

To Benita

An Illustrated Guide to Theoretical Ecology

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1 Exponential and Geometric Population Growth

A **population** is a group of individuals that belong to a single species and live in some defined area. Ecologists strive to understand the causes of variation in the sizes of populations and to predict trends in these numbers over time and from place to place. A population increases in size by births and the immigration of individuals into the population from outside. Deaths and emigration decrease population size. These inputs and outputs can be set up as an equation where the subscript t indicates a discrete point in time. The population at time $t + 1$ is N_{t+1} and its size is given by

$$N_{t+1} = N_t + \text{births} - \text{deaths} + \text{immigration} - \text{emigration}.$$

The births, deaths, immigration and emigration in this equation are those that occurred during the time interval between t and $t + 1$. If time is measured in years, then this equation says that the number of individuals at a specific time next year ($t + 1$) will equal the number that are present at the same time this year, plus all the positive and negative changes to population size that occurred during the year. Figure 1.1 summarizes these flows.

However, this diagram doesn't capture the long-term dynamics of population growth. Each new birth has the potential itself to give birth after that individual reaches sexual maturity. Thus the birth component of the input/output diagram forms a positive feedback loop with population size. The more births, the larger the population size becomes, and, as population size becomes larger, more individuals produce new young, and so on. Figure 1.2 modifies the diagram shown in Figure 1.1 to illustrate this positive feedback loop involving births.

This diagram still ignores many realistic complications: for example, different ages or different genotypes may have different rates of death, reproduction, and movement. These parameters may also vary over time and space and with population size. The rest of the book is devoted to adding and investigating these complications one at a time. For now, however, it is important for you to appreciate the inherent potential of exponential growth. The ability of populations to increase in a multiplicative way has tremendous ramifications for ecology, evolution, and economics. A pair of rabbits might produce 2 pairs, which can produce 4 pairs, which can produce 8 pairs, and so on. The larger the population size, the greater is its potential to grow still larger during the next time period (i.e. $N_{t+1} - N_t$, $N_{t+2} - N_{t+1}$, . . . , $N_{t+n} - N_{t+n-1}$). The end of each interval completes a **time step**.

MODELING POPULATION GROWTH

Population biologists trying to predict future population growth take different approaches to the mathematics of this growth. The first approach, "**discrete time**," as the name suggests, divides time into discrete chunks or intervals and forms equations that describe the growth of the population from one time step to the next. This method produces equations for population growth called **difference** equations; an example is

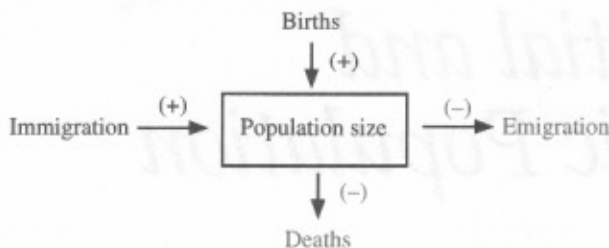


Figure 1.1
General factors increasing (+) and decreasing (-)
population size.

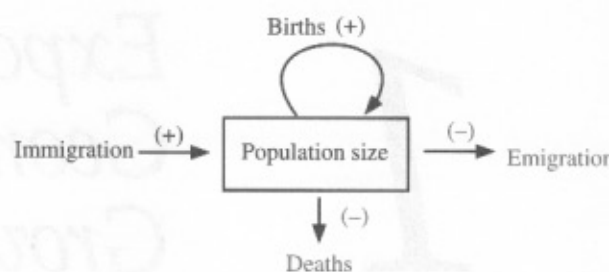


Figure 1.2
Births form a positive feedback loop with population size.

the opening equation of this chapter. The other approach considers time as a **continuous** variable and uses the calculus of differential equations to perform smooth, continuous projections over time. These different approaches are not based simply on mathematical convenience or an esoteric desire for completeness. We all know that time is continuous, nevertheless some organisms respond to time's arrow in a discontinuous, pulsed manner. Their breeding seasons may occur during brief intervals of the year. For other organisms, reproduction may go on continuously over the year, and for these species the mathematics of continuous time provides a more realistic description of their response. Most species are probably somewhere between these two extremes, but we could model them using either method as long as we recognize the minor errors involved. (The short Preparation section in Appendix 1 presents an overview of the strategy and syntax of model development in population biology.)

Box 1.1 shows side by side the basic equations for simple unlimited population growth in discrete time and continuous time. In both methods, we seek a **solution** that is an expression for population size at any arbitrary time in the future based on the population size that presently exists. In the discrete time approach, growth is formulated as

$$N_{t+1} = RN_t + N_t$$

This equation says that the population size, N , one time step (e.g., one year) later is equal to the present size of the population (at time t) plus some increment that represents the net change. This net change is given by a per capita rate R that then multiplies the number of individuals present at time t ; R may be positive or negative. Of course, R probably will vary over time, space, and individuals. However, the case in which it is constant is interesting and a good demonstration of the mathematical tools used in population projection. The goal is to find an expression for N , not for a single time step into the future, but rather for many time steps, say T . Box 1.1 shows that this expression is $N_T = N_0 \lambda^T$.

In the continuous time approach, the *instantaneous rate* of population change (dN/dt) is given as a function of the population size at the time t , $N(t)$, and a parameter r . (Later we determine the precise relationship between r and R in Box 1.2.) Note the differences in notation used in deriving the discrete time formula (use of subscripts and superscripts) and in deriving the continuous time formula (use of function notation).

For both methods we obtained **solutions** (Eqs. 1.3a and 1.3b) that give the population size any arbitrary time into the future, based on a knowledge of the initial population size, N_0 , a parameter describing population growth rate (either r or λ), and the growth model (either Eq. 1.1a or 1.1b).

Three examples of exponential population growth in continuous time are shown in Figure 1.3. All of these populations begin with a single inseminated female and, as time goes on, all approach infinity but at different rates.

When we plot the natural log of N (written $\ln N$), rather than N , the curves in Figure 1.3 become straight lines in Figure 1.4. Logarithms, regardless of the base chosen, convert multiplicative to additive processes (recall that $\ln(ab) = \ln a + \ln b$). The slope of each line equals $r = \ln \lambda$.

Box 1.1 Unrestricted Growth: Two Different Approaches When the Rate of Growth Is Constant

Discrete Time Using a Difference Equation (Geometric Growth)

The starting expression is

$$N_{t+1} = RN_t + N_b$$

where R is the net discrete (or geometric) per capita rate of growth. Collecting terms gives

$$N_{t+1} = (R + 1) N_t \quad (1.1a)$$

which we may also write as

$$N_{t+1} = \lambda N_t$$

where $\lambda = (R + 1)$ is the discrete (or geometric) per capita rate of growth; its units are per time period.

Similarly, for two time steps,

$$\begin{aligned} N_{t+2} &= \lambda N_{t+1} \\ &= \lambda \lambda N_t \\ &= \lambda^2 N_t \end{aligned}$$

and, for any arbitrary number of time steps into the future (say, T time steps),

$$N_{t+T} = \lambda^T N_t \quad (1.2a)$$

If we start with N_0 individuals at time $t = 0$, then at time T the number of individuals is

$$N_T = N_0 \lambda^T \quad (1.3a)$$

Equation (1.3a) is the "solution" for discrete time because it is a formula giving N for any arbitrary time period into the future.

Continuous Time Using a Differential Equation (Exponential Growth)

The starting expression is

$$\frac{dN}{dt} = rN(t) \quad (1.1b)$$

Initial conditions specify the beginning time ($t = 0$) and initial population size

$$N(\text{at } t = 0) = N(0).$$

In Eq. (1.1b), r is the intrinsic (or exponential) per capita rate of growth; its units are per time period.

To solve Eq. (1.1b) with its initial conditions, we separate the differentials and integrate both sides. Then we evaluate the integral from $t = 0$ to $t = T$:

$$\int_{N(0)}^{N(T)} \frac{dN(t)}{N} = r \int_0^T dt. \quad (1.2b)$$

From the integral formulas of calculus, the left-hand side of Eq. (1.2b) becomes

$$\ln N(T) - \ln N(0)$$

and the right-hand side of Eq. (1.2b) becomes

$$rT - r0 = rT.$$

After exponentiation of both sides,

$$\frac{N(T)}{N(0)} = e^{rT}.$$

Finally, rearranging yields

$$N(T) = N(0) e^{rT} \quad (1.3b)$$

Equation (1.3b) is the "solution" for continuous time because it is a formula giving $N(t)$ for any arbitrary time T into the future.

Comparing Eqs. (1.3a) and (1.3b), we see that $e^r = \lambda$.

Figure 1.3
Exponential growth for three different values of the intrinsic growth rate, r .

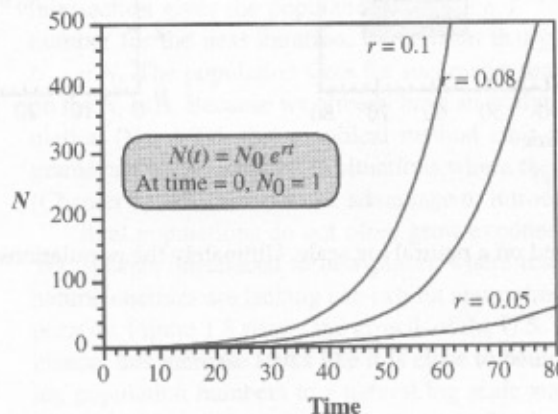
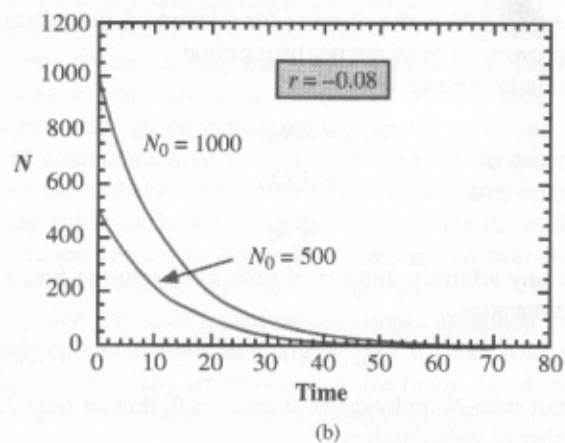
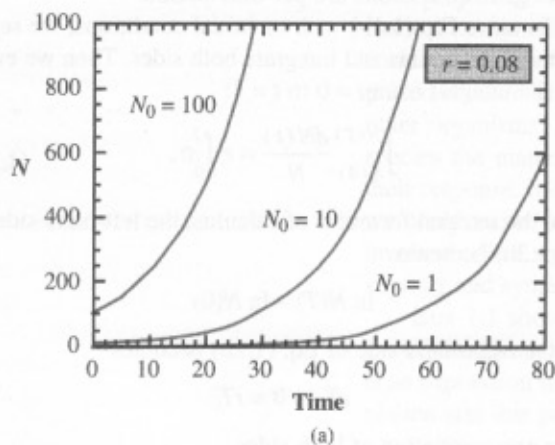
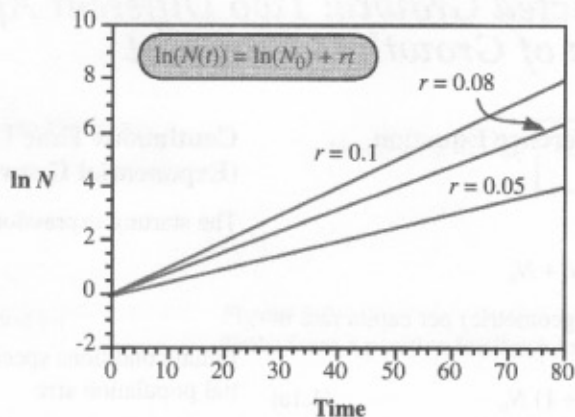
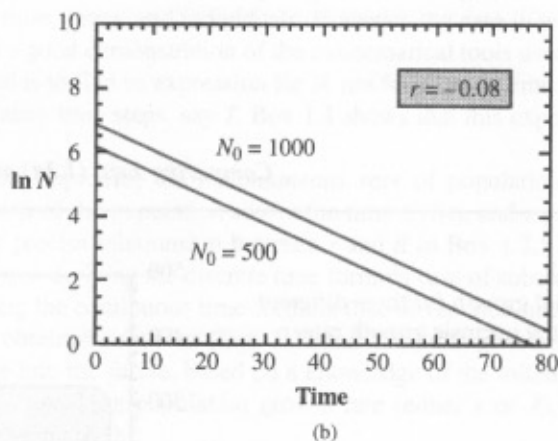
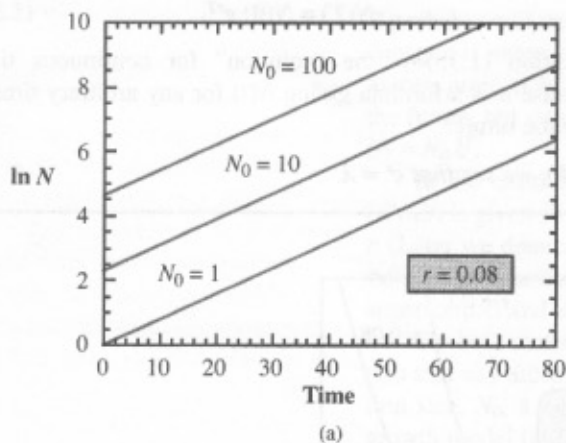


Figure 1.4

The three curves in Figure 1.3 plotted on a logarithmic scale for N . All populations begin at the same starting number of one inseminated female $\ln 1 = 0$.

**Figure 1.5**

The effect of different initial population sizes on the course of exponential growth: (a) $r > 0$ and (b) $r < 0$.

**Figure 1.6**

The results in Figure 1.5 plotted on a natural log scale. Ultimately the populations in (a) approach infinity and those in (b) approach zero.

Exercise: Use Eq. (1.3b) and the definition of the slope of a straight line to show that the slope of each line in Figure 1.4 is $r = \ln \lambda$.

Figure 1.5 shows the effect of varying the initial population size.

After conversion of N to a natural log scale, this plot produces the straight lines shown in Figure 1.6.

The lines for the different starting population sizes are parallel on the log scale. In Figure 1.6(a) it takes the $N_0 = 1$ population 75 years to reach 403 ($\ln 403 \approx 6$). Increasing the initial population size tenfold ($N_0 = 10$) reduces this time but only by about one-third, to about 46 years. Thus doubling the initial population size does *not* necessarily halve the time it takes for a population to reach some threshold size.

Question: One hundred rabbits are introduced onto a small island at the beginning of 1995. If this population has a geometric growth rate λ of 1.3/year on the island, what will be the population size at the beginning of 2000? At the beginning of 2005?

Answer: In this example, N_0 is the population size in 1995; label it $N_{1995} = 100$. Applying Eq. (1.3a), the number of rabbits in 2000 is

$$N_{2000} = N_{1995}(1.3^5) = (100)(3.713) \approx 371 \text{ rabbits.}$$

Or, equivalently, Eq. (1.3b) could be applied. After we take the natural log of both sides, that equation becomes

$$\ln N_{2000} = \ln(N_{1995}) + rt.$$

As $r = \ln \lambda$, this expression becomes

$$\ln N_{2000} = 4.605 + (0.2623)(5) = 5.9168.$$

The antilog of 5.9168 is $N_{2000} \approx 371$ rabbits.

The population size in 2005 is

$$N_{2005} = N_{1995}(1.3^{10}) = (100)(13.786) \approx 1379 \text{ rabbits.}$$

This quantitative equivalency between the dynamics of populations in discrete time and continuous time, with the substitution $e^r = \lambda$, does not extend to more complicated population dynamic models, as we show in Chapter 5 when we discuss density dependence.

A graphical technique helps illustrate the sequential change in the number of individuals over time by creating a “ladder” between N_{t+1} and N_t . The black diagonal line in Figure 1.7 is the line of equality $N_{t+1} = N_t$. Start the population with some number N_0 at time 0 and follow the dashed arrow up to the geometric growth line (slope = λ). This intersection gives the population size at $t + 1$. To translate this value into the starting number for the next iteration, move from that point horizontally to the diagonal line $N_{t+1} = N_t$. The population sizes for successive times $t = 1, 2$, and 3 are projected as dots on the N_t axis. Because we already have an analytical formula for the growth of the population (Eq. 1.3a), this graphical method isn’t really necessary. However, these diagrams can be generalized to situations where the growth rate, λ , is changing over time (Chapter 5), so there is some advantage to introducing the method for a simpler case.

Real populations do not often grow exponentially or geometrically for very long. Yet, species introduced to new places where resources are initially plentiful and their natural enemies are lacking can exhibit approximately exponential growth, at least temporarily. Figure 1.8 shows the growth of the U.S. population from 1790 to 1995. At first glance, this increase looks like it is close to being exponential. However, after converting population numbers to a natural log scale and then finding a best-fit linear regression line through the points, we see more clearly that the growth rate has been tapering off, as shown in Figure 1.9.

Figure 1.7

A graphical iteration method for determining discrete population growth. The initial population size is N_0 . (a) $\lambda = 1.3$. The population increases geometrically. (b) $\lambda = 0.8$. The population decreases geometrically.

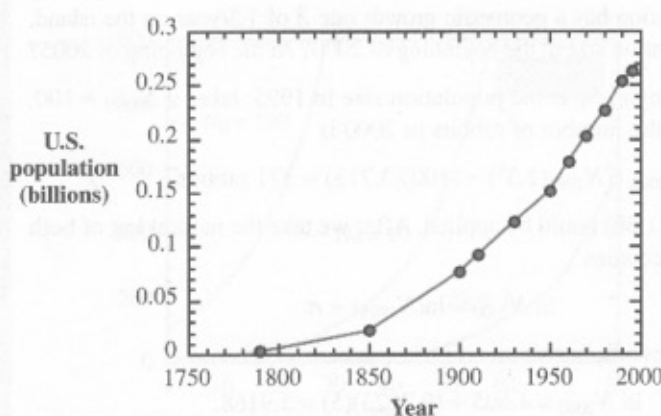
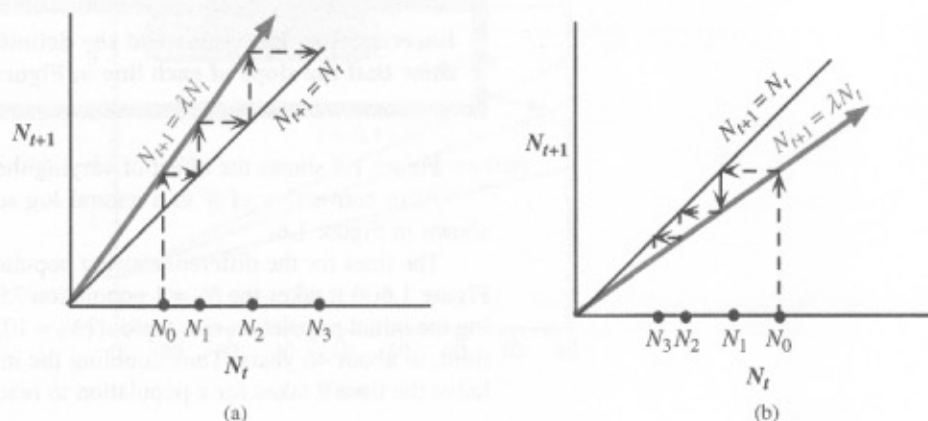


Figure 1.8

Population growth in the United States from 1790 to the present.

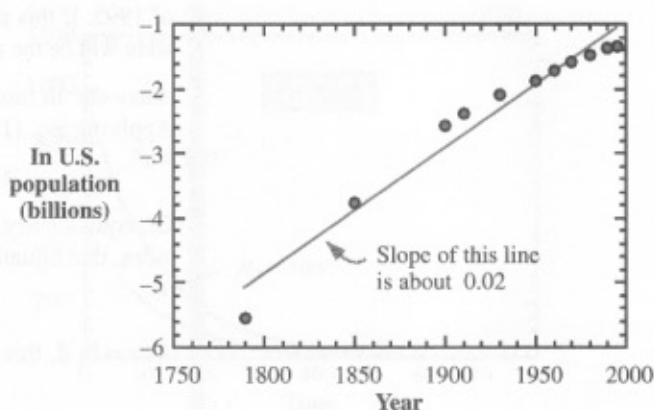


Figure 1.9

The data in Figure 1.8 plotted on a natural log scale. A regression line is shown through the points. It has a slope of about 0.02, meaning that the average rate of growth is about 2% per year. Note, however, that the actual points show a decline in growth rate over the past several decades.

The U.S. population has been growing at an average rate of about 2% per year, although current rates are less than 1%. The logarithmic plot reveals the decline in growth rate with time; note that the points are better described by a curve with a decreasing slope than by the straight line of constant r shown.

To give you a better understanding of geometric growth, in Figure 1.10 we show a simulation of a population of water lilies covering a pond. The open red squares represent the pond on selected days. The population of lily pads on those days is represented by the solid red areas. The black horizontal bars portray elapsed time. The simulation begins at day 0 with a single lily pad. Relative to the scale of the entire pond, this single lily pad is so small as to be invisible. The number of lily pads doubles every day ($\lambda = 2/\text{day}$) until the pads become visible on day 15 (lower left-hand corner of window). Ultimately the pond can hold 100 million lily pads. It is completely full at day 30 but was just half full 1 day before, on day 29. The point is that **geometric growth can sneak up on you**.

With a population doubling time of just 1 day, population size will get out of hand quickly, despite a very low initial number. However, the same kind of explosive growth occurs even with longer doubling times. The average growth rate in the United States since colonial times is only about 2%/year, translating to a doubling time of about 35 years. (See the section Solved Problems for this doubling time calculation.) The U.S. Geological Survey has produced a video showing the growth of urban and suburban areas in the Baltimore/Washington, D.C., area during this period. Figure 1.11 shows



Figure 1.10
Simulation of the growth of lily pads in a pond.

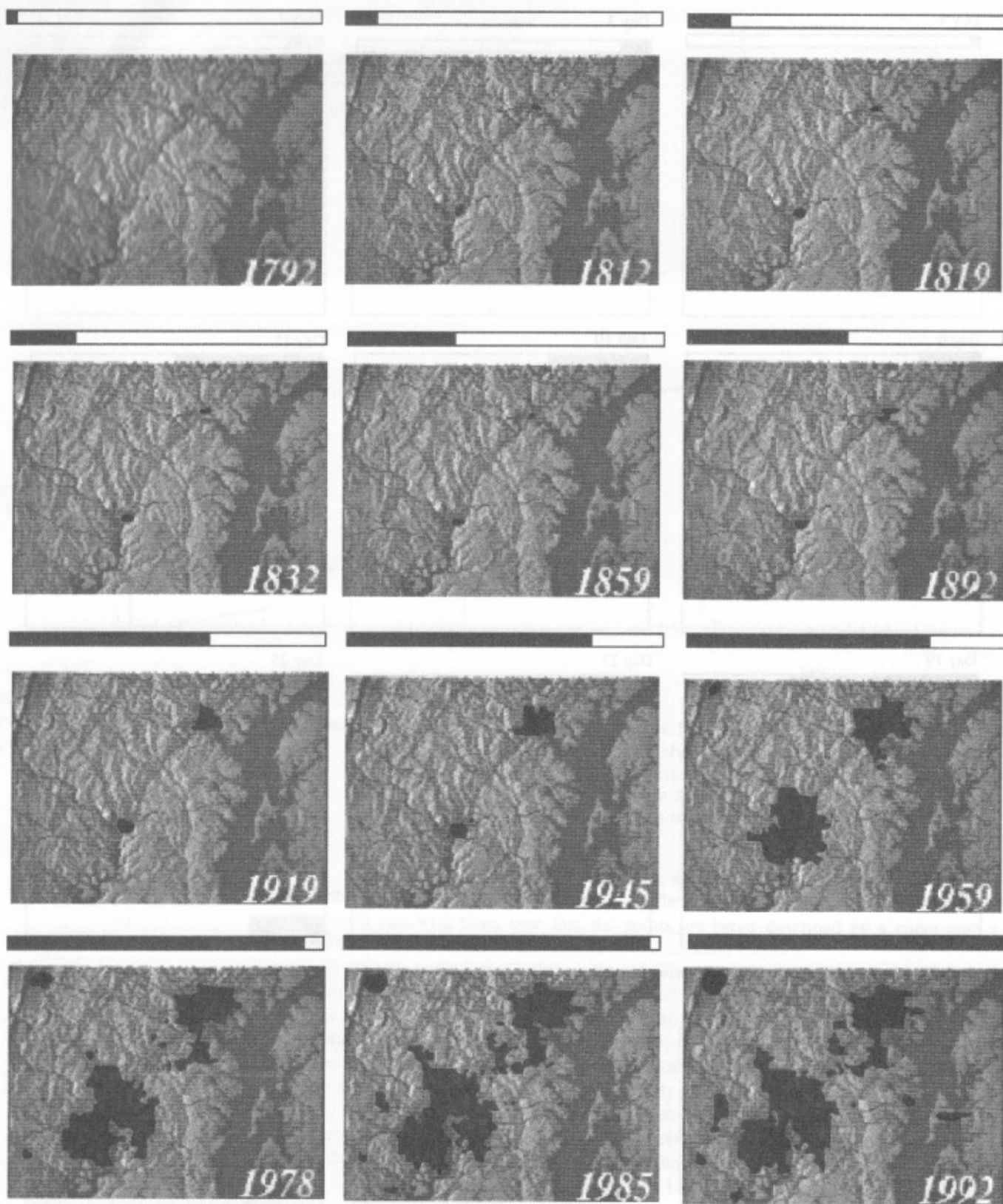


Figure 1.11

Historical growth of the Baltimore/Washington, D.C., urban area (shown in red). Adapted from a U.S. Geological Survey video.

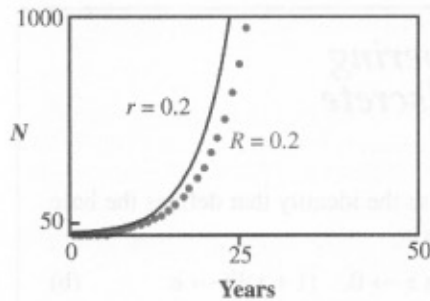


Figure 1.12

Comparison of exponential growth and geometric growth when $r = R = 0.2/\text{year}$.

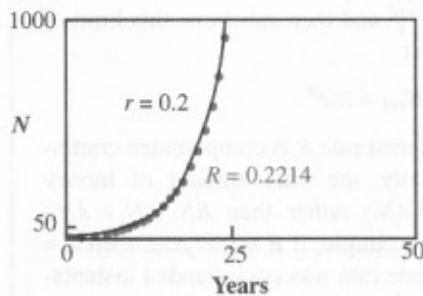


Figure 1.13

Exponential growth with $r = 0.2$ and discrete growth with $R = 0.2214$ give virtually identical time courses.

maps based on the same relative sequence of time slices as that for the lily pond simulation. Urbanized areas are shown in red, indicating clearly that development accelerated after World War II until the mid 1980s when it appears to have slowed.

EXPONENTIAL GROWTH: R VERSUS r

In financial circles R is called the *yield* or *annual yield* if expressed on a yearly basis, whereas r corresponds to what is called the *annual rate*. Financial institutions usually post both the annual yield and the annual rate in their advertisements. For example, a newspaper advertisement for a bank proclaims the following interest rates for its money market investments.

Annual yield	Annual rate
7.51%	7.25%

Note that the two rates are slightly different. To see how they are related, we plotted growth, N , over 25 years for $R = 0.2/\text{year}$ and for $r = 0.2/\text{year}$, as shown in Figure 1.12.

The two rates of growth shown in Figure 1.12 are not identical. The growth of the population (or money if we're talking about a financial investment) is larger for $r = 0.2$ than for $R = 0.2$. This difference makes sense because discrete growth *compounds* only once a year while continuous growth compounds much more frequently—in fact, instantaneously.

We may then reason that, if $R = 0.2/\text{year}$ in discrete time yields a slower rate of growth than $r = 0.2/\text{year}$ in continuous time, we need to make R larger if we want to superimpose its growth curve on that for $r = 0.2$. But how much larger?

You can immediately get an insight into this question by examining the two expressions at the bottom of Box 1.1. For geometric growth $N_T = N_0 \lambda^T$, and for exponential growth $N_T = N_0 e^{rT}$. These two expressions are identical after the substitution $\lambda = e^r$. And, since $R = \lambda - 1$,

$$R = e^r - 1. \quad (1.4)$$

Now let's work through this example. If $r = 0.2$, then we will get an identical curve, starting with the same initial numbers, if

$$R = e^{0.2} - 1 = 0.2214.$$

Thus in financial terms the annual yield would be 0.2214 (or 22.14%) if the annual rate was 0.20 (or 20.0%); \$1000.00 invested today would produce \$1221.40 one year later. The two curves are plotted in Figure 1.13.

The discrepancy between r and R decreases as r approaches 0. When the absolute value of r is much less than 1, we can apply a convenient approximation formula: $e^r \approx 1 + r$. So by Eq. (1.4), $R \approx 1 + r - 1 = r$. For example, for $r = 0.2$, the substitution yields $R = 1.02$, which is very close to the true value of 1.0202.

Exercise: Verify from an advertisement for money market interest rates that the two rates converge according to Eq. (1.4).

A word of caution: Here we have used r for the instantaneous growth rate and R for the discrete rate of population growth, but there is nothing sacred about this particular symbolism and it is not uniform in ecology texts. You will always be able to discern the meaning behind the symbols by looking at the equation, discrete or continuous time, in which they appear. A common alternative is to call r the **Malthusian parameter** and abbreviate it as m . Thomas Malthus was one of the first to realize the tremendous social implications of exponential growth for human beings. Charles Darwin attributed Malthus's 1798 book, *An Essay on the Principles of Population as It Affects*

Box 1.2 (Advanced) Exponential Growth: Recovering the Continuous from the Discrete

In discrete geometric growth, there is an implicit time lag of one time step (or one generation) each iteration. The population size is projected forward (or backward) in time, one step at a time. For example, in terms of yearly interest rates this time lag is like the compounding of interest on an investment only at the end of each year. If interest is compounded twice a year, then the time lag is reduced by half. With this modification, Eq. (1.1a) for discrete growth becomes

$$N_{t+1} = N_t \left(1 + \frac{R}{2}\right)^2,$$

where, as before, $t + 1$ means 1 year later than year t . Similarly if interest is compounded q times a year, then

$$N_{t+1} = N_t \left(1 + \frac{R}{q}\right)^q.$$

To reduce notational complexity, we can substitute the symbol x for R/q , leading to an expression for which calculus can provide a ready solution:

$$N_{t+1} = N_t(1 + x)^{R/x}. \quad (a)$$

From calculus we can use the identity that defines the base of the natural logarithms e :

$$\text{In the limit as } x \rightarrow 0, \quad (1 + x)^{1/x} \rightarrow e. \quad (b)$$

This equation is read as: In the limit, as x gets smaller and smaller, eventually approaching 0, then $(1 + x)^{1/x}$ comes closer and closer to the number e . For example, when $x = 0.1$, $(1 + x)^{1/x} = 1.1^{10} = 2.593$; and when $x = 0.01$, $(1 + x)^{1/x} = 1.01^{100} = 2.705$, thus approaching $e = 2.7183$

This is where our trick came in handy, allowing us to convert to something simpler. We also use the fact that $(1 + x)^{R/x} = [(1 + x)^{1/x}]^R$ and then substitute this limit of Eq. (b) into Eq. (a), to get

$$N_{t+1} = N_t e^R.$$

In other words, if the interest rate R is compounded continually rather than annually, the total amount of money after 1 year equals $(e^R)(N_t)$ rather than $RN_t + N_t = \lambda N_t$; the latter is smaller. For example, if $R = 8\%$ /year, then $\lambda = 1.08$ /year—but if this same rate was compounded instantaneously we would have $e^R = 1.083$, or 8.3% interest at the end of a year.

the Future Improvement of Society, to helping him crystallize his thinking on the theory of evolution by natural selection. Box 1.2 presents a more formal connection between r and R .

PROBLEM (ADVANCED)

Exponential Growth in the Consumption Rate of Resources

Question: If the present worldwide rate of consumption of petroleum increases by 2% every year, how long will it take to use up the earth's petroleum?

Answer: It is important to recognize that in this problem, unlike the problems considered so far in this chapter, the rate of change (in this case of petroleum consumption) is itself growing exponentially. Let's call the rate of petroleum consumption at time t , $C(t)$. Then we can express $C(t)$ as a function of present consumption ($C(0)$), at initial time 0:

$$C(t) = C(0)e^{rt}.$$

The rate constant, r , in units of per year can be determined by the condition $C(1) = 1.02C(0)$. Thus

$$e^{r(1)} = 1.02$$

and because $\ln(1.02) = 0.0198$,

$$r = 0.0198.$$

If $M(t)$ is the amount of petroleum remaining at time t , then the rate of change of $M(t)$ is

$$\frac{dM}{dt} = -C(t) = -C(0)e^{0.0198t}$$

Consumption depletes petroleum, so the minus sign is necessary on the right-hand side of the equation. This equation can be integrated to yield an expression for $M(t)$ versus t . If we call the integration variable t' , then we may write this integration as

$$\int_{M(0)}^{M(t)} dM = - \int_0^t C(0)e^{rt'} dt'. \quad (1.5)$$

Evaluating the integrals in Eq. (1.5) gives

$$M(t) - M(0) = \frac{-C(0)}{r} e^{rt} + \frac{C(0)}{r}. \quad (1.6)$$

[Do you see where the r 's came from in the denominators of Eq. (1.6)? The indefinite integral of e^t is just e^t but the indefinite integral of e^{rt} is e^{rt}/r .]

After collecting and rearranging terms, we have

$$M(t) = M(0) + \frac{C(0)}{r} (1 - e^{rt}). \quad (1.7)$$

The petroleum stock will be entirely consumed when $M(t)$ is 0. Let's call that particular time, when petroleum is depleted, T . (The capital T is not to be confused with the lowercase t , which we are using as the symbol for "generic" time.) Hence we defined T by setting $M(t)$ in Eq. (1.7) equal to 0, or

$$0 = M(0) + \frac{C(0)}{r} (1 - e^{rT}). \quad (1.8)$$

After collecting terms to get T on the left-hand side of the equals sign, we get

$$e^{rT} = 1 + \frac{rM(0)}{C(0)}.$$

Taking the log of both sides and dividing by r , we get

$$T = \frac{\ln \left[1 + \frac{rM(0)}{C(0)} \right]}{r}. \quad (1.9)$$

[Note that generally the logarithm of a sum of terms cannot be reduced to an expression involving the sum of the logarithms of the separate terms.]

As of 1995, the rate of petroleum consumption, $C(0)$, was about 24.163 billion barrels (bbl) per year and reserves were estimated at $M(0) = 1111$ billion barrels. Substituting these values and $r = 0.0198/\text{year}$ into eq (1.9), gives the final answer:

$$T = \frac{\ln \left[1 + \frac{(0.0198 / \text{year})(1111 \text{ bbl})}{24.163 \text{ bbl / year}} \right]}{0.0198 / \text{year}} = 32.2 \text{ years}.$$

If these estimates are accurate—and if the rates of consumption continue to increase exponentially—the world's petroleum reserves will be depleted by about 2027.

SOLVED PROBLEMS

1. How long would it take for a pair of individuals to produce the world population today (about 6 billion people) at the present rate of population growth ($r = 2\%$ per year)?

Solution:

Call the population size today N_{now} and assume a continuous time model:

$$N_{\text{now}} = N_0 e^{rt}$$

Take the natural log of both sides:

$$\ln N_{\text{now}} = \ln N_0 + rt \text{ and } t = \frac{\ln N_{\text{now}} - \ln N_0}{r}$$

The present population, N_{now} , is 6 billion, r is about 2% per year, and $N_0 = 2.0$. Hence

$$\begin{aligned} t &= \frac{\ln 6,000,000,000 - \ln 2}{0.02} \\ &= \frac{22.51 - 0.693}{0.02} \\ &= 1091 \text{ years.} \end{aligned}$$

2. What is the doubling time of this population?

Solution:

We denote the time until the population doubles as t_d and it occurs when

$$2N_0 = N_0 e^{rt_d}$$

Taking the natural log of both sides, we get

$$\ln[(2)N_0] = \ln(N_0) + rt_d$$

or

$$\ln 2 + \ln N_0 - \ln N_0 = rt_d$$

Rearranging to solve for the doubling time gives

$$t_d = \frac{\ln 2}{r} \quad (1.10)$$

This formula gives the doubling time of an exponentially growing population if r is known. In this case, Eq. (1.10) yields

$$t_d = \frac{0.693}{0.02} = 34.7 \text{ years.}$$

Note that for exponential growth the doubling time is independent of initial population size. A population growing at 2% per year will double about every 35 years. A population growing at 1% per year will double about every 69 years.

QUESTIONS

1. The population growth curves for two populations (A and B) are plotted in Figure 1.14. Both populations begin with 4 individuals. One population is growing continuously through time with $r = 0.25/\text{week}$, and the other population is growing discretely with $R = 0.25/\text{week}$ (i.e., $\lambda = 1.25/\text{week}$). Which is

a. Discrete? _____

Continuous? _____

b. What is the doubling time for population A? _____

c. What would the value of R need to be to exactly superimpose curve B on curve A? _____

d. What would the value of r need to be to exactly superimpose curve A on curve B? _____

e. Use the initial conditions $t_0 = 0$ and $N_0 = 10$ to write the growth equations for the two populations shown:

$$N_A(t) =$$

$$N_B(t_0 + n) =$$

2. A certain moth has a constant intrinsic per capita growth rate of $r = 0.4$ per generation ($\lambda = e^r = 1.492/\text{generation}$). If there are 10,000 moths now and the generation time is 10 days, how many moths will there be in 30 days?

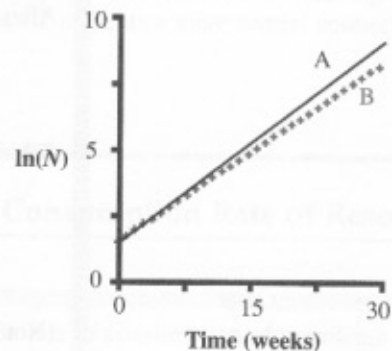


Figure 1.14

3. Another moth breeds only in the summer and survives the winter in the egg stage. A local population increased from 10,000 individuals to 12,000 individuals after one year. Predict the population size after two years, assuming that the per capita growth rate remains constant.

4. Mountain goats were introduced into the Olympic Peninsula in Washington state. The population increased from 12 individuals in 1929 to 1175 individuals in 1983 (Houston et al. 1994). Calculate r for this time frame, assuming a continuous and constant growth rate.

What is the doubling time of this population? Assuming that r remains constant in the future, in what year will the mountain goat population reach 10,000?

5. Mary is going to have an outdoor party in 15 days. She wants to have her backyard pond covered in water lilies before this party, so she goes to the nursery to buy some water lilies. Mary gives the clerk the

dimensions of her pool and the clerk, knowing the geometric growth rate of the water lilies that he stocks, calculates that if she purchases a single water lily, it will produce a population of $N = 10,000$ that will completely cover the surface of Mary's pool in 30 days. Mary reasons that if she buys two water lilies instead of one, she can meet her goal of having the pond surface covered in 15 days. Is anything wrong with her logic? If so, how many lilies will she need to buy to meet her goal?

in Birth and Death Rates

As you have seen in Chapter 1, populations have the capacity to grow exponentially as density is not taken into account. We think from experience, however, that natural populations are not starting to infinitely outpace growth as soon as the 10% interest suggested by exponential growth. Nature is more complicated than that. A population grows slower in some years than in others and in some places faster than in others. This irregular and spatial variation means that populations are seldom the idealized exponential case. In this chapter we will look at variation into two models for population growth. We explain these models with an eye toward testing if such variability can prevent explosions under biological, or simply delay them.

MOVEMENTS AND POPULATION GROWTH

Real populations occupy physical space and carry out their lives across this space. If we could measure the position of each individual—say through a high-resolution aerial view or GPS—we would have a snapshot of the population's distribution in that instant. If the population moved around a great deal, we could also depict the species' geographic range. Where individuals move more often over their lifetimes, the breadth of the geographic range may be larger, relatively speaking, even if it is smaller than that. There is one way to measure range: we can consider the smallest area where all individuals are reliably identified in terms of its ability to support population growth. That is, the species' efficiency to reproduce and recruit offspring. Imagine that we measure eight feet of that space with a few individuals of some kind growing in it, which the population also gains and so it grows by twice the individuals every 200 years. We call this area a *seed bank* because how quickly the population expands. To grow in the question we need to look up and for example we can see spread of a population where individuals only move, but do not die or get killed. Then we will approximate the first and last generation that give rise to a potential growth (from Chapter 1).

Random Walks and Diffusion

A strong place to think about the small-scale movement of individuals is through the random walk model. Figure 2.1 shows the lateral movement of individuals following that a walk in a plane (2D), in two dimensions. Each time period, an individual moves to one of the eight neighboring cells at random.

For most animals a random walk will probably be a poor approximation to how actual movements. Real animals will change their rate of movement over time, in different regions of space, or because of different opportunities that they have had. Importantly, real organisms certainly do not choose their direction to head just by chance alone. All these considerations produce deviations from a random walk model. Nevertheless, a random walk is a good starting place to explore the effect of the stochastic kinds of movement on population dynamics.