capture–recapture methods might be used more than once a year, for several years.

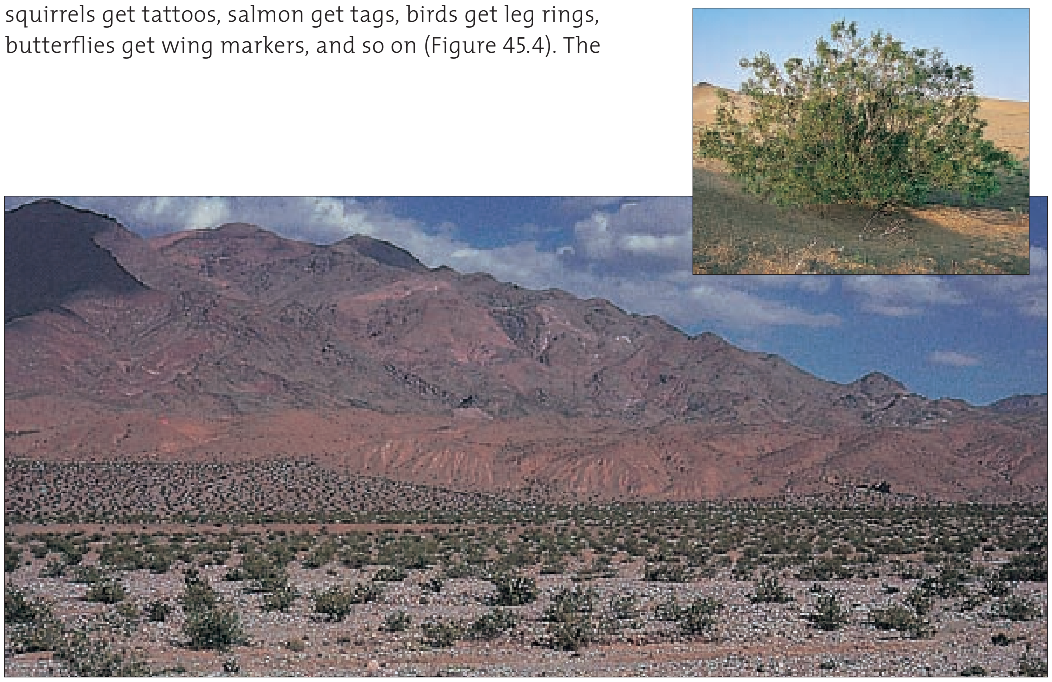


Figure 45.3 Near the eastern base of the Sierra Nevada, a population of creosote bushes showing nearly uniform distribution. The plants compete for scarce water in this desert climate zone, which has extremely hot, dry summers and mild winters.

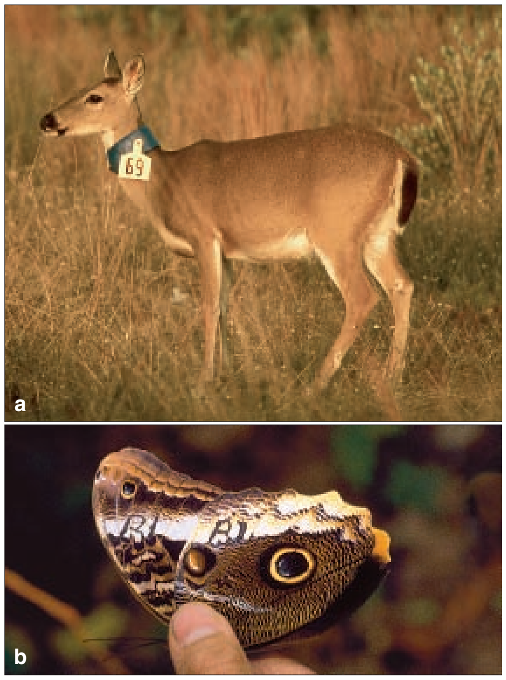


Figure 45.4 Two individuals marked for population studies. (**a**) Florida Key deer and (**b**) Costa Rican owl butterfly (*Caligo*).

45.3 Population Size and Exponential Growth

LINK TO SECTION 18.8

Populations are dynamic units of nature. Depending on the species, they may add or lose individuals every minute of every day, season, or year. Sometimes they glut portions of their habitat with individuals. Other times, individuals are scarce. Populations even drive themselves or are driven to extinction.

GAINS AND LOSSES IN POPULATION SIZE

You can measure change in population size in terms of birth rates, death rates, and how many individuals are entering and leaving during a specified interval.

Population size increases as a result of births and **immigration**, the arrival of new residents from other populations of the same species. Its size decreases as a result of deaths and **emigration**, the departure of individuals that take up permanent residence in some other place. As one example, Arnold Schwarzenegger emigrated from Austria to the United States, where he became a celebrated immigrant. His permanent move decreased the Austrian population by 1 and increased the United States population by 1.

For many species, population size changes during seasonal or daily migrations. However, **migration** is a recurring round trip between two distinct regions, so we need not consider its transient effects in this initial look at the nature of increases in population size.

FROM ZERO TO EXPONENTIAL GROWTH

To keep things simple, assume that immigration and emigration balance each other over time so that you can ignore the effects of both on population size. By doing so, you can define **zero population growth** as an interval in which the number of births is balanced by the number of deaths. During such an interval, the population size remains stable, with no net increase or decrease in the number of individuals.

Births, deaths, and the other variables that might change population size can be measured in terms of **per capita** rates, or rates per individual. *Capita* means head, as in head counts.

Visualize 2,000 mice living in a cornfield. Twenty or so days after their eggs get fertilized, the females give birth to a litter, then they nurse the offspring for a while. Then they get pregnant again. Suppose 1,000 mice are born in one month. The birth rate is 0.5 per mouse per month (1,000 births/2,000 mice). If 200 of the 2,000 die during that interval, the death rate will be 200/2,000 = 0.1 per mouse per month.

Assume further that the birth rate and death rate remain constant. By doing so, you can combine both variables into a single variable—the **net reproduction per individual per unit time**, or ***r*** for short. For our mice, r is 0.5 – 0.1 = 0.4 per mouse per month.

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

a

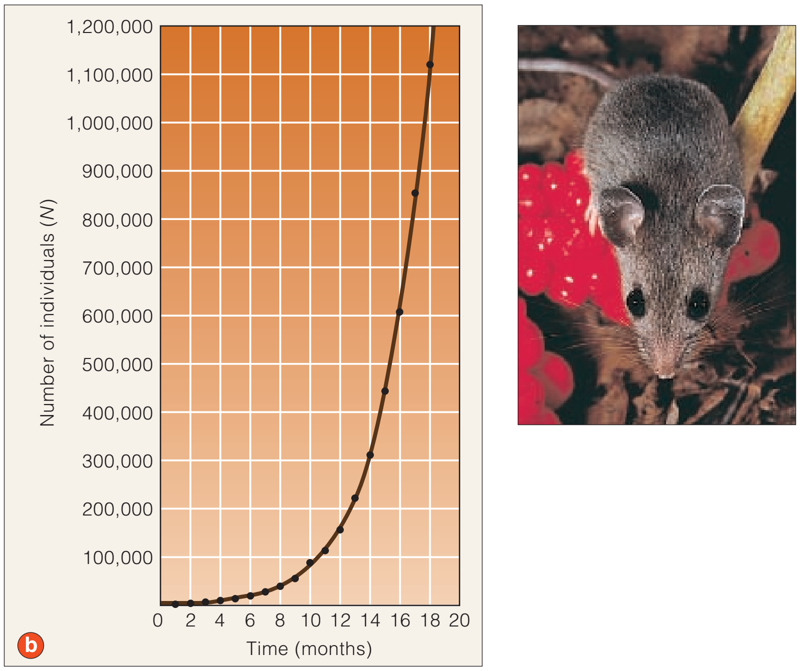


Figure 45.5 ***Animated!*** (**a**) Net monthly increases in a population of field mice living in a cornfield. Start to finish, the list shows a pattern typical of exponential growth. (**b**) Graph the numerical data and you end up with a J-shaped growth curve.

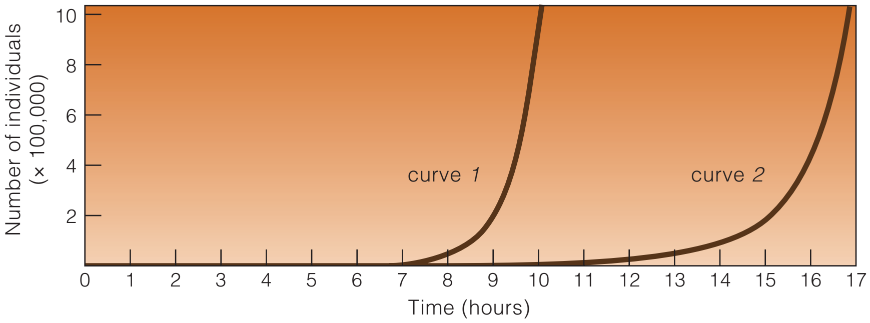


Figure 45.6 Effect of deaths on the rate of increase in two hypothetical populations of bacteria. Plot population growth for bacterial cells that reproduce every half hour and you get growth curve *1*. Plot the growth of a population of cells that divide every half hour, with 25 percent dying between divisions, and you get growth curve *2*. Deaths do slow the rate of increase, but as long as birth rate exceeds the death rate, exponential growth will continue.

Thus the hypothetical mice in a cornfield give us a simple way to represent population growth as:

$$\begin{array}{c}\text{population}\\\text{growth per}\\\text{unit time}\end{array} = \begin{array}{c}\text{net population}\\\text{growth rate}\\\text{per individual}\\\text{per unit time}\end{array} \times \begin{array}{c}\text{number of}\\\text{individuals}\end{array}$$

or, more simply, $G = rN$.

When the next month starts, 2,800 mice are living in the cornfield. The net increase of 800 fertile mice means the reproductive base has become larger. All of these mice reproduce, so the population size expands, for a net increase of 0.4 × 2,800 = 1,120. Population size is now 3,920. Suppose all mice in the population reproduce month after month. As Figure 45.5*a* shows, within two years, the number of mice in the cornfield will increase from 2,000 to more than 1 million!

Plot the monthly increases against time and you end up with a graph line in the shape of a "J," as in Figure 45.5*b*. When the growth of any population over time plots out as a J-shaped curve, you know that you are tracking exponential growth.

Exponential growth refers to any quantity that is growing at a rate proportional to its size. For instance, a population that is growing by a fixed percentage every day, month, or some other specified interval is growing exponentially. This does not necessarily mean eyepoppingly fast increases; a small population can grow exponentially, too, but at a slow rate. Even so, as long as *r* remains constant, the rate of growth will be proportional to the number of individuals that make up the reproductive base. A population that has 6,000 successfully reproducing individuals will grow three times faster in a given year than a population of 2,000. *The larger a population's reproductive base, the greater will be the rate of growth in a specified interval.*

Now look at other aspects of exponential growth. Start by supplying one bacterium in a culture flask with all the nutrients required for growth. After thirty minutes, the cell divides in two. Its two daughter cells divide, and so on every thirty minutes. Assume none of the cells dies between divisions. The population size doubles in each interval—from 1 to 2, then 4, 8, 16, 32, and so on. The time it takes for a population to double in size is its **doubling time**.

After 9–1/2 hours, or nineteen doublings, there are more than 500,000 cells. Ten hours (twenty doublings) later, there are more than a million. Curve *1* in Figure 45.6 is a plot of this outcome.

Will deaths put the brakes on exponential growth? Suppose that 25 percent of the descendant cells die every half hour. It now takes about seventeen hours, not ten, for the population to reach 1 million. *Deaths slowed the rate of increase but did not stop exponential growth* (curve *2* in Figure 45.6). As long as birth rates exceed death rates, exponential growth will continue.

WHAT IS THE BIOTIC POTENTIAL?

Now visualize a population in a habitat where living conditions are ideal. Every individual has sufficient shelter, food, and other vital resources. No predators, pathogens, or pollutants lurk anywhere in the habitat. The population may well display its **biotic potential**. This term refers to the maximum rate of increase per individual for any population that is growing under ideal conditions.

Each species has a characteristic maximum rate of increase. For many bacteria, it is 100 percent each half hour or so. For humans and other large mammals, the estimated biotic potential is 2 to 5 percent per year. The *actual* rate depends on how old individuals are at the onset of reproduction, how often they reproduce, and how many offspring they produce over a lifetime. The human population is not now displaying its full biotic potential, but it still is growing exponentially.

During a specified interval, population size is generally an outcome of births, deaths, immigration, and emigration.

A population that is growing at a rate proportional to the size of its reproductive base in a given interval is showing exponential growth.

As long as the per capita birth rate remains above the per capita death rate, a population will grow exponentially.

45.4 Limits on the Growth of Populations

LINKS TO
SECTIONS
17.3, 21.8

Many complex interactions take place within and between populations in nature, and it is not always easy to identify all the factors that can restrict population growth.

DENSITY-DEPENDENT LIMITING FACTORS

Most of the time, environmental circumstances keep a population from fulfilling its biotic potential. That is why sea stars—the females of which could produce 2,500,000 eggs each year—do not fill the oceans.

To get a sense of what some of the constraints may be, start again with a bacterial cell in a culture flask, where you can control the variables. First you enrich the culture medium with glucose and other nutrients necessary for bacterial growth. Then you sit back and let bacterial cells reproduce for many generations.

At first, growth may be exponential. Then it slows, and population size remains relatively stable. After a stable period, population size plummets until all of the bacterial cells are dead. *What happened?* The larger population required more nutrients. In time, nutrient levels declined, which acted as an environmental cue for cells to stop dividing. Even when growth stopped, the population continued to absorb nutrients until no nutrients were left, so the population died out.

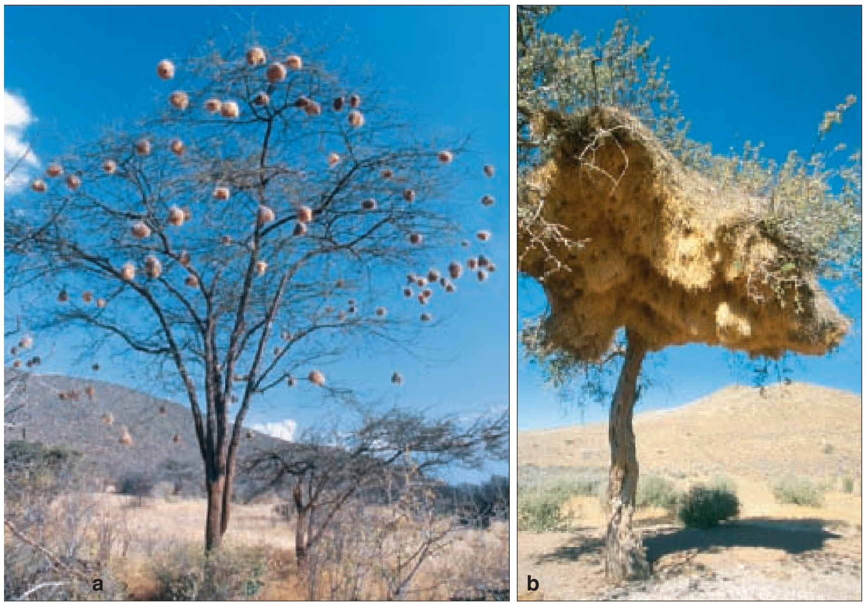


Figure 45.7 Response to a scarcity of nesting sites, a limiting factor for weaver bird populations in Africa.

(**a**) African weavers construct densely woven, cup-shaped nests that are only wide and deep enough for a hen and her nestlings. Many nests hang from the same spindly limbs. (**b**) This nest in Namibia is like an apartment house in a place where few trees are available. Between 100 and 300 pairs of sparrow weavers occupy their own flask-shaped nests, each with its own tubular entrance.

Any essential resource that is in short supply is a **limiting factor** on population growth. Food, mineral ions, refuge from predators, living space, and absence of pollutants are common examples (Figure 45.7). The number of limiting factors can be extensive, and their effects vary. Even so, one factor alone is often enough to put the brakes on population growth.

Suppose you kept freshening the nutrient supply. After growing exponentially, the population collapsed anyway. Like every other organism, bacteria generate metabolic wastes. The population produced so many wastes that it drastically altered the living conditions inside the culture flask. Collectively, the bacterial cells polluted the experimentally designed habitat and put a stop to further exponential growth.

CARRYING CAPACITY AND LOGISTIC GROWTH

Think of a small population of individuals dispersed through the habitat. As it increases in size, more and more individuals must compete for nutrients, living quarters, and other resources. The share available to each diminishes, fewer offspring are born, and more die from starvation or nutrient deficiencies. Now the population's growth rate declines until the births are balanced or outnumbered by deaths.

Ultimately, the *sustainable* supply of resources will determine population size. **Carrying capacity** is the maximum number of individuals of a population that a given environment can sustain indefinitely.

We can use the pattern of **logistic growth** to show how carrying capacity may affect population size. By this pattern, a small population starts growing slowly in size, then it grows rapidly, and finally its size levels off once the carrying capacity is reached. This pattern plots out as an S-shaped curve, as in Figure 45.8 (time A to C). We also may represent the pattern of logistic growth by the following equation:

$$\begin{array}{c}\text{population}\\\text{growth}\\\text{per unit}\\\text{time}\end{array} = \begin{array}{c}\text{maximum net}\\\text{population}\\\text{growth rate}\\\text{per individual}\\\text{per unit time}\end{array} \times \begin{array}{c}\text{number}\\\text{of}\\\text{individuals}\end{array} \times \begin{array}{c}\text{proportion}\\\text{of resources}\\\text{not yet}\\\text{used}\end{array}$$

The S-shaped curve is only an approximation of what goes on in nature. For instance, a population that grows too fast may drastically overshoot the carrying capacity. The death rate skyrockets and the birth rate plummets, which may well drive the population far below the carrying capacity. That is what happened to the St. Matthew reindeer (Figure 45.9).

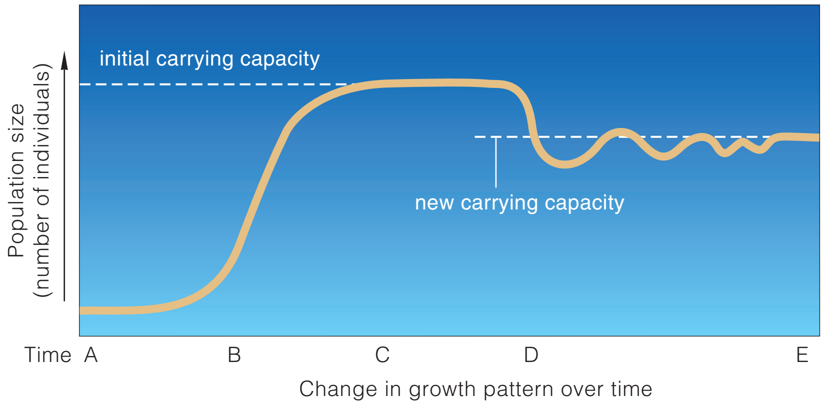


Figure 45.8 ***Animated!*** An idealized S-shaped curve, characteristic of logistic growth. Population growth slows after a phase of rapid increase (time A to C). The growth curve flattens as the carrying capacity is reached (time C to D). An S-shaped growth curve can show variations, as when changes in the environment lower the carrying capacity (time D to E).

Fluctuations in the pattern emerged after the bubonic plague swept through Europe's crowded cities in the fourteenth century. Remember the introduction to Chapter 18? One pandemic claimed 25 million lives.

Food and other essential resources are not the only factors that come into play when populations become too dense. When either exponential or logistic growth leads to overcrowding, many abiotic and biotic factors function as **density-dependent controls**, which means that they reduce the odds for individual survival.

For instance, interactions with predators or other species can drive the number of individuals below the maximum sustainable level. Predators, parasites, and pathogens have more intense effects in overcrowded populations of prey or host populations. In most cases, they thin out the population and thereby remove the very conditions that invited their controlling effect on population growth, as the next chapter explains.

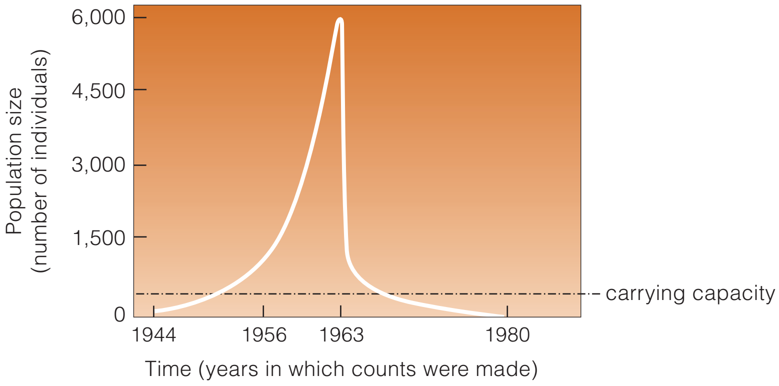


Figure 45.9 Growth curve for the reindeer herd barged over to St. Matthew Island in 1944, as described in the chapter introduction. This population did not recover after overshooting the carrying capacity.

DENSITY-INDEPENDENT LIMITING FACTORS

Density-independent factors can cause more deaths or fewer births regardless of population density. For instance, each year, millions of monarch butterflies fly from Canada to Mexico's forested mountains, where they spend the winter (Figure 45.10). Deforestation is going on in those mountains. In 2002 a sudden freeze —made worse by deforestation—killed off millions of them. That freeze would have killed them regardless of the density of the butterfly population.

Carrying capacity is the maximum number of individuals of a population that can be sustained indefinitely by the resources in a given environment.

With logistic growth, population growth is fast during times of low density, then it slows as the population approaches carrying capacity, where the numbers may level off.

Density-dependent factors, such the availability of a vital resource, exert control after populations become too dense as a result of exponential or logistic growth. Other factors exert control independently of population density.

Figure 45.10 Monarch butterflies at their wintering ground in Central Mexico. Each year these migratory insects travel hundreds of kilometers south to places that normally have been cool and humid in winter. If they were to stay in their northern breeding grounds, monarchs would risk being killed by more severe climatic conditions. Even so, deforestation and winter freezes in Mexico are now killing millions of them annually.

45.5 Life History Patterns

LINKS TO
SECTIONS 17.4,
25.11, 25.15

Researchers have identified age-specific adaptations that affect the survival, fertility, and reproduction of individuals for many kinds of species.

So far, we have looked at populations as if all of their members are identical in any given interval. For most species, however, different members are at different stages of development. Therefore, they are interacting in various ways with other organisms and with the environment. For instance, for part of their life cycle, they may be adapted to feed on a certain resource, as when larvae eat new leaves and butterflies sip nectar (Sections 25.11 and 25.15). They also may be more or less vulnerable to danger at that stage.

Table 45.1 Life Table for a Cohort of Annual Plants (*Phlox drummondii*)*

Age Interval (days)	Survivorship (number surviving at start of interval)	Number Dying During Interval	Death Rate (number dying/ number surviving)	"Birth" Rate during interval (number of seeds from each plant)
0–63	996	328	0.329	0
63–124	668	373	0.558	0
124–184	295	105	0.356	0
184–215	190	14	0.074	0
215–264	176	4	0.023	0
264–278	172	5	0.029	0
278–292	167	8	0.048	0
292–306	159	5	0.031	0.33
306–320	154	7	0.045	3.13
320–334	147	42	0.286	5.42
334–348	105	83	0.790	9.26
348–362	22	22	1.000	4.31
362–	0	0	0	0
		996		

* Data from W. J. Leverich and D. A. Levin, 1979.

Table 45.2 Life Table for the United States Human Population in 2001

Age Interval	Number at Start of Interval	Number Dying During Age Interval	Life Expectancy at Start of Interval	Reported Live Births
0–1	100,000	684	77.2	
1–5	99,316	132	76.7	
5–10	99,184	76	72.8	
10–15	99,108	96	67.9	7,315
15–20	99,012	330	62.9	525,493
20–25	98,682	468	58.1	1,022,106
25–30	98,214	471	53.4	1,060,391
30–35	97,743	554	48.6	951,219
35–40	97,189	801	43.9	453,927
40–45	96,388	1,154	39.2	95,788
45–50	95,234	1,682	34.7	5,244
50–55	93,552	2,373	30.3	263
55–60	91,179	3,474	26.0	
60–65	87,705	5,186	21.9	
65–70	82,519	7,397	18.1	
70–75	75,122	10,018	14.6	
75–80	65,104	13,284	11.5	
80–85	51,820	15,877	8.8	
85–90	35,943	16,147	6.5	
90–95	19,796	11,906	4.8	
95–100	7,890	5,845	3.6	
100+	2,045	2,045	2.7	

In short, each species has a **life history pattern**, or a set of adaptations that influence survival, fertility, and age at first reproduction. Each pattern reflects the individual's schedule of reproduction. In this section and the next, we consider a few of the environmental variables that underlie age-specific patterns.

LIFE TABLES

Each species has a characteristic life span, but few of its individuals survive to the maximum age possible. Death looms larger at particular ages. Individuals tend to reproduce during an expected age interval, and in some species they move out at an expected time.

Age-specific patterns in populations intrigue life insurance and health insurance companies as well as ecologists. Such investigators typically track a **cohort**, or a group of individuals recorded from the time of birth until the last one dies (Table 45.1). They also record the number of offspring born to individuals in each age interval. Life tables list the data for an age-specific death schedule, which are typically converted to much cheerier "survivorship" schedules that show the number of individuals actually reaching specified ages. Table 45.2 is a typical example. It lists data for the 2001 human population of the United States.

Dividing a population into age classes and noting the age-specific birth rates and mortality risks often yields useful information. Unlike a crude head count, for instance, the data can help people make decisions about pest management, endangered species habitats, or social planning for human populations. Birth and death schedules for the northern spotted owl are one case in point. They were cited in federal court rulings that halted mechanized logging in the owl's habitat—old-growth forests of the Pacific Northwest.

PATTERNS OF SURVIVAL AND REPRODUCTION

Evolution can occur by way of differences in survival and reproductive success. We measure reproductive success of individuals in terms of the number of their surviving offspring (Section 17.4). That number varies among species, which differ in how much energy and time are allocated to making gametes, securing mates, and providing parental care to offspring of one size or

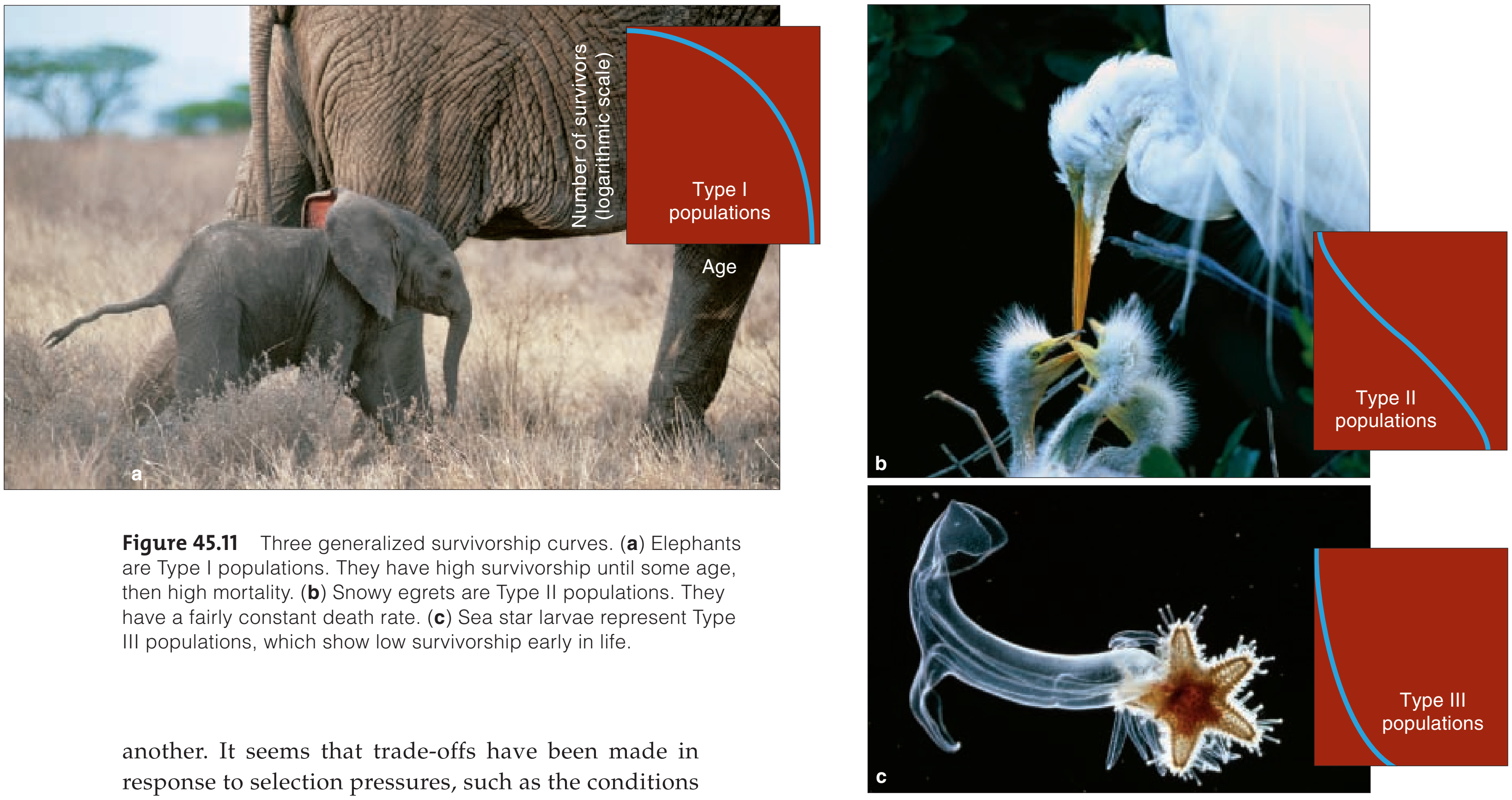


Figure 45.11 Three generalized survivorship curves. (**a**) Elephants are Type I populations. They have high survivorship until some age, then high mortality. (**b**) Snowy egrets are Type II populations. They have a fairly constant death rate. (**c**) Sea star larvae represent Type III populations, which show low survivorship early in life.

another. It seems that trade-offs have been made in response to selection pressures, such as the conditions prevailing in the habitat and species interactions.

A **survivorship curve** is a graph line that emerges when ecologists plot a cohort's age-specific survival in the habitat. Each species has a characteristic curve, and three types of curves are common in nature.

Type I curves reflect high survivorship until fairly late in life, then a large increase in deaths. Like many annual plants, the phlox species tracked in Table 45.1 show this type of pattern. So do large mammals that bear one or at most a few large-bodied offspring at a time, then engage in extended parental care (Figure 45.11*a*). For example, a female elephant gives birth to four or five calves in her lifetime and devotes several years to parenting each one.

Type I curves are typical of human populations in which the individuals have access to good health care services. However, in parts of the world where health care is poor, a sharp drop at the start of a survivorship curve reflects many infant deaths. After this, the curve levels off from childhood to early adulthood.

Type II curves reflect a fairly constant death rate at all ages. They are typical of organisms just as likely to be killed or die of disease at any age, such as lizards, small mammals, and large birds (Figure 45.11*b*).

Type III curves signify a death rate that is highest early in life. They characterize species that produce many small offspring and do little, if any, parenting.

Figure 45.11*c* shows how the curve plummets for sea stars. Sea stars release mind-boggling numbers of eggs. The tiny larvae must eat fast, grow, and finish developing on their own without support, protection, or guidance from parents. Corals and other animals quickly eat most of them, so their survivorship curve plummets. Such a curve is common for many marine invertebrates, insects, fishes, plants, and fungi.

At one time, ecologists thought selection processes favored *either* early, rapid production of many small offspring *or* late production of a few large offspring. They now see that the two patterns are only extremes at opposite ends of a range of possible life histories. Also, both patterns—as well as intermediate ones—sometimes unfold among different populations and at different times in the life cycle.

Tracking a cohort (a group of individuals) from birth until the last one dies reveals patterns of reproduction, death, and migration that typify the populations of a species.

Survivorship curves can reveal differences in age-specific survival among species. In some cases, such differences exist even between populations of the same species.

45.6 Natural Selection and Life Histories

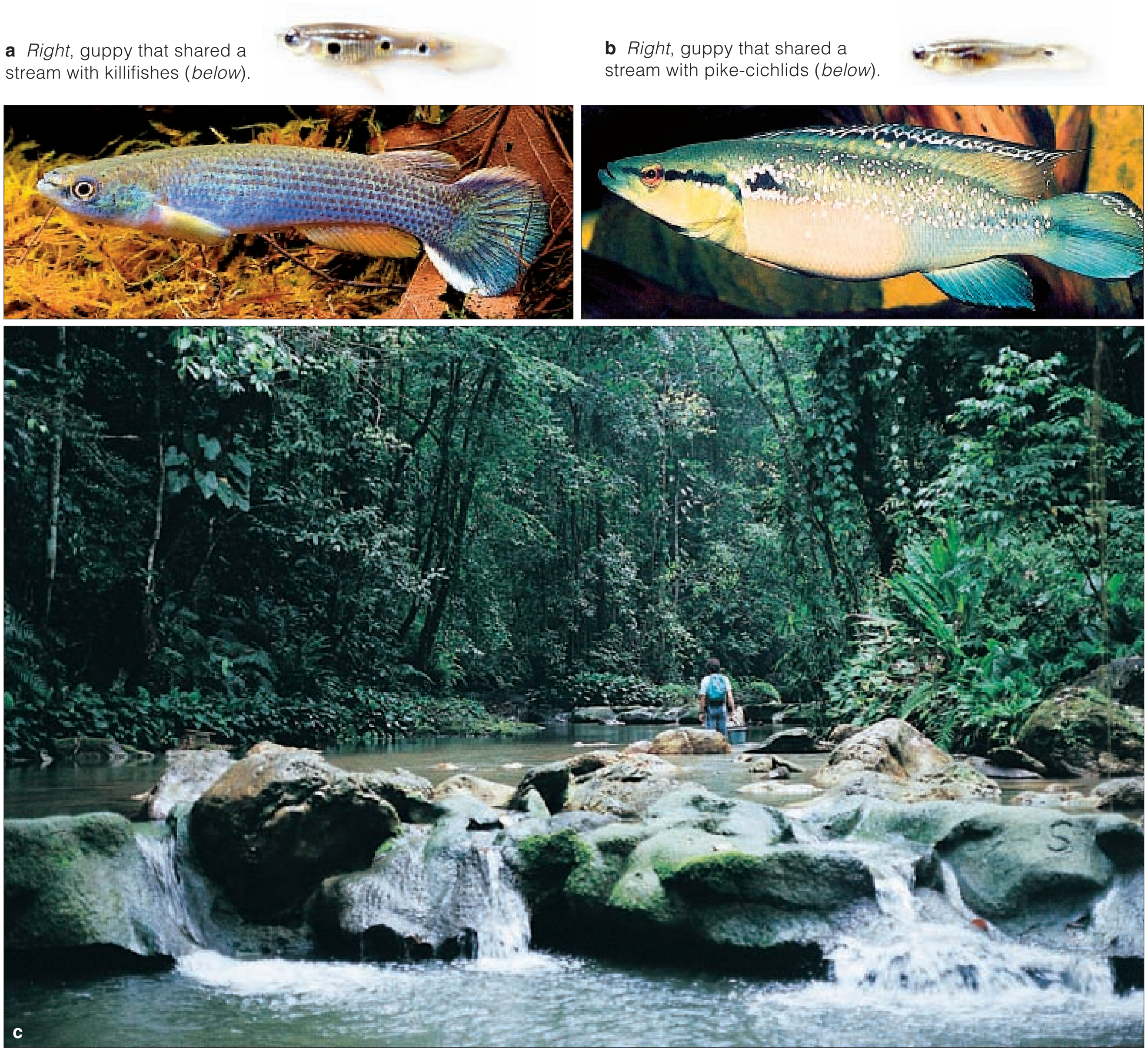
LINKS TO SECTIONS 1.4, 18.3, 26.2

Earlier you read that jaws evolved among certain fishes during the Cambrian. This key innovation led to adaptive radiations among predators and diverse defenses among prey. No one witnessed that coevolutionary arms race. However, experimental studies show that predators are still acting as selective agents, and prey are still evolving.

Several years ago, with fishnets in hand and drenched in sweat, two evolutionary biologists conducted fieldwork in the mountains of Trinidad, an island in the southern Caribbean Sea. They wanted to capture small fishes that live in the shallow freshwater streams (Figure 45.12). The fish were guppies (*Poecilia reticulata*). David Reznick and John Endler were starting an eleven-year study of the variables that help shape guppy life history patterns.

Male guppies are generally smaller and have brighter fish scales than females of the same age. The colors serve as visual signals for mating during the guppy's complex courtship rituals. Females are drab colored. Unlike males, they continue to grow after they reach sexual maturity.

Reznick and Endler were interested in the effects of predation on guppy evolution. They chose their study site because different predators act on different populations of guppies in the mountain streams of Trinidad. Different predators are present even along the length of the same



a *Right*, guppy that shared a stream with killifishes (*below*).

b *Right*, guppy that shared a stream with pike-cichlids (*below*).

Figure 45.12 (**a**,**b**) Two guppies (*Poecilia reticulata*) and two guppy eaters. (**c**) Biologist David Reznick contemplating interactions among guppies and their predators in a freshwater stream in Trinidad.

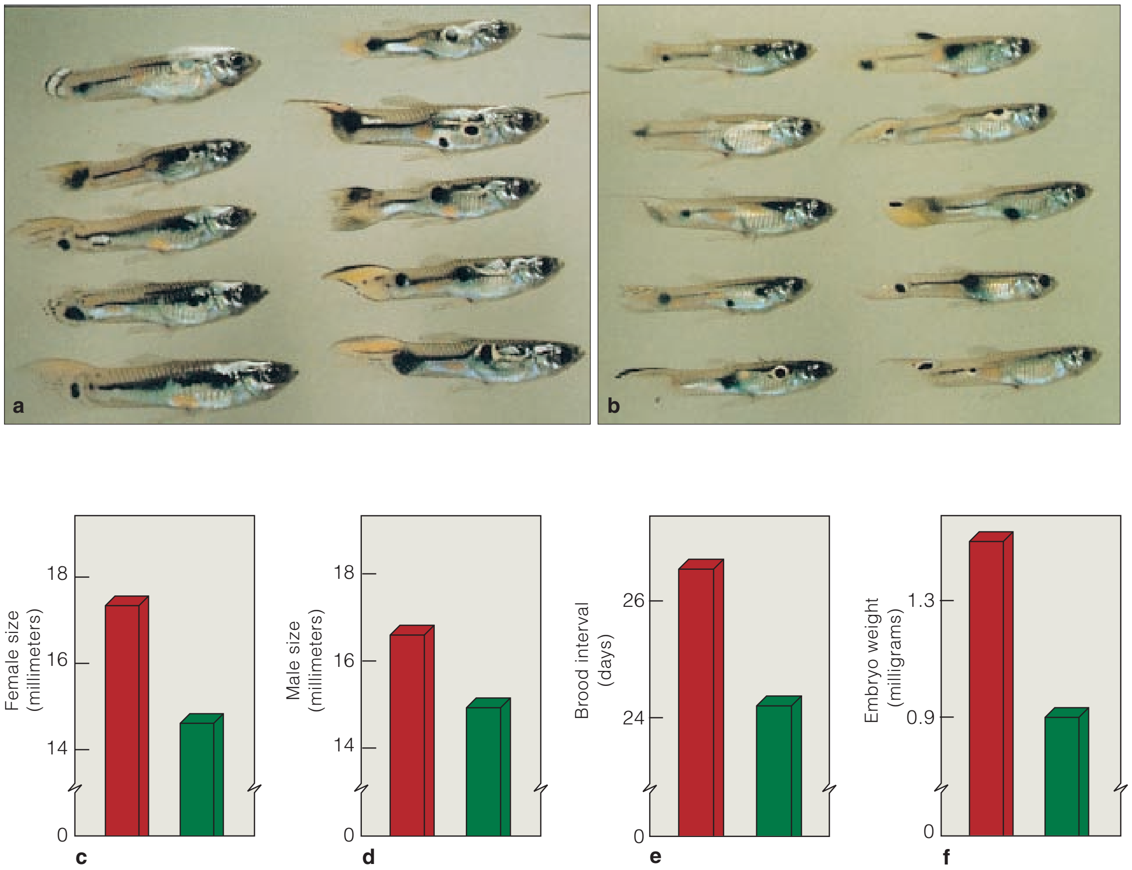


Figure 45.13 Typical size differences between (**a**) guppies that were preyed upon by killifishes and (**b**) guppies that were preyed upon by pike-cichlids.

(**c**–**f**) Graphs of some of the experimental evidence of natural selection among guppy populations that experimenters subjected to different predation pressures.

Compared to the guppies raised with killifish (*red* bars), guppies raised with pike-cichlids (*green* bars) differed in body size and length of time between broods. Killifish are small and prey on smaller guppies. Pike-cichlids are large fish and prey on larger guppies. The two predators select for differences in guppy life histories.

stream, because waterfalls prevent them from moving upstream or downstream from their habitat (Figure 45.12*c*).

Two major predators of guppies are killifishes (*Rivulus hartii*) and pike-cichlids (*Crenicichla*), as shown in Figure 45.12*a*,*b*. A killifish is not a very big fish. It preys efficiently on small, immature guppies but not on the larger adults. Pike-cichlids live in other streams. They prey on larger and sexually mature guppies and tend to ignore small ones.

Reznick and Endler hypothesized that predation is a selective agent that has shaped guppy life history patterns. As they knew, guppies in pike-cichlid streams grow faster and are smaller at maturity, compared with the guppies in killifish streams (Figure 45.13*a*,*b*). Also, guppies hunted by pike-cichlids reproduce earlier and more often, and they have more offspring per brood (Figure 45.13*c*–*f*).

Were these differences genetic, or did other variables influence life history patterns in killifish and pike-cichlid streams? To find out, the researchers shipped live guppies from each stream back to their laboratory in the United States. They allowed the guppies to reproduce in separate, predator-free aquariums for two generations. All other physical and chemical conditions in the artificial habitats were identical for the different experimental groups.

As it turned out, the experimental guppy populations displayed the same differences that the researchers saw in natural populations. The conclusion? *Differences between guppies preyed upon by different predators have a genetic foundation and therefore are subject to natural selection.*

What would happen if the selective pressure on a guppy population were to change? Reznick and Endler answered the question with sets of field experiments. For one set, they introduced guppies upstream from a small waterfall. Before the experiment, the waterfall had barred guppies and large pike-cichlids from emigrating upstream, where killifish were in the stream. Guppies introduced to the upstream experimental site were taken from a population that had evolved with pike-cichlids downstream from the waterfall.

Eleven years later, after thirty to sixty generations of guppies had been born, researchers revisited the stream. The experimental population had evolved. Guppies now had traits like those of guppies that had been living with killifishes for a longer time. The difference in the type of predator had influenced guppy body size, the frequency of reproduction, and other aspects of the life history patterns. Laboratory experiments with two generations of guppies confirmed that the differences have a genetic basis.

Reznick and Endler showed that life history traits, like other characteristics, can be inherited. They demonstrated that these traits can evolve. Traits that affect life history can be altered in a surprisingly short time in response to particular selection pressures.

45.7 Human Population Growth

LINKS TO
SECTIONS
21.8, 26.15

Human population size surpassed 6.4 billion in 2005. Take a look now at what the number means.

THE HUMAN POPULATION TODAY

Worldwide, the average rate of increase for the human population in 2004 was 1.3 percent. As long as birth rates continue to exceed death rates, annual additions to the population will drive a *larger* absolute increase each year into the foreseeable future.

Human population size is expanding even though more than 1 billion people are already confronted by limits to growth. They are malnourished or starving (Figure 45.14). They do not have clean drinking water, adequate shelter, access to health care systems, and sewage treatment facilities. Most of the population is expanding in already overcrowded parts of the world. Figure 45.15 is a graphic clue to what the expansion means with respect to the carrying capacity.

Even if it were possible to double food supplies to keep pace with growth, living conditions would still be marginal for most people. At least 10 million would continue to die each year from starvation.

For a time, it will be like the Red Queen's garden in Lewis Carroll's *Through the Looking Glass*, where one is forced to run as fast as one can to stay in the same place. What happens when our population doubles again? Can you brush the doubling aside as being too far in the future? *It is no farther removed from you than the sons and daughters of the next generation.*

Figure 45.14 Far from well-fed humans who live in the highly developed countries, an Ethiopian showing some morphological outcomes of starvation. Ethiopia is one of the poorest developing countries, with an annual per capita income of 120 dollars. Average caloric intake is more than 25 percent below the minimum required to maintain good health. The population has one of the highest annual rates of increase—about 2.7 percent in 2003. In that year Ethiopia's total fertility rate was 5.9 children per woman. In addition, Ethiopia is being torn apart by prolonged civil war. Even so, in 2003, its population of 74 million was expected to double in less than twenty-five years.

EXTRAORDINARY FOUNDATIONS FOR GROWTH

How did we get into this predicament? For most of its history, the human population grew slowly. Things started to pick up about 10,000 years ago, and in the past two centuries, growth rates skyrocketed. Three trends promoted the rates of increase. First, humans gradually developed the capacity to expand into new habitats and climate zones. Second, humans increased the carrying capacity of their existing habitats. Third, human populations sidestepped limiting factors that tend to restrain the growth of other species.

Reflect on the first point. Early humans evolved in woodlands, then in savannas. They were vegetarians, mostly, but they also scavenged bits of meat. Bands of hunter–gatherers moved out of Africa about 2 million years ago. By 40,000 years ago, their descendants were established in much of the world (Section 26.15).

Few species can expand into such a broad range of habitats. Having a truly complex brain, early humans drew on learning and memory to figure out how to build fires, make shelters, make clothing, make tools, and cooperate in hunts. With the advent of language, knowledge did not die with the individual. It spread quickly among groups. *The human population expanded into diverse environments far more rapidly compared to the long-term geographic dispersals of other species.*

Reflect on the second point. Starting about 11,000 years ago, many bands of hunter–gatherers shifted to agriculture. Instead of simply following the migratory game herds, they settled in fertile valleys and other regions that favored seasonal harvesting of fruits and grains. In this way, they developed a more dependable basis for life. A pivotal factor was the domestication of wild grasses, including species ancestral to modern wheat and rice. People harvested, stored, and planted seeds all in one place. They domesticated animals for food and pulling plows. They dug irrigation ditches and diverted water to croplands.

Agricultural productivity was a basis for increases in population growth rates. Towns and cities formed. Later in time, food supplies increased again, and yet again, by the use of chemical fertilizers, herbicides, and pesticides. Transportation improved, as did food distribution. *Thus, even at its simplest, management of food supplies through agriculture increased the carrying capacity for the human population.*

What about sidestepping of limiting factors? Until about 300 years ago, poor hygiene, malnutrition, and

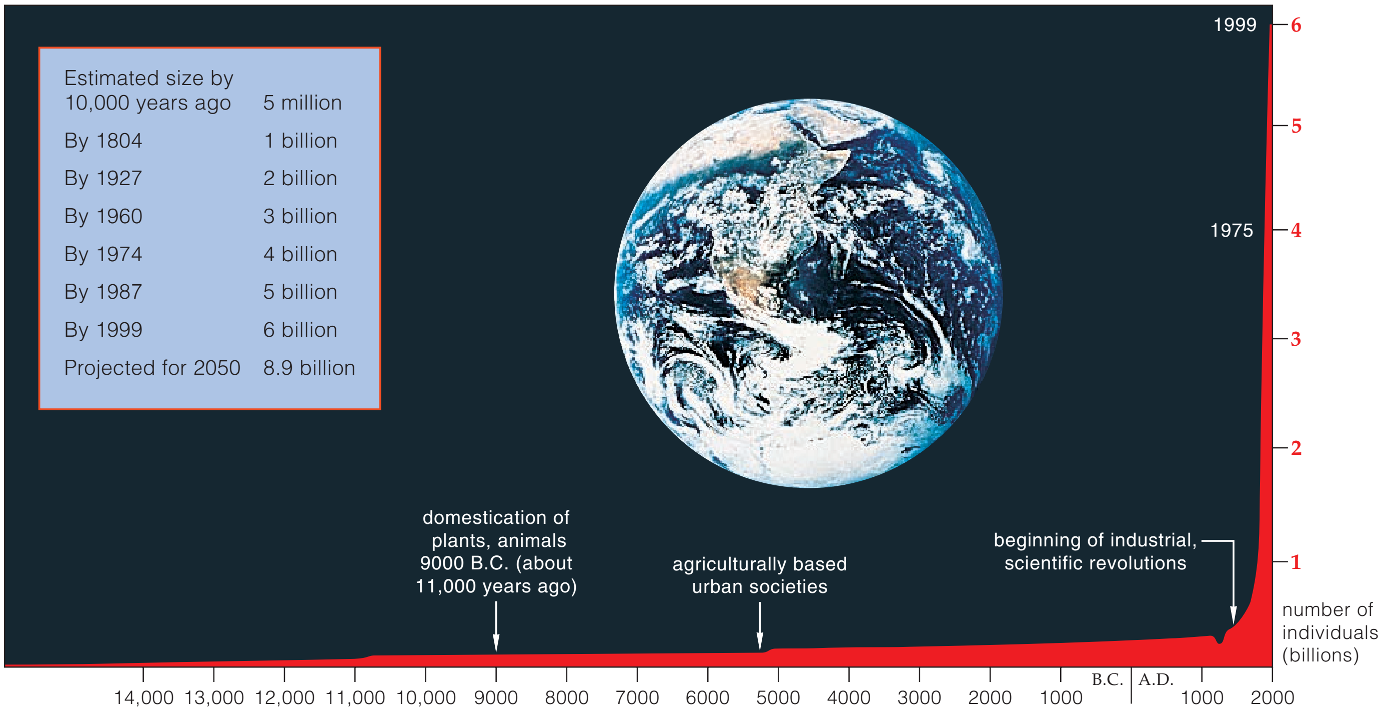


Figure 45.15 Growth curve (*red*) for the world human population. The *blue* box indicates how long it took for the human population to increase from 5 million to 6 billion. The dip between years 1347 and 1351 marks the time when 60 million people died during a bubonic plague, as explained in the Chapter 18 introduction.

infectious diseases kept death rates high enough to more or less balance birth rates. Infectious diseases became density-dependent controls. Epidemics swept through overcrowded settlements and cities that were infested with fleas and rodents. Then came plumbing and new methods of sewage treatment. Over time, vaccines, antibiotics, and other drugs were developed as weapons against many pathogens. The death rates dropped sharply. Births began to exceed deaths—and rapid population growth was under way.

In the industrial revolution of the mid-eighteenth century, people discovered how to harness the energy stored in fossil fuels, starting with coal. Within a few decades, large industrialized societies began to form in western Europe and North America. The urgency of World War I sparked the development of even more technologies. After the war, factories mass-produced cars, tractors, and other affordable goods. Advances in agriculture meant that fewer farmers were required to support a larger population.

In sum, by controlling disease agents and tapping into fossil fuels—forms of energy already concentrated for the taking—the human population has managed to sidestep big factors that had previously limited its rate of increase.

Where have the far-flung dispersals and stunning advances in agriculture, industrialization, and health care taken us? Starting with *Homo habilis*, it took about 2.5 million years for human population size to reach 1 billion. As Figure 45.15 shows, it took just 123 years to reach 2 billion, 33 more to reach 3 billion, 14 more to reach 4 billion, and then 13 more to get to 5 billion. It took only 12 more years to arrive at 6 billion! Given the principles governing population growth, we may expect the rate of increase to decline as birth rates fall or death rates rise. Alternatively, the rates of increase may continue to rise if breakthroughs in technology expand the carrying capacity. *Even so, continued growth cannot be sustained indefinitely*.

Why? Continuing increases in population size are invitations to certain density-dependent controls. For instance, globe-hopping travelers introduce pathogens to dense urban areas all around the world in a matter of weeks (Section 21.8). Also, emigration away from economic hardship and civil strife have put 50 million individuals on the move within and between nations. Will relocations of so many individuals be peaceable? How much food, clean water, and other resources will become available to them, wherever they end up?

Through expansion into new habitats, cultural interventions, and technological innovations, the human population has temporarily skirted environmental resistance to growth.

As population increases, density-dependent controls, such as disease and competition for resources, may slow growth.

45.8 Fertility Rates and Age Structure

LINK TO
SECTION
39.10

Acknowledgment of the risks posed by rising populations has resulted in increased family planning in almost every region. Putting the brakes on population growth is not easy, and numbers are expected to continue increasing.

Most governments recognize that population growth, resource depletion, pollution, and the quality of life are interconnected. Most are working to lower long-term birth rates, as with family planning programs. Details vary among countries, but most are offering information on available methods of fertility control.

The attempts are having impact. Birth rates are now slowing worldwide. Death rates are declining, mainly because improved diets and health care are lowering infant mortality rates: the number of infants per 1,000 who die in their first year. However, AIDS sent death rates soaring in some African countries (Section 39.10).

We still expect the world population to peak at 8.9 billion by 2050 and possibly to decline near the end of the century. Think about all the resources that will be required. We will have to boost food production and find more sources of energy and fresh water to meet even basic needs, something that still eludes close to half of the population. The large-scale manipulations of resources will intensify pollution.

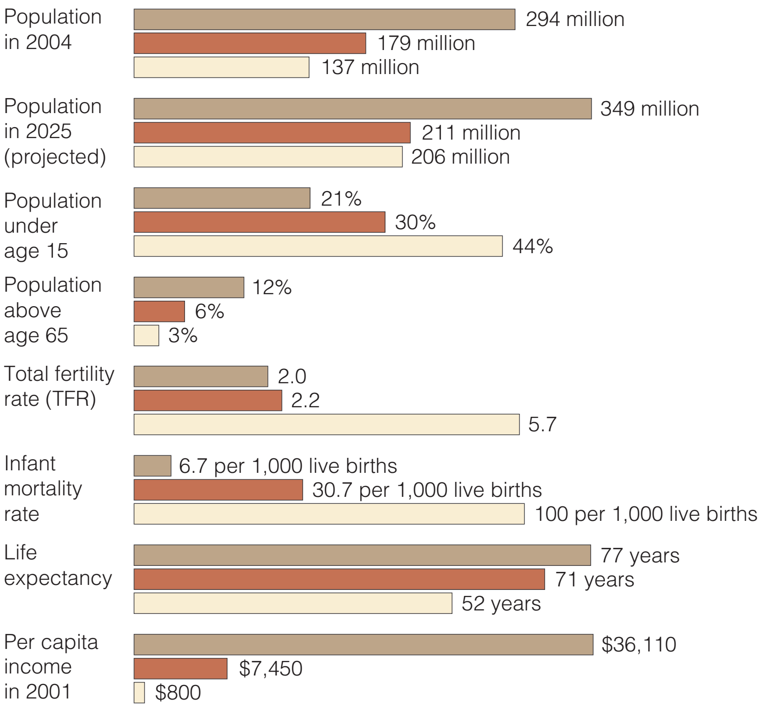


Figure 45.16 Key demographic indicators for three countries, mainly in 2004. The United States (*brown* bar) is highly developed, Brazil (*red* bar) is moderately developed, and Nigeria (*gold* bar) is less developed.

We expect to see the most growth in India, China, Pakistan, Nigeria, Bangladesh, and Indonesia, in that order. China (with 1.3 billion people) and India (with 1.09 billion) dwarf other countries; together, they make up 38 percent of the world population. Next in line is the United States, with 294 million.

The **total fertility rate** (TFR) is the average number of children born to the women of a population during their reproductive years. TFR estimates are based on current age-specific rates. In 1950, the worldwide TFR averaged 6.5. Currently it is 2.8, which is still far above the replacement level of 2.1—or the average number of children a couple must bear to replace themselves.

These numbers are averages. TFRs are at or below replacement levels in many developed countries; the developing countries in western Asia and Africa have the highest. Figure 45.16 has some examples of the disparities in demographic indicators.

Comparing the age structure diagrams for different populations is revealing. In Figure 45.17, focus on the reproductive age category for the next fifteen years. The average range for childbearing years is 15–49. We can expect populations with a broad base to increase in size at a faster rate. The United States population has a relatively narrow base and is undergoing slow growth, which has implications for 78 million *baby-boomers* (Figure 45.18). This cohort started forming in 1946 when American soldiers came home after World War II and began to raise families. The cohort is big, and the workforce must sustain their retirement.

Even if every couple decides to bear no more than two children, world population growth will not slow for sixty years, because 1.9 billion are about to enter the reproductive age bracket. *More than one-third of the world population is in the broad pre-reproductive base.*

China has the most wide-reaching family planning program. Its government discourages premarital sex; it urges people to delay marriage and limit families to one or two children. It offers abortions, contraceptives, and sterilization at no cost to married couples. Even in remote rural areas, paramedics and mobile units offer access to these measures. Couples who follow these guidelines receive more food, free medical care, better housing, and salary bonuses. Their offspring receive free tuition and preferential treatment when they are old enough to enter the job market. Parents who have more than two children lose government benefits and pay more taxes.

Although the policy might sound harsh, it works. Since 1972, China's TFR has fallen sharply, from 5.7 to 1.8. An unintended consequence has been a shift in the country's sex ratio. Traditional cultural preference

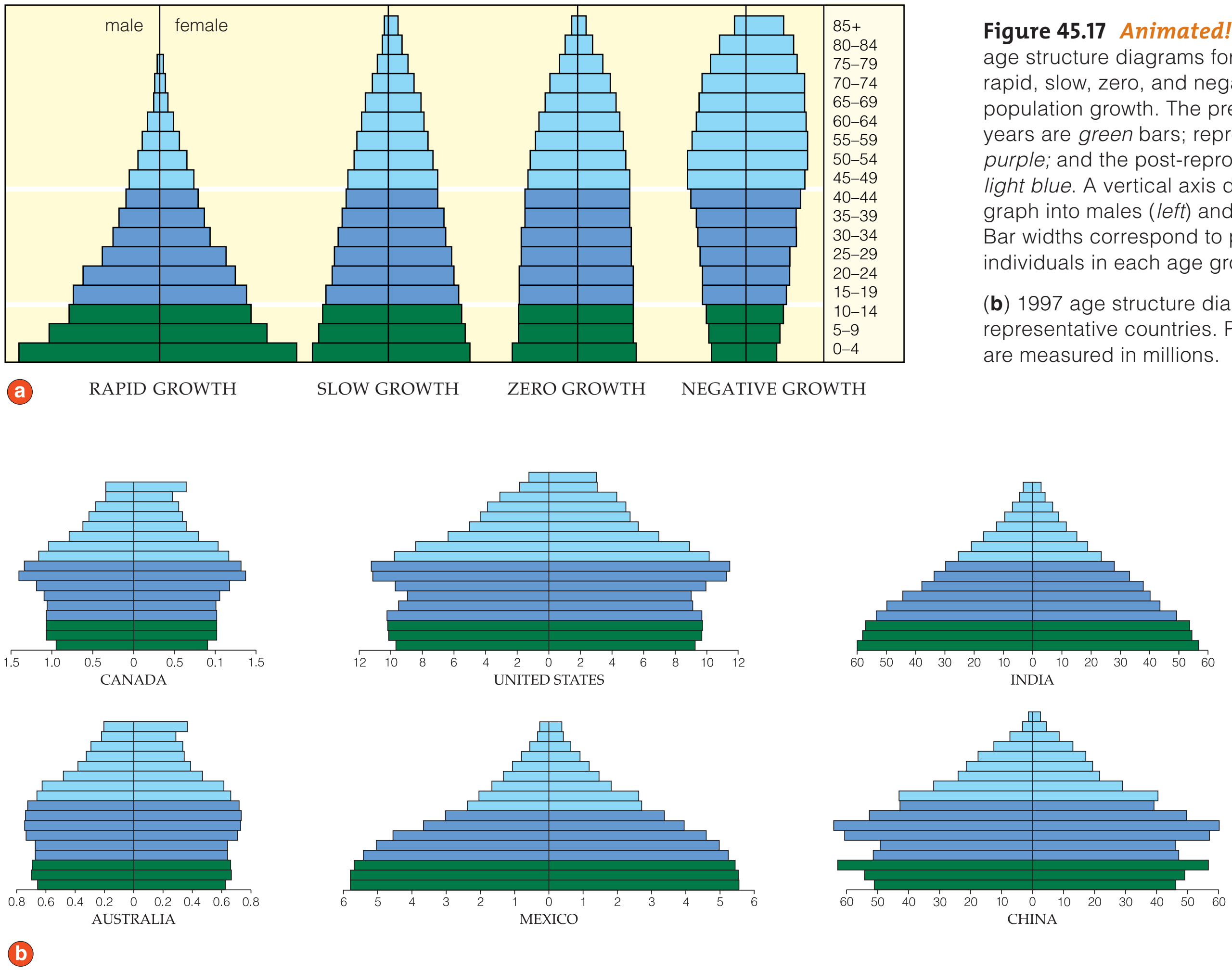


Figure 45.17 ***Animated!*** (**a**) General age structure diagrams for countries with rapid, slow, zero, and negative rates of population growth. The pre-reproductive years are *green* bars; reproductive years, *purple;* and the post-reproductive years, *light blue.* A vertical axis divides each graph into males (*left*) and females (*right*). Bar widths correspond to proportions of individuals in each age group.

(**b**) 1997 age structure diagrams for a few representative countries. Population sizes are measured in millions.

for sons, especially in the rural areas, has led some parents to abort developing females or even commit infanticide. Worldwide, 1.06 boys are born for every girl, but in China the latest census reports 1.19 boys per girl. Also, more than 100,000 girls are abandoned each year. The government now is offering additional cash and tax incentives to the parents of girls. In the meantime, China's population time bomb continues to tick. About 150 million Chinese girls are now in the pre-reproductive age category.

The worldwide total fertility rate has been dropping, but it is still above the replacement level that would move the population growth rate close to zero.

Most countries support family planning programs of some sort. Even with the slowdowns, the human population will continue to increase; its pre-reproductive base is immense.

At present, more than one-third of the human population is in a very broad pre-reproductive base.

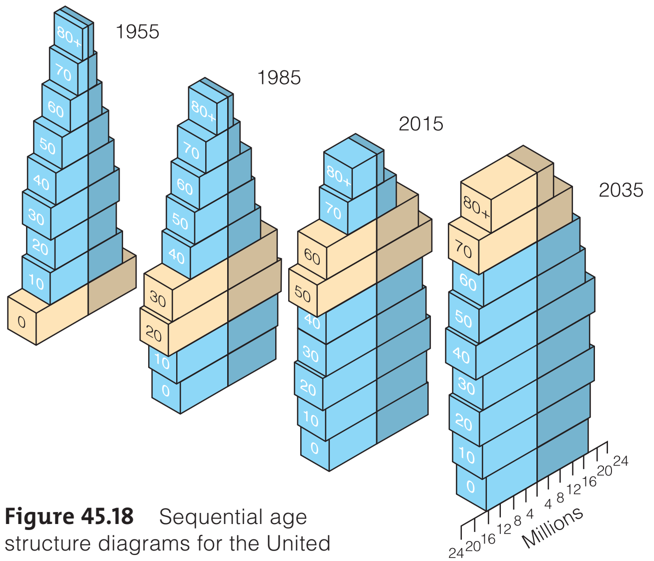


Figure 45.18 Sequential age structure diagrams for the United States population. *Gold* bars track the baby-boomer generation.

45.9 Population Growth and Economic Effects

LINK TO SECTION 39.10

The most highly developed countries have the slowest growth rates and use the most resources.

DEMOGRAPHIC TRANSITIONS

Changes in population growth rates often correlate with four stages of economic development, the heart of the **demographic transition model**. By this model, living conditions are harshest in a *preindustrial* stage, before technology and medical advances spread. Birth and death rates are high, so the rate of growth is low. In the *transitional* stage, industrialization begins. Food production and health care improve and death rates slow. Birth rates stay high in the agricultural societies, where big families provide help in the fields. Annual growth rates are between 2.5 and 3 percent. As living conditions improve and birth rates begin to decline, growth generally starts to level off (Figure 45.19).

In the *industrial* stage, industrialization is in full swing and growth slows. People move to cities, and couples often want small families. As they accumulate goods, many decide the time and cost of raising more than a few children conflict with their goals.

In the *postindustrial* stage, population growth rates become negative. The birth rate falls below the death rate, and population size slowly decreases.

The United States, Canada, Australia, and most of western Europe, Japan, and much of the former Soviet Union are in the industrial stage. Most developing countries, such as Mexico, are now in the transitional stage, without enough skilled workers to complete the transition to a fully industrial economy.

By some projections, many developing countries will make the demographic transition to an industrial stage in the next few decades. However, there also are signs that the still-rapid population growth in many of those countries will overwhelm economic growth, food production, and health care systems. If that were to happen, they would be trapped demographically, unable to pass through the transition stage.

Africa and some other developing countries already are caught in the demographic trap. Here you might wish to reflect again on the magnitude of the AIDS pandemic that is wreaking havoc on populations, as in sub-Saharan Africa (Section 39.10). One outcome is that many African populations are being driven back to the lowest stage of economic development.

The demographic transition model might not apply to many developing countries, because the conditions on which it is based no longer prevail in some places. For instance, how many can compete in a new global economy without a base of high-tech workers? How many have funds for fast economic growth? How much of what they do have is used to pay interest on debts already owed? Recognizing the problem, in 2004, the world's richest nations agreed to write off 40 billion dollars owed to them by the poorest nations.

A QUESTION OF RESOURCE CONSUMPTION

The industrialized nations use the most resources. For example, the United States has about 4.6 percent of the world's population and produces about 21 percent of all goods and services. Yet it requires thirty-five times

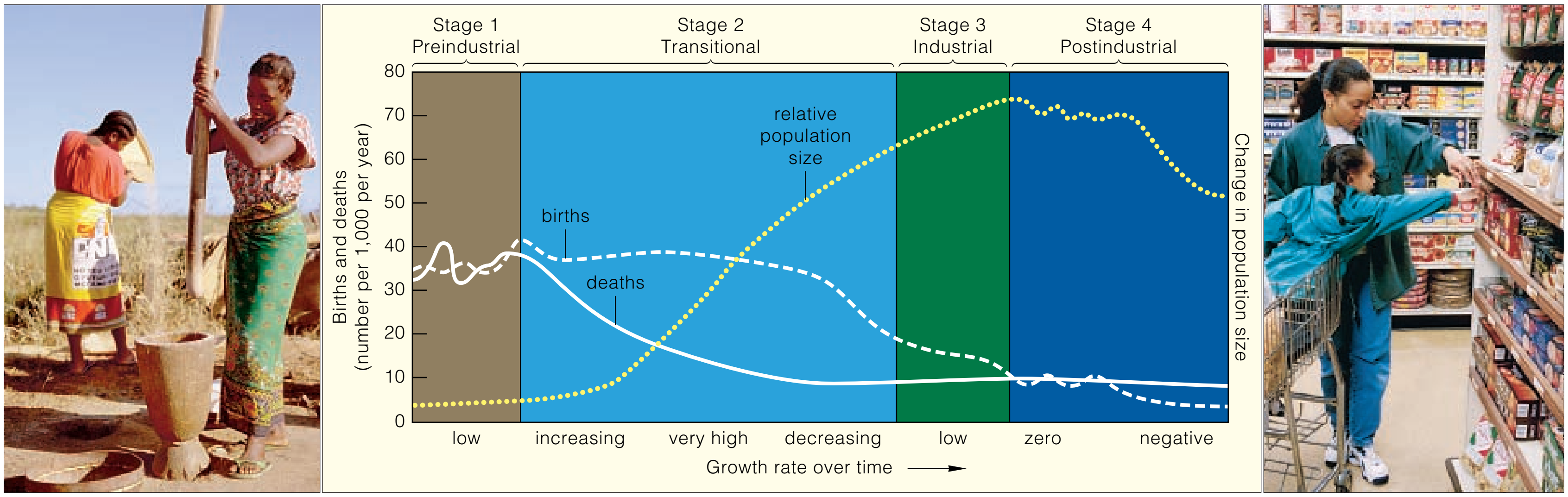


Figure 45.19 ***Animated!*** Demographic transition model for changes in population growth rates and sizes, correlated with long-term changes in the economy.

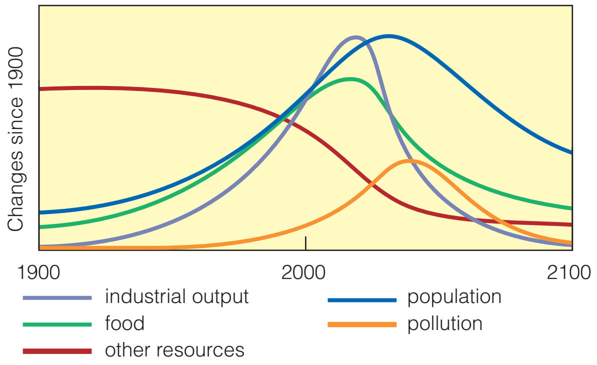


Figure 45.20 Computer-based projection of what might happen if human population size continues to skyrocket without dramatic policy changes and technological innovation. The assumptions were that the population has already overshot the carrying capacity and current trends will continue unchanged.

more goods and services than India. It uses 25 percent or so of the world's processed minerals and much of the available energy supplies. The United States is not alone in this. China and India are now demanding an ever increasing share of the economic pie.

G. Tyler Miller once estimated that it would take 12.9 billion impoverished individuals living in India to have as much impact on the environment as 284 million people living at the time in the United States. He pointed out that the projected increase in human population growth rates raises serious questions. Will there be enough food, energy, water, and other basic resources to sustain so many people? Will regional governments be able to provide adequate education, housing, medical care, and other social services for them? Computer models suggest not (Figure 45.20). Even so, some analysts claim we can adapt politically and socially to a more crowded world if innovative technologies improve harvests, if food resources are distributed more equitably, and if dietary preferences are shifted away from animal products.

There are no easy answers. If you have not been doing so, start following the arguments in the media. It is a good idea to become an informed participant in a debate that will have impact on your future.

Differences in population growth and resource consumption among countries can be correlated with levels of economic development. Growth rates are typically greatest during the transition to industrialization.

Global conditions have so changed that the demographic transition model may no longer apply to many nations.

45.10 Social Impact of No Growth

For humans, as for all species, the biological implications of exponential population growth are sobering. However, so are the social implications of what would happen if human population growth were to approach zero.

In a growing population, most of the individuals are in lower age brackets. When living conditions favor moderate growth, then the age distribution should guarantee a future workforce. But the distribution has social implications. Why? It takes a large workforce to support individuals in the higher age brackets.

In the United States, most seniors who have retired expect the government to subsidize their medical care and provide low-cost housing as well as many other social programs. Remember the baby-boomers?

However, as one outcome of better medicine and hygiene, people in these brackets are living far longer than seniors did when the nationwide social security program was established. Cash benefits now exceed contributions that individuals made to the program when *they* were younger.

If the human population does reach and maintain zero growth, a larger proportion of individuals will end up in higher age brackets. Even slower growth poses problems. Will these people continue to receive goods and services as the workforce carries more and more of the economic burden? Put it to yourself. How much economic hardship are you willing to bear for the sake of your parents? Your grandparents? How much will your children bear for you?

We have arrived at a turning point, not only in our biological evolution but in our cultural evolution as well. The decisions awaiting us are among the most pressing and difficult we will ever have to make.

All species face limits to growth. We might think we are different from the rest, and in some respects we are. The uniquely human capacity to undergo rapid cultural evolution has helped us postpone the action of most factors that limit growth. However, the crucial word is *postpone*. On the basis of all the models that are available to us, we can be fairly sure of this: Much of the human population will not escape the impact of limiting factors in the environment.

The human population has sidestepped a number of the constraints that typically restrict the population growth of other species.

By doing so, staggering numbers of individuals have now become more vulnerable to the laws of nature that cannot be repealed.

Summary

Sections 45.1, 45.2 A population is a group of individuals of the same species in a specified area. It is characterized in part by size, density, distribution, and age structure, which are measurable. Most populations in nature have a clumped distribution pattern.

Counting the number of individuals in quadrats is one way to estimate the density of a population in a specified area. Using capture–mark–recapture methods is a way to estimate the density for mobile animals.

BiologyNow
Learn how to estimate population size with the interaction on BiologyNow.

Section 45.3 The growth rate for a population in a specified interval depends on the rates of birth, death, immigration, and emigration. By putting aside the effects of immigration and emigration, we may then represent population growth (G) as

$$G = rN$$

where r is the net reproduction per individual per unit time and N is the number of individuals.

In cases of exponential growth, a population's rate of growth is proportional to its size. The reproductive base, and population size, increases at a fixed rate in a given interval. This trend plots out as a J-shaped growth curve. The rate of growth may be slow or rapid. As long as the population's per capita birth rate remains above its per capita death rate, it shows exponential growth.

BiologyNow
Observe a pattern of exponential growth with the animation on BiologyNow.

Section 45.4 The maximum number of individuals of a population that can be sustained indefinitely by the resources in their environment is called the carrying capacity. Food and other essential resources, disease, competition, and predation are examples of density-dependent factors that can limit population growth. Density-independent factors affect growth regardless of how crowded the individuals are.

Unlike exponential growth, a logistic growth pattern plots out as an S-shaped curve. As one example, a small population increases slowly in size, then rapidly, then levels off once the carrying capacity is reached.

BiologyNow
Learn about logistic growth on BiologyNow.

Sections 45.5. 45.6 Each species has a life history pattern characterized by the age at first reproduction, number of offspring per generation, life span, and other traits. Three general types of survivorship curves are common: a high death rate late in life, a constant rate at all ages, or a high rate early in life. Many aspects of life histories have a genetic basis, are subject to natural selection, and differ among populations and species.

Section 45.7 The human population has surpassed 6.4 billion. Its rapid growth in the past two centuries occurred through expansion into many diverse habitats and through agricultural, medical, and technological developments that raised carrying capacity.

Section 45.8 Family planning refers to societal efforts to slow population growth. The total fertility rate (TFR) is the average number of children born to women of a population during their reproductive years. The global TFR is declining. Even so, the pre-reproductive base of the world population is so large that human population size will continue to increase for at least sixty years.

BiologyNow
Compare age structure diagrams with the interaction on BiologyNow.

Section 45.9 The demographic transition model correlates industrial and economic development with changes in population growth rates, although global conditions have changed so much that the model may no longer apply to many of the developing nations. Per capita consumption of resources in developed nations is far higher than it is in developing nations.

BiologyNow
Learn about the demographic transition model with the animation on BiologyNow.

Section 45.10 Zero population growth has social repercussions, as when a population's age structure is such that the number of older individuals exceeds the number of young workers that must support them.

Self-Quiz

Answers in Appendix II

1. The rate at which a population grows or declines depends on the rate of ________ .
   a. births c. immigration e. a and b
   b. deaths d. emigration f. all of the above

2. Populations grow exponentially when ________ .
   a. its rate of increase is proportional to the size of its reproductive base in a given interval
   b. the size of a low-density population increases slowly, then quickly, then levels off once the carrying capacity is reached
   c. a and b are characteristics of exponential growth

3. For a given species, the maximum rate of increase per individual under ideal conditions is its ________ .
   a. biotic potential c. environmental resistance
   b. carrying capacity d. density control

4. Resource competition, disease, and predation are ________ controls on population growth rates.
   a. density-independent c. age-specific
   b. population-sustaining d. density-dependent

5. A life history pattern for a population is a set of adaptations that influence the individual's ________ .
   a. longevity c. age at reproductive maturity
   b. fertility d. all of the above

6. In 2004, the worldwide average rate of increase for the human population at midyear was ________ percent.
   a. 0 c. 1.3 e. 3.8
   b. 0.5 d. 2.7 f. 4.6

Figure 45.21 Saguaros (*Canegiea gigantea*) growing very slowly in Arizona's Sonoran desert.

Figure 45.22 A young Malian, with a 10 percent chance of becoming a mother by age fifteen, and a 50 percent chance before nineteen. Mali's TFR, about 7, is one of the world's highest.

7. Match each term with its most suitable description.

____	carrying capacity	a. maximum rate of increase per individual under ideal conditions
____	exponential growth	b. population growth plots out as an S-shaped curve
____	biotic potential	c. maximum number of individuals sustainable by the resources in a given environment
____	limiting factor	d. population growth plots out as a J-shaped curve
____	logistic growth	e. essential resource that restricts population growth when scarce

Additional questions are available on **Biology Now**™

Critical Thinking

1. If house cats that have not been neutered or spayed live up to their biotic potential, two can be the start of many kittens—12 the first year, 72 the second year, 429 the third, 2,574 the fourth, 15,416 the fifth, 92,332 the sixth, 553,019 the seventh, 3,312,280 the eighth, and 19,838,741 kittens the ninth year. Is this a case of logistic growth? Exponential growth? Irresponsible cat owners?

2. Reflect on Section 45.6. When researchers moved guppies from populations that were prey of pike-cichlids to a habitat with killifish, the life histories of the transplanted guppies evolved. They came to resemble those of guppy populations that had been preyed upon by killifish. The age of first reproduction increased, as did body size. The males became gaudier. Some of their scales formed larger, more colorful spots. How could a decrease in predation pressure on sexually mature fish influence male guppy coloration?

3. Each summer, a giant saguaro cactus produces tens of thousands of tiny black seeds. Most die, but a few land in a sheltered spot and sprout the following spring. The saguaro is a slow-growing CAM plant (Section 7.7). After fifteen years, it may be only knee high, and it will not flower for another fifteen years. It may live for 200 years. Saguaros share their habitat with annuals, such as poppies, that sprout, form seeds, and die in just a few weeks (Figure 45.21). Speculate on how these different life histories can both be adaptive in the same desert environment.

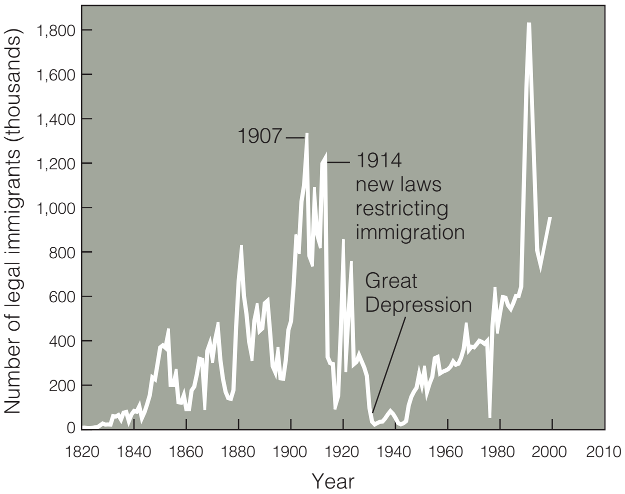


Figure 45.23 Chart of legal immigration to the United States between 1820 and 2000.

4. A third of the world population is younger than fifteen (Figure 45.22). Describe the effect this age distribution will have on the human population's growth rate. If you suspect it will have severe impact, what humane recommendations would you make to encourage individuals of this age group to limit their family size? What are some social, economic, and environmental factors that might prevent them from following the recommendations?

5. Figure 45.23 charts the legal immigration to the United States between 1820 and 2000. The greatest increase came after the Immigration Reform and Control Act of 1986 gave legal status to undocumented immigrants who proved they had lived in the country for years. Economic downturns in the 1980s and 1990s fanned resentment against immigrants.

Many people in the United States would like to limit legal immigration to 300,000–450,000 per year and to deport undocumented individuals. Others would like to have open borders; they say a rigidly enforced documentation policy would discriminate against legal immigrants of the same ethnic background. Do some research, then write an essay on the arguments on both sides of this volatile issue, which has social and economic ramifications.

6. Write a short essay about a population having one of the age structures signified by the diagrams at right. Speculate on that population's current economic status and the social and economic problems it may face in the future.