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## SENSITIVITY AND ELASTICITY ANALYSES

### Objectives

- Using the stage-based matrix model for a sea turtle population, conduct a sensitivity analysis of model parameters to determine the absolute contribution of each demographic parameter to population growth rate.
- Conduct an elasticity analysis on model parameters to determine the relative contribution of each demographic parameter to population growth rate.
- Interpret the meaning of the sensitivity and elasticity analyses from a conservation and management perspective.

*Prerequisite Exercise: Stage-Structured Matrix Models*

*Suggested Preliminary Exercises: Reproductive Value Exercises*

### INTRODUCTION

Let's imagine that you are a biologist working for an international conservation organization, and that your task is to suggest the best ways to manage the population of an endangered marine reptile, the sea turtle *Caretta caretta*. You have already constructed a stage-based matrix model (Exercise 14) for the population, and you want to manage it so that population growth,  $\lambda$ , increases. You know that the sea turtle has a complex life cycle, and that individuals can be classified into 1 of 5 classes: hatchlings ( $h$ ), small juveniles ( $sj$ ), large juveniles ( $lj$ ), subadults ( $sa$ ), and adults ( $a$ ). Individuals in each class have a specific probability of surviving; they can *either*: (1) survive and remain in the same class, denoted by the letter  $P$  followed by two identical subscripts (i.e., the probability that a small juvenile remains a small juvenile in the next year is  $P_{sj,sj}$ ); (2) survive and move into the next group, denoted by the letter  $P$  followed by two different subscripts (the probability that a small juvenile will become a large juvenile in the next year is  $P_{sj,lj}$ ); or (3) die, thus exiting the population. Only subadults and adults can breed, and the letter  $F_i$  denotes their fertilities. In this population, turtles are counted every year with a postbreeding census. The matrix for this population (Crowder et al. 1994) has the following form:

$$\mathbf{L} = \begin{bmatrix} P_{h,h} & F_{sj} & F_{lj} & F_{sa} & F_a \\ P_{h,sj} & P_{sj,sj} & 0 & 0 & 0 \\ 0 & P_{sj,lj} & P_{lj,lj} & 0 & 0 \\ 0 & 0 & P_{lj,sa} & P_{sa,sa} & 0 \\ 0 & 0 & 0 & P_{sa,a} & P_{a,a} \end{bmatrix}$$

Given the above  $\mathbf{L}$  matrix, the population reaches a stable stage distribution with all stage classes declining by 5% per year, or  $\lambda = 0.95$ . Your task is to suggest the best ways to manage the turtle population to increase the long-term asymptotic  $\lambda$ , and hence increase the population size. But  $\lambda$  can be increased in a variety of ways! Should you focus your efforts on increasing adult fertility? Should you focus your efforts on increasing the probability that hatchlings in year  $t$  will become small juveniles in year  $t + 1$ ? Or should you focus on increasing survivorship of adults? Finances and resources are limited, so it is not likely that you can do all these things at once.

In this exercise, you will extend the stage-based model you developed for *Caretta caretta* to conduct a **sensitivity** and/or **elasticity** analysis of each model parameter. These analyses will tell you how  $\lambda$ , population size, and the stable distribution might change as we alter the values of  $F_i$  and  $P_i$  in the  $\mathbf{L}$  matrix.

### Sensitivity Analyses

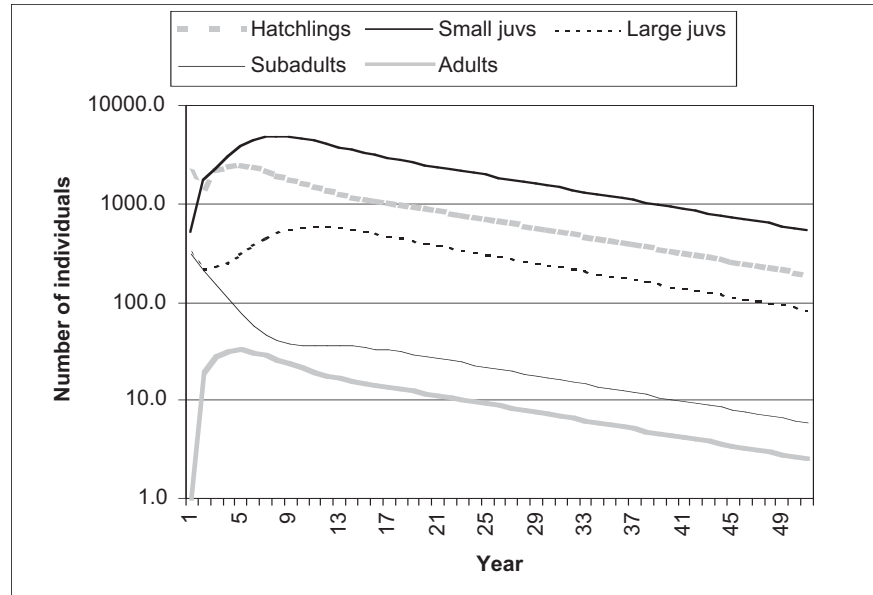
**Sensitivity analysis** reveals how very small changes in each  $F_i$  and  $P_i$  will affect  $\lambda$  when the other elements in the  $\mathbf{L}$  matrix are held constant. These analyses are important from several perspectives. From a conservation and management perspective, sensitivity analysis can help you identify the life-history stage that will contribute the most to population growth of a species. From an evolutionary perspective, such an analysis can help identify the life-history attribute that contributes most to an organism's fitness.

Conducting sensitivity analysis requires some basic knowledge of matrix algebra. While we will not delve into matrix formulations in detail here (see Caswell 2001), we will very briefly overview the concepts associated with sensitivity analysis. In the stage-based matrix models you developed earlier, you projected population size from time  $t$  to time  $t + 1$  by multiplying the  $\mathbf{L}$  matrix by a vector of abundance,  $\mathbf{n}$ , at time  $t$ . (Remember that uppercase boldface letters indicate a matrix, and lowercase boldface letters indicate a vector.) The result was a vector of abundances,  $\mathbf{n}$ , at time  $t + 1$ :

$$\mathbf{n}(t + 1) = \mathbf{L} \times \mathbf{n}(t) \quad \text{Equation 1}$$

After attaining the new vector of abundances, you repeated the process for the next time step and attained yet another vector of abundances. When the process was repeated over many time steps, eventually the system reached a stable stage distribution, where  $\lambda_t$  remained constant from one time step to the next. This stabilized  $\lambda_t$  is called the long-term or **asymptotic population growth rate**,  $\lambda$ . In the sea turtle exercise, the population stabilized within 100 years. If  $\lambda > 1$ , the numbers of individuals in the population increase geometrically; if  $\lambda < 1$ , the numbers of individuals in the population decline geometrically; and when  $\lambda = 1$ , the numbers of individuals in the population remain constant in numbers over time. Since  $\lambda = 0.95$  for the sea turtle population, number of individuals in the population decreases geometrically at 5% per time step. Graphically, the point in time in which the population reaches a stable stage distribution is the point where the population growth lines for *each* class become parallel (Figure 1). When  $\lambda_t$  has stabilized, the population can be described in terms of the *proportion* of each stage in the total population. When the population stabilizes, these proportions remain constant regardless of the value of  $\lambda$ .

Thus, given a matrix,  $\mathbf{L}$ , you can determine the stable stage distribution of individuals among the different classes, and the value of  $\lambda$  at this point. The value of  $\lambda$  when the population has stabilized is called an **eigenvalue** of the matrix. An **eigenvalue** is a



**Figure 1** The stage distribution of a population becomes stable when changes in numbers over time for each growth stage are parallel, regardless of the value of  $\lambda$ . At this point the proportion of each stage in the population remains the same into the future.

number (numbers in matrix algebra are called scalars) that, when multiplied by a vector of abundances, yields the same result as the  $L$  matrix multiplied by the same vector of abundances. For example, if  $\lambda$  is 1.15, the numbers of individuals in each class will increase by 15% from time step  $t$  to time step  $t + 1$ . If  $\lambda$  instead is 0.97, the numbers of individuals in each class will decrease by 3% from time step  $t$  to time step  $t + 1$ .

In order to conduct a sensitivity analysis on the parameters in the  $L$  matrix, we need to determine the stable-stage distribution of the population. For sea turtles, this was 23.9% hatchlings, 64.8% small juveniles, 10.3% large juveniles, 0.7% subadults, and 0.3% adults. We can convert these percentages into the proportions 0.239, 0.648, 0.103, 0.007, and 0.003. This vector of proportions is called a **right eigenvector** of the  $L$  matrix. The right eigenvector is represented by the symbol  $w$ . The  $w$  vector for the sea turtle population can be written as a column vector, where the first entry gives the proportion of the stabilized population that consists of hatchlings, and the last entry gives the proportion of the stabilized population that consists of adults:

$$w = \begin{bmatrix} .239 \\ .648 \\ .103 \\ .007 \\ .003 \end{bmatrix}$$

Note that the values sum to 1.

The final piece of information needed for compute sensitivities for the values of  $F_i$  and  $P_i$  in the  $L$  matrix is the **left eigenvector**, represented by the symbol  $v$ . The left eigenvector of the  $L$  matrix reveals the reproductive value for each class in the model. If you have completed the exercises on reproductive value, you know that reproductive value computes the “worth” of individuals of different classes (age, stage, or size) in terms of future offspring it is destined to contribute to the next generation, adjusted for the growth rate of the population (Fisher 1930). As Caswell (2001) states, “The amount of future reproduction, the probability of surviving to realize it, and the time required for the off-

spring 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 value of 0, since their contribution to future population growth is 0. Sea turtle newborns also may have low reproductive value because they probably have several years of living (and hence mortality risk) before they can start producing offspring

We need to compute the reproductive values for each class in order to conduct a sensitivity analysis of the  $F_i$ 's and  $P_i$ 's for the sea turtle population. The simplest way to compute  $\mathbf{v}$  for the  $\mathbf{L}$  matrix is to transpose the  $\mathbf{L}$  matrix, called  $\mathbf{L}'$ , then run the model until the population reaches a stable distribution, and then record the proportions of individuals that make up each class as with the  $\mathbf{w}$  vector. Transposing a matrix simply means switching the columns and rows around: Make the rows columns and the columns rows, as shown in Figure 2.

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

Figure 2

When  $\lambda$  is computed for the transposed matrix  $\mathbf{L}'$ , the right eigenvector of  $\mathbf{L}'$  gives the reproductive values for each class. This same vector is called the left eigenvector for the original matrix,  $\mathbf{L}$ . (Yes, it is confusing!) The  $\mathbf{v}$  vector for the sea turtle population is written as a row vector:

$$\mathbf{v} = [.002 \quad .003 \quad .013 \quad .207 \quad .776]$$

This vector gives, in order, the reproductive values of hatchlings, small juveniles, large juveniles, subadults, and adults. In this population, adults have the greatest reproductive value, followed by subadults. Large juveniles, small juveniles, and hatchlings have very small reproductive values. Oftentimes the reproductive value is standardized so that the first stage or age class has a reproductive value of 1. We can standardize the  $\mathbf{v}$  vector above by dividing each entry by 0.002 (the reproductive value of hatchlings) to generate standardized reproductive values. Our standardized vector would look like this:

$$\mathbf{v} = \left[ \begin{array}{ccccc} .002 & .003 & .013 & .207 & .776 \\ .002 & .002 & .002 & .002 & .002 \end{array} \right] = [1 \quad 1.4 \quad 7.5 \quad 115.6 \quad 434.4]$$

Thus, an adult individual is 434.4 times more “valuable” to the population in terms of future, adjusted offspring production than a single hatchling.

### Computing Sensitivities

Now we are ready to explore how the sensitivities of each  $P_i$  and  $F_i$  in the  $\mathbf{L}$  matrix are computed. Remember that sensitivity analyses reveal how very small changes in each  $F_i$  and  $P_i$  will affect  $\lambda$  when the other elements in the  $\mathbf{L}$  matrix are held constant. The steps for conducting a sensitivity analysis include: (1) running the projection model until the population reaches a stable distribution, (2) calculating the stable stage structure of the population, which is given by the vector  $\mathbf{w}$ , and (3) calculating the reproductive values for the different size classes, which is given by the vector  $\mathbf{v}$ . The sensitivity,  $s_{ij}$ , of an element in the  $\mathbf{L}$  matrix,  $a_{ij}$ , is given by

$$s_{ij} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{Equation 2}$$

where  $v_i$  is the  $i$ th element of the reproductive value vector,  $w_j$  is the  $j$ th element of the stable stage vector, and  $\langle \mathbf{w}, \mathbf{v} \rangle$  is the product of the  $\mathbf{w}$  and  $\mathbf{v}$  vectors, which is a single number (a **scalar**). Thus, the sensitivity of  $\lambda$  to changes in  $a_{ij}$  is proportional to the product of the  $i$ th element of the reproductive value vector and the  $j$ th element of the stable stage vector (Caswell 2001). You'll see how these calculations are made as you work through the exercise. We can also write Equation 2 as a partial derivative, because all but one of the variables of which  $\lambda$  is a function are being held constant:

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad \text{Equation 3}$$

How are the  $s_{ij}$ 's to be interpreted? A sensitivity analysis, for example, on the  $P_{aa}$  and  $F_{sa}$  might yield values of 0.1499 and 0.2287, respectively. These values answer the question, "If we change  $P_{aa}$  by a small amount in the  $\mathbf{L}$  matrix and hold the remaining matrix entries constant, what is the corresponding change in  $\lambda$ ?" The sensitivity of the  $P_{aa}$  matrix entry means, for example, that a small unit change in  $P_{aa}$  results in a change in  $\lambda$  by a factor of 0.1499. In other words, *sensitivity is represented as a slope*.

The most sensitive matrix elements produce the largest slopes, or the largest changes in the asymptotic growth rate  $\lambda$ . In our example above, where sensitivities were 0.1499 for the  $P_{aa}$  entry and 0.2287 for the  $F_{sa}$  entry, small changes in adult survival will not have as large an effect as changes in subadult fertility in terms of increasing growth, so you would recommend management efforts that aim to increase subadult fertility values.

### Elasticity Analysis

One challenge in interpreting sensitivities is that demographic variables are measured in different units. Survival rates are probabilities and they can only take values between 0 and 1. Fertility, on the other hand, has no such restrictions. Therefore, the sensitivity of  $\lambda$  to changes in survival rates may be difficult to compare with the sensitivities of fertility rates. This is where elasticities come into play. Elasticity analysis estimates the effect of a *proportional* change in the vital rates on population growth. The elasticity of a matrix element,  $e_{ij}$ , is the product of the sensitivity of a matrix element ( $s_{ij}$ ) and the matrix element itself ( $a_{ij}$ ), divided by  $\lambda$ . In essence, elasticities are proportional sensitivities, scaled so that they are dimensionless:

$$e_{ij} = \frac{a_{ij} s_{ij}}{\lambda} \quad \text{Equation 4}$$

Thus, you can directly compare elasticities among all life history variables. An elasticity analysis, for example, on the parameters hatchling survival and adult fecundity might yield values of 0.047 and 0.538, respectively. This means that a 1% increase in hatchling survival will cause 0.047% increase in  $\lambda$ , while a 1% increase in adult fecundity will cause a 0.538% increase in  $\lambda$ . In this situation, you would recommend management efforts that aim to increase adult fecundity values.

## PROCEDURES

The goal of this exercise is to introduce you to matrix methods of computing sensitivities and elasticities for the vital population parameters,  $P$  and  $F$ , for a population with stage structure. As always, save your work frequently to disk.

**INSTRUCTIONS**

**A. Set up the spreadsheet.**

1. Open the stage-based matrix model you created in Exercise 14 and save it under a new name. Retitle cell A1 to “Sensitivity and Elasticity Analysis.”

2. Enter the values shown in cells B4–F8. (You may have changed these values in your previous exercise).

**B. Calculate  $w$ , the stable-stage vector.**

1. Set up new column headings as shown in Figure 4.

2. In cell X5, calculate the proportion of total population in year 100 that consists of hatchlings.

**ANNOTATION**

Your spreadsheet headings should resemble Figure 3.

	A	B	C	D	E	F	G	H
1	<b>Sensitivity and Elasticity Analysis</b>							
2	<b>Loggerhead Sea Turtle Population</b>							<b>Initial population</b>
3		<b>F(h)</b>	<b>F(sj)</b>	<b>F(lj)</b>	<b>F(sa)</b>	<b>F(a)</b>		<b>vector</b>
4	<b>Hatchlings:</b>	0	0	0	4.665	61.896		2000
5	<b>Small juveniles:</b>	0.675	0.703	0	0	0		500
6	<b>Large juveniles:</b>	0	0.047	0.657	0	0		300
7	<b>Subadults:</b>	0	0	0.019	0.682	0		300
8	<b>Adults:</b>	0	0	0	0.061	0.8091		1
9								
10	<b>Year</b>	<b>Hatchlings</b>	<b>Small juvs</b>	<b>Large juvs</b>	<b>Subadults</b>	<b>Adults</b>	<b>Total</b>	$\lambda_t$

**Figure 3**

The stable stage distribution vector,  $w$ , is simply the proportion of individuals in the population that is made up of the different stage classes.

	X
3	<b>Stable stage distribution</b>
4	<b>vector, <math>w</math></b>
5	
6	
7	
8	
9	

**Figure 4**

The first entry, cell X5, is the proportion of the population that is made up of hatchlings (given that the population has reached a stable distribution). The second entry, cell X6, is the proportion of the population that is made up of small juveniles. Cells X7 and X8 will contain the proportions of large juveniles and subadults, and the last entry, cell X9, will contain the proportions of adults.

Enter the formula `=B111/$G$111` in cell X5.

In Exercise 14, you calculated the number of individuals in each class when the population has stabilized (remains constant over time). You might recall that the population stabilized at  $\lambda = 0.95$ , and that the stable population consists of 16.22 hatchlings, 44.05 small juveniles, 7.03 large juveniles, 0.50 subadults, and 0.21 adults. To calculate the  $w$  vector, we need to present these numbers in terms of proportions of the total population size. Rather than entering these values by hand, the above formula references the *proportion* of hatchlings listed in the last year of the projection.

3. In cells X6-X9, compute the proportions in the remaining classes.

4. Save your work. Your spreadsheet should now resemble Figure 5.

**C. Calculate  $v$ , the reproductive value vector.**

1. Set up new column headings as shown in Figure 6. Enter only the headings for now.

2. Use the **TRANSPOSE** function to transpose the original matrix, given in cells B4-F8, into cells K4-O8. Your spreadsheet should resemble Figure 7.

We entered the formulae

- X6 =C111/\$G\$111
- X7 =D111/\$G\$111
- X8 =E111/\$G\$111
- X9 =F111/\$G\$111

These equations assume the population has stabilized by year 100.

	X
3	<b>Stable stage distribution</b>
4	<b>vector, w</b>
5	0.239
6	0.648
7	0.103
8	0.007
9	0.003

**Figure 5**

The  $v$  vector gives the reproductive values for members in different stages of the population. The easiest way to do this is to transpose your original population matrix, then run the same type of analysis you ran to determine the  $w$  vector. *Transposing* a matrix simply means you interchange the rows and columns.

	I	J	K	L	M	N	O	P
1								
2			Reproductive value: transposed matrix					
3								
4		$F(h)$						
5		$F(sj)$						
6		$F(lj)$						
7		$F(sa)$						
8		$F(a)$						
9								
10	Year	Hatchlings	Small juvs	Large juvs	Subadults	Adults	Total	$\lambda_t$

**Figure 6**

The **TRANSPOSE** function in Excel is an array function. The mechanics of entering an array formula are a bit different than the typical (single cell) formula entry. Instead of selecting a single cell to enter a formula, you need to select a series of cells, then enter a formula, then press <Control>+<Shift>+<Enter> (Windows machines) to enter the formula for all of the cells you have selected. This function works best when you use the  $f_x$  key and follow the cues for entering a formula.

Select cells K4-O8 with your mouse, then use your  $f_x$  key to select Transpose. A dialog box will appear asking you to define an array that you wish to transpose. Use your mouse to highlight cells B4-F8, or enter this by hand. Instead of clicking OK, press <Control>+<Shift>+<Enter>, and the spreadsheet will return your transposed matrix. After you've obtained your results, examine the formulae in cells K4-O8. Your formula should look like this: {=TRANSPOSE(B4:F8)}. The { } symbols indicate that 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.

	J	K	L	M	N	O
2	Reproductive value: transposed matrix					
3						
4	$F(h)$	0	0.675	0	0	0
5	$F(sj)$	0	0.703	0.047	0	0
6	$F(lj)$	0	0	0.657	0.019	0
7	$F(sa)$	4.665	0	0	0.682	0.061
8	$F(a)$	61.896	0	0	0	0.8091

Figure 7

3. Set up a linear series from 0 to 100 in cells I11–I111.

4. Link the starting number of individuals of each class in year 0 to the original vector of abundances in cells H4–H8.

5. In cell O11, compute the total number of individuals in year 0.

6. In cell P11, enter a formula to compute  $\lambda_t$  for year 0.

7. Project the population over time as you did in your turtle matrix model, using the values from the transposed matrix for your calculations.

8. Compute  $\lambda_t$  for Year 1. Copy cells J12–P12 down to row 111 to complete the projection.

9. Set up new column headings as shown in Figure 8.

Enter 0 in cell I11.

Enter  $=1+I11$  in cell I12. Copy this formula down to cell I111.

You'll need to stick with the same initial population vector of abundances you used earlier in the exercise. We used the following formulae:

- J11 =H4
- K11 =H5
- L11 =H6
- M11 =H7
- N11 =H8

Enter the formula  $=SUM(J11:N11)$  in cell O11.

Enter the formula  $=O12/O11$  in cell P11.

We used the following formulae:

- J12 = $\$K\$4*J11+\$L\$4*K11+\$M\$4*L11+\$N\$4*M11+\$O\$4*N11$
- K12 = $\$K\$5*J11+\$L\$5*K11+\$M\$5*L11+\$N\$5*M11+\$O\$5*N11$
- L12 = $\$K\$6*J11+\$L\$6*K11+\$M\$6*L11+\$N\$6*M11+\$O\$6*N11$
- M12 = $\$K\$7*J11+\$L\$7*K11+\$M\$7*L11+\$N\$7*M11+\$O\$7*N11$
- N12 = $\$K\$8*J11+\$L\$8*K11+\$M\$8*L11+\$N\$8*M11+\$O\$8*N11$
- O12 = $SUM(J12:N12)$
- P12 = $O13/O12$

You should see that  $\lambda_t$  stabilizes at the same value it did for your original projections.

	Q	R	S	T	U	V	W
3				Small	Large		
4			Hatchlings	juveniles	juveniles	Subadults	Adults
5	v = reproductive value vector =						
6	Standardized reproductive value =						

Figure 8

10. In cell S5 enter a formula to compute the reproductive value of the hatchling stage.

11. In cells T5–W5, enter formulae to compute the reproductive value of the remaining stages.

12. Double-check your work.

13. In cells S6–W6, calculate the *standardized reproductive value* for each stage class.

14. Save your work.

**D. Calculate sensitivities of matrix parameters.**

1. Set up new column headings as shown in Figure 10. Enter only the headings (literals) for now.

Enter the formula =J111/\$O\$111 in cell S5.

As you did in computing the **w** vector, enter formula in these cells to reference the proportions listed in the last year of the projection. Thus, cell S5 gives the proportion of “hatchlings” in Year 100.

We entered the following formulae:

- T5 =K111/\$O\$111
- U5 =L111/\$O\$111
- V5 =M111/\$O\$111
- W5 =N111/\$O\$111

Cells S5–W5 should sum to 1.

Enter the formula =S5/\$S\$5 in cell S6. Copy this formula across to cell W6.

Reproductive values are often standardized such that the reproductive value of the first class (hatchlings) is 1. To standardize the reproductive values, divide each value by the value obtained for hatchlings. Your spreadsheet should now resemble Figure 9.

	Q	R	S	T	U	V	W
3				Small	Large		
4			Hatchlings	juveniles	juveniles	Subadults	Adults
5	v = reproductive value vector =		0.0018	0.0025	0.0133	0.2065	0.7759
6	Standardized reproductive value =		1.0	1.4	7.5	115.6	434.4

Figure 9

Now that you have calculated the **w** and **v** vectors, you are ready to perform a sensitivity analysis.

	R	S	T	U	V	W
7						
8	X = <w,v> =					
9						
10	Sensitivity matrix					
11			F(sj)	F(lj)	F(sa)	F(a)
12	Hatchlings					
13	Small juveniles					
14	Large juveniles					
15	Subadults					
16	Adults					
17						
18						
19	Elasticity matrix					
20		F(h)	F(sj)	F(lj)	F(sa)	F(a)
21	Hatchlings					
22	Small juveniles					
23	Large juveniles					
24	Subadults					
25	Adults					
26						

Figure 10

2. In cell S8, use the **MMULT** (matrix multiplication) function to multiply the **v** vector by the **w** vector.

3. In cell S12–W12, enter formulae to compute the sensitivity of fertility rates for each stage over time.

4. Copy cells S12–W12 down to cells S16–W16. Save your work.

### *E. Calculate elasticities of matrix parameters.*

1. In cell S21–W21, enter formulae to calculate the elasticity values for fertility at each stage for year 0.

2. Copy the formulae over the remaining years of the analysis.

3. Save your work.

### *F. Create graphs.*

1. Graph the elasticity values for fertility of the various stage classes.

Enter the formula **=MMULT(S5:W5,X5:X9)** in cell S8.

The **MMULT** function returns the matrix product of two arrays. The result is an array with the same number of rows as array 1 and the same number of columns as array 2. In our case, it ends up being a single digit (since our **v** vector consists of one row and our **w** vector consists of one column). This value is the denominator  $\langle \mathbf{w}, \mathbf{v} \rangle$  of the formula for calculating sensitivity values (Equation 3). This single-digit result is called a scalar; for purposes of the spreadsheet, we will call this value  $X$ .

Now you are ready to calculate the numerator of the sensitivities, and compute the sensitivity values for each entry in your matrix. Note that sensitivities are computed for all matrix entries, even those that are 0 in the original **L** matrix. For example, you will compute the sensitivity of subadult fertility ( $F_{sa,h}$ ) even though subadults cannot reproduce. This sensitivity value will allow you to answer, “If I could make subadults reproduce, it would increase  $\lambda$  at this rate. You may wish to shade the **L** matrix entries that have original cell entries that are equal to 0 a different color (as shown in Step 1).

Sensitivity of a population growth rate to changes in the  $a_{ij}$  element is simply the  $i$ th entry of **v** times the  $j$ th entry of **w**, divided by  $X$ . For example, to calculate the sensitivity of fertility rate of subadults (row 1, column 4), we would multiply the first element in the **v** vector by the fourth element in the **w** vector, and then divide that number by  $X$ . The formula in cell V12 would be **=(X8\*S5)/S8**. Enter formula in the remainder of the sensitivity matrix. Below are the formulae we used (note that we used absolute references for some cell addresses).

- S12 **=(X5\*S5)/S8**
- T12 **=(X6\*S5)/S8**
- U12 **=(X7\*S5)/S8**
- V12 **=(X8\*S5)/S8**
- W12 **=(X9\*S5)/S8**

Adjust your formulae in the formula bar to reference the appropriate cells in the **v** and **w** vectors. For example, in row 13, replace the reference to cell S6 with T5. In row 14, replace the reference to cell S7 with V5, etc. This completes the sensitivity analysis.

Enter the formula **=(B4\*S12)/H110** in cell S21. Copy this formula across to cell W21. The elasticity of  $a_{ij}$  is the sensitivity of  $a_{ij}$  times the value of  $a_{ij}$  in the original matrix, divided by  $\lambda$  when  $\lambda_t$  has stabilized. For example, the elasticity calculation of fecundities of the subadults would be **=(E4\*V12)/H110**. If the original matrix element was a 0 (such as the fecundities of the hatchling stage), the elasticity should be 0.

Copy the formulae in cells S21–W21 down to cells S25–W25. This will complete the elasticity analysis. The sum of the elasticities should add to be 1, since each elasticity value measures the proportional contribution of each element to  $\lambda$  (yours might be off by a bit due to rounding error).

Use a column graph and label your axes fully. Your graph should resemble Figure 11.

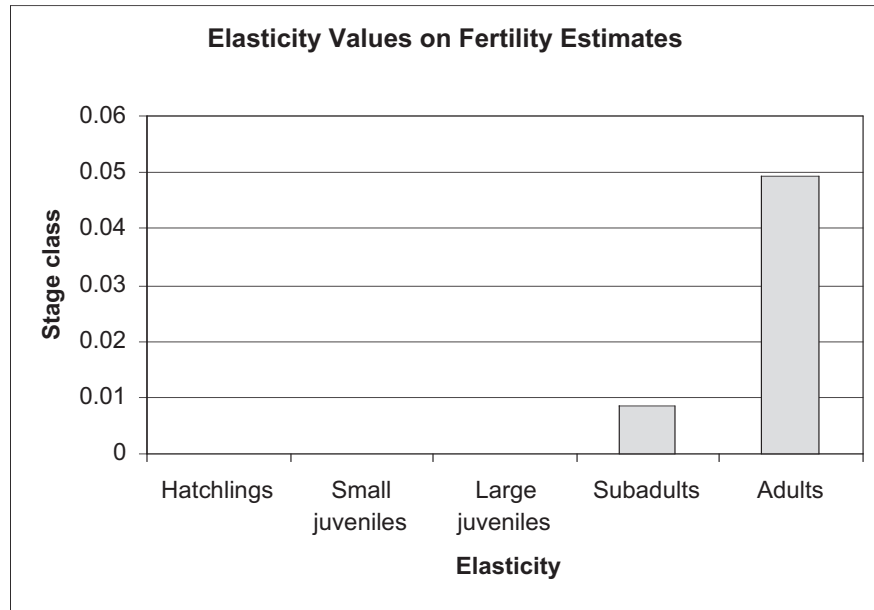


Figure 11

2. Graph the elasticity values for the survival values,  $P_{i,i}$  and  $P_{i,i+1}$  for each stage class.

You will have to manually select bars within the graph and color-code them to reflect within-stage survival ( $P_{i,i}$ ) or survival to the next stage ( $P_{i,i+1}$ ). Your graph should resemble Figure 12.

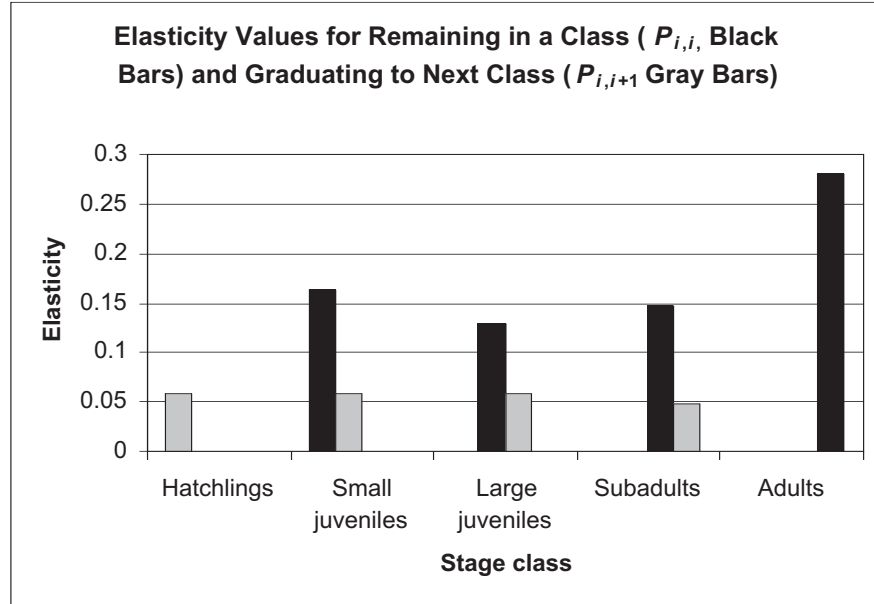


Figure 12

3. Save your work.

## QUESTIONS

1. Fully interpret the meaning of your sensitivity analysis. What management recommendations can you make for sea turtle conservation given your analysis?
2. Fully interpret the meaning of your elasticity analysis. What management recommendations can you make for sea turtle conservation given your elasticity analysis? Would your recommendations be different if you simply examined the sensitivities, and ignored elasticities? Which do you think is more appropriate for guiding management decisions?
3. As with all models in ecology and evolution, elasticity and sensitivity analyses have their assumptions (and weaknesses). Let's say you make some recommendations for sea turtle conservation based on the matrix parameters provided in the exercise. What kinds of assumptions are implicit in the model parameters? (What do you need to know about how the data were collected and the environmental and biological conditions in which the data were collected?)

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