7 GEOMETRIC AND EXPONENTIAL POPULATION MODELS

Objectives

- Understand the demographic processes that affect population size, including raw birth and death rates, per capita birth and death rates, and rates of immigration and emigration.
- Explore the derivations of of geometric (discrete-time) and exponential (continuous-time) models of populations.
- Investigate the relationship between geometric and exponential models.
- Set up spreadsheet models of geometric and exponential population growth and graph the results.

INTRODUCTION

The study of population dynamics has been and continues to be an important area of investigation in ecology. A **population** is a group of individual organisms belonging to the same species living in the same area at the same time. Members of a population are often considered to be actually or potentially interbreeding or exchanging genes.

The term **population dynamics** means change in population size (number of individuals) or population density (number of individuals per unit area) over time. In general, population dynamics are influenced by four fundamental **demographic processes**: birth, death, immigration (individuals moving into the population), and emigration (individuals moving out of the population).

In this exercise, we will ignore immigration and emigration so that we may concentrate on births and deaths. For many populations (e.g., the human population of the earth) this is a realistic simplification. Other populations (e.g., the human population of the United States) are more open, however, and immigration and emigration must be considered. Fortunately, the addition of immigration and emigration does not complicate the models very much.

We will begin by developing a model in discrete time. That is, we will treat time as if it moved in steps, rather than continuously. This allows us to use difference equations rather than differential equations, and thereby avoid the calculus. It is also a natural way to work in spreadsheets, and is realistic for many populations that have seasonal, synchronous reproduction. Strictly speaking, the discrete-time model represents **geometric population growth**. Later in the exercise, we will develop a continuous-time model, properly called an **exponential** model.

Many textbooks present only the continuous-time exponential model. The discrete-time geometric model developed in this exercise behaves very much like its continuous-time exponential counterpart, but there are some interesting differences, which we will explore at the end of the exercise.

Model Development

To begin, we can write a very simple equation expressing the relationship between population size and the four demographic processes. Let

N_t represent the size or density of the population at some arbitrary time t (we will ignore the distinction between population size and population density)
N_{t+1} represent population size one arbitrary time-unit later
B_t represent the total number of births in the interval from time t to time $t + 1$
D_t represent the total number of deaths in the same time interval
I_t represent the total number of immigrants in the same time interval
E_t represent the total number of emigrants in the same time interval

Then we can write

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

For simplicity, this exercise ignores immigration and emigration. Our equation becomes

$$N_{t+1} = N_t + B_t - D_t$$

This equation is easy to understand but inconvenient for modeling. The problem lies in the use of "raw" birth and death rates (B_t and D_t). We have no obvious, biologically reasonable starting assumptions about these numbers. However, if we switch from *raw* birth and death rates to *per capita* birth and death rates, we can do some fruitful modeling.

Geometric (Discrete-Time) Model of Population Growth

A **per capita** rate is a rate per individual; that is, the per capita birth rate is the number of births per individual in the population per unit time, and the per capita death rate is the number of deaths per individual in the population per unit time. Per capita birth rate is easy to understand, and seems a reasonable thing to model because reproduction (giving birth) is something individuals rather than whole populations do. Per capita death rate may seem strange at first; after all, an individual can die only once. But remember, this rate is calculated per unit time. You can think of per capita birth and death rates as *each individual's probability of giving birth or dying in a given unit of time*.

Keeping in mind that per capita rates are per individual rates, we can translate the raw rates B_t and D_t into per capita rates, which we will represent with lower-case letters (b_t and d_t) to distinguish them from the raw numbers. To calculate per capita rates, we divide the raw numbers by the population size. Thus,

$$b_t = B_t/N_t \quad \text{and} \quad d_t = D_t/N_t$$

Conversely,

$$B_t = b_t N_t \quad \text{and} \quad D_t = d_t N_t$$

Now we can rewrite our model in terms of per capita rates:

$$N_{t+1} = N_t + b_t N_t - d_t N_t$$

Perhaps this seems to have gotten us nowhere, but it turns out to be a very informative model if we make one further assumption. Let us assume, just to see what happens, that per capita rates of birth and death remain constant over time. In other words, let us assume that average number of births per unit time per individual in the popu-

lation and the average risk of dying per unit time remain unchanged over some period of time. What will happen to population size?

Because we assume constant per capita birth and death rates, we can make one further, minor modification to our equation by leaving off the time subscripts on b and d:

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

At this point, you're probably thinking that this assumption is unrealistic—that per capita rates of birth and death *are* likely to change over time for a variety of reasons.* You are quite correct, but the model is still useful for three reasons:

- It provides a starting point for a more complex and realistic model in which per capita rates of birth and death do change over time. (You will build such a model in the "Logistic Population Models" exercise.)
- It is a good *heuristic model*—that is, it can lead to insights and learning despite its lack of realism.
- Many populations *do* in fact grow as predicted by this model, under certain conditions and for limited periods of time.

Because per capita birth and death rates do not change in response to the size (or density) of the population, this model is said to be **density-independent**.

We can further simplify Equation 1 by factoring N_t out of the birth and death terms:

$$N_{t+1} = N_t + (b - d)N_t$$

The term $(b - d)$ is so important in population biology that it is given its own symbol, R. Thus $R = b - d$, and is called the **geometric rate of increase**. Substituting R for $(b - d)$ gives us

$$N_{t+1} = N_t + RN_t \qquad \text{Equation 2}$$

To further define R, we can calculate the *rate of change* in population size, ΔN_t, by subtracting N_t from both sides of Equation 2:

$$\Delta N_t = N_{t+1} - N_t = RN_t$$

Because $\Delta N_t = N_{t+1} - N_t$, we can simply write

$$\Delta N_t = RN_t \qquad \text{Equation 3}$$

In words, the rate of change in population size is proportional to the population size, and the constant of proportionality is R.

We can convert this to per capita rate of change in population size if we divide both sides by N_t:

$$\frac{\Delta N_t}{N_t} = R \qquad \text{Equation 4}$$

In other words, the parameter R represents the (discrete-time) per capita rate of change in the size of the population.

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*You may also wonder why we use this complex model (Equation 1) rather than the simpler forms of the geometric and exponential models presented in most textbooks (and developed in this exercise beginning with Equation 2). We prefer Equation 1 for three reasons:

- It emphasizes the roles of per capita birth and death rates rather than the more abstract quantities R or r (explained later).
- It allows you to manipulate per capita birth and death rates directly and separately, and discover that neither alone, but rather the difference between them, determines population growth rate.
- It allows you to discover that the per capita rate of population growth ($\Delta N_t/N_t$) is a constant, which you can then relate to R (and r if desired).

Moving on, we can simplify Equation 2 ($N_{t+1} = N_t + RN_t$) even further by factoring N_t out of the terms on the right-hand side, to get

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

The quantity $(1 + R)$ is often given its own symbol, λ (lambda), and its own name: the **finite rate of increase**. Substituting λ, we can write

$$N_{t+1} = \lambda N_t \qquad \text{Equation 5}$$

The quantity λ can be very useful in analyzing real population data. Some additional algebra will show us how.

If we divide both sides of Equation 5 by N_t, we get

$$\frac{N_{t+1}}{N_t} = \lambda \qquad \text{Equation 6}$$

In words, λ is the ratio of the population size at one time to its size one time-unit earlier. We can calculate λ from population counts at successive times, even if we do not know per capita rates of birth and death. You will use this tool to analyze human population data in Question 10 at the end of this exercise.

In Equations 2 and 5, we showed how to calculate the size of the population one time unit into the future. What if you wanted to know how big the population will be at some distant future time? You could carry out the one-time-step calculations many times, until you arrived at the desired answer, and you will do this in the spreadsheet. But there is also a shortcut. Let us start with Equation 5:

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

Starting at time 0, we can carry this calculation through a few times to calculate population sizes at time 1, time 2, and time 3. The population size at time 0 can be written N_0. Thus the populations at times 1, 2, and 3 would be

$$N_1 = \lambda N_0$$

$$N_2 = \lambda N_1 = \lambda(\lambda N_0)$$

$$N_3 = \lambda N_2 = \lambda[\lambda(\lambda N_0)]$$

Do you see a pattern here? Population size at time 1 is $\lambda^1 N_0$, at time 2 it is $\lambda^2 N_0$, and at time 3 it is $\lambda^3 N_0$. In general, we can write

$$N_t = \lambda^t N_0 \qquad \text{Equation 7}$$

This expression may strike you as rather abstract. One way to understand its impact is to use Equation 7 to calculate doubling time (t_{double})—that is, the time required for the population to double in size.* If we plug the doubling time into Equation 7, we get

$$N_{t_{double}} = \lambda^{t_{double}} N_0$$

We can derive doubling time by exploiting the fact that the population at time t_{double} is, by definition, twice the population at time 0:

$$N_{t_{double}} = 2N_0$$

Substituting $2N_0$ for $N_{t\,double}$ gives us

*This derivation follows Gotelli (2001).

$$2N_0 = \lambda^{t_{\text{double}}} N_0$$

If we divide both sides by N_0, we get

$$2 = \lambda^{t_{\text{double}}}$$

Taking the logarithm of both sides gives us

$$\ln 2 = t_{\text{double}} \ln \lambda$$

Dividing both sides by $\ln\lambda$, we get

$$\frac{\ln 2}{\ln \lambda} = t_{\text{double}} \qquad\qquad \text{Equation 8}$$

What does this mean? Suppose $R = 0.1$ individuals/individual/year. Therefore, $\lambda = 1 + R = 1.1$. This implies that the population increases by 10% per year, which doesn't sound like much. But, if you plug this value of λ into Equation 8, you'll find that the population doubles in about 7.27 years, which seems more impressive.

   You may be wondering how a population that grows in discrete intervals of a year can double in a non-integer number of years. It can't, of course. This calculation really means that the population will not quite double in 7 years, and will more than double in 8 years.

Exponential (Continuous-Time) Model of Population Growth

Population growth can also be modeled in continuous time, which is more realistic for populations that reproduce continuously, rather than seasonally. Continuous-time models also allow use of the calculus, which provides many powerful analytical tools. In this exercise, we will eschew the calculus, and simply present some results.

   Most textbooks begin with the continuous-time analog of Equation 3:

$$dN/dt = rN \qquad\qquad \text{Equation 9}$$

The left-hand side of Equation 9 represents the **instantaneous** rate of change in population size, which is different from the rate of change over some discrete time interval, $\Delta N_t/N_t$, that we looked at in Equation 7. Therefore, we use a lowercase r to distinguish the continuous-time exponential model from the discrete-time geometric model. The symbol r is called the **instantaneous rate of increase** or the **intrinsic rate of increase**. The parameters r and R are *not* equal, although they are related, as we will show below.

   As we did with the discrete-time model, we can calculate the per capita rate of population growth by dividing both sides of Equation 9 by N:

$$\frac{(dN/dt)}{N} = r \qquad\qquad \text{Equation 10}$$

You can use the calculus to operate on Equation 10 and calculate the size of the population at any time. We will spare you the derivation, but the resulting equation is

$$N_t = N_0 e^{rt} \qquad\qquad \text{Equation 11}$$

where e is the root of the natural logarithms ($e \cong 2.71828$).

   You can derive the relationship between r and R as follows. Suppose we start two populations with the same initial number of individuals, N_0, and both grow at the same rate. However, one grows in continuous time and the other grows in discrete time. Because they grow at the same rate, at some later time, t, they will have reached the same size, N_t. If we write the discrete-time population on the left and the continuous-time population on the right we can derive as follows:

$$N_t = N_t$$

$$N_0 \lambda^t = N_0 e^{rt}$$

$$\lambda^t = e^{rt}$$

$$\ln(\lambda^t) = \ln(e^{rt})$$

$$t \ln\lambda = rt \ln e$$

$$\ln\lambda = r \hspace{4cm} \text{Equation 12}$$

$$\lambda = e^r \hspace{4cm} \text{Equation 13}$$

So we can convert back and forth between continuous-and-discrete time models. Remember that $\lambda = 1 + R$.

Suppose we have a population growing in continuous time with some value of r, and a population growing in discrete time with the same value of R, i.e., $r = R$. Which will grow faster? As we did with the geometric model, we can derive the doubling time for the exponential model (Gotelli 2001). We begin with Equation 11, and plug in t_{double}:

$$N_{t_{double}} = N_0 e^{rt_{double}}$$

Substituting $2N_0$ for Nt_{double}, we get

$$2N_0 = N_0 e^{rt_{double}}$$

Dividing both sides by N_0 gives us

$$2 = e^{rt_{double}}$$

and taking the natural logarithm of both sides yields

$$\ln 2 = rt_{double}$$

Finally, we divide both sides by r, and rearrange, to get

$$t_{double} = \frac{\ln 2}{r}$$

Parallel to our earlier example, let us suppose $r = 0.1$ individuals/individual/year. As before, this implies a 10% annual increase in the population, but now this increase occurs continuously rather than in discrete time intervals. How long does it take for this population to double? Plugging in the value 0.1 for r yields a doubling time of 6.93 years, somewhat faster than indicated by the geometric model.

PROCEDURES

The following exercises will set up spreadsheets and allow you to graph both the geometric and exponential growth of populations. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Geometric (discrete-time) model.

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
1	Geometric Model of Population Growth								
2	Assumes constant per capita rates of birth and death.								
3				Variables				Constants	
4	t	Nt	Total births	Total deaths	ΔN_t	$(\Delta N_t)/N_t$	b	d	R
5	0						1.25	0.50	0.75
6	1								
7	2								

Figure 1

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

In cell A5, enter the number 0.
In cell A6, enter the formula **=A5+1**.
Copy cell A6. Select cells A7–A25. Paste.

3. Enter the values shown for per capita birth and death rates, *b* and *d*.

In cell G5, enter the number 1.25.
In cell H5, enter the number 0.50.

4. Enter a formula to calculate *R* in cell I5.

In cell I5, enter the formula **=G5-H5**.

5. Enter an initial population size of 100.

In cell B5, enter the number 100.

6. Enter the formulae for total births (bN_t) and deaths (dN_t) into cells C5 and D5.

In cell C5, enter the formula **=$G$5*B5**.
In cell D5, enter the formula **=$H$5*B5**.

Note that references to per capita birth rate (**$G$5**) and per capita death rate (**$H$5**) use absolute addresses, but the references to current population size (**B5**) use a relative address. This is because you will later copy these formulae down their columns, and you want them to refer, respectively, to constants—per capita birth and death rates—and to a variable—the population size at time *t*.

7. Enter the formula for N_{t+1} into cell B6.

In cell B6, enter the formula **=B5+C5-D5**.

Note that this formula uses the total births and deaths you have already calculated. This mimics the chain of biological cause and effect: per capita rates of birth and death, in conjunction with the number of individuals in the population, determine the total number of births and deaths, which in turn determine the size of the population at the next time.

8. Copy the formulae for total births and deaths into cells C6 and D6.

Select cells C5 and D5. Copy.
Select cells C6 and D6. Paste.

9. Copy the formulae for N_t, total birth and total deaths, down their columns.

See annotation at Step 8 for the commands involved.

10. In cell E5, enter a formula to calculate the change in population size (ΔN_t) from time 0 to time 1.

In cell E5, enter the formula **=B6-B5**.

Note that this change in population size is calculated for the coming time interval. You could do it differently, but this way gives an interesting result, seen in the next step.

11. In cell F5, enter a formula for the per capita change in population size ($\Delta N_t/N_t$) from time 0 to time 1.

In cell F5, enter the formula **=E5/B5**.

Like all per capita rates, this one is calculated by dividing the change in population size by the current population size. How does the value of ($\Delta N_t/N_t$) compare to the value of R?

12. Copy the formulae for ΔN_t and $\Delta N_t/N_t$ down their columns.

See step 8 for the commands involved.
Your model is now complete and you are ready to create graphs.
Save your work.

13. Graph N_t, total births, total deaths, ΔN_t, and $\Delta N_t/N_t$ against time.

Select cells A4–F24. Note that you should include column headings in your selection, so that the legend will be labeled properly. Do not include row 25 because ΔN_t, and $\Delta N_t/N_t$ are undefined there.

Click on the Chart Wizard button or open Insert | Chart. (Details are given in the Introduction, "Spreadsheet Hints and Tips," and in Exercise 1, "Mathematical Functions and Graphs.") Follow the prompts in the resulting dialog boxes to set up an XY chart (Scatterplot) with time on the *x*-axis. *Do not use a line chart*.

14. Edit your graph for readability. The result should resemble Figure 2.

Put $\Delta N_t/N_t$ on the secondary *y*-axis and scale that axis from 0 to 1. (Again, refer to the Introduction and to Exercise 1; or just try clicking on things in the graph, and see what happens.)
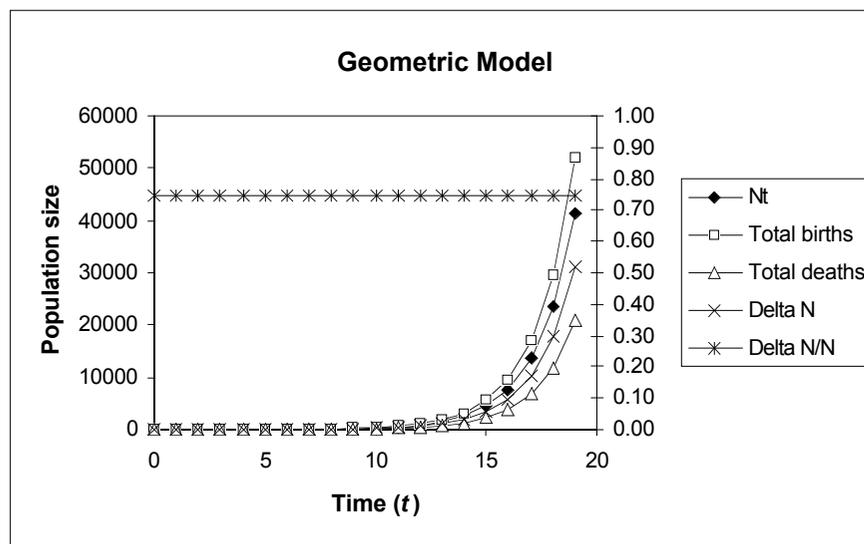

Figure 2

Strictly speaking, the graph in Figure 2 is inaccurate, because it implies that population size increases smoothly and continuously between time steps. Actually, population size remains unchanged from one time (t) to the next ($t + 1$), and then instantaneously takes its new value. Thus, the graph should look like a flight of stairs that gets steeper exponentially. However, such a graph is difficult to produce in Excel, so we will have to settle for this one and bear this inaccuracy in mind.

15. Graph total births, total deaths, and ΔN_t on the vertical axis against population size on the horizontal axis.

Select cells B4–E24. Note that this differs from your previous graph in that you do *not* include time (column A). Include column headings in your selection so that the legend will be labeled properly.

Click on the Chart Wizard or open Insert | Chart. Follow the prompts in the resulting dialog boxes to set up an XY chart (Scatterplot) with N_t on the *x*-axis. *Do not use a line chart*.

16. Edit your graph for readability. The result should resemble Figure 3.
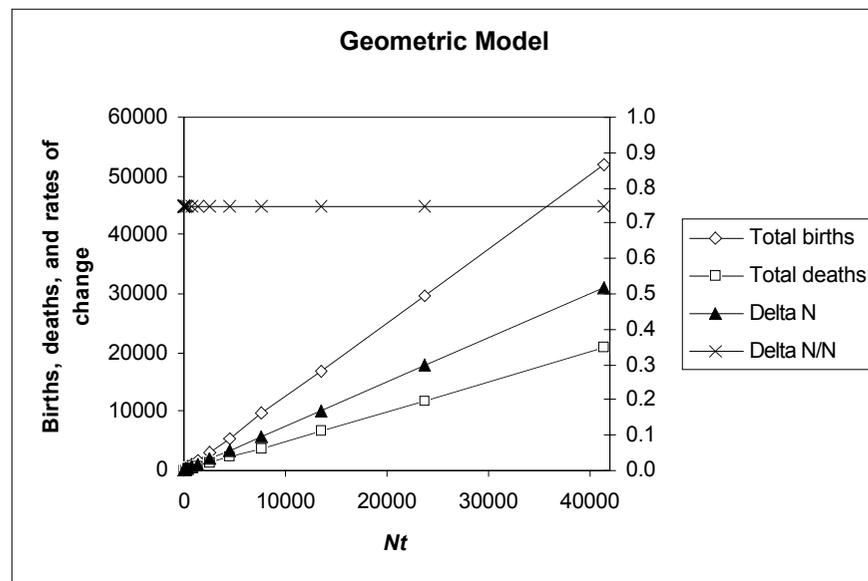
See Step 2 above.

Figure 3

B. Exponential (continuous-time) model.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 4. Enter the values shown for *r* and *R*.

These are all literals, so just select the appropriate cells and type them in. We will set up an exponential (continuous-time) model and a geometric (discrete-time) model side-by-side for comparison.

	A	B	C	D	E
1	Comparison of Exponential and Geometric Models				
2		Constants			
3		r =	0.25		
4		R =	0.25		
5				Calculated values	
6		Nt	Nt	r	R
7	Time(t)	Exponential	Geometric	Exponential	Geometric
8	0				
9	1				
10	2				

Figure 4

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

Enter the value 0 in cell A8.
In cell A9, enter the formula **=1+A8**. Copy cell A9 and paste into cells A10–A28.

3. In cells B8 and C8, enter initial population sizes for the two populations.

Enter the value 1.00 into cells B8 and C8. Later, you can change these values to see the effect on population growth.

4. In cell B9, enter a formula to calculate the size of the exponential population at time 1.

In cell B9, enter the formula **=$B$8*EXP($C$4*A9).**
This corresponds to Equation 11, $N_t = N_0 e^{rt}$. The function **EXP($C$4*A9)** is the spreadsheet version of e^{rt}. Note that the reference to the initial population size (a constant) uses an absolute cell address (**$B$8**), as does the reference to r (**$C$4**), but the reference to time (**A9**) is relative (a variable).

Note that the reference to the initial population size (a constant) uses an absolute cell address (**$B$8**), as does the reference to r (**$C$4**), but the reference to time (**A9**) is relative (a variable).

5. In cell C9, enter a formula to calculate the size of the geometric population at time 1.

In cell C9, enter the formula **=(1+$C$5)^A9*$C$8**.
This corresponds to Equation 7: $N_t = \lambda^t N_0$. The term **(1+$C$5)** calculates λ, (which is 1 + R, remember) and the expression **^A9** raises λ to the power t. Note that the reference to the initial population size uses an absolute cell address (**$C$8**), as does the reference to R (**$C$5**), but the reference to time (**A9**) is relative.

6. Copy the formulae in cells B9 and C9 down their columns.

Select cells B9 and C9. Copy.
Select cells B10–C28. Paste.

7. Enter a formula in cell D8 to calculate r from the population sizes in cells B8 and B9.

In cell D8, enter the formula **=LN(B9/B8)**.
This formula calculates λ from the population sizes at times 0 and 1, as if the population were growing in discrete time, and then converts λ to the continuous-time r by taking the natural logarithm of λ. Review Equation 12 for the derivation of this relationship.

We use this roundabout method to set the stage for analyzing real population data, as you will do in answering Question 10 at the end of this exercise. In some cases, we may know population sizes at different times, but not per capita rates of birth and death. Using this method allows us to determine r from population sizes, and predict population dynamics without knowing per capita birth and death rates.

8. Enter a formula in cell E8 to calculate *R* from the population sizes in cells C8 and C9.

In cell E8, enter the formula **=C9/C8-1**.
Remember that $\lambda = 1 + R$, so $R = \lambda - 1$. The rationale for this calculation is the same as for our calculation of *r* in step 7.

9. Copy the formulae in cells D8 and E8 down their columns to row 27.

Do not copy the formulae into cells D28 and E28 because they become undefined there.

10. Save your work.

11. Graph population size against time for exponential and geometric models on the same graph.

See "Spreadsheet Hints and Tips" and Exercise 2, "Spreadsheet Functions and Graphs," for detailed instructions. Your finished graph should resemble Figure 5.
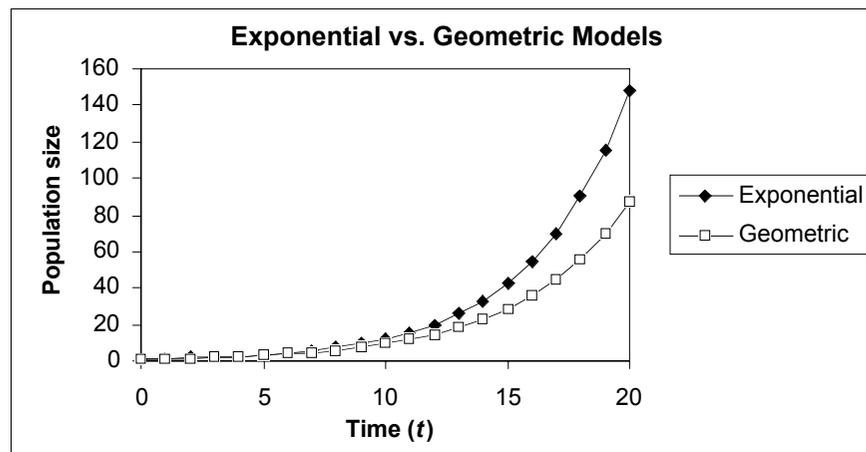

Figure 5

QUESTIONS

1. Under the assumptions $b > d$ and both *b* and *d* constant, how does the population grow? How can you verify your answer?

2. How does population size change over time if $b < d$? Before you start plugging values into the model, sketch what you think the graph of N_t against time will look like.

3. How does population size change over time if $b = d$?

4. Which of the following determine the rate of population growth (ΔN_t)?
    - per capita birth rate
    - per capita death rate
    - the product of the two
    - the ratio of the two
    - the difference between the two

5. How does the rate of population growth (ΔN_t) change over time?

6. How do total births, total deaths, and ΔN_t relate to population size?

7. How does per capita rate of population growth ($\Delta N_t/N_t$) relate to population size (N_t)?

8. Which grows faster, the continuous-time population or the discrete-time population? Why?

9. How much larger than r must R be in order to produce equal population growth rates?

10. How has the human population grown over the past 12 centuries or so? Analyze the following data from the U.S. Census Bureau website (http://www.census.gov):

Date (year C.E.)	Time (years elapsed since 500 C.E.)	Estimated population size
500	0	190,000,000
600	1	200,000,000
700	2	207,000,000
800	3	220,000,000
900	4	226,000,000
1000	5	254,000,000
1100	6	301,000,000
1200	7	360,000,000
1300	8	360,000,000
1400	9	350,000,000
1500	10	425,000,000
1600	11	545,000,000
1700	12	600,000,000
1800	13	813,000,000
1900	14	1,550,000,000

LITERATURE CITED

Gotelli, N. J. 2001. *A Primer of Ecology*, 3rd Edition. Sinauer Associates, Sunderland, MA.