11

AGE-STRUCTURED MATRIX MODELS

Objectives

- Set up a model of population growth with age structure.
- Determine the stable age distribution of the population.
- Estimate the finite rate of increase from Leslie matrix calculations.
- Construct and interpret the age distribution graphs.

Suggested Preliminary Exercises: Geometric and Exponential Population Models; Life Tables and Survivorship Curves

INTRODUCTION

You've probably seen the geometric growth formula many times by now (Exercise 7). It has the form

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

where b is the per capita birth rate and d is the per capita death rate for a population that is growing in discrete time. The term $(b - d)$ is so important in population biology that it is given its own symbol, R. It is called the **intrinsic** (or **geometric**) **rate of natural increase**, and represents the per capita rate of change in the size of the population. Substituting R for $b - d$ gives

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

We can factor 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 called the finite rate of increase, λ. Thus we can write

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

where N is the number of individuals present in the population, and t is a time interval of interest. Equation 1 says that the size of a population at time $t + 1$ is equal to the size of the population at time t multiplied by a constant, λ. When $\lambda = 1$, the population will remain constant in size over time. When $\lambda < 1$, the population declines geometrically, and when $\lambda > 1$, the population increases geometrically.

Although geometric growth models have been used to describe population growth, like all models they come with a set of assumptions. What are the assump-

tions of the geometric growth model? The equations describe a population in which there is no genetic structure, no age structure, and no sex structure to the population (Gotelli 2001), and all individuals are reproductively active when the population census is taken. The model also assumes that resources are virtually unlimited and that growth is unaffected by the size of the population. Can you think of an organism whose life history meets these assumptions? Many natural populations violate at least one of these assumptions because the populations have **structure**: They are composed of individuals whose birth and death rates *differ* depending on age, sex, or genetic make-up. All else being equal, a population of 100 individuals that is composed of 35 prere-productive-age individuals, 10 reproductive-age individuals, and 55 postreproduc-tive-age individuals will have a different growth rate than a population where all 100 individuals are of reproductive age. In this exercise, you will develop a **matrix model** to explore the growth of populations that have age structure. This approach will enable you to estimate λ in Equation 1 for structured populations.

Model Notation

Let us begin our exercise with some notation often used when modeling populations that are structured (Caswell 2001; Gotelli 2001). For modeling purposes, we divide individuals into groups by either their **age** or their **age class**. Although age is a continuous variable when individuals are born throughout the year, by convention individuals are grouped or categorized into discrete time intervals. That is, the age class of 3-year-olds consists of individuals that just had their third birthday, plus individuals that are 3.5 years old, 3.8 years old, and so on. In age-structured models, *all* individuals within a particular age group (e.g., 3-year-olds) are assumed to be equal with respect to their birth and death rates. The age of individuals is given by the letter x, followed by a number within parentheses. Thus, newborns are $x(0)$ and 3-year-olds are $x(3)$.

In contrast, the age class of an individual is given by the letter i, followed by a subscript number. A newborn enters the first age class upon birth (i_1), and enters the second age class upon its first birthday (i_2). Caswell (2001) illustrates the relationship between age and age class as:
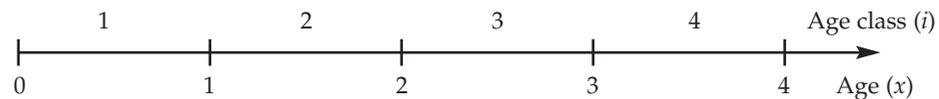

Thus, whether we are dealing with age classes or ages, individuals are grouped into discrete classes that are of equal duration for modeling purposes. In this exercise, we will model age classes rather than ages. A typical life cycle of a population with age-class structure is:
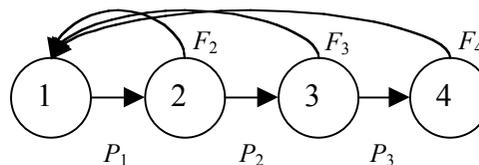
The age classes themselves are represented by circles. In this example, we are considering a population with just four age classes. The horizontal arrows between the circles represent survival probabilities, P_i—the probability that an individual in age class i will survive to age class $i + 1$. Note that the fourth age class has no arrow leading to a fifth age class, indicating that the probability of surviving to the fifth age class is 0. The curved arrows at the top of the diagram represent births. These arrows all lead to age class 1 because newborns, by definition, enter the first age class upon birth. Because

"birth" arrows emerge from age classes 2, 3, and 4 in the above example, the diagram indicates that all three of these age classes are capable of reproduction. Note that individuals in age class 1 do not reproduce. If only individuals of age class 4 reproduced, our diagram would have to be modified:
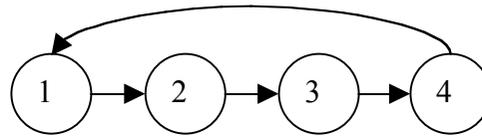
The Leslie Matrix

The major goal of the matrix model is to compute λ, the finite rate of increase in Equation 1, for a population with age structure. In our matrix model, we can compute the **time-specific growth rate** as λ_t. The value of λ_t can be computed as

$$\lambda_t = N_{t+1}/N_t \qquad \text{or} \qquad \lambda_t = \frac{N_{t+1}}{N_t} \qquad\qquad \text{Equation 2}$$

This time-specific growth rate is not necessarily the same λ in Equation 1. (We will discuss this important point later.) To determine N_t and N_{t+1}, we need to count individuals at some standardized time period over time. We will make two assumptions in our computations. First, we will assume that the time step between N_t and N_{t+1} is one year, and that age classes are defined by yearly intervals. This should be easy to grasp, since humans typically measure time in years and celebrate birthdays annually. (If we were interested in a different time step—say, six months—then our age classes would also have to be 6-month intervals.) Second, we will assume for this exercise that our population censuses are completed once a year, immediately after individuals breed (a **postbreeding census**). The number of individuals in the population in a census at time $t + 1$ will depend on how many individuals of each age class were in the population at time t, as well as the birth and survival probabilities for each age class.

Let us start by examining the **survival probability**, designated by the letter P. P is the probability that an individual in age class i will survive to age class $i + 1$. The small letter l gives the number of individuals in the population at a given time:

$$P_i = \frac{l(i)}{l(i-1)}$$

This equation is similar to the $g(x)$ calculations in the life table exercise. For example, let's assume the probability that individuals in age class 1 survive to age class 2 is $P_1 = 0.3$. This means 30% of the individuals in age class 1 will survive to be censused as age class 2 individuals. By definition, the remaining 70% of the individuals will die. If we consider survival alone, we can compute the number of individuals of age class 2 at time $t + 1$ as the number of individuals of age class 1 at time t multiplied by P_1. If we denote the number of individuals in class i at time t as $n_i(t)$, we can write the more general equation as

$$n_{i+1}(t + 1) = P_i n_i(t) \qquad\qquad \text{Equation 3}$$

This equation works for calculating the number of individuals at time $t + 1$ for each age class in the population except for the first, because individuals in the first age class arise only through birth. Accordingly, let's now consider birth rates.

There are many ways to describe the occurrence of births in a population. Here, we will assume a simple **birth-pulse model**, in which individuals give birth the moment they enter a new age class. When populations are structured, the birth rate is called the **fecundity**, or the average number of offspring born per unit time to an individual female of a particular age. If you have completed the exercise on life tables, you might recall
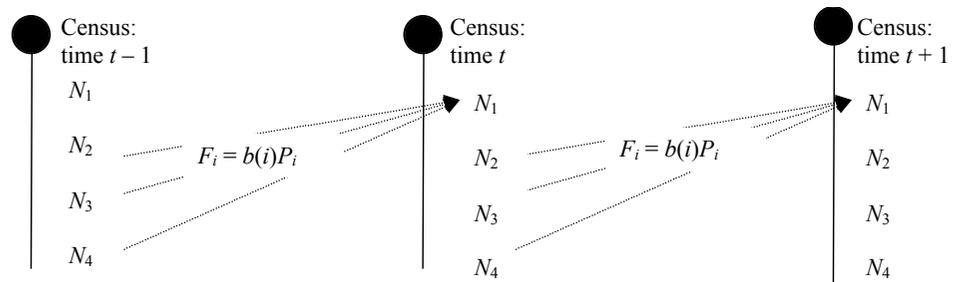
Figure 1 In this population, age classes 2, 3, and 4 can reproduce, as represented by the dashed arrows that lead to age class 1 in the next step. Births occur in a birth pulse (indicated by the filled circle and vertical line) and individuals are censused immediately after young are born. (After Akçakaya et al. 1997.)

that fecundity is labeled as $b(x)$, where b is for birth. Individuals that are of prereproductive or postreproductive age have fecundities of 0. Individuals of reproductive age typically have fecundities > 0.

Figure 1 is a hypothetical diagram of a population with four age classes that are censused at three time periods: time $t - 1$, time t, and time $t + 1$. In Figure 1, all individuals "graduate" to the next age class on their birthday, and since all individuals have roughly the same birthday, all individuals counted in the census are "fresh"; that is, the newborns were just born, individuals in age class 2 just entered age class 2, and so forth. With a postbreeding census, Figure 1 shows that the number of individuals in the first age class at time t depends on the number of breeding adults in the previous time step.

If we knew how many adults actually bred in the previous time step, we could compute fecundity, or the average number of offspring born per unit time per individual (Gotelli: 2001). However, the number of adults is not simply N_2 and N_3 and N_4 counted in the previous time step's census; these individuals must survive a long period of time (almost a full year until the birth pulse) before they have another opportunity to breed. Thus, we need to discount the fecundity, $b(i)$, by the probability that an adult will actually survive from the time of the census to the birth pulse (P_i), (Gotelli 2001). These adjusted estimates, which are used in matrix models, are called **fertilities** and are designated by the letter F.

$$F_i = b(i)P_i \qquad \text{Equation 4}$$

The adjustments are necessary to account for "lags" between the census time and the timing of births. Stating it another way, F_i indicates the number of young that are produced per female of age i in year t, given the appropriate adjustments. Be aware that various authors use the terms fertility and fecundity differently; we have followed the notation used by Caswell (2001) and Gotelli (2001). The total number of individuals counted in age class 1 in year $t + 1$ is simply the fertility rate of each age class, multiplied by the number of individuals in that age class at time t. When these products are summed together, they yield the total number of individuals in age class 1 in year $t + 1$. Generally speaking,

$$n_1(t+1) = \sum_{i=1}^{k} F_i n_i(t)$$

Once we know the fertility and survivorship coefficients for each age class, we can calculate the number of individuals in each age at time $t + 1$, given the number of individuals in each class at time t:

$$n_1(t + 1) = F_1 n_1(t) + F_2 n_2(t) + F_3 n_3(t) + F_4 n_4(t)$$
$$n_2(t + 1) = P_1 n_1(t)$$
$$n_3(t + 1) = P_2 n_2(t)$$
$$n_4(t + 1) = P_3 n_3(t)$$

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix}$$

Figure 2 The specific form of a Leslie matrix, based on a population with four age classes. The letters used to designate a mathematical matrix are conventionally uppercase, boldface, and not italic. The rows and columns of the matrix are enclosed in large brackets. See P. H. Leslie's original paper (Leslie 1945) for the classic discussion.

How can we incorporate the equations in Equation 4 into a model to compute the constant, λ, from Equation 1? Leslie (1945) developed a matrix method for predicting the size and structure of next year's population for populations with age structure. A **matrix** is a rectangular array of numbers; matrices are designated by uppercase, bold letters. **Leslie matrices**, named for the biologist P. H. Leslie, have the form shown in Figure 2.

Since our population has only four age classes, the Leslie matrix in Figure 2 is a four row by four column matrix. If our population had five age classes, the Leslie matrix would be a five row by five column matrix. The fertility rates of age classes 1 through 4 are given in the top row. Most matrix models consider only the female segment of the population, and define fertilities in terms of female offspring. The survival probabilities, P_i, are given in the subdiagonal; P_1 through P_3 are survival probabilities from one age class to the next. For example, P_1 is the probability of individuals surviving from age class 1 to age class 2. All other entries in the Leslie matrix are 0. The composition of our population can be expressed as a column **vector**, $\mathbf{n}(t)$, which is a matrix that consists of a single column. Our column vector will consist of the number of individuals in age classes 1, 2, 3, and 4:

$$\mathbf{n}(t) = \begin{bmatrix} w \\ x \\ y \\ z \end{bmatrix}$$

When the Leslie matrix, $\mathbf{A}$, is multiplied by the population vector, $\mathbf{n}(t)$, the result is another population vector (which also consists of one column); this vector is called the **resultant vector** and provides information on how many individuals are in age classes 1, 2, 3, and 4 in year $t + 1$. The multiplication works as follows:

$$\begin{bmatrix} a & b & c & d \\ e & f & g & h \\ i & j & k & l \\ m & n & o & p \end{bmatrix} \times \begin{bmatrix} w \\ x \\ y \\ z \end{bmatrix} = \begin{bmatrix} aw + bx + cy + dz \\ ew + fx + gy + hz \\ iw + jx + ky + lz \\ mw + nx + oy + pz \end{bmatrix}$$

$$\mathbf{A} \quad \times \quad \mathbf{n} \quad = \quad \text{Resultant vector}$$

The first entry in the resultant vector is obtained by multiplying each element in the first row of the $\mathbf{A}$ matrix by the corresponding element in the $\mathbf{n}$ vector, and then summing the products together. In other words, the first entry in the resultant vector equals the total of several operations: multiply the first entry in the first row of the $\mathbf{A}$ matrix by the first entry in $\mathbf{n}$ vector, multiply the second entry in the first row of the $\mathbf{A}$ matrix by the second entry in the $\mathbf{n}$ vector, and so on until you reach the end of the first row of the $\mathbf{A}$ matrix, then add all the products. In the example above, a 4×4 matrix on the left is multiplied by a column vector (center). The resultant vector is the vector on the right-hand side of the equation.

Rearranging the matrices so that the resultant vector is on the left, we can compute the population size at time $t + 1$ by multiplying the Leslie matrix by the population vector at time t.

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} \times \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{bmatrix} \qquad \text{Equation 4}$$

For example, assume that you have been following a population that consists of 45 individuals in age class 1, 18 individuals in age class 2, 11 individuals in age class 3, and 4 individuals in age class 4. The initial vector of abundances is written

$$\begin{bmatrix} 45 \\ 18 \\ 11 \\ 4 \end{bmatrix}$$

Assume that the Leslie matrix for this population is

$$\begin{bmatrix} 0 & 1 & 1.5 & 1.2 \\ .8 & 0 & 0 & 0 \\ 0 & .5 & 0 & 0 \\ 0 & 0 & .25 & 0 \end{bmatrix}$$

Following Equation 4, the number of individuals of age classes 1, 2, 3, and 4 at time $t + 1$ would be computed as

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{bmatrix} = \begin{bmatrix} 0 & 1 & 1.5 & 1.2 \\ .8 & 0 & 0 & 0 \\ 0 & .5 & 0 & 0 \\ 0 & 0 & .25 & 0 \end{bmatrix} \times \begin{bmatrix} 45 \\ 18 \\ 11 \\ 4 \end{bmatrix} = \begin{bmatrix} 0 \times 45 + 1 \times 18 + 1.5 \times 11 + 1.2 \times 4 \\ 0.8 \times 45 + 0 \times 18 + 0 \times 11 + 0 \times 4 \\ 0 \times 45 + .5 \times 18 + 0 \times 11 + 0 \times 4 \\ 0 \times 45 + 0 \times 18 + .25 \times 11 + 0 \times 4 \end{bmatrix} = \begin{bmatrix} 39.3 \\ 36 \\ 9 \\ 2.75 \end{bmatrix}$$

The time-specific growth rate, λ_t, can be computed as the total population at time $t + 1$ divided by the total population at time t. For the above example,

$$\lambda_t = (39.3 + 36 + 9 + 2.75)/(45 + 18 + 11 + 4) = 87.05/78 = 1.116$$

As we mentioned earlier, λ_t is not necessarily equal to λ in Equation 1. The Leslie matrix not only allows you to calculate λ_t (by summing the total number of individuals in the population at time $t + 1$ and dividing this number by the total individuals in the population at time t), but also to evaluate how the composition of the population changes over time. If you multiply the Leslie matrix by the new vector of abundances, you will project population size for yet another year. Continued multiplication of a vector of abundance by the Leslie matrix eventually produces a population with a **stable age distribution**, where the proportion of individuals in each age class remains constant over time, and a stable (unchanging) time-specific growth rate, λ_t. When the λ_t's converge to a constant value, this constant is an estimate of λ in Equation 1. Note that this λ has no subscript associated with it. Technically, λ is called the **asymptotic growth rate** when the population converges to a stable age distribution. At this point, if the population is growing or declining, all age classes grow or decline at the same rate. In this exercise you'll set up a Leslie matrix model for a population with age structure. The goal is to project the population size and structure into the future, and examine properties of a stable age distribution. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Set up the spread-sheet.

1. Set up new column headings as shown in Figure 3.

	A	B	C	D	E	F	G
1	*Age-Structured Matrix Models*						
2							
3			**Age class**				**n**
4		**1**	**2**	**3**	**4**		
5		0	1	1.5	1.2		45
6	**A =**	0.8	0	0	0		18
7		0	0.5	0	0		11
8		0	0	0.25	0		4
9							
10							
11	**Time**	**1**	**2**	**3**	**4**	**Total pop**	λ_t

Figure 3

2. Enter values in the Leslie matrix in cells B5–E8 as shown.

Remember that the Leslie matrix has a specific form. Fertility rates are entered in the top row. Survival rates are entered on the subdiagonal, and all other values in the Leslie matrix are 0.

3. Enter values in the initial population vector in cells G5–G8 as shown.

The initial population vector, **n**, gives the number of individuals in the first, second, third, and fourth age classes. Thus our population will initially consist of 45 individuals in age class 1, 18 individuals in age class 2, 11 individuals in age class 3, and 4 individuals in age class 4.

4. Set up a linear series from 0 to 25 in cells A12–A37.

We will track the numbers of individuals in each age class over 25 years.
Enter 0 in cell A12.
Enter **=1+A12** in cell A13.
Copy your formula down to cell A37.

5. Enter formulae in cells B12–E12 to link to values in the initial vector of abundances (G5–G8).

Enter the following formulae:
- B12 **=G5**
- C12 **=G6**
- D12 **=G7**
- E12 **=G8**

6. Sum the total number of individuals at time 0 in cell F12.

Enter the formula **=SUM(B12:E12)**. Your result should be 78.

7. Compute λ_t for time 0 in cell G12.

8. Save your work.

Enter the formula **=F13/F12**. Your result will not be interpretable until you compute the population size at time 1. You can generate the λ symbol by typing in the letter l, highlighting this letter in the formula bar, and then changing its font to the symbol font.

B. Project population size over time.

1. In cells B13–E13, enter formulae to calculate the number of individuals in each age class in year 1. In your formulae, use the initial vector of abundances listed in row 12 instead of column G.

Now we are ready to project the population sizes into the future. Remember, we want to multiply the Leslie matrix by our initial set of abundances to generate a resultant vector (which gives the abundances of the different age classes in the next time step). Recall how matrices are multiplied to generate the resultant vector:

$$\begin{bmatrix} a & b & c & d \\ e & f & g & h \\ i & j & k & l \\ m & n & o & p \end{bmatrix} \times \begin{bmatrix} w \\ x \\ y \\ z \end{bmatrix} = \begin{bmatrix} aw + bx + cy + dz \\ ew + fx + gy + hz \\ iw + jx + ky + lz \\ mw + nx + oy + pz \end{bmatrix}$$

See if you can follow how to calculate the resultant vector, and enter a formula for its calculation in the appropriate cell—it's pretty easy to get the hang of it. The cells in the Leslie matrix should be absolute references, while the cells in the vector of abundances should be relative references. We entered the following formulae:

- B13 **=$B$5*B12+$C$5*C12+$D$5*D12+$E$5*E12**
- C13 **=$B$6*B12+$C$6*C12+$D$6*D12+$E$6*E12**
- D13 **=$B$7*B12+$C$7*C12+$D$7*D12+$E$7*E12**
- E13 **=$B$8*B12+$C$8*C12+$D$8*D12+$E$8*E12**

2. Copy the formula in cell F12 into cell F13.

3. Copy the formula in cell G12 into cell G13. Your spreadsheet should now resemble Figure 4.

	A	B	C	D	E	F	G
11	**Time**	**1**	**2**	**3**	**4**	**Total pop**	λ_t
12	0	45	18	11	4	78	1.1153846
13	1	39	36	9	3	87	0

Figure 4

4. Select cells B13–G13, and copy their formulae into cells B14–G37. Save your work.

This will complete your population projection over 25 years.

C. Create graphs.

1. Graph the number of individuals in each age class over time, as well as the total number of individuals over time. Use the scatter graph option, and label your axes clearly. Your graph should resemble Figure 5.
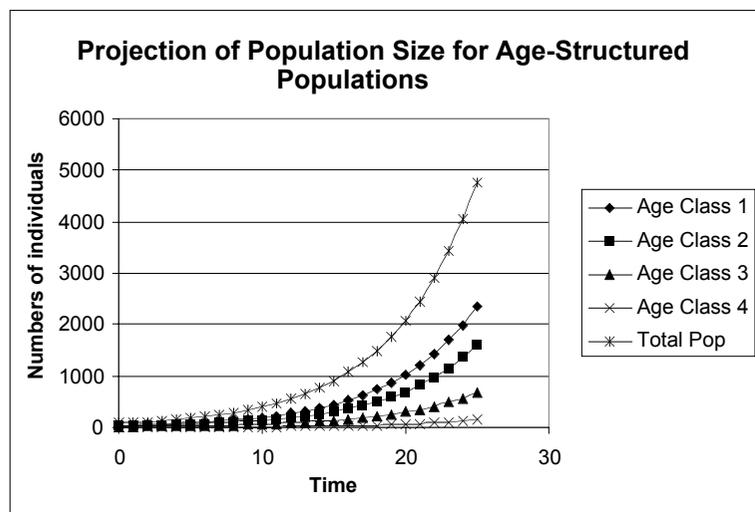

Figure 5

It's often useful to examine the logarithms of the number of individuals instead of the raw data. This takes the bending nature out of a geometrically growing or declining population (see Exercise 1). To adjust the scale of the *y*-axis, double click on the values in the *y*-axis. A dialog box (Figure 6) will appear:
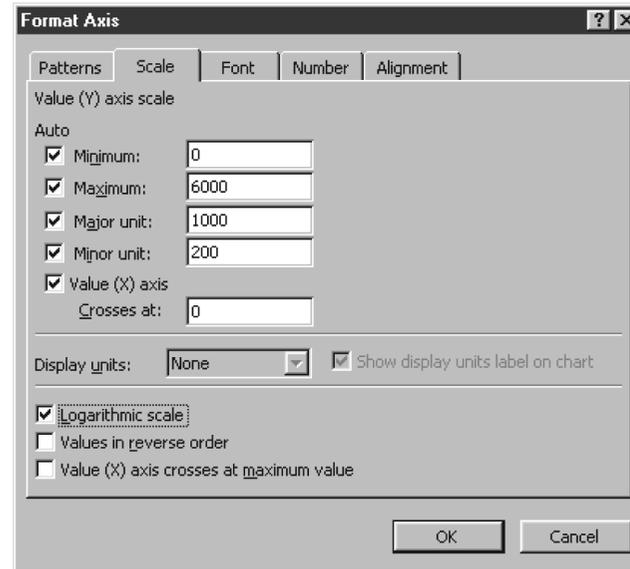

Figure 6

Toward the bottom of the screen is a box labeled Logarithmic scale. Click on that box, and then click the OK button, and your scale will be automatically adjusted. It's sometimes easier to interpret your population projections with a log scale.

2. Generate a new graph of the same data, but use a log scale for the *y*-axis.
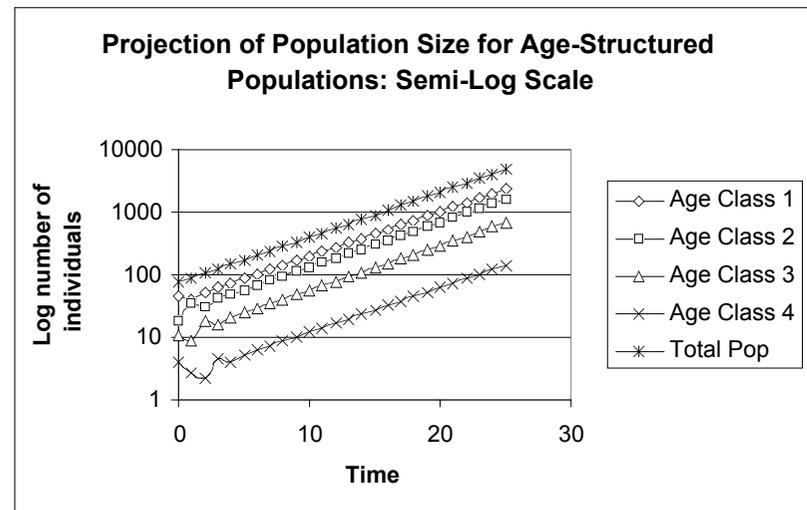
3. Save your work.

Figure 7

QUESTIONS

1. Examine your first graph (Figure 5). What is the nature of the population growth? Is the population increasing, stable, or declining? How does λ_t change with time?

2. Examine your semi-log graph (Figure 7) and your spreadsheet projections (column G). At what point in the 25-year projection does λ_t not change (or change very little) from year to year? When the λ_t's do not change over time, they are an estimate of λ, the asymptotic growth rate, or an estimate of λ in Equation 1 in the Introduction. What is λ for your population, and how does this affect population growth? If you change entries in your Leslie matrix, how does λ change?

3. Return your Leslie matrix parameters to their original values. What is the composition of the population (the proportion of individuals in age class 1, age class 2, age class 3, and age class 4) when the population has reached a stable distribution? Set up headings as shown:

	H	I	J	K
10	**Stable Age Distribution**			
11	**1**	**2**	**3**	**4**

In cell H12, enter a formula to calculate the proportion of the total population in year 25 that consists of individuals in age class 1. Enter formulae to compute the proportions of the remaining age classes in cells I12–K12. Cells H12–K12 should sum to 1 and give the stable age distribution.

4. How does the initial population vector affect λ_t, λ and the stable age distribution? How does it affect λ_t and the age distribution prior to stabilization? Change the initial vector of abundances so that the population consists of 75 individuals in age class 1, and 1 individual in each of the remaining age classes. Graph and interpret your results. Do your results have any management implications?

5. What are the assumptions of the age-structured matrix model you have built?

6. Assume that the population consists of individuals that can exist past age class 4. Suppose that these individuals have identical fertility functions (*F*) as the fourth age class and have a probability of surviving from year t to year $t + 1$ with a probability of 0.25. Draw the life cycle diagram, and adjust your Leslie matrix to incorporate these older individuals. How does this change affect the stable age distribution and λ at the stable age distribution?

LITERATURE CITED

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