

CHAPTER 1

Exponential Population Growth



Model Presentation and Predictions

ELEMENTS OF POPULATION GROWTH

A **population** is a group of plants, animals, or other organisms, all of the same species, that live together and reproduce. Just as an individual grows by gaining weight, a population grows by gaining individuals. What controls population growth? In this chapter, we will build a simple mathematical model that predicts population size. In later chapters, we will flesh out this model by including resource limitation (Chapter 2), age structure (Chapter 3), and migration (Chapter 4). We will also introduce other players: populations of competitors (Chapter 5) and predators (Chapter 6) that can control growth. But for now, we will concentrate on a single population and its growth in a simple environment.

The variable N will be used to indicate the **size of the population**. Because population size changes with time, we will use the subscript t to indicate the point in time we are talking about. Thus, N_t is the number of individuals in the population at time t . By convention, we use $t = 0$ to indicate the starting point. For example, suppose we census a population of tarantulas and count 500 spiders at the beginning of our study. We revisit the population in one year and count 800 spiders. Thus, $N_0 = 500$ and $N_1 = 800$.

The units of t , in contrast to their numerical values, depend on the organism we are studying. For rapidly growing populations of bacteria or protozoa, t might conveniently be measured in minutes. For long-lived sea turtles or bristlecone pines, t would be measured in years or decades. Whatever units we use, we are interested in predicting the future population size (N_{t+1}) based on its current size (N_t).

The biological details of population growth vary tremendously among different species, and even among different populations within the same species. The factors that cause a tarantula population to increase from 500 to 800 spiders will be very different from the factors that cause an endangered condor population to decrease from 10 to 8 birds. Fortunately, all changes in population size can be classified into just four categories. Populations increase because of births and decrease because of deaths. Population size also changes if individuals move between sites. Populations increase when new individuals arrive (**immigration**) and decrease when resident individuals depart (**emigration**).

These four factors operate at different spatial scales. Births and deaths depend on current population size, as we will explain in a moment. To understand births and deaths, we need to study only the target population. By contrast, emigration and immigration depend on the movement of individuals. If

we want to describe these processes, we must keep track of not just one, but several interconnected populations.

Any combination of the four factors will change population size. For our tarantula example, the initial population of 500 spiders might have produced 400 new spiderlings during the year and lost 100 adult spiders to death, with no movement of individuals. Alternatively, there might have been 50 births and 50 deaths, with 300 residents leaving (emigration) and 600 spiders arriving from other populations (immigration). Either scenario leads to an increase of 300 spiders.

These four factors can be incorporated into a mathematical expression for population growth. In this expression, B represents the number of births, D is the number of deaths, I is the number of new immigrants entering the population, and E is the number of emigrants leaving the population between time t and $t + 1$:

$$N_{t+1} = N_t + B - D + I - E \quad \text{Expression 1.1}$$

Expression 1.1 says that population size in the next time period (N_{t+1}) equals the current population size (N_t) plus births (B) and immigrants (I), minus deaths (D) and emigrants (E). We are interested in the change in population size (ΔN), which is simply the difference in population size between last time and this time. We get this by subtracting N_t from both sides of Expression 1.1:

$$N_{t+1} - N_t = N_t - N_t + B - D + I - E \quad \text{Expression 1.2}$$

$$\Delta N = B - D + I - E \quad \text{Expression 1.3}$$

To simplify things, we will assume that our population is **closed**; in other words, there is no movement of individuals between population sites. This assumption is often not true in nature, but it is mathematically convenient and it allows us to focus on the details of local population growth. In Chapter 4, we will examine some models that allow for movement of individuals between patches. If the population is closed, both I and E equal zero, and we do not need to consider them further:

$$\Delta N = B - D \quad \text{Expression 1.4}$$

We will also assume that population growth is **continuous**. This means that the time step in Expression 1.1 is infinitely small. As a consequence, population growth can be described by a smooth curve. This assumption allows us to model **population growth rate** (dN/dt) with a **continuous differential equation** (see Appendix). Thus, population growth is described as the change in population size (dN) that occurs during a very small interval of time (dt):

$$\frac{dN}{dt} = B - D \quad \text{Expression 1.5}$$

Now we will focus on B and D . Because this is a continuous differential equation, B and D now represent respectively the **birth** and **death rates**, the number of births and deaths per unit time during a very short time interval. What factors control birth and death rates? The birth rate will certainly depend on population size. For example, a population of 1000 warblers will produce many more eggs over a short time interval than a population of only 25 birds. If each individual produces the same number of offspring during that time interval, the birth rate (B) in the population will be directly proportional to population size. Let b (lowercase!) denote the **instantaneous birth rate**. The units of b are number of births per individual per unit time [births/(individual \cdot time)]. Because of these units, note that b is a rate that is measured **per capita**, or per individual. Over a short time interval, the number of births in the population is the product of the instantaneous birth rate and the population size:

$$B = bN \quad \text{Expression 1.6}$$

Similarly, we can define an **instantaneous death rate** d , with units being number of deaths per individual per unit time [deaths/(individual \cdot time)]. Of course, an individual either dies or it doesn't, but this rate is measured for a continuously growing population over a short time interval. Again, the product of the instantaneous death rate and the population size gives the population death rate:*

$$D = dN \quad \text{Expression 1.7}$$

These simple functions will not always apply in the real world. In some cases, the birth rate may not depend on the current population size. For example, in some plant populations, seeds remain dormant in the soil for many years in a **seed bank**. Consequently, the number of emergent seedlings (births) may reflect the structure of the plant population many years ago. A model for such a population would include a **time lag** because the current growth rate actually depends on population size at a much earlier time.

Expressions 1.6 and 1.7 also imply that b and d are constant. No matter how large the population gets, individuals have the same per capita birth and death rates! But in the real world, birth and death rates may be affected by crowding: the larger the population, the lower the per capita birth rate and

*Note that dN in the numerator of the expression for continuous population growth (dN/dt) is not the same as dN in Expression 1.7. In Expression 1.7, dN is the product of the instantaneous death rate (d) and the current population size (N).

the higher the per capita death rate. We will explore this sort of **density-dependent model** in Chapter 2. For now, we will develop our model assuming a constant per capita birth rate (b) and a constant per capita death rate (d). Substituting Expressions 1.6 and 1.7 into Expression 1.5 and rearranging the terms gives us:

$$\frac{dN}{dt} = (b - d)N \quad \text{Expression 1.8}$$

Let $b - d$ equal the constant r , the **instantaneous rate of increase**. Sometimes r is called the **intrinsic rate of increase**, or the **Malthusian parameter** after the Reverend Thomas Robert Malthus (1766–1834). In his famous “Essay on the Principle of Population” (1798), Malthus argued that food supply could never keep pace with human population growth, and that human suffering and misery were an inevitable consequence.

The value of r determines whether a population increases exponentially ($r > 0$), remains constant in size ($r = 0$), or declines to extinction ($r < 0$). The units of r are individuals per individual per unit time [individuals/(individual • time)]. Thus, r measures the per capita rate of population increase over a short time interval. That rate is simply the difference between b and d , the instantaneous birth and death rates. Because r is an instantaneous rate, we can change its units by simple division. For example, because there are 24 hours in a day, an r of 24 individuals/(individual • day) is equivalent to an r of 1 individual/(individual • hour). Substituting r back into Expression 1.8, we arrive at our first model of population growth:

$$\frac{dN}{dt} = rN \quad \text{Equation 1.1}$$

Equation 1.1 is a simple model of **exponential population growth**. It says that the population growth rate (dN/dt) is proportional to r and that populations only increase when the instantaneous birth rate (b) exceeds the instantaneous death rate (d), so that $r > 0$. If r is positive, population growth continues unchecked and is proportional to N : the larger the population, the faster its rate of increase.

When will our model population not grow? A population will neither increase nor decrease when the population growth rate equals zero ($dN/dt = 0$). For Equation 1.1, there are only two cases when this is true. The first is when $N = 0$. Because of migration, population growth in nature will not necessarily stop when the population reaches zero. But in our simple model immigration is not allowed, so the population will stop growing if it ever hits the “floor” of zero individuals. The population will also stop growing if r should equal zero. In other words, if the per capita birth and death rates are

exactly balanced, the population will neither increase nor decrease in size. In all other cases, the population will either increase exponentially ($r > 0$) or decline to extinction ($r < 0$).

PROJECTING POPULATION SIZE

Equation 1.1 is written as a differential equation. It tells us the population growth rate, but not the population size. However, if Equation 1.1 is integrated (following the rules of calculus; see Appendix), the result can be used to project, or predict, population size:

$$N_t = N_0 e^{rt} \quad \text{Equation 1.2}$$

N_0 is the initial population size, N_t is the population size at time t , and e is a constant, the base of the natural logarithm ($e \approx 2.718$). Knowing the starting population size and the intrinsic rate of increase, we can use Equation 1.2 to forecast population size at some later time. Equation 1.2 is similar to the formula used by banks to calculate compound interest on a savings account.

Figure 1.1a illustrates some population trajectories that were calculated from Equation 1.2 for five different values of r . In Figure 1.1b, these same data are shown on a semilogarithmic plot, in which the y axis is the natural logarithm (base e) of population size. This transformation converts an exponential growth curve to a straight line. The slope of this line is r .

These graphs show that when $r > 0$, populations increase exponentially, and that the larger the value of r , the faster the rate of increase. When $r < 0$, populations decline exponentially. Mathematically, such populations never truly reach zero, but when the population reaches a projected size of less than one individual, extinction has occurred (by definition).

CALCULATING DOUBLING TIME

One important feature of a population (or a savings account) that is growing exponentially is a constant **doubling time**. In other words, no matter how large or small the population, it will always double in size after a fixed time period. We can derive an equation for this doubling time, t_{double} , by noting that, if the population has doubled in size, it is twice as large as the initial population size:

$$N_{t_{\text{double}}} = 2N_0 \quad \text{Expression 1.9}$$

Substituting back into Equation 1.2 gives an expression in terms of initial population size:

$$2N_0 = N_0 e^{rt_{\text{double}}} \quad \text{Expression 1.10}$$

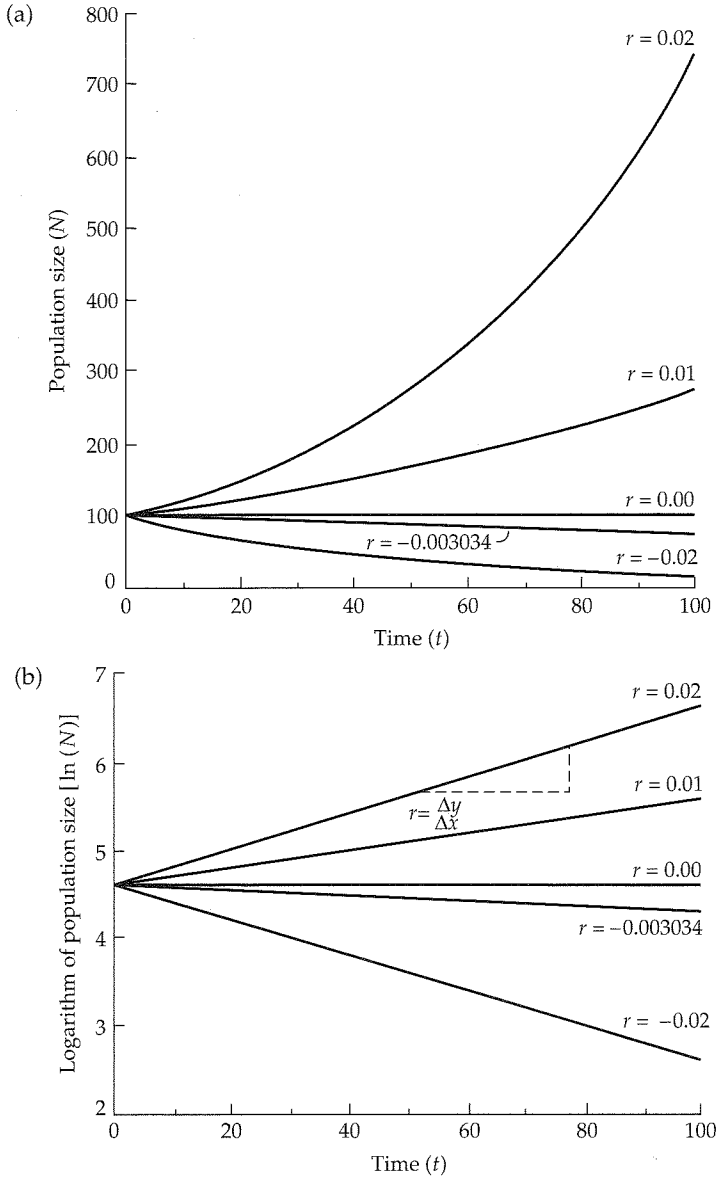


Figure 1.1 (a) Trajectories of exponential population growth, calculated from a starting population size of 100 individuals. The estimated r of -0.003034 [individuals / (individual \cdot year)] corresponds to the projection for the grizzly bear (*Ursus arctos horribilis*) population of Yellowstone National Park (see Figure 1.6). (b) Exponential growth curves plotted on a semilogarithmic graph. The same data are used as in (a), but the y axis (population size) shows the natural logarithm (base e) of population size. In this type of graph, an exponential curve becomes a straight line; the slope of that line is r , the intrinsic rate of increase.

Table 1.1 Estimates of r and doubling times for different organisms.

<i>Species</i>	<i>Common name</i>	<i>r [individuals / (individual • day)]</i>	<i>Doubling time</i>
T phage	Virus	300.0	3.3 minutes
<i>Escherichia coli</i>	Bacterium	58.7	17 minutes
<i>Paramecium caudatum</i>	Protozoan	1.59	10.5 hours
<i>Hydra</i>	Hydra	0.34	2 days
<i>Tribolium castaneum</i>	Flour beetle	0.101	6.9 days
<i>Rattus norvegicus</i>	Brown rat	0.0148	46.8 days
<i>Bos taurus</i>	Domestic cow	0.001	1.9 years
<i>Avicennia marina</i>	Mangrove	0.00055	3.5 years
<i>Nothofagus fusca</i>	Southern beech	0.000075	25.3 years

From Fenchel (1974).

Dividing through by N_0 eliminates it from both sides of the equation:

$$2 = e^{rt_{\text{double}}} \quad \text{Expression 1.11}$$

Taking the natural logarithm of both sides gives:

$$\ln(2) = rt_{\text{double}} \quad \text{Expression 1.12}$$

Expression 1.12 can be rearranged to solve for doubling time:

$$t_{\text{double}} = \frac{\ln(2)}{r} \quad \text{Equation 1.3}$$

Thus the larger r is, the shorter the doubling time. Table 1.1 gives some estimated values of r (with their corresponding doubling times) for different species of plants and animals. Among species, r varies considerably, and much of this variation is related to body size: small-bodied organisms grow faster and have larger rates of population increase than large-bodied organisms. For example, bacteria and protozoa can reproduce by asexual fission every few minutes and have high population growth rates. Larger organisms, such as primates, have delayed reproduction and long generation times, which lead to low values of r . Corresponding doubling times range from minutes for viruses to decades for beech trees.

Note, however, that even “slow-growing” populations eventually will reach astronomical sizes if they increase exponentially. Table 1.2 projects the future population size for a hypothetical herd of 50 Vermont cows [$r = 0.365$

Table 1.2 Exponential growth of a herd of 50 cattle, with $r = 0.365$ cows/(cow • year).

<i>Year</i>	<i>Herd size</i>
0	50.0
1	72.0
2	103.8
3	149.5
4	215.3
5	310.1
10	1923.7
50	4.2×10^9
100	3.6×10^{17}
150	3.0×10^{25}
200	2.5×10^{33}

Population sizes calculated from Equation 1.2.

cows/(cow • year)]. After 150 years of exponential growth, the model predicts a herd of 3×10^{25} cattle, the weight of which would exceed that of the planet earth!

Model Assumptions

What are the assumptions of Equation 1.1? In other words, what is the underlying biology of a population that is growing exponentially? This is a critical question that must be asked for any mathematical model we construct. The predictions of a mathematical model depend on its underlying assumptions. If certain assumptions are violated, or changed, the predictions of the model will also change. Other assumptions may be less critical to the predictions of the model; the model is **robust** to violations of these assumptions. We make the following assumptions for a population growing according to Equation 1.1:

✓ **No I or E.** The population is “closed;” changes in population size depend only on local births and deaths. We made this simplifying assumption in Expression 1.4, so that we could model the growth of a single population without having to keep track of organisms moving between populations. In Chapter 4, we will relax this assumption and build some simple models in which there is migration between populations.

- ✓ **Constant b and d .** If a population is going to grow with constant birth and death rates, an unlimited supply of space, food and other resources must be available. Otherwise, the birth rate will decrease and/or the death rate will increase as resources are depleted. Constant birth and death rates also imply that b and d do not change randomly through time. Later in this chapter, we will incorporate variable birth and death rates in the model to see how the predictions are affected.
- ✓ **No genetic structure.** Equation 1.1 implies that all the individuals in the population have the same birth and death rates, so there cannot be any underlying genetic variation in the population for these traits. If there is genetic variation, the genetic structure of the population must be constant through time. In this case, r represents an *average* of the instantaneous rate of increase for the different genotypes in the population.
- ✓ **No age or size structure.** Similarly, there are no differences in b and d among individuals due to their age or body size. Thus, we are modeling a sexless, parthenogenetic population in which individuals are immediately reproductive when they are born. A growing population of bacteria or protozoa most closely approximates this situation. In Chapter 3, we will relax this assumption and examine a model of exponential growth in which individuals have different birth and death rates as they age. If there are differences among ages, the population must have a stable age structure (see Chapter 3); in this case, r is an average calculated across the different age classes.
- ✓ **Continuous growth with no time lags.** Because our model is written as a simple differential equation, it assumes that individuals are being born and dying continuously, and that the rate of increase changes instantly as a function of current population size. Later in this chapter, we will relax the assumption of continuous growth and examine a model with discrete generations. In Chapter 2, we will explore models with time lags, in which population growth depends not on current population size, but on its size at some time in the past.

The most important assumption on this list is that of constant b and d , which implies unlimited resources for population growth. Only if resources are unlimited will a population continue to increase at an accelerating rate. If the other assumptions are violated, populations may still increase exponentially, although migration and time lags will complicate the picture.

But unlimited resources do not occur in nature, and we know that no real population increases without bound. So, why does the exponential growth

model form the cornerstone of population biology? Although no population can increase forever without limit, all populations have the *potential* for exponential increase. Indeed, this potential for exponential increase in population size is one of the key factors that can be used to distinguish living from non-living objects. The exponential model recognizes the multiplicative nature of population growth and the positive feedback that gives populations the potential to increase at an accelerating rate.

Exponential population growth is also a key feature of Charles Darwin's (1809–1882) theory of natural selection. Darwin read Malthus' writings and recognized that the surplus of offspring resulting from exponential growth would allow natural selection to operate and bring about evolutionary change. Finally, although no population can increase forever, resources may be *temporarily* unlimited so that populations go through phases of exponential increase. Outbreaks of insect pests, invasions of "weedy" plant species, and the plight of overcrowded human populations are compelling evidence of the power of exponential population growth.

Model Variations

CONTINUOUS VERSUS DISCRETE POPULATION GROWTH

We will now explore some variations on our exponential growth model. For many organisms, time does not really behave as a continuous variable. For example, in seasonal environments, many insects and annual desert plants reproduce only once, then die; the offspring that survive form the basis for next year's population. If birth and death rates are constant (as in the exponential model), then the population will increase or decrease by the same factor each year. This population has **non-overlapping generations** and is modeled with a **discrete difference equation** rather than a continuous differential equation. Suppose the population increases (or decreases) each year by a constant proportion r_d , the **discrete growth factor**. Thus, if the population increased annually by 36%, $r_d = 0.36$. The population size next year would be:

$$N_{t+1} = N_t + r_d N_t \quad \text{Expression 1.13}$$

Combining terms gives:

$$N_{t+1} = N_t(1 + r_d) \quad \text{Expression 1.14}$$

Let $1 + r_d = \lambda$, the **finite rate of increase**. Then:

$$N_{t+1} = \lambda N_t \quad \text{Expression 1.15}$$

λ is always a positive number that measures the proportional change in population size from one year to the next. Thus, λ is the ratio of the population size during the next time period to the population size for the current time period (N_{t+1}/N_t). After two years, the population size will be:

$$N_2 = \lambda N_1 = \lambda(\lambda N_0) = \lambda^2 N_0 \quad \text{Expression 1.16}$$

Notice that the “output” of Expression 1.15 (N_{t+1}) forms the “input” (N_t) for the calculation in the next time step. The general solution to this **recursion equation** after t years is:

$$N_t = \lambda^t N_0 \quad \text{Equation 1.4}$$

Equation 1.4 is analogous to Equation 1.2, which we used to project population size in the continuous model. What does population growth look like with the discrete model? The answer depends on the precise timing of birth and death events. Imagine that births are pulsed each spring and that deaths occur continuously throughout the year. The population growth curve will resemble a jagged saw blade, with a sharp vertical increase from births each spring, followed by a gradual decrease from deaths during the rest of the year. In spite of this decrease, the overall curve will rise exponentially, because annual births exceed annual deaths (Figure 1.2). The size of each “tooth” in the growth curve will increase year after year because the same fractional increase will add more individuals to a large population than to a small one. For example, if $\lambda = 1.2$, the population increases by 20% each year.

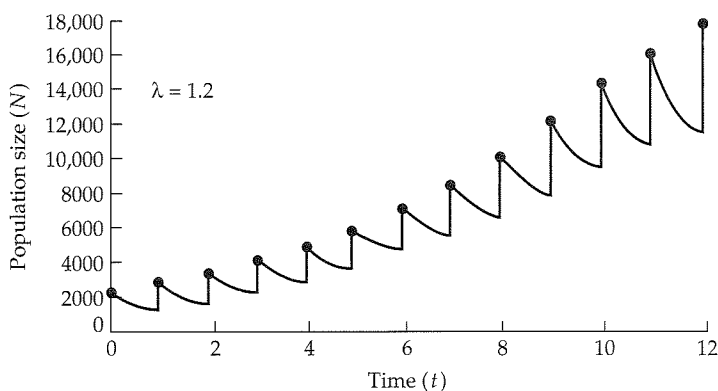


Figure 1.2 Discrete population growth. In this example, births are pulsed at the beginning of the year, and deaths occur continuously.

If the population size is 100, it will increase by 20 in one year. But when the population size is 1000, it will increase by 200 in one year.

Suppose our population reproduced twice a year, as is the case for some insects. Now we would have a “tooth” on the graph every six months. If the time step between reproductive periods becomes shorter and shorter, the teeth on the graph will be closer and closer together. Finally, if the time step is infinitely small, the curve is no longer jagged but is smooth, and we have arrived again at the continuous model of exponential growth (Equation 1.2). The continuous model essentially “connects the dots” of time in the discrete model. The continuous model is equivalent to a discrete difference equation with an infinitely small time step. Thus, we can use the rules of calculus to solve for the limit of $(1 + r_d)$ and show that:

$$e^r = \lambda \quad \text{Equation 1.5}$$

We can express Equation 1.5 in equivalent logarithmic form as:

$$r = \ln(\lambda) \quad \text{Equation 1.6}$$

where \ln is the natural logarithm (base e). This relationship between r and λ also establishes the following numerical equivalents:

$$r > 0 \leftrightarrow \lambda > 1 \quad \text{Expression 1.17}$$

$$r = 0 \leftrightarrow \lambda = 1 \quad \text{Expression 1.18}$$

$$r < 0 \leftrightarrow 0 < \lambda < 1 \quad \text{Expression 1.19}$$

Because λ is a ratio of population sizes, it is a **dimensionless number** with no units. However, λ is associated with the particular time step of the equation and cannot be changed by a simple scaling. For example, a λ of 1.2 measured with a yearly time step is *not* equivalent to a λ of 0.1 measured with a monthly time step. A λ of 1.2 yields a 20% annual increase, whereas a λ of 0.1 yields a 90% monthly decrease! If you need to change the time step for λ , first convert λ to r using Equation 1.6. Then scale r to the appropriate time units and convert back to λ with Equation 1.5. In this example, $\lambda = 1.2$ is equivalent to $r = 0.18232$ individuals/(individual \cdot year). Dividing by 12 (months) gives $r = 0.01519$ individuals/(individual \cdot month). From Equation 1.5, $\lambda = 1.0153$, with a monthly time step. As a check on this calculation, we can use Equation 1.4 to show that, after 12 months:

$$N_t = (1.0153)^{12} N_0 \quad \text{Expression 1.20}$$

$$N_t = 1.2N_0 \quad \text{Expression 1.21}$$

This calculation demonstrates that $\lambda = 1.0153$ for a monthly time step is equivalent to $\lambda = 1.2$ for a yearly time step.

In summary, the predictions of the discrete and continuous models of exponential population growth are qualitatively similar to one another. In Chapter 2, we will see that discrete models behave very differently when we incorporate resource limitation.

ENVIRONMENTAL STOCHASTICITY

Equation 1.2 is entirely deterministic. If we know N_0 , r , and t , we can calculate the predicted population size to the last decimal place. If we started over with the same set of conditions, the population would grow to precisely the same size. In such a **deterministic model**, the outcome is determined solely by the inputs, and nothing is left to chance.

Deterministic models represent an idealized view of a simple, orderly world. But the real world tends to be complex and uncertain. Think of public transportation. Does any commuter ever expect their bus or train to arrive at *precisely* the time indicated in the printed schedule? At least in American cities, buses are delayed, trains break down, and subways travel at irregular speeds, all of which introduce uncertainty (and anxiety) into the daily commute.

Could we incorporate all of the complex sources of variation into a public transportation model? Not very easily. But we could measure, each day, the arrival time of our bus. After many commuting days, we could calculate two numbers that would help us to estimate the uncertainty. The first number is the average or **mean** arrival time of the bus. If we use the variable x to indicate the time the bus arrives, the mean is depicted as \bar{x} . Approximately half of all buses will arrive later than \bar{x} and half will arrive earlier. The second number we could calculate is the **variance** in arrival times (σ_x^2). The variance measures the variability or uncertainty associated with the mean. If the variance is small, then we know that most days the bus will arrive within, say, two minutes of the mean. But if the variance is large, the arrival time of the bus on any given morning could be as much as 20 minutes earlier *or* 20 minutes later than \bar{x} . Obviously, our “commuting strategy” will be affected by both the mean and the variance of x .

How can we incorporate this type of uncertainty into an exponential growth model? Suppose that the instantaneous rate of increase is no longer a simple constant, but instead changes unpredictably with time. Uncertainty in r means there are good times and bad times for population growth. During good times, the birth rate is much larger than the death rate, and the popula-

tion can increase rapidly. During bad times, the difference between birth and death rates is much smaller, or perhaps even negative, so that the population increases slowly, or even decreases, for a short time period. Without specifying all of the biological causes of good and bad years, we can still develop a **stochastic** model of population growth in a varying environment. Variability associated with good and bad years for population growth is known as **environmental stochasticity**.

Imagine that a population is growing exponentially with a **mean r** (\bar{r}) and a **variance in r** (σ_r^2). We will use this model to predict the **mean population size** at time t (\bar{N}_t) and the **variance in population size** ($\sigma_{N_t}^2$). Make sure you understand the difference between these two averages and the two variances: the average and variance in r are used to predict the average and variance in N .

The derivation of this model is beyond the scope of this primer, but the results are straightforward. First, the average population size for a population growing with environmental stochasticity is:

$$\bar{N}_t = N_0 e^{\bar{r}t} \quad \text{Equation 1.7}$$

This is no different from the deterministic model (Equation 1.2) except that we use the average r to predict the average N_t . However, like the “average family” with 2.1 children, \bar{N}_t may not be a very accurate descriptor of any particular population. Figure 1.3 shows a computer simulation of a population growing with environmental stochasticity. Although the population achieves exponential increase in the long run, it fluctuates considerably from one time period to the next. The variance in population size at time t is given by (May 1974a):

$$\sigma_{N_t}^2 = N_0^2 e^{2\bar{r}t} \left(e^{\sigma_r^2 t} - 1 \right) \quad \text{Equation 1.8}$$

Other mathematical expressions for this variance are possible, depending on precisely how the model is formulated.* Equation 1.8 tells us several things about the variance of the population. First, population variance increases with time. Like stock-market projections or weather forecasts, the further

*Technically, we are replacing r in Equation 1.2 by $r + \sigma_r^2 W_t$, where W_t is a “white noise” distribution. This is a stochastic differential equation, which unfortunately does not have a unique solution. I have followed May (1974a), who presents the Ito solution to this problem. Biologically, the Ito solution is appropriate because it arises as a diffusion approximation to a discrete model of geometric random growth, similar to Expression 1.15. Interested readers should consult May (1973, 1974a) and Roughgarden (1979) for more details.

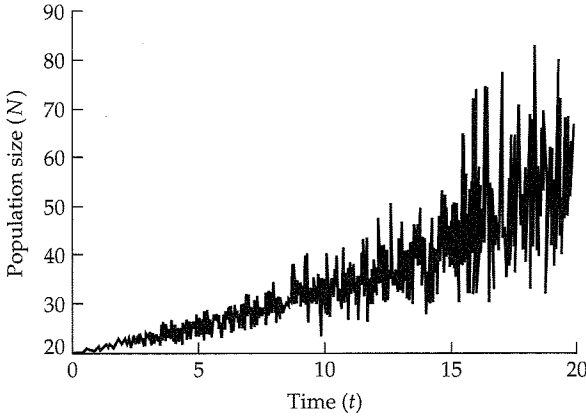


Figure 1.3 Exponential growth with environmental stochasticity. In this model, the instantaneous rate of increase fluctuates randomly through time. Here $N_0 = 20$; $r = 0.05$; $\sigma_r^2 = 0.0001$.

into the future we try to predict population size, the more uncertain our estimate. Consequently, the population growth curve resembles a funnel that flares out with increasing time (Figure 1.3). Second, the variance of N_t is proportional to both the mean and variance of r . Populations that are growing rapidly, or have a variable r , fluctuate more than slow-growing populations or those with a relatively constant r . Finally, if the variance of r is zero, Equation 1.8 collapses to zero—there is no variance in N_t , so we have returned to the deterministic model.

There is a limit to how much the population can vary in size and still persist. If N fluctuates too violently, the population may “crash” to zero. This can happen even if \bar{r} is large enough to ensure rapid growth for the “average” population. Extinction from environmental stochasticity will almost certainly happen if the variance in r is greater than twice the average of r (May 1974a):

$$\sigma_r^2 > 2\bar{r}$$

Equation 1.9

In our deterministic model, the population increased exponentially as long as r was greater than zero. With environmental stochasticity, the average population size also increases exponentially as a function of \bar{r} . However, if the variance in r is too large, there is a measurable risk of population extinction.

DEMOGRAPHIC STOCHASTICITY

Environmental stochasticity is not the only source of variability that can affect populations. Even if r is constant, populations may still fluctuate because of

demographic stochasticity. Demographic stochasticity arises, in part, because most organisms reproduce themselves as discrete units: an ostrich can lay 2 eggs or 3, but not 2.6! Some clonal plants and corals can reproduce by fragmentation and asexual budding, and in that sense, “pieces” of individuals may contribute to population increase (see Chapter 3). But for most organisms, population growth is an integer process.

If we were to follow a population over a short period of time, we would see that births and deaths are not perfectly continuous, but instead occur sequentially. Suppose that the birth rate is twice as large as the death rate. This means that a birth would be twice as likely to occur in the sequence as a death. In a perfectly deterministic world, the sequence of births and deaths would look like this: ...BBDBBDBBDBBD... But with demographic stochasticity, we might see : ...BBBDBBDBBBD... By chance, we may hit a run of four births in a row before seeing a death in the population. This demographic stochasticity is analogous to genetic drift, in which allele frequencies change randomly in small populations.* In a model of demographic stochasticity, the probability of a birth or a death depends on the relative magnitudes of b and d :

$$P(\text{birth}) = \frac{b}{(b+d)} \quad \text{Equation 1.10}$$

$$P(\text{death}) = \frac{d}{(b+d)} \quad \text{Equation 1.11}$$

Suppose that, for a chimpanzee population, $b = 0.55$ births/(individual • year) and that $d = 0.50$ deaths/(individual • year). This yields an r of 0.05 individuals/(individual • year), with a corresponding doubling time of 13.86 years (Equation 1.3). From Equations 1.10 and 1.11, the probability of birth is $[0.55/(0.55 + 0.50)] = 0.524$, and the probability of death is

*As in the analysis of environmental stochasticity, the equations depend on the particular biological details of the model. One formulation for demographic stochasticity is that individuals in a population live and die independently of one another for random durations. Lifetimes have an exponential distribution with a mean of $1/(b+d)$. At the end of its life, an individual either replicates itself with probability $b/(b+d)$ (Equation 1.10) or it dies with probability $d/(b+d)$ (Equation 1.11). The independence of individual births and deaths leads to Equation 1.15, which gives the overall probability of population extinction.

An alternative formulation for demographic stochasticity is that change in population size is described by a matrix (Markov) transition model. In this case, the population persists with N individuals for a time that has an exponential distribution with a mean of $1/N(b+d)$. At the end of this time, the population either increases to $N+1$ with probability $b/(b+d)$ (Equation 1.10) or it decreases to $N-1$ with probability $d/(b+d)$ (Equation 1.11). Interested readers should consult Iosifescu and Tăutu (1973) for more details.

$[0.50/(0.55 + 0.50)] = 0.476$. Note that these probabilities must add to 1.0, because the only “events” that can occur in this population are births or deaths. Because a birth is more likely than a death, the chimpanzee population will, on average, increase. However, population size can no longer be projected precisely; by chance, there could be a run of births or a run of deaths in the population. Figure 1.4 shows a computer simulation of four populations that each began with 20 individuals and grew with stochastic births and deaths. Two of these populations actually declined below N_0 , even though r was greater than zero.

As in our analysis of environmental stochasticity, we are interested in the average population size and its variance. The average population size at time t is again given by:

$$\bar{N}_t = N_0 e^{rt}$$

Equation 1.12

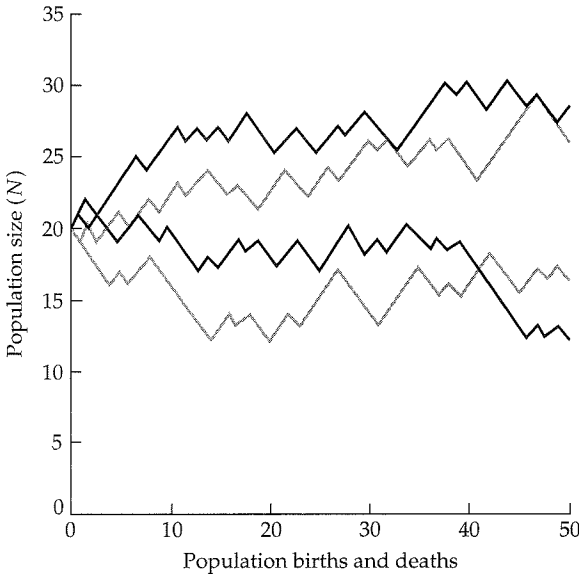


Figure 1.4 Computer simulation of population growth with demographic stochasticity. Each population track starts with an N of 20 individuals. $b = 0.55$ births / (individual \cdot year) and $d = 0.50$ deaths / (individual \cdot year). Although the starting conditions are identical, two of the populations actually dipped below the initial population size by the end of the simulation. Note that the x axis is not absolute time, but the number of sequential population events (births and deaths).

which is the same as in the deterministic model. The equation for variance of population size depends on whether the birth and death rates are equal or not. If b and d are exactly equal, the population will not increase on average, and the variance in population size at time t is (Pielou 1969):

$$\sigma_{N_t}^2 = 2N_0bt \quad \text{Equation 1.13}$$

If b and d are not equal, use the following:

$$\sigma_{N_t}^2 = \frac{N_0(b+d)e^{rt}(e^{rt}-1)}{r} \quad \text{Equation 1.14}$$

As in the model of environmental stochasticity, the variance in population size increases with time, and there is a risk of extinction even for populations with positive r . Demographic stochasticity is especially important at small population sizes because it doesn't take very many sequential deaths to drive a small population to extinction. Consequently, the probability of extinction depends not only on the relative sizes of b and d , but also on the initial population size. This probability of extinction is:

$$P(\text{extinction}) = \left(\frac{d}{b}\right)^{N_0} \quad \text{Equation 1.15}$$

For the chimpanzee example, if there were 50 chimps initially, the chance of extinction would be $(0.50/0.55)^{50} = 0.009 = 0.9\%$. However, if the initial population size were only 10 chimps, the chance of extinction would be $(0.50/0.55)^{10} = 0.386 = 38.6\%$.

Equations 1.13 and 1.14 also show that demographic stochasticity depends not only on the difference between b and d , but on the absolute sizes of b and d . Populations with high birth and death rates will be more variable than populations with low rates. Thus, a population with $b = 1.45$ and $d = 1.40$ will fluctuate more than a population with $b = 0.55$ and $d = 0.50$. In both populations, $r = 0.05$, but in the first, there is a much faster turnover of individuals, and thus a much greater chance for a run of several consecutive births or deaths.

To summarize, the average population size in stochastic models of exponential growth is the same as in the deterministic model we originally derived. In a stochastic world, populations can fluctuate because of changes in the environment that affect the intrinsic rate of increase (environmental stochasticity) and because of random birth and death sequences (demo-

graphic stochasticity). For both types of variability, a population can fluctuate so much that extinction is likely, even if the average intrinsic rate of increase is positive. Demographic stochasticity is much more important as a cause of extinction at small population sizes than at large.

Empirical Examples

PHEASANTS OF PROTECTION ISLAND

Humans have introduced many species into new environments, both intentionally and accidentally. Some of these introductions have turned out to be interesting ecological experiments. For example, in 1937, eight pheasants (*Phasianus colchicus torquatus*) were introduced onto Protection Island off the coast of Washington State (Lack 1967). The island had abundant food resources and no foxes or other bird predators. The island was too far from the mainland for pheasants to fly to it, so migration did not influence population size. From 1937 to 1942, the population increased to almost 2000 birds (Figure 1.5a,b). The curve shows a jagged increase that is similar to our discrete model of population growth. This increase reflects the fact that pheasant chicks hatch in the spring, and mortality continues throughout the year.

The initial population of eight birds had increased to 30 by the beginning of 1938. If we assume that resources were not limiting growth at this time, we can estimate λ as $(30/8) = 3.75$, with a corresponding r of $\ln(3.75) = 1.3217$ pheasants/(pheasant \cdot year). We can use this estimate to predict population size from the exponential growth model, and compare it to the actual size of the pheasant population each year. The initial predictions of this model were reasonably accurate, but after 1940, the model overestimated population size. By 1942, the population had grown to 1898 birds, whereas the model prediction was three times larger (5933 birds). This difference probably reflects depletion of food resources on the island by the increasing pheasant population. Unfortunately, this interesting ecological experiment ended abruptly when the U.S. Army set up a training camp for World War II on the island, and promptly ate the pheasants!

GRIZZLY BEARS OF YELLOWSTONE NATIONAL PARK

The grizzly bear (*Ursus arctos horribilis*) was once widespread throughout most of North America. Today, its range in the lower 48 states consists of only six fragmented populations in the northwest, some of which have fewer than 10 individuals. Yellowstone National Park supports one of the largest remaining populations, which fluctuates markedly from year to year (Figure 1.6).

The grizzly bear population data obviously do not conform to a simple exponential growth model, but they can be described by a more complex

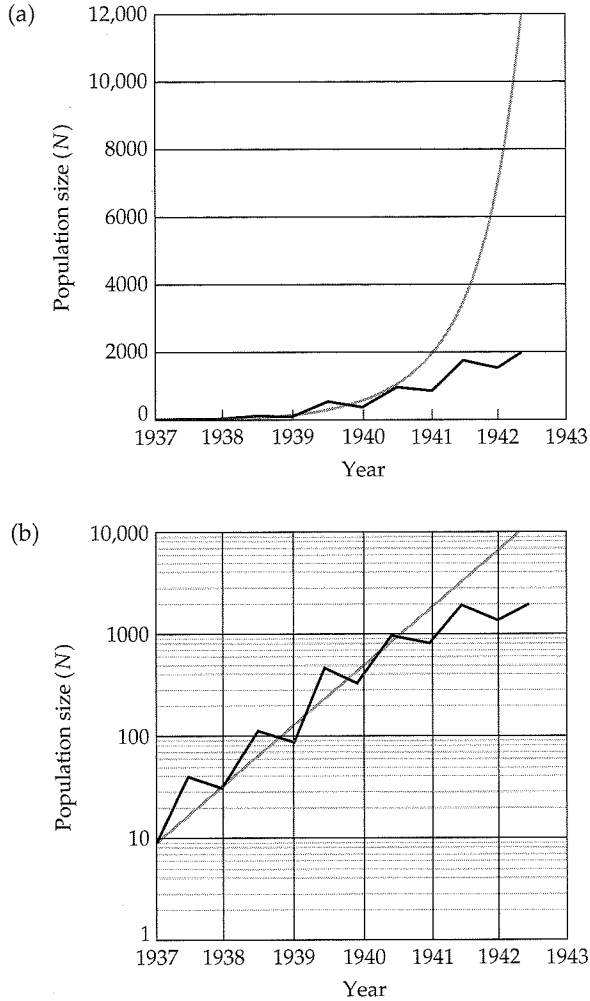


Figure 1.5 Growth of pheasant (*Phasianus colchicus torquatus*) population introduced to Protection Island. The thin line shows the hypothetical exponential growth curve, with $r = 1.3217$ individuals / (individual \cdot year); the thick line shows the observed population size. For comparison, population sizes are plotted on a linear scale in (a) and a logarithmic scale in (b). Note that the logarithmic scale is base 10, not base e . (Data from Lack 1967.)

exponential model that incorporates environmental stochasticity (Dennis et al. 1991). The estimate of r that emerged from this model is -0.003034 bears/(bear \cdot year), suggesting that the population will decline slowly in the long run. However, the variance for this estimate was relatively large, so we should not be surprised to see periods of population increase. Based on this

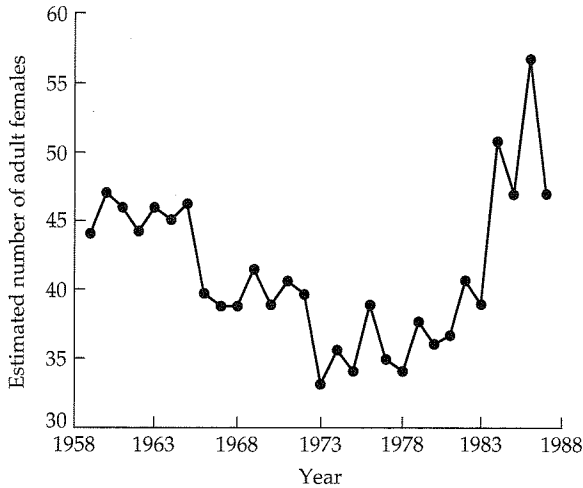


Figure 1.6 Population size of grizzly bears (*Ursus arctos horribilis*) in Yellowstone National Park. These data were used to construct a model of exponential population growth that incorporates environmental stochasticity. The estimate of r from this model was -0.003034 individuals / (individual \cdot year). (From Dennis et al. 1991.)

model, the prognosis for the Yellowstone grizzly bear population is not good. The model forecasts that the population is certain to drop below 10 individuals, at which point extinction is almost guaranteed. However, because r is close to zero and its variance is large, the estimated time to extinction is 200 years. Thus, the model suggests that it is unlikely the grizzly bear population is in immediate danger of extinction, but that the population is likely to reach a dangerously small size in the long run.

This projection assumes that background variability in b and d will continue in the future. Thus, the model does not incorporate catastrophic events, such as the 1988 Yellowstone fire, or future changes in human activity and management strategy, such as the 1970–1971 closure of the park garbage dumps, an important food source for the bears. Because this model is one of exponential population growth in a stochastic environment, it does not incorporate resource limitation, which might lead to different predictions (see Chapter 2). Finally, the predictions of the model will change as additional data from yearly censuses become available. Increasingly, conservation biologists and park managers are using quantitative population models to estimate the risk of extinction for endangered species. Many of these models are based on the principles of exponential population growth that we have developed in this chapter.

Problems

- 1.1. In 1993, when the first edition of this book was written, the world's human population was expected to double in size in approximately 50 years. Assuming population growth is continuous, calculate r for the human population. If the population size in 1993 was 5.4 billion, what was the projected population size for the year 2000?

The future is here! On August 2, 2000 the best estimate of the world population size was 6.087 billion—a bit higher than that projected by the model in 1993. To find out the current estimate of the world population size, visit this website maintained by the U.S. Census Bureau:

<http://www.census.gov/main/www/popclock.html>

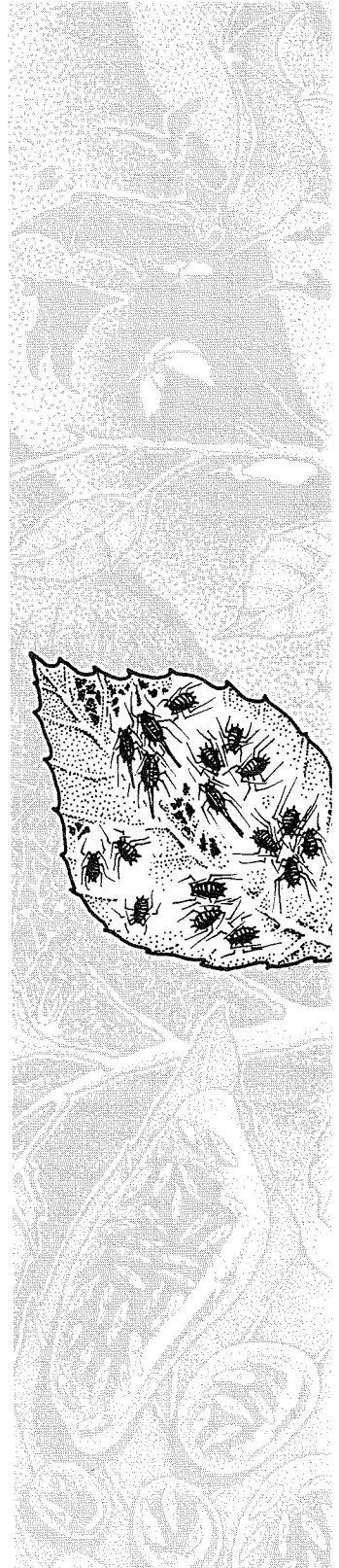
This website has a “real-time clock” that shows the estimated world and U.S. population sizes. What is today's date for you, reader, and how large is the human population now?

- 1.2. You are studying a population of beetles of size 3000. During a one-month period, you record 400 births and 150 deaths in this population. Estimate r and project the population size in 6 months.
- 1.3. For five consecutive days, you measure the size of a growing population of flatworms as 100, 158, 315, 398, and 794 individuals. Plot the logarithm (base e) of population size to estimate r .
- 1.4. A population of annual grasses increases in size by 12% every year. What is the approximate doubling time?
- *1.5. You are studying an endangered population of orchids, for which $b = 0.0021$ births/(individual \cdot year) and $d = 0.0020$ deaths/(individual \cdot year). The current population size is 50 plants. A new shopping mall is planned that will eliminate part of the orchid habitat and reduce the population to 30 plants. Estimate the effect of the proposed development on the probability of extinction.

* Advanced problem

CHAPTER 2

Logistic Population Growth



Model Presentation and Predictions

In Chapter 1, we assumed (unrealistically) that resources for population growth were unlimited. Consequently, the per capita birth and death rates, b and d , remained constant. We did explore some models in which b and d fluctuated through time (environmental stochasticity), but those fluctuations were **density-independent**; in other words, birth and death rates did not depend on the size of the population. In this chapter, we assume that resources for growth and reproduction are limited. As a consequence, birth and death rates depend on population size. To derive this more complex **logistic growth model**, we will start with the familiar growth equation:

$$\frac{dN}{dt} = (b' - d')N \quad \text{Expression 2.1}$$

but now we will modify b' and d' so they are density-dependent and reflect crowding.

DENSITY DEPENDENCE

In the face of increased crowding, we expect the per capita birth rate to *decrease* because less food and fewer resources are available for organisms to use for reproduction. The simplest formula for a decreasing birth rate is a straight line (see Figure 2.1):

$$b' = b - aN \quad \text{Expression 2.2}$$

In this expression, N is population size, b' is the per capita birth rate, and b and a are constants. From Expression 2.2, the larger N is, the lower the birth rate. On the other hand, if N is close to zero, the birth rate is close to b . The constant b is the birth rate that would be achieved under ideal (uncrowded) conditions, whereas b' is the actual birth rate, which is reduced by crowding. Thus, b has the same interpretation as in the original exponential growth model: it is the instantaneous per capita birth rate when resources are unlimited. The constant a measures the strength of density dependence. The larger a is, the more sharply the birth rate drops with each individual added to the population. If there is no density dependence, then $a = 0$, and the birth rate equals b , regardless of population size. Thus, the exponential growth model is a special case of the logistic model in which there are no crowding effects on the birth rate ($a = 0$) or on the death rate ($c = 0$).

Using similar reasoning, we can modify the death rate to reflect density dependence. In this case, we expect the death rate to *increase* as the population grows:

$$d' = d + cN \quad \text{Expression 2.3}$$

Again, the constant d is the death rate when the population size is close to zero, and the population is growing (almost) exponentially. The constant c measures the increase in the death rate from density dependence.

Expressions 2.2 and 2.3 are the simplest mathematical descriptions of the effects of crowding on birth and death rates. In real populations, the functions may be more complex. For example, b' and d' may not change in a linear fashion; instead, there may be no change in b' or d' until a critical threshold density is reached. Some animals can reproduce, hunt, care for their offspring, or avoid predators more efficiently in groups than they can by themselves. For these populations, b' may actually increase and d' decrease as the population grows. This **Allee effect** (Allee et al. 1949) is usually important when the population is small, and may generate a critical minimum population size, below which extinction occurs (see Problem 2.3). But as the population grows, we expect negative density effects to appear as resources are depleted.

Note that *both* birth and death rates are density-dependent in this model. But it might be that only the death rate is affected by population size, and the birth rate remains density-independent, or vice versa. Fortunately, the algebra of this case works out exactly the same (see Problem 2.5). As long as either the birth rate *or* the death rate shows a density-dependent effect, we arrive at the logistic model.

Now we substitute Expressions 2.2 and 2.3 back into 2.1:

$$\frac{dN}{dt} = [(b - aN) - (d + cN)]N \quad \text{Expression 2.4}$$

After rearranging the terms:

$$\frac{dN}{dt} = [(b - d) - (a + c)N]N \quad \text{Expression 2.5}$$

Next, we multiply Expression 2.5 by $[(b - d)/(b - d)]$. This term equals 1.0, so it does not change the results, but allows us to simplify further:

$$\frac{dN}{dt} = \left[\frac{(b - d)}{(b - d)} \right] [(b - d) - (a + c)N]N \quad \text{Expression 2.6}$$

$$\frac{dN}{dt} = [(b - d)] \left[\frac{(b - d)}{(b - d)} - \frac{(a + c)}{(b - d)}N \right] N \quad \text{Expression 2.7}$$

Treating $(b - d)$ as r , we have:

$$\frac{dN}{dt} = rN \left[1 - \frac{(a + c)}{(b - d)}N \right] \quad \text{Expression 2.8}$$

CARRYING CAPACITY

Because a , c , b , and d are all constants in Expression 2.8, we can define a new constant K :

$$K = \frac{(b-d)}{(a+c)} \quad \text{Expression 2.9}$$

The constant K is used for more than just mathematical convenience. It has a ready biological interpretation as the **carrying capacity** of the environment. K represents the maximum population size that can be supported; it encompasses many potentially limiting resources, including the availability of space, food, and shelter. In our model, these resources are depleted incrementally as crowding increases. Because K represents maximum sustainable population size, its units are numbers of individuals. Substituting K back into Expression 2.8 gives:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad \text{Equation 2.1}$$

Equation 2.1 is the logistic growth equation, which was introduced to ecology in 1838 by P.-F. Verhulst (1804–1849). It is the simplest equation describing population growth in a resource-limited environment, and it forms the basis for many models in ecology.

The logistic growth equation looks like the equation for exponential growth (rN) multiplied by an additional term in parentheses ($1 - N/K$). The term in parentheses represents the **unused portion of the carrying capacity**. As an analogy, think of the carrying capacity as a square frame that will hold a limited number of flat tiles, which are the individuals. If the population should ever exceed the carrying capacity, there would be more tiles than could fit in the frame. The unused portion of the carrying capacity is the percentage of the area of the frame that is empty (Krebs 1985).

For example, suppose $K = 100$ and $N = 7$. The unused portion of the carrying capacity is $[1 - (7/100)] = 0.93$. The population is relatively uncrowded and is growing at 93% of the growth rate of an exponentially increasing population [$rN(0.93)$]. In contrast, if the population is close to K ($N = 98$), the unused carrying capacity of the environment is small: $[1 - (98/100)] = 0.02$. Consequently, the population grows very slowly, at 2% of the exponential growth rate [$rN(0.02)$]. Finally, if the population should ever exceed carrying capacity ($N > K$), the term in parentheses becomes negative, which means that the growth rate is less than zero, and the population declines towards K . Thus, density-dependent birth and death rates provide an effective brake on exponential population growth.

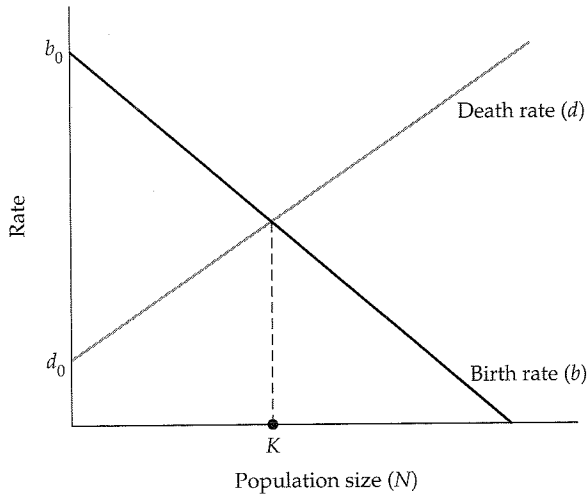


Figure 2.1 Density-dependent birth and death rates in the logistic model. The graph illustrates how the per capita rates of birth and death change as a function of crowding. The population reaches a stable equilibrium ($N = K$) at the intersection of the curves, where birth and death rates are equal.

When will the population stop growing? As in the exponential model, the rate of population growth (dN/dt) is zero when either r or N equals zero. But in the logistic model, the population will also stop growing when $N = K$. This is illustrated in Figure 2.1, which shows the density-dependent birth and death functions in the same graph. The two curves intersect at the point $N = K$ and form a **stable equilibrium**. The equilibrium is stable because no matter what the starting size of the population, it will move towards K . If N is less than K , we are at a point to the left of the intersection of the birth and death curves. In this region of the graph, the birth rate exceeds the death rate, so the population will increase. If we are to the right of the intersection point, the death rate is higher than the birth rate, and the population will decline (see Appendix).

As with the exponential growth model, we can use the rules of calculus to integrate the growth equation and express population size as a function of time:

$$N_t = \frac{K}{1 + \left[\frac{K - N_0}{N_0} \right] e^{-rt}} \quad \text{Equation 2.2}$$

From Equation 2.2, the graph of N versus time for logistic growth is a characteristic S-shaped curve (Figure 2.2). When the population is small, it

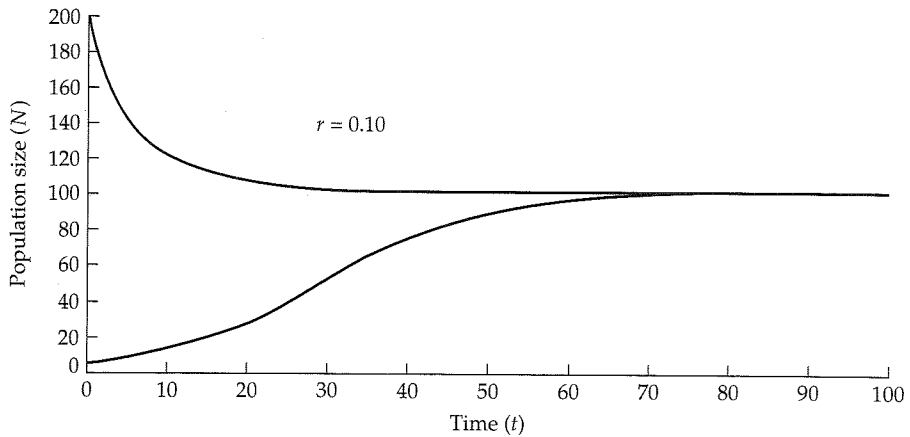


Figure 2.2 Logistic growth curve. The graph of N versus time increases in a characteristic S-shaped fashion when the population begins below carrying capacity. Above carrying capacity, the curve drops rapidly to the equilibrium point. In this example, $K = 100$, and the starting population size is 5 or 200.

increases rapidly, at a rate slightly less than that predicted by the exponential model. The population grows at its highest rate when $N = K/2$ (the steepest point on the curve), and then growth decreases as the population approaches K (Figure 2.3a). This is in contrast to the exponential model, in which the population growth rate increases linearly with population size (Figure 2.3b). In the logistic model, if the population should begin above K , Equation 2.1 takes on a negative value, and N will decline towards carrying capacity.

Regardless of the initial number of individuals (N_0), a population growing according to the logistic model will quickly reach a fixed carrying capacity, which is determined solely by K . However, the time it takes to reach that equilibrium is proportional to r ; faster-growing populations reach K more quickly.

Model Assumptions

Because the logistic model is derived from the exponential model, it shares the assumptions of no time lags, migration, genetic variation, or age structure in the population. But resources are limited in the logistic model, so we make two additional assumptions:

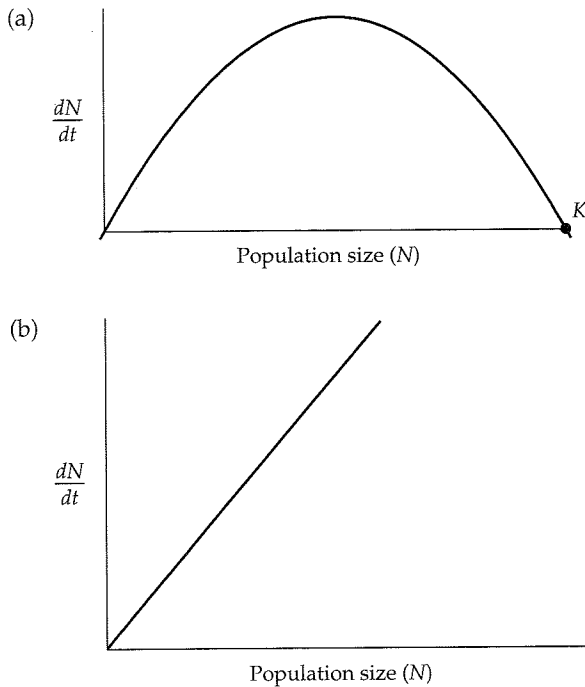


Figure 2.3 Population growth rate (dN/dt) as a function of population size. (a) Logistic growth. (b) Exponential growth.

✓ **Constant carrying capacity.** In order to achieve the S-shaped logistic growth curve, we must assume that K is a constant: resource availability does not vary through time. Later in this chapter, we will relax this assumption.

✓ **Linear density dependence.** The logistic model assumes that each individual added to the population causes an incremental decrease in the per capita rate of population growth. This is illustrated in Figure 2.4a, which shows the **per capita population growth rate** $(1/N)(dN/dt)$ as a function of population size. This per capita rate is at its maximum value of $(b - d) = r$ when N is close to zero, then declines linearly to zero when N reaches K . If N exceeds K , the per capita growth rate becomes negative. Although b and d are constants, the actual birth and death rates (b' and d') now change as a function of population size (Expressions 2.2 and 2.3). In contrast, the corresponding graph for the exponential growth model is a horizontal line because the per capita growth rate is independent of population size (Figure 2.4b).

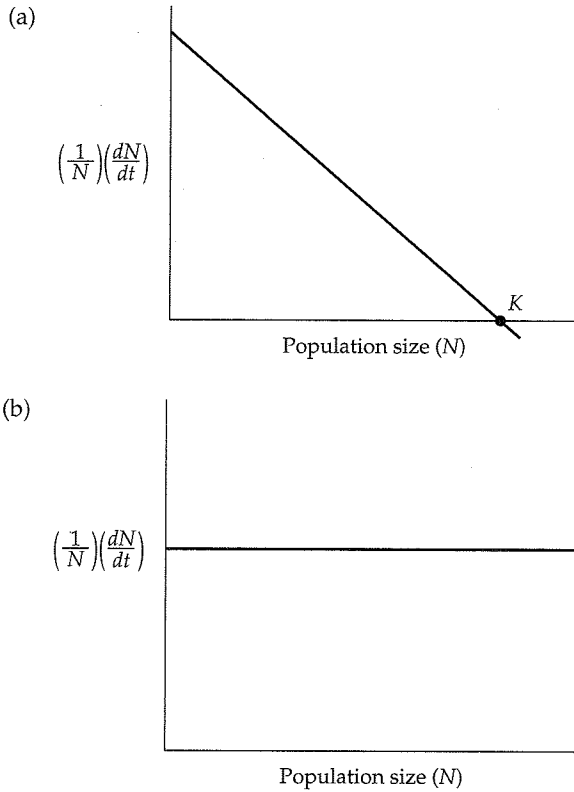


Figure 2.4 Per capita growth rates $(1/N)(dN/dt)$ as a function of population size. (a) Logistic growth. (b) Exponential growth.

Model Variations

TIME LAGS

The logistic growth model assumes that when another individual is added to the population, the per capita growth rate decreases immediately. But in many populations there may be **time lags** in the density-dependent response. For example, if a population of gulls increases in size in the fall, density dependence may not be expressed until the following spring, when females lay eggs. In a tropical rain forest, density-dependent mortality of mahogany trees (*Swietenia mahogany*) may occur in the seedling stage, but density-dependent reproduction may not occur until 50 years later, when the trees first begin to flower. Individuals do not immediately adjust their growth and reproduction when resources change, and these delays can affect population

dynamics. Seasonal availability of resources, growth responses of prey populations, and age and size structure of consumer populations can introduce important time lags in population growth.

How can time lags be incorporated into our model? Suppose there is a time lag of length τ between the change in population size and its effect on population growth rate. Consequently, the growth rate of the population at time t (dN/dt) is controlled by its size at time $t - \tau$ in the past ($N_{t-\tau}$). Incorporating this time lag into the logistic growth equation gives:

$$\frac{dN}{dt} = rN \left(1 - \frac{N_{t-\tau}}{K} \right) \quad \text{Equation 2.3}$$

The behavior of this **delay differential equation** depends on two factors: (1) the length of the time lag τ , and (2) the “response time” of the population, which is inversely proportional to r (May 1976). Populations with fast growth rates have short response times ($1/r$).

The ratio of the time lag τ to the response time ($1/r$), or $r\tau$, controls population growth. If $r\tau$ is “small” ($0 < r\tau < 0.368$), the population increases smoothly to carrying capacity (Figure 2.5a). If $r\tau$ is “medium” ($0.368 < r\tau < 1.570$), the population first overshoots, then undershoots the carrying capacity; these **damped oscillations** diminish with time until K is reached (Figure 2.5b). The exact numerical values for these trajectories are not important. What is important is to understand how the behavior of the model changes as $r\tau$ is increased.

If $r\tau$ is “large” ($r\tau > 1.570$) the population enters into a **stable limit cycle**, periodically rising and falling about K , but never settling on a single equilibrium point (Figure 2.5c). The carrying capacity is the midpoint between the high and low points in the cycle. The cycle is stable because if the population is perturbed, it will return to these characteristic oscillations. When $r\tau$ is large, the time lag is so much longer than the response time that the population repeatedly overshoots and then undershoots K . The population resembles a heating system with a faulty thermostat that constantly overheats and then overcools, never achieving an equilibrium temperature.

Cyclic populations are characterized by their **amplitude** and **period** (Figure 2.5c). The amplitude is the difference between the maximum and the average population size. It is measured on the y axis of the graph of N vs. t , and its units are number of individuals. The larger the amplitude, the greater the population fluctuations. If the amplitude is too large, the population may hit the “floor” of zero and go extinct. The period is the amount of time it takes for one complete population cycle to occur. It is measured on the x axis, in units of time. The longer the period, the greater the amount of time between population peaks.

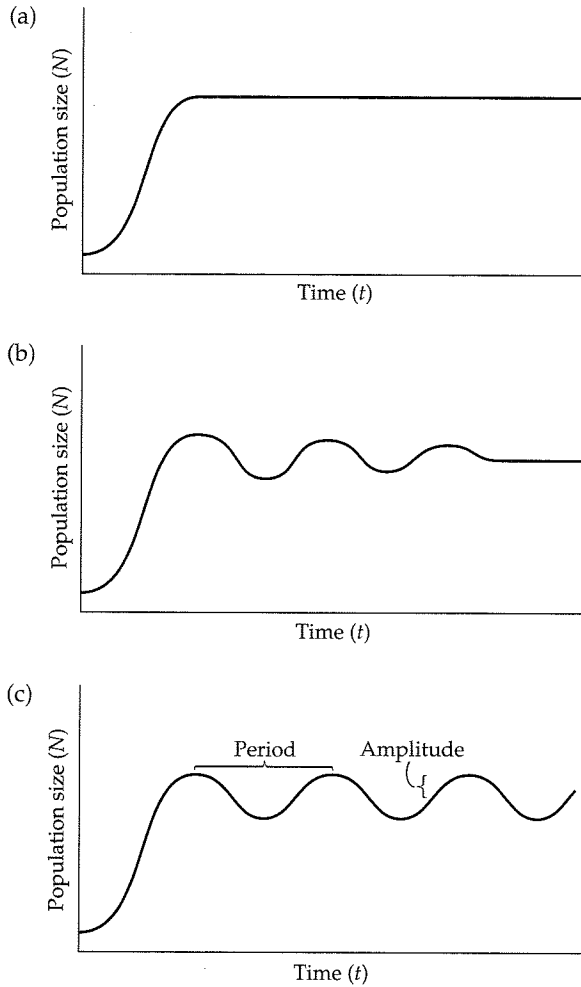


Figure 2.5 Logistic growth curves with a time lag. The behavior of the model depends on $r\tau$, the product of the intrinsic rate of increase and the time lag. (a) “Small” $r\tau$ behaves like the model with no time lag. (b) “Medium” $r\tau$ generates damped oscillations and convergence on carrying capacity. (c) “Large” $r\tau$ generates a stable limit cycle and does not converge on the carrying capacity.

In a logistic model with a time lag, the amplitude of the cycle increases with increasing values of $r\tau$. This makes intuitive sense—if the population is growing very rapidly, or if the time lag is very long, the population will greatly overshoot K before it begins a phase of decline.

The period of the cycle is always about 4τ , regardless of the intrinsic rate of increase. Thus, a population with a time lag of one year can be expected to reach a peak density every four years. Why should the period of the cycle be four times as long as the lag? When the population reaches K , it will continue to increase for a length of time τ before starting to decrease. The distance from K to the population peak is about one-quarter of the cycle, so the length of the entire cycle is approximately 4τ . This result may explain the observation that many populations of mammals in seasonal, high-latitude environments cycle with peaks every three or four years (May 1976; see Chapter 6).

DISCRETE POPULATION GROWTH

We will now explore a model in which population growth is discrete rather than continuous. A discrete version of the logistic equation is:

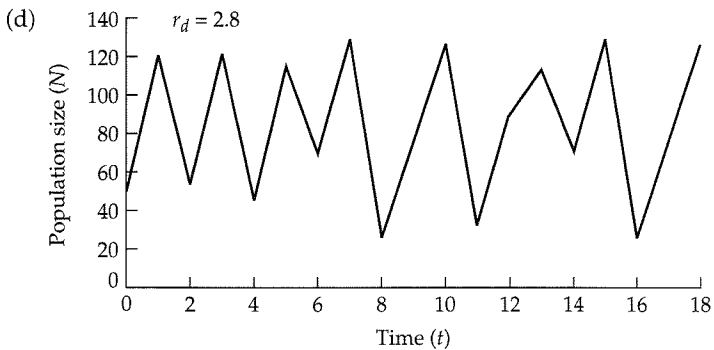
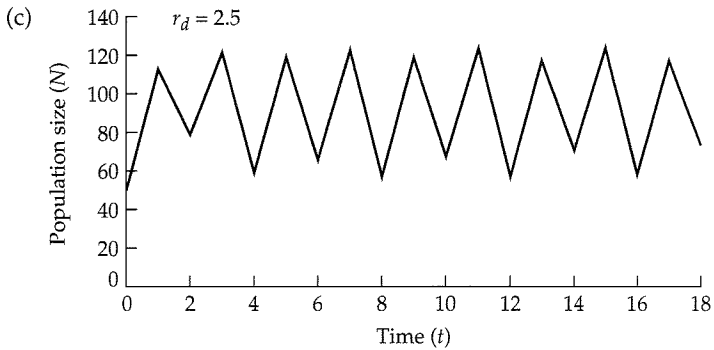
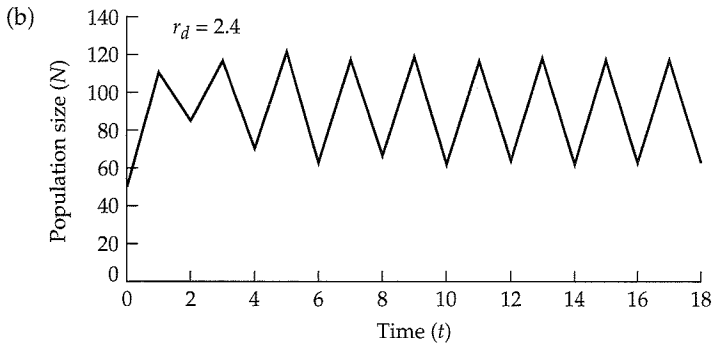
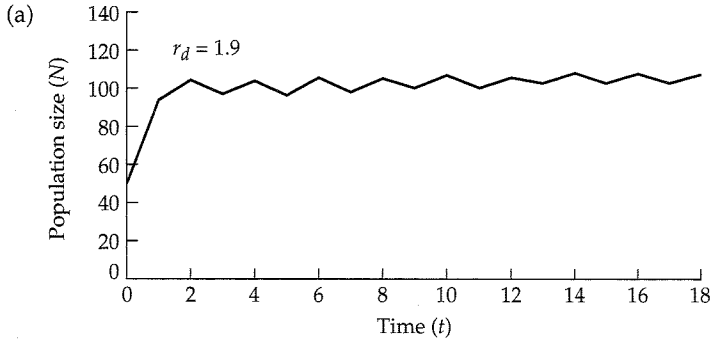
$$N_{t+1} = N_t + r_d N_t \left(1 - \frac{N_t}{K} \right) \quad \text{Equation 2.4}$$

This discrete growth logistic equation is analogous to the continuous model (Equation 2.1) in the same way that Equation 1.4 was analogous to the original exponential model (Equation 1.2). Note that the growth rate is the discrete growth factor r_d , described in Chapter 1.

A discrete population growth model has a built-in time lag of length 1.0. The population size at one time step in the future (N_{t+1}) depends on the current population size (N_t). In the last section, we saw that the product $r\tau$ controls the dynamics when a time lag is present. For the discrete model, the lag is of length 1.0, so the dynamics depend solely on r_d .

If r_d is not large, the behavior of this discrete equation is similar to that of its continuous cousin. At “small” r_d ($r_d < 2.000$), the population approaches K with damped oscillations (Figure 2.6a). At “less small” r_d ($2.000 < r_d < 2.449$), the population enters into a stable two-point limit cycle. This is similar to the continuous model, except that the population rises and falls to sharp “points,” rather than following a smooth curve. The points in the discrete model correspond to peaks and valleys of the cycle (Figure 2.6b). Between an r_d of 2.449 and an r_d of 2.570, the population grows with more complex limit cycles. For example, a four-point limit cycle has two distinct peaks and two distinct valleys before it starts to repeat. The number of points in the limit cycle increases geometrically (2, 4, 8, 16, 32, 64, etc.) as the value of r_d is increased in this interval (Figure 2.6c).

But if r_d is larger than 2.570, the limit cycles break down, and the population grows in a complex, nonrepeating pattern known as **chaos** (Figure 2.6d). Mathematical models of chaos are important in many areas of science, from the description of turbulent flow to the prediction of major weather patterns.



- ◀ **Figure 2.6** The behavior of the discrete logistic growth curve is determined by the size of r_d . (a) “Small” r_d generates damped oscillations ($r_d = 1.9$). (b) “Less small” r_d generates a stable two-point limit cycle ($r_d = 2.4$). (c) “Medium” r_d generates a more complex four-point limit cycle ($r_d = 2.5$). (d) “Large” r_d generates a chaotic pattern of fluctuations that appears random ($r_d = 2.8$).

Population biologists were among the first to appreciate that simple discrete equations may generate complex patterns (May 1974b). What is interesting about chaos is that seemingly random fluctuations in population size can emerge from a model that is entirely deterministic. Indeed, the track of a chaotic population may be so complex that it is difficult to distinguish from the track of a stochastic population.

However, chaos does not mean stochastic, or random, change. The fluctuations in a chaotic population have nothing to do with chance or randomness. Once the parameters of the model are specified (K , r_d , and N_0), the same erratic population track will be produced each time we run the model. The source of these erratic fluctuations is the density-dependent feedback of the logistic equation, combined with the built-in time lag of the discrete model. A characteristic of a chaotic population is sensitivity to initial conditions. If we alter the starting conditions, say, by changing the initial population size (N_0), the populations will diverge more and more as time goes on (Figure 2.7).

In contrast, a truly stochastic population fluctuates because one or more of its parameters (r_d or K) changes with each time step. In a stochastic model, if we alter the starting population slightly, but retain the same pattern of variation in r_d or K , the two population tracks will be slightly different, but they will not diverge as in Figure 2.7. In the next section we explore stochastic models in which the carrying capacity varies with time.

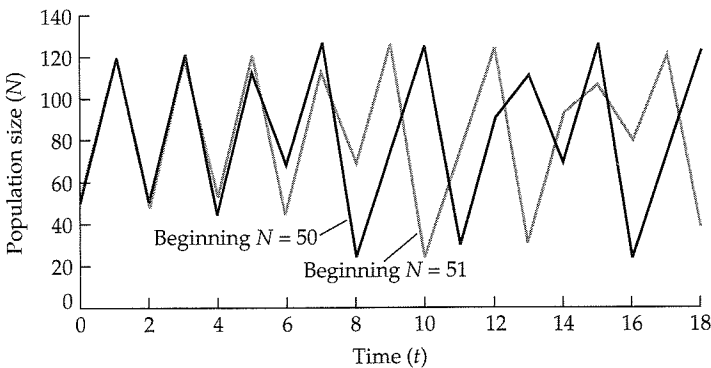


Figure 2.7 Divergence of population tracks with chaos. Both populations followed the same logistic equation, but the starting N for one of the populations was 50 and the other was 51. Note that, as more time passes, the two populations begin to diverge from one another.

RANDOM VARIATION IN CARRYING CAPACITY

In our analysis of environmental stochasticity (Chapter 1), we assumed that resources were unlimited, but that r varied randomly with time. For the logistic model, we will now assume that r is fixed, but that the carrying capacity varies randomly with time. Random variation in K means that the maximum population size that the environment can support changes unpredictably with time. How does this variation in resources affect the behavior of the logistic model? There are several mathematical approaches to the problem (May 1973; Roughgarden 1979), none of which yields a simple answer.

When r varied randomly in our exponential model, we found that the average population size was the same as in the deterministic model ($\bar{N}_t = N_0 e^{rt}$). So, you might reason that the average population size in the logistic model should approximate the average carrying capacity (\bar{K}). But this is not the case. Instead, \bar{N} will always be *less* than \bar{K} . Why should this be so? When a population is above K , it declines faster than a population that is increasing from a corresponding level below K (see Problem 2.4). This asymmetry is reflected in Figure 2.2, which shows that the population tracks above and below carrying capacity are not mirror images of one another. If the carrying capacity is described by its mean (\bar{K}) and variance (σ_K^2), a rough approximation to the average population size is (May 1974a):

$$\bar{N} \approx \bar{K} - \frac{\sigma_K^2}{2} \quad \text{Equation 2.5}$$

Thus, the more variable the environment, the smaller the average population size. The pattern of population fluctuations also depends on r (Levins 1969). Populations with large r are very sensitive to changes in K , and they will tend to track these fluctuations quite closely. Consequently, the average population size will be only slightly less than the average carrying capacity. In contrast, populations with small r are relatively sluggish and will not exhibit large increases or decreases (Figure 2.8); \bar{N} will be somewhat smaller than for populations with large r .

PERIODIC VARIATION IN CARRYING CAPACITY

Instead of random fluctuations in carrying capacity, suppose K varies repeatedly, in a cyclic fashion. Cyclic fluctuations in carrying capacity probably characterize many populations in seasonal temperate latitudes, and can be described with a cosine function (May 1976):

$$K_t = k_0 + k_1[\cos(2\pi t / c)] \quad \text{Equation 2.6}$$

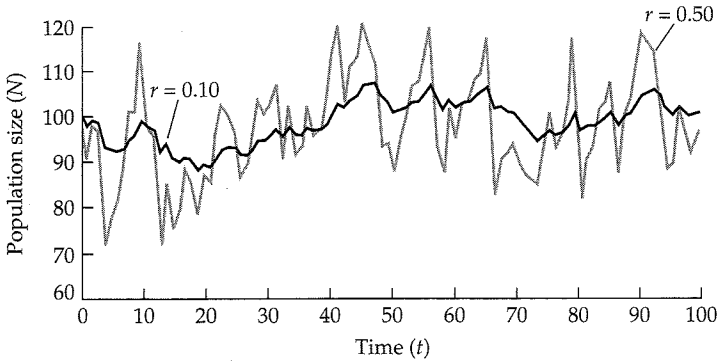


Figure 2.8 Logistic population growth with random variation in carrying capacity. Note that the population with the larger growth rate ($r = 0.50$) tracks the fluctuations in carrying capacity, whereas the population with the small growth rate ($r = 0.10$) is less variable and does not respond as quickly to fluctuations in resources.

Here, K_t is the carrying capacity at time t , k_0 is the mean carrying capacity, k_1 is the amplitude of the cycle, and c is the length of the cycle. As t increases, the cosine term in parentheses varies cyclically from -1 to 1 . Thus, during a single cycle of length c , the carrying capacity of the environment varies from a minimum of $k_0 - k_1$ to a maximum of $k_0 + k_1$.

How does this cyclic variation in carrying capacity affect population growth? The length of the carrying capacity cycle functions as a kind of time lag, so once again, the behavior of the model depends on rc . If rc is small ($\ll 1.0$), the population tends to “average” the fluctuations in the environment and persists at roughly:

$$\bar{N} \approx \sqrt{k_0^2 - k_1^2} \quad \text{Equation 2.7}$$

Thus, if rc is small, \bar{N} is less than \bar{K} , and the reduction is greater when the amplitude of the cycle is large; both patterns are similar to the results for a population in which K varies stochastically. If rc is large ($\gg 1.0$), the population tends to track the fluctuations in the environment:

$$N_t \approx k_0 + k_1 \cos(2\pi t/c) \quad \text{Equation 2.8}$$

although at a value slightly less than the actual carrying capacity (Figure 2.9).

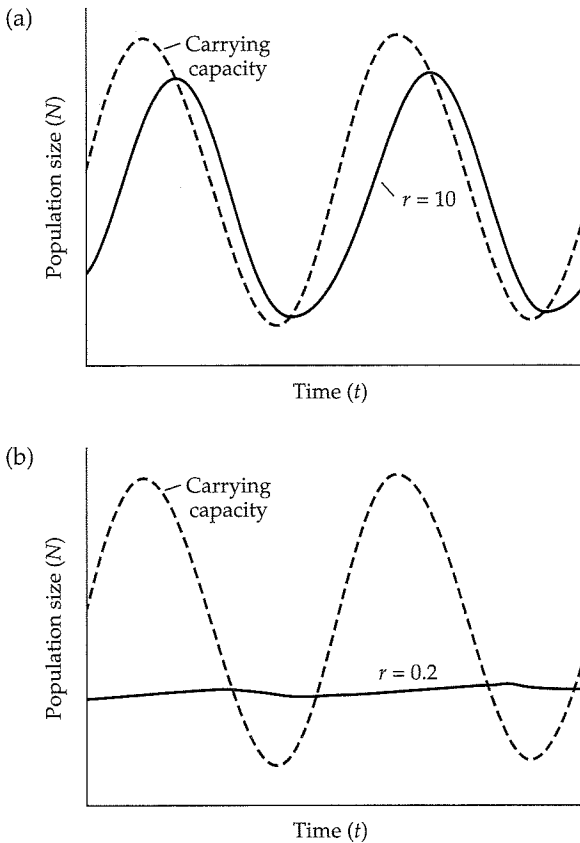


Figure 2.9 Logistic growth with periodic variation in the carrying capacity. The carrying capacity of the environment varies according to a cosine function. As with random variation, the population with the large growth rate ($r = 10$) tends to track the variation (a), and the population with the small growth rate ($r = 0.2$) tends to average it (b). The dashed line indicates K . (From May 1976.)

In conclusion, both stochastic and periodic variation in carrying capacity reduce populations, and the more variable the environment, the lower the average population size. In a variable environment, populations with large r , such as most insects, may be expected to track variation in carrying capacity, whereas populations with small r , such as large mammals, may be expected to average the environmental variation and remain relatively constant.

Empirical Examples

SONG SPARROWS OF MANDARTE ISLAND

Mandarte Island is a rocky, 6-hectare island off the coast of British Columbia. The island is home to a population of song sparrows (*Melospiza melodia*) that has been studied for many decades (Smith et al. 1991). On average, only one new female migrant joins this population each year, so most of the changes in population size are due to local births and deaths. Over the past 30 years, the population has varied between 4 and 72 breeding females and between 9 and 100 breeding males. The sparrow population of Mandarte Island does not conform to a simple logistic growth model; population size is variable and there have been periods of increase followed by rapid declines (Figure 2.10). Some of these, such as the crash in 1988, were caused by an unusually cold winter and an increased death rate. Other declines were not correlated with any obvious change in the environment.

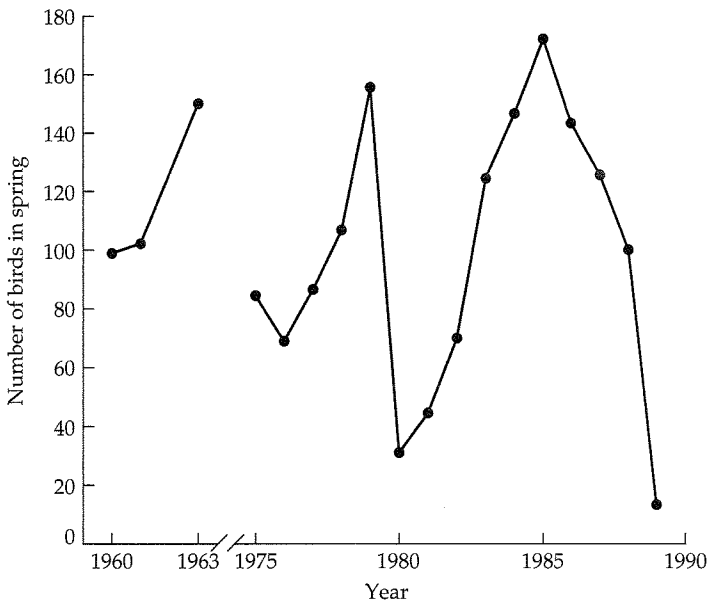


Figure 2.10 Population size of the song sparrow (*Melospiza melodia*) on Mandarte Island. (After Smith et al. 1991.)

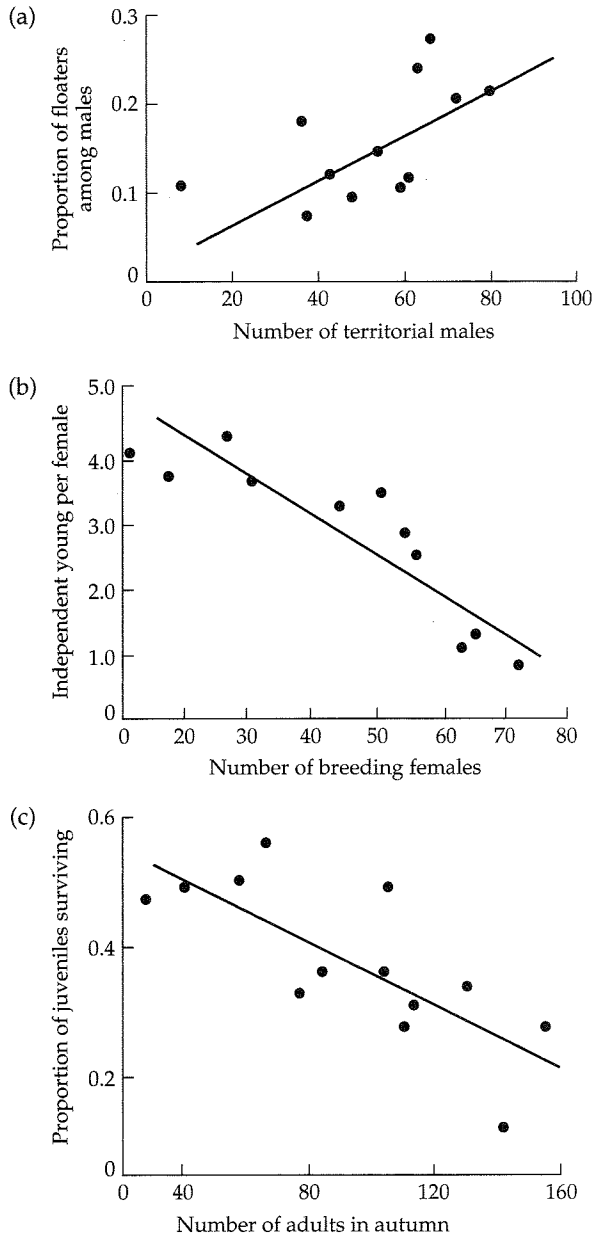


Figure 2.11 Density dependence in the Mandarte Island song sparrow (*Melospiza melodia*) population. As the population becomes more crowded (a) the proportion of nonterritorial “floater” males increases; (b) the number of surviving young produced per female decreases; (c) juvenile survival decreases. (After Arcese and Smith 1988 and Smith et al. 1991.)

Although this population is clearly buffeted by density-independent changes, there is good evidence of underlying density dependence. Male song sparrows defend territories that determine their breeding success, but limited food resources and space prevent many males from ever establishing territories. These nonterritorial “floaters” are behaviorally submissive individuals. Their proportion increased in a density-dependent fashion as the population became more crowded (Figure 2.11a). When the resident territory holders were experimentally removed, floater males quickly took over their territories, so the total breeding population size remained relatively constant.

Density dependence is also seen in the number of surviving young produced per female (Figure 2.11b), and in the survival of juveniles (Figure 2.11c), both of which decreased as the population size increased. Experimental studies confirmed that food limitation was the controlling factor: when food levels for sparrows were artificially enhanced, female reproductive output increased fourfold (Arcese and Smith 1988). Thus, both territoriality and food limitation generated density-dependent birth and death rates in song sparrows.

Nevertheless, although density dependence has the potential to control population sizes, the risk of extinction for Mandarte Island sparrows probably comes from unpredictable environmental catastrophes and other density-independent forces. Somewhat paradoxically, it is these density-independent fluctuations that allow us to detect density dependence, because they push the population above or below its equilibrium and reveal the underlying dynamics of birth and death rates.

POPULATION DYNAMICS OF SUBTIDAL ASCIDIANS

Ascidians, or “sea squirts,” are filter-feeding invertebrates that live attached to pier pilings and rock walls. These animals are important components of subtidal “fouling” communities throughout the world. Ascidians are actually primitive chordates that disperse with a sexually produced tadpole larva. The perennial ascidian *Ascidia mentula* has been the subject of a long-term study of population dynamics on vertical rock walls off the Swedish west coast (Svane 1984).

Six populations were monitored continually for 12 years with photographs of permanent plots. At sheltered sites within a fjord, density was highest in shallow plots; at exposed stations, density was highest in deep-water plots. At all sites, populations fluctuated considerably (Figure 2.12), in contrast to the predictions of the basic logistic model. Mortality was primarily due to “bulldozing” by sea urchins and temperature fluctuations. These factors seemed to operate in a density-independent fashion, because there was no relationship between mortality rate and population size (Figure 2.13a). In

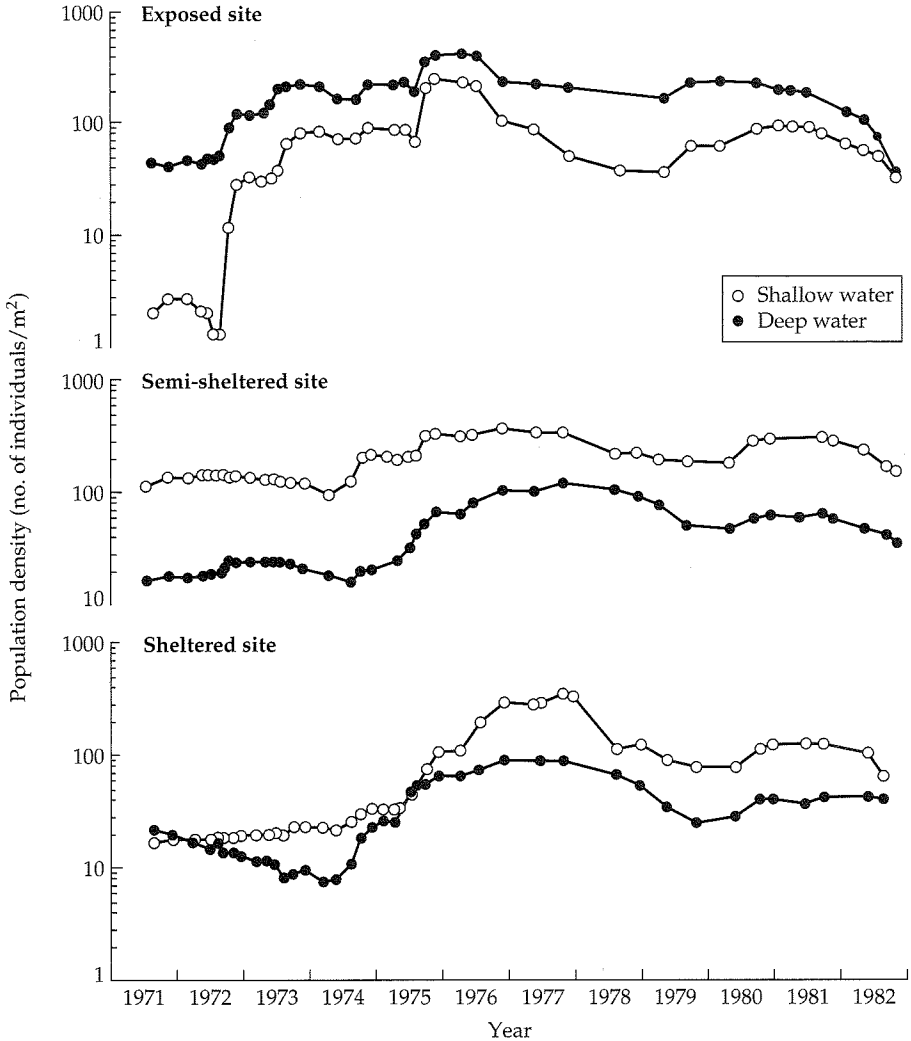


Figure 2.12 Population density of ascidians (*Ascidia mentula*) at six subtidal sites off the coast of Sweden. Population densities are greater in shallow water than in deep, except at the exposed site. Note the use of a logarithmic scale for the y axis, which diminishes the appearance of population fluctuations. (After Svane 1984.)

contrast, reproduction (as measured by larval recruitment) was density-dependent and decreased at high densities. At low densities, there was evidence of an Allee effect: recruitment actually increased with population density until a density of approximately 100 animals per square meter was

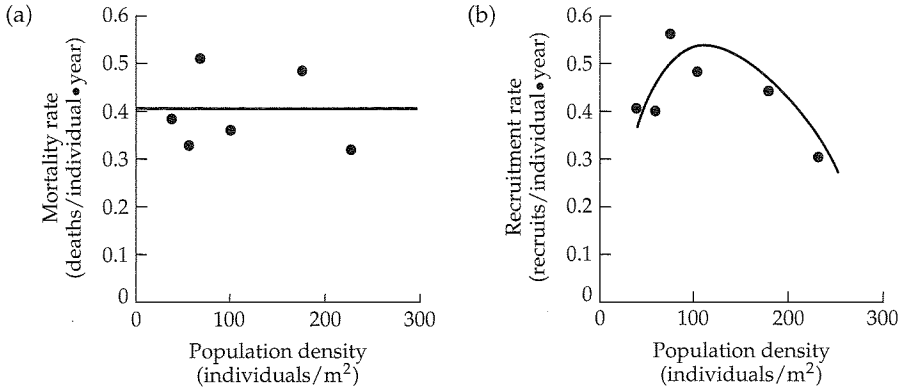


Figure 2.13 (a) Density-independent mortality rates. The mortality rate of ascidians (*Ascidia mentula*) at the six population sites appears to be independent of population size. (b) Density-dependent recruitment rates. The rate of recruitment of new juveniles into ascidian populations is density-dependent and is lower in more dense populations. Note the appearance of a possible Allee effect, as recruitment is also decreased at sites with very low abundance. (After Svane 1984.)

reached (Figure 2.13b). Possible explanations for this Allee effect include the behavioral attraction of larvae to established adults and entrapment of larvae by local water currents.

Like the Mandarte Island sparrows, these ascidians showed some evidence of underlying density dependence, although the population never reached a steady carrying capacity. Both the ascidian and sparrow populations were affected by temperature fluctuations, although these effects seemed more subtle and long-term for the ascidians. Unlike the isolated sparrow population, the ascidian populations were potentially linked by larval dispersal between sites, so that a realistic model of population dynamics might be especially complex (see Chapter 4).

LOGISTIC GROWTH AND THE COLLAPSE OF FISHERIES POPULATIONS

How many tons of fish should be harvested each year to maximize long-term yield? This **optimal yield** problem has been very important to commercial fisheries because of the huge amounts of money involved and because overfishing has been a problem since at least the 1920s, when commercial stocks of many species started to decline. The logistic growth curve provides a simple, though often unpopular, prescription for optimal fishing strategies.

The optimal strategy is the one that maximizes the population growth rate, because this rate determines how quickly fish can be removed from the pop-

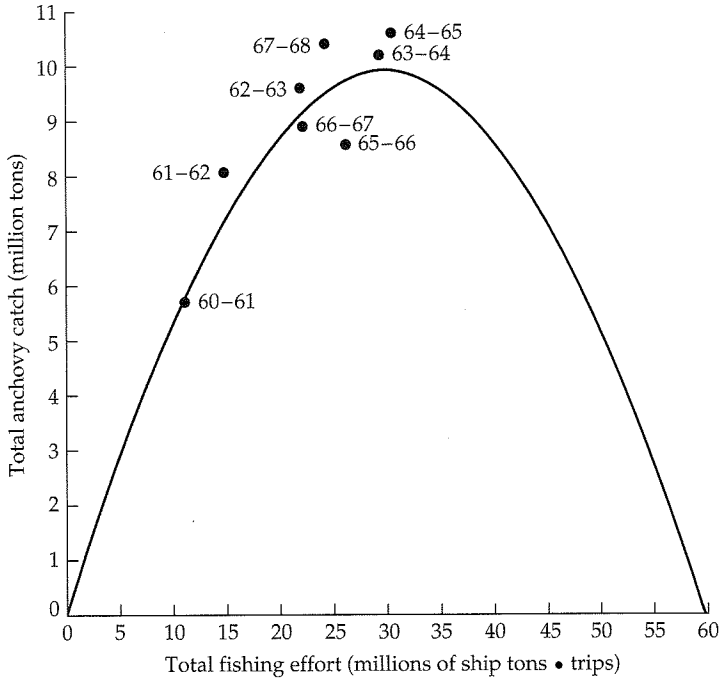


Figure 2.14 Relationship between fishing effort and total catch for the Peruvian anchovy (*Engraulis ringens*) fishery. Each point represents the fishing catch and effort for a particular year. The data include fishing effort by humans and fish catches by seabird populations. The parabola is drawn by fitting the logistic model to data from Boerema and Gulland (1973). (After Krebs 1985.)

ulation while still maintaining a constant stock for future production. If a population is growing according to the logistic equation, maximum population growth rate occurs if the population is held at $K/2$, half the carrying capacity (Figure 2.3a). Two other strategies are guaranteed to produce low yields. The first is to be extremely conservative and remove very few animals at each harvest. This keeps the standing stock large, but the yield is low because the population is close to carrying capacity and grows slowly. The other strategy is to harvest the population down to a very small size. This also produces low yield because there are so few individuals left to reproduce.

Unfortunately, this latter strategy of overdepletion has been followed by all the world's fisheries. Figure 2.14 shows the yearly catch of Peruvian anchovy (*Engraulis ringens*) fitted to the predictions of a simple logistic model. The model predicts a maximum sustained yield of approximately 10 to 11

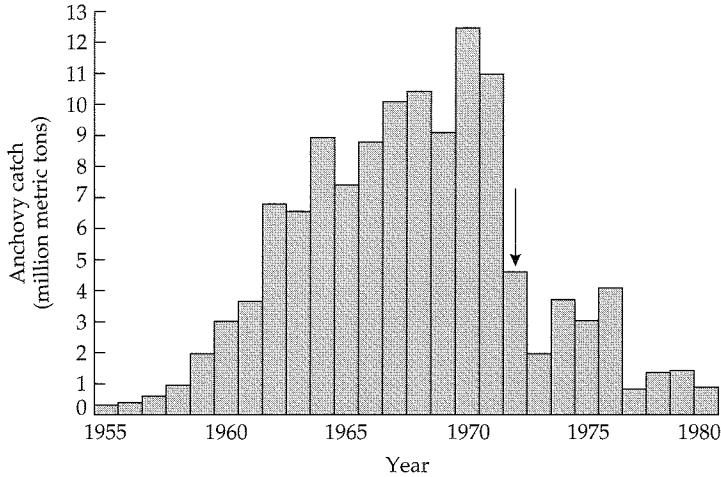


Figure 2.15 Total catch for the Peruvian anchovy (*Engraulis ringens*) fishery from 1955 to 1981. This was the largest fishery in the world until its collapse in 1972. (After Krebs 1985; unpublished data from M. H. Glanz.).

million metric tons per year. The annual catch was close to this sustained maximum from 1964 to 1971. In 1972, the Peruvian anchovy fishery collapsed, in part due to overfishing, and in part due to an El Niño event, in which a warm tropical water mass moved off the coast of Peru and greatly reduced productivity. Although fishing was reduced to allow stocks to recover, anchovy populations have never reached their former abundance and fishing yields remain low (Figure 2.15). Increasingly sophisticated technology and large factory-ships have depleted world stocks of many fish populations to the point where the industry itself is doomed to economic collapse. In 1989, for example, the cost of operating the world's 3 million fishing vessels was estimated at \$92 billion, whereas the total catch was worth only \$72 billion (Pitt 1993). The disappearance of human societies that depend on fishing is also inevitable.

The situation can only be remedied by worldwide restrictions on fishing and short-term reductions in catch. Unfortunately, this will not be easy because each individual fishing vessel tries to maximize its short-term yield by intensive fishing. Migratory fish populations do not obey political boundaries, making international policies difficult to enforce. The problem of short-term versus long-term profits in the exploitation of natural resources is known as "the tragedy of the commons" (Hardin 1968).