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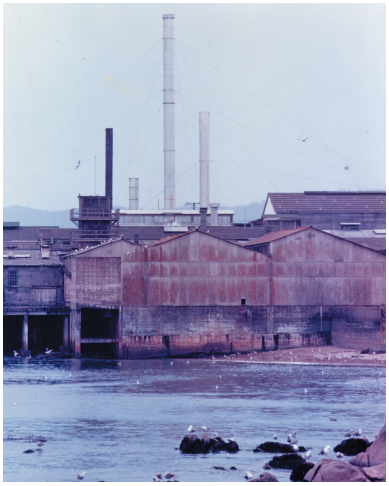


Cannery Row, Monterey, California, 1973.

10

Balancing Birth and Death

Cannery Row in Monterey in California is a poem, a stink, a grating noise, a quality of light, a habit, a nostalgia, a dream. . . . In the morning when the sardine fleet has made its catch, the purse-seiners waddle heavily into the bay blowing their whistles. The deep-laden boats pull in against the coast where canneries dip their tails into the bay.

These words from John Steinbeck's *Cannery Row* describe a sardine fishery thriving off the coast of Central California. Yet shortly after *Cannery Row* was written in 1945, the sardine population vanished. Today Cannery Row is a tourist attraction. What happened to the sardines is now an ecological mystery.

Did the sardines off the coast of California simply move to a different habitat? Or did the fishing industry drive the population to extinction? To answer these questions we need to understand how populations grow in number, and we need to uncover the biology that determines growth.

Many factors affect the growth of a population. Some depend on the size, or *density,* of the population, particularly how crowded it is. For this reason, these factors are called *density dependent*. Other factors may not depend on population size. One such factor is dispersal, the movement of individuals between populations. Of course, weather and other features of the physical environment affect the growth of populations, as well as their dispersal.

Population growth affects natural selection, and natural selection in turn shapes population growth. Interrelationships between population growth and natural selection provide fascinating intersections of ecology with evolution. Some of our most important insights into the natural world have come from the study of the subtle ways in which populations grow in number. ❖

The Population Bomb

10.1 Populations are collections of interbreeding individuals and the basic units of ecology and evolution

In his influential book, *The Population Bomb* (1968), renowned population biologist Paul Ehrlich describes a night he experienced in Delhi, India:

> The temperature was well over 100, and the air was a haze of dust and smoke. The streets seemed alive with people. People eating, people washing, people sleeping. People visiting, arguing, and screaming. People thrusting their hands through the taxi window begging. People defecating and urinating. People clinging to buses. People herding animals. People, people, people, people. . . . since that night I've known the *feel* of overpopulation.

The recent history of the human population is one of almost unfettered growth. It is shocking to realize how quickly the planet is becoming populated. In 6000 B.C. there may have been about 5 million humans. Before that, it probably took 1 million years for the population to increase from 2.5 to 5 million. We call the time it takes for the population to double in size a **doubling time**. From 6000 B.C. to A.D. 1650, the doubling time averaged about 1000 years. However, by 1850 the population had again doubled from its level in 1650. By 1930 the doubling time had fallen to 80 years. By the time *The Population Bomb* first appeared in 1968, the doubling time was about 35 years, and the world human population was about 3 billion.

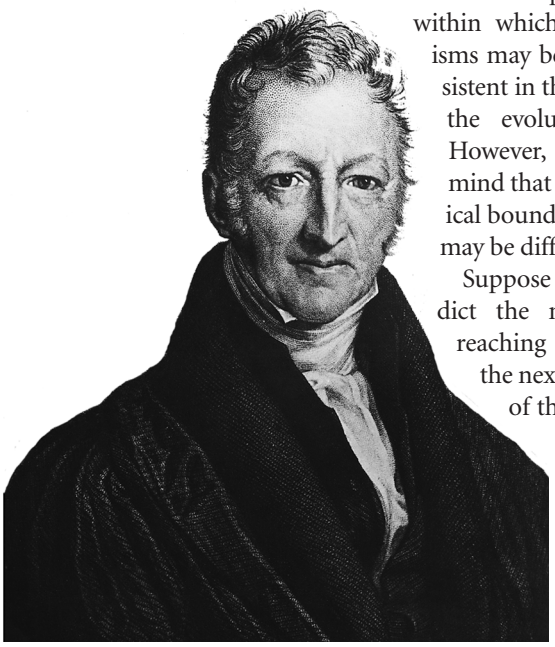
One important prediction of exponential growth is that if births exceed deaths, then—if we are also given unlimited time—the population will get infinitely large. But it is impossible for a planet of limited size and resources to sustain exponential growth of any population forever. Thomas Robert Malthus (Figure 10.1A) was one of the first to articulate this idea in 1789 when he wrote, "The power of population is so superior to the power in earth to produce subsistence for man, that premature death must in some shape or other visit

the human race." The logic behind these conclusions is so simple, we may consider a fundamental principle of ecology to be that *no population will grow exponentially forever*.

The ideas of Malthus were so persuasive to Darwin that they became a crucial component in the development of his own thinking, as we saw in Chapter 1. According to Malthus, populations will tend to produce an excess of progeny that cannot all survive. For Darwin the important question was, which individuals will die and which will survive? He answered the question with his theory of natural selection: Those individuals possessing traits that better adapted them to their environment should be most likely to survive.

The temperature was well over 100, and the air was a haze of dust and smoke.

In evolutionary biology a **population** is a group of individuals that regularly exchange genes. It is this exchange of genetic material that links the evolution of the population's members. Ecologists are often less concerned with the exchange of genes than with the physical boundaries within which individual organisms may be found. To be consistent in this book, we will use the evolutionary definition. However, we need to bear in mind that defining the ecological boundaries of populations may be difficult.



Suppose we wanted to predict the number of people reaching retirement age in the next 20 years. Estimates of these numbers can be most easily made with the help of a mathematical model of population growth. As with most models in population biology, however, there is seldom a single model that we can apply to all organisms. So before turning to the models, we must address the general life cycle of the organism. There are two major categories of life cycles we could model. Both were introduced in Chapter 7.

The first life cycle is one with **discrete generations**. This means that reproduction is synchronized among the adults: There is a breeding season. We often see manifestations of this life cycle during springtime in temperate climates. Released from the rigors of winter, adults greet each other with a view to participating in sex and other reproductive activities. The offspring from this round of breeding then develop and enter the population of breeding adults in the next generation. Among the many organisms that actually follow this life cycle are many annual plants, insects that produce one generation per year, and salmon. When generations are discrete, time moves in sudden jerks. It does not flow.

The second major type of life cycle involves organisms with continuous reproduction. Instead of discrete pulses of reproduction, reproduction provides a continuous flow of new recruits into the population. Therefore, this type of life cycle is represented by continuous time. There are no jerks in the ecological process, only a seamless procession.

Because discrete time models do not require knowledge of calculus, we will use them exclusively in this chapter. Often the biological conclusions are qualitatively the same with both models. We are not usually sacrificing valuable ecological insights by limiting ourselves to discrete-time models.

Another important aspect of models of population growth is age structure. Organisms whose adults may reproduce multiple times and live for an extended period have an **age structure;** that is, they consist of individuals of many different ages in different proportions. This means we need to know something about how mortality and survival change with age. It is easier to describe the growth of populations without age structure, and so Modules 10.2 through 10.14 focus on these types of populations.

FIGURE 10.1A Thomas Malthus forecast the outcome of exponential growth.

T. R. Malthus (1766–1834)

Thomas Robert Malthus graduated from Jesus College, Cambridge, with honors in mathematics. Although Malthus was concerned about overpopulation, he was apparently not concerned about inbreeding; he married his cousin, Harriet Eckersall, and had three children. His most lasting work—*An Essay on the Principle of Population, as it Affects the Future Improvement of Society with Remarks on the Speculations of Mr. Godwin, M. Condorcet, and Other Writers*—was published in 1798 anonymously. This essay met with success, and Malthus published several revisions and summaries of this work. Malthus was appointed Professor of Political Economy at East India College in 1805, where he worked until his death.

Malthus conjectured that there were two principal mechanisms to halting population growth: *Preventive checks* included mechanisms like postponed marriage, abstinence, homosexuality, birth control, and abortion. *Positive checks* were the more severe forms of population control, which entailed increased death rates from sources like war and famine. Malthus was keenly aware that these positive checks would not be meted out evenly and that the poorest would suffer most. Consequently, he favored the use of preventive checks like postponed marriage as a means of avoiding the devastation of positive checks.

10.2 Populations may grow exponentially for short periods of time

We start with the exponential model of population growth, a model that almost never applies to any real population—or, if it does, will apply for only brief periods of time. This does not mean the model is useless. In fact, by learning the predictions of the exponential model, we are led to more realistic descriptions of population growth.

The development of this model requires some assumptions about the organism's life cycle. For simplicity we focus attention in Figure 10.2A on asexual organisms, which reproduce synchronously. This bout of reproduction can be thought of as a breeding season. Limiting this discussion to asexual organisms may seem extreme, but in fact the inclusion of two sexes does not substantially alter the predictions of the exponential model.

We also assume that each individual dies after it has reproduced, and the next generation is constituted only from the surviving offspring. Many organisms have this type of life cycle: annual plants, black widow spiders, Pacific salmon, and others described in Chapter 7. If we allowed some adults to survive to the next generation we would get similar results, but the development of the model would be a bit tricky.

The key assumption of the model is that each individual, on average, produces a constant number of offspring,

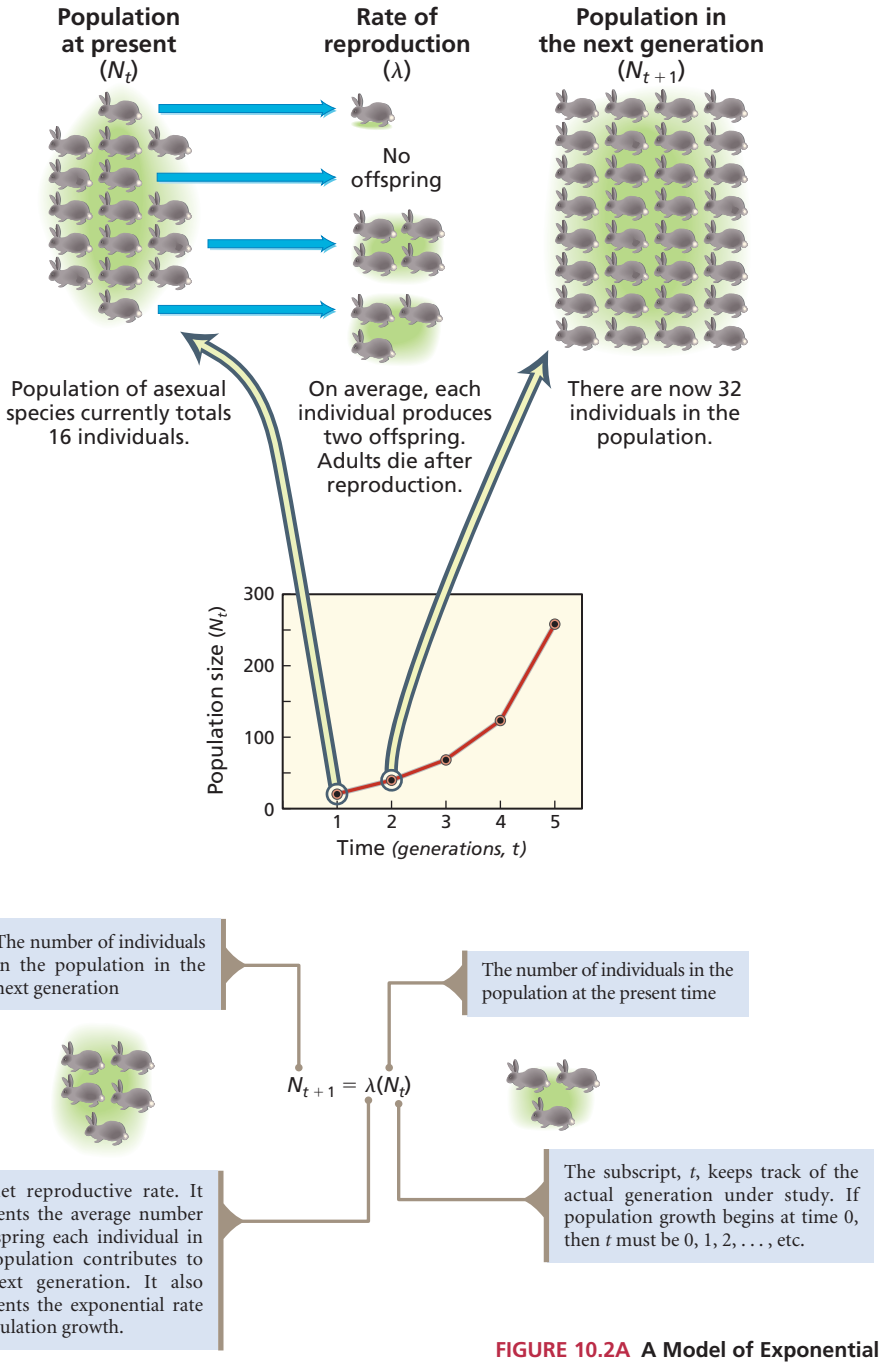


FIGURE 10.2A A Model of Exponential Population Growth

referred to as λ (lambda). We also call λ the **net reproductive rate**. We assume that this rate of reproduction does not change over time or as the population increases in size.

Figure 10.2A shows a model of exponential population growth using the example of an asexual population that starts out with 16 members and grows at a net reproductive rate (λ) of 2. This population increases in size over time, and the numbers that are added to the population each generation get larger. As long as each individual in the population produces a slight excess beyond replacement ($\lambda > 1.0$), the population will grow in this manner. These are the characteristic signs of exponential growth. Not only do the numbers increase by larger amounts in each generation, but as a great deal of time passes, the population size is predicted to get infinitely large. This is the major defect in this model,

since we know from common sense and practical experience that no population on Earth can become infinitely large. There must be some forces at work in natural populations that prevent this growth. We will discuss some of those forces later in this module.

In the very unlikely case that $\lambda = 1.0$, the population will remain at a constant size that equals its initial size. The likelihood of this occurring is effectively zero. If the average individual in the population does not replace itself ($\lambda < 1.0$), then the population will decline in size every generation until it goes extinct.

The following box shows how to predict mathematically what the size of an exponentially growing population will be in the distant future.

Population Growth over Multiple Generations

The model of exponential growth in Figure 10.2A shows how population size changes over a single generation. Is there some way to predict the population size at some distant time in the future for exponentially growing populations? In fact, there is an easy way to do this. Remember that the relationship shown in Figure 10.2A holds for any generation. So if we start with some arbitrary time in the future, time t, then we know that

$$N_t = \lambda N_{t-1}. \qquad (1)$$

In other words, the size of the present generation equals the net reproductive rate times the size of the previous generation.

It would be helpful to have N_t on the left-hand side of the equation and some simple relationship involving the initial population size (N_0) on the right-hand side. To do this we must replace N_{t-1} with some other relationship. We know from the figure that if we take the right-hand side of this equation and replace N_{t-1} in equation (1) above with this value we get, $N_t = \lambda(\lambda N_{t-2}) = \lambda^2 N_{t-2}$. If we continue with these substitutions, we get the useful result, $N_t = \lambda^t N_0$.

From this relationship we can easily produce figures, like Figure 10.2B here, showing the long-term behavior of exponentially growing populations. Thus, an initial group of 50 mice that had a net reproductive rate of 2.0 would grow to 200 mice (50×2^2) after two generations, and to 51,200 mice after 10 generations (50×2^{10}).

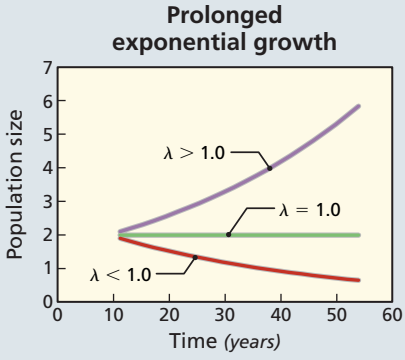


FIGURE 10.2B
Prolonged Exponential Growth

10.3 In crowded populations, survival and fertility decline

No biological population can grow exponentially forever. Eventually, populations become so crowded that food, shelter, and other essential resources are difficult to find. Individuals that cannot find sufficient resources may die, or if they survive, their capacity to reproduce may be impaired. Accordingly, the net reproductive rate, which we call λ, can be divided into two components as follows:

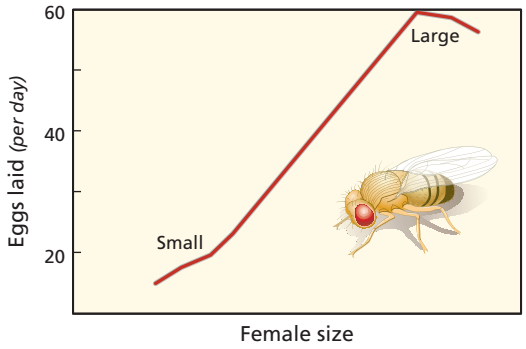
λ = (*number of offspring produced*) × (*probability that each offspring survives to reproduce in the next generation*)

The two components are given in parentheses above. The first is the total number of offspring produced by each individual—sometimes called fertility—in the previous generation. The second is the probability that each of those offspring will survive to reproduce—sometimes called viability—in the next generation.

Crowding can reduce the number of newborn offspring, reduce offspring survival, or both. The specifics will vary among organisms. For example, larval growth in insects and amphibians can determine the size of the reproductive adult. If food is scarce, larvae may grow slowly and produce small adults. These small adults may then have fewer offspring, as shown in Figure 10.3A. If food levels are very low, death may result, as illustrated in Figure 10.3B. Likewise, if adults starve, they may have reduced fertility. For example, human females whose body fat has been reduced due to starvation or intense exercise may fail to ovulate.

Crowded populations may also suffer from increased disease. This could arise from increased transmission of infectious disease from one individual to the next, thanks to more frequent contact. Or it may come from the accumulation of feces, urine, and other waste products that accompany crowded conditions. The black plague in Europe may have been one such example, as the following box describes.

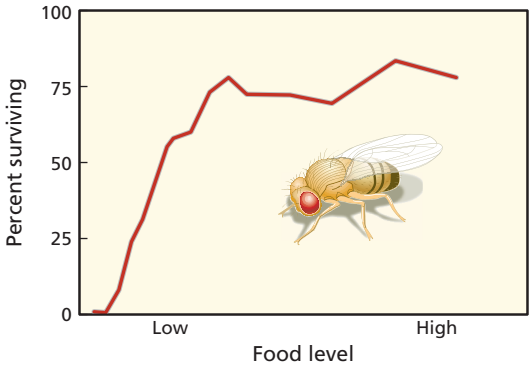
Another consequence of crowding is increased susceptibility to predators. Predators sometimes concentrate their efforts on the most common prey in a given area, all but ignoring acceptable but less common species. Thus the most numerous species may also suffer increased mortality from its popularity with predators.



Fertility may be reduced by:
- limited food for adults
- increased behavioral interactions
- reduced size of adults due to crowding of prereproductive individuals

FIGURE 10.3A **The Relationship between Female Body Size and Egg Laying in Laboratory Fruit Flies**

In mammals, crowding can stimulate the formation of steroids such as cortisone, cortisol and corticosterone, which help the organism adapt to stress by creating ready reserves of carbohydrate for quick energy. However, prolonged stress and production of these steroids have adverse side effects, which include the weakening of the immune system and sometimes death.



Survival may be reduced by:
- limited food
- increased waste products
- increased susceptibility to predators
- increased stress
- infanticide and cannibalism
- disease

FIGURE 10.3B The Relationship between Food Level and Survival in Laboratory Fruit Flies

In general, the deleterious effects of high population size get more severe as the level of crowding increases. This will lead to further reductions in fertility and survival, which in turn will further reduce the value of λ. Ultimately, the net reproductive rate will either equal one or be less than one. At this point the population will cease growing. A goal of Module 10.6 will be to predict when a population will cease growing and thus how many individuals can be reasonably supported by a particular environment.

The Black Plague

Humankind has experienced three worldwide epidemics of the deadly disease known as the black plague (Figure 10.3C). The second pandemic, which ravaged Asia and Europe for three centuries, may have killed 25 million people in Europe during the fourteenth century—nearly one quarter of the total population. This disease results in death in 50 percent or more of those who are afflicted and untreated. It is caused by the bacteria *Pasteurella pestis,* which infects rats and humans and is primarily transmitted by fleas.

As Eurasian populations grew during the Middle Ages, the lack of sanitation helped maintain large populations of rats. When epidemics of the plague killed large numbers of rats, the fleas would move to their less favored human hosts with devastating effects. Although the cause of the disease was unknown until 1894, ancient civilizations were aware of important aspects of its epidemiology. The fifth-century Indian medical work, *Bhagavata Purana,* implores people to leave their homes, "when rats fall from the roofs above, jump about and die." The Venetian Republic was so concerned about the disease that in 1374 it required all ships coming from plague-infested territories to wait 40 days before landing, so any infections could run their course. This 40-day period, or *quaranti giorni,* is the root of the English word *quarantine,* meaning enforced isolation to prevent the spread of disease.

FIGURE 10.3C *The Plague*, by Arnöld Bocklin

10.4 Space is the important limiting resource for some populations

The *rocky intertidal zone*, shown in Figure 10.4A, has been the site of many important studies in ecology. Land in the intertidal zone is splashed and partially submerged by the ocean. The duration of these periods of submersion depends on the tides, the local weather conditions, and the distance from the ocean—criteria that subdivide the intertidal into two zones. The *upper intertidal zone* is mostly splashed, only occasionally submerged during the highest tides. Animals and plants that live here must be able to withstand heat and water loss. The *lower intertidal zone* is only briefly exposed to the air each day. Animals and plants here, such as the barnacles and algae in Figure 10.4A, are constantly pounded by the surf and must be securely fastened to rocks; otherwise they will be washed out to sea.

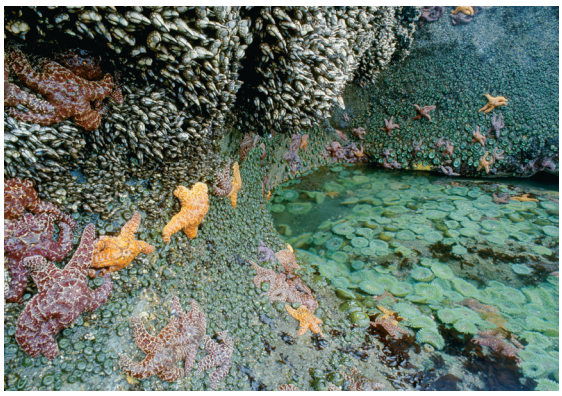


FIGURE 10.4A The Rocky Intertidal Zone in the Pacific Northwest

Many intertidal animals survive by filtering food brought in by the tides and surf. Many small, often microscopic, plants and animals live near the surface of the ocean. They are called *plankton*. Mucus secreted by *filter-feeding* animals traps plankton, which is then used as food. For a filter-feeding animal, the intertidal can be a luxurious place to live because the continuous movement of water ensures a constant supply of food. In many intertidal habitats, the first resource to vanish when population size is high is not food but open space for attachment. Thus, one limit to plant and animal numbers may simply be the available space. Any environmental factor that limits the distribution or abundance of an organism is called a **limiting resource**.

The relationship between free space and animal numbers was demonstrated by Paul Dayton. He created two experimental regions in an intertidal zone. The control region (Figure 10.4B) contained undisturbed populations of sea anemones (*Anthopleura elegantissima*) and barnacles (*Balanus cariosus*). The test region was the same except that 45 percent of the barnacles were removed, creating more free space. As Figure 10.4C shows, the number of sea anemones stayed relatively constant in the control region. But in the test region, the numbers of sea anemones fluctuated widely. Their numbers increased rapidly in the fall and winter as they occupied the newly cleared space. In the summer the number of anemones declined due to the drying heat and wind.

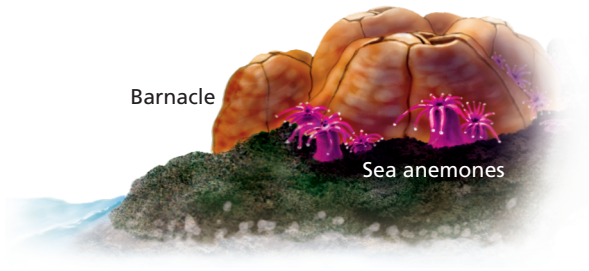


FIGURE 10.4B On the San Juan Islands in Washington State, sea anemones and barnacles live in the same area of the intertidal zone. The sea anemones are often clumped below large barnacles and thereby protected from drying in the air.

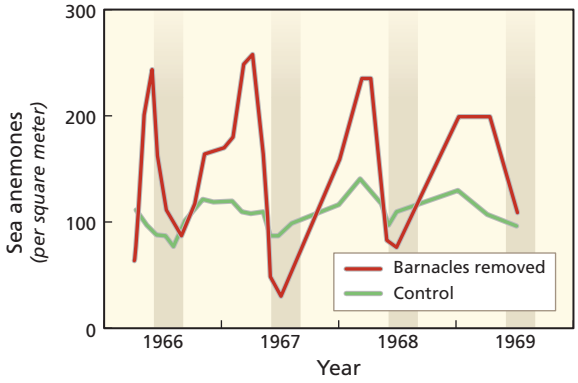


FIGURE 10.4C Paul Dayton removed 45 percent of the barnacles in some areas and none in others (control areas). In the winter and fall sea anemones grew rapidly in the area lacking barnacles, due to the extra free space. In the summer the numbers of anemones declined due to warm, drying conditions.

Although space can be a limiting resource in the intertidal zone, as Dayton's experiment shows, it is not always a limiting resource. Other aspects of the physical environment may also determine when space is limiting. For example, although sea anemones can reproduce by a vegetative process of budding, many invertebrates, such as barnacles, broadcast large numbers of larvae out to sea. These larvae must develop and then be washed by tidal currents onto open space. In Oregon and Washington, it appears that there are always large numbers of these invertebrate larvae settling, leaving little free space (Figure 10.4A). In California the nearshore currents carry the larvae farther from shore, increasing the likelihood that the larvae will die before settling. Consequently, there is more free space in the California intertidal zone than in the Northwest, as Figure 10.4D shows.

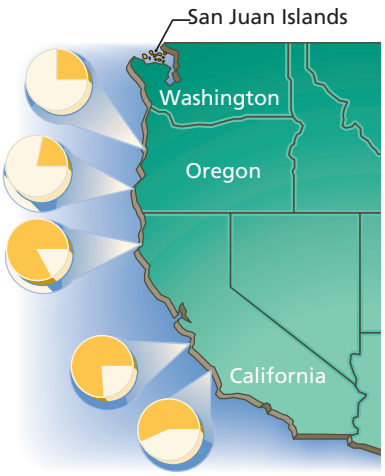


FIGURE 10.4D The amount of free space (orange) in the intertidal zone increases from Oregon to California.

Experimental and theoretical ecology began with investigations of single-species population growth 10.5

How do Malthus's "positive checks," such as famine, affect growing populations? Rather than generating catastrophes, they usually act by creating gradual declines in reproductive rates as population size increases. Ecologists refer to the operation of such checks on population increase as **density-dependent population growth**, with *density* referring to the numbers of organisms inhabiting a particular area.

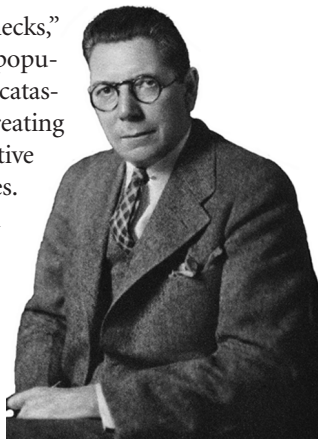


FIGURE 10.5A Raymond Pearl

In fact, the relationship between population growth and density was the first focus of ecological theory. Raymond Pearl (Figure 10.5A) vigorously explored this relationship in the early part of the twentieth century. Pearl championed the use of a mathematical model, called the *logistic equation* (see Module 10.6), to describe density-dependent population growth. Much of Pearl's experimental research was used to support the logistic equation.

Pearl initiated a strong experimental laboratory research program to investigate the theory of density-dependent population growth. The use of experimental laboratory research is still not as common in ecology as it is in many areas of science, despite early laboratory research by Pearl (see the box), Gause (see Module 12.6), and others. Ultimately, ecologists are interested in understanding the forces and principles responsible for determining the abundance and distribution of organisms in their natural environments. Experimental laboratory research involves environments that are different from those in nature, and usually simpler. This difference has led some ecologists to question the validity of inferences made from laboratory systems.

The use of simplified laboratory systems has served other branches of science very well. As an example, a physicist may be interested in understanding the laws that govern the motion of objects in the Earth's atmosphere or on its surface. In these types of "environments," friction affects the velocity and acceleration of objects. However, physicists have found it helpful first to study the laws governing the motion of objects in the absence of friction. Introductory courses in physics still begin instruction with these simple models of motion. After developing and testing these simple theories, physicists then modified their laws of motion to include the complications of friction.

The science of ecology is not nearly as advanced as physics. Ecologists are still developing very basic models. Thus, although we accept the notion that the growth of most populations will be affected by factors other than density, many of our models are focused on the idea of density dependence by itself. However, progress in ecology will require the careful development and testing of additional ideas, which must of necessity start out simply.

Ecology has also advanced by carefully designed experiments using natural populations. In addition, we have learned much through careful observation of organisms in their natural habitats.

Many organisms experience a decline in net reproductive rates with increasing population density. In effect, increasing population size regulates the ultimate number of individuals in the population. However, this regulation may be far from perfect. A basic issue in ecology is the extent to which fluctuations in population size are due either to the environment or reproductive regulatory mechanisms, as seen in Chapter 1.

Some species regularly experience periods of crowding. These organisms are often able to endure severe crowding, managing to survive and reproduce. These abilities are rooted in adaptations of behavior or morphology. As we will see in Module 10.7, these adaptations are important for understanding how organisms live in changing environments.

Raymond Pearl (1879–1940), the Founder of Experimental Ecology

After obtaining his Ph.D. from the University of Michigan, Raymond Pearl studied in Europe with the biostatistician Karl Pearson. Pearson instilled in Pearl an appreciation for mathematical approaches to biology. Pearson also taught a method of achieving scientific generalizations that appealed to Pearl. This method was to take a wide variety of scientific observations and reduce them to a brief formula or a few words, called a law.

With this background Pearl was eager to find the laws that governed population growth. He undertook research at the Institute for Biological Research at Johns Hopkins University, which he had established with support from the Rockfeller Foundation. Pearl did experimental research with fruit flies to test models of population growth. He was also interested in predicting the growth of human populations with the logistic model. Pearl's work was criticized for his attempts to extrapolate human population growth from the logistic model. Some scientists thought that the only way to control human population growth was through the genetically based improvement of human intelligence. Pearl's theory seemed to contradict this approach by suggesting that a variety of natural factors will predictably and reliably slow down population growth. Ultimately, the long-term predictions of the logistic model were not very accurate. In the 1920s Pearl predicted that the population of the United States would be about 197 million by the year 2000. In fact the real number was closer to 272 million, although it had been boosted by immigration.

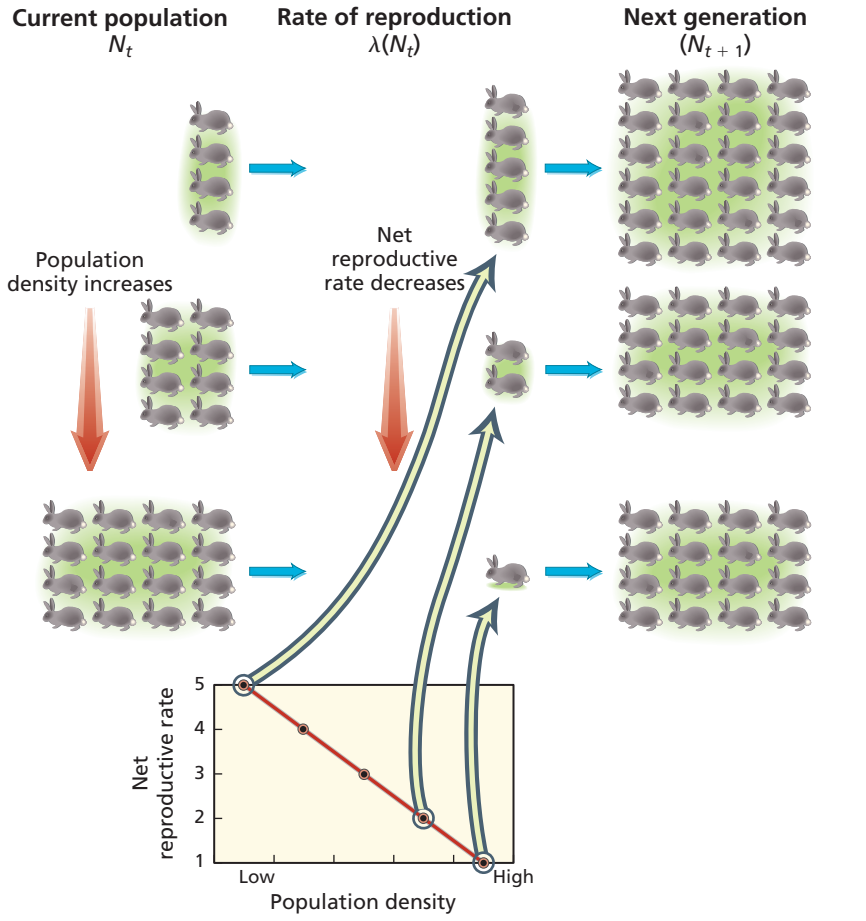
10.6 Density-regulated populations do not grow without bound

The effects of growth-limiting factors increase with population density. If net reproductive rates decline as population density increases, the population will reach a density where the net reproductive rate is exactly one, and each individual in the population simply replaces itself. When this happens, the population will cease growing until population densities decrease and net reproductive rates are again greater than one. It is also possible for the population size to get so large that net reproductive rates drop below one. In that case, the population size will decrease until the net reproductive rates again rise to one.

To make these predictions more quantitative, we need to define the mathematical relationship between population size and net reproductive rate. No single equation will apply to all organisms. Indeed, we expect this relationship to vary from one species to another, and perhaps between populations of the same species. But many important consequences of density-dependent population growth can be understood by examining simple models.

One such model, known as the *logistic model,* is based on a linear relationship between density and net reproductive rate. In contrast to the exponential model that we examined in Module 10.2, which sees the net reproductive rate as constant, the logistic model assumes that the reproductive rate decreases linearly as population density increases, as the graph in Figure 10.6A shows. The properties of the logistic model depend on numerical constants called parameters. The logistic model uses only two parameters. The first is *r,* the **intrinsic rate of increase**. This parameter determines the maximum rate of growth at low densities. The second parameter, *K,* is called the carrying capacity. The **carrying capacity** reflects the maximum number of individuals that the environment can support.

In Figure 10.6A we see that as the number of individuals in the population (N_t) gets close to zero, the population size in the next generation is approximately $(1 + r)N_t$. If $r > 0$, then the population is growing at an exponential rate equal to $1 + r$. As the population grows, the rate of exponential growth slows, reflecting the combined effects of reduced fertility and increased mortality brought about by crowding. (Mathematically, the slowing occurs because $-rN_t/K$ becomes significantly less than zero and this quantity is added to the exponential growth term, $1 + r$.) As the population size gets closer to the value K (the carrying capacity of the environment), the net reproductive rate declines and gets closer to one. When the population size is exactly equal to K, the population ceases to change size. We call this point $N_t = K$ an *equilibrium* of the



Let $\lambda(N_t) = 1 + r - \frac{rN_t}{K}$. Then, $N_{t+1} = \lambda(N_t)\, N_t$

This looks the same as the exponential growth model, except we have added (N_t) next to the λ to emphasize that reproductive value depends on density.

$$N_{t+1} = \left(1 + r - \frac{rN_t}{K}\right)N_t$$

r, the intrinsic rate of increase, is a constant. At low density the reproductive rate is greatest and close to $1 + r$.

K, the carrying capacity is a constant. Its value will depend on how many individuals can be supported by the environment. When $N_t = K$, each individual just replaces itself and the population size stays constant.

FIGURE 10.6A A Model of Logistic Population Growth

logistic model because population size does not change at that population density.

This simple mathematical result illustrates the general principle that density-dependent population growth causes populations to grow toward their equilibrium density whether they start at low or high densities. Ecologists use this theoretical pattern to explain the maintenance of steady population densities in both experimental and natural populations. In some species, the logistic model does a reasonable job of predicting population growth (see box).

Logistic Population Growth in Real Populations

How does the growth of real populations compare with the predictions of the logistic model? The growth of real biological populations can be studied by examining the total change in population size as a function of density. The total change in population size is simply the present population size minus the size in the previous generation, or in terms of the notation we developed earlier, $N_{t+1} - N_t$. This change can then be compared to the change predicted by the logistic equation. Using the results developed in Figure 10.6A, a little algebra shows that $N_{t+1} - N_t = rN_t - rN_t^2/K$. For the unicellular ciliate, *Paramecium caudatum*, r has been estimated from the observations in Figure 10.6B to be 0.922 and K as 200. Thus, when the density of *P. caudatum* is 100 animals per 0.5 cc, the expected change in population size is $0.922 \times 100 - 0.922 \times 100^2/200 = 46.1$. The solid line in Figure 10.6B shows the predicted changes in population size from the logistic equation. The observed changes, shown by the circles, generally are fairly close to the predicted changes.

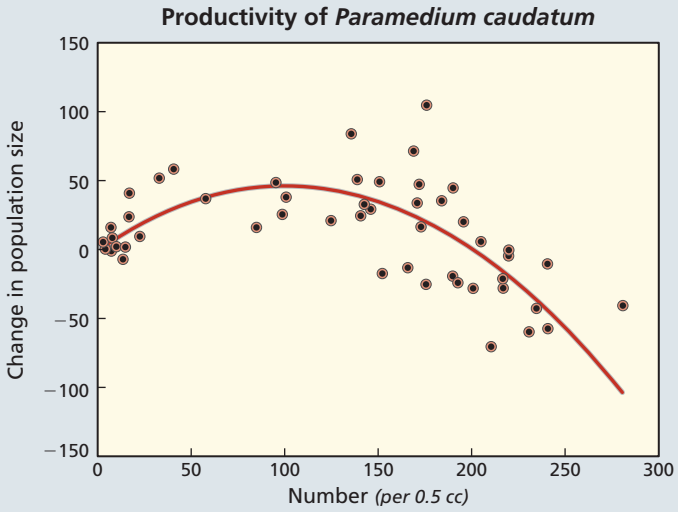


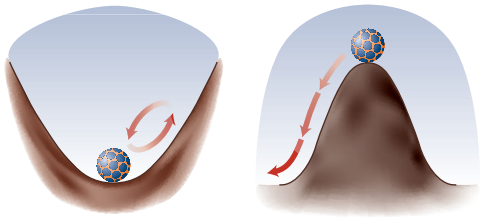
FIGURE 10.6B The growth of *Paramecium caudatum* as a function of population density. The solid line shows the predicted change in population size from the logistic equation; the symbols show the observed change.

10.7 Density-regulated populations may exhibit chaotic behavior

For the logistic model of population growth, when net reproductive rates are equal to one, the population size should stay constant. The population size at which the population ceases growing is an equilibrium. Many factors other than population density may affect the population size. Environmental fluctuations, such as those produced by weather, may lead to either additional deaths or enhanced survival, changing population size by small amounts above or below the equilibrium. This type of small change is called a **perturbation**.

Will the population return to the equilibrium size after a perturbation, or will it move to some new equilibrium? The answer to this question hinges on a property of the equilibrium known as its **stability**. If the population returns to the equilibrium after a perturbation, we say the *equilibrium is stable*. If the population moves away from the equilibrium size, this is evidence of an *unstable equilibrium*. Figure 10.7A presents a visual analogy for stable and unstable equilibria.

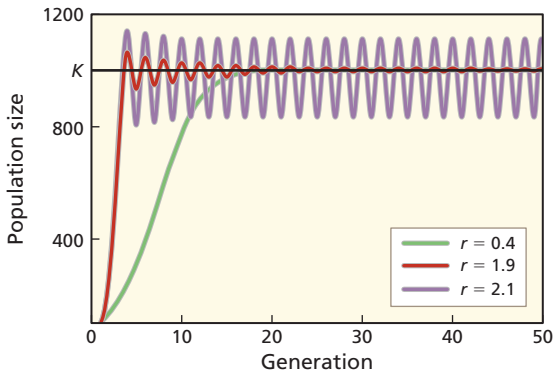
For the logistic model the stability of the equilibrium, $N_t = K$, is determined by the magnitude of r, the intrinsic rate of increase. If r is greater than zero but less than two (the red curve in Figure 10.7B), the equilibrium at K, the carrying capacity, is stable. Let's try to make sense of this condition. If r is less than zero, net reproductive rates are less than one at all densities and the population will die out (recall that at very low density the net reproductive rate will be approximately $1 + r$). When r is greater than zero but less than two, net reproductive rates are



STABLE EQUILIBRIUM
If the ball is moved up the valley, it is returned by the force of gravity to its equilibrium position at the bottom.

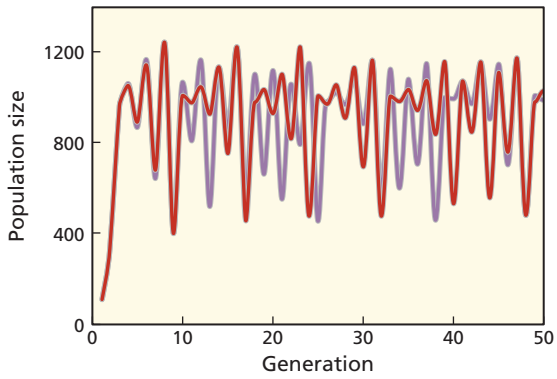
UNSTABLE EQUILIBRIUM
In this case, any slight perturbation of the ball from its resting position causes the ball to continue moving away from its equilibrium position at the top of the hill.

FIGURE 10.7A Types of Equilibria



For the logistic model, the stability of the equilibrium point, $N_t = K$, is determined by the value of r.

FIGURE 10.7B Stability of the Logistic Model



If r is very large, population size fluctuates in a seemingly erratic fashion. This behavior is called chaos. Populations that display chaotic dynamics are very sensitive to small displacements.

The graph shows the population size predicted from the logistic equation with $r = 2.7$ and $K = 1000$. The only difference between the two curves is that the red line started at 100 individuals and the blue line started at 101.

FIGURE 10.7C Chaos

greater than one and the population size increases at low density. As population size increases, the net reproductive rate decreases, slowly approaching one and allowing the population size to gradually approach the carrying capacity (green curve). As r gets larger the population tends to overshoot and then undershoot the equilibrium size, oscillating but eventually approaching the carrying capacity (red curve). Eventually, when $r > 2.0$ (blue curve), the overshoots and undershoots continue indefinitely.

When r gets very large (which for the logistic model means $r > 2.57$), the population dynamics become very erratic. This type of behavior is called **chaos**. Chaos is a type of behavior exhibited by many things besides population growth—from electrical circuits to economies. One property of chaos in populations is that population sizes can change abruptly and dramatically in a single generation—as shown in Figure 10.7C, where a theoretical population with a carrying capacity of 1000 occasionally drops to 360 individuals. It isn't easy to predict the future of a chaotic population. Figure 10.7C shows how different the future population sizes are in two chaotic populations that start at almost the same sizes (100 vs. 101). With real populations, prediction is even more complicated because population size also varies due to random environmental factors.

The box below demonstrates stable and unstable equilibria in two laboratory environments. Laboratory experiments, like the one below, aid the ecologists in dissecting the important events that determine population stability. In flour beetle populations adults often cannibalize pupae. The stability of the flour beetle populations depends critically on these rates of pupal cannibalism. It also turns out that flour beetle larvae cannibalize eggs and occasionally pupae. However, larval cannibalism is less important for stability of the beetle populations. Ultimately, high levels of adult cannibalism and high adult mortality can lead to population cycles and even chaos.

Stability of Laboratory Populations of Fruit Flies

Below are data from laboratory populations of the fruit fly *Drosophila melanogaster*. Figure 10.7D shows five populations kept under conditions that result in a stable carrying capacity. During the first five generations there is a slow and steady increase in the population size. After generation five, the populations fluctuate around their carrying capacity. The populations in Figure 10.7E are in a different environment, where the carrying capacity is not stable. These populations show large increases in size immediately followed by large decreases. For *Drosophila* an unstable environment is one in which adult food levels are high and larval food levels are low. The high food level provided to adults results in substantial increases in egg production, thus effectively increasing the value of r.

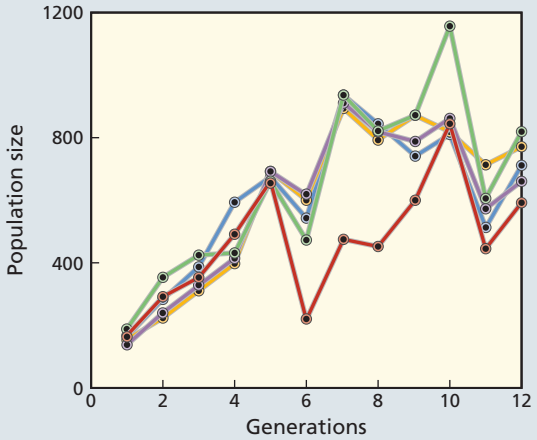


FIGURE 10.7D

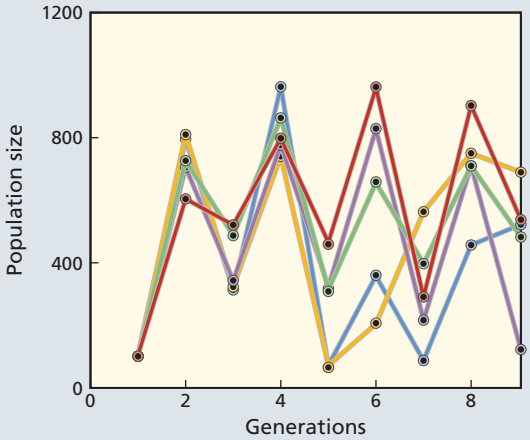


FIGURE 10.7E

10.8 Many organisms have complex life cycles that are density regulated

The logistic equation is based on the premise that crowding reduces survival and fertility. What are the biological mechanisms that generate these effects? Here, we consider some of the biological mechanisms that occur in organisms with complex life cycles. Some organisms start life as small versions of adults and then grow to their adult size. Other organisms, including some frogs and insects have juvenile and adult forms that are morphologically quite different. They may even live in different habitats. For example, many insects start life as crawling or burrowing larvae with limited ability to move large distances. After an active period of larval growth, they form a resting phase as a pupa. Usually the pupa is covered with a protective case, inside of which the insect undergoes a dramatic metamorphosis to the adult form. Usually the adult can fly. Likewise, amphibians normally begin life as an aquatic organism with gills. To become adult, their bodies undergo a metamorphosis to form legs that permit the animal to travel on land (see Figure 10.8A). The combination of two distinct life-forms into one life cycle has led ecologists to call the typical insect and amphibian life cycle *complex*.

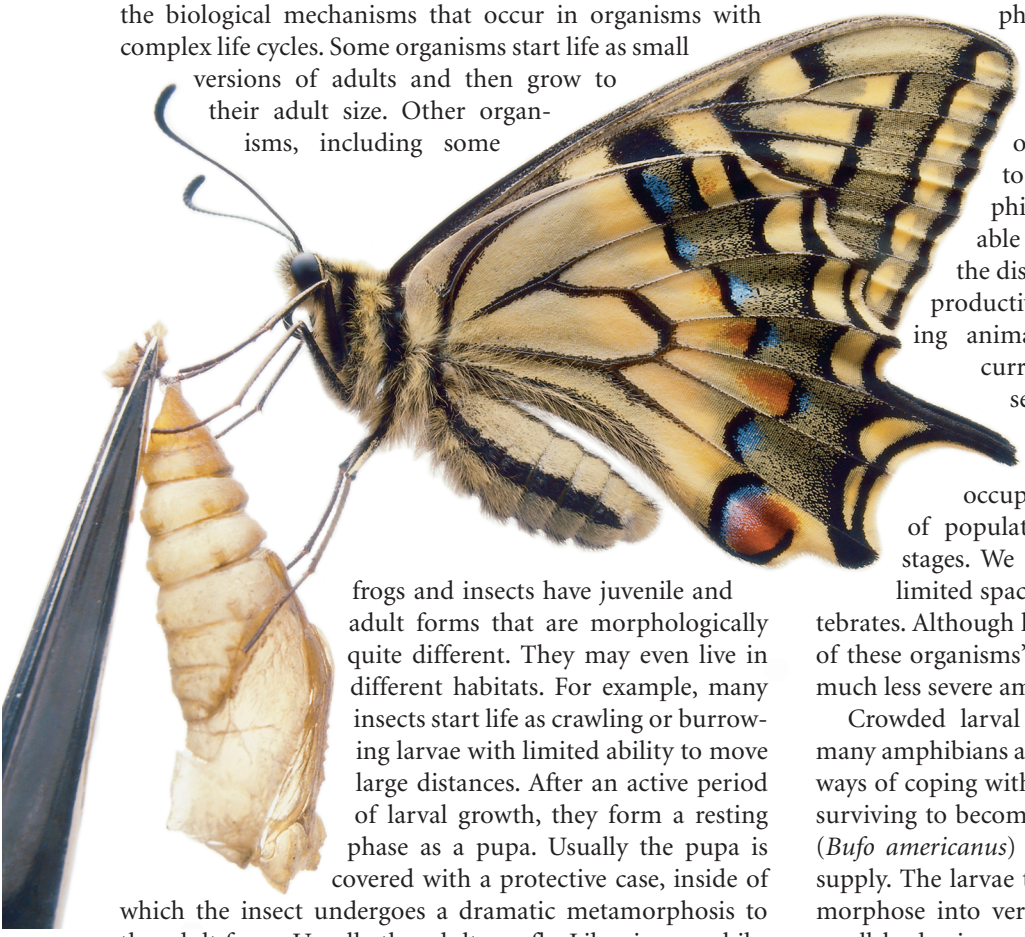


Figure 10.8A is a generalized illustration of a **complex life cycle**. Organisms with such life cycles devote the first part of the cycle to growth and the second part to reproduction. For the insect and amphibian life cycles, the adult phase is better able to disperse. But in marine invertebrates the dispersal cycle is often reversed. The pre-reproductive stages live as zooplankton, small floating animals that are dispersed by the ocean currents. To mature, the larval zooplankton settle out and attach to rock, only then beginning reproduction.

Because the different life stages may occupy very different environments, the effects of population crowding may differ between life stages. We have already discussed the problems of limited space faced by many marine intertidal invertebrates. Although less is known about the planktonic phase of these organisms' life cycle, the effects of density must be much less severe among plankton.

Crowded larval conditions are probably common for many amphibians and insects. These organisms have evolved ways of coping with crowding that increase their chances of surviving to become adults. For instance, when some toads (*Bufo americanus*) are crowded as larvae, food is in short supply. The larvae then grow much more slowly and metamorphose into very small adults (see Figure 10.8B). This small body size reduces the number of offspring they can produce as adults. However, had the larva died from starvation, they would not have had offspring at all.

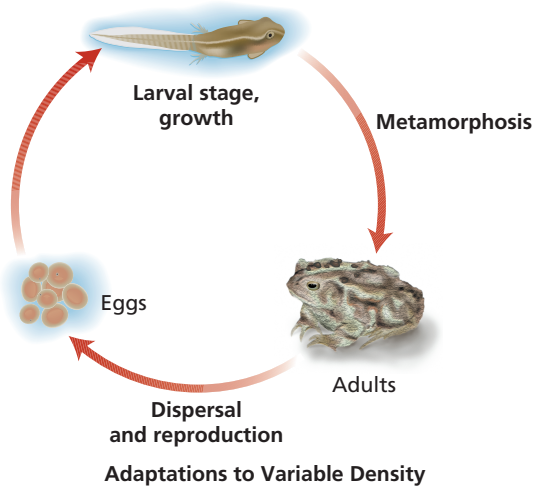


FIGURE 10.8A A Generalized Complex Life Cycle

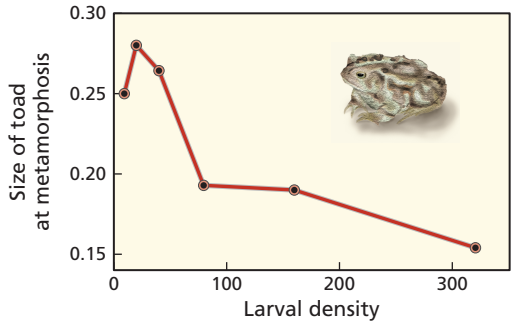


FIGURE 10.8B Adaptations to Variable Density: Toads When toads are crowded, the tadpoles may metamorphose at a small size and thus avoid death by starvation. Interestingly, when the density is very low there are probably too few larvae to stir up all the food and keep it suspended in the water column. As a result, there is a small decline in body size at the lowest larval density.

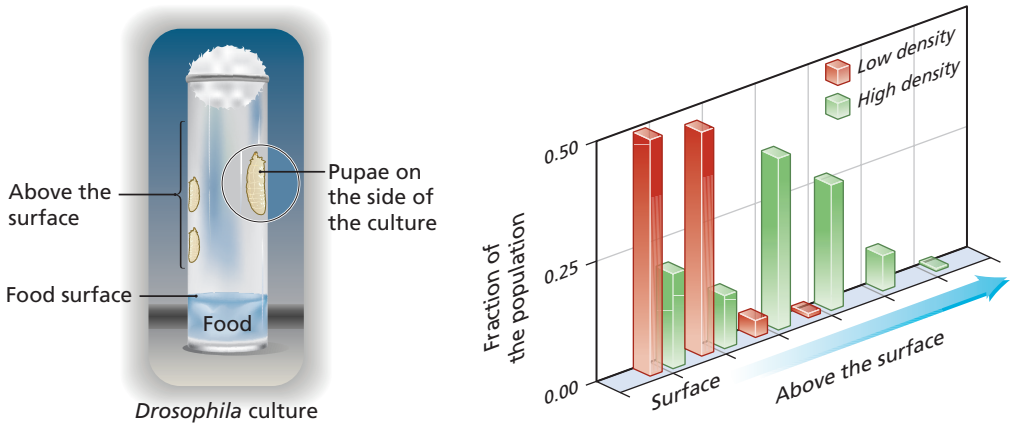


FIGURE 10.8C Adaptations to Variable Density: Flies Larvae of the fruit fly, *Drosophila*, often form pupal cases on the surface of the food medium in uncrowded cultures. If the cultures are crowded, the pupae can sink into the soft food and drown. In such crowded cultures the larvae try to avoid pupating on the surface and tend to crawl up the sides of the culture, away from the food surface.

In laboratory cultures of fruit flies (*Drosophila melanogaster*), the consistency of the food depends on the numbers of larvae that are feeding in it. When there are few larvae, the food may remain relatively hard and dry. With many larvae, the food becomes a fluid mess, much like quicksand. To become adults, the larvae must find a place to form their pupal case and undergo metamorphosis. In uncrowded cultures, they tend to pupate on the surface of the food or close to it (Figure 10.8C). But in crowded cultures pupating on the surface is dangerous because the pupae would sink into the food and die. Under these conditions, the larvae tend to avoid the surface of the food, instead crawling high up the side of the culture as shown in Figure 10.8C.

Tribolium, the common flour beetle, also has a complex life cycle—although all life stages are typically found in a common environment. For these species an important component of population regulation is cannibalism (Figure 10.8D). As more larvae are produced, they consume more eggs. Since eggs become larvae, high numbers of larvae will reduce the numbers of larvae in the future through their consumption of eggs.

The levels of cannibalism may also respond to natural selection. When *Tribolium* are experimentally provided eggs from close relatives, their propensity to cannibalize them decreases over time due to group selection. This type of natural selection is described in more detail in Chapter 20.

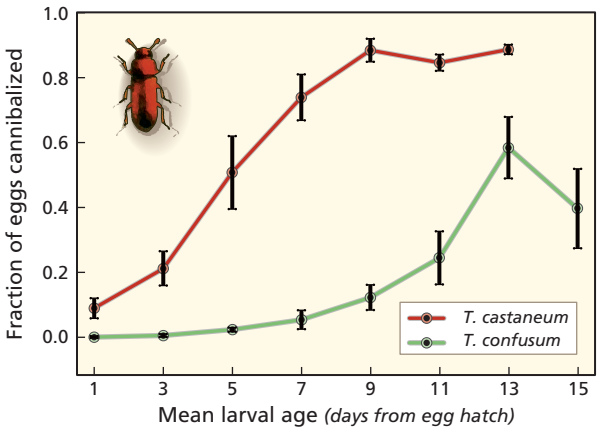
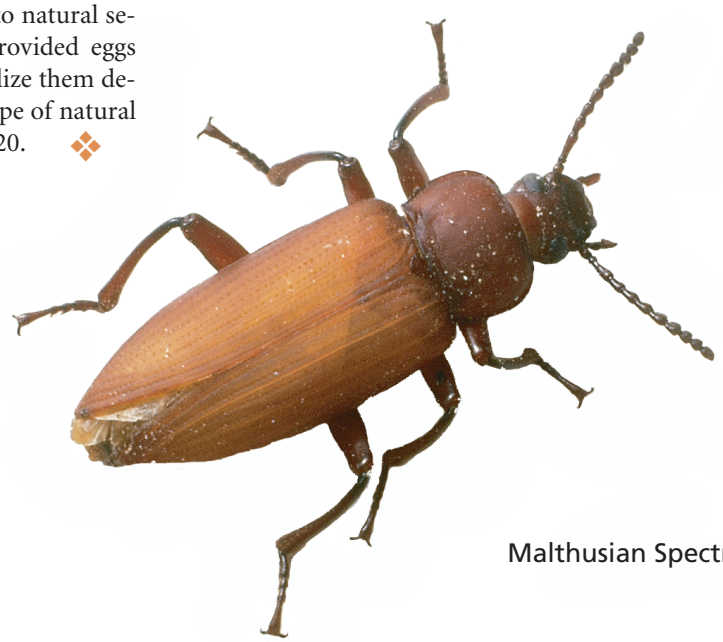


FIGURE 10.8D Cannibalism is an important mechanism of population regulation for flour beetles. At a fixed egg density, *Tribolium* larvae consume more eggs as they get older. As more eggs are eaten, fewer larvae are produced; this relaxes the intensity of regulation on egg numbers.



Density-Dependent Natural Selection

10.9 The early theories of *r*- and *K*-selection were verbal

The importance of the natural environment in shaping the adaptations of organisms is inescapable. Yet evolutionary biology in the first half of this century paid little attention to ecology. In 1930 the great English statistician and population geneticist, Sir Ronald Fisher, proposed that natural selection will always increase the mean fitness of a population. Fisher called this theory the Fundamental Theorem of Natural Selection. In 1962 the American ecologist, Robert MacArthur (see the box), tried to redirect the course of evolutionary thought by developing an ecological analogue to Fisher's Fundamental Theorem of Natural Selection. This attempt of MacArthur's did not result in a lasting theory, but it did illustrate the point that ecology and evolution might be combined, and biologists in both fields have continued to explore this intersection.

Ecologists devote much attention to the response of population growth to density. And some evolutionary biologists study adaptation to population density. Combined, these two efforts yield an evolutionary biology based directly on the ecology of populations. Part of this union is the field of *density-dependent natural selection*. It is the first success of evolutionary ecology. In this module we outline its basic theory and key experiments.

Some of the seminal ideas behind density-dependent selection were first summarized in 1967 by MacArthur and E. O. Wilson. They called the theory ***r*- and *K*-selection**, where *r* and *K* refer to the parameters of the logistic model. Specifically, *r* is the intrinsic rate of increase, or maximum rate of growth at low population densities, and *K* is the carrying capacity, or the maximum number of individuals that the environment can support. Over the last 30 years, various experiments have tested these ideas. The history of this research provides important lessons for research methodologies in evolution and ecology. We review some of these lessons here.

The original development of this theory was qualitative. MacArthur and Wilson argued that for populations living at low density with abundant resources, natural selection would favor traits that contribute to *r*, the intrinsic rate of increase in the logistic equation. It was not clear exactly what traits could make this contribution, so there were many suggested candidates. (These candidate traits are referred to as **life-history characters** since they are associated with the timing and process of reproduction. You will be familiar with these characters from Chapter 7.) For instance, some suggested that decreases in **generation time**, the average time between birth and the production of offspring, and increases in fecundity would be the most likely changes brought about by life at low population densities. Others suggested that increasing *r* could be accomplished by a decrease in body size.

At high densities the opposite suite of traits would evolve, causing an increase in the carrying capacity for individuals with these traits. For example, if individuals became more efficient at extracting energy from the available food, a given envi-

FIGURE 10.9A Experimental Tests of *r*- and *K*-selection Cattails studied by McNaughton. The *r*-selected populations had more rapid development and produced more seed, but invested less energy in each seed compared to the *K*-selected populations.

ronment could support a larger number of these efficient individuals.

A central thesis of *r*- and *K*-selection is the notion that evolution cannot simultaneously maximize *r* and *K,* so there are trade-offs. As a result, the suite of traits that are favored at low densities are different from those favored at high densities. So while selection at low density may favor increased fecundity, that increase may be accompanied by a decline in competitive ability at high densities. It is hard to predict what these trade-offs will be like, or if they will even exist. Fortunately, experimental tests have given insights into the nature of these trade-offs.

Some early tests of these predictions compared different species that lived under different density conditions. The idea was that each species represented a different end product of evolution and that the differences between the species were largely due to the different densities at which they lived. We review two of the classic studies in this field, from the early 1970s. McNaughton compared two species of cattail (*Typha,* Figure 10.9A) and concluded that species from the northern United States had traits consistent with *r*-selection, whereas species from the southern United States had traits consistent with *K*-selection. Of course it is hard to be sure that environmental density was the only important difference between these species; or that other factors, such as climate or genetic drift, did not contribute to the observed differences.

Some other early studies focused on different populations of one species. Gadgil and Solbrig studied populations of dandelions (Figure 10.9B). They found that a genotype of dandelion prevalent in an undisturbed site was a better competitor but produced fewer seeds than a genotype common in a disturbed site. The assumption was that population densities should be higher in the undisturbed sites. However, there was no way to know what the past densities had been at these sites, or if there were factors other than density that varied between sites and affected the evolution of competitive ability and seed number. Gadgil and Solbrig looked at competitive ability and seed number because the measurement of actual rates of population growth in nature is difficult.

FIGURE 10.9B Experimental Tests of *r*- and *K*-selection Gadgil and Solbrig found that the predominant genotype of dandelion in undisturbed areas (*K*-selected) was a better competitor than the predominant genotypes in the disturbed area (*r*-selected). However, the *r*-selected genotype produced more seeds than the *K*-selected genotype did.

Robert H. MacArthur, Innovative Theoretical Ecologist (1930–1972)

FIGURE 10.9C
Robert H. MacArthur

Much of the interest in selection at varying densities was inspired by the theoretical work of Robert MacArthur (Figure 10.9C). MacArthur's short career was marked by the development of highly original theories concerning species diversity, life histories, and many other important problems in ecology. MacArthur emphasized theory that could explain general patterns in ecology, as opposed to searching for hypotheses that might apply to only a few species. Critics of MacArthur pointed out that many of his theories were overly simplistic.

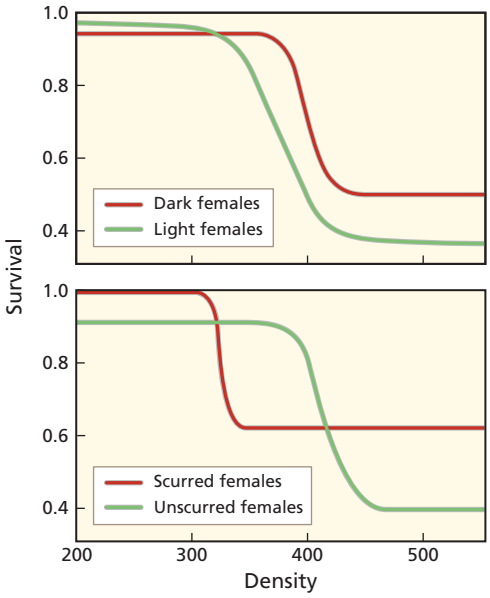
The most extensive development of his theory for density-dependent population growth appeared in his 1967 book with E. O. Wilson, *Island Biogeography*. MacArthur and Wilson called their theory of density-dependent selection *r*- and *K*-selection, emphasizing the consequences of selection at extreme densities. At very low density, they argued that the genotypes with highest *r* values would be favored; at very high densities, the genotypes with the highest *K*-values would win. These ideas were attractively intuitive, but at times their application was exaggerated, which caused scientists to dismiss them prematurely. However, the theory of *r*- and *K*-selection has been made more rigorous (as outlined in Module 10.11) and the predictions from this type of theory have been tested, as described in this chapter. The groundwork laid by MacArthur has led to substantial advances in our understanding of ecology and evolution.

10.10 Great differences exist within species in their ability to tolerate crowding

A major goal in the field of evolutionary ecology has been to determine the relationship between *life-history characteristics* (traits associated with the timing and rate of reproduction) and *fitness*. The chance of surviving to become an adult, **viability**, must be related to fitness. But viability alone is not equivalent to fitness, because the organism must also leave offspring. Therefore the number of offspring produced will be related to fitness. But fertility alone is not fitness if the organism never finds a mate. There is certainly no single, easily measured character that we can assume is equal to fitness.

Nevertheless, some characters may be very closely related to fitness. For example, the *per capita contribution to population growth* is a plausible measure of fitness. This measure, which can be related to the number of offspring left in the next generation, depends on both survival and fertility. Population growth rates will vary with population density. At high density the carrying capacity of a genotype may be equivalent to fitness. This is a somewhat abstract concept, but in principle refers to the ability of a genotype to withstand crowding. While at low densities, the initial reproductive rate may be more important for fitness. For these reasons, it is attractive to think of *fitness* as an organism's contribution to population growth.

If we utilize this definition of fitness, then natural selection may shape population growth rates if population growth rate varies genetically within populations. Figures 10.10A and 10.10B show two examples of this type of genetic variation. The first example (Figure 10.10A) comes from a natural population of Soay sheep (*Ovis aries;* Figure 10.10C) living in Scotland. In these populations, there is clearly strong selection in favor of sheep with dark coats and scurred (small, twisted) horns during periods of high density. The reason these genotypes survive better is unknown, but they are a remarkable example of density-dependent selection in a natural population.



In Soay sheep a single locus determines the color of the sheep's coat. The allele that produces light-colored coats when homozygous is recessive to the allele that produces dark brown coats.

These same sheep also show genetically based differences in horn shape. Some sheep have scurred horns (small and twisted), while others are unscurred. The horn type is determined by one or two loci.

In 1996 Paul Moorcroft and his colleagues analyzed eight years of survival data from natural populations of Soay sheep in Scotland. The survival of females at different densities is shown on the right.

From these results it appears that at low density all phenotypes survive well, but at high density the dark phenotype does better than the light phenotype and the scurred phenotype does better than the unscurred.

FIGURE 10.10A Different genotypes of Soay sheep vary in their ability to survive crowding.

The second example (Figure 10.10B) involves populations of fruit flies (*Drosophila melanogaster*) in the laboratory. Fruit-fly chromosomes were manipulated to create different populations of flies. All individuals in a population were made homozygous for their second chromosome. When rates of population growth were estimated, large differences were found between genetically different populations. For this collection of genotypes, the differences in fitness, measured as net reproductive rates, were greatest at low densities. These net reproductive rates are the same as those defined in Module 10.2.

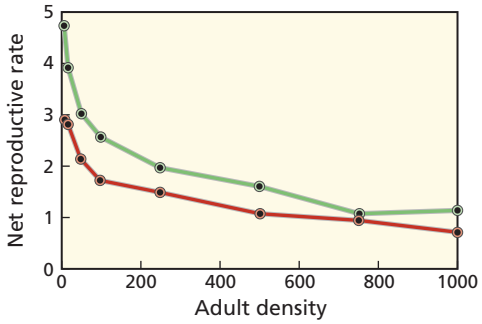


FIGURE 10.10B Net Reproductive Rates Vary among Genetically Different Populations of Fruit Flies Populations of fruit flies (*Drosophila melanogaster*) can be rendered homozygous for large portions of their genome. The graph shows two such populations and their net reproductive rates at a variety of densities. Note that at very low density, one population grows 50 percent faster than the second population.

FIGURE 10.10C Soay Sheep

Because rates of population growth depend on both the survival and fertility of individuals, genetically based differences in population growth rates will affect fitness, and natural selection may change the frequencies of genotypes. As we saw with Soay sheep and fruit flies, the differences between the growth rates of particular genotypes can vary with density. Soay sheep are differentiated at high density, and fruit flies show the greatest growth rate differences among genotypes at low density.

We can determine the outcome of selection with varying population density using a simple genetic model with two alleles (A_1 and A_2) at a single locus. If we assume population growth follows the logistic equation, then we can summarize the growth characteristics of each genotype by its specific values of r and K (Figure 10.11A). In the example in Figure 10.11B, the A_1A_1 homozygotes have highest fitness at low density, the A_2A_2 homozygotes have highest fitness at high densities, and the heterozygotes are intermediate. These fitness differences reflect the fact that the A_1A_1 homozygotes have high values of r but low values of K, relative to the A_2A_2 homozygotes (Figure 10.11C).

$$W_{A_1A_1} = 1 + r_{11} - \frac{r_{11}N}{K_{11}}$$

$$W_{A_2A_2} = 1 + r_{22} - \frac{r_{22}N}{K_{22}}$$

- r_{11}: Intrinsic rate of growth for the A_1A_1 homozygote
- K_{11}: Carrying capacity for the A_1A_1 homozygote
- N: Total population size, which is the sum of all three genotypes

FIGURE 10.11A Fitness equals each genotype's net reproductive rate.

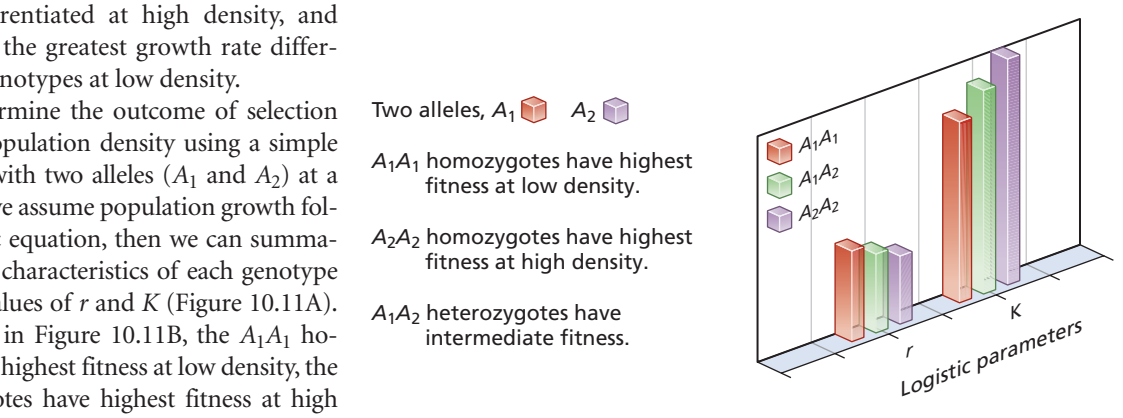


FIGURE 10.11B Genetic variation for population growth.

What then is the outcome of natural selection? The outcome of natural selection depends on the environment. In crowded environments, the A_2A_2 homozygotes have the highest growth rates and the highest fitness and therefore increase in frequency to fixation (i.e., their frequency approaches 100 percent; Figure 10.11D). In those environments where population density is kept low, the A_1A_1 homozygotes have highest fitness, and they increase in frequency at the expense of the genotypes carrying the A_2 alleles.

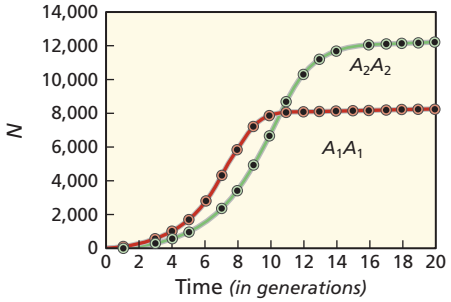


FIGURE 10.11C This figure demonstrates that when the homozygous genotypes are kept in isolation, they grow logistically and attain their carrying capacities. The carrying capacity of the A_2A_2 genotype is greater than that of the genotype.

The particular density conditions experienced by natural populations vary. In stable environments, populations may have long periods of uninterrupted growth, reach their carrying capacity, and thus experience strong selection for those traits that increase growth rates at high densities. It is also possible that, in some environments, floods, drought, and winter freezes keep population numbers well below the carrying capacity. In these environments, we would expect selection to favor those traits that will increase growth rates at low density.

Natural constraints may prevent any single genotype from being best for both r and K. One explanation for the existence of such constraints may be that organisms have limited energy stores, so that energy devoted to high reproduction at low densities may not be available for surviving stressful conditions at high population densities. For instance, an individual could increase r by producing more eggs. One way to tolerate crowded conditions, and thus periods of reduced food, is to store fat. But eggs and fat both require energy, so they may trade off against each other. This type of trade-off may be fairly common.

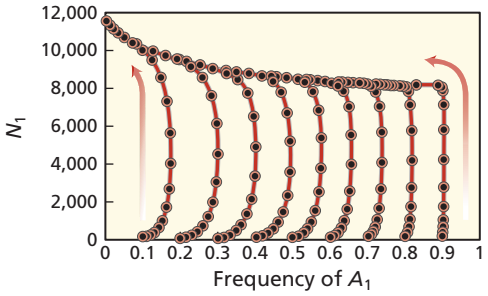


FIGURE 10.11D Changes in allele frequency and population size over time from several different initial allele frequencies. When population density is low, the curves lean to the right, indicating that the A_1 allele is increasing due to the superior fitness of A_1 carrying genotypes at low density. At far left in the figure, the A_2 allele has become fixed while the total population has grown and become crowded.

10.12 Natural selection often cannot increase population growth rates at high and low density simultaneously

If trade-offs exist between the responses to selection at different densities, then the genotypes favored by natural selection in uncrowded environments should be different from the ones favored in crowded environments. One way to test this idea is to create populations that differ only in the density they are exposed to as they evolve over many generations. Will the growth rates of these populations then fit the theory of density-dependent selection?

Just such an experiment has been carried out with fruit flies. The experiment, illustrated in Figure 10.12A, used three populations that had been maintained in the laboratory at low densities for 198 generations. From each of these three populations, a new population was created that was maintained with crowding. After 25 generations of evolution at high densities, the rates of population growth (measured as net reproductive rates per week) were measured in both the low-density and high-density populations, at both high and low densities. Because there were three replicate populations, genetic differences that appear in all three high-density populations must have arisen due to natural selection as opposed to a random process like genetic drift.

We use the net reproductive rates to estimate relative fitness. A generation in these environments takes about three weeks, so relative fitness was estimated as the growth rate of the low-density population divided by the growth rate of the high-density population cubed. From the graph in Figure 10.12A we see that at a test density of 10 larvae, the relative fitness of the low-density populations is greater than 1.0, due to their superior growth rates. At the two higher test densities, 750 and 1000, the average relative fitness of the low-density populations is less than 1.0, indicating the superior fitness of the high-density populations. However, natural selection has been unable to produce a genotype that does best at all densities. This is consistent with the underlying hypothesis that there will be insurmountable trade-offs in an organism's ability to do well at both extreme densities.

These results show that evolution has affected population growth rates. However, individual traits have also evolved in response to crowding. Three of these traits are well-defined larval behaviors. A behavior called pupation height refers to the distance traveled by a larva up the side of its culture prior to settling and becoming a pupa. Some larvae do not travel at all but will pupate the surface of the food. Other larvae may travel to the very top of the culture. The populations that have evolved at high density are more likely to travel far up the side of the culture and less likely to pupate on the surface of the food compared to the populations that have evolved at low density. In a crowded culture, nearly 80 percent of pupae that pupate on the surface of the food die, so avoiding the surface as a pupation site is clearly adaptive in crowded environments.

A second behavior that has changed in response to density-dependent natural selection is a measure of the feeding rate

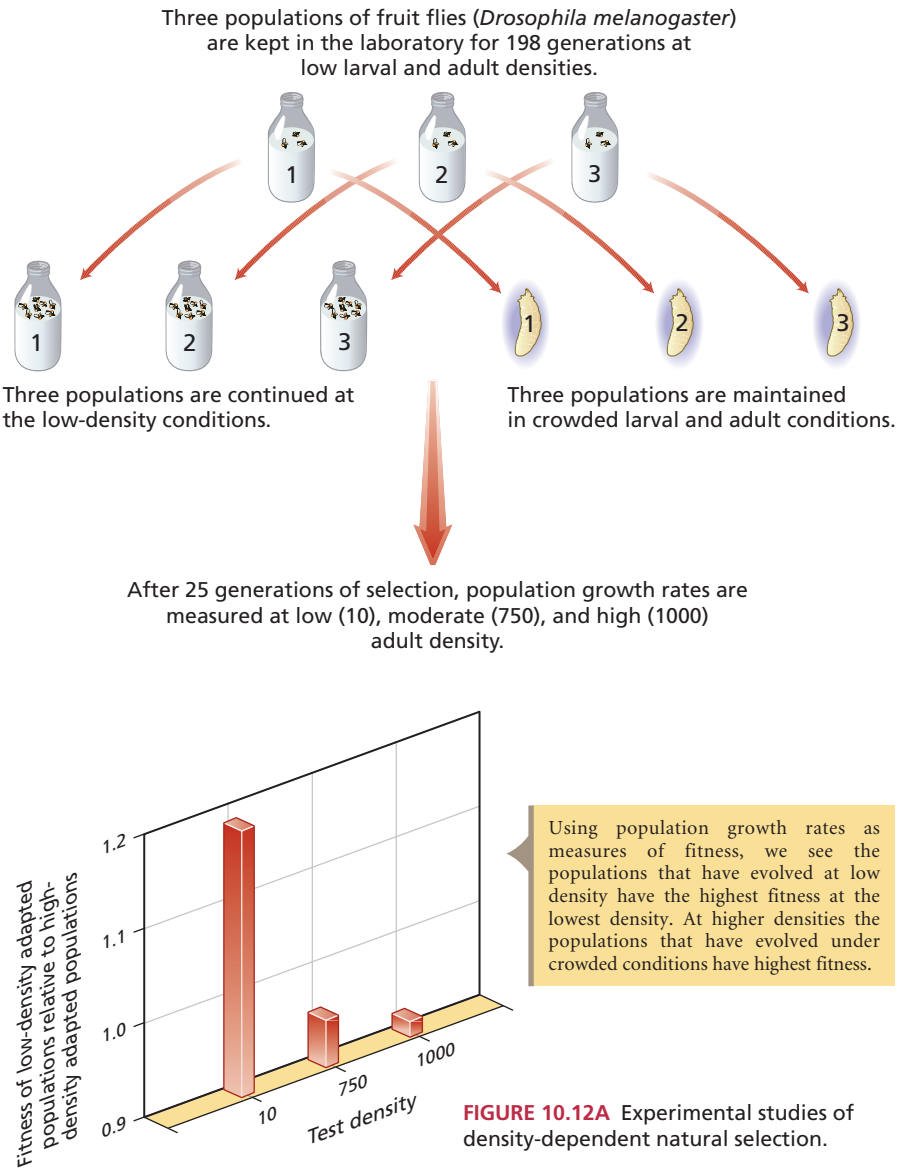


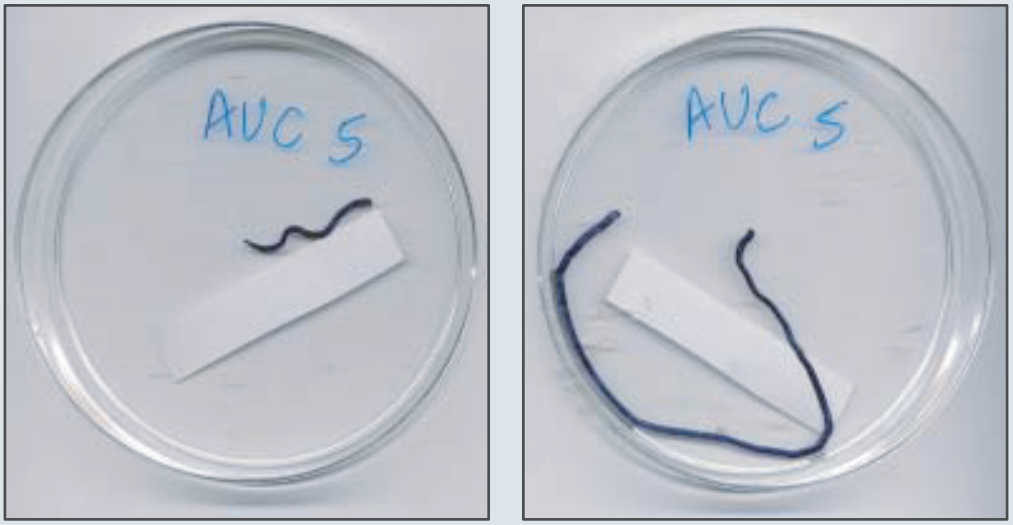
FIGURE 10.12A Experimental studies of density-dependent natural selection.

of larvae. Fruit fly larvae have only one goal—to grow. The larvae feed and grow continuously until they surpass a minimum size required to successfully metamorphose and become an adult. In environments with limited food it turns out that the best competitors have the highest feeding rates (see Module 12.2). Consequently, the populations of fruit flies that have evolved at high population density have evolved much higher feeding rates than their low-density counterparts. A third behavior is called the foraging path length and is described in the box below.

Behavior Evolves in Response to Density

Density-dependent natural selection can even affect the evolution of behavior. Consider fruit-fly larvae, which show genetic polymorphism for foraging. When larvae are put on a flat surface, some—called *rovers*—move a lot, and some—called *sitters*—do not (Figure 10.12B). Larvae from populations that have low densities are mostly sitters, whereas rovers are more common in populations that have been kept at high densities for many generations.

How can we explain the evolution of these foraging behaviors? In crowded environments, rovers are probably better at finding food and avoiding waste. In uncrowded environments, the extra movement of rovers may just waste energy. This sitter-rover polymorphism appears to be controlled by a gene that codes for a cyclic guanosine monophosphate-dependent protein kinase. This protein has been implicated in nervous system function in other organisms.



(**A**) Sitter (**B**) Rover

FIGURE 10.12B
The foraging path length of sitters (left) and rovers (right). The trails are paths left by larvae in a yeast solution.

10.13 The stability of populations is affected by the environment, but not selection

The logistic model produces sustained fluctuations when r is sufficiently large, as we saw in Module 10.7. Although r is a parameter that reflects genetically based components of survival and fertility, r may also be affected by environmental factors. For example, the number of offspring an individual produces may be affected by either the amount or the quality of food the organism eats. Some environments may be uncrowded but have poor food quality, such as low levels of protein and carbohydrate, which may depress r and enhance population stability. The converse is also true.

Blowflies are insects with a flying adult stage and a crawling larval stage. These insects are a significant agricultural pest in Australia, where they infest grazing animals. In Figure 10.13A we give an example of a blowfly population whose stability is affected by environmental factors. In the 1950s, A. J. Nicholson studied the factors that affect population stability in blowflies. His research was not motivated by recent theoretical results concerning population stability, but it has recently been of great interest to ecologists. In Nicholoson's experiment, the blowfly larvae and adults received food independently. The first 630 days of observations, during which the adults were given large quantities of food, show dramatic population cycles, as Figure 10.13A shows. After that period, when the level of adult food were reduced, the cycles were significantly attenuated.

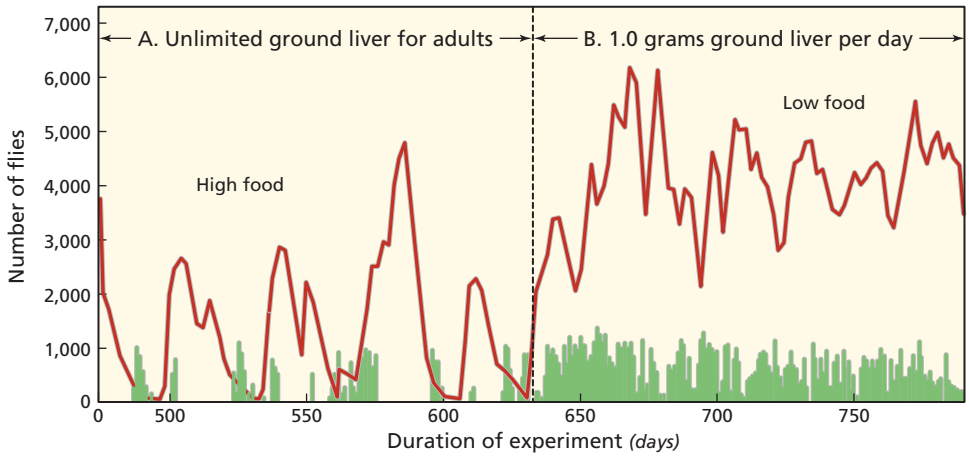


FIGURE 10.13A Environmental Factors Affect Population Stability Populations of blowflies show changes in stability when adult food levels are changed. High levels of food cause increases in female fecundity, and the population becomes unstable. The red line indicates the total number of adults and the green vertical lines represent the number of new recruits added to the adult population. During the first part of the experiment almost all new adult recruits are produced only when the total population size is low.

Besides environmental factors, genetic changes in populations may also affect the value of *r* in the logistic equation, and hence population stability. To investigate this problem, Mueller and his colleagues introduced five populations of fruit flies, which had evolved for 43 generations at low larval and adult densities, into environments with low levels of larval food and high levels of adult food. This resulted in very crowded larval cultures and population sizes that cycled around an equilibrium but never settled down to stable population densities.

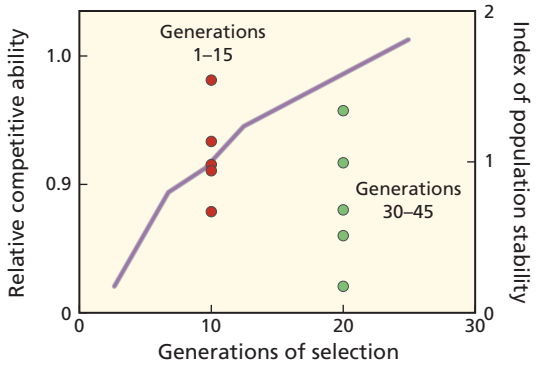


FIGURE 10.13B Evolution of Population Stability Over the first 25 generations in environments with crowded larval conditions, there was strong selection for increased competitive ability as the larvae adapted to the cultures (see blue line). However, the stability of these populations seems unaffected by the evolution of life-history traits in response to crowding. An index of population stability shows roughly the same range and magnitude of effects in the first 15 generations of selection (red circles) as it does in the last 15 generations of selection (green circles).

What happened in this experiment? During the first 25 generations, the populations evolved in response to crowding. They adapted to the crowded larval conditions, and this adaptation is reflected in measurable improvements in competitive ability, as the blue line in the graph of Figure 10.13B shows. Changes in population size were recorded every generation and used to compute an index of population stability. The closer this index is to zero the more stable the population. As the red and green circles on the graph in Figure 10.13B show, there was little change in the stability of the populations; the population stability indices overlap extensively when early generations are compared with later generations. These results suggest that over ecological time spans—perhaps from dozens to a few hundred generations—the stability of a population is more likely to be influenced by changes in the local environment than it is to be influenced by changes in the genetic composition of the population.

Ecological interactions between different life stages have important consequences for the stability of flour beetle populations too. This simple experimental system is described in more detail in the following box.

Cannibalism Affects Population Stability of Flour Beetles

The dynamics and stability of flour beetle (*Tribolium castaneum*) populations are affected by adult cannibalism of pupae as well as adult mortality. It is thus possible to study the dynamics of flour beetle populations by manipulating these events. Theoretically, we expect that low rates of adult mortality and cannibalism should result in the population gradually approaching a stable equilibrium, while high rates of adult mortality and cannibalism should destabilize the population. Figures 10.13C and 10.13D show that when adult mortality was manipulated, the populations behaved as predicted, gaining or losing stability as expected.

Cannibalism may be affected by levels of crowding and by natural selection. It is not clear whether natural selection on flour beetles would have different effects on stability than those we saw in fruit flies.

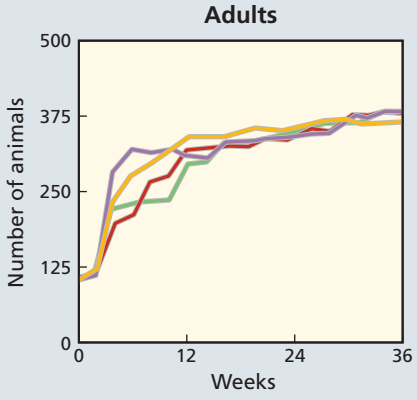


FIGURE 10.13C In this experiment adult mortality was kept low, and the population approaches a stable equilibrium point of about 375 adults. Each line shows an independent replicate population.

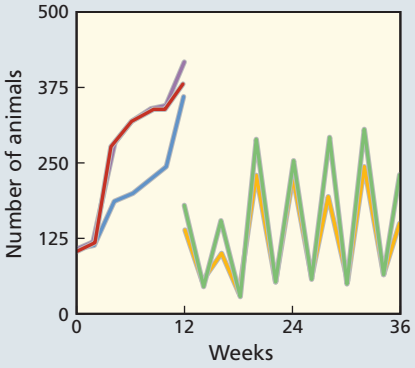


FIGURE 10.13D In this experiment, researchers increased the adult mortality rate after 12 weeks. This caused the population to move away from the stable point and enter a two-point cycle. The peak of the cycle occurs at about 225–250 animals, and the trough is at 50–75 animals.

The Bomb Did Not Blow

10.14 A combination of increased food production and changes in demographic patterns has helped humans avert Malthusian catastrophes

If there is one principle we can derive from this chapter, it is that no biological population can grow exponentially forever. This principle also applies to the human population. Is the human population indeed headed for global starvation and ecological catastrophe, caused by our overabundance? In this module we review two major trends suggesting there is hope that human population growth can avoid the worst possible scenarios. This is not to say that some regions of the world will not suffer starvation and severe disease from time to time. Even with no further increase in the human population, its current members will continue to deplete natural resources, and replacements for these must be found. Nevertheless, gains that have been made in food production and in decreasing human fertility might prevent the population bomb from exploding.

Humans practiced animal and plant breeding long before we had any understanding of genetic mechanisms. Indeed, Darwin used the great success that breeders had in creating animal breeds to support his theory of adaptation by natural selection. For Darwin, nature employed the same mechanisms of differential selection, with the most important traits being those that helped individuals survive and reproduce in their environment.

However, as we have added to our knowledge of the genetic basis of natural and artificial selection, improvements in these techniques have become possible. For instance, we now understand that most of the progress achieved in any artificial selection program that uses outbreeding organisms depends on pre-existing genetic variation in the population. Consequently, preserving genetic variation in economically important species is vital to the long-term success of any breeding program. In addition, most scientists now realize that evolution is never static. Today's super corn variety may need to be modified in the future as new insect or microbial pests evolve.

Many agricultural breeding programs now include the preservation of genetically diverse stocks and ancestral populations as important sources of genetic variation. The levels of genetic variation in some of these species is impressive. For instance, store-bought corn (maize) is remarkable for its consistent appearance. As a species, however, maize harbors tremendous levels of genetic variation—some of which is visible in the color and shape of its seeds (Figure 10.14A).

However, wild populations and stocks of maize are not the only avenue now available for the improvement of agricultural stocks. With the advances in genetic engineering of the last 20 years, it is now possible to introduce genes from other species into agricultural stocks for their improvement. In this module we review some of the impressive gains that have been made with genetically engineered crops.

The gradual decline in mortality among developed countries has been associated with a decline in fertility, thus preventing rapid population growth. However, in the first half of the twentieth century, underdeveloped countries experienced very rapid declines in mortality as modern medical advances were introduced. The result was unprecedented population growth in these countries. Are there any indications that these countries have made any progress decreasing fertility?

Although fertility has been generally lower in developed countries than underdeveloped countries, many developed countries—including the United States—had fertility rates above replacement in the middle of the twentieth century. However, as we see in Figure 10.14B, fertility has shown a steady decline in the United States since the 1950s. This trend has also been observed in other developed countries. Female

FIGURE 10.14A The Range of Corn Seed Phenotypes

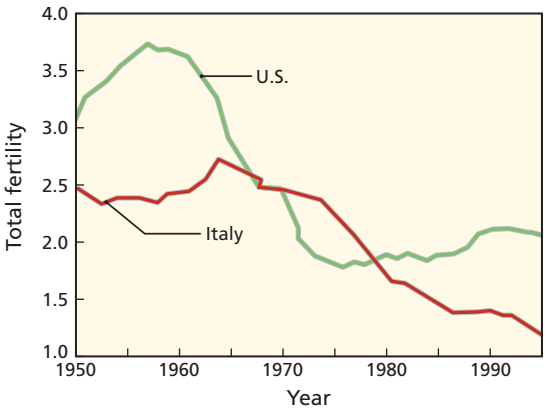


FIGURE 10.14B **Observed Total Fertility in Italy and the United States**

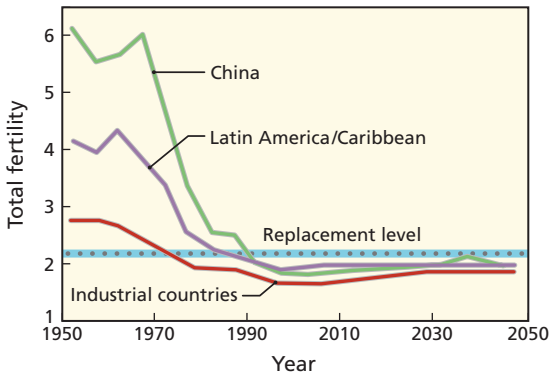


FIGURE 10.14C **Past and Projected Total Fertility in Different World Regions**

fertility in Italy, for instance, has dropped below replacement levels since the late 1970s.

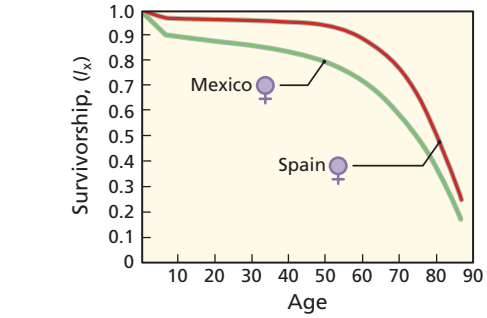
However, no country has shown a more dramatic decline than China, which has dropped from nearly six offspring per female in 1970 to two in 1990 (Figure 10.14C). More importantly, many other regions of the world have experienced similar declines (Figure 10.14C). The major reason for these declines in the developing countries has been changes in the behavior of people. Many couples have chosen to limit their families to two children through the use of contraceptives. These changes in behavior have been aided by massive international efforts to instill family planning in these countries. In many developing countries, there has also been a postponement of marriage and child bearing. In 1950, most Asian women were married by the time they were 20. In 1980 the average age of Asian women at their first marriage was 20–25 years.

This transition to lower fertility in the more developed world is quite different from events in the less developed countries. In Europe and North America, lower fertility was often reached without the aid of modern contraceptive techniques—and in many instances, despite social and religious forces opposing such practices. Next we will learn more about how these reductions in fertility affect population growth projections for the next century.

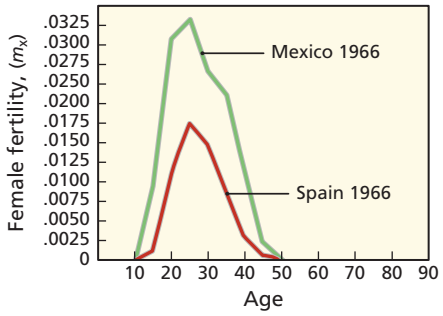
10.15 Forecasting trends in human populations relies on knowledge of human birth and death patterns

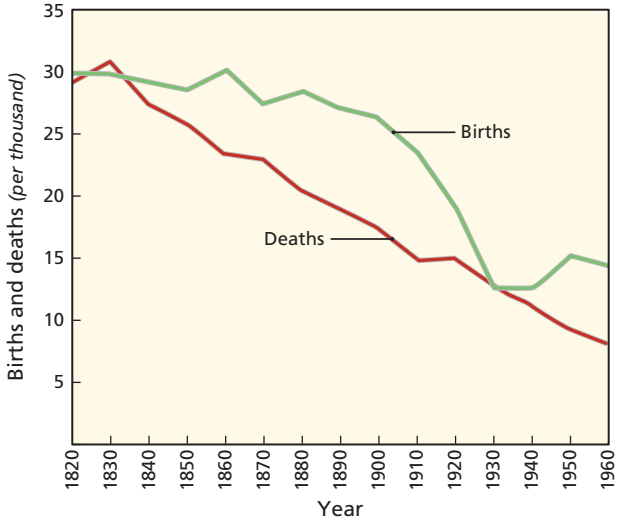
In more developed countries, such as the United States, the rate of population growth was much lower than that in a less developed country like Mexico. These differences separate many developed and less developed countries today. What is the cause of these differences?

Very broadly, the differences in population growth rates may be due to differences in birthrates, death rates, or both. To summarize the survival of human populations, the maximum life span is broken into intervals of five or ten years. If the age classes were spaced at five-year intervals, then the first age class would represent newborns and children up to the age of five years, and the second age class would be children just over five years up to ten years, etc. The chance that an individual survives from the first age class to age class x is often represented by the symbol l_x. The estimated chances of survival for females in Mexico and Spain are shown at the top of Figure 10.15A. For the same age classes, fertility of females may be summarized as the number of offspring born to females in age class x. This value is often represented by the symbol, m_x. Female fertility for the Mexican and Spanish populations is also shown in Figure 10.15A (middle). In 1966 the Mexican population had higher death rates, especially at young ages, compared to the Spanish population, but still had higher population growth rates. The reason for this is that female fertility in Mexico was often substantially higher than in Spain at all ages.



A sharp distinction between the developed and undeveloped countries exists in age-specific patterns of survival and fertility. The figure on the left shows the survival and fertility of females in Spain and Mexico in 1966. The major differences in survival are at very young ages, when Mexican females have a much greater chance of dying. Mexican females have more children than Spanish females do at all ages.





The transition to low rates of population growth in European populations was made gradually by reductions in both fertility and mortality. The patterns shown in the figure are for Sweden between 1820 and 1960.

FIGURE 10.15A Human Demographic Patterns

Many European populations had much higher birthrates 200 years ago. However, as modern medical technology and hygiene were introduced to Europe, mortality gradually declined, especially among infants. This was accompanied by a gradual decline in the birthrate (Figure 10.15A). Of course, until recently the less developed countries lacked modern medical technology. The rapid introduction of antibiotics and other modern medical practices to less developed countries has suddenly reduced mortality with hardly any change in fertility. The result is rapid population growth.

We can summarize patterns of births and deaths in human populations with a few simple demographic parameters. If the total number of individuals in the populations is N, then the **crude birthrate** of a population in any year is simply the total number of births in that year (B) divided by the population size (N). The **crude death rate** is the number of deaths (D) in a given year divided by the total population size (N). The **crude rate of population increase** is simply births minus deaths divided by the total population size: $(B - D)/N$.

TABLE 10.15A World Demographic Parameters, 1995–2000

Country or Area	Growth Rate (%)	Crude Birthrate (per thousand)	Crude Death Rate (per thousand)
World Total	1.3	22	9
Developed regions[a]	0.3	11	10
Less developed regions[b]	1.6	25	9
Least developed regions[c]	2.4	39	15

[a] All regions of Europe and North America, Australia/New Zealand, and Japan.
[b] All regions of Africa, Asia (excluding Japan), Latin America and the Caribbean, and the regions of Melanesia, Micronesia, and Polynesia.
[c] According to the United Nations in 1998, these consisted of 48 countries; 33 are in Africa, 9 in Asia, 1 in Latin America and the Caribbean, and 5 in Oceania.

As an example, let's consider Mexico in 2000. The demographic parameters for that country were as follows: $N = 100{,}350{,}000$, $B = 2{,}310{,}000$, and $D = 502{,}000$. Thus, the crude birthrate expressed as a rate per thousand is $(2{,}310{,}000/100{,}350{,}000) \times 1000 = 23$. The death rate is 5 per thousand, and the rate of increase is 18 per thousand, or 1.8 percent.

Based on birth and death rates, the world's populations generally fall into three categories (see Table 10.15A): (1) High birth and high death rates are found in the least developed countries; (2) High birth and low death rates are found in the less developed countries; and (3) Low birth and low death rates are found in the developed countries.

Many of the developed countries have very low growth rates, and in some cases population sizes are decreasing. Nevertheless, the world population is still growing rapidly. The total world population passed 6 billion in 1999. During this period the population was adding 1 billion new people every 12 years. In the early part of the twentieth century, it took nearly 33 years for the world population to add 1 billion people. The United Nations predicts that the world population will reach 8.9 billion by the year 2050.

10.16 The use of selection and genetic engineering vastly expanded agricultural productivity—though their long-term ecological effects are not known

The production of food in modern agriculture faces a variety of problems that set limits not only to the productivity of existing farms but also to where farming can be carried out. These limits include insect, bacterial, and fungus pests; lack of nutrients in the soil; weed species that compete for those nutrients; and water. Other problems are more subtle but of growing importance. For instance, in many arid areas of the world, crops can be raised with irrigation. However, the high rates of evaporation result in increasing soil salinity, sometimes to the point that plants are unable to grow. Genetic engineering is now being used or considered as a solution for all the problems we have just reviewed. The result of these efforts is increasing agricultural productivity. Let us review some of these recent advances.

The general methodology of genetically engineering crops is shown in Figure 10.16A. A gene of interest, say one that fixes nitrogen from the atmosphere, is carried in bacterial cells. The gene of interest and the bacterial host are together called the **transgenic construct**. This gene is introduced into a susceptible genotype, or **transformation variety**, of the crop species. The presence of the target gene in any particular plant can be determined by a genetic analysis of tightly linked marker loci. Inbreeding will make the target gene homozygous. Then by a series of crosses with the genotype actually used for growing crops, the so-called **elite variety,** the gene of interest is brought into the useful elite variety.

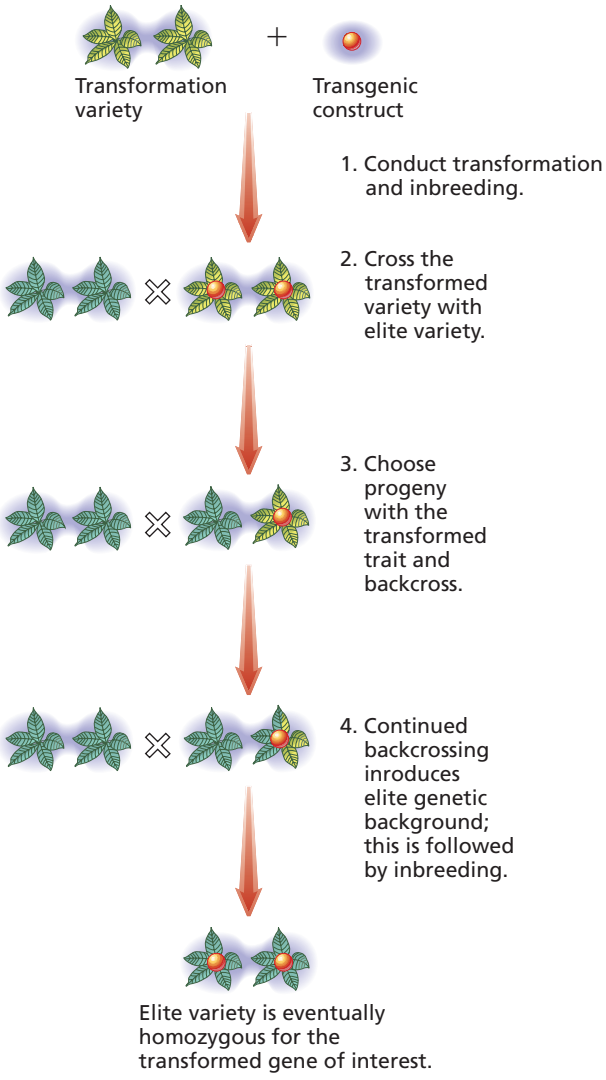
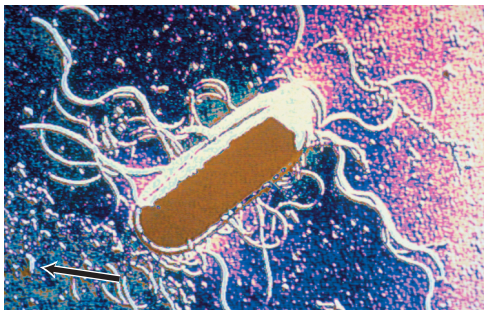


FIGURE 10.16A Genetic Engineering of Crop Species

(**A**) Crown gall infecting a rosebush

(**B**) Crown gall infecting (arrows) a grapevine



(**C**) *Bacillus thuringiensis* spores and Bt toxin crystals (arrow).

FIGURE 10.16B Examples of genetic engineering in crop species.

FIGURE 10.16C Genetic analysis of wild-type, domesticated, and hybrid tomatoes allows identification of important genes that affect color and shape of the fruits. These lines serve as reservoirs of important genetic information.

Crown gall (Figure 10.16B) is caused by a bacterium (*Agrobacterium tumefaciens*) with a small, circular piece of DNA called a plasmid (explained in Chapter 5) that infects many plant species, including roses, grapes, cherries, and peaches. The bacterium invades wounds in the plant and injects the plasmid into plant tissue. The plasmid DNA then integrates into the plant nuclear DNA and causes the plant cells to build the gall. Ironically, the ability to transfer DNA from a plasmid into plant nuclear DNA has made *A. tumefaciens* a useful vector for making transgenic constructs. The growth of crown gall is inhibited by another bacteria, *Agrobacterium radiobacter. A. radiobacter* was genetically engineered so that it could not pass on its genetic information to *A. tumefaciens*. These genetically engineered *A. radiobacter,* known as strain K1026, are now used quite effectively to control crown gall.

A soil bacterium, *Bacillus thuringiensis*, makes a protein, Bt toxin, that kills a variety of insect pests (Figure 10.16B). The gene coding for Bt toxin has been introduced into more than 50 different crop species. These plants thus have continuous protection from pests, eliminating the need for costly pesticide spraying. As with man-made pesticides, some insects are now developing a resistance to Bt toxin. In addition, plants that make Bt toxin excrete it into the soil, where it can persist for long periods of time. It now appears that this lingering Bt toxin can have detrimental affects on "good" insect species that naturally consume pest species. More research will be needed to see if there are ways to avoid these undesirable effects of Bt toxin.

The ancestral species (*Lycoperscion pennellii*) of today's cultivated tomato (*Lycoperscion esculentum*) looks very different from contemporary domesticated plants (Figure 10.16C). However, the ancestral species is a reservoir of genetic variability that can be useful for developing new varieties of crops. By making crosses between the cultivated tomato and the ancestral species, hybrids with intermediate traits can be created. By measuring these traits in the hybrids and the two parents, it is possible to map the genes that affect important color, shape, and other tomato characters. These genes can then be isolated in varieties for future use in tomato breeding programs.

10.17 Humans began to restrict their reproduction

We began Module 10.14 with a review of evidence that many countries have undergone a decline in fertility in the last 50 years. This trend is expected to continue in the developing countries of the world well into the twenty-first century. These declines imply that populations that are now growing will eventually stop growing and even start decreasing in size. Because it is impossible to know exactly how quickly fertility will decline in the future, scientists have estimated the most probable changes. These estimates can then be used to predict when certain populations will start declining in size (Figure 10.17A).

For the entire world population, there is a 50 percent chance that numbers will start declining by the year 2075.

From these estimates we see, for instance, that in the European part of the former USSR there is about a 90 percent chance that the populations will start declining in size by 2015. Less developed countries like China and sub-Saharan Africa lag behind, but show an increasing likelihood of population decline as the twenty-first century progresses (Figure 10.17A). For the entire world population, there is a 50 percent chance that numbers will start declining by the year 2075.

We show what this means for total population size in Figure 10.17B. By 2050, the total world population is predicted to be about 3 billion more than the current number of 6 billion. However, growth is expected to slow by the end of the twenty-first century and not to exceed 10 billion. In fact, current estimates suggest there is about a 15 percent chance that in the year 2100, the world population will be less than it is today.

These predictions depend on the projections of fertility decline. What evidence suggests that fertility will not increase in the future? In fact, this could happen; and then these predictions would be of little use. However, recent historical trends suggest it is unlikely for countries that have experienced fertility declines to show a later increase in fertility. In Figure 10.17C, the changes in fertility between 1950 and 1990 have been recorded. The number of countries that fall into one of four categories of fertility in 1950–55 and 1990–95 are listed in this figure. Very few countries show an increase in fertility (e.g., numbers in the orange zone). Most countries show movement to lower fertility (the blue zone) or no change (the purple zone). If these trends continue to hold, then the widespread drop in fertility is not likely to show a reversal in the next century.

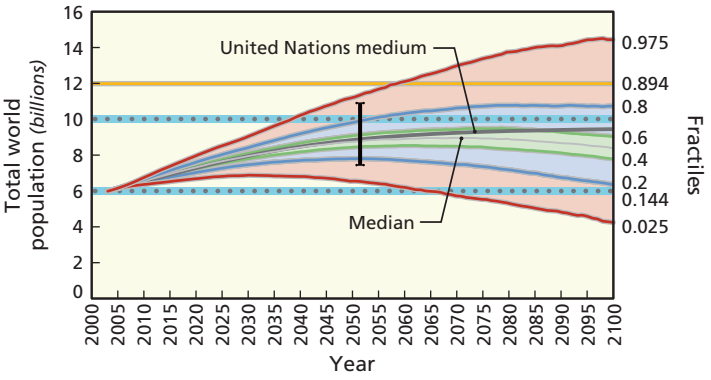


FIGURE 10.17B Projected world population size. Based on information about fertility declines around the world, the best estimates of the total human population are shown here as a dark grey line labeled, "United Nations medium." Due to some uncertainty about this projection, the various shaded bands give some indication of the range of uncertainty in these predictions.

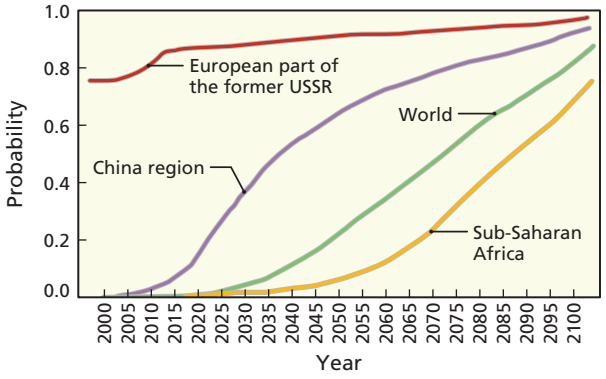


FIGURE 10.17A Probability of population decline. Due to declines in human fertility, populations are predicted to stop growing in the future. This figure shows the probability (y-axis) that a given region in the world will start its population decline at some time in the future. By the year 2100, current predictions suggest there is a very high chance that almost all parts of the world will have started their population decline.

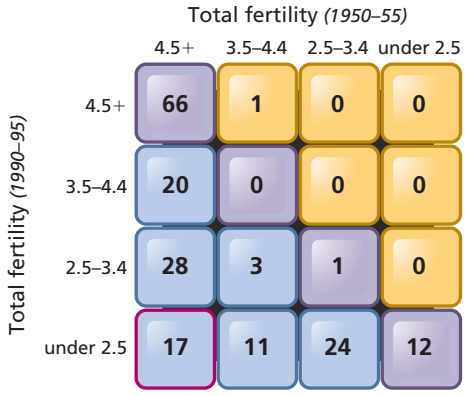


FIGURE 10.17C Fertility change over 40 years. Numbers indicate number of countries in each category.

SUMMARY

1. When birth and death rates are constant, populations grow or decline exponentially.
   a. When births exceed deaths, this means that a population will increase in size indefinitely.
   b. The most obvious factor that will prevent exponential growth is the effect of crowding on fertility and on survival.
   c. Food and space are two resources that will be in short supply as density increases.
2. A simple model of density-dependent population growth is the logistic model.
   a. This model has two parameters, r and K. K is called the carrying capacity, and it determines the equilibrium population numbers that can be supported by the environment.
   b. The second parameter, r, determines the maximum rate of population growth at low densities.
   c. The parameter r of the logistic model also determines whether the carrying capacity is a stable equilibrium.
   d. When r is greater than 2.0 the equilibrium becomes unstable; the population may exhibit cycles or even seemingly random variation called chaos.
3. Natural selection may also affect population growth. If there is genetic variation for traits that affect r or K of the logistic, we expect per capita rates of population growth to increase evolutionarily through a combination of increases in either r or K, or in both r and K.
4. In populations of fruit flies kept at either very high or very low densities, we observe appropriate improvements in population growth rates. However, there are trade-offs such that the genotypes that do well at high densities do not do well at low density, and vice-versa.
5. The human population may avoid large-scale catastrophes from overpopulation. This is a consequence of two major events.
   a. Advances in agriculture in the last 50 years have allowed food production to keep pace with population growth.
   b. There are signs that many countries are undergoing reductions in fertility. The long-term consequence of this decrease is that world population size may stabilize or even decline by the year 2100.

REVIEW QUESTIONS

1. The exponential growth model predicts that population size will be constant when λ is exactly equal to one. Why do you think the exponential model is rarely offered as an explanation for the growth of populations that exhibit stable population size?
2. In a population growing exponentially with $\lambda = 1.5$, how many generations would be required to increase the current population size by tenfold?
3. List some factors that may slow rates of population growth at high densities, and give some specific examples.
4. In a logistically growing population with $r = 1$ and $K = 1000$, there are two population sizes that result in no change in population size over time. What are these population sizes?
5. At a single locus with two alleles (A and a), the genotypic values of r and K are as follows:

Genotype	*r*	*K*
AA	1.0	900
Aa	1.2	1100
aa	1.5	1000

   If this population is allowed to grow to an ecological equilibrium, what will happen to the frequency of the A allele?
6. The stability of some populations is affected by aspects of their ecology. Give some examples for which the biological factors affecting stability are well documented.
7. Are the crude rates of human population growth density-dependent or density-independent estimates of future growth?

KEY TERMS

age structure
carrying capacity
chaos
complex life cycle
crude birthrate
crude death rate
crude rate of population increase
density-dependent population growth
discrete generations
doubling time
elite variety
equilibrium
equilibrium population size
exponential population growth
generation time
intrinsic rate of increase
life history characters
limiting resource
logistic population growth
net reproductive rate
perturbation
population
r- and *K*-selection
stability
transformation variety
transgenic construct
viability

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