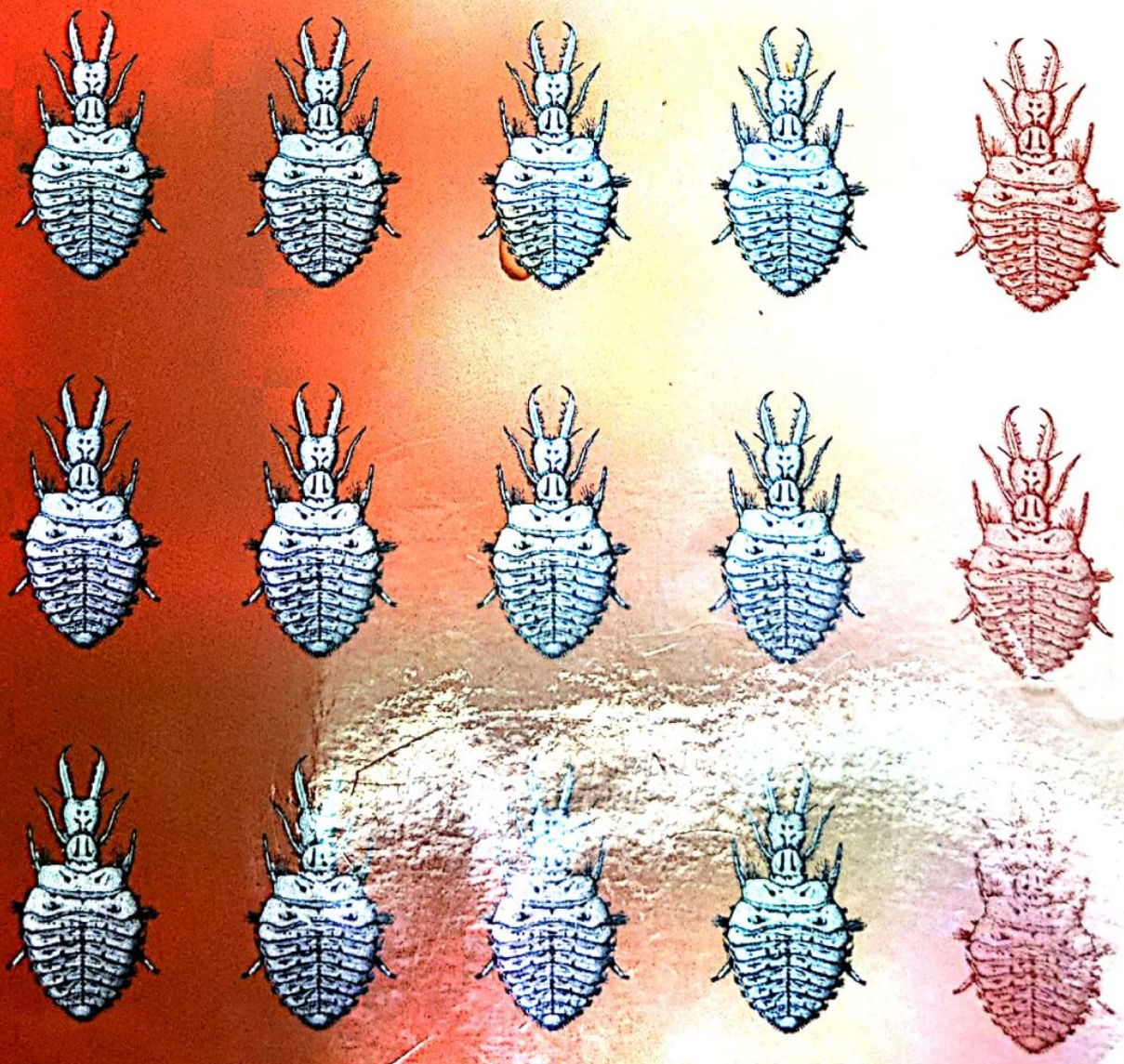
NICHOLAS J. GOTELLI

A Primer of Ecology

THIRD EDITION



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A Primer of Ecology

Third Edition

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The Cover

Third-instar larvae of the North American ant lion, *Myrmeleon immaculatus*. From *Demons of the Dust* by William Morton Wheeler (W. W. Norton, New York, 1930).

The Frontispiece

A portrayal of the complexity of ecological interactions in nature. Each chapter of the primer highlights a particular interaction from this figure. Original artwork by Shahid Naeem, University of Washington.

A PRIMER OF ECOLOGY, Third Edition

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To the Student

The most common question beginning ecology students ask me is, "Why do we have to use so much mathematics to study ecology?" Many students enroll in my ecology course expecting to hear about whales, global warming, and the destruction of tropical rain forests. Instead they are confronted with exponential growth, doubling times, and per capita rates of increase. The two lists of topics are not unrelated. But before we can begin to solve complex environmental problems, we have to understand the basics. Just as a mechanical engineer must learn the principles of physics to build a dam, a conservation biologist must learn the principles of ecology to save a species.

The science of ecology is the study of distribution and abundance. In other words, we are interested in predicting where organisms occur (distribution), and the sizes of their populations (abundance). Ecological studies rely on measurements of distribution and abundance in nature, so we need the tools of mathematics and statistics to summarize and interpret these measurements.

But why do we need the mathematical models? One answer is that we need models because nature is so complex. We could spend a lifetime measuring different components of distribution and abundance and still not have a very clear understanding of ecology. The mathematical models act as simplified road maps, giving us some direction and idea of exactly what things we should be trying to measure in nature.

The models also generate testable predictions. By trying to verify or refute these predictions, we will make much faster progress in understanding nature than if we try to go out and measure everything without a plan. The models highlight the distinction between the *patterns* we see in nature and the different *mechanisms* that might cause those patterns.

There are two dangers inherent in the use of mathematical models in ecology. The first danger is that we build models that are too complex. When this happens, the models may contain many variables that we can never measure in nature, and the mathematical solutions may be too complex. Consequently, the most useful ecological models are often the simplest ones, and these have been emphasized throughout this primer.

The second danger is that we forget that the models are abstract representations of nature. However logical a model might appear, nothing says that nature must follow its rules. By carefully focusing on the assumptions of the model, we may be able to pinpoint the places where it departs from reality. As

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you will see from the examples in this primer, the models often tell us more about nature when their predictions do not match our field observations.

The purpose of this primer is to de-mystify the mathematical models used in ecology. Many of the equations in this primer can also be found in your textbook. However, your textbook may provide little or no explanation for where these equations come from, whereas the primer develops them step by step. I hope this primer will help you to understand the mathematical models and to appreciate their strengths and limitations.

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CHAPTER 1

Exponential Population Growth

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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

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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 $t + 1$:

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

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:

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

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

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:

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

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):

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

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 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 • 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:

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

Similarly, we can define an **instantaneous death rate** d, with units being number of deaths per individual per unit time [deaths/(individual • 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:*

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

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).

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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:

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

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:

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

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

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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:

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

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:

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

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

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

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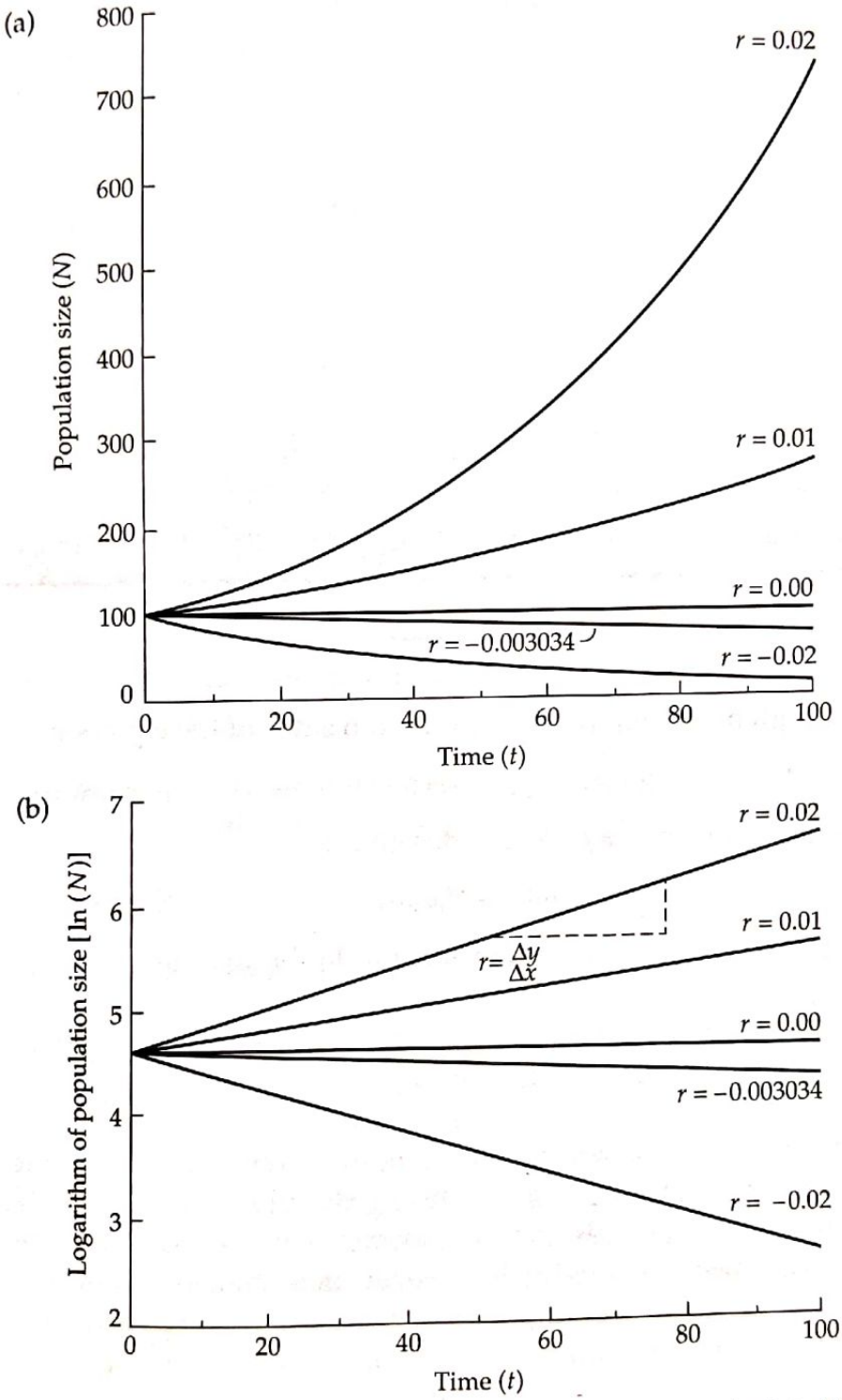

Figure 1.1 (a) Trajectories of exponential population growth, calculated from a starting population size of 100 individuals. The estimated r of −0.003034 [individuals/(individual • year)] corresponds to the projection for the grizzly bear (*Ursus arctos horribilis*) population of Yellowstone National 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.

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

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

From Fenchel (1974).

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

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

Taking the natural logarithm of both sides gives:

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

Expression 1.12 can be rearranged to solve for doubling time:

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

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 [$r = 0.365$

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

Year	*Herd size*
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.

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✓ ***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

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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 nonliving 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:

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

Combining terms gives:

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

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

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

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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:

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

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:

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

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.

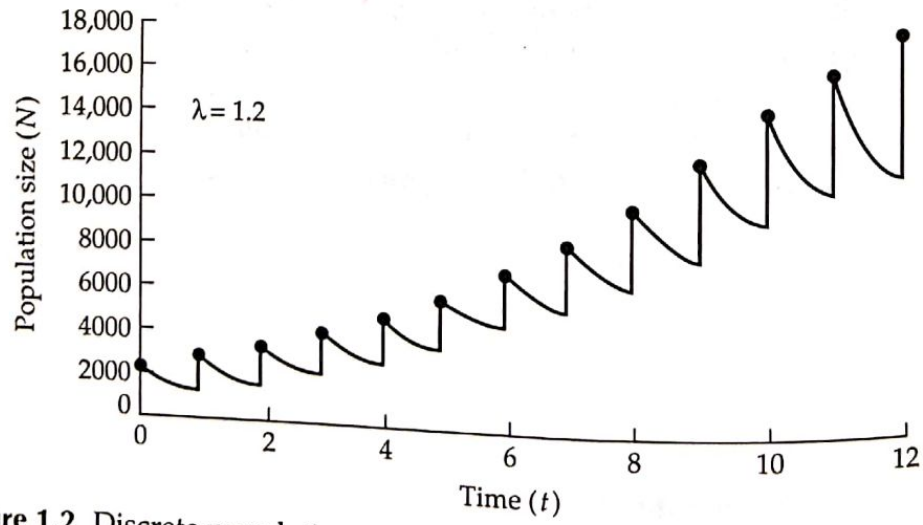

Figure 1.2 Discrete population growth. In this example, births are pulsed at the beginning of the year, and deaths occur continuously.

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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:

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

We can express Equation 1.5 in equivalent logarithmic form as:

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

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

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

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

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

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 • year). Dividing by 12 (months) gives $r = 0.01519$ individuals/(individual • 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:

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

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

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-

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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:

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

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):

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

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.

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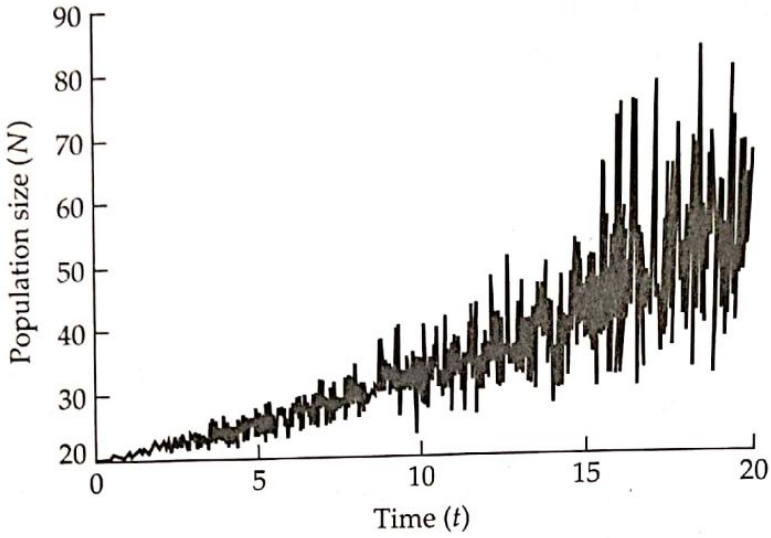

Figure 1.3 Exponential growth with environmental stochasticity. In this model, the instantaneous rate of increase fluctuates randomly through time. Here $N_0 = 20$; $r = 0.05$; $\sigma_r^2 = 0.0001$.

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):

$$\sigma_r^2 > 2\bar{r} \qquad \text{Equation 1.9}$$

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

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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 : ...BBBDDBDBBBBD.... 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:

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

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

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.

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[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:

$$\overline{N}_t = N_0 e^{rt} \qquad \text{Equation 1.12}$$

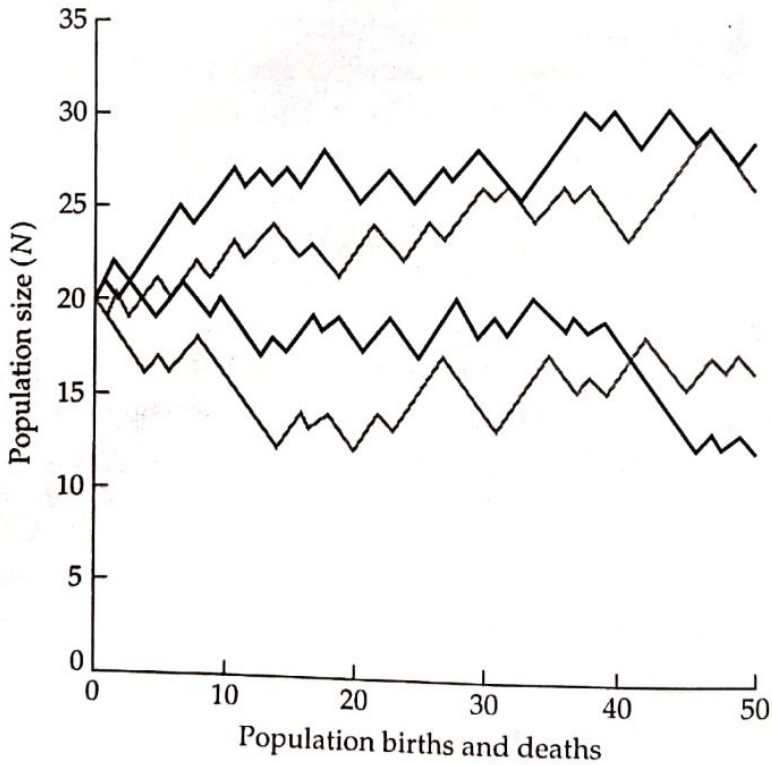

Figure 1.4 Computer simulation of population growth with demographic stochasticity. Each population track starts with an N of 20 individuals. b = 0.55 births / (individual • year) and d = 0.50 deaths / (individual • year). Although the starting conditions are identical, two of the populations actually 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).

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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):

$$\sigma^2_{N_t} = 2N_0bt \qquad \text{Equation 1.13}$$

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

$$\sigma^2_{N_t} = \frac{N_0(b+d)e^{rt}\left(e^{rt}-1\right)}{r} \qquad \text{Equation 1.14}$$

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:

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

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-

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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 • 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

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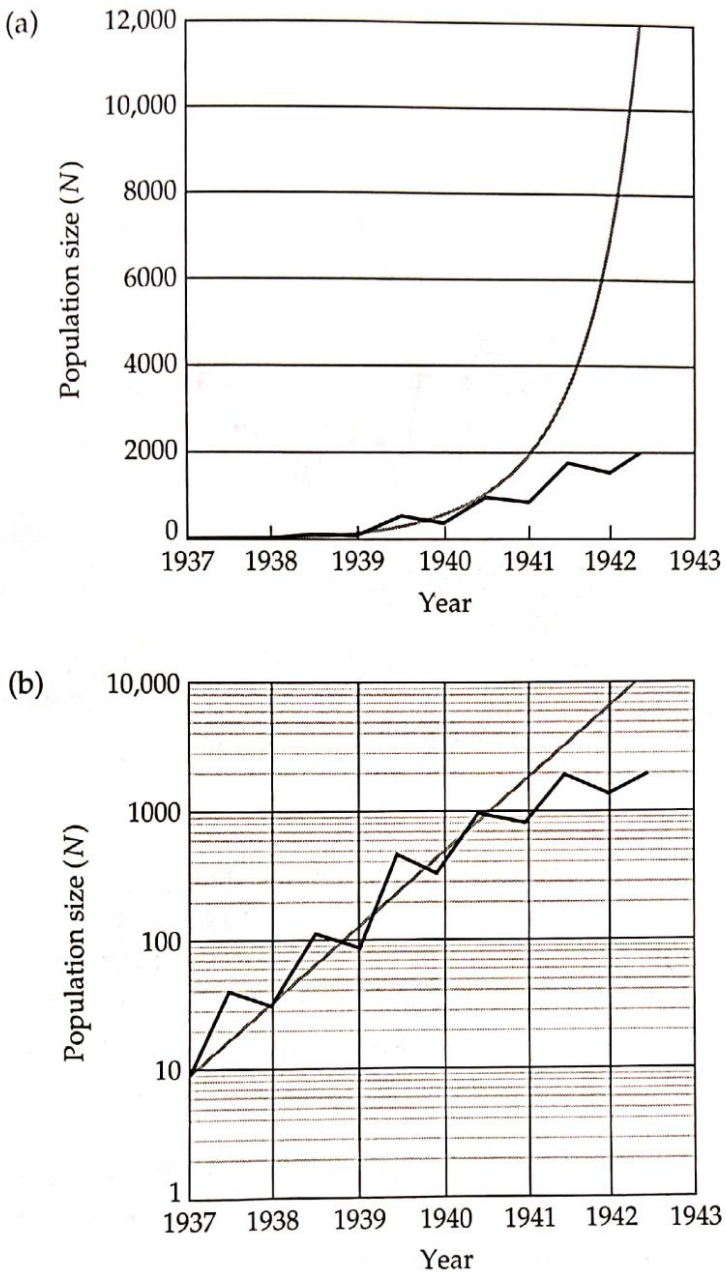

Figure 1.5 Growth of pheasant (*Phasianus colchicus torquatus*) population introduced to Protection Island. The thin line shows the hypothetical exponential growth curve, with $r = 1.3217$ individuals / (individual • year); the thick line shows the observed population size. For comparison, population 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 • 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

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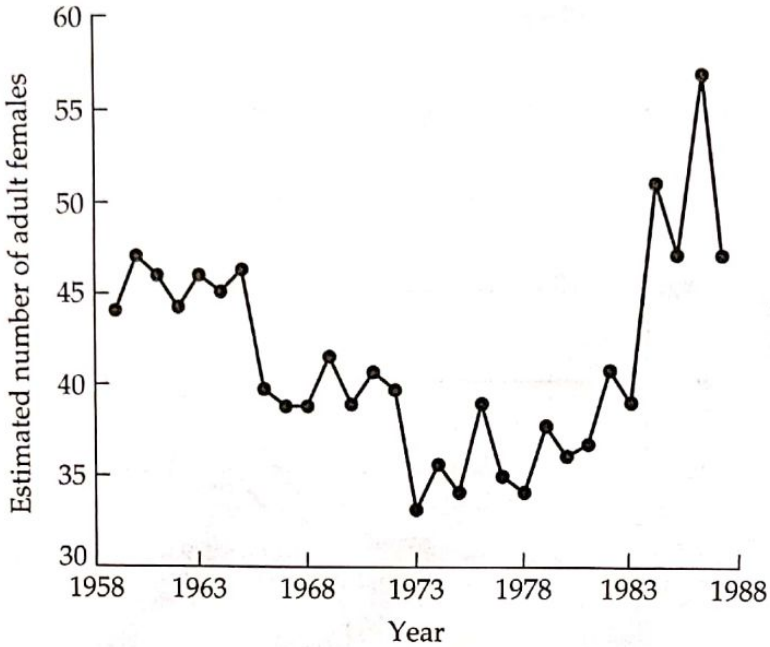

Figure 1.6 Population size of grizzly bears (*Ursus arctos horribilis*) in Yellowstone National Park. These data were used to construct a model of exponential population growth that incorporates environmental stochasticity. The estimate of r from this model was –0.003034 individuals / (individual • year).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

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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 • year) and d = 0.0020 deaths/(individual • 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

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