13 REPRODUCTIVE VALUE: MATRIX APPROACH

Objectives

- Develop a Leslie matrix population growth model.
- Calculate reproductive values from the matrix model with the "inoculate" method.
- Calculate reproductive values from the matrix model with the "transpose vector" method.
- Evaluate how life history strategy affects reproductive values.

Suggested Preliminary Exercise: Age-Structured Matrix Models

INTRODUCTION

A basic premise in ecology and evolution is that not all individuals are created equal. In ecology, some individuals in a population are more "valuable" than others in terms of the number of offspring they are expected to produce over their remaining lifespan. Take, for example, a hypothetical population that consists of newborns, reproductively active 1-year-olds, reproductively active 2-year-olds, and postreproductive 3-year-olds. Which individuals are likely to produce the greatest number of offspring in the future?

If our population consisted solely of postreproductive individuals, it would go extinct because they are too old to reproduce. Clearly, this age class is not the most valuable in terms of future offspring production. Newborns may be valuable to the population in terms of future offspring because, although they cannot reproduce right now, they have their entire reproductive life ahead of them. However, they must survive to a reproductive age, and their value right now may be low if their chances of making it to a reproductive age in the future are slim. The 1-year-olds are valuable because they have already "made it" to the age of reproduction and are producing young. They may even be more valuable than the 2-year-olds because 2-year-olds are in their final year of breeding. But they may be less valuable than 2-year-olds if they have a slim chance of surviving to a second year *and/or* if they produce fewer offspring than the 2-year-olds.

Biologists are often interested in knowing the value of the different individuals from a practical standpoint because this information can suggest which individuals should be harvested, killed, transplanted, and so forth from a conservation or wildlife management perspective. For example, assuming the numbers of individuals in each age or stage class were equal, if you were trying to eliminate or control a pest species, you would attempt to kill individuals with the highest value because those individuals affect future population size more than any other age group. Conversely, if you were trying to save a threatened species by introducing it into a new area, you would want to "inoculate" the area with individuals of the highest value because those individuals will allow more rapid establishment of a population than other individuals.

An individual's potential for contributing offspring to future generations is called its **reproductive value**. R. A. Fisher introduced the concept of reproductive value in 1930, and defined it as the number of future offspring expected to be produced by an individual of age x over its remaining life span, adjusted by the growth rate of the population. Why the adjustment? To Fisher, the expected number of future offspring wasn't quite the same thing as the "value" of those offspring. Fisher treated offspring like money. If the economy is growing, a dollar received today is worth more than a dollar received next week, because that same dollar will be "diluted" by all the extra money around next week, and even more so in the following year. Similarly, if the population size is changing, the value of future individuals depends on whether the population is increasing, decreasing, or remaining constant over time. The value of each offspring produced by individuals in the future is diluted when the population is increasing (i.e., when the finite rate of increase, λ, is greater than 1), and the value of each offspring is increased when the population is decreasing ($\lambda < 1$). When the population remains constant over time ($\lambda = 1$), no adjustments are needed. (Refer to the next exercise, "Reproductive Value: Life Table Approach," for more details.) To make these adjustments, we divide the expected number of future offspring by the amount the population will have grown or declined when those offspring are produced. The discrete-time version of Fisher's formula to compute v_i, the reproductive value of an individual of age i, is

$$v_i = \sum_{j=i}^{s} \left(\prod_{h=i}^{j-1} P_h \right) F_j \lambda^{i-j-1} \qquad \text{Equation 1}$$

This equation is not so daunting as it might at first appear. Recall that F_j is the fertility of an individual in age class j, and P_h is the probability that an individual in age class h will survive to age class $h + 1$. The Σ symbol indicates that we are summing values starting with the current age class of our individual (i) and going up to the oldest age class (s). Thus, if we are calculating the reproductive value of an individual in age class 2 ($i = 2$), and this species has four age classes ($s = 4$), there will be only three values of j to consider in the summation ($j = 2$, $j = 3$, and $j = 4$). Using these values for i, s, and j, we can expand Equation 1 as follows:

$$\begin{aligned} v_2 &= \sum_{j=2}^{4} \left(\prod_{h=2}^{j-1} P_h \right) F_j \lambda^{2-j-1} \\ &= \left(\prod_{h=2}^{2-1} P_h \right) F_2 \lambda^{2-2-1} + \left(\prod_{h=2}^{3-1} P_h \right) F_3 \lambda^{2-3-1} + \left(\prod_{h=2}^{4-1} P_h \right) F_4 \lambda^{2-4-1} \\ &= \left(\prod_{h=2}^{1} P_h \right) F_2 \lambda^{-1} + \left(\prod_{h=2}^{2} P_h \right) F_3 \lambda^{-2} + \left(\prod_{h=2}^{3} P_h \right) F_4 \lambda^{-3} \end{aligned}$$

The Π symbol is a shorthand for repeated multiplication in the same way that the Σ symbol is a shorthand for repeated addition. For example,

$$\prod_{h=2}^{3} P_h = P_2 P_3$$

Note that in the first product of our expanded expression for v_2 (when $j = 2$), h goes from 2 to 1—a step backwards. In this case, we just consider the product to be equal to 1. We can now complete our expansion of Equation 1 for v_2:

$$v_2 = F_2\lambda^{-1} + P_2F_3\lambda^{-2} + P_2P_3F_4\lambda^{-3}$$

Translating this equation into English, the reproductive value of an individual in age class 2 is its fertility at age class 2 adjusted for one year's population change ($F_2\lambda^{-1}$) plus its fertility at age class 3 adjusted for the probability that it will survive age class 2 and for two years' population change ($P_2F_3\lambda^{-2}$) plus its fertility at age class 4 adjusted for the probability that it will survive age classes 2 *and* 3 and for three years' population change ($P_2P_3F_4\lambda^{-3}$).

As Caswell (2001) states, "The amount of future reproduction, the probability of surviving to realize it, and the time required for the offspring to be produced all enter into the reproductive value of a given age or stage class. Typical reproductive values are low at birth, increase to a peak near the age of first reproduction, and then decline." Individuals that are postreproductive have a reproductive value of 0 since their contribution to future population growth is 0. Newborns also might have low reproductive value because they may have several years of living (and hence mortality risk) before they can start producing offspring. In this exercise, you will calculate reproductive value with matrix calculations. We will begin with a brief review of the major Leslie matrix calculations, and then discuss the reproductive value computations.

Leslie Matrix Calculations

You might recall that an age-based (Leslie) matrix has the form

$$A = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} \qquad \text{Equation 2}$$

The matrix shown is a 4×4 square, which indicates that there are four age classes under consideration. The fertility rates of age classes 1 through 4 are given in the top row. The survival probabilities, P, 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. When the Leslie matrix, **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 new resultant vector is then multiplied by the Leslie matrix to generate the vector of abundances in the next time step. When this process is repeated over time, eventually the population reaches a stable age distribution, in which the proportion of individuals in each age class remains constant over time.

$$\begin{bmatrix} N_{1(t+1)} \\ N_{2(t+1)} \\ N_{3(t+1)} \\ N_{4(t+1)} \end{bmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix} \times \begin{bmatrix} N_{1(t)} \\ N_{2(t)} \\ N_{3(t)} \\ N_{4(t)} \end{bmatrix} \qquad \text{Equation 3}$$

There are two ways to examine reproductive value with matrices. One way is what we call the **inoculate method** (Case 2000). In this method, assume that a number of individuals can be introduced into a completely empty habitat. Should you introduce (inoculate) the habitat with individuals from age class 1, 2, 3, or 4? This approach answers the question *"Which age class will produce the largest population size after the population has reached a stable distribution?"* The answer is the age class with the highest reproductive value. For example, suppose a population has a Leslie matrix with fertilities and survival probabilities as shown in Figure 1. If the habitat was inoculated with 200 individuals from age class 1, the vector of abundances would be 200 individuals from age class 1 and 0 individuals for age classes 2, 3, and 4.

	B	C	D	E	F	G
3	**Leslie matrix**					
4	***1***	***2***	***3***	***4***		***Initial vector***
5	0.0	30.0	100.0	0.0	N_1=	200
6	0.2	0.0	0.0	0.0	N_2=	0
7	0.0	0.2	0.0	0.0	N_3=	0
8	0.0	0.0	0.5	0.0	N_4=	0

Figure 1

We then determine the long-term (asymptotic) λ by running the matrix model until the population has reached a stable distribution. We could repeat the process with a different inoculate, say 200 individuals in age class 2, and 0 individuals in age classes 1, 3, and 4. Although the asymptotic λ will be the same, we can compare the overall size of the population to determine the reproductive value of each age class. The age class "seed" with the highest reproductive value will generate the largest population size. We used this method to generate a hypothetical example in Figure 2, where numbers of individuals were tracked over 10 years for different kinds of inoculates. Age class 1 has the highest reproductive value, followed closely by age class 2.

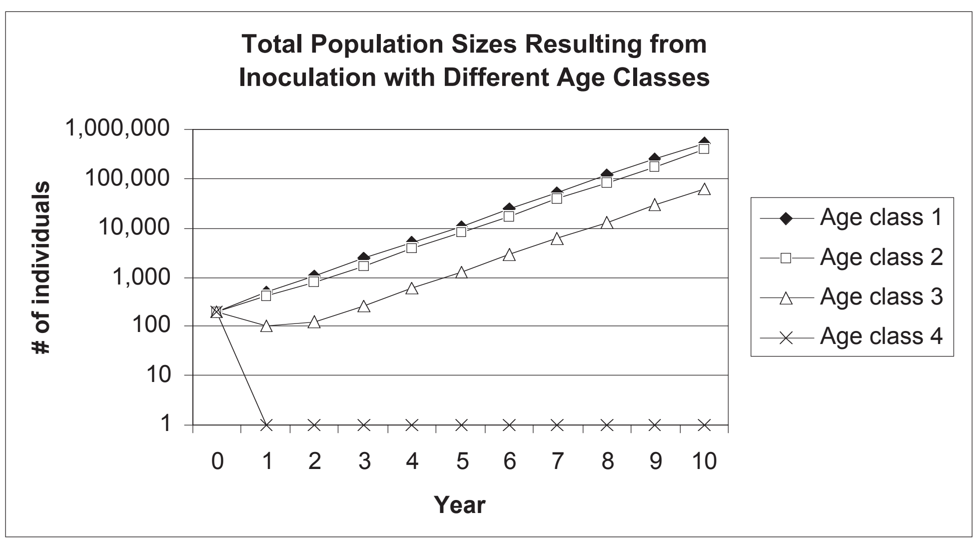

Figure 2

The inoculate method demonstrates clearly the concept of reproductive value, but it is not usually used to *calculate* reproductive value. A faster way to calculate reproductive value involves transposing the Leslie matrix vector and then calculating the proportion of the population that consists of age classes 1, 2, 3, and 4 when the population has reached a stable distribution. This method generates reproductive values very quickly.

Think back once again to your Leslie matrix exercise and how you computed the stable age distribution. You ran your model until λ_t stabilized over time, and computed the proportion of the population that consisted of each age class. These proportions can be written as a vector, **w**. This vector is called a **right eigenvector** of the matrix **A**. For example, the **w** vector for a population that consists of four age classes might be

$$\mathbf{w} = \begin{bmatrix} 0.70 \\ 0.20 \\ 0.05 \\ 0.05 \end{bmatrix}$$

which indicates that when the population growth rate (λ_t) has stabilized, 70% of the total population consists of individuals from age class 1, 20% of the total population consists of individuals from age class 2, 5% of the total population consists of individuals from age class 3, and 5% consists of individuals from age class 4. Thus, the right eigenvector (**w**) of the matrix **A** reveals the stable-age distribution of the population.

In contrast to the right eigenvector, the **left eigenvector** (**v**) of the matrix **A** reveals the reproductive value for each class in the matrix model (Caswell 2001). The simplest way to compute **v** for the **A** matrix is to transpose the **A** matrix (we call the transposed matrix $\mathbf{A}^{\mathrm{T}}$), run the model until the population reaches a stable distribution, and then record the proportions of individuals that make up each class as you did with your original Leslie matrix model. Transposing a matrix simply means switching the columns and rows around—make the rows columns and the columns rows, as in Figure 3.

Original matrix				Transposed matrix		
A	B	C		A	D	G
D	E	F		B	E	H
G	H	I		C	F	I

Figure 3

When λ_t has stabilized for the transposed matrix, $\mathbf{A}^{\mathrm{T}}$, the right eigenvector of $\mathbf{A}^{\mathrm{T}}$ gives the reproductive values for each class. This same vector is called the **left eigenvector** for the original matrix, **A**. (Yes, it is confusing!) A left eigenvector, **v**, for a hypothetical population with four age classes is written as a row vector:

$$\mathbf{v} = \begin{bmatrix} 0.01 & 0.04 & 0.25 & 0.70 \end{bmatrix}$$

Note that the values sum to 1. This vector gives, in order, the reproductive values of age classes 1, 2, 3, and 4. In this hypothetical population, individuals in age class 4 have the greatest reproductive value, followed by individuals in age class 3. The first two age classes have very small reproductive values. Frequently, the reproductive value is **standardized** so that the first stage or age class has a reproductive value of 1. We can standardize the **v** vector above by dividing each entry by the reproductive value of the first age class. Our standardized vector would look like this:

$$\mathbf{v} = \begin{bmatrix} \frac{0.01}{0.01} & \frac{0.04}{0.01} & \frac{0.25}{0.01} & \frac{0.70}{0.01} \end{bmatrix} = \begin{bmatrix} 1 & 4 & 25 & 70 \end{bmatrix}$$

In this example, an individual in age class 4 is 70 times more "valuable" to the population in terms of (adjusted) future offspring production than an individual in age class 1. Let's now go back and consider how Fisher's computation of reproductive value (Equation 1) was derived. Recall that Equation 1 computes v_i, the reproductive value of an individual currently in age class *i*:

$$v_i = \sum_{j=i}^{s}\left(\prod_{h=i}^{j-1} P_h\right)F_j\lambda^{i-j-1}$$

Since our computations for reproductive value assume that λ_t has stabilized, multiplying **v**, the vector with reproductive values of each age class, by the original Leslie matrix, **A**,

$$\begin{pmatrix} v_1 & v_2 & v_3 & v_4 \end{pmatrix} \times \begin{pmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix} \qquad \text{Expression 1a}$$

is the same thing as multiplying **v** by λ:

$$\lambda\begin{pmatrix} v_1 & v_2 & v_3 & v_4 \end{pmatrix} \qquad \text{Expression 1b}$$

To multiply a matrix or vector by a single value, simply multiply each element of the matrix or vector by that value. Thus, Expression 1b is equal to the vector (λv1 λv2 λv3 λv4). Let's assume that reproductive values are standardized such that the reproductive value of age class 1 is 1 (v1 = 1). Since Expression 1a is equal to Expression 1b, we can write

$$\lambda v_1 = v_1 F_1 + v_2 P_1 + v_3 0 + v_4 0 = F_1 + v_2 P_1 \qquad \text{Expression 1c}$$

$$\lambda v_2 = v_1 F_2 + v_2 0 + v_3 P_2 + v_4 0 = F_2 + v_3 P_2 \qquad \text{Expression 1d}$$

$$\lambda v_3 = v_1 F_3 + v_2 0 + v_3 0 + v_4 P_3 = F_3 + v_4 P_3 \qquad \text{Expression 1e}$$

$$\lambda v_4 = v_1 F_4 + v_2 0 + v_3 0 + v_4 0 = F_4 \qquad \text{Expression 1f}$$

Now let's solve for v_1 in terms of only F's, P's and λ to see how these four equations are equivalent to Equation 1. Starting with Expression 1f (and recalling that 1/λ = λ^{-1}), we can compute v_4 as

$$v_4 = F_4\lambda^{-1} \qquad \text{Expression 1g}$$

Now let's plug Expression 1g back into Expression 1e:

$$v_3 = \frac{F_3 + F_4\lambda^{-1}P_3}{\lambda} = F_3\lambda^{-1} + P_3F_4\lambda^{-2} \qquad \text{Expression 1h}$$

Now let's plug Expression 1h back into Expression 1d:

$$\begin{aligned} v_2 &= \frac{F_2 + v_3P_2}{\lambda} = \frac{F_2 + (F_3\lambda^{-1} + P_3F_4\lambda^{-2})P_2}{\lambda} \\ &= F_2\lambda^{-1} + P_2F_3\lambda^{-2} + P_2P_3F_4\lambda^{-3} \end{aligned} \qquad \text{Expression 1i}$$

Note that Expression 1i is the expansion of Equation 1 that we worked out earlier for $i = 2$ and $s = 4$. Finally, substituting Expression 1i into Expression 1c gives:

$$\begin{aligned} v_1 = 1 &= \frac{F_1 + v_2P_1}{\lambda} = \frac{F_1 + (F_2\lambda^{-1} + P_2F_3\lambda^{-2} + P_2P_3F_4\lambda^{-3})P_1}{\lambda} \\ &= F_1\lambda^{-1} + P_1F_2\lambda^{-2} + P_1P_2F_3\lambda^{-3} + P_1P_2P_3F_4\lambda^{-4} \end{aligned}$$

which is the expansion of Equation 1 when $i = 1$ and $s = 4$:

$$v_1 = \sum_{j=1}^{s} \left(\prod_{h=1}^{j-1} P_h \right) F_j \lambda^{-j}$$

PROCEDURES

In this exercise, you'll learn how to calculate the reproductive value of different individuals in a population. You will then be able to alter the Leslie matrix to reflect different life history schedules, and determine how such changes affect the reproductive value of different age classes. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Set up a Leslie matrix.

1. Open a new spreadsheet and set up headings as shown in Figure 4.

	A	B	C	D	E	F	G
1	***Reproductive Value Model: Matrix Approach***						
2							
3		**Leslie matrix**					
4		***1***	***2***	***3***	***4***		***Initial vector***
5		1.6	1.5	0.25	0		200
6		0.8	0	0	0		0
7		0	0.5	0	0		0
8		0	0	0.25	0		0
9							
10		**Age class**					
11	**Time**	**1**	**2**	**3**	**4**	**Total pop**	**λ**

Figure 4

2. Complete the entries in the Leslie matrix in cells B5–E8.

Describe each cell's entry in the space below:

D5 ________________________________

E5 ________________________________

B6 ________________________________

C7 ________________________________

D8 ________________________________

3. Enter the vector of abundances shown in cells G5–G8.

4. Set up a linear series from 0 to 50 in cells A12–A62.

Enter the value 0 in cell A12.
In cell A13, enter **=A12+1**.
Copy your formula down to cell A62.
This will track the growth of our age-structured population for 50 years.

5. Enter formulae in cells B12–E12 that link abundance at time 0 to the initial vector of abundances.

Enter the formulae

- B12 **=G5**
- C12 **=G6**
- D12 **=G7**
- E12 **=G8**

6. Calculate the total population size in Year 0 in cell F12. Copy your formula down one row.

Enter the formula **=SUM(B12:E12)**.

7. Enter formulae in cells B13–E13 to project population growth for Year 1.

Enter 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**

8. Calculate lambda, λ, as N_{t+1}/N_t in cell G12. Copy this formula down to cell G13.

Enter the formula =**F13/F12**.

9. Select cells B13:G13, and copy their formulae down to row 62.

This completes your 50-year projection. Your spreadsheet should look like the one in Figure 5.

	A	B	C	D	E	F	G
1	***Reproductive Value Model: Matrix Approach***						
2							
3				**Leslie matrix**			
4		***1***	***2***	***3***	***4***		***Initial vector***
5		1.6	1.5	0.25	0		200
6		0.8	0	0	0		0
7		0	0.5	0	0		0
8		0	0	0.25	0		0
9							
10				**Age class**			
11	**Time**	**1**	**2**	**3**	**4**	**Total pop**	**λ**
12	0	200	0	0	0	200	2.4
13	1	320	160	0	0	480	2.266666667
14	2	752	256	80	0	1088	2.166176471

Figure 5

10. Graph population growth over time (graph the first 10 years).

Use a semi-log graph and the line graph option, and label your axes fully. The resulting graph should resemble Figure 6. (You may wish to *not* use a semi-log graph because the spreadsheeet will generate a message, "zero values cannot be plotted correctly on log charts." This message will appear frequently if you choose to use a semi-log graph where some entries are 0.)

11. Save your work.

B. Calculate the reproductive value: Inoculate method.

Now we are ready to compute the reproductive values using a matrix approach. There are two ways to generate reproductive values from matrices, the "inoculation" approach and the "transpose vector" approach. We'll start with the inoculation approach. To get an idea of what reproductive value means, we'll inoculate our population with 200 individuals from age class 1 (the other age classes will have 0 individuals), and then record

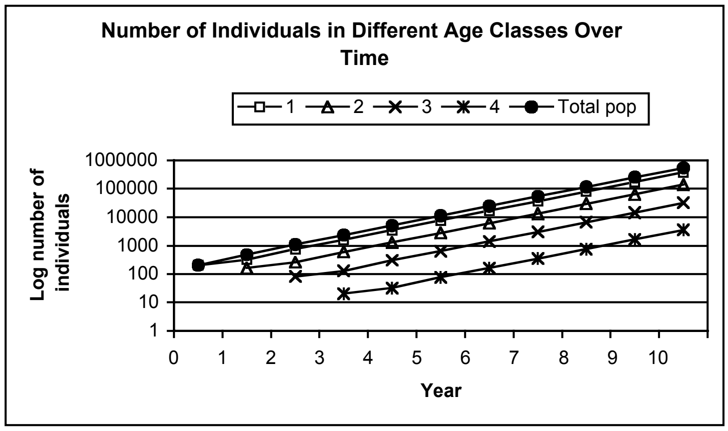

Figure 6

the total population size over 50 years of time in cells I12–I62 (Figure 7). We'll also record final population size at year 50 in cell J5. We'll repeat the process for inoculate of the remaining age classes. For example, for age class 2, our inoculate will consist of 200 individuals of age class 2 (the other age classes will have 0 individuals). We'll record the total population size over 50 years of growth in cells J12–J62. We'll record the final population size at Year 50 in cell J6. The process will be repeated for age classes 3 and 4.

1. Set up new headings as shown in Figure 7.

	I	J	K	L	M
2	**Reproductive value**				
3		Inoculate method		Transpose method	
4	**Age class**	**Final pop size**	**RV**	**RV**	**Standardized**
5	1				
6	2				
7	3				
8	4				
9					
10	**Total pop when initial population consists of only:**				
11	**Age class 1**	**Age class 2**	**Age class 3**	**Age class 4**	

Figure 7

2. Set cell G5 to 200, and the other vector elements in cells G6–G8 to 0.

First we'll inoculate our population with 200 individuals from age class 1. Your projections should be automatically updated. If not, make sure that your Calculation setting is set to automatic (Tools | Options | Calculation).

3. Copy cells F12 to F62 into cells I12 and down.

Use the Paste Special option and paste the values.
By copying the total population size with an inoculate of age class 0, we can determine how "fast" the population grows relative to other kinds of inoculates.

4. Select cell F62; copy and paste its value into cell J5.

Cell F62 gives the total population size at Year 50 when our inoculate consists of 200 individuals from age class 1.

5. Repeat steps 2-4 for the remaining age class inoculates and enter results into appropriate cells.

Your finished spreadsheet should look like Figure 8.

	I	J	K	L	M
2	**Reproductive value**				
3		Inoculate method		Transpose method	
4	**Age class**	**Final pop size**	**RV**	**RV**	**Standardized**
5	1	1.64938E+19			
6	2	1.18204E+19			
7	3	1.89731E+18			
8	4	0			
9					
10	**Total pop when initial population consists of only:**				
11	**Age class 1**	**Age class 2**	**Age class 3**	**Age class 4**	
12	200	200	200	200	
13	480	400	100	0	
14	1088	770	120	0	
15	2356.8	1692	272	0	
16	5124.48	3671.2	589.2	0	

Figure 8

6. Graph population growth from year 0 to year 10 for each of the inoculates.

Use the line graph option and label your axes. Your graph should resemble Figure 9.

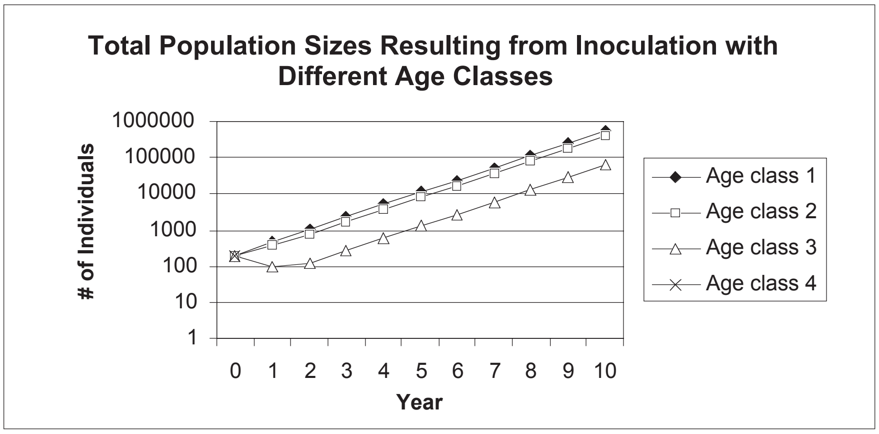

Figure 9

Interpret your graph. Which age class inoculate generated the largest population size after 10 years?

7. Enter the formula **=J5/$J$5** in cell K5; copy your formula down to cell K8. Interpret your results.

Now we can compute reproductive values. As mentioned in the Introduction, reproductive values can be scaled so that the reproductive value of the first age class is 1. The formula **=J5/$J$5** does this scaling. We set cell K5 = 1, then the reproductive values indicate the value of each age class compared to age class 1 (Figure 10).

	I	J	K
3		Inoculate method	
4	**Age class**	**Final pop size**	**RV**
5	1	1.64938E+19	1
6	2	1.18204E+19	0.71665214
7	3	1.89731E+18	0.11503129
8	4	0	0

8. Save your work.

Figure 10

C. Calculate the reproductive value: Transpose vector method.

The second method for computing reproductive values using a matrix approach is the transpose vector approach. It is perhaps quicker than the first approach, and is the method commonly used to compute reproductive values with matrices (Caswell 2001).

The first step is to transpose your Leslie matrix by inverting the rows and columns. For example, if your Leslie matrix has the form

$$\begin{bmatrix} 1.6 & 1.5 & 0.25 & 0 \\ 0.8 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{bmatrix}$$

then the transposed matrix is

$$\begin{bmatrix} 1.6 & 0.8 & 0 & 0 \\ 1.5 & 0 & 0.5 & 0 \\ 0.25 & 0 & 0 & 0.25 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

1. Modify the spreadsheet from section A.

Select cells A3–G12 and open Edit | Copy. Select cell N3 and paste the cells. Modify the heading in row 3 to read "Transposed Leslie Matrix."

2. Set up a linear series from 0 to 50 in cells N12–N62.

3. Select cells O5–R8, and use the **TRANSPOSE** function to transpose the original Leslie matrix (cells B5–E8).

The **TRANSPOSE** formula is an array formula because it is entered into a block of cells rather than a single cell. You may want to review the mechanics of working with an array formula, described on pages 10–11.

Select cells O5–R8 with your mouse. Use the f_x key to select the **TRANSPOSE** function. The dialog box will ask you to define an array that you wish to transpose. Use your mouse to highlight cells B5–E8, or enter this by hand. Instead of clicking OK, press <Control><Shift><Enter> (or <Enter>) and the function will return your transposed matrix.

Once you've obtained your results, examine the formulae in cells O5–R8. This formula should read **{=TRANSPOSE(B5:E8)}**. (Remember that the **{ }** symbols indicate the formula is part of an array. If for some reason you get "stuck" in an array formula, press the <Escape> key and start over.) Your spreadsheet should now look like Figure 11.

	N	O	P	Q	R	S	T
3		**Transposed Leslie matrix**					
4		***1***	***2***	***3***	***4***		***Initial vector***
5		1.6	0.8	0	0		200
6		1.5	0	0.5	0		0
7		0.25	0	0	0.25		0
8		0	0	0	0		0
9							
10		**Age class**					
11	**Time**	**1**	**2**	**3**	**4**	**Total pop**	λ
12	0	200	0	0	0	200	

Figure 11

4. Compute λ in cell T12.

In cell T12 enter the equation **=S13/S12** to compute λ.

5. Enter formulae to project the population over time in cells O13–R13, as you did in Part A.

Enter the formulae

- O13 **=$O$5*O12+$P$5*P12+$Q$5*Q12+$R$5*R12**
- P13 **=$O$6*O12+$P$6*P12+$Q$6*Q12+$R$6*R12**
- Q13 **=$O$7*O12+$P$7*P12+$Q$7*Q12+$R$7*R12**
- R13 **=$O$8*O12+$P$8*P12+$Q$8*Q12+$R$8*R12**

6. Copy cells O13–T13 down to row 62 to complete the projection.

At this point, your population projection should show the same λ values as before. If λ is *not* the same value, you made a mistake somewhere.

7. Calculate the proportion of individuals in age class 1 after 50 years of population growth in cell L5.

Enter the formula **=O62/$S$62** in cell L5. The result should be the unstandardized reproductive value for individuals in age class 1.

8. Compute the reproductive values for the other age classes in cells L6–L8.

Enter the formulae

- L6 **=P62/$S$62**
- L7 **=Q62/$S$62**
- L8 **=R62/$S$62**

The results are your reproductive values.

9. Compute the standardized reproductive values in cells M5–M8.

Once again we need to standardize so that the reproductive value for the first age class is equal to 1. By dividing each value by the value in the first age class, you will set age class 1 to a value of 1, so that the reproductive values of the remaining age classes indicate the reproductive value of a particular class compared to age class 1. We used the following formula:

- M5 **=L5/$L$5**
- M6 **=L6/$L$5**
- M7 **=L7/$L$5**
- M8 **=L8/$L$5**

10. Save your work.

Your results should match the values obtained with the inoculate method, and your spreadsheet should resemble Figure 12.

	I	J	K	L	M
2	**Reproductive value**				
3		Inoculate method		Transpose method	
4	**Age class**	**Final pop size**	**RV**	**RV**	**Standardized**
5	1	1.64938E+19	1	0.54594587	1
6	2	1.18204E+19	0.71665214	0.39125327	0.716652136
7	3	1.89731E+18	0.11503129	0.06280086	0.11503129
8	4	0	0	0	0

Figure 12

D. Create graphs.

1. Graph the reproductive values for the various age classes.

Use the column graph option and label your axes fully. Your graph should resemble Figure 13.

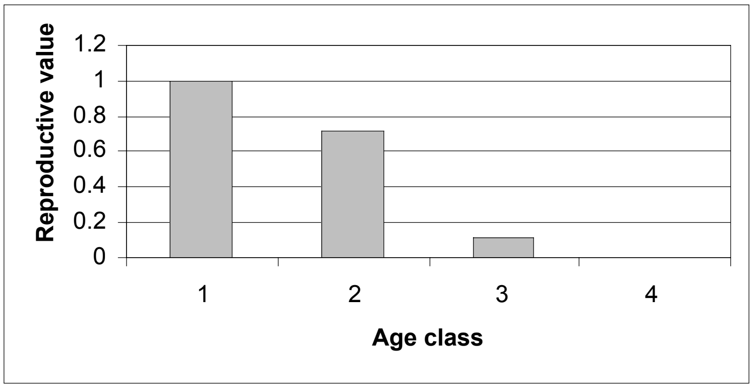

Figure 13

QUESTIONS

1. Interpret the graph from the inoculate method. In what way does the graph show the reproductive values for the various age classes?
2. Interpret the reproductive values from your models from the standpoint of conservation of a game species whose populations are harvested and maintained at a high level, versus a pest species whose populations you would like to reduce or eliminate, versus a threatened species that is being reintroduced to an area. For each situation, which actions would you recommend based on your knowledge of reproductive values (e.g., which age class should be harvested; which age class should be reintroduced?) Does it matter how abundant each age class is when the population stabilizes?
3. Change the Leslie matrix to reflect a population with a Type I survival curve. Compare the reproductive value of the different age classes with a Type I survival schedule versus the original schedule (which was a Type II curve). Use the transpose method to assess reproductive value because your results will automatically be calculated.
4. Change the Leslie matrix to reflect a population with a Type III survival curve. Compare the reproductive value of the different age classes with a Type I and Type II schedule. Use the transpose method to assess reproductive value because your results will automatically be calculated.
5. Find the life history schedule of an organism of interest to you and enter Leslie matrix parameters to the best of your knowledge. How do small changes in different matrix elements affect reproductive value? How might the environment in which your organism resides help shape its life history?

LITERATURE CITED

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