CHAPTER

36

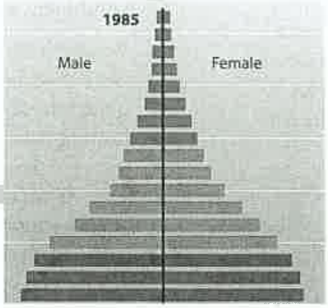
Population Ecology

BIG IDEAS

Population Structure and Dynamics

(36.1–36.8)

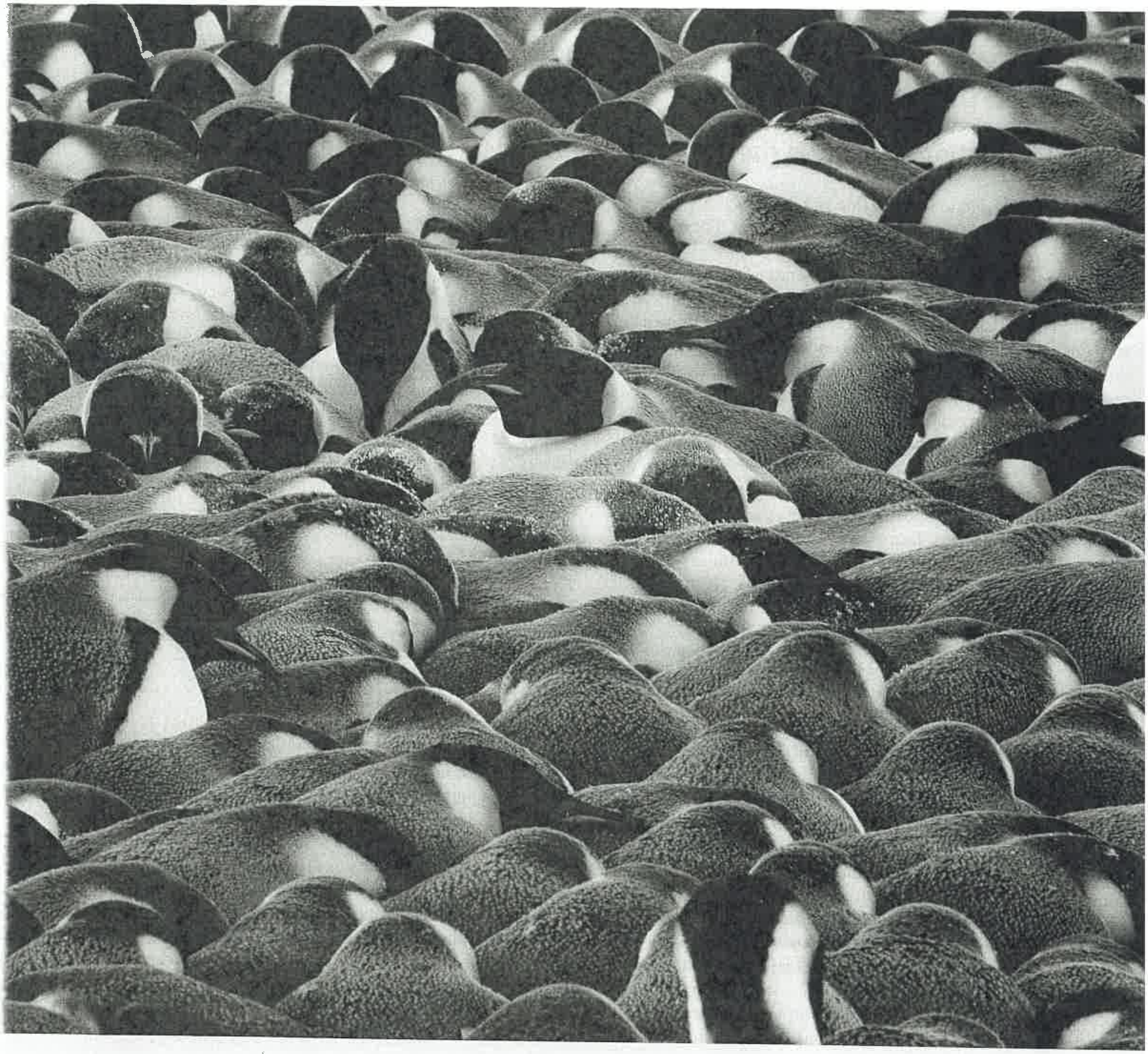
Population ecology is concerned with characteristics that describe populations, changes in population size, and factors that regulate populations over time.



The Human Population

(36.9–36.11)

The principles of population ecology can be used to describe the growth of the human population and its limits.



Emperor penguins, shown above, are one of the few species adapted to life on the polar ice. Their outer feathers form a waterproof cover for foraging in the icy sea, while a downy underlayer provides insulation. Beneath their skin, their bodies are swaddled in a thick layer of fat that adds insulation as well as storing energy. Reproduction is especially challenging in this environment. After the female lays an egg, she passes it to the male for safekeeping while she trudges many miles to the sea to feed. Throughout the frigid Antarctic winter, the male penguins huddle together in a shifting mass of bodies, each protecting its precious egg from the bitter cold and howling winds. Weeks later, the females return, and the males trek to the sea to replenish their depleted energy stores. In the following months, the parents make multiple trips to the sea to fetch food, which they regurgitate for their hungry offspring. Even chicks that receive food regularly are not assured of survival—predatory birds known as giant petrels carry off many of the young.

As an individual, each penguin faces the rigors of the Antarctic climate, the threat of predators, and the struggle to reproduce. In terms of population ecology, however, the fates of individuals are merged into group characteristics—each chick that escapes being a petrel's prey feeds into the percentage of chicks that survive their first year; the breeding success of one pair of birds feeds into the growth rate of the population.

In this chapter, you'll learn about the structure and dynamics of populations and the factors that regulate populations over time. As ecologists gain greater insight into natural populations, we become better equipped to develop sustainable food sources, assess the impact of human activities, and balance human needs with the conservation of biodiversity and resources.

Population Structure and Dynamics

36.1 Population ecology is the study of how and why populations change

Ecologists usually define a **population** as a group of individuals of a single species that occupy the same general area. These individuals rely on the same resources, are influenced by the same environmental factors, and are likely to interact and breed with one another. For example, the emperor penguins living near Dumont d'Urville Station, where *March of the Penguins* was filmed, are a population. When a researcher chooses a population to study, he or she defines it by boundaries appropriate to the species being studied and to the purposes of the investigation.

Population ecology is concerned with changes in population size and the factors that regulate populations over time. A population ecologist might use statistics such as the number and distribution of individuals to describe a population. Population ecologists also examine population dynamics, the interactions between biotic and abiotic factors that cause variation in population sizes. One important aspect of population dynamics—and a major topic for this chapter—is population growth. The penguin population at Dumont d'Urville Station increases through births and the immigration of penguins from nearby colonies. Deaths and the emigration of individuals away from Dumont d'Urville Station decrease the population. Population ecologists might investigate how various environmental factors, such as availability of food, predation by killer whales, or the extent of sea ice, affect the size, distribution, or dynamics of the population.

Population ecology plays a key role in applied research. For example, population ecology provides critical information for identifying and saving endangered species. Population ecology is being used to manage wildlife populations and to develop sustainable fisheries throughout the world. The population ecology of pests and pathogens provides insight into controlling their spread. Population ecologists also study human population growth, one of the most critical environmental issues of our time.

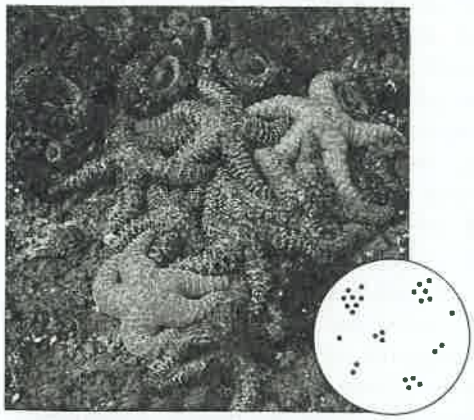
? What is the relationship between a population and a species?

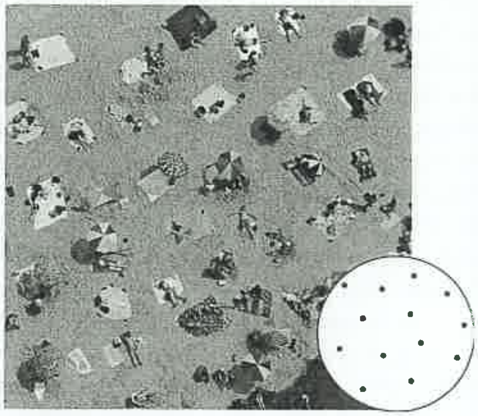
A population is a localized group of individuals of a single species.

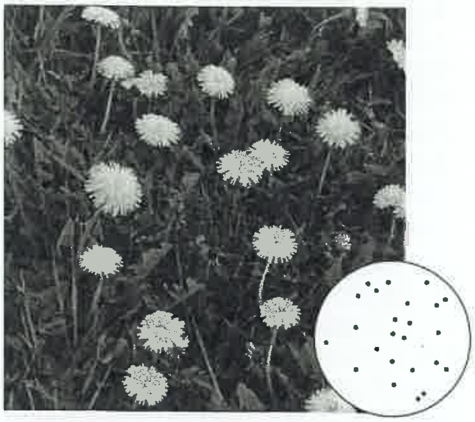
36.2 Density and dispersion patterns are important population variables

Two important aspects of population structure are population density and dispersion pattern. **Population density** is the number of individuals of a species per unit area or volume—the number of oak trees per square kilometer (km^2) in a forest, for instance, or the number of earthworms per cubic meter (m^3) in forest soil. Because it is impractical or impossible to count all individuals in a population in most cases, ecologists use a variety of sampling techniques to estimate population densities. For example, they might base an estimate of the density of alligators in the Florida Everglades on a count of individuals in a few sample plots of 1 km^2 each. The larger the number and size of sample plots, the more accurate the estimates. In some cases, population densities are estimated not by counts of organisms but by indirect indicators, such as number of bird nests or rodent burrows.

Within a population's geographic range, local densities may vary greatly. The **dispersion pattern** of a population refers to the way individuals are spaced within their area. A **clumped dispersion pattern**, in which individuals are grouped in patches, is the most common in nature. Clumping often results from an unequal distribution of resources in the environment. For instance, plants or fungi may be clumped in areas where soil conditions and other factors favor germination and growth. Clumping of animals often results from uneven food distribution. For example, the sea stars shown in **Figure 36.2A** group together where food is abundant. Clumping may


▲ **Figure 36.2A** Clumped dispersion of ochre sea stars at low tide


▲ **Figure 36.2B** Uniform dispersion of sunbathers at Coney Island


▲ **Figure 36.2C** Random dispersion of dandelions

also reduce the risk of predation, or be associated with social behavior.

A **uniform dispersion pattern** (an even one) often results from interactions between the individuals of a population. For instance, some plants secrete chemicals that inhibit the germination and growth of nearby plants that could compete for resources. Animals may exhibit uniform dispersion as a result of territorial behavior. **Figure 36.2B** (on the previous page) shows the uniform dispersion of sunbathers at a popular New York beach.

In a **random dispersion pattern**, individuals in a population are spaced in an unpredictable way, without a pattern. Plants, such as dandelions (**Figure 36.2C**, previous page), that grow from windblown seeds might be randomly dispersed. However, varying habitat conditions and social interactions make random dispersion rare.

Estimates of population density and dispersion patterns enable researchers to monitor changes in a population and to compare and contrast the growth and stability of populations in different areas. The next module describes another tool that ecologists use to study populations.

? **What dispersion pattern would you predict in a forest population of termites, which live in damp, rotting wood?**

Clumped (in fallen logs or dead trees)

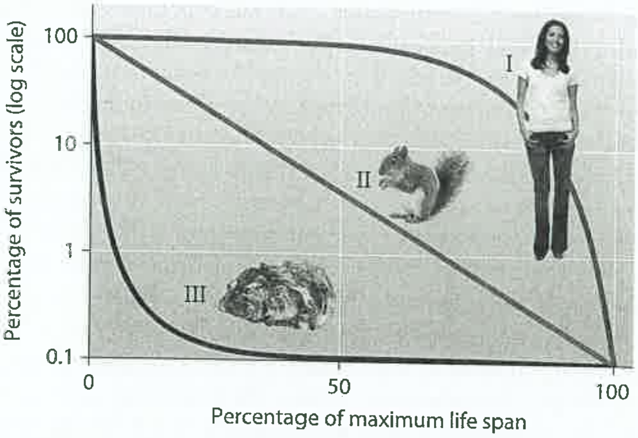
36.3 Life tables track survivorship in populations

Life tables track survivorship, the chance of an individual in a given population surviving to various ages. Starting with a population of 100,000 people, **Table 36.3** shows the number who are expected to be alive at the beginning of each age interval, based on death rates in 2004. For example, 93,735 out of 100,000 people are expected to live to age 50. The chance of surviving to age 60, shown in the last column of the table, is 0.939. The chance of surviving to age 90, however, is only 0.412. The life insurance industry uses life tables to predict how long, on average, a person will live. Population ecologists have adopted this technique and constructed life tables for various other species. By identifying the most vulnerable stages of an organism's life, life table data help conservationists develop effective measures for maintaining a viable population.

Life tables can be used to construct **survivorship curves**, which plot survivorship as the proportion of individuals from an initial population that are alive at each age (**Figure 36.3**). By using a percentage scale instead of actual ages on the *x*-axis, we can compare species with widely varying life spans on the same graph. The curve for the human population shows that most people survive to the older age intervals, as we saw in the life table. Ecologists refer to the shape of this curve as Type I survivorship. Species that exhibit a Type I curve—humans and many other large mammals—usually produce few offspring but give them good care, increasing the likelihood that they will survive to maturity.

In contrast, a Type III curve indicates low survivorship for the very young, followed by a period when survivorship is high for those few individuals who live to a certain age. Species with this type of survivorship curve usually produce very large numbers of offspring but provide little or no care for them. Some fishes, for example, can produce millions of eggs at a time, but most offspring die as larvae from predation or other causes. Many invertebrates, such as oysters, also have Type III survivorship curves.

A Type II curve is intermediate, with survivorship constant over the life span. That is, individuals are no more vulnerable at one stage of the life cycle than at another. This type of survivorship has been observed in some invertebrates, lizards, and rodents.



▲ **Figure 36.3** Three types of survivorship curves

TABLE 36.3 | LIFE TABLE FOR THE U.S. POPULATION IN 2004

Age Interval	Number Living at Start of Age Interval (*N*)	Number Dying During Interval (*D*)	Chance of Surviving Interval 1 – (*D*/*N*)
0–10	100,000	871	0.991
10–20	99,129	419	0.996
20–30	98,709	933	0.991
30–40	97,776	1,259	0.987
40–50	96,517	2,781	0.971
50–60	93,735	5,697	0.939
60–70	88,038	11,847	0.865
70–80	76,191	22,267	0.708
80–90	53,925	31,706	0.412
90+	22,219	22,219	0.000

? **How does the chance of survival change with age in organisms with a Type III survivorship curve?**

The chance of survival is initially low but increases after an individual reaches a certain age.

36.4 Idealized models predict patterns of population growth

Population size fluctuates as new individuals are born or immigrate into an area and others die or emigrate. Some populations—for example, trees in a mature forest—are relatively constant over time. Other populations change rapidly, even explosively. Consider a single bacterium that divides every 20 minutes. There would be two bacteria after 20 minutes, four after 40 minutes, eight after 60 minutes, and so on. In just 12 hours, the population would approach 70 billion cells. If reproduction continued at this rate for a day and a half—a mere 36 hours—there would be enough bacteria to form a layer a foot deep over Earth's entire surface. Using idealized models, population ecologists can predict how the size of a particular population will change over time under different conditions.

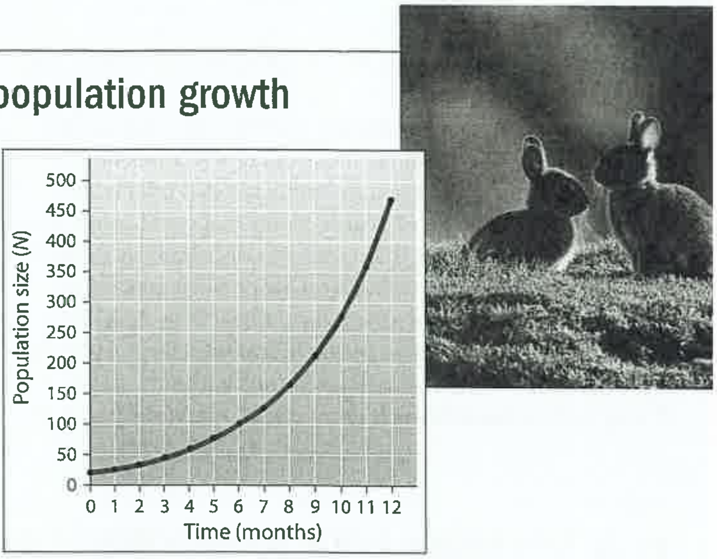
The Exponential Growth Model The rate of population increase under ideal conditions, called exponential growth, can be calculated using the simple equation $G = rN$. The G stands for the growth rate of the population (the number of new individuals added per time interval); N is the population size (the number of individuals in the population at a particular time); and r stands for the **per capita rate of increase** (the average contribution of each individual to population growth; per capita means "per person").

How do we estimate the per capita rate of increase? Population growth reflects the number of births minus the number of deaths (the model assumes that immigration and emigration are equal). Suppose a population of rabbits has 100 individuals, and there are 50 births and 20 deaths in one month. The net increase is 30 rabbits. The per capita increase in the population, or r, is 30/100, or 0.3.

In a population growing in an ideal environment with unlimited space and resources, r is the maximum capacity of members of that population to reproduce. Thus, the value of r depends on the kind of organism. For example, rabbits have a higher r than elephants, and bacteria have a higher r than rabbits.

TABLE 36.4A | EXPONENTIAL GROWTH OF RABBITS, $r = 0.3$

Time (months)	N	$G = rN$
0	20	6
1	26	8
2	34	10
3	44	13
4	57	17
5	74	22
6	96	29
7	125	38
8	163	49
9	212	64
10	276	83
11	359	108
12	467	140



▲ **Figure 36.4A** Exponential growth of rabbits

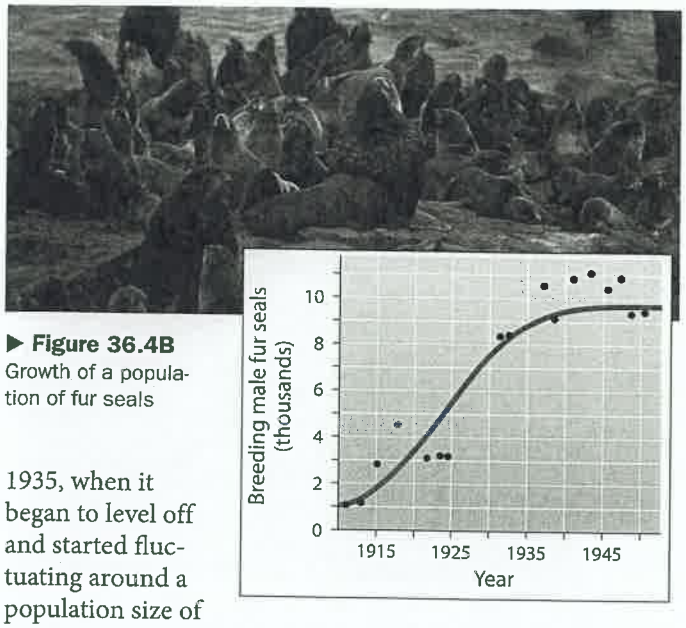
When a population is expanding without limits, r remains constant and the rate of population growth depends on the number of individuals already in the population (N). In **Table 36.4A**, a population begins with 20 rabbits. The growth rate (G) for this population, using $r = 0.3$, is shown in the right-hand column. Notice that the larger the population size, the more new individuals are added during each time interval.

Graphing these data in **Figure 36.4A** produces a J-shaped curve, which is typical of exponential growth. The lower part of the J, where the slope of the line is almost flat, results from the relatively slow growth when N is small. As the population increases, the slope becomes steeper.

The **exponential growth model** gives an idealized picture of unlimited population growth. There is no restriction on the abilities of the organisms to live, grow, and reproduce. Even elephants, the slowest breeders on the planet, would increase exponentially if enough resources were available. Although elephants typically produce only six young in a 100-year life span, Charles Darwin estimated that it would take only 750 years for a single pair to give rise to a population of 19 million. But any population—bacteria, rabbits, or elephants—will eventually be limited by the resources available.

Limiting Factors and the Logistic Growth Model In nature, a population that is introduced to a new environment or is rebounding from a catastrophic decline in numbers may grow exponentially for a while. Eventually, however, one or more environmental factors will limit its growth rate as the population reaches its maximum sustainable size. Environmental factors that restrict population growth are called **limiting factors**.

You can see the effect of population-limiting factors in the graph in **Figure 36.4B** (see top of facing page), which illustrates the growth of a population of fur seals on St. Paul Island, off the coast of Alaska. (For simplicity, only the mated bulls were counted. Each has a harem of a number of females, as shown in the photograph.) Before 1925, the seal population on the island remained low because of uncontrolled hunting, although it changed from year to year. After hunting was controlled, the population increased rapidly until about



▶ **Figure 36.4B** Growth of a population of fur seals

1935, when it began to level off and started fluctuating around a population size of about 10,000 bull seals. At this point, a number of limiting factors, including some hunting and the amount of space suitable for breeding, restricted population growth.

The fur seal growth curve fits the **logistic growth model**, a description of idealized population growth that is slowed by limiting factors as the population size increases. **Figure 36.4C** compares the logistic growth model (red) with the exponential growth model (blue). As you can see, the logistic curve is J-shaped at first, but gradually levels off to resemble an S.

To model logistic growth, the formula for exponential growth, rN, is multiplied by an expression that describes the effect of limiting factors on an increasing population size:

$$G = rN\,\frac{(K - N)}{K}$$

This equation is actually simpler than it looks. The only new symbol in the equation is K, which stands for carrying capacity. **Carrying capacity** is the maximum population size that a particular environment can sustain ("carry"). For the fur seal population on St. Paul Island, for instance, K is about 10,000 mated males. The value of K varies, depending on the species and the resources available in the habitat. K might be considerably less than 10,000 for a fur seal population on a smaller island with fewer breeding sites. Even in one location, K is not a fixed number. Organisms interact with other organisms in their communities, including predators, parasites, and food sources, that may affect K. Changes in abiotic factors may also increase or decrease carrying capacity. In any case, the concept of carrying capacity expresses an essential fact of nature: Resources are finite.

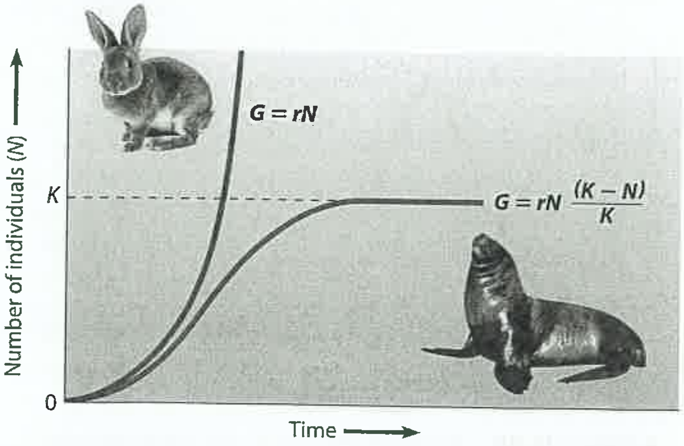
Table 36.4B demonstrates how the expression $(K - N)/K$ in the logistic growth model produces the S-shaped curve. At the outset, N (the population size) is very small compared to K (the carrying capacity). Thus, $(K - N)/K$ nearly equals K/K, or 1, and population growth (G) is close to rN—that is, exponential growth. As the population increases and N gets closer to carrying capacity, $(K - N)/K$ becomes an increasingly smaller fraction. The growth rate slows as rN is multiplied by that fraction. At carrying capacity, the population is as large as it can theoretically get in its environment; at this point, $N = K$, and $(K - N)/K = 0$. The population growth rate (G) becomes zero.

What does the logistic growth model suggest to us about real populations in nature? The model predicts that a population's growth rate will be small when the population size is *either* small or large, and highest when the population is at an intermediate level relative to the carrying capacity. At a low population level, resources are abundant, and the population is able to grow nearly exponentially. At this point, however, the increase is small because N is small. In contrast, at a high population level, limiting factors strongly oppose the population's potential to increase. There might be less food available per individual or fewer breeding territories, nest sites, or shelters. These limiting factors cause the birth rate to decrease, the death rate to increase, or both. Eventually, when the birth rate equals the death rate, the population stabilizes at the carrying capacity (K).

It is important to realize that the logistic growth model presents a mathematical ideal that is a useful starting point for studying population growth and for constructing more complex models. Like any good starting hypothesis, the logistic model has stimulated research, leading to a better understanding of the factors affecting population growth. We take a closer look at some of these factors next.

? In logistic growth, at what population size (in terms of K) is the population increasing most rapidly? Explain why.

When N is $\frac{1}{2}K$. At this population size, there are more reproducing individuals than at lower population sizes and still lots of space or other resources available for growth.



▲ **Figure 36.4C** Logistic growth and exponential growth compared

TABLE 36.4B EFFECT OF K ON GROWTH RATE AS N APPROACHES K, $K = 1{,}000$, $r = 0.1$

N	rN	(K – N)/K	G = rN(K – N)/K
10	1	0.99	0.99
100	10	0.9	9.00
400	40	0.6	24.00
500	50	0.5	25.00
600	60	0.4	24.00
700	70	0.3	21.00
900	95	0.05	0.25
1,000	100	0.00	0.00

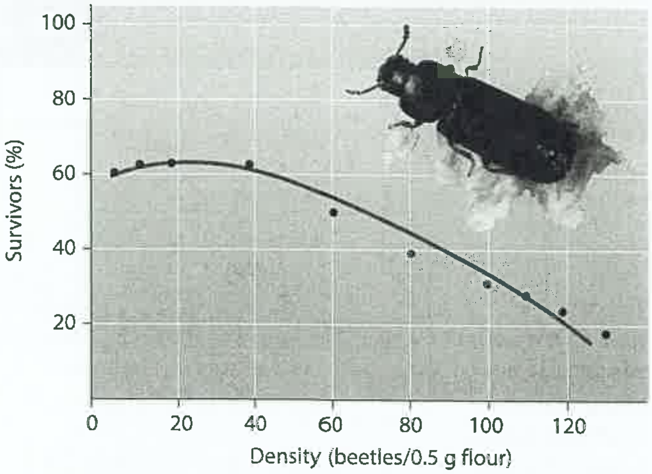
36.5 Multiple factors may limit population growth

The logistic growth model predicts that population growth will slow and eventually stop as population density increases. That is, at higher population densities, the birth rate decreases, the death rate increases, or both. What are the possible causes of these density-dependent changes in birth and death rates?

Several **density-dependent factors**—limiting factors whose intensity is related to population density—appear to limit growth in natural populations. The most obvious is **intraspecific competition**—competition between individuals of the same species for limited resources. As a limited food supply is divided among more and more individuals, birth rates may decline as individuals have less energy available for reproduction. In **Figure 36.5A**, clutch size (the number of eggs a female bird lays in a "litter") declines as the population density, and therefore the number of competitors, increases.

Density-dependent factors often depress a population's growth by increasing the death rate. In a laboratory experiment with flour beetles, for example, survivorship declined with increasing population density **(Figure 36.5B)**. In a natural setting, plants that grow close together may experience increased mortality as competition for resources increases. And those that survive will likely produce fewer flowers, fruits, and seeds than uncrowded individuals. In an animal population, the death rate may climb as a result of increased disease transmission under crowded conditions or the accumulation of toxic waste products. Predation may also be an important cause of density-dependent mortality. A predator may concentrate on a particular kind of prey as that prey becomes abundant.

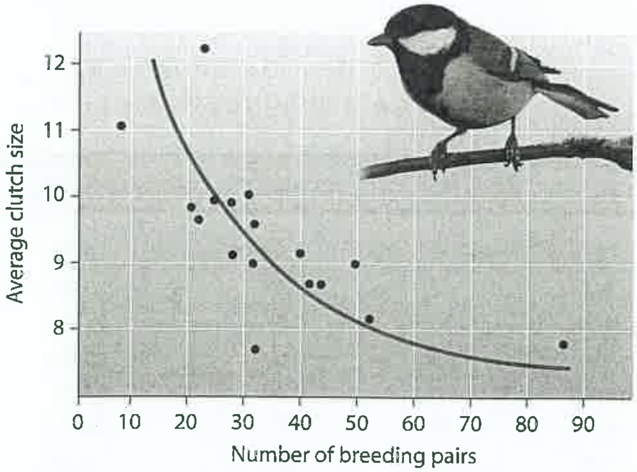
A limiting factor may be something other than food or nutrients. In many vertebrates that defend a territory, the availability of space may limit reproduction. For instance, the number of nesting sites on rocky islands may limit the population size of seabirds such as gannets. Or, like a game of musical chairs, the number of safe hiding places may limit a prey population by exposing some individuals to a greater risk of predation.



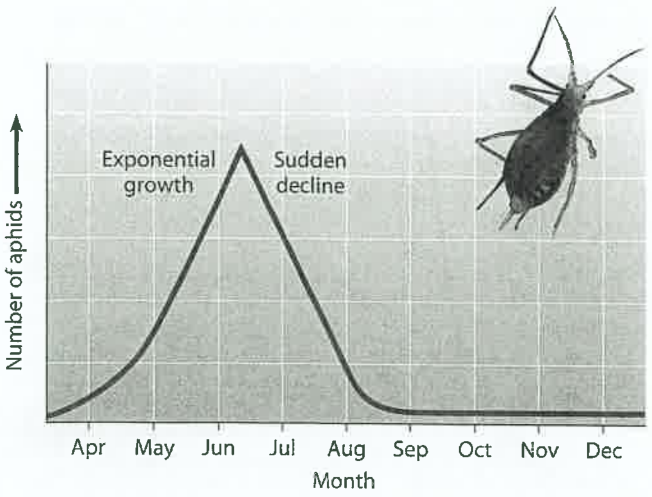
▲ **Figure 36.5B** Decreasing survival rates with increasing density in a population of flour beetles

For some animal species, physiological factors may regulate population size. White-footed mice in a small field enclosure will multiply from a few to a colony of 30 to 40 individuals, but reproduction then declines until the population ceases to grow. This drop in reproduction occurs even when additional food and shelter are provided. High population densities in mice appear to induce a stress syndrome in which hormonal changes can delay sexual maturation, cause reproductive organs to shrink, and depress the immune system. In this case, high densities cause both a decrease in birth rate and an increase in death rate. Similar effects of crowding have been observed in wild populations of other rodents.

In many natural populations, abiotic factors such as weather may affect population size well before density-dependent factors become important. A population-limiting factor whose intensity is unrelated to population density is called a **density-independent factor**. If we look at the growth curve of such a



▲ **Figure 36.5A** Decreasing birth rate with increasing density in a population of great tits



▲ **Figure 36.5C** Weather change as a density-independent factor limiting aphid population growth population, we see something like exponential growth followed by a rapid decline, rather than a leveling off. **Figure 36.5C** (on the previous page) shows this effect for a population of aphids, insects that feed on the sugary phloem sap of plants. These and many other insects undergo virtually exponential growth in the spring and then rapidly die off when the weather turns hot and dry in the summer. A few individuals may survive, and these may allow population growth to resume if favorable conditions return. In some populations of insects—many mosquitoes and grasshoppers, for instance—adults die off entirely, leaving only eggs, which initiate population growth the following year. In addition to seasonal changes in the weather, disturbances—such as fire, storms, and habitat disruption by human activity—can affect a population's size regardless of its density.

Over the long term, most populations are probably regulated by a mixture of factors. Some populations remain fairly stable in size and are presumably close to a carrying capacity that is determined by biotic factors such as competition or predation. Most populations for which we have long-term data, however, show fluctuations in numbers. Thus, the dynamics of many populations result from a complex interaction of both density-dependent factors and density-independent abiotic factors such as climate and disturbances.

? List some of the factors that may reduce birth rate or increase death rate as population density increases.

Food and nutrient limitations, insufficient territories, increase in disease and predation, accumulation of toxins

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36.6 Some populations have "boom-and-bust" cycles

Some populations of insects, birds, and mammals undergo dramatic fluctuations in density with remarkable regularity. "Booms" characterized by rapid exponential growth are followed by "busts," during which the population falls back to a minimal level. A striking example is the boom-and-bust growth cycles of lemming populations that occur every three to four years. (Lemmings are small rodents that live in the tundra.) Some researchers hypothesize that natural changes in the lemmings' food supply may be the underlying cause. Another hypothesis, as discussed in Module 36.5, is that stress from crowding during the "boom" may reduce reproduction, causing a "bust."

Figure 36.6 illustrates another well-known example—the cycles of snowshoe hare and lynx. The lynx is one of the main predators of the snowshoe hare in the far northern forests of Canada and Alaska. About every 10 years, both hare and lynx populations show a rapid increase followed by a sharp decline.

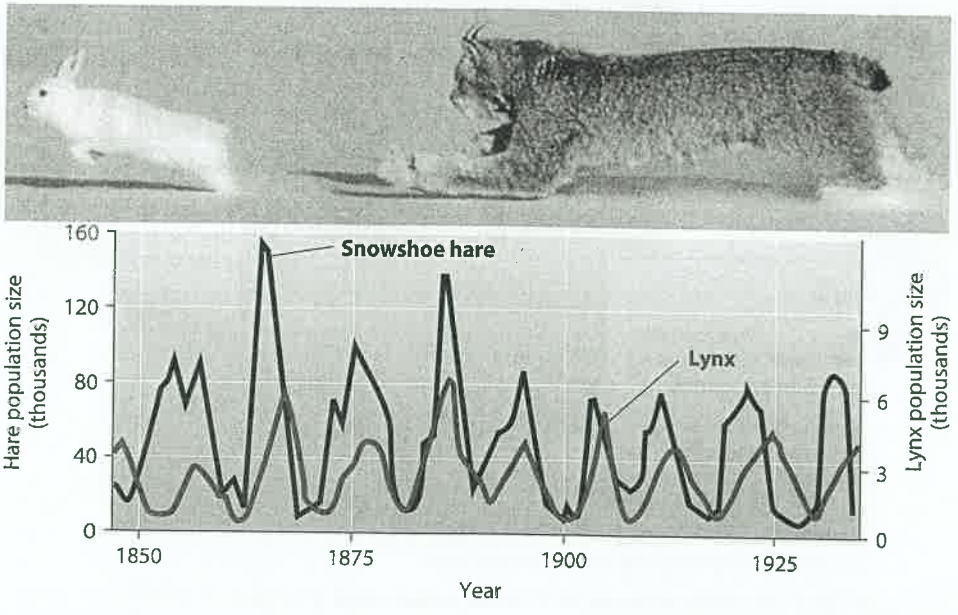
What causes these boom-and-bust cycles? Since ups and downs in the two populations seem to almost match each other on the graph, does this mean that changes in one directly affect the other? For the hare cycles, there are three main hypotheses. First, cycles may be caused by winter food shortages that result from overgrazing. Second, cycles may be due to predator-prey interactions. Many predators other than lynx, such as coyotes, foxes, and great-horned owls, eat hares, and the combination of predators might overexploit their prey. Third, cycles could be affected by a combination of limited food resources and excessive predation. Recent field experiments support the hypothesis that the 10-year cycles of the snowshoe hare are largely driven by excessive predation, but are also influenced by fluctuations in the hare's food supplies.

For the lynx and many other predators that depend heavily on a single species of prey, the availability of prey can have a strong influence on population size. Thus, the 10-year cycles in the lynx population probably do result at least in part from the 10-year cycles in the hare population. As the lynx population declines, the prey population—released from predator pressure—rebounds. Long-term studies are the key to unraveling the complex causes of such population cycles.

Now that we have looked at patterns of population growth, we turn our attention to the differences in reproductive patterns of populations and how they are shaped by natural selection.

? In one experiment, providing more food to hares increased their population density, but the population continued to show cyclic collapses. What might you conclude from these results?

Hare population cycles are not primarily caused by food shortages.



▲ **Figure 36.6** Population cycles of the snowshoe hare and the lynx

EVOLUTION CONNECTION

36.7 Evolution shapes life histories

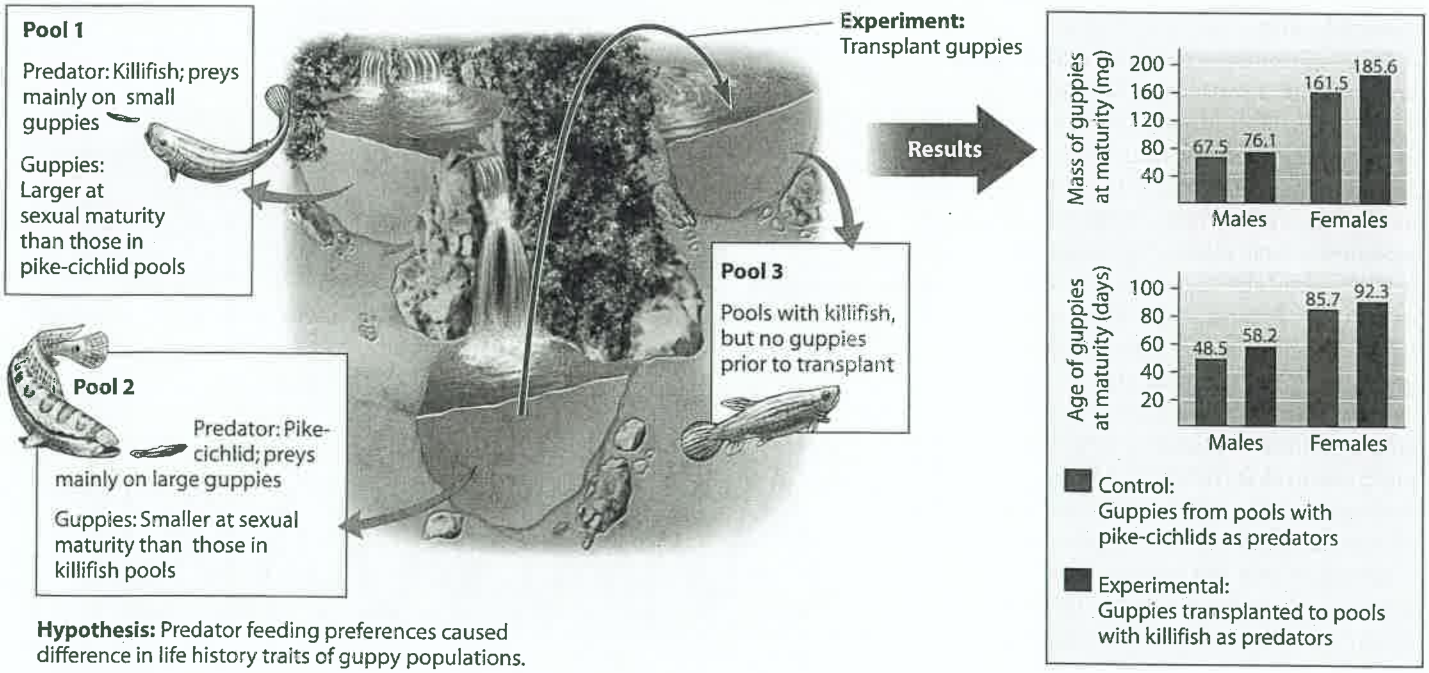
The traits that affect an organism's schedule of reproduction and death make up its **life history**. Some key life history traits are the age of first reproduction, the frequency of reproduction, the number of offspring, and the amount of parental care given. Natural selection cannot optimize all of these traits simultaneously because an organism has limited time, energy, and nutrients. For example, an organism that gives birth to a large number of offspring will not be able to provide a great deal of parental care. Consequently, the combination of life history traits in a population represents trade-offs that balance the demands of reproduction and survival. Because selective pressures vary, life histories are very diverse. Nevertheless, ecologists have observed some patterns that are useful for understanding how life history characteristics have been shaped by natural selection.

One life history pattern is typified by small-bodied, short-lived animals (for example, insects and small rodents) that develop and reach sexual maturity rapidly, have a large number of offspring, and offer little or no parental care. A similar pattern is seen in small, nonwoody plants such as dandelions that produce thousands of tiny seeds. Ecologists hypothesize that selection for this set of life history traits occurs in environments where resources are abundant, permitting exponential growth. It is sometimes called ***r*-selection** because *r* (the per capita rate of increase) is maximized. Most *r*-selected species have an advantage in habitats that experience unpredictable disturbances, such as fire, floods, hurricanes, drought, or cold weather, which create new opportunities by suddenly reducing a population to low levels. Human activity is a major cause of disturbance, producing road cuts, freshly cleared fields and woodlots, and poorly maintained lawns that are commonly colonized by *r*-selected plants and animals.

In contrast, large-bodied, long-lived animals (such as bears and elephants) develop slowly and produce few, but well-cared-for, offspring. Plants with comparable life history traits include coconut palms, which produce relatively few seeds that are well stocked with nutrient-rich material—the plant's version of parental care. Ecologists hypothesize that selection for this set of life history traits occurs in environments where the population size is near carrying capacity (*K*), so it is sometimes called ***K*-selection**. Population growth in these situations is limited by density-dependent factors. Because competition for resources is keen, *K*-selected organisms gain an advantage by allocating energy to their own survival and to the survival of their descendants. Thus, *K*-selected organisms are adapted to environments that typically have a stable climate and little opportunity for rapid population growth.

The hypothesis of *r*- and *K*-selection has been criticized as an oversimplification, and most organisms fall somewhere between the extremes. However, this hypothesis has stimulated a vigorous subfield of ecological research on the evolution of life histories.

A long-term project in Trinidad has provided direct evidence that life history traits can be shaped by natural selection. For years, researchers have been studying guppy populations living in small, relatively isolated pools. As shown in **Figure 36.7**, some guppy populations live in pools with predators called killifish, which eat mainly small, immature guppies (Pool 1).



▲ **Figure 36.7** The effect of predation on the life history traits of guppies

Other guppy populations live where larger fish, called pike-cichlids, eat mostly mature, large-bodied guppies (Pool 2). Guppies in populations exposed to these pike-cichlids tend to be smaller, mature earlier, and produce more offspring at a time than those in areas with killifish. Thus, guppy populations differ in certain life history traits, depending on the kind of predator in their environment. For these differences to be the result of natural selection, the traits should be heritable. And indeed, guppies from both populations raised in the laboratory without predators retained their life history differences.

To test whether the feeding preferences of different predators caused these differences in life histories by natural selection, researchers introduced guppies from a pike-cichlid habitat into a guppy-free pool inhabited by killifish (Pool 3). The scientists tracked the weight and age at sexual maturity in the experimental guppy populations for 11 years, comparing these guppies with control guppies that remained in the pike-cichlid pools. The average weight and age at sexual maturity of the transplanted populations increased significantly as compared with the control populations. These studies demonstrate not only that life history traits are heritable and shaped by natural selection, but also that questions about evolution can be tested by field experiments.

As we have seen, population ecology involves theoretical model building as well as observations and experiments in the field. Next we look at how the principles of population ecology can be applied to conservation and management.

? Refer to Module 36.3. Which type of survivorship curve would you expect to find in a population experiencing *r*-selection? *K*-selection?

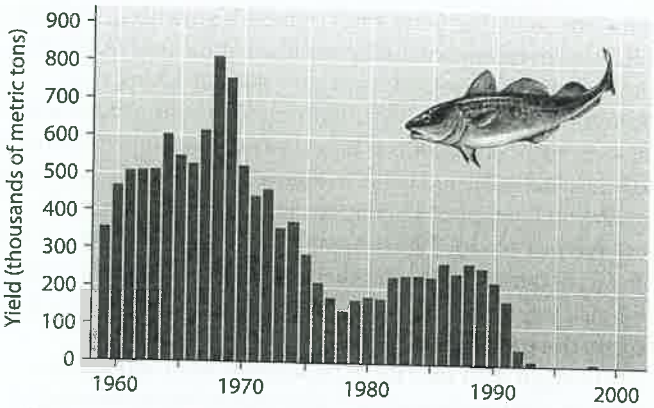
Type III for a population experiencing *r*-selection; Type I for *K*-selection

CONNECTION 36.8 Principles of population ecology have practical applications

Principles of population ecology can help guide us toward resource management goals, such as increasing populations we wish to harvest or save from extinction or decreasing populations we consider pests. Wildlife managers, fishery biologists, and foresters try to use **sustainable resource management**: harvesting crops without damaging the resource. In terms of population growth, this means maintaining a high population growth rate to replenish the population. According to the logistic growth model, the fastest growth rate occurs when the population size is at roughly half the carrying capacity of the habitat. Theoretically, a resource manager should achieve the best results by harvesting the populations down to this level. However, the logistic model assumes that growth rate and carrying capacity are stable over time. Calculations based on these assumptions, which are not realistic for some populations, may lead to unsustainably high harvest levels that ultimately deplete the resource. In addition, economic and political pressures often outweigh ecological concerns, and the amount of scientific information is frequently insufficient.

Fish, the only wild animals still hunted on a large scale, are particularly vulnerable to overharvesting. For example, in the northern Atlantic cod fishery, estimates of cod population sizes were too high, and the practice of discarding young cod (below legal size) at sea caused a higher mortality rate than predicted. The fishery collapsed in 1992 and has not recovered **(Figure 36.8)**. Following the decline of many other fish and whale populations, resource managers are trying to minimize the risk of resource collapse by setting minimum population sizes or imposing protected, harvest-free areas. For species that are in decline or facing extinction, resource managers may try to provide additional habitat or improve the quality of existing habitat to raise the carrying capacity and thus increase population growth.

Reducing the size of a population may also be a challenging task. Simply killing many individuals will not usually decrease the size of a pest population. Many insect and weed species have life history traits that are *r*-selected and have adaptations that promote rapid population growth. Also, most pesticides kill both the pest and their natural predators. Because prey species often have a higher reproductive rate than predators, pest populations rapidly rebound before their predators can.



▲ **Figure 36.8** Collapse of northern cod fishery off Newfoundland

Integrated pest management (IPM) uses a combination of biological, chemical, and cultivation methods to control agricultural pests. IPM relies on knowledge of the population ecology of the pest and its associated predators and parasites, as well as crop growth dynamics.

As you've learned, there are many factors that influence a population's size. To effectively manage any population, we must identify those variables, account for the unpredictability of the environment, consider interactions with other species, and weigh the economic, political, and conservation issues. These same issues apply to the growth of the human population, which we explore next.

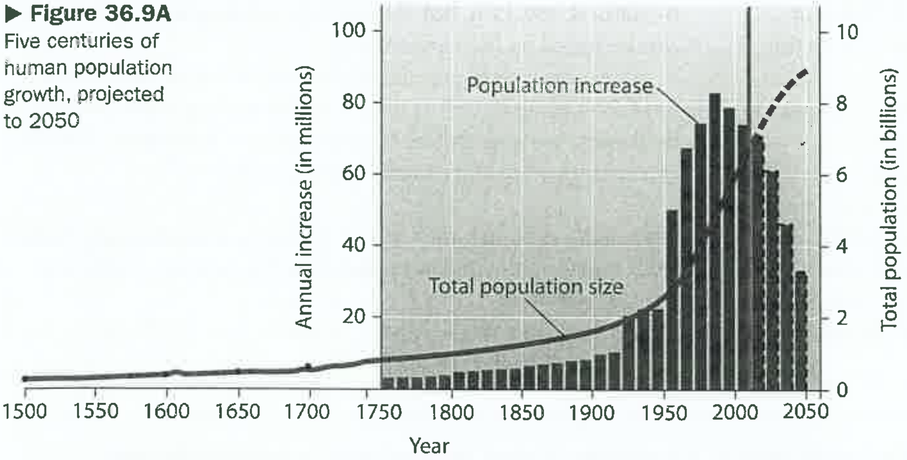
? Explain why managers often try to maintain populations of fish and game species at about half their carrying capacity.

To protect wildlife from overharvest yet maintain lower population levels so that growth rate is high and mortality from resource limitation is reduced

The Human Population

36.9 The human population continues to increase, but the growth rate is slowing

▶ **Figure 36.9A** Five centuries of human population growth, projected to 2050



In the few seconds it takes you to read this sentence, 21 babies will be born somewhere in the world and nine people will die. The statistics may have changed a bit since this book was printed, but births will still far outnumber deaths. An imbalance between births and deaths is the cause of population growth (or decline), and as the red curve in **Figure 36.9A** shows, the human population is expected to continue increasing for at least the next several decades. The bar graph in Figure 36.9A tells a different part of the story. The number of people added to the population each year has been declining since the 1980s. How do we explain these patterns of human population growth?

Let's begin with the rise in population from 480 million people in 1500 to the current population of more than 6.8 billion. In our simplest model (see Module 36.4), population growth depends on *r* (per capita rate of increase) and *N* (population size). Because the value of *r* was assumed to be constant in a given environment, the growth rate in the examples we used in Module 36.4 depended wholly on the population size. Throughout most of human history, the same was true of people. Although parents had many children, mortality was also high, so *r* (birth rate − death rate) was only slightly higher than 0. As a result, population growth was very slow. (If we extended the *x*-axis of Figure 36.9A back in time to year 1, when the population was roughly 300 million, the line would be almost flat for 1,500 years.) The 1 billion mark was not reached until the early 19th century.

As economic development in Europe and the United States led to advances in nutrition and sanitation and later, medical care, people took control of their population's rate of increase (*r*). At first, the death rate decreased, while the birth rate remained the same. The net rate of increase rose, and population growth began to pick up steam as the 20th century began. By mid-century, improvements in nutrition, sanitation, and health care had spread to the developing world, spurring growth at a breakneck pace as birth rates far outstripped death rates.

As the world population skyrocketed from 2 billion in 1927 to 3 billion just 33 years later, some scientists became alarmed. They feared that Earth's carrying capacity would be reached and that density-dependent factors (see Module 36.5) would maintain that population size through human suffering and death. But the overall growth rate peaked in 1962. In the more developed nations, advanced medical care continued to improve survivorship, but effective contraceptives held down the birth rate. As a result, the overall growth rate of the world's population began a downward trend.

Demographic Transition The world population is undergoing a change known as a **demographic transition**, a shift from zero population growth in which birth rates and death rates are high but roughly equal, to zero population growth characterized by low but roughly equal birth and death rates. **Figure 36.9B** shows the demographic transition of Mexico, which is projected to approach zero population growth with low birth and death rates in the next few decades. Notice that the death rate dropped sharply from 1925 to 1975 (the spike corresponds to the worldwide flu epidemic of 1918–1919), while the birth rate remained high until the 1960s. This is a typical pattern for demographic transitions.

Because economic development has occurred at different times in different regions, worldwide demographic transition is a mosaic of the changes occurring in different countries. The most developed nations have completed or are nearing completion of their demographic transitions. In these countries collectively, the rate of increase per 1,000 individuals was estimated at 0.4 in 2009 (**Table 36.9**, on the facing page). In the developing world, death rates have dropped, but high birth rates persist. As a result, these populations are growing rapidly. Of the more than 74 million people added to the world in 2009, more than 71 million were in developing nations.

Reduced family size is the key to the demographic transition. As women's status and education increase, they delay

▲ **Figure 36.9B** Demographic transition in Mexico

TABLE 36.9 POPULATION CHANGES IN 2009 (Estimated)

Population	Birth Rate (per 1,000)	Death Rate (per 1,000)	Rate of Increase (per 1,000)
World	19.5	8.3	11.2
More developed nations	10.9	10.5	0.4
Less developed nations	21.4	7.8	13.6

reproduction and choose to have fewer children. This phenomenon has been observed in both developed and developing countries, wherever the lives of women have improved. Given access to affordable contraceptive methods, women generally practice birth control, and many countries now subsidize family planning services and have official population policies. In many other countries, however, issues of family planning remain socially and politically charged, with heated disagreement over how much support should be provided for family planning.

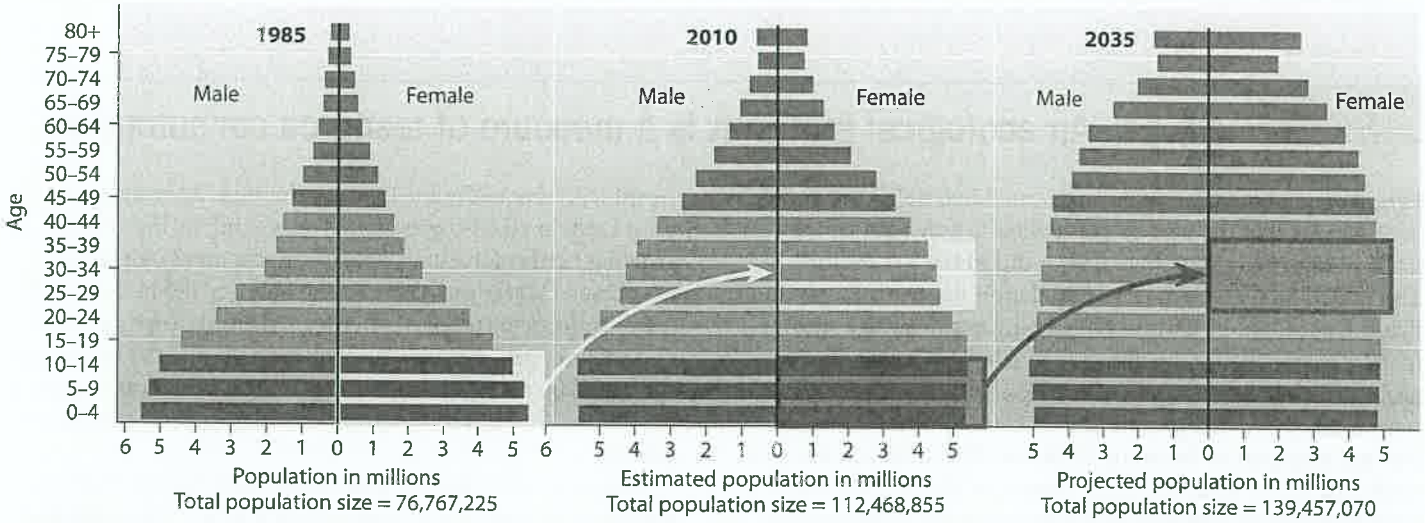
Age Structures A demographic tool called an age-structure diagram is helpful for predicting a population's future growth. The **age structure** of a population is the number of individuals in different age-groups. **Figure 36.9C** shows the age structure of Mexico's population in 1985, its estimated 2010 age structure, and its projected age structure in 2035. In these diagrams, green represents the portion of the population in their prereproductive years (0–14), pink indicates the part of the population in prime reproductive years (15–44), and blue is the proportion in postreproductive years (45 and older). Within each of these broader groups, each horizontal bar represents the population in a 5-year age-group. The area to the left of each vertical center line represents the number of males in each age-group; females are represented on the right side of the line.

An age structure with a broad base, such as Mexico's in 1985, reflects a population that has a high proportion of children and a high birth rate. On average, each woman is substantially exceeding the replacement rate of two children per couple. As Figure 36.9B shows, the birth rate and the rate of increase have dropped 25 years later, but the population continues to be affected by its earlier expansion. This situation, which results from the increased proportion of women of childbearing age in the population, is known as **population momentum**. Girls 0–14 in the 1985 age structure (outlined in yellow) are in their reproductive years in 2010, and girls who are 0–14 in 2010 (outlined in purple) will carry the legacy of rapid growth forward to 2035. Putting the brakes on a rapidly expanding population is like stopping a freight train—the end result takes place long after the decision to do it was made. Even when fertility is reduced to replacement rate, the total population will continue to increase for several decades. The percentage of individuals under the age of 15 gives a rough idea of future growth. In the developing countries, about 29% of the population is in this age-group. In contrast, roughly 16% of the population of developed nations is under the age of 15. Population momentum also explains why the population size in Figure 36.9A continues to increase even though fewer people are added to the population each year.

In the next module, we examine the age structure of the United States.

? **During the demographic transition from high birth and death rates to low birth and death rates, countries usually undergo rapid population growth. Explain why.**

The death rate declines before the birth rate declines, creating a period when births greatly outnumber deaths. This also sets up population momentum.



▲ **Figure 36.9C** Population momentum in Mexico

CONNECTION

36.10 Age structures reveal social and economic trends

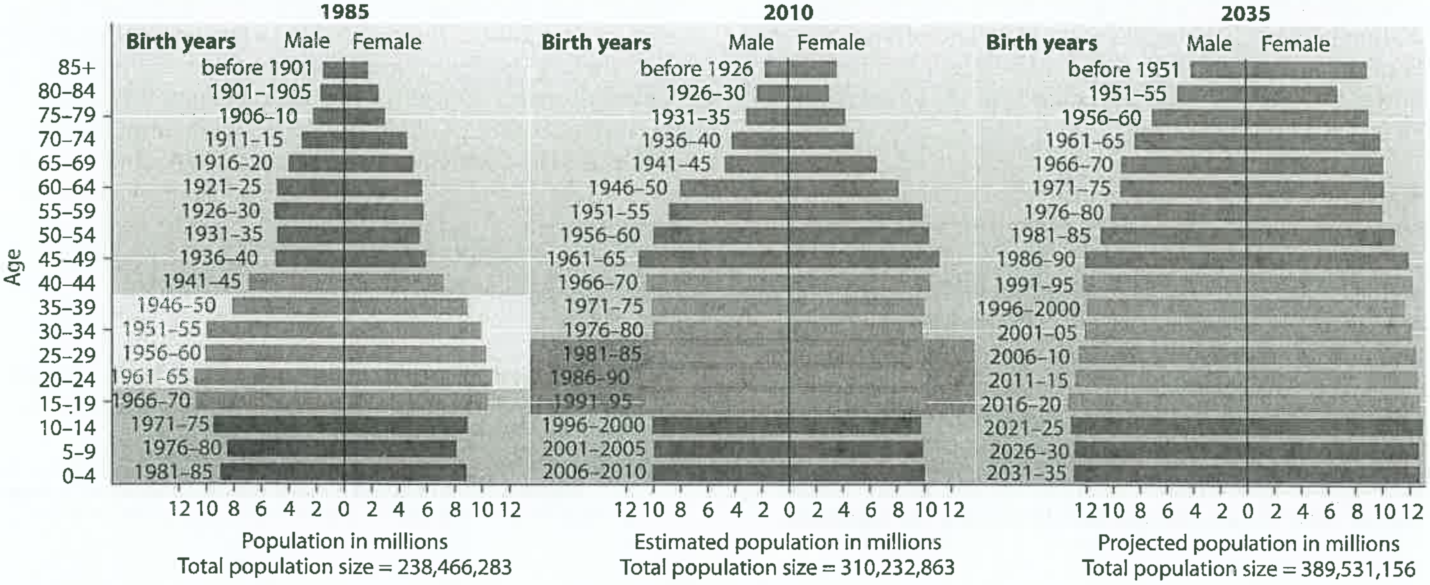
Age-structure diagrams not only reveal a population's growth trends, they also indicate social conditions. For instance, an expanding population has an increasing need for schools, employment, and infrastructure. A large elderly population requires that extensive resources be allotted to health care. Let's look at trends in the age structure of the United States from 1985 to 2035 **(Figure 36.10)**.

The large bulge in the 1985 age structure (tan screen) corresponds to the "baby boom" that lasted for about two decades after World War II ended in 1945. The large number of children swelled school enrollments, prompting construction of new schools and creating a demand for teachers. On the other hand, graduates who were born near the end of the boom faced stiff competition for jobs. Because they make up such a large segment of the population, boomers have had an enormous influence on social and economic trends. They also produced a boomlet of their own, seen in the 0–4 age-group in 1985 and the bump (purple screen) in the 2010 age structure.

Where are the baby boomers now? The leading edge has reached retirement age, which will place pressure on programs such as Medicare and Social Security. In 2010, 60% of the population was between 20 and 64, the ages most likely to be in the workforce, and 13% of the population was over 65. In 2035, the percentages are projected to be 54 and 20. In part, the increase in the elderly population is because people are living longer. The percentage of the population over 80, which was 2.5% in 1985, is projected to rise to nearly 6%—more than 23 million people—in 2035.

? Point out an example of population momentum in Figure 36.10.

The 1981–1995 "boomlet" is a consequence of rapid reproduction in 1946–1965, as girls born during the baby boom entered their reproductive years.



▲ **Figure 36.10** Age structures for the United States in 1985, 2010 (estimated), and 2035 (projected)

CONNECTION

36.11 An ecological footprint is a measure of resource consumption

How large a population of humans can Earth hold? In Module 36.9, we saw that the world's population is growing exponentially, though at a slower rate than it did in the last century. The rate of increase, as well as population momentum, predict that the populations of most developing nations will continue to increase for the foreseeable future. The U.S. Census Bureau projects a global population of 8 billion within the next 20 years and 9.5 billion by the mid-21st century. But these numbers are only part of the story. Trillions of bacteria can live in a petri dish *if* they have sufficient resources. Do we have sufficient resources to sustain 8 or 9 billion people? To accommodate all the people expected to live on our planet by 2025, the world will have to double food production. Already, agricultural lands are under pressure. Overgrazing by the world's growing herds of livestock is turning vast areas of grassland into desert. Water use has risen sixfold over the past 70 years, causing rivers to run dry, water for irrigation to be depleted, and levels of groundwater to drop. And because so much open space will be needed to support the expanding human population, many thousands of other species are expected to become extinct.

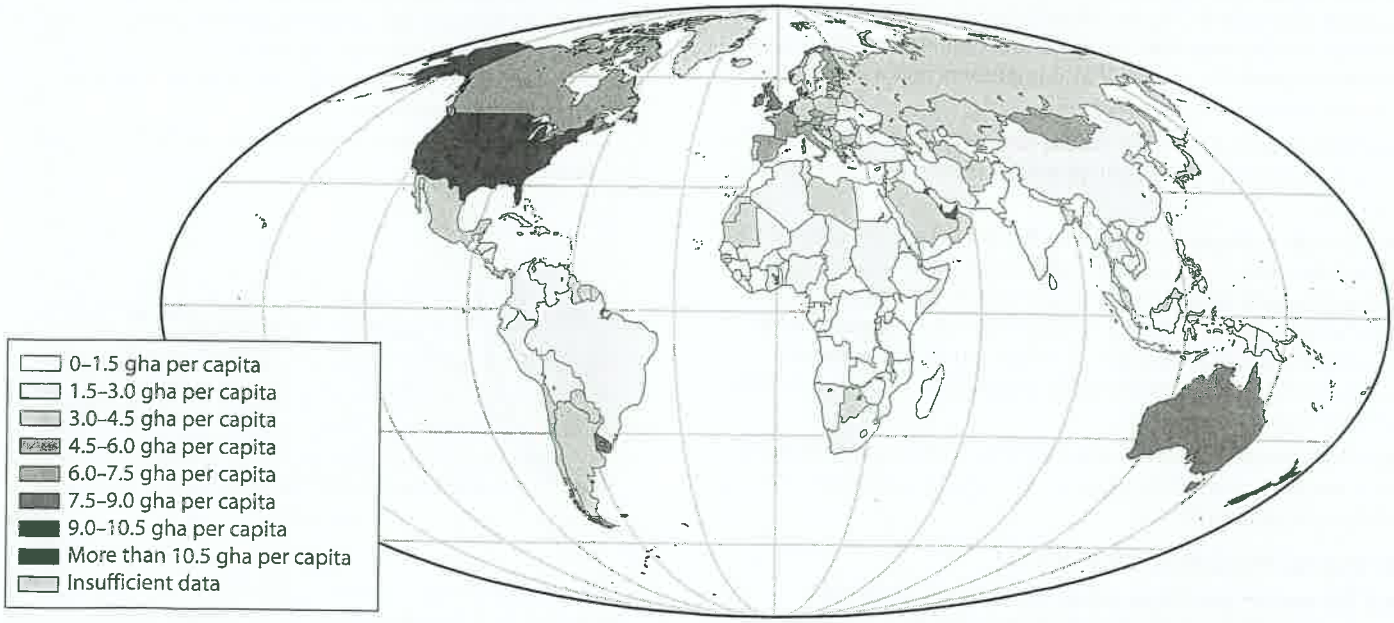
The concept of an ecological footprint is one approach to understanding resource availability and usage. An **ecological footprint** is an estimate of the amount of land required to

▲ **Figure 36.11A** Families in India (left) and the United States (right) display their possessions

provide the raw materials an individual or a nation consumes, including food, fuel, water, housing, and waste disposal. When the total area of ecologically productive land on Earth is divided by the global population, we each have a share of about 2.1 global hectares (1 hectare, or ha, = 2.47 acres; a *global hectare* is a hectare with world-average ability to produce resources and absorb wastes). According to the World Wildlife Fund, in 2005 (the most recent year for which data are available), the average ecological footprint for the world's population was 2.7 global hectares (gha)—we have already overshot the planet's capacity to sustain us.

The United States has a bigger ecological footprint (9.4 gha per person) than its own land and resources can support (5 gha per person)—it has a large ecological deficit. Looking at **Figure 36.11A**, it is not difficult to understand why. Compared with a family in rural India, Americans have an abundance of possessions. Americans also consume a disproportionate amount of food and fuel. By this measure, the ecological impact of affluent nations such as the United States is potentially as damaging as unrestrained population growth in the developing world. So the problem is not just overpopulation, but overconsumption. **Figure 36.11B** shows the ecological footprint of each country. The world's richest countries, with 15% of the global population, account for 36% of humanity's total footprint. Some researchers estimate that providing everyone with the same standard of living as the United States would require the resources of 4.5 planet Earths.

? **What is your ecological footprint? Do a Web search to find a site that calculates personal resource consumption.**



▲ **Figure 36.11B** Ecological footprints around the world

CHAPTER 36 REVIEW

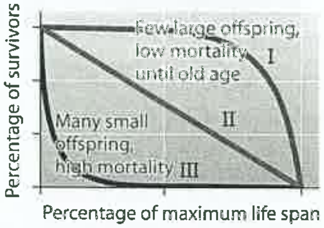
For Practice Quizzes, BioFlix, MP3 Tutors, and Activities, go to www.masteringbiology.com.

Reviewing the Concepts

Population Structure and Dynamics (36.1–36.8)

36.1 Population ecology is the study of how and why populations change.

36.2 Density and dispersion patterns are important population variables. Population density is the number of individuals in a given area or volume. Environmental and social factors influence the spacing of individuals in various dispersion patterns: clumped (most common), uniform, or random.



36.3 Life tables track survivorship in populations. Life tables and survivorship curves predict an individual's statistical chance of dying or surviving during each interval in its life. The three types of survivorship curves reflect species' differences in reproduction and mortality.

36.4 Idealized models predict patterns of population growth. Exponential growth is the accelerating increase that occurs when growth is unlimited. The equation $G = rN$ describes this J-shaped growth curve; G = the population growth rate, r = an organism's inherent capacity to reproduce, and N = the population size. Logistic growth is the model that represents the slowing of population growth as a result of limiting factors and the leveling off at carrying capacity, which is the number of individuals the environment can support. The equation $G = rN(K - N)/K$ describes a logistic growth curve, where K = carrying capacity and the term $(K - N)/K$ accounts for the leveling off of the curve.

36.5 Multiple factors may limit population growth. As a population's density increases, factors such as limited food supply and increased disease or predation may increase the death rate, decrease the birth rate, or both. Abiotic, density-independent factors such as severe weather may limit many natural populations. Most populations are probably regulated by a mixture of factors, and fluctuations in numbers are common.

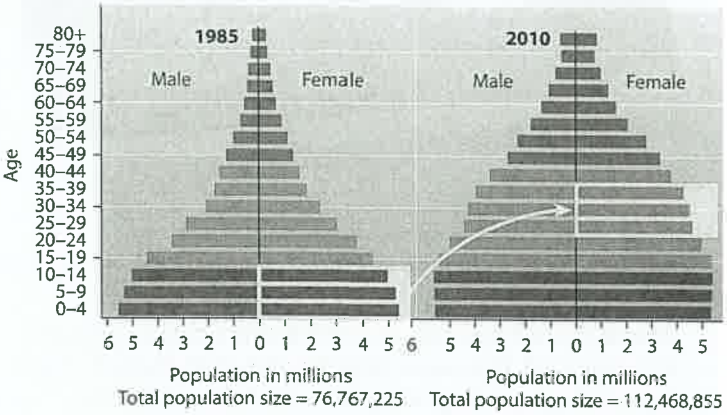
36.6 Some populations have "boom-and-bust" cycles. Boom-and-bust cycles alternate population growth and decline at regular intervals.

36.7 Evolution shapes life histories. Natural selection shapes a species' life history, the series of events from birth through reproduction to death. Populations with so-called r-selected life history traits produce many offspring and grow rapidly in unpredictable environments. Populations with K-selected traits raise few offspring and maintain relatively stable populations. Most species fall between these extremes.

36.8 Principles of population ecology have practical applications. For example, resource managers use population ecology to determine sustainable yields.

The Human Population (36.9–36.11)

36.9 The human population continues to increase, but the growth rate is slowing. The human population grew rapidly during the 20th century and currently stands at more than 6.8 billion. Demographic transition, the shift from high birth and death rates to low birth and death rates, has lowered the rate of growth in developed countries. In the developing nations, death rates have dropped, but birth rates are still high. The age structure of a population—the proportion of individuals in different age-groups—affects its future growth. Population momentum is the continued growth that occurs despite reduced fertility and is a result of girls in the 0–14 age-group of a previously expanding population reaching their childbearing years.

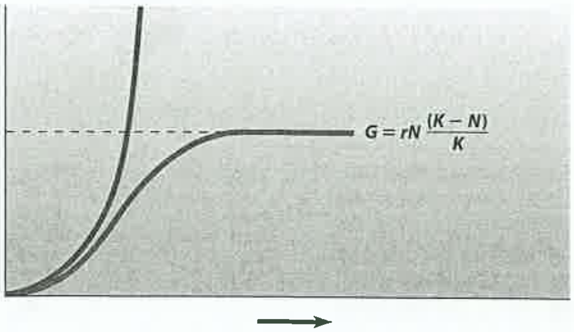


36.10 Age structures reveal social and economic trends.

36.11 An ecological footprint is a measure of resource consumption. An ecological footprint estimates the amount of land required by each person or country to produce all the resources it consumes and to absorb all its wastes. The global ecological footprint already exceeds a sustainable level. There is a huge disparity between resource consumption in more developed and less developed nations.

Connecting the Concepts

1. Use this graph of the idealized exponential and logistic growth curves to complete the following.
   a. Label the axes and curves on the graph.
   b. Give the formula that describes the blue curve.
   c. What does the dotted line represent?
   d. For each curve, indicate and explain where population growth is the most rapid.
   e. Which of these curves best represents global human population growth?



2. The graph at the top of the next page shows the demographic transition for a hypothetical country. Many developed countries that have achieved a stable population size have