Sensitivity and Elasticity Analyses

Learning Objectives:
1. 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.
2. Interpret the meaning of the sensitivity and elasticity analyses from a conservation and management perspective.
3. Learn more about how to use the remarkable functionality of Excel 2013 to plot and analyze wildlife population data.

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 loggerhead sea turtle, *Caretta caretta.* Let's say that you have already constructed a stage-based matrix model for the population (you did that in the *Stage-Structured Lefkovitch Matrix Population Modeling* problem set) 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. You count the turtles in your population 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, you found (in the *Stage-Structured Lefkovitch Matrix Population Modeling* problem set) the population reached a stable stage distribution (SSD) and that all stage classes declined by 5% per year (λ = 0.95). Your task is to suggest the best ways to manage the turtle population to increase λ . But λ can be increased in a variety of ways. Should you focus your efforts on (1) increasing the probability that hatchlings in year *t* will become small juveniles in year *t* + 1, (2) increasing adult fecundity, or (3) should you focus on increasing adult survival? As always, money 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 loggerhead sea turtles in the *Stage-Structured Lefkovitch Matrix Population Modeling* problem set to conduct a **sensitivity** and **elasticity** analysis of each model parameter. These analyses will tell you how λ, population size, and the SSD might change as we alter the values of F_i and P_i in the **L** matrix.

Analytical Sensitivity Analysis

Analytical sensitivity analysis reveals how very small changes in a F_i or P_i will affect λ when the other elements in the **L** matrix are held constant. The word "sensitivity" as it is used here refers to how sensitive λ is to tiny changes in different vital rates (*Fi* or *Pi*). These analyses are important from several perspectives. From a conservation and management perspective, analytical sensitivity analysis can help you identify the life-history stage that will contribute the most to population growth of a species. From an ecological perspective, such an analysis can help identify the life-history attribute that contributes most to an organism's fitness.

Conducting analytical 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 analytical 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. *R*emember that 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, which produces yet another vector of abundances. When the process is repeated over n time steps, eventually the system reaches a SSD, where λ_t remains constant from 1 time step to the next. This stabilized λ_t is called the **asymptotic population growth rate**, λ. In our loggerhead sea turtle *Stage-Structured Lefkovitch Matrix Population Modeling* problem set, we saw that the population stabilized at year 58 when $\lambda = 0.95158$. Graphically, the point in time in which the population reaches a SSD 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 in the total population. When the population stabilizes, these proportions remain constant regardless of the value of λ.

Thus, given a matrix, **L**, you can determine the SSD of individuals among the different stage classes, and the value of λ at this point. The value of λ when the population has stabilized (reached a SSD) is called an **eigenvalue** of the matrix. An **eigenvalue** is a number or scalar (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 $t + 1$.

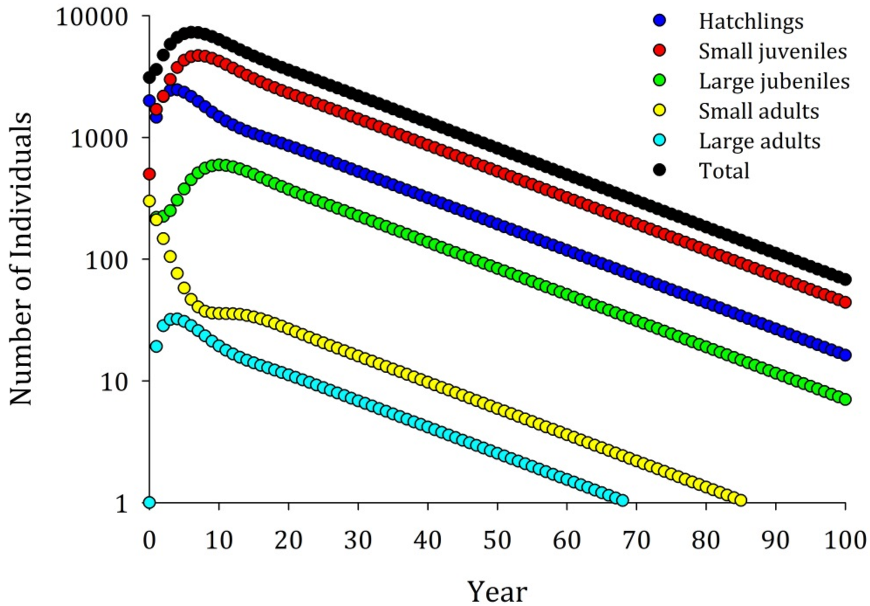


Figure 1. The stage distribution of a population becomes stable when changes in numbers over time for each growth stage are parallel, regardless of the value of λ. At this point the proportion of each stage in the population remains the same into the future.

In order to conduct a sensitivity analysis on the parameters in the **L** matrix, we need to determine the SSD of the population. In our loggerhead sea turtle example from the *Stage-Structured Lefkovitch Matrix Population Modeling* problem set, this was 24% hatchlings, 65% small juveniles, 10% large juveniles, 0.07% subadults, and 0.03% adults. Of course, 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 $\boldsymbol{w}$. The $\boldsymbol{w}$ 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 large adults:

$$w = \begin{bmatrix} 0.239 \\ 0.648 \\ 0.103 \\ 0.007 \\ 0.003 \end{bmatrix}$$

Note that the values sum to 1.

The final piece of information needed to compute sensitivities for values of F_i or P_i in the matrix is the **left eigenvector**, represented by the symbol $\boldsymbol{v}$. The left eigenvector of the **L** matrix reveals the reproductive value for each stage class in the model. Reproductive value computes the "worth" of individuals of different stage classes in terms of future offspring they are 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 hatchlings have low reproductive value because they have several years of living (and hence mortality risk) before they can start producing offspring.

We need to compute the reproductive values for each stage class in order to conduct a sensitivity analysis of the F_i's or P_i's for the sea turtle population. The simplest way to compute $\boldsymbol{v}$ for the **L** matrix is to transpose the **L** matrix, called **L′**, then run the model until the population reaches a SSD, and then to record the proportions of individuals that make up each class as with the $\boldsymbol{w}$ 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 $\mathbf{L}'$, the right eigenvector of $\mathbf{L}'$ gives the reproductive values for each stage class. This same vector is called the left eigenvector for the original matrix, **L**. (Yes, I know. It is confusing.) The ***v*** vector for our loggerhead sea turtle population is written as a row vector:

$$\boldsymbol{v} = [0.002\ 0.003\ 0.013\ 0.207\ 0.776]$$

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. The reproductive value is typically standardized so that the first stage class has a reproductive value of 1. We can standardize the ***v*** vector above simply by dividing each entry by 0.002 (the reproductive value of hatchlings) to generate standardized reproductive values. Our standardized vector would look like this:

$$\mathbf{v} = \begin{bmatrix} \frac{0.002}{0.002} & \frac{0.003}{0.002} & \frac{0.013}{0.002} & \frac{0.207}{0.002} & \frac{0.776}{0.002} \end{bmatrix} = [1 \quad 1.4 \quad 7.5 \quad 115.6 \quad 434.4]$$

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

Now we are ready to explore how sensitivities of a P_i or F_i in the **L** matrix are computed. Remember that analytical sensitivity analysis reveals how very small changes in a F_i or P_i affect λ when the other elements in the **L** matrix are held constant. The steps for conducting an analytical sensitivity analysis include:

1. Running the projection model until the population reaches a SSD;

2. Calculating the SSD 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 *i*th element of the reproductive value vector, w_j is the *j*th element of the stable stage vector, and <***w***,***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 *i*th element of the reproductive value vector and the *j*th element of the stable stage vector (Caswell 2001). You'll understand more about these calculations as you work through the exercise.

How are the s_{ij}'s to be interpreted? Let's say that a sensitivity analysis, for $P_{a,a}$ and $F_{s,a}$ yield values of 0.1499 and 0.2287, respectively. These values answer the question, "If we change $P_{a,a}$ 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 $P_{a,a}$ matrix entry means, for example, that a small unit change in $P_{a,a}$ 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 λ. In our example above, where sensitivities were 0.1499 for the $P_{a,a}$ and 0.2287 for the F_{sa}, small changes in adult survival will not have as large an effect as changes in subadult fecundity in terms of increasing λ. Thus you would recommend management efforts that aim to increase subadult fecundity values (i.e., more subadult loggerhead sea turtles in your population of interest need to get pregnant and lay eggs).

Analytical 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. Fecundity, on the other hand, has no such restrictions. Therefore, the sensitivity of λ to changes in survival rates is difficult to compare with the sensitivities of fecundity rates. This is where elasticity comes into play. Elasticity analysis estimates the effect of a *proportional* change in the vital rates on λ. 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:

$$e_{ij} = \frac{a_{ij} s_{ij}}{\lambda}$$ Equation 3

In essence, elasticities are proportional sensitivities, scaled so that they are dimensionless. 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 analytical sensitivities and elasticities for the vital population parameters, *P* and *F*, for a loggerhead sea turtle population with stage structure.

A. Open the Excel spreadsheet you constructed for the *Stage-Structured Lefkovitch Matrix Population Modeling* problem set as seen in Figure 3. Note that Figure 3 shows only the first 25 years of the loggerhead sea turtle population projection. Your file should have population projection data for 100 years. Save the file with a different name.

	A	B	C	D	E	F	G	H	I
1	Sensitivity and Elasticity Analysis							Initial	
2	Loggerhead sea turtle population							Population	
3		F (h)	F (sj)	F (lj)	F (sa)	F (a)		vector	
4		0	0	0	4.665	61.896		2000	
5		0.675	0.703	0	0	0		500	
6	M =	0	0.047	0.657	0	0	n =	300	
7		0	0	0.019	0.682	0		300	
8		0	0	0	0.061	0.8091		1	
9									
10	Year	Hatch.	S. juvs	L. juvs	Subadult	Adults	Total	λ_t	
11	0	2000	500	300	300	1	3101	1.16508	
12	1	1461	1702	221	210	19	3613	1.31397	
13	2	2164	2183	225	148	28	4747	1.22635	
14	3	2440	2995	250	105	32	5822	1.13877	
15	4	2464	3752	305	76	32	6630	1.07333	
16	5	2350	4301	377	58	31	7116	1.02661	
17	6	2171	4609	450	47	28	7305	0.99358	
18	7	1974	4706	512	40	26	7258	0.97055	
19	8	1786	4641	558	37	23	7044	0.95504	
20	9	1618	4468	584	36	21	6728	0.94528	
21	10	1477	4233	594	36	19	6360	0.93993	
22	11	1362	3973	589	36	18	5978	0.93787	
23	12	1268	3712	574	35	17	5606	0.93811	
24	13	1191	3466	552	35	16	5259	0.93981	
25	14	1128	3241	525	34	15	4943	0.94225	
26	15	1073	3039	497	33	14	4657	0.94488	
27	16	1024	2861	470	32	13	4401	0.94732	
28	17	979	2703	443	31	13	4169	0.94934	
29	18	937	2561	418	30	12	3957	0.95085	
30	19	896	2433	395	28	12	3763	0.95188	
31	20	856	2315	374	27	11	3582	0.95247	
32	21	817	2205	354	25	11	3412	0.95273	
33	22	779	2101	336	24	10	3250	0.95275	
34	23	742	2003	320	23	10	3097	0.95262	
35	24	706	1909	304	22	9	2950	0.95242	
36	25	672	1819	290	21	9	2810	0.95220	

Figure 3

B. Calculate ***w***, the SSD vector.

1. Set up new column headings in cells X3 and X4 as shown in Figure 4. Highlight the cells X5-X9 with a color of your choice. Remember, **w**, the SSD vector, is simply the proportion of individuals in the population that is made up of the different stage classes.

	X	Y
1		
2		
3	Stable stage distribution	
4	vector, **w**	
5	0.239	
6	0.648	
7	0.103	
8	0.007	
9	0.003	
10		

Figure 4

2. The first entry, cell X5, is the proportion of the population that is made up of hatchlings (given that the population has reached a SSD). 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. The last entry, cell X9, will contain the proportion of adults.
3. In cell X5, calculate the proportion of total population in year 100 that consists of hatchlings. Enter the formula **=B111/$G$111** in cell X5.
4. In cells X6:X9 compute the proportions in the remaining classes. Enter the following formulas:

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

Your spreadsheet should now resemble Figure 5.

	X	Y
1		
2		
3	Stable stage distribution	
4	vector, **w**	
5	0.239	
6	0.648	
7	0.103	
8	0.007	
9	0.003	
10		

Figure 5

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

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

	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							

Figure 6

3. Transpose the original matrix, given in cells B4:F8, into cells K4:O8. Here are the steps.
   a. Select the original matrix (cells B4:F8) and copy it to the Clipboard.
   b. Select the top-left cell of the range you want to copy the transposed data to (cell K4).
   c. Click Paste.
   d. Choose Transpose.
4. Your spreadsheet should now resemble Figure 7.

	J	K	L	M	N	O	P
1							
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	
9							

Figure 7

5. 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.

6. Link the starting number of individuals of each class in year 0 to the original vector of abundances in cells H4:H8. Use the following formulas:
   - J11=**H4**
   - K11=**H5**
   - L11=**H6**
   - M11=**H7**
   - N11=**H8**

7. In cell O11, compute the total number of individuals in year 0. Enter the formula **=SUM(J11:N11)** in cell O11.
8. In cell P11, enter a formula to compute λ_t for year 0. Enter the formula **=O12/O11** in cell P11.
9. Project the population for 100 years as you did in your *Stage-Structured Lefkovitch Matrix Population Modeling* problem set, using the values from the transposed matrix for your calculations. Use the following formulas:

   - 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**

10. Compute λ_t for Year 1. Copy cells J12:P12 down to row 111 to complete the projection. Note that λ_t stabilized at the same value (0.95158) it did for your original projections.
11. Set up new column headings as shown in Figure 8.

	R	S	T	U	V	W
1						
2						
3			Small	Large		
4		Hatchlings	juveniles	juveniles	Subadults	Adults
5	**v** = reproductive value vector =					
6	Standardized reproductive value =					
7						

Figure 8

12. In cell S5 enter a formula to compute the reproductive value of the hatchling stage. Enter the formula **=J111/$O$111** in cell S5. Thus, cell S5 gives the proportion of "hatchlings" in Year 100.
13. In cells T5:W5, enter formulas to compute the reproductive value of the remaining stages:

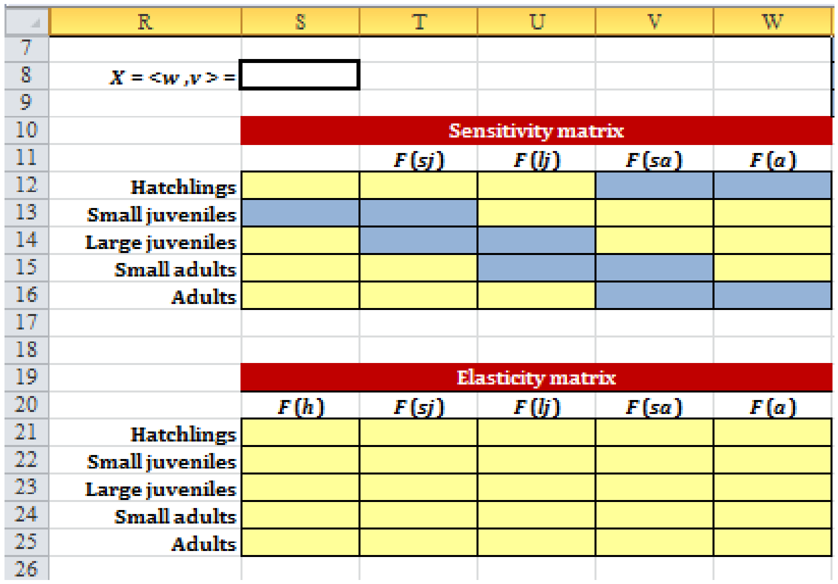
    - T5**=K111/$O$111**
    - U5**=L111/$O$111**
    - V5**=M111/$O$111**
    - W5**=N111/$O$111**

14. Double-check your work. Cells S5:W5 should sum to 1.
15. 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 reproductive value for the other stage classes by the value obtained for hatchlings. To do that 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
1							
2							
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	0.239
6	Standardized reproductive value =	1	1.4	7.5	115.6	434.4	0.648
7							0.103
8							0.007
9							0.003

Figure 9

16. Now that you have calculated the **w** and **v** vectors, you are ready to perform a sensitivity analysis. 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*(*sj*)	*F*(*lj*)	*F*(*sa*)	*F*(*a*)
12	Hatchlings					
13	Small juveniles					
14	Large juveniles					
15	Small adults					
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	Small adults					
25	Adults					
26						

Figure 10

17. 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 (the ***v*** vector) and the same number of columns as array 2 (the ***w*** vector). 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 this exercise, we will call this value X.
18. 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 fecundity (F_{sa}) 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.
19. In cell S12:W12, enter formulas to compute the sensitivity of fecundity rates for each stage over time. Sensitivity of λ 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 fecundity 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**=($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**

20. Copy cells S12:W12 down to cells S16:W16. Adjust your formulas 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. You will need to adjust the formulas for cells S13:W13 as well. This completes the sensitivity analysis. Your spreadsheet should now look like Figure 11.

	R	S	T	U	V	W
1						
2						
3			Small	Large		
4		Hatchlings	juveniles	juveniles	Subadults	Adults
5	ctive value vector =	0.0018	0.0025	0.0133	0.2065	0.7759
6	productive value =	1.0	1.4	7.5	115.6	434.4
7						
8	*X* = <*w*,*v*> =	0.0073566				
9						
10		Sensitivity matrix				
11			*F(sj)*	*F(lj)*	*F(sa)*	*F(a)*
12	Hatchlings	0	0	0	0.00177	0.00076
13	Small juveniles	0.08164	0.22170	0	0	0
14	Large juveniles	0	1.17255	0.18708	0	0
15	Small adults	0	0	2.90051	0.20443	0
16	Adults	0	0	0	0.76820	0.32889

Figure 11

D. Calculate elasticities of matrix parameters.

1. In cell S21:W21, enter formulas to calculate the elasticity values for fecundity 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.

21. Copy the formulas 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. Your spreadsheet should now look like Figure 12.

	R	S	T	U	V	W
19		Elasticity matrix				
20		*F(h)*	*F(sj)*	*F(lj)*	*F(sa)*	*F(a)*
21	**Hatchlings**	0	0	0	0.00867	0.04924
22	**Small juveniles**	0.05791	0.16378	0	0	0
23	**Large juveniles**	0	0.05791	0.12916	0	0
24	**Small adults**	0	0	0.05791	0.14651	0
25	**Adults**	0	0	0	0.04924	0.27964

Figure 12

E. Create graphs.

1. Graph the elasticity values for fecundity at each stage for year 0. Highlight cells S20:W20 and the open **Insert | Charts | Column | Clustered Column**. Label your axes, add a chart title, and remove horizontal bars. Your graph should resemble Figure 13.

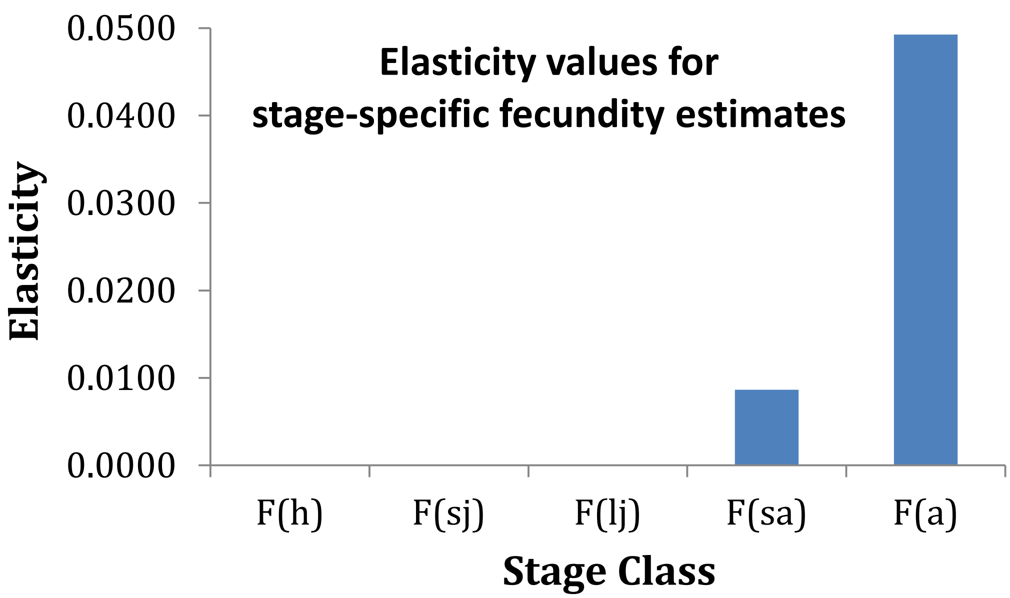


Figure 13

2. Graph the elasticity values for the survival values, $P_{i,i}$ and $P_{i,i+1}$ for each stage class. Highlight cells S22: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 14.

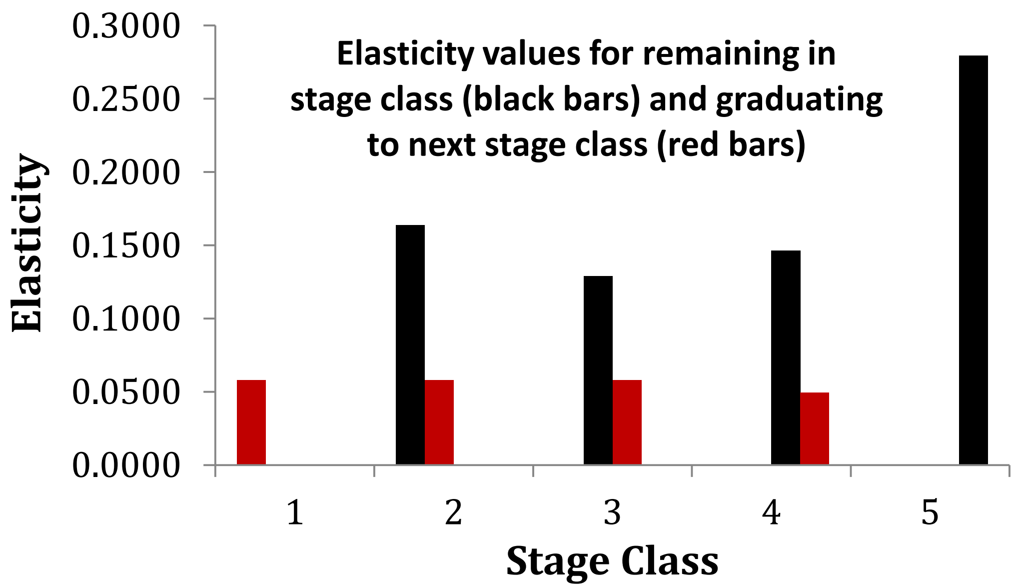


Figure 14

Discussion Questions

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

2. Fully interpret the meaning of your elasticity analysis. What management recommendations can you make for loggerhead sea turtle conservation given your results? Would your recommendations be different if you simply examined the sensitivities and ignored elasticities? Which do you think is more appropriate, elasticities or sensitivities, for guiding management decisions?

3. As with all models in wildlife ecology, elasticity and sensitivity analyses come with assumptions, including 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?

Literature Cited

Caswell, H. 2001. Matrix population models, 2nd ed. Sinauer Associates, Sunderland, Massachusetts, USA.

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, England.

Acknowledgement

This problem set was adapted from Exercise 19: Sensitivity and elasticity analysis, pages 253-264 *in* Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA. This publication is available at http://www.uvm.edu/rsenr/vtcfwru/spreadsheets/?Page=ecologyevolution/EE24.htm.

Your write-up should include the following: (1) a paragraph explaining the objectives of this problem set, and (2) your answers to the 3 discussion questions above. Email me (whited@uamont.edu) your spreadsheet model.