Population Ecology

16

CHAPTER 16

Chapter Outline

Key Concepts	Applications
Recognize that populations vary in gene frequency, age distribution, sex ratio, size, and density.	• State how age distribution, sex ratio, and density can affect the rate of population growth.
Understand why the size of a population tends to increase.	• Describe and draw the stages of a typical population growth curve. • Identify key components that cause population growth. • Identify the factors that ultimately limit population size. • State the importance of the birth and death rates to population growth.
Recognize that human populations obey the same rules of growth as populations of other types of organisms.	• State why the human population must have an upper limit. • List methods that would effectively control human population size.

16.1 Population Characteristics

A **population** is a group of organisms of the same species located in the same place at the same time. Examples are the number of dandelions in your front yard, the rat population in the sewers of your city, or the number of people in your biology class. On a larger scale, all the people of the world constitute the human population. The terms *species* and *population* are interrelated because a species is a population—the largest possible population of a particular kind of organism. The term *population,* however, is often used to refer to portions of a species by specifying a space and time. For example, the size of the human population in a city changes from hour to hour during the day and varies according to where you set the boundaries of the city.

Because each local population is a small portion of a species, we should expect distinct populations of the same species to show differences. One of the ways in which they can differ is in gene frequency. Chapter 11 on population genetics introduced you to the concept of **gene frequency,** which is a measure of how often a specific gene shows up in the gametes of a population. Two populations of the same species often have quite different gene frequencies. For example, many populations of mosquitoes have high frequencies of insecticide-resistant genes, whereas others do not. The frequency of the genes for tallness in humans is greater in certain African tribes than in any other human population. Figure 16.1 shows that the frequency of the allele for type B blood differs significantly from one human population to another.

Because members of a population are of the same species, sexual reproduction can occur, and genes can flow from one generation to the next. Genes can also flow from one place to another as organisms migrate or are carried from one geographic location to another. **Gene flow** is used to refer to both the movement of genes within a species because of migration and the movement from one generation to the next as a result of gene replication and sexual reproduction. Typically both happen together as individuals migrate to new regions and subsequently reproduce, passing their genes to the next generation in the new area.

Another feature of a population is its **age distribution,** which is the number of organisms of each age in the population. In addition, organisms are often grouped into the following categories:

1. Prereproductive juveniles—insect larvae, plant seedlings, or babies
2. Reproductive adults—mature insects, plants producing seeds, or humans in early adulthood
3. Postreproductive adults no longer capable of reproduction—annual plants that have shed their seeds, salmon that have spawned, and many elderly humans.

A population is not necessarily divided into equal thirds (figure 16.2). In some situations, a population may be made up of a majority of one age group. If the majority of the population is prereproductive, then a "baby boom" should be anticipated in the future. If a majority of the population is reproductive, the population should be growing rapidly. If the majority of the population is postreproductive, a popula-

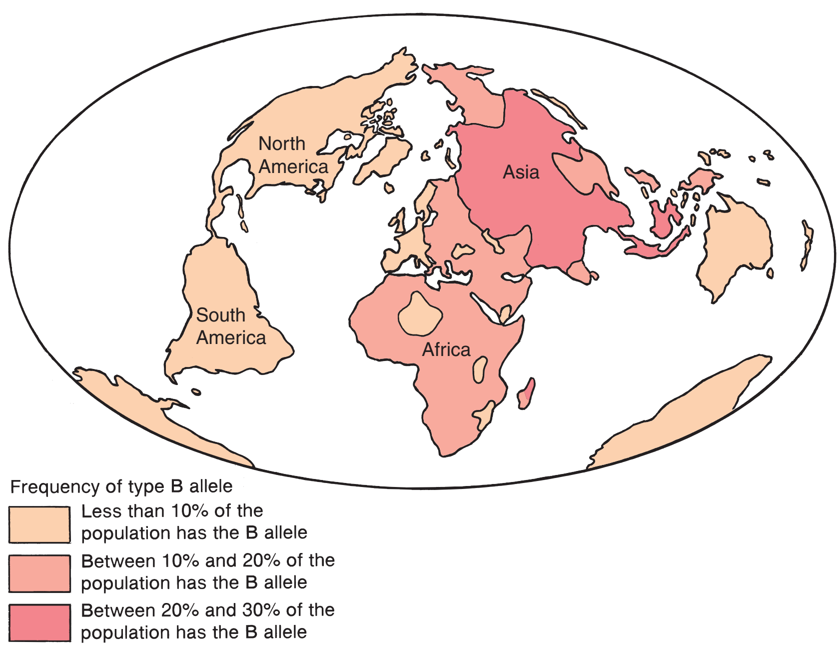


Figure 16.1

Distribution of the Allele for Type B Blood
The allele for type B blood is not evenly distributed in the world. This map shows that the type B allele is most common in parts of Asia and has been dispersed to the Middle East and parts of Europe and Africa. There has been very little flow of the allele to the Americas.

tion decline should be anticipated. Many organisms that live only a short time and have high reproductive rates can have age distributions that change significantly in a matter of weeks or months. For example, many birds have a flurry of reproductive activity during the summer months. Therefore, if you sample the population of a specific species of bird at different times during the summer you would have widely different proportions of reproductive and prereproductive individuals.

Populations can also differ in their sex ratios. The **sex ratio** is the number of males in a population compared to the number of females. In bird and mammal species where strong pair-bonding occurs, the sex ratio may be nearly one to one (1:1). Among mammals and birds that do not have strong pair-bonding, sex ratios may show a larger number of females than males. This is particularly true among game species, where more males than females are shot, resulting in a higher proportion of surviving females. Because one male can fertilize several females, the population can remain large even though the females outnumber the males. However, if the population of these managed game species becomes large enough to cause a problem, it becomes necessary to harvest some of the females as well because their number determines how much reproduction can take place. In addition to these examples, many species of animals like bison, horses, and elk have mating systems in which one male maintains a harem of females. The sex ratio in these small groups is quite different from a 1:1 ratio (figure 16.3). There are very few situations in which the number of males exceeds the number of

Figure 16.3

Sex Ratio in Elk
Some male animals defend a harem of females; therefore the sex ratio in these groups is several females per male.

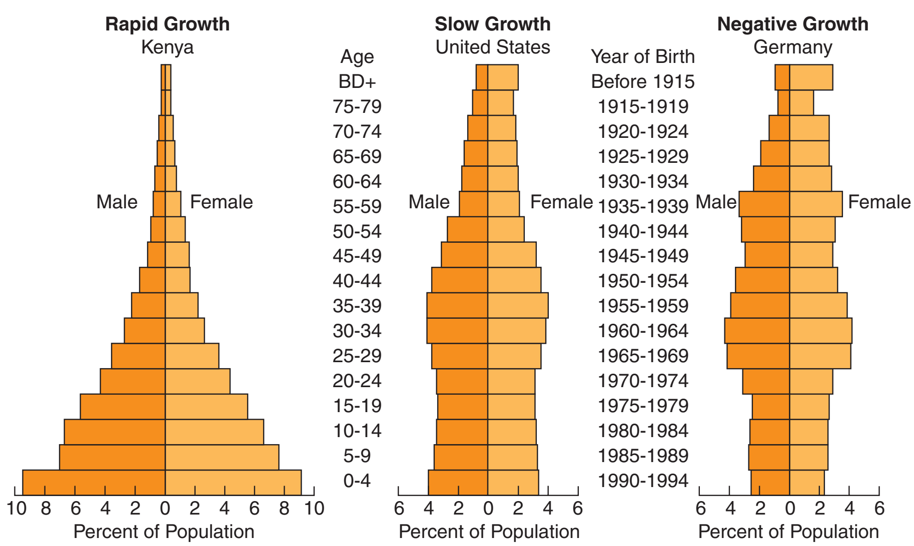


Figure 16.2

Age Distribution in Human Populations
The relative number of individuals in each of the three categories (prereproductive, reproductive, and postreproductive) can give a good clue to the future of the population. Kenya has a large number of young individuals who will become reproducing adults. Therefore this population will grow rapidly and will double in about 25 years. The United States has a declining proportion of prereproductive individuals but a relatively large reproductive population. Therefore it will continue to grow for a time but will probably stabilize in the future. Germany's population has a large proportion of postreproductive individuals and a small proportion of prereproductive individuals. Its population is beginning to fall.

Source: U.S. Bureau of the Census and the United Nations, as reported in Joseph A. McFalls, Jr., "Population: A Lively Introduction," *Population Bulletin,* vol. 46, no. 2. Washington, D.C.: Population Reference Bureau, Inc., October 1991.

(a)

(b)

Figure 16.4

Changes in Population Density
This population of lodgepole pine seedlings consists of a large number of individuals very close to one another (*a*). As the trees grow, many of the weaker trees will die, the distance between individuals will increase, and the population density will be reduced (*b*).

females. In some human and other populations, there may be sex ratios in which the males dominate if female mortality is unusually high or if some special mechanism separates most of one sex from the other.

Regardless of the sex ratio of a population, most species can generate large numbers of offspring, producing a concentration of organisms in an area. **Population density** is the number of organisms of a species per unit area. Some populations are extremely concentrated in a limited space; others are well dispersed. As the population density increases, competition among members of the population for the necessities of life increases. This increases the likelihood that some individuals will explore new habitats and migrate to new areas. Increases in the intensity of competition that cause changes in the environment and lead to dispersal are often referred to as **population pressure.** The dispersal of individuals to new areas can relieve the pressure on the home area and lead to the establishment of new populations. Among animals, it is often the juveniles who participate in this dispersal process. Female bears generally mate every other year and abandon their nearly grown young the summer before the next set of cubs is to be born. The abandoned young bears tend to wander and disperse to new areas. Similarly, young turtles, snakes, rabbits, and many other common animals disperse during certain times of the year. That is one of the reasons you see so many road-killed animals in the spring and fall.

If dispersal cannot relieve population pressure, there is usually an increase in the rate at which individuals die because of predation, parasitism, starvation, and accidents. In plant populations, dispersal is not very useful for relieving population density; instead, the death of weaker individuals usually results in reduced population density. In the lodgepole pine, seedlings become established in areas following fire and dense thickets of young trees are established. As the stand ages, many small trees die and the remaining trees grow larger as the population density drops (figure 16.4).

16.2 Reproductive Capacity

Sex ratios and age distributions within a population have a direct bearing on the rate of reproduction. Each species has an inherent **reproductive capacity** or **biotic potential,** which is the theoretical maximum rate of reproduction. Generally, this biotic potential is many times larger than the number of offspring needed simply to maintain the population. For example, a female carp may produce 1 million to 3 million eggs in her lifetime. This is her reproductive capacity. However, only two or three of these offspring ever develop into sexually mature adults. Therefore, her reproductive rate is much smaller than her reproductive potential.

A high reproductive capacity is valuable to a species because it provides many slightly different individuals for the

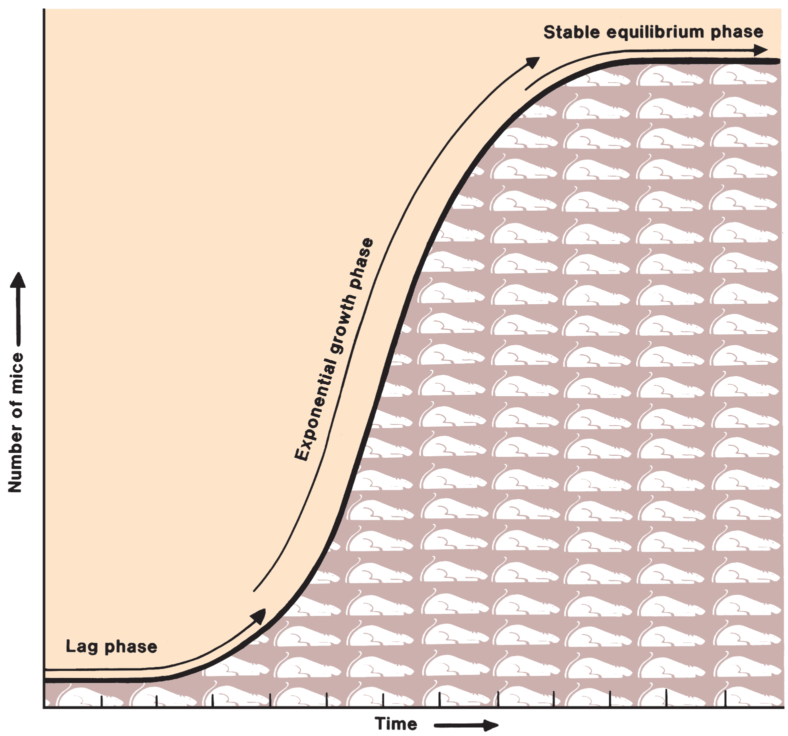


Figure 16.5

A Typical Population Growth Curve
In this mouse population, the period of time in which there is little growth is known as the lag phase. This is followed by a rapid increase in population as the offspring of the originating population begin to reproduce themselves; this is known as the exponential growth phase. Eventually the population reaches a stable equilibrium phase, during which the birthrate equals the deathrate.

environment to select among. With most plants and animals, many of the potential gametes are never fertilized. An oyster may produce a million eggs a year, but not all of them are fertilized, and most that are fertilized die. An apple tree with thousands of flowers may produce only a few apples because the pollen that contains the sperm cells was not transferred to the female part of each flower in the process of pollination. Even after the new individuals are formed, mortality is usually high among the young. Most seeds that fall to the earth do not grow, and most young animals die. But, usually, enough survive to ensure continuance of the species. Organisms that reproduce in this way spend large amounts of energy on the production of gametes and young, without caring for the young. Thus the probability that any individual will reach reproductive age is small.

A second way of approaching reproduction is to produce relatively fewer individuals but provide care and protection that ensure a higher probability that the young will become reproductive adults. Humans generally produce a single offspring per pregnancy, but nearly all of them live. In effect, energy has been channeled into the care and protection of the young produced rather than into the production of incredibly large numbers of potential young. Even though fewer young are produced by animals like birds and mammals, their reproductive capacity still greatly exceeds the number required to replace the parents when they die.

16.3 The Population Growth Curve

Because most species of organisms have a high reproductive capacity, there is a tendency for populations to grow if environmental conditions permit. For example, if the usual litter size for a pair of mice is 4, the 4 would produce 8, which in turn would produce 16, and so forth. Figure 16.5 shows a graph of change in population size over time known as a **population growth curve.** This kind of curve is typical for situations where a species is introduced into a previously unutilized area.

The change in the size of a population depends on the rate at which new organisms enter the population compared to the rate at which they leave. The number of new individuals added to the population by reproduction per thousand individuals is called **natality.** The number of individuals leaving the population by death per thousand individuals is called **mortality.** When a small number of organisms (two mice) first invade an area, there is a period of time before reproduction takes place during which the population remains small and relatively constant. This part of the population growth curve is known as the **lag phase.** During the lag phase both natality and mortality are low. The lag phase occurs because reproduction is not an instantaneous event. Even after animals enter an area they must mate and produce young. This may take days or years depending on the animal. Similarly, new plant introductions must grow to maturity, produce flowers, and set seed. Some annual plants may do this in less than a year, whereas some large trees may take several years of growth before they produce flowers.

In organisms that take a long time to mature and produce young, such as elephants, deer, and many kinds of plants, the lag phase may be measured in years. With the mice in our example, it will be measured in weeks. The first litter of young will be able to reproduce in a matter of weeks. Furthermore, the original parents will probably produce an additional litter or two during this time period. Now we have several pairs of mice reproducing more than just once. With several pairs of mice reproducing, natality increases and mortality remains low; therefore the population begins to grow at an ever-increasing (accelerating) rate. This portion of the population growth curve is known as the **exponential growth phase.**

The number of mice (or any other organism) cannot continue to increase at a faster and faster rate because, eventually, something in the environment will become limiting and cause an increase in the number of deaths. For animals, food, water, or nesting sites may be in short supply, or predators or disease may kill many individuals. Plants may lack water, soil nutrients, or sunlight. Eventually, the number of individuals entering the population will come to equal the number of individuals leaving it by death or migration, and the population size becomes stable. Often there is both a decrease in natality and an increase in mortality at this point. This portion of the population growth curve is known as the **stable equilibrium phase.** It is important to recognize that this is still a population with births, deaths, migration, and a changing mix of individuals; however the size of the population is stable.

16.4 Population-Size Limitations

Populations cannot continue to increase indefinitely; eventually, some factor or set of factors acts to limit the size of a population, leading to the development of a stable equilibrium phase or even to a reduction in population size. The identifiable factors that prevent unlimited population growth are known as **limiting factors.** All the different limiting factors that act on a population are collectively known as **environmental resistance,** and the maximum population that an area can support is known as the **carrying capacity** of the area. In general, organisms that are small and have short life spans tend to have fluctuating populations and do not reach a carrying capacity, whereas large organisms that live a long time tend to reach an optimum population size that can be sustained over an extended period (figure 16.6). A forest ecosystem contains populations of many insect species that fluctuate widely and rarely reach a carrying capacity, but the number of specific tree species or large animals such as owls or deer is relatively constant. Each is at the carrying capacity of the ecosystem for its species.

Carrying capacity is not an inflexible number, however. Often such environmental differences as successional changes, climate variations, disease epidemics, forest fires, or floods can change the carrying capacity of an area for specific species. In aquatic ecosystems one of the major factors that determine the carrying capacity is the amount of

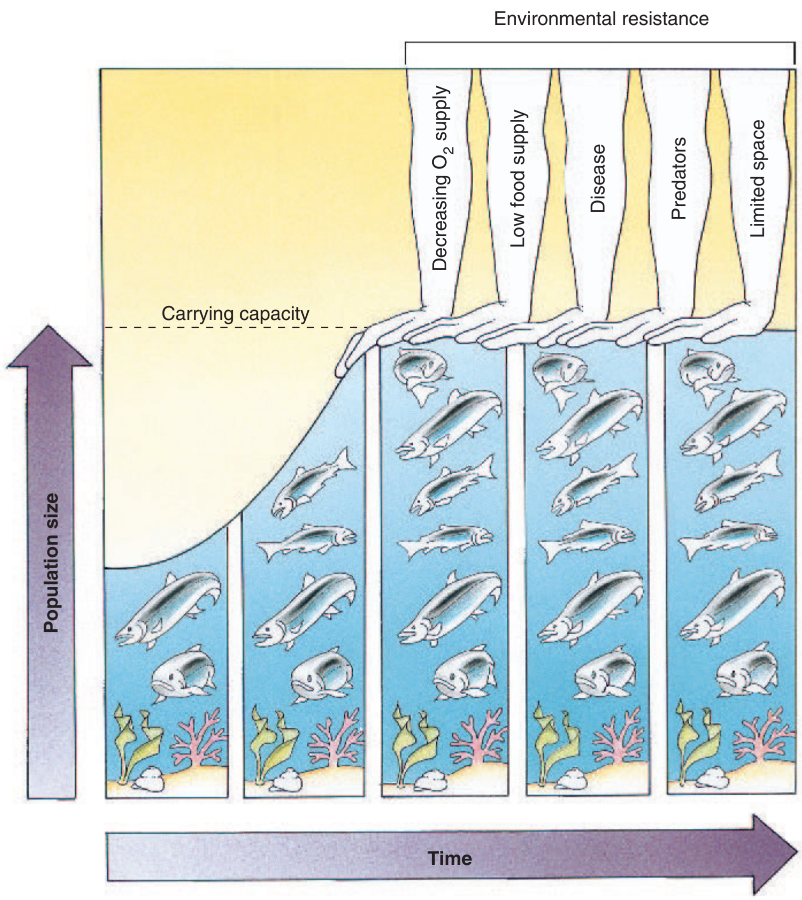


Figure 16.6

Carrying Capacity
A number of factors in the environment, such as food, oxygen supply, diseases, predators, and space determine the number of organisms that can survive in a given area—the carrying capacity of that area. The environmental factors that limit populations are collectively known as environmental resistance.

nutrients in the water. In areas where nutrients are abundant, the numbers of various kinds of organisms are high. Often nutrient levels fluctuate with changes in current or runoff from the land, and plant and animal populations fluctuate as well. In addition, a change that negatively affects the carrying capacity for one species may increase the carrying capacity for another. For example, the cutting down of a mature forest followed by the growth of young trees increases the carrying capacity for deer and rabbits, which use the new growth for food, but decreases the carrying capacity for squirrels, which need mature, fruit-producing trees as a source of food and old, hollow trees for shelter.

Wildlife management practices often encourage modifications to the environment that will increase the carrying capacity for the designated game species. The goal of wildlife managers is to have the highest sustainable population available for harvest by hunters. Typical habitat modifications include creating water holes, cutting forests to provide young growth, and encouraging the building of artificial nesting sites.

In some cases the size of the organisms in a population also affects the carrying capacity. For example, an aquarium of a certain size can support only a limited number of fish, but the size of the fish makes a difference. If all the fish are tiny, a large number can be supported, and the carrying capacity is high; however, the same aquarium may be able to support only one large fish. In other words, the biomass of the population makes a difference (figure 16.7). Similarly, when an area is planted with small trees, the population size is high. But as the trees get larger, competition for nutrients and sunlight becomes more intense, and the number of trees declines while the biomass increases.

16.5 Categories of Limiting Factors

Limiting factors can be placed in four broad categories:

1. Availability of raw materials
2. Availability of energy
3. Production and disposal of waste products
4. Interaction with other organisms

The first category of limiting factors is the *availability of raw materials.* For example, plants require magnesium for the manufacture of chlorophyll, nitrogen for protein production, and water for the transport of materials and as a raw material for photosynthesis. If these substances are not present in the soil, the growth and reproduction of plants is inhibited. However, if fertilizer supplies these nutrients, or if irrigation is used to supply water, the effects of these limiting factors can be removed, and some other factor becomes limiting. For animals, the amount of water, minerals, materials for nesting, suitable burrow sites, or food may be limiting factors. Food for animals really fits into both this category and the next because it supplies both raw materials and energy.

The second major type of limiting factor is the *availability of energy.* The amount of light available is often a limiting factor for plants, which require light as an energy source for photosynthesis. Because all animals use other living things as sources of energy and raw materials, a major limiting factor for any animal is its food source.

The *accumulation of waste products* is the third general category of limiting factors. It does not usually limit plant populations because they produce relatively few wastes. However, the buildup of high levels of self-generated

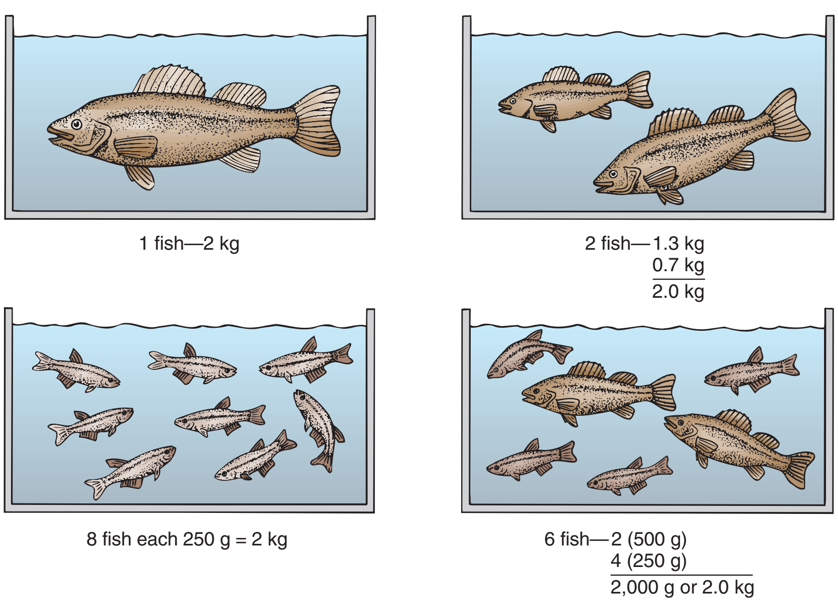
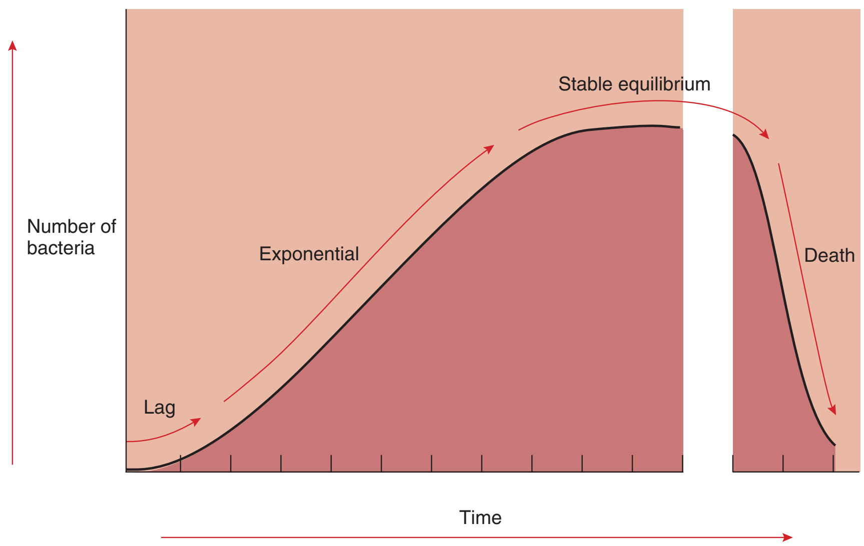


Figure 16.7

The Effect of Biomass on Carrying Capacity
Each aquarium can support a biomass of 2 kilograms of fish. The size of the population is influenced by the body size of the fish in the population.

Figure 16.8

Bacterial Population Growth Curve
The rate of increase in the population of these bacteria is typical of population growth in a favorable environment. When the environmental conditions change as a result of an increase in the amount of waste products, the population first levels off, then begins to decrease. This period of decreasing population size is known as the death phase.



waste products is a problem for bacterial populations and populations of tiny aquatic organisms. As wastes build up, they become more and more toxic, and eventually reproduction stops, or the population may even die out. When a few bacteria are introduced into a solution containing a source of food, they go through the kind of population growth curve typical of all organisms. As expected, the number of bacteria begins to increase following a lag phase, increases rapidly during the exponential growth phase, and eventually reaches stability in the stable equilibrium phase. But as waste products accumulate, the bacteria literally drown in their own wastes. When space for disposal is limited, and no other organisms are present that can convert the harmful wastes to less harmful products, a population decline known as the **death phase** follows (figure 16.8).

Wine makers deal with this situation. When yeasts ferment the sugar in grape juice, they produce ethyl alcohol. When the alcohol concentration reaches a certain level, the yeast population stops growing and eventually declines. Therefore wine can naturally reach an alcohol concentration of only 12% to 15%. To make any drink stronger than that (of a higher alcohol content), water must be removed (to distill) or alcohol must be added (to fortify).

In small aquatic pools like aquariums, it is often difficult to keep populations of organisms healthy because of the buildup of ammonia in the water from the waste products of the animals. This is the primary reason that activated charcoal filters are commonly used in aquariums. The charcoal removes many kinds of toxic compounds and prevents the buildup of waste products.

The fourth set of limiting factors is *organism interaction.* As we learned in chapter 15 on community interaction, organisms influence each other in many ways. Some organisms are harmed and others benefit. The population size of any organism is negatively affected by parasitism, predation, or competition. Parasitism and predation usually involve interactions between two different species, although cannibalism of others of the same species does occur in some animals. Competition among members of the same species is often extremely intense. This is true for all kinds of organisms, not just animals.

On the other hand many kinds of organisms perform services for others that have beneficial effects on the population. For example, decomposer organisms destroy toxic waste products, thus benefiting populations of animals. They also recycle materials needed for the growth and development of all organisms. Mutualistic relationships benefit both populations involved. The absence of such beneficial organisms would be a limiting factor.

Often, the population sizes of two kinds of organisms are interdependent because each is a primary limiting factor of the other. This is most often seen in parasite-host relationships and predator-prey relationships. A good example is the relationship of the lynx (a predator) and the varying hare (the prey) as it was studied in Canada. The varying hare has a high reproductive capacity. In peak reproductive years, a female varying hare can produce 16 to 18 young. As with many animals a primary cause of death is predation. The varying hare population is a good food source for a variety of predators including the lynx. When the population of varying hares increases it provides an abundant source of food for the lynx and the size of the lynx population rises, and when the population of hares decreases so does that of the lynx. This pattern repeats itself in a ten-year cycle (figure 16.9).

Recent studies indicate that one of the causes of the decline in varying hare populations is a reduction in their

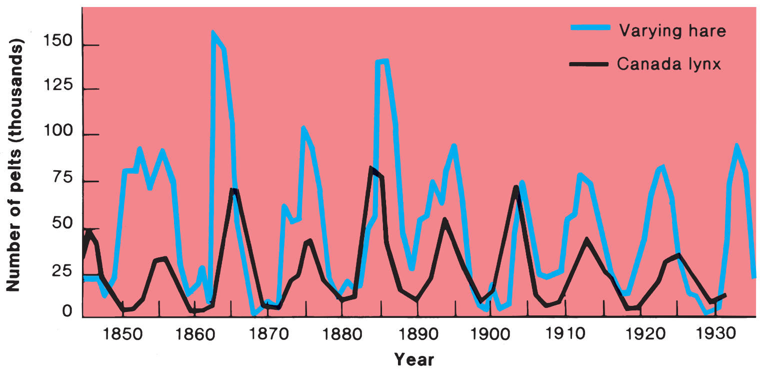


Figure 16.9

Organism Interaction
The interaction between predator and prey species is complex and often difficult to interpret. These data were collected from the records of the number of pelts purchased by the Hudson Bay Company. It shows that the two populations fluctuate, with changes in the lynx population usually following changes in varying hare populations.

Source: Data from D. A. MacLulich, *Fluctuations in the Numbers of the Varying Hare (Lepus americanus),* University of Toronto Press, 1937, (reprinted 1974), Toronto, Canada.

reproductive rate. The causes of this reduction rate may be related to a variety of factors including: reduced quality of food and higher levels of stress resulting from greater difficulty in finding food and avoiding predators. With reduced reproduction and continued high predation the varying hare population drops. With reduced numbers of hares, lynx populations drop. Eventually the reproductive rate of hares increases and the population rebounds followed by a rebound in the lynx population as well. It appears that both food availability and predation are important limiting factors that determine the size of the varying hare population and the number of varying hares is a primary limiting factor for the lynx.

Extrinsic and Intrinsic Limiting Factors

Some factors that help control populations come from outside the population and are known as **extrinsic factors.** Predators, loss of a food source, lack of sunlight, or accidents of nature are all extrinsic factors. However, many kinds of organisms self-regulate their population size. The mechanisms that allow them to do this are called **intrinsic factors.** For example, a study of rats under crowded living conditions showed that as conditions became more crowded, abnormal social behavior became common. There was a decrease in litter size, fewer litters per year were produced, mothers were more likely to ignore their young, and many young were killed by adults. Thus changes in the behavior of the members of the rat population itself resulted in lower birthrates and higher deathrates, leading to a reduction in the population growth rate. As another example, trees that are stressed by physical injury or disease often produce extremely large numbers of seeds (offspring) the following year. The trees themselves alter their reproductive rate. The opposite situation is found among populations of white-tailed deer. It is well known that reproductive success is reduced when the deer experience a series of severe winters. When times are bad, the female deer are more likely to have single offspring rather than twins.

Density-Dependent and Density-Independent Limiting Factors

Many populations are controlled by limiting factors that become more effective as the size of the population increases. Such factors are referred to as **density-dependent factors.** Many of the factors we have already discussed are density-dependent. For example, the larger a population becomes, the more likely it is that predators will have a chance to catch some of the individuals. A prolonged period of increasing population allows the size of the predator population to increase as well. Large populations with high population density are more likely to be affected by epidemics of parasites than are small populations of widely dispersed individuals because dense populations allow for the easy spread of parasites from one individual to another. The rat example discussed previously is another good example of a density-dependent factor operating because the amount of abnormal behavior increased as the density of the population increased. In general, whenever there is competition among members of a population, its intensity increases as the population increases. Large organisms that tend to live a long time and have relatively few young are most likely to be controlled by density-dependent factors.

Density-independent factors are population-controlling influences that are not related to the size of the population. They are usually accidental or occasional extrinsic factors in nature that happen regardless of the size or density of a population. A sudden rainstorm may drown many small plant seedlings and soil organisms. Many plants and animals are killed by frosts that come late in spring or early in the fall. A small pond may dry up, resulting in the death of many organisms. The organisms most likely to be controlled by density-independent factors are small, short-lived organisms that can reproduce very rapidly.

So far we have looked at populations primarily from a nonhuman point of view. Now it is time to focus on the human species and the current problem of world population growth.

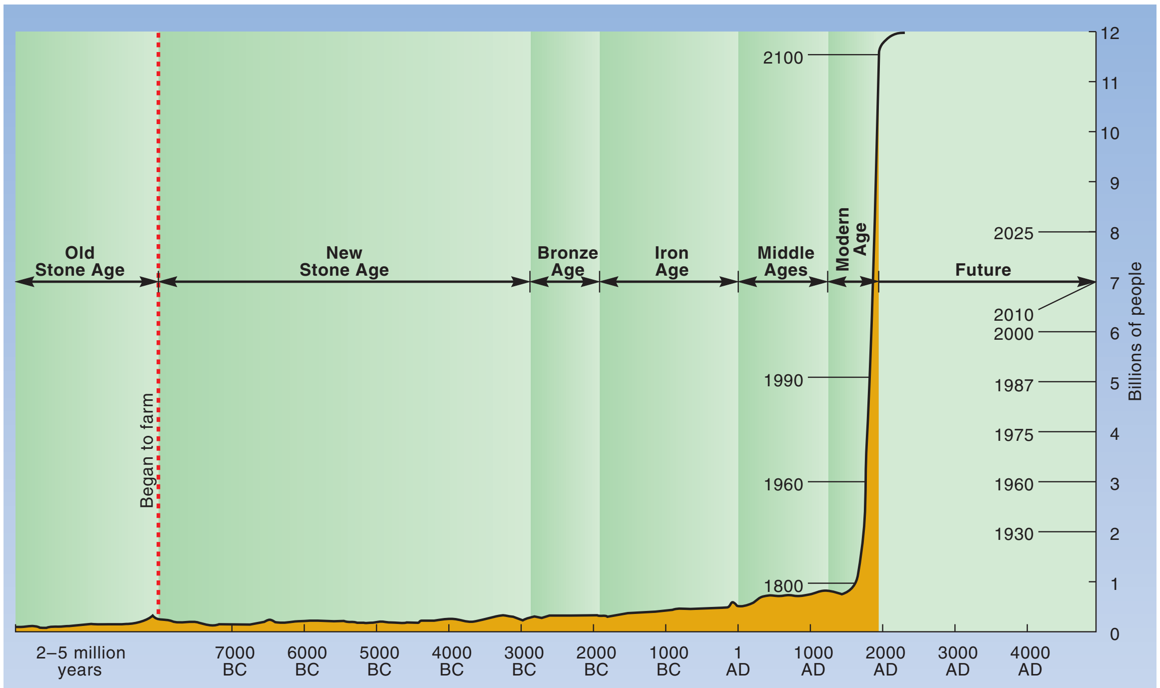


Figure 16.10

Human Population Growth

The number of humans doubled from A.D. 1800 to 1930 (from 1 billion to 2 billion), doubled again by 1975 (4 billion), and is projected to double again by the year 2025. How long can the human population continue to double before the Earth's ultimate carrying capacity is reached?

Source: Data from Jean Van Der Tak, et al., "Our Population Predicament: A New Look," in *Population Reference Bureau,* Washington, D.C.

16.6 Limiting Factors to Human Population Growth

Today we hear differing opinions about the state of the world's human population. On one hand we hear that the population is growing rapidly. By contrast we hear that some countries are afraid that their populations are shrinking. Other countries are concerned about the aging of their populations because birthrates and deathrates are low. In magazines and on television we see that there are starving people in the world. At the same time we hear discussions about the problem of food surpluses and obesity in many countries. Some have even said that the most important problem in the world today is the rate at which the human population is growing; others maintain that the growing population will provide markets for goods and be an economic boon. How do we reconcile this mass of conflicting information?

It is important to realize that human populations follow the same patterns of growth and are acted upon by the same kinds of limiting factors as are populations of other organisms. When we look at the curve of population growth over the past several thousand years, estimates are that the human population remained low and constant for thousands of years but has increased rapidly in the past few hundred years (figure 16.10). For example, it has been estimated that when Columbus discovered America, the Native American population was about 1 million and was at or near its carrying capacity. Today, the population of North America is over 300 million people. Does this mean that humans are different from other animal species? Can the human population continue to grow forever?

The human species is no different from other animals. It has an upper limit set by the carrying capacity of the environment but the human population has been able to increase astronomically because technological changes and displacement of other species has allowed us to shift the carrying capacity upward. Much of the exponential growth phase of the human population can be attributed to the removal of diseases, improvement in agricultural methods, and replacement of natural ecosystems with artificial agricultural ecosystems. But even these conditions have their limits. There will be some limiting factors that eventually cause a leveling off of our population growth curve. We cannot increase beyond our ability to get raw materials and energy, nor can we ignore the waste products we produce or the other organisms with which we interact.

HOW SCIENCE WORKS 16.1

Thomas Malthus and His Essay on Population

In 1798 Thomas Robert Malthus, an Englishman, published an essay on human population. It presented an idea that was contrary to popular opinion. His basic thesis was that human population increased in a geometric or exponential manner (2, 4, 8, 16, 32, 64, etc.), whereas the ability to produce food increased only in an arithmetic manner (1, 2, 3, 4, 5, 6, etc.). The ultimate outcome of these different rates would be that population would outgrow the ability of the land to produce food. He concluded that wars, famines, plagues, and natural disasters would be the means of controlling the size of the human population. His predictions were hotly debated by the intellectual community of his day. His assumptions and conclusions were attacked as erroneous and against the best interest of society. At the time he wrote the essay, the popular opinion was that human knowledge and "moral constraint" would be able to create a world that would supply all human needs in abundance. One of Malthus's basic postulates was that "commerce between the sexes" (sexual intercourse) would continue unchanged; other philosophers of the day believed that sexual behavior would take less procreative forms and human population would be limited. Only within the past 50 years, however, have really effective conception-control mechanisms become widely accepted and used, and they are used primarily in developed countries.

Malthus did not foresee the use of contraception, major changes in agricultural production techniques, or the exporting of excess people to colonies in the Americas. These factors, as well as high deathrates, prevented the most devastating of his predictions from coming true. However, in many parts of the world today, people are experiencing the forms of population control (famine, epidemic disease, wars, and natural disasters) predicted by Malthus in 1798. Many people believe that his original predictions were valid—only his time scale was not correct—and that we are seeing his predictions come true today.

Another important impact of Malthus's essay was the effect it had on the young Charles Darwin. When Darwin read it, he saw that what was true for the human population could be applied to the whole of the plant and animal kingdoms. As over-reproduction takes place, there would be increased competition for food, resulting in the death of the less fit organisms. This was an important part of the theory he called *natural selection.*

Available Raw Materials

To many of us, raw materials consist simply of the amount of food available, but we should not forget that in a technological society, iron ore, lumber, irrigation water, and silicon chips are also raw materials. However, most people of the world have much more basic needs. For the past several decades, large portions of the world's population have not had enough food. Although it is biologically accurate to say that the world can currently produce enough food to feed all the people of the world, there are many reasons why people can't get food or won't eat it. Many cultures have food taboos or traditions that prevent the use of some available food sources. For example, pork is forbidden in some cultures. Certain groups of people find it almost impossible to digest milk. Some African cultures use a mixture of cow's milk and cow's blood as food, which people of other cultures might be unable to eat.

In addition, there are complex political, economic, and social issues related to the production and distribution of food. In some cultures, farming is a low-status job, which means that people would rather buy their food from someone else than grow it themselves. This can result in underutilization of agricultural resources. Food is sometimes used as a political weapon when governments want to control certain groups of people. But probably most important is the fact that transportation of food from centers of excess to centers of need is often very difficult and expensive.

A more fundamental question is whether the world can continue to produce enough food. In 2001 the world population was growing at a rate of 1.3% per year. This amounts to about 160 new people added to the world population every minute, which will result in a doubling of the world population in about 50 years. With a continuing increase in the number of mouths to feed, it is unlikely that food production will be able to keep pace with the growth in human population (How Science Works 16.1). A primary indicator of the status of the world food situation is the amount of grain produced for each person in the world (per capita grain production). World per capita grain production peaked in 1984. The less-developed nations of the world have a disproportionately large increase in population and a decline in grain production because they are less able to afford costly fertilizer, machinery, and the energy necessary to run the machines and irrigate the land to produce their own grain.

Availability of Energy

The availability of energy is the second broad limiting factor that affects human populations as well as other kinds of organisms. All species on Earth ultimately depend on sunlight for energy—including the human species. Whether one produces electrical power from a hydroelectric dam, burns fossil fuels, or uses a solar cell, the energy is derived from the Sun. Energy is needed for transportation, building and maintaining homes, and food production. It is very difficult to develop unbiased, reasonably accurate estimates of global energy "reserves" in the form of petroleum, natural gas, and coal. Therefore, it is difficult to predict how long these "reserves" might last. We do know, however, that the quantities are limited and that the rate of use has been increasing.

If the less-developed countries were to attain a standard of living equal to that of the developed nations, the global energy "reserves" would disappear overnight. Because the United States constitutes approximately 4.6% of the world's population and consumes approximately 25% of the world's energy resources, raising the standard of living of the entire world population to that of the United States would result in a tremendous increase in the rate of consumption of energy and reduce theoretical reserves drastically. Humans should realize that there is a limit to our energy resources; we are living on solar energy that was stored over millions of years, and we are using it at a rate that could deplete it in hundreds of years. Will energy availability be the limiting factor that determines the ultimate carrying capacity for humans, or will problems of waste disposal predominate?

Production of Wastes

One of the most talked-about aspects of human activity is the problem of waste disposal. Not only do we have normal biological wastes, which can be dealt with by decomposer organisms, but we generate a variety of technological wastes and by-products that cannot be efficiently degraded by decomposers. Most of what we call pollution results from the waste products of technology. The biological wastes usually can be dealt with fairly efficiently by building wastewater treatment plants and other sewage facilities. Certainly these facilities take energy to run, but they rely on decomposers to degrade unwanted organic matter to carbon dioxide and water. Earlier in this chapter we discussed the problem that bacteria and yeasts face when their metabolic waste products accumulate. In this situation, the organisms so "befoul their nest" that their wastes poison them. Are humans in a similar situation on a much larger scale? Are we dumping so much technological waste, much of which is toxic, into the environment that we are being poisoned? Some people believe that disregard for the quality of our environment will be a major factor in decreasing our population growth rate. In any case, it makes good sense to do everything possible to stop pollution and work toward cleaning our nest.

Interactions with Other Organisms

The fourth category of limiting factors that determine carrying capacity is interaction among organisms. Humans interact with other organisms in as many ways as other animals do. We have parasites and occasionally predators. We are predators in relation to a variety of animals, both domesticated and wild. We have mutualistic relationships with many of our domesticated plants and animals because they could not survive without our agricultural practices and we would not survive without the food they provide. Competition is also very important. Insects and rodents compete for the food we raise, and we compete directly with many kinds of animals for the use of ecosystems.

As humans convert more and more land to agriculture and other purposes, many other organisms are displaced. Many of these displaced organisms are not able to compete successfully and must leave the area, have their populations reduced, or become extinct. The American bison (buffalo), African and Asian elephants, panda, and grizzly bear are a few species that are considerably reduced in number because they were not able to compete successfully with the human species. The passenger pigeon, Carolina parakeet, and great auk are a few that have become extinct. Our parks and natural areas have become tiny refuges for plants and animals that once occupied vast expanses of the world. If these refuges are lost, many organisms will become extinct. What today might seem to be an insignificant organism that we can easily do without may tomorrow be seen as a link to our very survival. We humans have been extremely successful in our efforts to convert ecosystems to our own uses at the expense of other species.

Competition with one another (intraspecific competition), however, is a different matter. Because competition is negative to both organisms, competition between humans harms humans. We are not displacing another species, we are displacing some of our own kind. Certainly, when resources are in short supply, there is competition. Unfortunately, it is usually the young that are least able to compete, and high infant mortality is the result.

Control of Human Population Is a Social Problem

Humans are different from most other organisms in a fundamental way: We are able to predict the outcome of a specific course of action. Current technology and medical knowledge are available to control human population and improve the health and well-being of the people of the world. Why then does the human population continue to grow, resulting in human suffering and stressing the environment in which we live? Because we are social animals that have freedom of choice, we frequently do not do what is considered "best" from an unemotional, unselfish, biological point of view. People make decisions based on historical, social, cultural, ethical, and personal considerations. What is best for the population as a whole may be bad for you as an individual (Outlooks 16.1).

The biggest problems associated with control of the human population are not biological problems but, rather, require the efforts of philosophers, theologians, politicians, and sociologists. As population increases, so will political, social, and biological problems; individual freedom will diminish, intense competition for resources will intensify, and famine and starvation will become even more common. The knowledge and technology necessary to control the human population are available, but the will is not. What will eventually limit the size of our population? Will it be lack of resources, lack of energy, accumulated waste products, competition among ourselves, or rational planning of family size?

Recent studies of the changes in the population growth rates of different countries indicates that a major factor determining the size of families is the educational status of women. Regardless of other cultural differences, as girls and

OUTLOOKS 16.1

Government Policy and Population Control

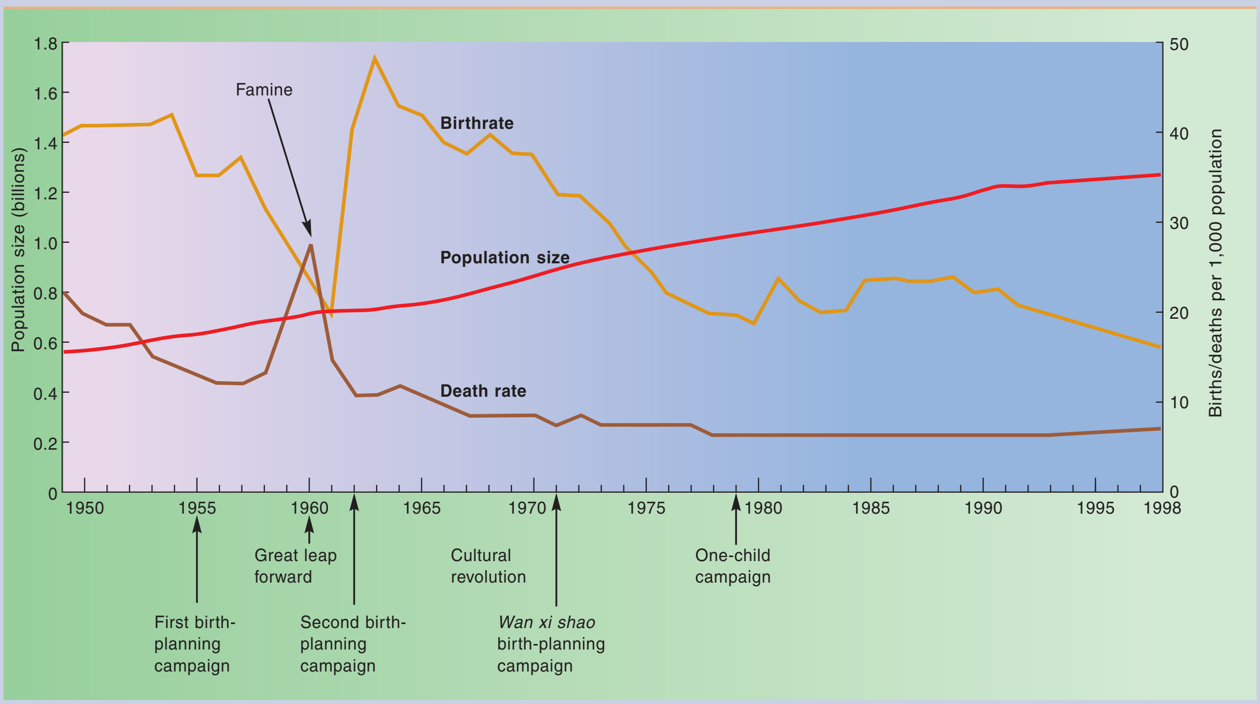
The actions of government can have a significant impact on the population growth patterns of nations. Some countries have policies that encourage couples to have children. The U.S. tax code indirectly encourages births by providing tax advantages to the parents of children. Some countries in Europe are concerned about the lack of working-age people in the future and are considering ways to encourage births.

China and India are the two most populous countries in the world. Both have over 1 billion people. However, China has taken steps to control its population and now has a total fertility rate of 1.8 children per woman while India has a total fertility rate of 3.2. The total fertility rate is the average number of children born to a woman during her lifetime. The differences in total fertility rates between these two countries are the result of different policy decisions over the last 50 years. The history of China's population policy is an interesting study of how government policy affects reproductive activity among its citizens. When the People's Republic of China was established in 1949, the official policy of the government was to encourage births because more Chinese would be able to produce more goods and services, and production was the key to economic prosperity. The population grew from 540 million to 614 million between 1949 and 1955 while economic progress was slow. Consequently, the government changed its policy and began to promote population control.

The first family-planning program began in 1955, as a means of improving maternal and child health. Birthrates fell (see graph). But other social changes resulted in widespread famine and increased deathrates and low birthrates in the late 1950s and early 1960s.

The present family-planning policy began in 1971 with the launching of the *wan xi shao* campaign. Translated, this phrase means "later" (marriages), "longer" (intervals between births), and "fewer" (children). As part of this program the legal ages for marriage were raised. For women and men in rural areas, the ages were raised to 23 and 25, respectively; for women and men in urban areas the ages were raised to 25 and 28, respectively. These policies resulted in a reduction of birthrates by nearly 50% between 1970 and 1979.

An even more restrictive one child campaign was begun in 1978–1979. The program offered incentives for couples to restrict their family size to one child. Couples enrolled in the program would receive free medical care, cash bonuses for their work, special housing treatment, and extra old-age benefits. Those who broke their pledge were penalized by the loss of these benefits as well as other economic penalties. By the mid-1980s less than 20% of the eligible couples were signing up for the program. Rural couples, particularly, desired more than one child. In fact, in a country where over 60% of the population is rural, the rural total fertility rate was 2.5 children per woman. (The total



Source: Data from H. Yuan Tien, "China's Demographic Dilemmas," in *Population Bulletin, 1992,* Population Reference Bureau, Inc., Washington, D.C., and Natural Family Planning Commission of China; and more recent data taken from Population Reference Bureau, Inc.

OUTLOOKS 16.1 (*continued*)

fertility rate is the number of children born per woman per lifetime.) In 1988 a second child was sanctioned for rural couples if their first child was a girl, which legalized what had been happening anyway.

The programs appear to have had an effect because the current total fertility rate has fallen to 1.8 children per woman. Replacement fertility, the total fertility rate at which the population would eventually stabilize, is 2.1 children per woman per lifetime. Furthermore, over 80% of couples use contraception. Abortion is also an important aspect of this program, with a ratio of more than 600 abortions per 1,000 live births.

By contrast, during the same 50 years India has had little success in controlling its population. In 2000 a new plan was unveiled which includes the goal of bringing the total fertility rate from its current 3.2 children per woman to 2 (replacement rate) by 2010. In the past the emphasis of government programs was on meeting goals of sterilization and contraceptive use but this has not been successful. Today less than 50% of couples use contraceptives. This new plan will emphasize improvements in the quality of life of the people. The major thrusts will be to reduce infant and maternal death, immunize children against preventable disease, and encourage girls to attend school. It is hoped that improved health will remove the perceived need for large numbers of births. Currently, less than 50% of the women in India can read and write. The emphasis on improving the educational status of women is related to the experiences of other developing countries. In many other countries it has been shown that an increase in the education level of women has been linked to lower fertility rates.

It seems overly optimistic to think that the total fertility rate can be reduced from 3.2 to 2 in just ten years, but programs that emphasize improvements in maternal and child health and increasing the educational level of women have been very effective in reducing total fertility in other countries.

women become educated they have fewer children. Several reasons have been suggested for this trend. Higher levels of education allow women to get jobs with higher pay, which makes them less dependent on males for their support. Being able to read may lead to better comprehension of how methods of birth control work. Regardless of the specific reasons, improving educational levels of women has now become a major technique employed by rapidly growing countries that hope to eventually control their populations.

SUMMARY

A population is a group of organisms of the same species in a particular place at a particular time. Populations differ from one another in gene frequency, age distribution, sex ratio, and population density. Organisms typically have a reproductive capacity that exceeds what is necessary to replace the parent organisms when they die. This inherent capacity to overreproduce causes a rapid increase in population size when a new area is colonized. A typical population growth curve consists of a lag phase in which population rises very slowly, followed by an exponential growth phase in which the population increases at an accelerating rate, followed by a leveling off of the population in a stable equilibrium phase as the carrying capacity of the environment is reached. In some populations, a fourth phase may occur, known as the death phase. This is typical of bacterial and yeast populations.

The carrying capacity is the number of organisms that an area can sustain over a long time. It is set by a variety of limiting factors. Availability of energy, availability of raw materials, accumulation of wastes, and interactions with other organisms are all categories of limiting factors. Because organisms are interrelated, population changes in one species sometimes affect the size of other populations. This is particularly true when one organism uses another as a source of food. Some limiting factors operate from outside the population and are known as extrinsic factors; others are properties of the species itself and are called intrinsic factors. Some limiting factors become more intense as the size of the population increases; these are known as density-dependent factors. Other limiting factors that are more accidental and not related to population size are called density-independent factors.

Humans as a species have the same limits and influences that other organisms do. Our current problems of food production, energy needs, pollution, and habitat destruction are outcomes of uncontrolled population growth. However, humans can reason and predict, thus offering the possibility of population control through conscious population limitation.

THINKING CRITICALLY

If you return to figure 16.10, you will note that it has very little in common with the population growth curve shown in figure 16.5. What factors have allowed the human population to grow so rapidly? What natural limiting factors will eventually bring this population under control?

What is the ultimate carrying capacity of the world? What alternatives to the natural processes of population limitation could bring human population under control?

Consider the following in your answer: reproduction, death, diseases, food supply, energy, farming practices, food distribution, cultural biases, and anything else you consider relevant.

CONCEPT MAP TERMINOLOGY

Construct a concept map to show relationships among the following concepts.

biotic potential
carrying capacity
exponential growth phase
extrinsic limiting factors
intrinsic limiting factors
lag phase
mortality
natality
population density
sex ratio
stable equilibrium phase

KEY TERMS

age distribution
biotic potential
carrying capacity
death phase
density-dependent factors
density-independent factors
environmental resistance
exponential growth phase
extrinsic factors
gene flow
gene frequency
intrinsic factors
lag phase
limiting factors
mortality
natality
population
population density
population growth curve
population pressure
reproductive capacity
sex ratio
stable equilibrium phase

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Topics	Questions	Media Resources
16.1 Population Characteristics	1. Why do populations grow?	**Quick Overview** • Scientific ways to describe a population **Key Points** • Population characteristics **Animations and Review** • Introduction • Characteristics **Interactive Concept Maps** • Population characteristics
16.2 Reproductive Capacity	2. List four ways in which two populations of the same species could be different.	**Quick Overview** • Predicting population growth **Key Points** • Reproductive capacity
16.3 The Population Growth Curve	3. Draw the population growth curve of a yeast culture during the wine-making process. Label the lag, exponential growth, stable equilibrium, and death phase.	**Quick Overview** • Typical stages of population maturation **Key Points** • The population growth curve **Animations and Review** • Growth **Interactive Concept Maps** • Growth curve
16.4 Population-Size Limitations		**Quick Overview** • Slowing down population growth **Key Points** • Categories of limiting factors

(*continued*)

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Topics	Questions	Media Resources
16.5 Categories of Limiting Factors	4. List four kinds of limiting factors that help set the carrying capacity for a species. 5. How do the concepts of biomass and population size differ? 6. Differentiate between density-dependent and density-independent limiting factors. Give an example of each. 7. Differentiate between intrinsic and extrinsic limiting factors. Give an example of each.	**Quick Overview** • Limiting factors **Key Points** • Limiting factors **Animations and Review** • Size regulation • Concept quiz **Interactive Concept Maps** • Text concept map
16.6 Limiting Factors to Human Population Growth	8. As the human population continues to grow, what should we expect to happen to other species? 9. How does the population growth curve of humans compare with that of other kinds of animals? 10. All organisms over-reproduce. What advantages does this give to the species? What disadvantages?	**Quick Overview** • A story of removing limiting factors **Key Points** • Human population growth **Animations and Review** • Food needs • Food production • Food quality • Future prospects • Concept quiz **Experience This!** • Plot the growth of a population