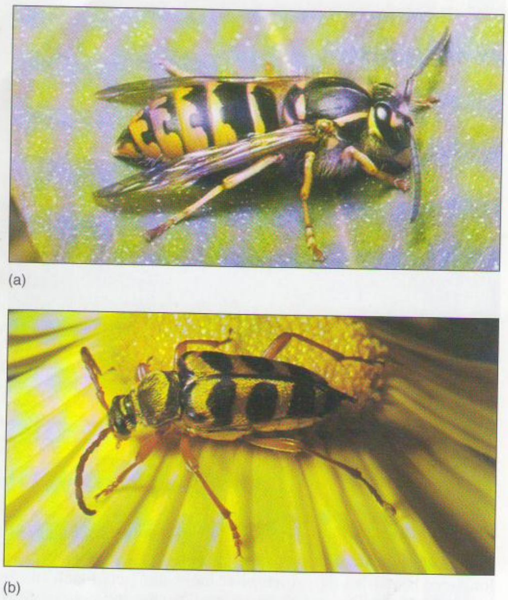


FIGURE 3.15 *An example of Batesian mimicry.* (a) *This dangerous wasp has bold yellow and black bands to warn away predators.* (b) *The much rarer longhorn beetle has no poisonous stinger, but looks and acts like a wasp and thus avoids predators as well.*

other times of the year for pollination and seed-dispersal would disappear as well.

Even microorganisms can play vital roles. In some forest ecosystems, mycorrhizae (fungi associated with tree roots) are essential for mineral mobilization and absorption. If the fungi die, so do the trees and many other species that depend on a healthy forest community. Rather than being a single species, mycorrhizae are actually a group of species that together fulfill a keystone function.

Often a number of species are intricately interconnected in biological communities so that it is difficult to tell which is the essential key. In the kelp "forests" off the California coast, the giant kelp (a kind of algae) provides shelter for many fish and shellfish species and so could be regarded as the key to community structure (fig. 3.16). However, kelp depends on sea otters, which eat the sea urchins that graze on the kelp. Are kelp or otters most important? Each depends on and affects the other. Perhaps we should think in terms of a "keystone set" of organisms in some ecosystems. Some ecological communities are functionally redundant in the sense that if one important species disappears, another will replace it, and essential ecological functions will continue without much change. Such a community might be said to have no keystone species. We'll discuss the role of keystone species in preserving biodiversity in chapter 5.

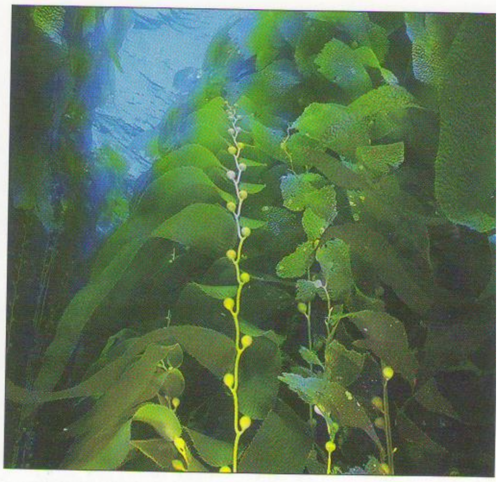


FIGURE 3.16 *Giant kelp is a massive alga that forms dense "forests" off the Pacific coast of California. It is a keystone species in that it provides food, shelter, and structure essential for a whole community. Removal of sea otters allows sea urchin populations to explode. When the urchins destroy the kelp, many other species suffer as well.*

POPULATION DYNAMICS

Many biological organisms can produce amazing numbers of offspring, given optimum environmental resources (fig. 3.17). Consider the example of the common fruitfly (*Drosophila melanogaster*). Under ideal conditions, 24 fly generations can be produced in a year. Typically, each female lays 50 to 100 eggs per generation. If one female fly were to lay 100 eggs and if all her offspring lived long enough to reproduce at the same rate with the same survival success, in a single year she would have about 6×10^{40} offspring. That's 60 billion trillion quadrillion insects! If this rate of reproduction continued for a decade, the whole earth would be covered several meters deep in fruitflies. Fortunately for us, fruitfly reproduction, like that of most organisms, is limited by a variety of environmental factors. This example demonstrates, however, the remarkable potential amplification of biological reproduction. Population dynamics describes the changes in number of organisms in a population.

Population Growth

We call the unrestricted increase in populations **exponential growth** because its rate can be expressed as a constant fraction, or exponent, by which the existing population is multiplied. The mathematical formula for exponential growth is:

$$\frac{dN}{dt} = rN$$

FIGURE 3.17 *High reproductive rates give many organisms the potential to expand populations explosively. The cockroaches in this kitchen could have been produced in only a few generations. A single female cockroach can produce up to 80 eggs every six months. This exhibit is in the Smithsonian Institute's National Museum of Natural History.*

That is, the change in numbers of individuals (*dN*) per change in time (*dt*) equals the rate of growth (*r*) times the number of individuals in the population (*N*). The *r* term is a fraction representing the average individual contribution to population growth, perhaps 1.2 if each individual produces 1.2 times its own number in each time step. If *r* is less than 1, then the population is shrinking. If *r* is exactly 1, then there is no change, and $dN/dt = 0$.

This equation for population growth is also referred to as **biotic potential**, the potential of a population to grow if nothing were limiting its expansion. Note that the equation is a very simple *model* (an idealized, simple description of the real world). In reality, many factors prevent most populations from growing at their biotic potential. (The same equation is used to calculate growth in your bank account due to interest rates; unfortunately, many factors also may keep your savings from growing at their potential rate.)

Boom and Bust Population Cycles

A graph of exponential population growth is described as a **J curve** (left portion of fig. 3.18) because of its shape. As you can see in this graph, the number of individuals added to a population at the beginning of an exponential growth curve can be rather small. But within a very short time, the numbers begin to increase quickly because a fixed percentage becomes a much larger amount as the population increases.

In the real world, however, there are limits to growth. We call the maximum number of individuals of any species that can be supported by a particular ecosystem on a sustainable basis the **carrying capacity**. When a population **overshoots**, or surpasses the carrying capacity of its environment, death rates will begin to surpass birth rates. The growth curve becomes negative rather than positive, and the population may decrease as fast as, or faster, than it grew. We call this dieback a population crash. Populations may go through repeated oscillating cycles of population growth and decline as shown in fig. 3.18. These cycles may be very regular if they depend on a few simple factors, such as the seasonal light- and temperature-dependent bloom of algae in a lake. They also may be very irregular if they depend on complex environmental and biotic relationships that control cycles, such as the outbreaks of migratory locusts in the desert or tent caterpillars in northern forests. We call long periods of low population size followed by a sudden population explosion irruptive growth.

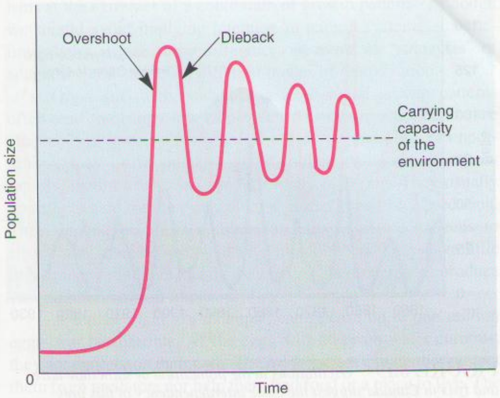


FIGURE 3.18 *Population oscillations. Some species demonstrate a pattern of cyclic overshoot and dieback.*

Sometimes, predator and prey populations oscillate in a sort of synchrony with each other as is shown in fig. 3.19. This is a classic study of the number of furs brought into Hudson Bay Company trading posts in Canada between 1840 and 1930. As you can see, the numbers of Canada lynx fluctuate on about a ten-year cycle that is similar to, but slightly out of phase with, the population peaks of snowshoe hares. When the hare population is high and food is plentiful, lynx reproduction is very successful, and lynx populations grow rapidly.

Eventually, declining food supplies limit hare populations. For awhile lynx populations continue to grow because starving hares are easier to catch than healthy ones. As hares become more scarce, however, so do the lynx. When hares are at their lowest levels, food supplies recover and population growth of both prey and predator begins again. This predator-prey oscillation is known as the Lotka-Volterra model, after the scientists who first described it mathematically.

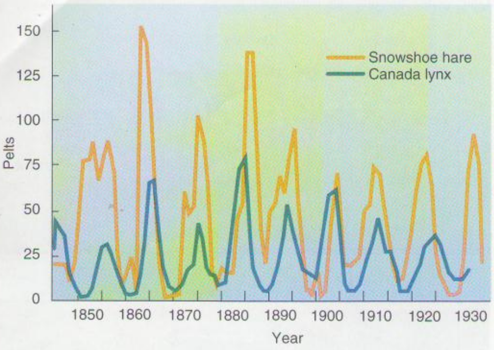


FIGURE 3.19 *Oscillations in the population of snowshoe hare and lynx in Canada suggest the close interdependency of this prey-predator relationship. These data are based on the number of pelts received by the Hudson Bay Company. Both predator and prey show a ten-year cycle in population growth and decline.*

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

Growth to a Stable Population

Not all biological populations go through these cycles of exponential overshoot and catastrophic diebacks. Many species are regulated by both internal and external factors so that they come into equilibrium with their environmental resources and maintain relatively stable population sizes. These species may grow exponentially when resources are unlimited, but their growth slows as they approach the carrying capacity of the environment. This pattern is called **logistic growth** because of its constantly changing rate.

Mathematically, this growth pattern is described by the following equation, which adds a term for carrying capacity (K) to the biotic potential growth equation:

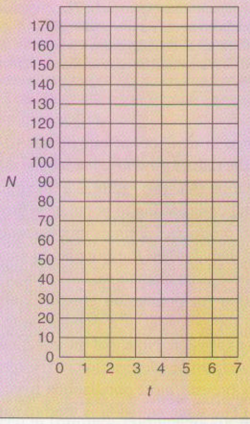
$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right)$$

This equation says that the change in numbers over time (dN/dt) equals the exponential growth rate (r times N) *times the portion of the carrying capacity* (K) *represented by the population size* (N). The term ($1 - N/K$) represents the relationship between N at any given time step and K, the number of individuals the environment can support. If N is less than K, say 100 compared to 120, then ($1 - N/K$) is a positive number ($1 - 100/120 = 0.17$), and population growth, dN/dt, is slow but positive. If N is greater than K, that is, if the population is greater than the environment can support, then ($1 - N/K$) is a negative number. For example, if N is 150 and K is 120, then ($1 - N/K$) is ($1 - 150/120$), which is equal to ($1 - 1.25$), or -0.25. In this case, the growth rate is negative. The logistic growth model, then, describes a population that decreases if its numbers exceed carrying capacity.

APPLICATION: Calculate Population Growth

Think of exponential growth as occurring in time steps. Start with ten cockroaches that can produce enough young to increase at a rate of 150 percent per month ($r = 1.5$). Calculate the number of roaches after seven time steps: for each t, multiply r times the N of the previous time step (round N to the nearest whole number). Then graph the results.

$t = 0$ (start): $N = 10$
$t = 1$: $N = 1.5 \times 10 = 15$
$t = 2$: $N = 1.5 \times 15 = 22$
$t = 3$: $N = 1.5 \times 22 =$ _______
$t = 4$: $N = 1.5 \times$ _______ = _______
$t = 5$: $N = 1.5 \times$ _______ = _______
$t = 6$: $N = 1.5 \times$ _______ = _______
$t = 7$: $N = 1.5 \times$ _______ = _______



Answer: The final graph should be a J-shaped curve.

How does the growth curve of a stable population differ from the J curve of an exploding population? Figure 3.20 shows an idealized comparison between exponential and logistic growth. The J curve on the left in this figure represents the growth without restraint toward the biotic potential, or the maximum number a species might possibly attain. The curve to the right represents logistic growth. We call this later pattern an **S curve** or sigmoidal curve (for the Greek letter sigma).

Limiting Factors

In many species, population growth is regulated both by internal and external factors. Maturity, body size, and hormonal status are

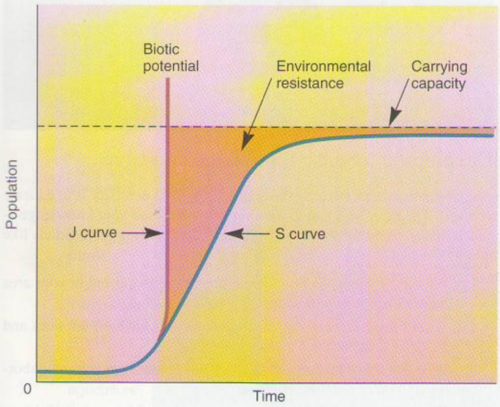


FIGURE 3.20 *J and S population curves. The J curve represents theoretical unlimited growth. The S curve represents population growth and stabilization in response to environmental resistance.*

examples of internal factors. Habitat and food availability, or interactions with other organisms, are examples of external factors. Some of these limits are dependent on population density. Food and water, for example, become more limited as populations grow. Disease, stress, and exposure to predators or parasites can all increase mortality rates as populations increase. These factors are called *density-dependent.*

Other limits to growth are *density-independent.* Many of these factors are abiotic: drought or early frost can reduce populations of mosquitoes drastically, regardless of how many mosquitoes there were to start with. Habitat destruction—because of floods, landslides, or human activities—can also limit population growth.

Together, factors that tend to reduce population growth rates are called **environmental resistance**. The area between the two curves in fig. 3.20 is the cumulative effect of environmental resistance. Note that the resistance becomes larger and the rate of logistic growth becomes smaller as the population approaches the carrying capacity of the environment.

K-adapted and *r*-adapted Species

Some organisms, such as dandelions, persist by depending on a high rate of reproduction and growth (*rN*). These organisms are described as **r-adapted.** They tend to have rapid reproduction and high mortality of offspring, and they may frequently overshoot carrying capacity and die back. Other organisms tend to reproduce more slowly as they approach the carrying capacity (*K*) of their environment. These species are referred to as **K-adapted.**

Many species don't fit neatly into either exponential (r-adapted) or logistic (K-adapted) growth patterns. Still, it's useful to contrast the advantages and disadvantages of some organisms at the extremes of a continuum of growth patterns. Although we should avoid implying intention in natural systems, it sometimes helps us see these differences in terms of "strategies" of adaptation and "logic" in different modes of reproduction.

Organisms with *r*-adapted or exponential growth patterns often tend to occupy low trophic levels in their ecosystems (see chapter 2) or to be successional pioneers. As generalists or opportunists, they move quickly into disturbed environments, grow rapidly, mature early, and produce many offspring. They usually do little to care for their offspring or protect them from predation. They depend on sheer numbers and dispersal mechanisms to ensure that some offspring survive to adulthood. They have little investment in individual offspring, using their energy to produce vast numbers instead (table 3.2).

A female clam, for example, can release up to one million eggs over her lifetime. As the eggs drift away on water currents, they are entirely on their own. The mother clam can neither protect them from predators nor help them find food or a place to live. The vast majority of all young clams die before reaching maturity, but if even a few survive, the species will continue. Many marine invertebrates, parasites, insects, rodents, and annual plants follow this reproductive strategy. Predators or other external factors generally limit their numbers. Also included in this group are the weeds, pests, or other species we consider nuisances that reproduce profusely, adapt quickly to environmental change, and survive under a broad range of conditions.

So-called *K*-adapted organisms are usually larger, live longer, mature more slowly, produce fewer offspring in each generation, and have fewer natural predators than the species below them in the ecological hierarchy. Elephants, for example, are not reproductively mature until they are 18 to 20 years old. During

TABLE 3.2 Reproductive Strategies

R ADAPTED SPECIES	*K* ADAPTED SPECIES
1. Short life	1. Long life
2. Rapid growth	2. Slower growth
3. Early maturity	3. Late maturity
4. Many, small offspring	4. Few, large offspring
5. Little parental care and protection	5. High parental care or protection
6. Little investment in individual offspring	6. High investment in individual offspring
7. Adapted to unstable environment	7. Adapted to stable environment
8. Pioneers, colonizers	8. Later stages of succession
9. Niche generalists	9. Niche specialists
10. Prey	10. Predators
11. Regulated mainly by intrinsic factors	11. Regulated mainly by extrinsic factors
12. Low trophic level	12. High trophic level

youth and adolescence, a young elephant is part of a complex extended family that cares for it, protects it, and teaches it how to behave. A female elephant normally conceives only once every four or five years after she matures. The gestation period is about 18 months; thus, an elephant herd doesn't produce many babies in a given year. Since they have few enemies and live a long life (often 60 or 70 years), however, this low reproductive rate usually produces enough elephants to keep the population stable, given appropriate environmental conditions.

An important underlying question to much of the discussion in this book is which of these strategies do humans follow. Do we more closely resemble wolves and elephants in our population growth, or does our population growth pattern more closely resemble that of moose and rabbits? Will we overshoot our environment's carrying capacity (or are we already doing so), or will our population growth come into balance with our resources?

COMMUNITY PROPERTIES

The processes and principles that we have studied thus far in this chapter—tolerance limits, species interactions, resource partitioning, evolution, and adaptation—play important roles in determining the characteristics of populations and species. In this section, we will look at some fundamental properties of biological communities and ecosystems—productivity, diversity, complexity, resilience, stability, and structure—to learn how they are affected by these factors.

Productivity

A community's **primary productivity** is the rate of biomass production, or the conversion of solar energy into chemical energy stored in living (or once-living) organisms. Since much energy is used in respiration, a more useful term is often *net* primary productivity, or the amount of biomass stored after respiration. Productivity depends on light levels, temperature, moisture, and nutrient availability. Figure 3.21 shows approximate productivity levels for some major ecosystems. As you can see, tropical forests, coral reefs, and estuaries (bays or inundated river valleys wher rivers meet the ocean) have high levels of productivity becaus they have abundant supplies of all the required resources. I deserts, lack of water limits photosynthesis. On the arctic tundra c in high mountains, low temperatures inhibit plant growth. In th open ocean, a lack of nutrients reduces the ability of algae to mak use of plentiful sunshine and water.

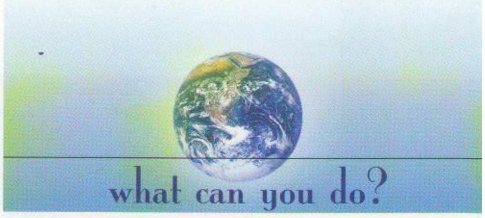
Even the most photosynthetically active ecosystems captur only a small percentage of the available sunlight and use it t make energy-rich compounds. In a temperate-climate oak fores leaves absorb only about half the available light on a midsumme day. Of this absorbed energy, 99 percent is used to evaporate wate

APPLICATION: ***K*-Adapted and *r*-Adapted Species**

Do *K*-adapted or *r*-adapted characteristics best describe the following species (or are some attributes of each appropriate)?

ant ______
housefly ______
bald eagle ______
bison ______
wildebeest ______
antelope ______
cheetah ______
shark ______

Answer: The ant, housefly, bison, wildebeest, and antelope are generally considered *r*-adapted, while the bald eagle, cheetah, and shark are best described as *K*-adapted.



what can you do?

Developing a Sense for Where You Live

One of the first steps toward conserving biological diversity is to educa yourself. The more you know, the more you can share your knowledge- and skills—to help the natural world. Look for answers to questions lik these:

- What ecosystems and biological communities existed in your ar before European settlement?
- What impact, if any, did indigenous people have on the flora ar fauna of your area?
- What are the dominant species (besides humans) in your neighbo hood? Where did they originate?
- How much rain falls in your region each year? Is precipitation se sonal? Is water a limiting factor for biological communities?
- What are the seasonal high and low temperatures where you live How do native plants and animals adapt to seasonal variations?
- Is there a keystone species or group of species especially importa in determining the structure and functions of your local ecosy tems? What factors might threaten those keystone components?
- Where do your drinking water, food, and energy come from? Wh local and regional environmental impacts are caused by produ tion, use, and disposal of those resources? Could you lessen thos impacts by changing your sources or use patterns of resources?
- Is there a park or wildlife refuge near where you live? Does it co tain any rare, threatened, or endangered species? What makes the rare, threatened, or endangered?
- Are there opportunities for volunteer work to improve your loc environment, such as planting native species, cleaning up a river lake, restoring a wetland, recycling trash, or helping to maintain refuge or park?