Chapter 4

Population Growth

Figure 4.1 Elephants reproduce slowly, but have the potential to generate large populations.

INTRODUCTION

The great 19th century biologist **Charles Darwin** developed an important ecological idea while reading a book on population growth by **Thomas Malthus** (*An Essay on the Principle of Population*, 1798). Although Malthus was an economist concerned about an expanding human population with a limited food supply, Darwin saw in Malthus' thesis a more general ecological principle. He realized that populations of all species have the potential to grow, and if that growth continues unchecked, competition for resources will eventually limit the size of every population in nature. Darwin documented the staggering growth rate of rapidly breeding organisms such as insects and weedy plants in his *Origin of Species* (1859), but he most effectively illustrated the universal impact of population growth with an example at the opposite end of the life history spectrum: the long-lived and slowly reproducing elephant. In Darwin's own words, "The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair" (*Origin of Species*, Ch. 3).

How did Darwin arrive at this amazing result? Let's try to duplicate his calculations. If an elephant begins breeding at age 30, then let's assume its generation length is close to 40 years of age. If a pair of elephants has an average family size of "three pair of young," then the population triples every generation. In other words, Darwin's elephants would have the capacity to triple their numbers in approximately 40 years. To keep our model simple, we will ignore post-reproductive survival and mortality, simply counting each new generation as it replaces the old. With these simplifying assumptions, let's look at the projected growth for Charles Darwin's hypothetical population of elephants:

Year	Population Size
0	2
40	6
80	18
120	54
160	162
200	486
240	1458
280	4374
320	13,122
360	39,366
400	118,098
440	354,294
480	1,062,882
520	3,188,646
560	9,565,938

Indeed, before year 600, Darwin's elephants have passed the nine million mark! Darwin probably used a more complex population model, keeping track of surviving adult elephants and overlapping elephant generations, but even in our oversimplified calculation, the conclusion is clear. Any population can overrun its environment if parents continue to produce more offspring than are needed to replace themselves.

Exponential Growth

Let's look at our calculations of elephant growth in the form of a graph (Figure 4.2). The x-axis shows time in years, with year 0 marking the beginning of our calculations. The y-axis shows population numbers, in millions. Although the rate of growth is a constant, tripling every 40 years, the consequences begin to show dramatically after generation 12. This kind of increase is called **exponential population growth,** and a standard plot of its numbers always produces this kind of J-shaped curve. Although we would need different time scales to graph population growth for fruit flies or dandelions, their exponential growth curves would follow a similar pattern. Darwin's prolific pachyderms provide a good general model for population growth any time resources are in abundant supply and surviving offspring outnumber their parents.

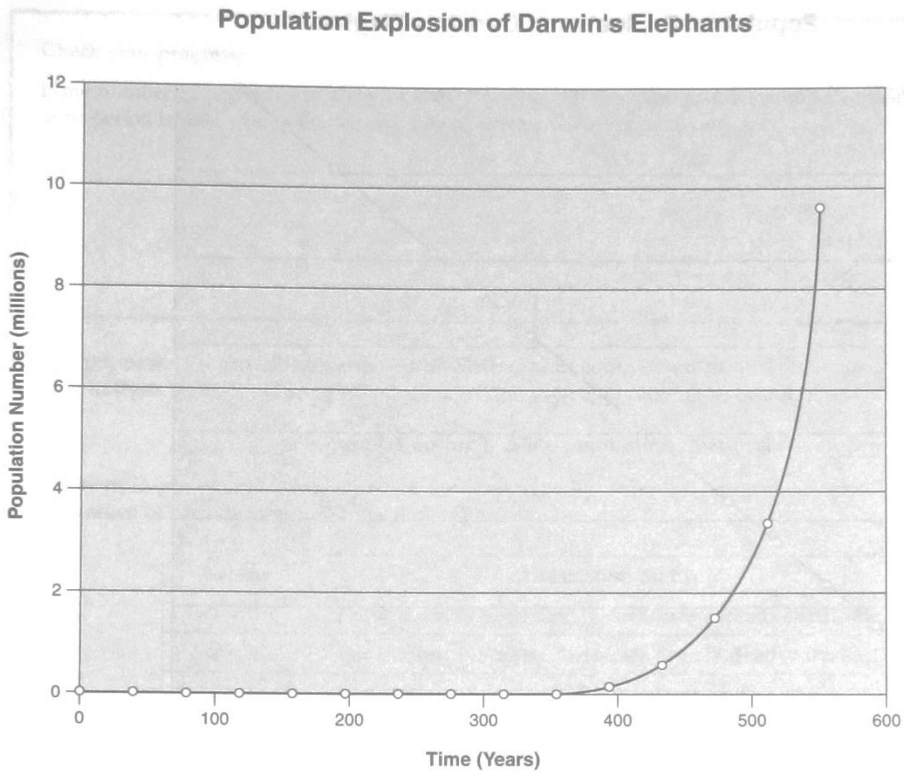

Figure 4.2 Projection of population size in Darwin's elephant example. The curve indicating population size bends upward in a J-shape, as is typical of exponential growth.

Why use the term *exponential growth?* Take a look at Figure 4.3. This graph shows exactly the same population growth numbers, and the x-axis is identical to Figure 4.2. You will notice, however, that the y-axis shows numbers in powers of ten (1, 10, 100, 1000, 10000, etc.). Another way of writing this series is to use *exponents* of ten. The y-axis would then show 10^0, 10^1, 10^2, 10^3, 10^4, and so on. These *exponents* increase at a constant rate on the population growth line in Figure 4.2, so we say this population demonstrates *exponential* growth. Another name for a variable exponent attached to a constant base (base 10 in this example) is a *logarithm*. For this reason, graphs in the form of Figure 4.3 are called ***logarithmic plots***. *Population ecologists find logarithmic graphs (or log plots for short) very handy, since they straighten out exponential curves, and display a broad range of data on a single axis.*

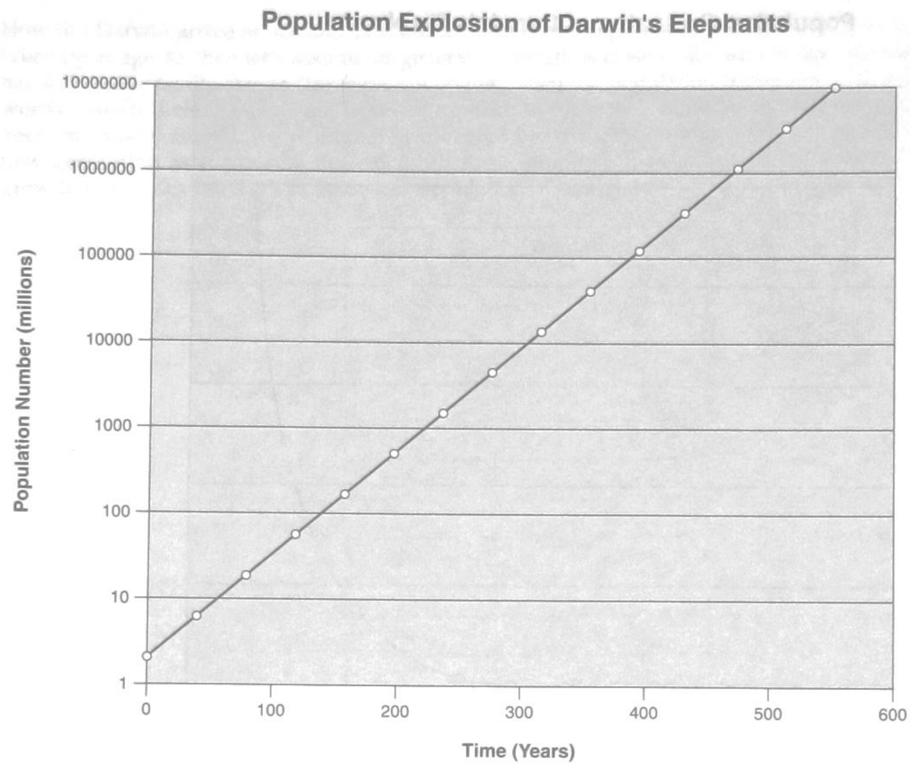

Figure 4.3 Logarithmic plot of Darwin's elephant example. Note that the y-axis shows numbers in a scale that increases by factors of ten. This changes the exponential growth curve to a straight line.

To describe the growth of an exponentially reproducing population accurately, we need a measure of its growth rate. The symbol used for this measure by ecologists is **r**, the **intrinsic rate of population increase**. One way to calculate r is to compare birth rates and death rates. The birth rate is simply the number of new individuals added to the population over a unit time period divided by the total population size. In the human population of a city, for example:

Birth rate = (newborns in the past year)/(total city population)

Similarly, the death rate is the number of deaths over a unit of time divided by the population size. For the city example:

Death rate = (deaths in the past year)/(total city population)

For humans, we chose a year as a convenient unit of time, but the appropriate time scale depends on the organism's life history. For fruit flies, we may want to calculate birth and death rate in days; for bacteria, the appropriate time scale may be minutes. Calculating r over a short time interval relative to the life of the organism is important, since r theoretically provides an instantaneous measure of the population's growth trajectory at a particular moment in its history.

Check your progress:

If the number of newborns in a city of 300,000 was 15,000 this year, and the number of deaths during the same period is 9000, what is the intrinsic rate of increase for the population?

Answer: $r = 0.02$

Since a population's growth depends on its birth rate in comparison to its death rate, we can define r for our city in these terms, assuming no net change due to people moving in or out of town:

r = population birth rate – population death rate

In exponential growth calculations, r is a constant, usually a small fraction near zero. The following table shows values of r for different biological situations:

r value	Population status
$r < 0$	**Population is declining. Death rate exceeds birth rate.**
$r = 0$	**Population is stable. Birth rate equals death rate.**
$r > 0$	**Population is growing. Birth rate exceeds death rate.**

Once you know the value of r, you can use a simple exponential equation to predict next year's population size:

Exponential Growth Equation (Discrete Form)

$$N_{t+1} = N_t + N_t(r)$$

N_{t+1} = population size at the next time interval
N_t = population size at the current time
r = intrinsic rate of population increase

To state this equation in words, we would say the population next year is equal to the population this year plus the new individuals added. The number of new individuals added equals the current population size times the intrinsic rate of growth. We will call this the "discrete form" of the equation, since it calculates growth in a series of discrete steps. To predict two years ahead, you must use the equation to generate N_1, and then plug that number in as the new value of N_t and repeat the calculation to get N_2. For a hundred years of growth, you would have to repeat the calculation 100 times!

Check your progress:

If $r = 0.02$ for a city, and the current population is 300,000, then what will the population be next year?

Answer: $N_{t+1} = 306{,}000$

The discrete form of the exponential growth equation can be repeated as many times as you wish to make long-range projections, but this is a cumbersome method, and it tends to magnify small errors as you repeat the calculations. A form of the exponential growth equation that provides continuous tracking of population growth over time is as follows:

Exponential Growth Equation (Continuous Form)

$$N_t = N_0\,(e^{rt})$$

N_t = population size at any time in question
N_0 = population size at the beginning
e = base of natural logarithms ≅ 2.718
r = intrinsic rate of population increase
t = time

To demonstrate the power of this formula, let's return to the city example. For a population of 300,000 with r = 0.02, what is the projected population size 10 years in the future?

$$\begin{aligned} N_{10} = N_0\,(e^{rt}) &= 300{,}000\ (2.718)^{.02\,(10)} \\ &= 300{,}000\ (2.718)^{.2} \\ &= 300{,}000\ (1.22) \\ &= 366{,}000 \end{aligned}$$

Note that the number of individuals added in ten years (66,000) is more than ten times the number added in one year (6000). Like compound interest, the number of babies born each year increases as the number of parents increases, so additions to the population accelerate over time to produce a J-shaped curve.

There is one more form of the exponential growth equation you will find useful. By taking the natural logarithm of both sides of the equation, we can convert the J-shaped curve to a straight line, just as we saw in the log 10 plot of elephant numbers in Figure 4.3.

$$\ln N_t = \ln N_0 + r\,t$$

ln means "natural log of"
N_t = population size at time t
N_0 = population size at the beginning
r = intrinsic rate of population increase
t = time

Note that *ln* N_0 is a constant, as is r. The equation is therefore in the form of a straight line, y = a + bx. Furthermore, r represents the slope of that line. To calculate r from population numbers over time, simply take the natural logarithm of all population size data, and plot time on the x-axis vs. *ln* (population size) on the y-axis. Then calculate the slope of that line, which you may recall is the change in y divided by the change in x. The slope of the resulting line is a good estimate of the intrinsic rate of increase, r. (See Figure 4.4.)

Check your progress:

Use the formula to predict the number of individuals in a city of 300,000 with r = 0.02 after 20 years of exponential growth.

Answer: N_{20} = 447, 529

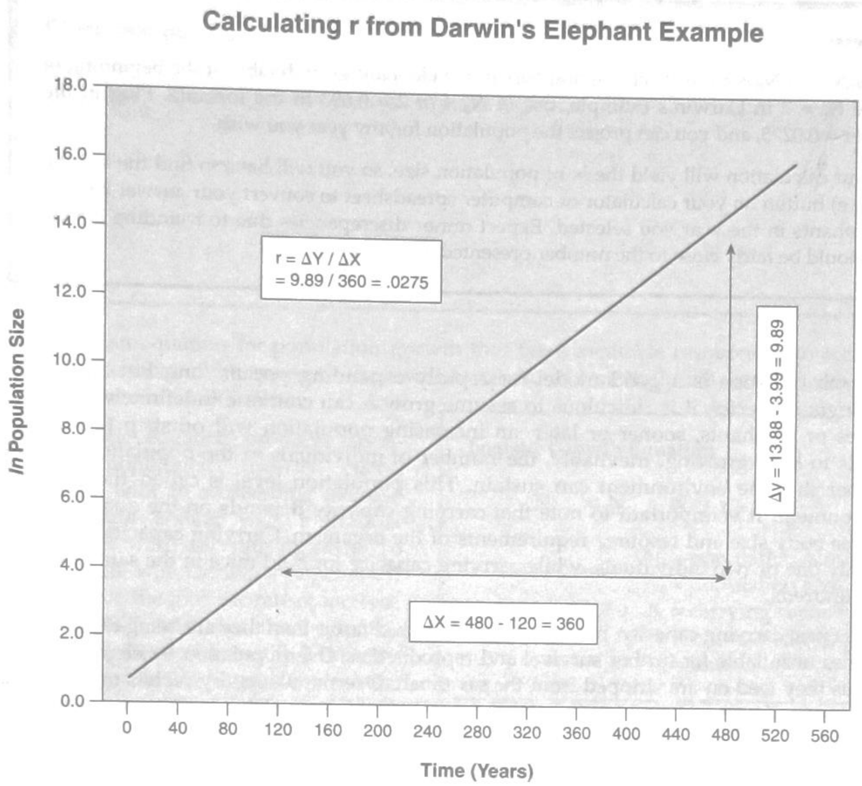

Figure 4.4 Calculating r from exponentially growing population numbers. If time in years is plotted against the natural log of population size, then r is the slope of the resulting straight line. To calculate the slope, pick two points on the line. Change in Y (denoted as Δ Y) is simply the difference between the *ln* population sizes of the two points. Change in X (denoted as Δ X) is the difference between the years designated by the two points. To calculate the slope, divide Δ Y/Δ X, as shown in the figure. For Darwin's elephants, r is approximately 0.0275.

You may choose any two points on the line to calculate the slope; let's choose two points near the beginning and end of the elephant growth calculations as follows:

	x value (year)	y value (*ln* population size)
Point 1	120	3.99
Point 2	480	13.88

To calculate the slope, $r = \Delta y / \Delta x$

$$= (y_2 - y_1)/(x_2 - x_1)$$

$$= (13.88 - 3.99)/(480 - 120) = 0.0275$$

Check your progress:

Use the formula $ln\ N_t = ln\ N_0 + r\ t$ to check the numbers in the elephant growth table at the beginning of this chapter. Since $N_0 = 2$ in Darwin's example, use $ln\ N_0 = ln\ 2 = 0.693$ in the formula. Plug in the calculated value of $r = 0.0275$, and you can project the population for any year you wish.

Remember that your calculation will yield the *ln* of population size, so you will have to find the inverse *ln* (or anti-log base e) button on your calculator or computer spreadsheet to convert your answer back to the number of elephants in the year you selected. Expect minor discrepancies due to rounding errors, but your answer should be fairly close to the number presented in the table.

Logistic Growth

The exponential growth equation is a good model for rapidly expanding populations, but as Darwin pointed out in the *Origin of Species*, it is ridiculous to assume growth can continue indefinitely. Whether made up of fruit flies or elephants, sooner or later, an increasing population will outstrip the natural resource base it needs to keep growing. Inevitably, the number of individuals in the population reaches the maximum number that the environment can sustain. This population level is called the **carrying capacity** of the environment. It is important to note that carrying capacity depends on the quality of the habitat, but also on the body size and resource requirements of the organism. Carrying capacity for elk in a meadow may be only one or two individuals, while carrying capacity for field mice in the same location may number in the hundreds.

If the population grows past carrying capacity, resources are being used faster than they are being regenerated, and the habitat becomes unsuitable for further survival and reproduction. Overpopulation by elephants may mean the woody plants they feed on are stripped from the savannah. Overpopulation by rabbits may mean a shortage of hiding places, and easy hunting for their predators. Overpopulation by oak trees may mean too much shade for seedlings to survive.

Some species tend to overshoot carrying capacity, and then crash to local extinction when they degrade their own habitat. These organisms tend to exhibit drastic fluctuations in population size, with "boom and bust" cycles throughout their range. Other species tend to slow their reproductive rate as they approach carrying capacity. Reproductive success in these organisms is **density-dependent**, that is, sensitive to the numbers of individuals per unit area. Population growth in these species is called **logistic growth**, because their rate of increase is adjusted as the population grows. As an example, many songbirds defend a territory large enough to rear a nest of young. If the population size grows too large, many birds fail to reproduce because all the nesting sites are taken. As a result, per-capita production of nestlings stabilizes as the population size approaches carrying capacity.

Ecologists use the symbol **K** to represent carrying capacity. If we can imagine a population occupying resource space in its habitat, then K represents the number of individuals that would completely fill that space. Recall that N represents the size of the population. The number of "empty spaces" in the environment could therefore be expressed as K – N. If we wanted to measure the *proportion* of habitat space still available for newcomers, we could divide empty spaces by total capacity, which would be:

$$\textbf{Proportion of habitat space available} = \frac{K - N}{K}$$

K = carrying capacity
N = population size

For example, if carrying capacity K = 100, and there are 80 animals in the population, then the proportion of the habitat still open for additions to the population would be (K – N)/K = 0.20, or 20%.

Check your progress:

If carrying capacity = 1500, and the population size is 600, what proportion of the resource base is still available?

Answer: 0.60 or 60%

To create an equation for population growth that takes available resources into account, we simply take the discrete form of the exponential growth equation, and multiply the growth term by our expression for available resources as follows:

Logistic Growth Equation

$$N_{t+1} = N_t + N_t \cdot r \cdot \frac{K - N_t}{K}$$

N_t = population size at time t
N_0 = population size at the beginning
K = carrying capacity
r = intrinsic rate of population increase
t = time

The Logistic equation produces an S-shaped population growth curve, beginning with an accelerating increase in size, and ending with a gradual approach toward carrying capacity. To demonstrate with Darwin's elephants, if we presume the intrinsic rate of increase is still 0.0275, and that the beginning number of elephants is still 2, but the population occupies a grassland biome that can support a carrying capacity of no more than 500,000 individuals, then Figure 4.5 illustrates the resulting logistic population growth reaching a plateau at about 600 years. Compare Figures 4.2 and 4.5 to see the difference between exponential and logistic growth.

Check your progress:

If carrying capacity = 500,000, the intrinsic rate of increase is 0.0275, and the population size is 350,000 in time t, what does the logistic model predict for time t+1?

Answer: N_{t+1} = 352,887.5

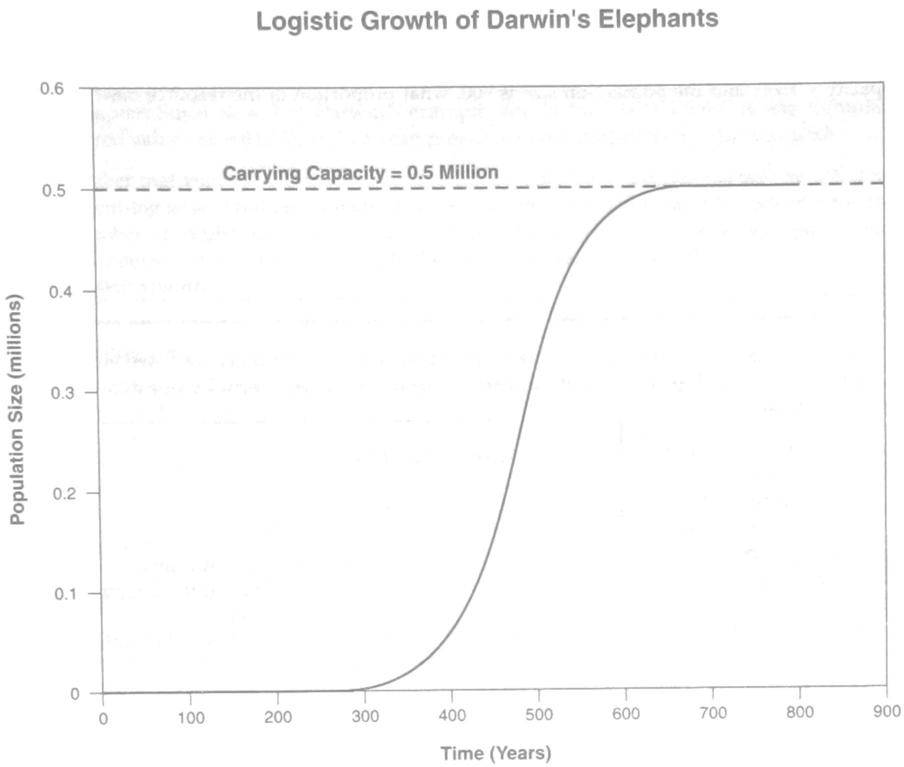

Figure 4.5 Logistic growth approaches carrying capacity as an S-shaped curve.

One final thought: in logistic growth models, K is treated as a constant. For general predictions of population behavior in relatively stable ecosystems, this is an appropriate assumption. We must realize, however, that carrying capacities in nature fluctuate with the weather, with changes in prey or predator numbers, and with many other kinds of environmental disturbance. Ecologists use growth models to understand basic patterns of population biology, but superimposed on these patterns we almost always see an overlay of random perturbation and continuous population adjustment. If a population fluctuates within definable limits, we say it is in **dynamic equilibrium**. The changing nature of carrying capacities does not negate the value of models such as the logistic growth equation, but variable upper limits to population size do need to be considered in applications to ecological problems such as wildlife management and biological pest control.

METHOD A: CALCULATING r FROM A PUBLISHED DATA SET

[Laboratory activity]

Research Question

How rapidly did populations of the Egyptian goose grow in the Netherlands?

Preparation

Students will need calculators with natural log functions or access to computers with spreadsheet software for this exercise. Extra graph paper may be useful for students attempting log plots.

Materials (per laboratory team)

Calculator or computer with spreadsheet software to calculate *ln* values

Ruler

Background

Figure 4.6 illustrates an Egyptian goose (*Alopochen aegyptiacus*), a species broadly distributed in Africa. Population biologist Rob Lensink documented exponential population growth of the Egyptian goose in the Netherlands in the years following its introduction to that country (Lensink, 1998). The following population numbers are cumulative census data from Lensink's observations along three rivers during the period 1985–1994. Each count included an entire winter's observations. For example, the population number for 1985 is the number observed during the winter of 1985–86.

Figure 4.6 Egyptian goose.

Year	Population Size
1985	259
1986	277
1987	501
1988	626
1989	897
1990	1324
1991	2475
1992	2955
1993	5849
1994	7259

Procedure

1. Enter the year and population size for each of the numbers above in the calculation page for *Method A.*
2. Calculate the log base e, also called *ln*, of each population number, and enter those data in the calculation page. This number is *ln* N.
3. Plot time in years (on the x-axis) vs. *ln* N (on the y-axis) on the graph following the calculation page.
4. Using a ruler, draw the best straight line you can through the points on the graph. If some points fall off the line, try to leave the same number of points above and below the line you draw.
5. Use the method explained in the Introduction to calculate the slope of the line. The slope is an estimate of r for Egyptian geese in the Netherlands during this period. Be sure to choose two points on your line for the calculations.
6. Use the population growth equation to project the numbers of geese in the winter of 2000, assuming continued exponential growth.

CALCULATIONS (METHOD A)

Year	Population Size	*ln* Population Size
1985	259	
1986	277	
1987	501	
1988	626	
1989	897	
1990	1324	
1991	2475	
1992	2955	
1993	5849	
1994	7259	

METHOD B: COMPARING EXPONENTIAL AND LOGISTIC GROWTH

[Computer activity]

Research Question

How do projections of the exponential and logistic growth models compare?

Preparation

Students will need a basic understanding of spreadsheet software such as Microsoft's Excel©. Corel's Quattro Pro© is also suitable, but the cell formulas in Quattro will require an opening parenthesis (rather than an equals sign =) as a first character. Graphing population data works best with the scatter-plot option in Excel.

Materials (per laboratory team)

One computer work station, equipped with spreadsheet software

Background

Wildlife biologists Anna Whitehouse and Anthony Hall-Martin studied growth of the elephant population of Addo National Elephant Park in South Africa over a 23-year time span. Hunting prior to 1950 had reduced elephants to low numbers, but the population recovered after Addo Park was established for their protection. The study generated the following population data (Whitehouse and Hall-Martin, 2000).

Year	Population Size
1976	94
1977	96
1978	96
1979	98
1980	103
1981	111
1982	113
1983	120
1984	128
1985	138
1986	142
1987	151

Year	Population size
1988	160
1989	170
1990	181
1991	189
1992	199
1993	205
1994	220
1995	232
1996	249
1997	261
1998	284

Procedure

1. Using a spreadsheet program, set up a spreadsheet, labeled as shown in the following table.
2. Use the first row as column labels, "Year" in A1, "Observed Number" in B1, "Exponential Model" in C1, and "Logistic Model" in D1 as shown.
3. In column A, enter years 1976 through 1998 in cells A2 through A24. Make sure you enter all of the 23 years of data in your spreadsheet.
4. In column C, enter the beginning population size of 94 in cell C2. This number is N_t in the exponential population growth equation. Likewise, enter the beginning population size of 94 in cell D2 to supply a starting population number for the Logistic growth model.

	A	B	C	D
1	Year	Observed Population Size	Exponential Model r = 0.0525	Logistic Model r = 0.0525 K = 500
2	1976	94	94	94
3	1977	96	= C2 + (C2*0.0525)	= D2 + (D2*0.0525*(500–D2)/500)
4	1978	96	copy previous cell	copy previous cell
5	1979	98	copy previous cell	copy previous cell
6	1980	103	copy previous cell	copy previous cell
7	1981	111	copy previous cell	copy previous cell
8	etc.	etc.	etc.	etc.

5. Type the equation **= C2 + (C2*0.0525)** in cell C3. This is the spreadsheet version of the discrete form of the exponential growth equation $\mathbf{N_{t+1} = N_t + N_t\,(r)}$ discussed in the Introduction. Compare the equation with the spreadsheet formula. We have already said that C2 is the number we have entered to represent $\mathbf{N_t}$. The number **0.0525** is an estimate of this elephant population's value for **r**, calculated from these data estimated from the slope of a log plot, as demonstrated in Method A. Note that we are using the population size in cell C2, which stands for $\mathbf{N_t}$, and placing the result in cell C3, which holds the value for $\mathbf{N_{t+1}}$.
6. Now COPY the spreadsheet formula in cell C3, and PASTE it in every cell from C4 to C24. By dragging to highlight the entire area before you select PASTE, you can do this in one step. You have now commanded the spreadsheet to make a series of annual calculations, computing the population size for each year from the previous year's population size, located just above it in column C.
7. Type the equation **= D2 + (D2*0.0525*(500 – D2)/500)** in cell D3. This is the spreadsheet version of the discrete form of the logistic growth equation $\mathbf{N_{t+1} = N_t + [\, N_t \cdot r \cdot (K - N)/K \,]}$ which was discussed in the Introduction. Note that the cell D2 holds the initial population size represented in the equation by $\mathbf{N_t}$. We have used 0.0525 as our value for the intrinsic rate of increase **r**, and 500 as our value for the carrying capacity **K**. Note that we are basing our calculation on the population number in cell D2, which holds the value for $\mathbf{N_t}$, and placing the result in cell D3, which holds the value for $\mathbf{N_{t+1}}$.
8. Now COPY the spreadsheet formula in cell D3, and PASTE it in every cell from D4 to D24. By dragging to highlight the entire area before you select PASTE, you can do this in one step. You have now commanded the spreadsheet to make a series of annual calculations, computing the population size for each year from the previous year's population size, located just above it in column D.
9. Use your spreadsheet software to produce a graph. The x-axis should show time in years, the y-axis population numbers. To simplify the y-axis labels, you can display population numbers in millions, or billions if you choose. You should be able to produce three lines on the graph: the actual population growth over time, an exponential curve, and a logistic curve. Which model best projects the actual growth of this population?
10. Copy and paste the formulas in columns C and D through C49 and D49 to predict the fate of the Addo elephant population 25 years into the future. Repeat the graphing procedure in step 9 to show the fate of the elephants in Addo Park, as described by these two models of population growth. Remember that in column D you presumed the carrying capacity of the park was 500. This carrying capacity figure is NOT based on data from Whitehouse and Hall-Martin, so you may try substituting other values for K, and recopying the formulas in column D to produce alternative logistic projections if you wish.
11. Print out your graph and spreadsheet to attach to the Questions for Method B.