8 | *LOGISTIC POPULATION MODELS*

Objectives

- Explore various aspects of logistic population growth models, such as per capita rates of birth and death, population growth rate, and carrying capacity.
- Understand the concepts of density dependence and density independence.
- Set up spreadsheet models and graphs of logistic population growth.
- Compare the model to real populations.

Suggested Preliminary Exercise: Geometric and Exponential Population Models

INTRODUCTION

This exercise builds on the models developed in Exercise 7, "Geometric and Exponential Population Models." If you have not already done that exercise, you should do it first, or at least read its introduction.

As in the earlier exercise, we begin with a model of population dynamics in discrete time, with explicit parameters for per capita rates of birth and death. We choose the discrete-time model as the starting point for several reasons:

- It emphasizes the roles of per capita birth and death rates (b and d) rather than the more abstract quantities r (or R) and K (explained later).
- It allows you to manipulate, directly and separately, per capita birth and death rates and density-dependent rates of change in per capita birth and death rates. You will discover that none of these alone, but rather the relationship between them, determines logistic population growth and whether the population eventually stabilizes.
- It allows you to discover that for a population to stabilize, per capita birth and death rates must change as the population grows, and they must become equal at some equilibrium population size.
- It drives home, in ways that algebraically simpler models cannot, the meaning of density dependence: change in per capita birth and death rates in response to change in population size.

The logistic model with explicit birth and death rates, presented first here, lies at the heart of this particular exercise. For the sake of compatibility with a variety of textbooks, and to provide background for other exercises in this book, we present two other logistic models: a more commonly encountered discrete-time version incorporating carrying capacity (*K*), and a continuous-time version. We see no need to build all three versions; which one you do will depend on your instructor's aims. To instructors, we strongly suggest that the first version, with explicit per capita birth and death rates, is the best learning tool, for the reasons given above. In our experience, students have no difficulty switching to the *R-K* version for later exercises.

Model Development: Logistic Model with Explicit Birth and Death Rates

In Exercise 7, we developed the following geometric model of population dynamics:

$$N_{t+1} = N_t + bN_t - dN_t \qquad \text{Equation 1}$$

where

N_t = population size at time *t*
N_{t+1} = population size one time unit later
b = per capita birth rate
d = per capita death rate

As you discovered in the earlier exercise, this model produces geometric population growth (the discrete-time analog of exponential growth) if *b* and *d* are held constant and $b > d$. However, the assumption that per capita rates of birth and death remain constant is unrealistic, so in this exercise you will develop a model in which these rates change.

Birth and death rates may change for many reasons, such as changes in climate conditions, food supply, or populations of natural enemies (competitors, predators, parasites, and pathogens). To keep our model manageable, in this exercise we will consider only one cause of changes in per capita birth and death rates: the size of the population itself. In other words, we will assume that environmental conditions, food supply, and so on remain constant; only the size of the population itself changes. Because per capita rates of birth and death *do* change in response to population size or density, logistic models are **density-dependent**, in contrast to geometric and exponential models, which are density-independent. As the population grows, less food and water, fewer nesting and hiding sites, and fewer resources in general are available to each individual, affecting both an individual's rate of reproduction and its risk of death. Our model will thus include **intraspecific competition** (competition among members of the same species) for resources.

We now add two new terms to our model to represent changes in per capita rates of birth and death:

b' = the amount by which the per capita birth rate changes in response to the addition of one individual to the population
d' = the amount by which the per capita death rate changes in response to the addition of one individual to the population

We can now add these terms to our geometric model to produce a discrete-time logistic model:

$$N_{t+1} = N_t + (b + b'N_t)N_t - (d + d'N_t)N_t \qquad \text{Equation 2}$$

This model replaces the simple per capita birth rate *b* with the more complex expression $(b + b'N_t)$, and it replaces *d* with $(d + d'N_t)$. The symbols *b* and *d* now represent per capita rates of birth and death when the population is very small. The terms $(b + b'N_t)N_t$ and $(d + d'N_t)N_t$ represent total births and total deaths, respectively. Thus, our model still represents the fundamental insight that

$$N_{t+1} = N_t + \text{Births} - \text{Deaths} \qquad \text{Equation 3}$$

Most textbooks that use this model use a slightly different form, in which the birth term is written $(b - b'N_t)N_t$, because per capita birth rate normally decreases as population size increases. We prefer to add $b'N_t$ rather than subtract it, because our way forces you to use a negative number for b', reinforcing the idea of decreasing per capita births. It also allows you to experiment with the model to see what happens if per capita birth rate *increases* with population size.

All four parameters (b, b' d, and d') are assumed to remain constant, as you can tell from the absence of time subscripts. Let's try to visualize what happens to per capita rates of birth and death as the population grows according to this model. When the population is small, there are plenty of resources for each individual, so per capita birth rate should be high, per capita death rate should be low, and the population will grow larger. As new individuals are added, available resources will be divided among more individuals, and each individual will get less. We would expect per capita birth rate to decline (so b' should be less than zero) in proportion to the number of individuals in the population (so we multiply b' by N_t). We would also expect per capita death rate to increase (so d' should be greater than zero), also in proportion to population size (so we multiply d' by N_t as well).

As simple as it is, this model has proven useful in several contexts. Many populations grow as predicted by this model, and (in the form of Equation 7, below) it was one of the origins of chaos theory. Logistic models are used in studying interspecific as well as intraspecific competition and predator-prey relationships. These models also inform practical decisions in the management of fisheries and game animal populations and are used to predict the growth of the human population.

The rate of population growth is not easy to visualize from this equation, so you will explore its behavior using the spreadsheet. However, we can see informally that when the population is very small, it will grow almost geometrically (exponentially), because the parameters b' and d' are multiplied by a small number (N_t is small), and thus the model reduces (almost) to a geometric model. As the population grows larger, however, the influence of b' and d' increases, and population growth slows. What will be the endpoint of this slowing rate of growth? Will the population stabilize, will it continue to grow at an ever-decreasing rate, or will it decrease in size?

We can show formally that there is an **equilibrium population size** in this model. In other words, appropriate values of b, d, b', and d' will produce a model population that grows until it reaches a stable size. To prove that such an equilibrium exists, we try a commonly used tactic: We will *assume* that the equilibrium population size exists, and try to calculate its value. If the equilibrium does not exist, this procedure will lead us to a logical contradiction. If the equilibrium exists, we will find its value.

Let us begin with Equation 2:

$$N_{t+1} = N_t + (b + b'N_t)N_t - (d + d'N_t)N_t$$

Assume that an equilibrium population size exists, and call it N_{eq}. If N_{eq} exists, then plugging it into Equation 2 in place of N_t should produce no change in population size. Therefore N_{t+1} will also equal N_{eq}. If we substitute N_{eq} for N_t and N_{t+1}, we get

$$N_{eq} = N_{eq} + (b + b'N_{eq})N_{eq} - (d + d' N_{eq})N_{eq}$$

Subtracting N_{eq} from both sides gives us

$$0 = (b + b'N_{eq})N_{eq} - (d + d' N_{eq})N_{eq}$$

Adding $(d + d' N_{eq})N_{eq}$ to both sides, we get

$$(d + d' N_{eq})N_{eq} = (b + b'N_{eq})N_{eq}$$

In words, the population is at equilibrium when *total* deaths equal *total* births (compare to Equation 3 above). This seems a sensible result. Let us continue by dividing both sides by N_{eq}, to get

$$d + d'N_{eq} = b + b'N_{eq}$$

This tells us that the population is at equilibrium when *per capita* rates of birth and death are equal, which also makes sense.

Subtracting d and $b'N_{eq}$ from both sides gives us

$$d'N_{eq} - b'N_{eq} = b - d$$

Factoring N_{eq} out of the left-hand side produces

$$(d' - b')N_{eq} = b - d$$

and dividing both sides by $(d' - b')$ gives us

$$N_{eq} = \frac{b - d}{d' - b'} \qquad \text{Equation 4}$$

Note that the numerator on the right-hand side of Equation 4 is the geometric growth factor *R*, as defined in Exercise 7, "Geometric and Exponential Population Growth."

Equation 4 gives us our equilibrium population size. The derivation shows that values of b, d, b', and d' exist that will produce a stable population. Be aware, however, that it does not show that *any* values of these parameters will do so—that is, there also may exist values of these parameters that will produce population growth that does *not* reach equilibrium. It also shows that the equilibrium population depends on all four parameters, in the particular way shown in Equation 4.

Logistic Model with Explicit Carrying Capacity

Because the equilibrium defined in Equation 4 is so important in population biology, it is given its own name—the **carrying capacity**. The carrying capacity is defined as the largest population that can be supported indefinitely, given the resources available in the environment. Most logistic models presented in textbooks represent this carrying capacity with its own parameter, *K*, and build it into the model explicitly. We develop this model below.

Most textbooks present logistic population growth in terms of a differential equation in continuous time:

$$\frac{dN}{dt} = rN\left(\frac{K - N}{K}\right) \qquad \text{Equation 5}$$

The discrete-time analog of this equation is

$$\Delta N_t = RN_t\left(\frac{K - N_t}{K}\right) \qquad \text{Equation 6}$$

In Equation 6, ΔN_t represents the difference between the population size at time $t + 1$ and at time t. We can therefore write $\Delta N_t = N_{t+1} - N_t$ and substitute that into Equation 6. This gives us

$$N_{t+1} - N_t = RN_t\left(\frac{K - N_t}{K}\right)$$

Adding N_t to both sides gives us our discrete-time model of logistic population growth; we get

$$N_{t+1} = N_t + RN_t\left(\frac{K - N_t}{K}\right) \qquad \text{Equation 7}$$

Because this model has fewer parameters, it is more convenient to use in studying interspecific competition, predator-prey relationships, and harvesting populations.

The behavior of Equation 7 is not difficult to visualize. If we begin with a very small population, the term $(K - N_t)/K$ is very nearly equal to K/K, or 1. The model will then behave like a geometric model, and the population will grow, provided $R > 1$. The population will grow slowly at first, because the parameter R is also being multiplied by a number (N_t) that is nearly equal to zero, but it will grow faster and faster, at least for a while. At some point, however, population growth will begin to slow because the term $(K - N_t)/K$ is getting smaller and smaller as N_t gets larger and closer to K.

At the other extreme, imagine a population that starts out at a size very close to its carrying capacity, K. The term $(K - N_t)/K$ becomes nearly equal to zero, and population growth is extremely slow. When $N_t = K$, the population stops growing altogether.

The actual dynamics of this model can be much more complex, as you will see when you build the spreadsheet model and play around with its parameters. With some values of b, d, b', and d', or of R and K, the population can temporarily overshoot its carrying capacity, oscillate around it, or become chaotic.

The two discrete-time models (expressed in Equations 2 and 7) are mathematically equivalent. This is not obvious from the equations, and the proof is not directly relevant to our modeling concerns, but if you're curious you can read the proof at the end of the exercise (pp. 121–122).

Continuous-Time Logistic Model

As we said above, most textbooks begin with the model given by Equation 5:

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

As stated, this tells you only the rate of change in population size, not the population size at any time t. To derive the equation for population size requires the calculus, so we will simply give the result (Roughgarden 1998):

$$N_t = \frac{K}{1 + \left[(K - N_0)/N_0\right]e^{-rt}} \qquad \text{Equation 8}$$

This model behaves as described for the discrete-time version. An important difference, however, is that the continuous-time model always grows smoothly to its carrying capacity and stabilizes there. The discrete-time model can display more interesting behavior.

PROCEDURES

Your instructor may assign all of the following three parts, or only one or two. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATIONS
Part 1. Discrete-Time Logistic Model with Explicit Birth and Death Rates *A. Set up the spreadsheet.* 1. Open a new spreadsheet and set up titles and column headings as shown in Figure 1.	 Enter only the text items for now. These are all literals, so just select the appropriate cells and type them in.

	A	B	C	D	E	F	G	H	I	J	K
1	Logistic Model of Population Growth										
2	Includes explicit terms for per capita rates of birth and death, and for changes in these rates										
3					Variables						
4			Per capita	Total	Per capita	Total				Constants	
5	Time (t)	N_t	birth rate	births	death rate	deaths	ΔN_t	$(\Delta N_t)/N_t$	b	d	R
6	0								1.2500	0.50	0.75
7	1								b'	d'	K
8	2								-0.010	0.005	50.00
9	3										
10	4										

Figure 1

2. Set up a linear time series from 0 to 20 in column A.

In cell A6, enter the number **0**.
In cell A7, enter the formula **=A6+1**.
Copy cell A7.
Select cells A8–A26. Paste.

3. Enter the values shown in Figure 1 for per capita birth and death rates, b and d, and per capita rates of change in b and d, b' and d'.

Be sure to enter a negative number for b'. This indicates that per capita birth rate *decreases* as each new member is added to the population. A positive value of d' indicates that per capita death rate *increases* as each new member is added to the population.

4. Enter formulae to calculate R and K.

In cell K6, enter the formula **=I6-J6**. Remember, by definition, $R = b - d$.
In cell K8, enter the formula **=(I6-J6)/(J8-I8)**. This is the spreadsheet version of Equation 4 in the Introduction. It represents the largest population that can be sustained indefinitely on the resources available.

5. Enter an initial population size of 1.00.

In cell B6, enter the value 1.00.

6. Enter formulae for per capita birth and death rates (b and d).

In cell C6, enter the formula **=$I$6+$I$8*B6**.
In cell E6, enter the formula **=$J$6+$J$8*B6**.
These formulae correspond to the per capita birth and death rates, $(b + b'N_1)$ and $(d + d'N_1)N_1$, in Equation 2.
We calculate per capita births and deaths explicitly because it is important to understand how these rates respond to changes in population size. You will graph these quantities later in the exercise.

7. Enter formulae for total births and total deaths.

In cell D6, enter the formula **=C6*B6**.
In cell F6, enter the formula **=E6*B6**.
These formulae correspond to the total births, $(b + b'N_t)N_t$, and total deaths, $(d + d'N_t)N_t$, in Equation 2. We calculate total births and deaths as an intermediate step in calculating N_{t+1} (see next step).

8. Enter a formula to calculate the size of the population at time 1.

In cell B7, enter the formula **=B6+D6-F6**.
This corresponds to Equation 3, $N_{t+1} = N_t +$ Births $-$ Deaths.

9. Copy the formulae in cells C6–F6 into cells C7–F7.

See "Spreadsheet Hints and Tips" for instructions on copying and pasting.

10. Copy the formulae from cells B7–F7 into cells B8–F26.

11. Enter a formula for ΔN_t.

In cell G6, enter the formula **=B7-B6**.
Note that we calculate ΔN_t over the coming time interval, as we did in Exercise 7, "Geometric and Exponential Population Models."

12. Enter a formula for $\Delta N_t / N_t$.

In cell H6, enter the formula **=G6/B6**.
This is the *per capita* rate of change in population size over the interval from time 0 to time 1. Like ΔN_t, it is calculated over the coming time interval.

13. Copy the formulae in cells G6 and H6 into cells G7–H25.

Note that we do *not* paste these formulae into cells G26 and H26. This is because ΔN_t and $\Delta N_t / N_t$ are calculated over the coming time interval, and would therefore be undefined for the last population size calculated (cell B26).

B. Create graphs.

1. Graph N_t against time, and edit your graph for readability.

Select cells A5–B26. Note that you should include column headings in your selection, so that the legend will be labeled properly.

Click on the Chart Wizard or open Insert | Chart. Details of the steps involved are given in "Spreadsheet Hints and Tips" and in Exercise 2, "Mathematical Functions and Graphs." Follow the prompts in the dialog boxes to set up an XY chart (Scatter graph) with time on the *x*-axis. Do not use a line chart.
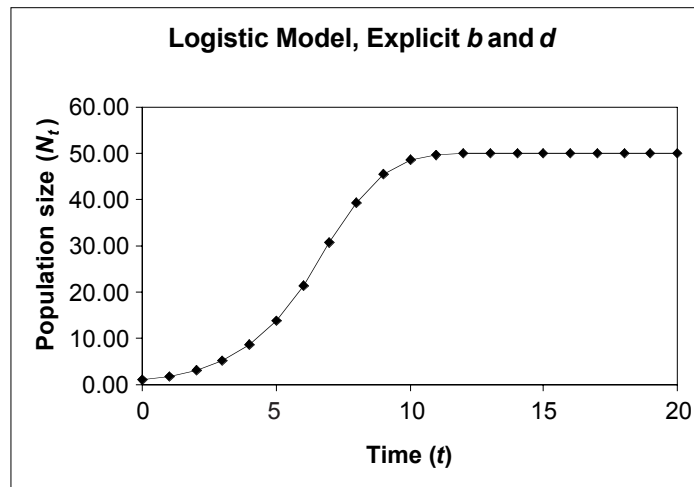
Your graph should resemble Figure 2.

Figure 2

2. Graph per capita birth and death rates against N_t, and edit your graph for readability.

Note that you are *not* graphing against time. Select cells B5–C26.
Hold down the <Control> or ⌘ key and select cells E5–E26.
Make an XY chart (Scatter graph) (see previous step).
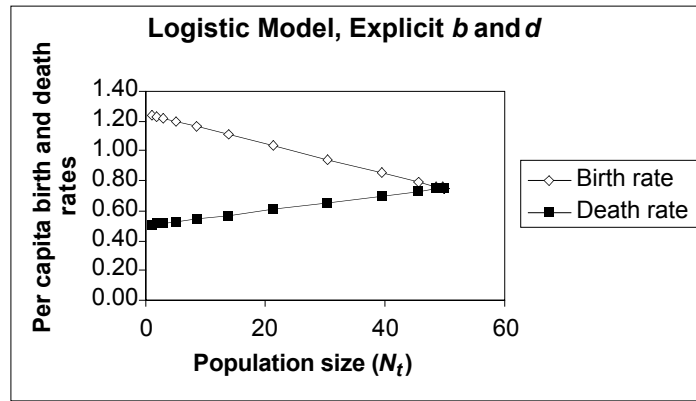
Your graph should resemble Figure 3.

Figure 3

3. Graph ΔN_t and $\Delta N_t/N_t$ against N_t.

Select cells B5–B25. Note that you should *not* include cell B26 in your selection.
Hold down the <Control> or key and select cells G5–H25.
Make an XY chart, per the previous step.
Because the ranges of values taken by ΔN_t is so much larger than the range of $\Delta N_t/N_t$, the latter gets squashed down against the *x*-axis. You will fix this in the next step.

4. Graph ΔN_t on a second *y*-axis of the same graph.

Select the curve for ΔN_t in your graph by double-clicking on the line or on one of the data points.
In the dialog box that pops up, select the Axis tab, and then click the button for Secondary axis, as shown in Figure 4. Click on the OK button.
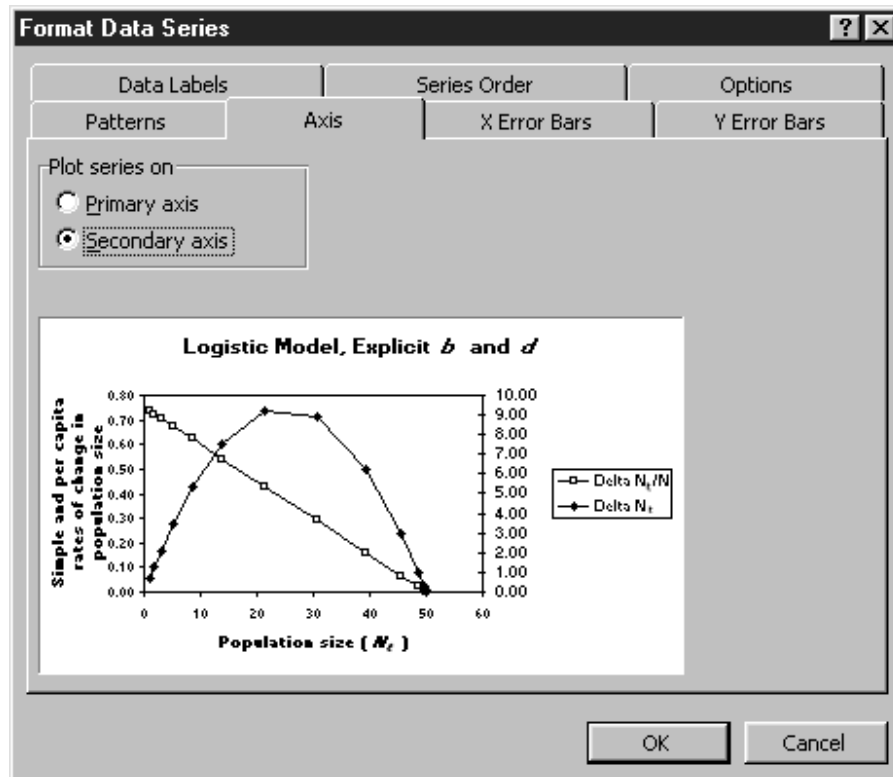

Figure 4

5. Edit your graph for readability.

Set the minimum of the left-hand *y*-axis to zero: Double-click on the left-hand *y*-axis. In the dialog box that pops up, click the tab for Scale, and enter the value 0 in the Minimum box. This will make no difference now, but it will prevent graphing errors later in the exercise.
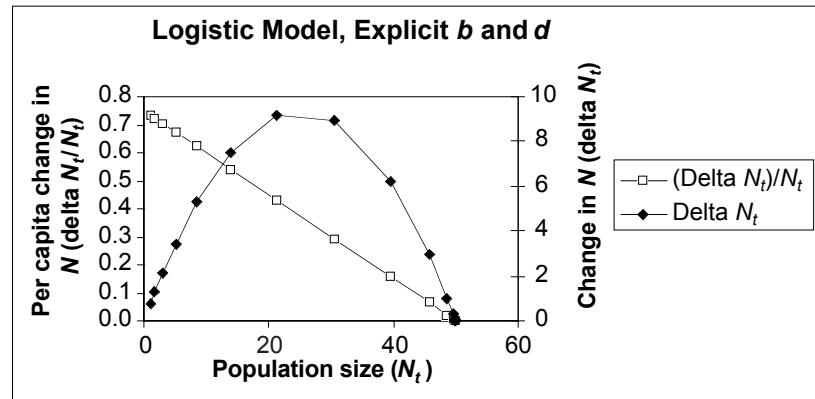

Figure 5

Your graph should resemble Figure 5. To label the right-hand *y*-axis, select the whole chart by clicking once inside it. Then open Chart|Chart Options|Titles. Enter the label for the right-hand *y*-axis in the text box for Second value (Y) axis.

Part 2. Discrete-Time Logistic Model with Explicit Carrying Capacity

C. Set up the spreadsheet.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 6.

	A	B	C	D	E	F	G
1	Logistic Model of Population Growth						
2	Assumes density-dependent changing per capita rates of birth and death.						
3							
4			Variables		Constants		
5	Time (*t*)	N_t	ΔN_t	(ΔN_t)/N_t	*R*	*K*	
6	0				0.75	50.00	
7	1						
8	2						
9	3						

Figure 6

Enter only the text items for now. These are all literals, so just select the appropriate cells and type them in.

2. Set up a linear time series from 0 to 20 in column A.

In cell A6, enter the value 0.
In cell A7, enter the formula **=A6+1**.
Copy the formula in cell A7 into cells A8–A26.

3. Enter the values shown for initial population size, R, and K.

In cell B6, enter the value 1.00.
In cell E6, enter the value 0.75.
In cell F6, enter the value 50.

4. Enter a formula to calculate the size of the population at time 1.

In cell B7, enter the formula **=B6+$E$6*B6*($F$6-B6)/$F$6**.
This corresponds to the right-hand side of Equation 7:

$$N_t + RN_t\left(\frac{K - N_t}{K}\right)$$

5. Extend the population-size calculation down its column.

Copy the formula in cell B7 into cells B8–B26.

6. Enter formulae to calculate ΔN_t and $\Delta N_t/N_t$, and copy them down their columns.

In cell C6, enter the formula **= B7-B6**. In cell D6, enter the formula **=C6/B6**.
Note that we calculate ΔN_t and $\Delta N_t/N_t$ over the coming time interval, as we did "Geometric and Exponential Population Models."
Copy the formulae in cells C6 and D6 into cells C7–D25.
Do not copy these formulae into cells C26 and D26, because they would be undefined for the last population size calculated.

D. Create graphs.

1. Select cells A5–B26. Create an XY graph. Your graph should resemble Figure 7.

1. Graph N_t against time and edit your graph for readability.

Logistic Model, Explicit *R* and *K*

(graph: Population size (N_t) vs Time (t))

Figure 7

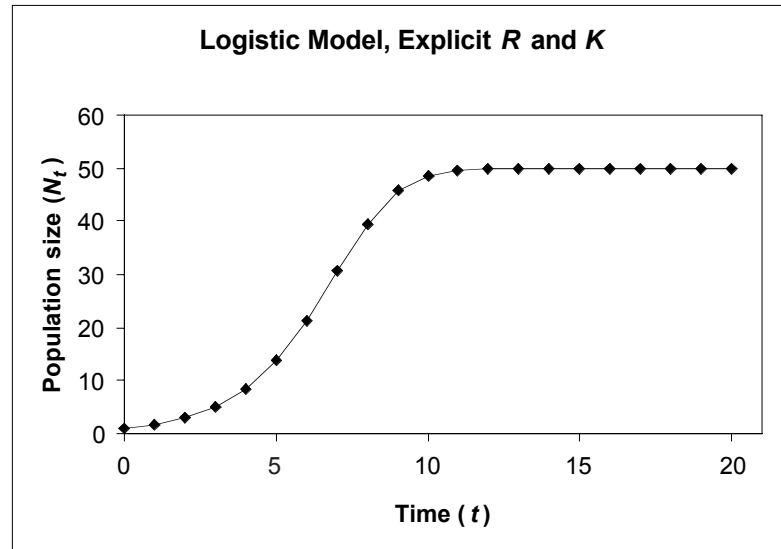2. Graph ΔN_t and $\Delta N_t/N_t$ against N_t.

Select cells B5–D25 and make an XY graph.
Because the range of values taken by ΔN_t is so much larger than the range of $\Delta N_t/N_t$, the latter gets squashed down against the *x*-axis. You will fix this in the next step.

3. Graph ΔN_t on a second *y*-axis of the same graph.

Select the curve for ΔN_t in your graph, by double-clicking on the line or on one of the data points.
In the dialog box that pops up, select the Axis tab, and then click the button for Secondary axis (see Figure 4). Click on the OK button.

4. Edit your graph for readability.

Set the minimum of the left-hand *y*-axis to zero. Double-click on the left-hand *y*-axis. In the dialog box that pops up, click the tab for Scale, and enter the value 0 in the Minimum box. This will make no difference now, but it will prevent graphing errors later in the exercise. Your graph should resemble Figure 8.
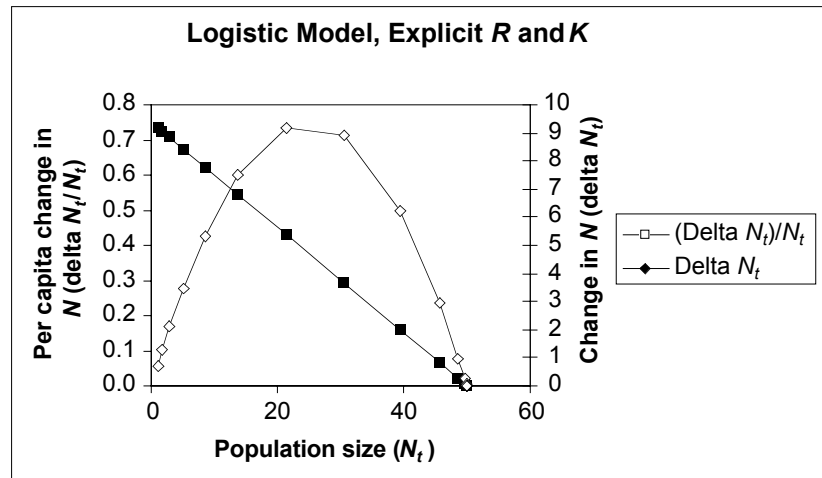

Figure 8

To label the right-hand *y*-axis, select the whole chart by clicking once inside it. Then open Chart|Chart Options|Titles. Enter the label for the right-hand *y*-axis in the text box for Second value (Y) axis.

Part 3. Continuous-Time Logistic Model

E. Set up the spread-sheet.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 9.

Enter only the text items for now. These are all literals, so just select the appropriate cells and type them in. Note that we use the differential notation dN/dt and $(dN/dt)/N$ instead of the difference notation ΔN_t and $\Delta N_t/N_t$, and r in place of R.

	A	B	C	D	E	F
1	Logistic Model of Population Growth					
2	Continuous-time version					
3						
4			Variables		Constants	
5	Time (t)	N_t	dN/dt	$(dN/dt)/N$	r	K
6	0				0.75	50.00
7	1					
8	2					
9	3					

Figure 9

2. Set up a linear time series from 0 to 20 in column A.

In cell A6, enter the value 0.
In cell A7, enter the formula **=A6+1**.
Copy the formula in cell A7 into cells A8–A26.

3. Enter the values shown for initial population size, *r*, and *K*.

In cell B6, enter the value 1.00.
In cell E6, enter the value 0.5. Note the use of lowercase *r*, to distinguish the continuous-time model from the discrete-time version.
In cell F6, enter the value 50.

4. Enter a formula to calculate the size of the population at time 1.

In cell B7, enter the formula **=$F$6/(1+(($F$6-$B$6)/$B$6)*EXP(-1*$E$6*A7))**.
This corresponds to Equation 8:

$$N_t = \frac{K}{1+\left[(K-N_0)/N_0\right]e^{-rt}}$$

5. Extend the population-size calculation down its column.

Copy the formula in cell B7 into cells B8–B26.

6. Enter formulae to calculate *dN/dt* and (*dN/dt*)/*N* and copy them down their columns. (Hint: Refer to Equation 5.)

In cell C6, enter the formula **=$E$6*B6*($F$6-B6)/$F$6**.
This corresponds to Equation 5:

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

In cell D6, enter the formula **=C6/B6**.
Copy the formulae in cells C6 and D6 into cells C7–D26. In this case, we *do* copy these formulae into cells C26 and D26, because we are calculating them instantaneously from the current N_t. This is an important difference between this model and the two previous discrete-time logistic models. If we had used the same difference method to calculate these rates of change as we used before, we would get different values.

F. *Create graphs.*

1. Graph N_t against time and edit your graph for readability.

Select cells A5–B26. Make an XY graph and edit for readability. Your graph should resemble Figure 10.

Figure 10

2. Graph *dN/dt* and (*dN/dt*)/*N* against N_t.

Select cells B5–D26 and make an XY graph.
Because the ranges of values taken by *dN/dt* is so much larger than the range of (*dN/dt*)/*N*, the latter gets squashed down against the *x*-axis. You will fix this in the next step.

3. Graph *dN/dt* on a second *y*-axis of the same graph.

Select the curve for *dN/dt* in your graph by double-clicking on the line or on one of the data points.
In the dialog box that pops up, select the Axis tab, and then click the button for Secondary axis (see Figure 4). Then click on the OK button.

4. Edit your graph for readability.

Set the minimum of the left-hand *y*-axis to zero. Double-click on the left-hand *y*-axis. In the dialog box that pops up, click the tab for Scale, and enter the value 0 in the Minimum box. Your graph should resemble Figure 11.

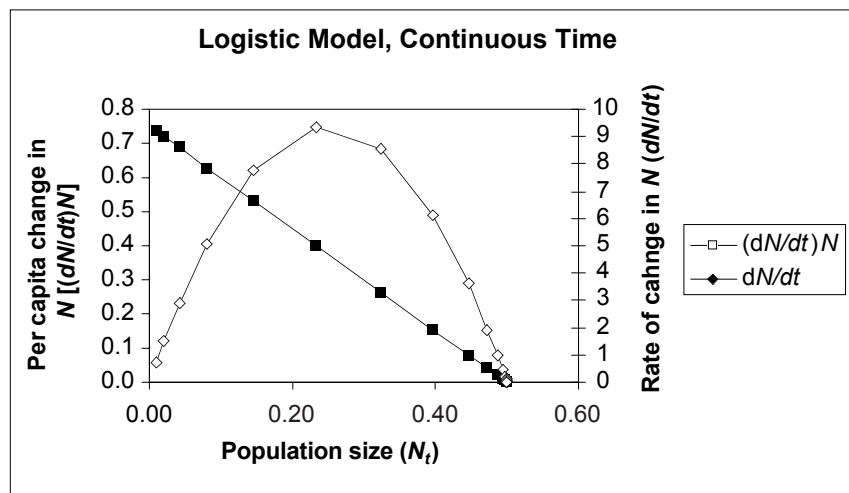This will make no difference now but will prevent graphing errors later in the exercise.

Logistic Model, Continuous Time

Figure 11

To label the right-hand *y*-axis, select the whole chart by clicking once inside it. Then open Chart|Chart Options|Titles. Enter the label for the right-hand *y*-axis in the text box for Second value (Y) axis.

Proof That the Two Discrete-Time Models Are Equivalent

The following proof* demonstrates that the two discrete-time models (Equation 2 and Equation 7) are in fact equivalent. Begin with Equation 7:

$$N_{t+1} = N_t + RN_t\left(\frac{K - N_t}{K}\right)$$

Equation 7

Rewrite the term in parentheses:

$$N_{t+1} = N_t + RN_t\left(\frac{K}{K} - \frac{N_t}{K}\right)$$

Because $K/K = 1$, we can write

$$N_{t+1} = N_t + RN_t\left(1 - \frac{N_t}{K}\right)$$

We showed early in the exercise that $K = (b-d)/d' - b')$, so we can substitute

$$N_{t+1} = N_t + RN_t \left(1 - \frac{N_t}{\left(\frac{b-d}{d'-b'} \right)} \right)$$

Rearranging gives us

$$N_{t+1} = N_t + RN_t \left(1 - \frac{(d'-b')N_t}{b-d} \right)$$

Because $R = b - d$ by definition, we can substitute

$$N_{t+1} = N_t + (b-d)N_t \left(1 - \frac{(d'-b')N_t}{b-d} \right)$$

and carry out the multiplication across the parentheses:

$$N_{t+1} = N_t + (b-d)N_t - \frac{(b-d)(d'-b')N_t^2}{(b-d)}$$

Canceling terms gives us

$$N_{t+1} = N_t + (b-d)N_t - (d'-b')N_t^2$$

Factoring out N_t, we get

$$N_{t+1} = N_t + N_t[(b-d) - (d'-b')N_t]$$

Carrying out the multiplication inside the square brackets, we get

$$N_{t+1} = N_t + N_t[b - d - d'N_t + b'N_t]$$

Rearranging terms gives us

$$N_{t+1} = N_t + N_t[(b + b'N_t) - (d + d'N_t)]$$

Multiplying through by N_t gives us Equation 2:

$$N_{t+1} = N_t + (b + b'N_t)N_t - (d + d'N_t)N_t \qquad \text{Equation 2}$$

Unfortunately, the graph does not indicate which axis relates to which curve. You must look at the values in the spreadsheet to see that the left-hand y-axis relates to $dN/dt/N$ because that ratio takes values from 0.74 to 0 (see column D). Likewise, the right-hand axis relates to dN/dt because that difference takes values from 9.33 to 0 (see column C).

QUESTIONS

1. How does the behavior of the logistic model differ from that of the geometric and exponential models in the previous exercise?

2. Why does the population stabilize at the carrying capacity?

3. How do ΔN_t and $\Delta N_t / N_t$, or dN/dt and $(dN/dt)/N$, change as the population grows? How does the behavior of these quantities differ from the geometric and exponential models?

4. What is the y-intercept of the $\Delta N_t / N_t$ line in the graph of $\Delta N_t / N_t$ against N_t? What is the x-intercept? If you used the continuous-time version, ask the same questions about the $(dN/dt)/N$ line. Answering this question will lead you to a powerful tool for analyzing real populations for density-dependence, and for estimating R (or r) and K.

5. What happens if the population overshoots its carrying capacity? This might happen, for example, if resources decreased dramatically from one year to the next, causing the carrying capacity to decrease. If population were at its old carrying capacity, it would suddenly find itself above its new carrying capacity. What would happen?

6. Is the carrying capacity a *stable equilibrium* or an *unstable equilibrium*? If an equilibrium is stable, the system (the population, in this case) will tend to return to equilibrium after a disturbance. If an equilibrium is unstable, the system will show no tendency to return to equilibrium after disturbance.

7. We have assumed so far that as the population grows, per capita births decrease and per capita deaths increase. However, that need not be the case. Per capita births may increase as the population grows if, for example, mates become easier to find. Per capita deaths may decrease if, for example, a bigger herd is safer from predators.

   What happens if per capita birth rate increases with increasing N_t, or if per capita death rate decreases with increasing N_t?

8. What happens if the per capita birth rate and per capita death rate change equally (so that the difference between them remains constant) as the population grows?

9. What happens if the difference between per capita birth and death rates increases as the population grows?

10. So far, we have kept the population growth rate relatively slow, and population size has changed smoothly and predictably. What happens if the population grows more rapidly?

11. Has the human population grown exponentially or logistically since 1963? Can you estimate r and K for the human population? Estimating K is especially important because it amounts to a prediction of the size of our population when (and if) it stabilizes. Estimating r will allow you to predict when the population may stabilize.

LITERATURE CITED

Roughgarden, Jonathan. 1998. *Primer of Ecological Theory*. Prentice Hall, Upper Saddle River, NJ.

U.S. Census Bureau Web site *http://www.census.gov/*