Problem Set #8: Sensitivity and Elasticity Analyses

Objectives

- Using a stage-based matrix model for a Loggerhead 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.

Introduction

Let's imagine that you are a biologist working for an international conservation organization and your task is to suggest the best ways to manage the population of an endangered marine reptile, the loggerhead sea turtle, *Caretta caretta.* Let's say that you have already constructed a stage-based matrix model for the population and you want to manage it so that population growth, λ, increases. You know that loggerhead sea turtles have a complex life cycle, and that individuals can be classified into 1 of 5 stages: hatchlings (*h*), small juveniles (*sj*), large juveniles (*lj*), subadults (*sa*), and adults (*a*). Individuals in each stage have a specific probability of surviving; they can *either:*

1. survive and remain in the same stage class, denoted by the letter *P* followed by 2 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 stage class, denoted by the letter *P* followed by 2 different subscripts (i.e., 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. Turtles in our population are counted every year postbreeding. 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 this **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 λ, and hence increase the population size. But λ, of course, 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? As always, finances and resources are limited, so it is not likely that you can do all these things at once.

In this problem set, you will extend a stage-based model developed for loggerhead sea turtles to conduct a **sensitivity** and/or **elasticity** analysis of each model parameter. These analyses will inform you on how λ, population size, and the stable distribution might change as we alter the values of F_i and P_i in the **L** matrix.

Sensitivity Analyses

Sensitivity analysis reveals how very small changes in each F_i and P_i will affect λ when the other elements in the **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 for a comprehensive discussion), we will very briefly overview the concepts associated with sensitivity analysis.

In stage-based matrix models, the population size is projected from time t to time $t + 1$ by multiplying the **L** matrix by a vector of abundance, **n**, at time t (in matrix algebra, uppercase boldface letters (**L**) indicate a matrix and lowercase boldface letters (**n**) indicate a vector). The result is a vector of abundances, **n**, at time $t + 1$:

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

After attaining a new vector of abundances, the process is repeated for the next time step; yet another vector of abundances is attained. When the process is repeated over many time steps, eventually the system reaches a stable stage distribution, where λ_t remains constant from 1 time step to the next. This stabilized λ_t is called the long-term or **asymptotic population growth rate**, λ. In our sea turtle example, the population stabilizes 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 our sea turtle population, the 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 λ_t has stabilized, the population can be described in terms of the *proportion* of each stage class in the total population. When the population stabilizes, these proportions remain constant regardless of the value of λ.

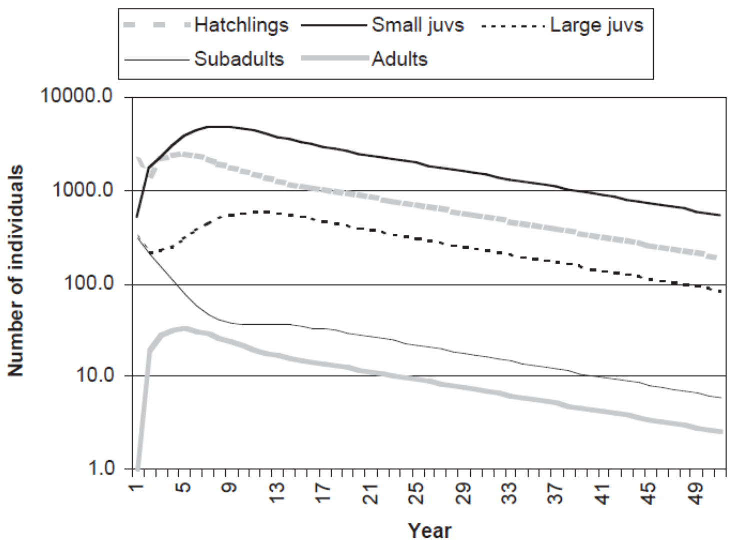

Figure 1. The stage distribution of a population becomes stable when changes in numbers over time for each growth stage are parallel, regardless of the value of λ. At this point the proportion of each stage in the population remains the same into the future.

Thus, given a matrix, **L**, you can determine the stable stage distribution of individuals among the different classes, and the value of λ at this point. The value of λ when the population has stabilized is called an **eigenvalue** of the matrix. An **eigenvalue** is a 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 λ is 1.15, the numbers of individuals in each class will increase by 15% from time step t to time step $t + 1$. If λ 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 proportions: 0.239, 0.648, 0.103, 0.007, and 0.003, respectively. 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 our loggerhead 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:

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

Note that the values sum to 1.

The final piece of information needed to compute sensitivities for the values of F_i and P_i in the 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. 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 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 value of 0, since their contribution to future population growth is 0. Loggerhead 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 **v** for the **L** matrix is to transpose the **L** matrix, called **L**′, then run the model until the population reaches a stable distribution, and then to record the proportions of individuals that make up each class as with the **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. Transposing a matrix.

When λ is computed for the transposed matrix **L**′, the right eigenvector of **L**′ gives the reproductive values for each class. This same vector is called the left eigenvector for the original matrix, **L**. (Yes, it is confusing!) The **v** vector for our loggerhead sea turtle population is written as a row vector:

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

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 (by far), 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 **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:

$$\mathbf{v} = \begin{bmatrix} \frac{.002}{.002} & \frac{.003}{.002} & \frac{.013}{.002} & \frac{.207}{.002} & \frac{.776}{.002} \end{bmatrix} = \begin{bmatrix} 1 & 1.4 & 7.5 & 115.6 & 434.4 \end{bmatrix}$$

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

Computing Sensitivities

Now we are ready to explore how the sensitivities of each P_i and F_i in the **L** matrix are computed. Remember that sensitivity analyses reveal how very small changes in each F_i and P_i will affect λ when the other elements in the **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 **w**; and

3. Calculating the reproductive values for the different stage classes, which is given by the vector **v**.

The sensitivity, s_{ij}, of an element in the **L** matrix, a_{ij}, is given by

$$s_{ij} = \frac{v_i w_j}{<\mathbf{w},\mathbf{v}>} \qquad \text{Equation 2}$$

where v_i is the ith element of the reproductive value vector, w_j is the jth element of the stable stage vector, and $<\mathbf{w},\mathbf{v}>$ is the product of the **w** and **v** vectors, which is a single number (a **scalar**). Thus, the sensitivity of λ to changes in a_{ij} is proportional to the product of the ith element of the reproductive value vector and the jth element of the stable stage vector (Caswell 2001). You'll understand more about these calculations as you work through the exercise. We can also write Equation 2 as a partial derivative, because all but 1 of the variables of which λ is a function are being held constant:

$$s_{ij} = \frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i w_j}{<\mathbf{w},\mathbf{v}>} \qquad \text{Equation 3}$$

How are the s_{ij}'s to be interpreted? A sensitivity analysis, for example, on the $P_{a,a}$ 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 **L** matrix and hold the remaining matrix entries constant, what is the corresponding change in λ?" The sensitivity of the P_{aa} matrix entry means, for example, that a small unit change in P_{aa} results in a change in λ 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 λ. 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 λ to changes in survival rates may be difficult to compare with the sensitivities of fertility rates. This is where elasticity comes 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 λ. In essence, elasticities are proportional sensitivities, scaled so that they are dimensionless:

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

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 λ, while a 1% increase in adult fecundity will cause a 0.538% increase in λ. 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 for computing sensitivities and elasticities for the vital population parameters, *P* and *F*, for a loggerhead sea turtle population with stage structure.

Set up the spreadsheet

1. Open the Microsoft Excel spreadsheet provided to you ("SensitivityElasticityAnalysis") and add the headings seen in Figure 3.

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

Figure 3. Sensitivity and elasticity analysis spreadsheet.

2. Enter the values shown in cells B4:F8 and in cells H4:H8.

Calculate w, the stable-stage vector

1. Set up new column headings in cells X3 and X4 as shown in Figure 4. To highlight cells with a certain color, select the cells you would like to highlight, open **Home | Font**, click on the highlight submenu button, and choose a color. To create a border around a group of cells, select the group of cells around which you would like to draw a border, open **Home | Font**, click on the borders submenu button, and select **Outside Borders** from the list. 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	**Stable stage distribution**
4	**vector, *w***
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.

2. In cell X5, calculate the proportion of the total population in year 100 that consists of hatchlings. Enter the formula **=B111/$G$111** in cell X5.

   In the data provided in the spreadsheet, you should note the number of individuals in each class when the population stabilized (remains constant over time). You might notice that the population stabilized at $\lambda = 0.95$, and that the stable population consists of 16.2 hatchlings, 44.0 small juveniles, 7.0 large juveniles, 0.5 subadults, and 0.2 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. Enter the following 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.

4. Your spreadsheet should now resemble Figure 5.

	X
3	**Stable stage distribution**
4	**vector, *w***
5	0.238535412
6	0.647720163
7	0.007283541
8	0.007283541
9	0.003118266

Figure 5.

Calculate v, the reproductive value vector

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, and 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.

1. Set up new column headings as shown in Figure 6.

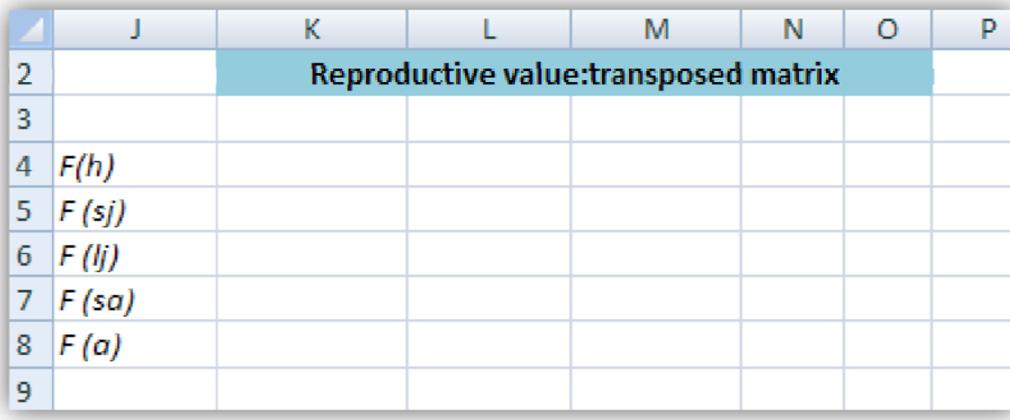

Figure 6.

2. Use the **TRANSPOSE** function to transpose the original matrix, given in cells B4:F8, into cells K4:O8. 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> to enter the formula for all of the cells you have selected. This function works best when you use the  key and follow the cues for entering a formula.

   Select cells K4:O8 with your mouse then use your  key to find and select the **Transpose** function. 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 (B4:F8). 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.

   Your spreadsheet should now resemble Figure 7.

	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. Enter 0 in cell I11. Enter **=1+I11** in cell I12. Copy this formula down to cell I111.

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

5. In cell O11, compute the total number of individuals in year 0. Enter the formula **=SUM(J11:N11)** in cell O11.

6. In cell P11, enter a formula to compute λ_t for year 0. Enter the formula **=O12/O11** in cell P11.

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

8. Compute λ_t for Year 1. Copy cells J12:P12 down to row 111 to complete the projection. You should see that λ_t stabilizes at the same value it did for your original projections.

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

	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 the formula **=J111/$O$111** 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:

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

12. Double-check your work. Cells S5:W5 should sum to 1.

13. In cells S6:W6, calculate the *standardized reproductive value* for each stage class. 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. Enter the formula **=S5/$S$5** in cell S6. Copy this formula across to cell W6. Your spreadsheet should now resemble Figure 9.

	R	S	T	U	V	W	X
3			Small	Large			Stable stage distribution
4		Hatchlings	juveniles	juveniles	Subadults	Adults	vector, *w*
5	*v* = reproductive value vector =	0.0018	0.0025	0.0133	0.2065	0.7759	0.238535412
6	Standardized reproductive value =	1.0	1.4	7.5	115.6	434.4	0.647720163
7							0.007283541
8							0.007283541
9							0.003118266

Figure 9.

Calculate sensitivities of matrix parameters

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

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

	R	S	T	U	V	W
7						
8	*X* = <*w*,*v*> =					
9						
10		**Sensitivity matrix**				
11		***F*(*h*)**	***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**					

Figure 10.

2. In cell S8, use the **MMULT** (matrix multiplication) function to multiply the **v** vector by the **w** vector. Enter the formula **=MMULT(S5:W5,X5:X9)** in cell S8. The **MMULT** function returns the matrix product of 2 arrays. The result is an array with the same number of rows as array 1 and the same number of columns as array 2. This value is the denominator <**w,v**> of the formula for calculating sensitivity values (Equation 3). This 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 the question: "If I could make subadults reproduce, it would increase λ 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).

3. In cell S12:W12, enter formulae to compute the sensitivity of fertility rates for each stage over time. Sensitivity of a population growth rate to changes in the a_{ij} element is simply the ith entry of **v** times the jth 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 I used (note that I used absolute references for some cell addresses).

   - S12 **=($X$5*S5)/$S$8**
   - T12 **=($X$6*S5)/$S$8**

- U12 =**($X$7*S5)/$S$8**
- V12 =**($X$8*S5)/$S$8**
- W12 =**($X$9*S5)/$S$8**

4. Copy cells S12:W12 down to cells S16:W16. 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 U5. In row 15, replace the reference to cell S8 with V5. In row 16, replace the reference to cell S9 with W5. This completes the sensitivity analysis.

   With the exception of the elasticity matrix (we haven't completed those calculations yet), your spreadsheet should now look like Figure 11

	R	S	T	U	V	W
7						
8	*X* = <w,v> =	0.0060773				
9						
10		**Sensitivity matrix**				
11		***F(h)***	***F(sj)***	***F(lj)***	***F(sa)***	***F(a)***
12	**Hatchlings**	0.0701	1904	0.0021	0.0021	0.0009
13	**Small juveniles**	0.0988	0.2684	0.0030	0.0030	0.0013
14	**Large juveniles**	0.5227	1.4194	0.0160	0.0160	0.0068
15	**Subadults**	8.1042	22.0062	0.2475	0.2475	0.1059
16	**Adults**	30.4543	82.6957	0.9299	0.9299	0.3981
17						
18						
19		**Elasticity matrix**				
20		***F(h)***	***F(sj)***	***F(lj)***	***F(sa)***	***F(a)***
21	**Hatchlings**	0	0	0	0.010494	0.05961
22	**Small juveniles**	0.0701043	0.198258	0	0	0
23	**Large juveniles**	0	0.070104	0.01102	0	0
24	**Subadults**	0	0	0.004941	0.1773531	0
25	**Adults**	0	0	0	0.0596104	0.338505

Figure 11.

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. Enter the formula **=(B4*S12)/$H$110** in cell S21. Copy this formula across to cell W21. The elasticity of a_{ij} is the sensitivity of a_{ij} times the value of a_{ij} in the original matrix, divided by λ when λ_t has stabilized. For example, the elasticity calculation of fecundities of the subadults would be **=(E4*V12)/$H$110**. If the original matrix element was a 0 (such as the fecundities of the hatchling stage), the elasticity should be 0.

2. 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 λ (yours might be off by a bit due to rounding error).

Create graphs

1. Graph the elasticity values for fertility at each stage for year 0. Highlight cells S21:W21 and the open **Insert | Charts | Column | Clustered Column**. Label your axes, add a chart title, and remove horizontal bars. Your graph should resemble Figure 12.

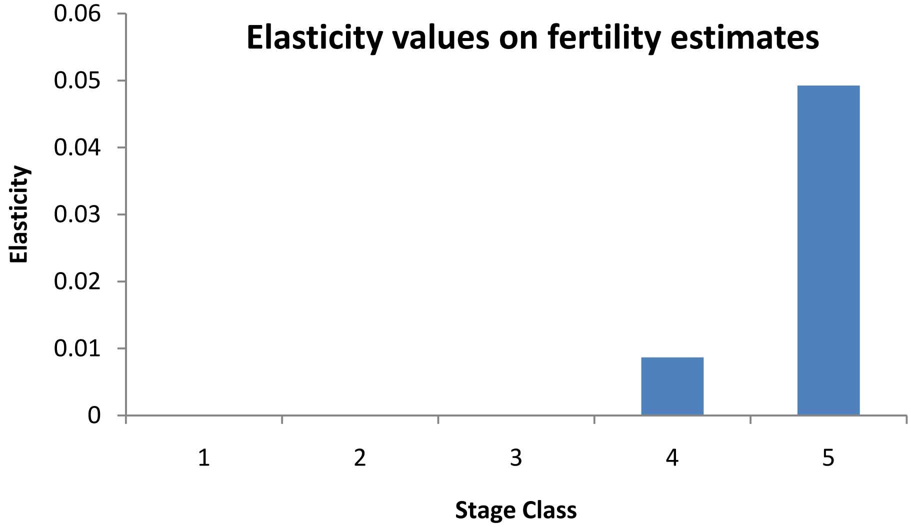

Figure 12.

2. Graph the elasticity values for the survival values, $P_{i,i}$ and $P_{i,i+1}$ for each stage class. Highlight cells S22:S25, T22:T25, U22:U25, V22:V25, and W22:W25. Open **Insert | Charts | Column | Clustered Column**. Label your axes, add a chart title, and remove horizontal bars. You will also have to manually select bars within the graph and color-code them (Black or Gray) to reflect within-stage survival ($P_{i,i}$) or survival to the next stage ($P_{i,i+1}$). Your graph should resemble Figure 13.

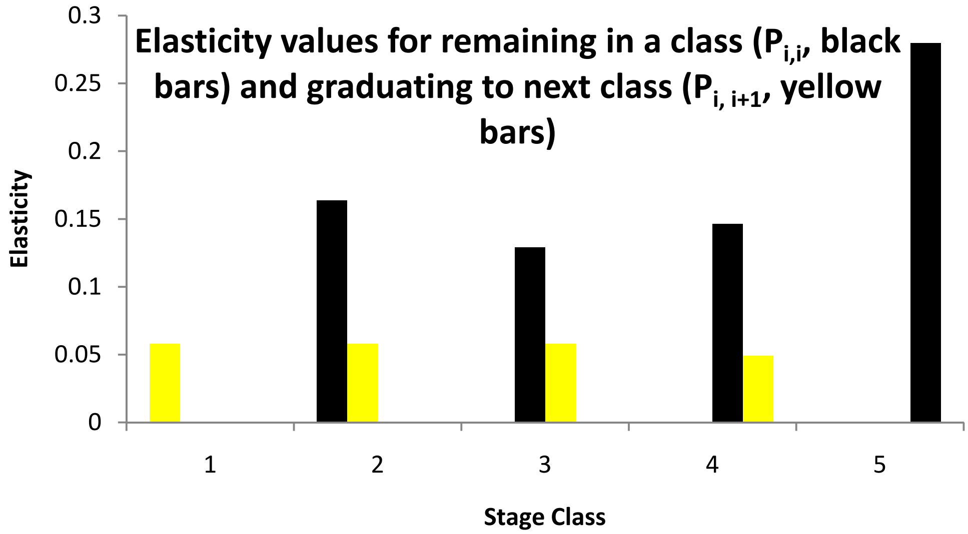

Figure 13.

Questions

1. Fully interpret the meaning of your sensitivity analysis. What management recommendations can you make for loggerhead sea turtle conservation given your analysis?

2. Fully interpret the meaning of your elasticity analysis. What management recommendations can you make for loggerhead sea turtle conservation given your elasticity analysis? Would your recommendations be different if you simply examined the sensitivies, 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 loggerhead sea turtle conservation based on the matrix parameters provided in the exercise. What kinds of assumptions are implicit in the model parameters? That is, what do you need to know about how the data were collected and the environmental and biological conditions in which the data were collected?

Literature Cited

Caswell, H. 2001. Matrix Population Models, 2nd Ed. Sinauer Associates, Sunderland, MA.

Crowder, L.B., D.T. Crouse, S.S. Heppell and T.H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4: 437–445.

Fisher, R.A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.