APPM 2360 Project 2:
Exploring Stage-Structured Population Dynamics with Loggerhead Sea Turtles

Due: March 22, 2018 by 11:59 PM
Submit to the Dropbox on D2L as a PDF

1 Introduction

In this lab, you will use a stage-based population model for Loggerhead Sea Turtles. This model uses a special type of transition matrix, called a Lefkovitch matrix, to advance the population forward in time while keeping track of how the population is distributed among several stage-classes. This model gives us a close estimate of the population growth rate. We will use sensitivity and elasticity analysis to identify population stages where conservation efforts should be focused so as to have the largest positive effect on the growth rate.

2 Mathematical Model

In the simple population models we have discussed in class, a population can either grow or decay according to the differential equation, $\frac{dP}{dt} = rP$, where r gives the intrinsic growth rate. As you know, solving this ODE gives the expression $P(t) = P_0 e^{rt}$ for the population, P, at any time, t. This model assumes that the given population has no structure; that is, all individuals are equally likely to reproduce or die at any time. However, most populations do not obey this assumption. In humans, for example, there is a period of about 30 years during which females are able to reproduce and, in general, likelihood of death increases with age. Therefore, we would expect population evolution in a group of humans to behave differently if that group were composed of equal numbers of babies, children, teenagers, adults, and elderly people, as opposed to a group of 50 babies, 10 children, 15 teenagers, 7 adults, and 3 elderly people.

In a similar way, the life cycle of turtles, and many other animals, can be divided into life stages, each with its own probability of survival and/or reproduction. Here, we will consider population evolution in *discrete time* and use a matrix to advance the population while keeping track of the number of individuals in each stage-class. We are interested in the growth rate of the population as a whole but, breaking the population down in this way will give more detailed information and aid us in assessing appropriate conservation efforts.

Let $\mathbf{n}_t$ be a vector where each component contains, in order, the number of individuals in each stage-class at time t. Multiplying this vector by the transition matrix, $\mathbf{L}$, advances the population by one time step, yielding the following equation:

$$\mathbf{n}_{t+1} = \mathbf{L}\mathbf{n}_t. \tag{1}$$

Given an initial population distribution, $\mathbf{n}_0$, Equation (1) will give the stage-class distribution at any time t. In this way,

$$\mathbf{n}_t = \mathbf{LLL} \overset{t \text{ times}}{\cdots} \mathbf{L}\mathbf{n}_0 = \mathbf{L}^t\mathbf{n}_0. \tag{2}$$

How should $\mathbf{L}$ be constructed? At each time step, an individual can either:

(1) Survive but remain in the same life stage. This probability is denoted by P_s where s is the given life stage.

(2) Survive and advance to the next life stage. This is denoted by G_s.

(3) Die.

Additionally, if individuals in a certain stage have reached a reproductive age, we consider the stage-specific fecundity, F_s. This is a measure of reproductive output calculated as the birth-rate for this stage times the number of surviving individuals. New births enter the population at the first stage, $s = 1$. In our model, F_s is given as the number of eggs produced per surviving stage-class member.

2.1 Example Bee Problem

The following schematic shows how a population of bees, which have four distinct life-stages, might evolve. Notice, an individual may remain in each of the four stage-classes for longer than one time step and, only adult bees can reproduce.

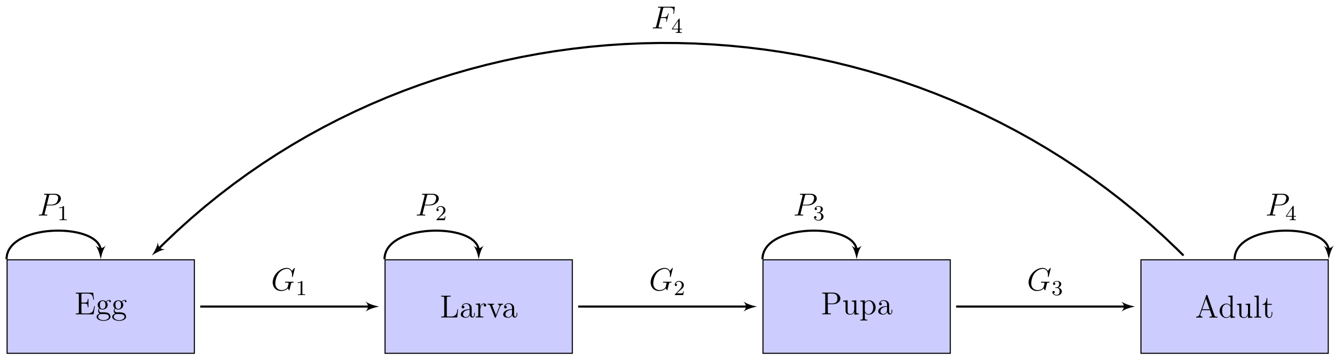

Figure 1: A diagram of structured population evolution in bees.

The schematic above may be translated into the matrix given below where multiplying the current population, $\mathbf{n}_t$, by $\mathbf{L}$ advances the population by one time step.

$$\mathbf{L} = \begin{bmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{bmatrix}, \quad \text{and } \mathbf{n}_t = \begin{bmatrix} n^{(1)} = & \text{(number of eggs)} \\ n^{(2)} = & \text{(number of larva)} \\ n^{(3)} = & \text{(number of pupa)} \\ n^{(4)} = & \text{(number of adults)} \end{bmatrix}_t \tag{3}$$

2.2 Model for Loggerhead Sea Turtles, Caretta Caretta

The Loggerhead Sea Turtle population can be divided into seven stage-classes: (1) Eggs and hatchlings, (2) small juveniles, (3) large juveniles, (4) sub-adults, (5) novice breeders, (6) 1st-year remigrants, and (7) mature breeders. Use the table of values below to form the transition matrix, $\mathbf{L}$, for the sea turtle population (in MATLAB, no need to include this matrix in your report).

Model Parameters				
Stage-Class	F_s	P_s	G_s	Initial Population
1	0	0	0.68	100
2	0	0.74	0.05	150
3	0	0.67	0.01	40
4	0	0.69	0.05	20
5	127	0	0.82	15
6	6	0	0.79	10
7	95	0.83		5

Table 1: Use these parameter and initial values in your simulation.

2.3 Questions

1. Using what you know about matrix multiplication, specifically multiplication of $\mathbf{L}\mathbf{n}_t$, explain the structure of the transition matrix, $\mathbf{L}$, for the bee example. What values are found along the diagonal, the subdiagonal, the first row, and why?

2. Corroborate this by giving the equation for each component of $\mathbf{n}_t$ for the bee population.

3. Why do we not include a parameter for death?

4. Advance the turtle population forward 100 time steps. Plot the total population as well as the number of individuals in each stage-class on the same axes from $t = 0$ to $t = 100$, include a legend. What does this plot show?

5. Repeat the above but, change the y-axis to be on a logarithmic scale using the MATLAB command `semilogy` in place of `plot`. What does this plot tell you about the growth rate of each stage-class? How does the slope of each curve compare?

6. Repeat (5) and (6) above with a few different sets of initial conditions. Do not include these plots in your report but comment on what you observe.

3 Model Analysis using the Power Method

After applying the transition matrix repeatedly to a population vector, the system reaches a steady-state distribution. That is, the fraction of individuals in each class remains constant, even as the number of individuals continues to change. This section describes what is known as the Power Method and shows how we can find this steady-state distribution directly.

We can write any vector $\mathbf{x} \in \mathbb{R}^n$ as a linear combination of the eigenvectors, $\mathbf{v}_i$, $i = 1, 2, \cdots n$, of a matrix $\mathbf{A} \in \mathbb{R}^{n\times n}$ so long as the $\mathbf{v}_i$ are linearly independent:

$$\mathbf{x} = c_1\mathbf{v}_1 + c_2\mathbf{v}_2 + \cdots + c_k\mathbf{v}_k. \tag{4}$$

Since $\mathbf{v}_i$ are the eigenvectors of $\mathbf{A}$, multiplying by $\mathbf{A}$ on the left is equivalent to:

$$\mathbf{A}\mathbf{x} = c_1\lambda_1\mathbf{v}_1 + c_2\lambda_2\mathbf{v}_2 + \cdots + c_k\lambda_k\mathbf{v}_k \tag{5}$$

where λ_i are the corresponding eigenvalues. Repeating this multiplication N-times gives:

$$\mathbf{A}^N\mathbf{x} = c_1\lambda_1^N\mathbf{v}_1 + c_2\lambda_2^N\mathbf{v}_2 + \cdots + c_k\lambda_k^N\mathbf{v}_k. \tag{6}$$

Assuming our eigenvalues are distinct in magnitude and we've ordered them such that $|\lambda_1| > |\lambda_2| > \cdots > |\lambda_k|$, we can factor out the largest eigenvalue (in magnitude), λ_1, to get:

$$\mathbf{A}^N\mathbf{x} = \lambda_1^N[c_1\mathbf{v}_1 + c_2(\lambda_2/\lambda_1)^N\mathbf{v}_2 + c_3(\lambda_3/\lambda_1)^N\mathbf{v}_3 + \cdots + c_k(\lambda_k/\lambda_1)^N\mathbf{v}_k]. \tag{7}$$

In the limit as $N \to \infty$, all terms like $c_j(\lambda_j/\lambda_1)^N\mathbf{v}_j$ go to zero since λ_1 is the eigenvalue with the largest magnitude and thus, the ratio λ_j/λ_1 is strictly less than one for all $j \neq 1$. This tells us that, after an initial growth period, or for N large enough, the population distribution at time N is given by:

$$\mathbf{A}^N\mathbf{n}_0 = c_1\lambda_1^N\mathbf{v}_1. \tag{8}$$

The dominant eigenvalue, λ_1, gives the **asymptotic population growth rate**, λ, and is equal to e^r where r is the intrinsic population growth rate. The dominant eigenvector, $\mathbf{v}_1$, is then **normalized** (such that the sum of its components is equal to one, e.g. `v = v/sum(v)`) to give the fraction of the population in each stage-class.

- Note: Use the MATLAB command `[V, D] = eig(L)` in answering the following questions. Some of the eigenvalues or eigenvectors may contain a nonzero imaginary part, don't worry about this. Use the command `real(V(:, k))` to isolate the real part of the dominant eigenvector. (See: Perron-Frobenius Theorem)

3.1 Questions

1. The determinant of $\mathbf{V}$, the matrix whose columns are the eigenvectors of $\mathbf{L}$, is nonzero. This shows that the eigenvectors of $\mathbf{L}$ are linearly independent. How does this justify Equation (4)?

2. What does it imply for the population if λ is equal to 1? less than 1? greater than 1?

3. Find the asymptotic growth rate and intrinsic growth rate of the turtle population. What are the implications for population survival?

4. Find (and normalize) the steady-state stage-class distribution for the turtle population.

5. Most conservation efforts focus on saving turtle eggs or helping hatchlings into the ocean. Change the parameter representing survival/advancement in the first stage-class to 1. How does this change the growth rate? What does this tell you?
   $\star$ Don't forget to change back afterwards!

4 Sensitivity and Elasticity Analysis

To devise a conservation plan for this endangered population, we need to assess which interventions will be most effective. Sensitivity and elasticity analyses will guide us in this endeavor by showing which parameters have the largest effect on overall population growth rate.

In order to carry out this analysis, we need to first calculate the **left eigenvector**. We're used to working with right eigenvectors which satisfy $\mathbf{A}\mathbf{v}_i = \lambda_i \mathbf{v}_i$. Left eigenvectors are row-vectors that satisfy $\mathbf{w}_i\mathbf{A} = \lambda_i\mathbf{w}_i$. Finding the left eigenvectors of a matrix $\mathbf{A}$ is equivalent to finding the right eigenvectors of $\mathbf{A}^T$. The left eigenvector corresponding to the dominant eigenvalue, λ with the greatest magnitude, of our transition matrix, $\mathbf{L}$, gives the reproductive value or worth of each stage-class in terms of the future offspring they will produce.

Sensitivity analysis tells us how small changes in parameter values will affect λ if all other elements are held constant. The sensitivity of the matrix element l_{ij} in $\mathbf{L}$ is given by:

$$s_{ij} = \frac{\mathbf{w}^{(i)}\mathbf{v}^{(j)}}{\mathbf{v} \cdot \mathbf{w}}. \tag{9}$$

Superscripts, as in $\mathbf{x}^{(i)}$, refer to the i^{th} component of a vector. Calculated sensitivities, s_{ij}, are interpreted as the factor by which λ will change if a small change is made to l_{ij}. This information has some value but, it is difficult to compare across all matrix entries. For example, in our model, P_s and G_s represent probabilities and are therefore assigned values between 0 and 1; however, fecundity rates, F_s, are measured in number of eggs produced.

Elasticity gives a more useful measure in that it calculates the effect of a *proportional* change to λ and can be thought of as a dimensionless sensitivity. The elasticity of l_{ij} is given by:

$$e_{ij} = \frac{l_{ij} \cdot s_{ij}}{\lambda} = \frac{l_{ij}}{\lambda} \frac{\mathbf{w}_i \mathbf{v}_j}{\mathbf{v} \cdot \mathbf{w}}. \tag{10}$$

Elasticity values, e_{ij}, give the percent by which λ will increase for a $\delta\%$ increase in a given parameter. For example, if the elasticity for some parameter p is calculated to be 0.025, increasing this parameter by $\delta\%$ will increase λ by $\delta \times 0.025\%$ so, if originally $p = 2$ and $\lambda = 1$, increasing p by 2% to 2.04 will change λ to 1.05. In performing these analyses, be sure to *normalize* the eigenvectors so that their components add up to one.

4.1 Questions

1. Show that if $\mathbf{x}_i$ is a right eigenvector of $\mathbf{A}^T$, then $\mathbf{x}_i^T$ is a left eigenvector of $\mathbf{A}$.

2. Using the normalized left and right eigenvectors, $\mathbf{w}$ and $\mathbf{v}$, respectively, perform a sensitivity analysis on the nonzero elements in the transition matrix $\mathbf{L}$. Include this in your report by making a bar graph of the sensitivities for the survival parameters, P_s and G_s, and for the fecudity parameters, F_s. (Note: You can get these two graphs all on one figure by using `subplot(m, n, p)` before each call to `bar`). Be sure to title each graph and label your axes.

3. Using the sensitivities found above, perform an elasticity analysis on $\mathbf{L}$. Include this in your report by plotting the elasticities for P_s, G_s, and F_s (all on the same plot) with stage-classes on the x-axis, be sure to include a legend.

4. Based on your plot and calculations, which parameters have the largest effect on λ and in what way?

5. How would you use this information to guide future conservation efforts?

6. Google search for Turtle Excluder Device (TED) and briefly describe what you found. Has this device been effective?

5 Report Guidelines

Your group will submit your project on D2L, in the appropriate dropbox (you can find these under the "assessments" tab in D2L). Adhere to the following guidelines:

- Do not put off finding a group, do this early. You should have a group set up within one week of the project assignment date.
- Submit your project in pdf format. Contents of .zip files will not necessarily be graded. (Word documents not acceptable because equations are commonly jumbled around by D2L.)

- Submit ALL code used for your project (.nb files for Mathematica, .m files for MatLab, etc). Code may be included in an appendix if you wish. DO NOT submit anything on D2L as a .zip file.
- Have only ONE group member submit the project. Having multiple people in your group submit the project to D2L will result in multiple grades, and we will take the LOWEST one.
- Include the names of all group members working on the project.

Your report needs to accurately and consistently describe the steps you took in answering the questions asked. This report should have the look and feel of a technical paper. Presentation and clarity are very important. Here are some important items to remember:

- Absolutely make sure your recitation number is on your submitted report.
- Start with an introduction that describes what you will discuss in the body of your document. A brief summary of important concepts used in your discussion could be useful here as well.
- Summarize what you have accomplished in a conclusion. No new information or new results should appear in your conclusion. You should only review the highlights of what you wrote about in the body of the report.
- Always include units in your answers.
- Always label plots and refer to them in the text. The main body of your paper should NOT include lengthy calculations. These should be included in an appendix, and referred to in the main body.
- Labs must be typed. Including the equations in the main body (part of your learning experience is to learn how to use an equation editor). An exception can be made for lengthy calculations in the appendix, which can be hand written (as long as they are neat and clear), and minor labels on plots, arrows in the text and a few subscripts.
- Your report does not have to be long. You need quality, not quantity of work. Of course you cannot omit any important piece of information, but you need not add any extras.
- DO NOT include printouts of computer software screens. You simply need to state which software you used in each step, and what it did for you.
- You must include any plot that supports your conclusions or gives you insight in your investigations.
- Write your report in an organized and logical fashion. Section headers such as Introduction, Background, Problem Statement, Calculations, Results, Conclusion, Appendix, etc... are not mandatory, but are highly recommended. They not only help you write your report, but help the reader navigate through your paper, besides giving it a clearer look.
- Remember: you are expected to submit a complete report for this project. Documents submitted with numbered responses will be deducted points.