Overview

A structured population model tracks not just the size of a population, but also the number of individuals in each of a number of stages of development. For example, a basic model might track the number of immature, adolescent, and adult individuals. Doing so allows modeling of dynamics within the population, and also allows direct modeling of the effects of age dependent phenomena on the population size. For example, death rates might be different for different age groups, and females of different ages may have different fertility rates.

In this lab we study **Leslie models**, a kind of structured population model that only involves linear interactions.

Exercise 1: Suppose we divide our population is divided into only two classes: children and adults. Let c_n denote the number of children at time step n and a_n the number of adults. The population evolves according to the following rules:

$$c_{n+1} = \frac{1}{8}c_n + 6a_n$$

$$a_{n+1} = \frac{1}{5}c_n.$$

We denote the whole population by a vector

$$\mathbf{p}_n = \begin{bmatrix} c_n \\ a_n \end{bmatrix},$$

so in matrix notation

$$\mathbf{p}_{n+1} = \begin{bmatrix} \frac{1}{8} & 6 \\ \frac{1}{5} & 0 \end{bmatrix} \mathbf{p}_n.$$

The matrix appearing above is called a **Leslie matrix**.

Suppose $\mathbf{p}_0 = (40, 0)$ (i.e. we start with 40 children and no adults). What is $\mathbf{p}_1$? Explain what happened during this time step in everyday language.

Suppose $\mathbf{p}_0 = (0, 100)$ (i.e. we start with no children and 100 adults). What is $\mathbf{p}_1$? Explain what happened during this time step in everyday language.

Suppose $\mathbf{p}_0 = (40, 100)$. How is $\mathbf{p}_1$ related to the similar computation in the previous two examples? How many of the children in $\mathbf{p}_1$ were children in $\mathbf{p}_0$?

Exercise 2: We will now track the population starting from an initial population of $\mathbf{p}_0 = (10, 10)$. You can think of the population being measured in thousands to make these numbers more realistic. In Matlab, enter the matrix from the previous problem as A. Then enter the following commands

```
p = [10;10];
P = [p];

p = A*p;
P= [P p];
```

```
p = A*p;
P = [P p];

p = A*p;
P = [P p];

plot(P')
```

Explain what the contents of P are at the end of this.

Exercise 3: We could build a graph of the population over time by entering more and more steps like the ones above. But that's tedious. In Matlab, enter the following.

```
p = [10; 10];
P = [p];

for k=1:8
  p = A*p;
  P = [P p];
end

plot(P')
```

Observe what the new plot is. Then modify these lines to generate a graph of the population over 25 generations, and sketch the population graph.

Exercise 4: Repeat Exercise 3 for different initial conditions, e.g. $\mathbf{p}_0 = (19, 1)$ and $\mathbf{p}_0 = (1, 19)$. Sketch two of the resulting graphs.

Exercise 5: Qualitatively, describe the common features of the way the populations in the last two questions change over time. Do you see population growth or decay? Do the populations oscillate or not? If there are oscillations, do they grow in size or decay?

Exercise 6: Generate a matrix P containing the population history starting from $\mathbf{p}_0 = (10, 10)$ up to 100 subsequent generations. Plot `log(P')` and describe what you see. Your plot shows that for large values of n, a_n can be modeled by a function of the form

$$a_n = C\lambda^n$$

How can you measure C and λ from the graph?

Exercise 7: Use Matlab to find the least-squares best fit line to the graph of `log(P'(:,1))`. For full credit, your solution must involve the command `vander` from the first lab, and must set up and solve the normal equations. Record the Matlab commands you used to do this, and the equation of the line of best fit. Then find the line of best fit to `log(P'(:,2))` as well.

Exercise 8: Use your results from the previous exercise to predict the long term ratio c_n/a_n. Explain the computations you do to arrive at this number.

Exercise 9: The empirical results of the last two exercises can be predicted mathematically using eigenvalues and eigenvectors of the matrix A. We will be discussing these in class soon, but this lab is self contained and contains an introduction to these concepts.

An **eigenvector** of a square matrix B is a nonzero vector that satisfies

$$B\mathbf{v} = \lambda\mathbf{v}$$

for some scalar λ. For example, $\mathbf{v} = (1, 1)$ is an eigenvector of

$$B = \begin{bmatrix} 1 & 2 \\ 2 & 1 \end{bmatrix}$$

because

$$B\mathbf{v} = \begin{bmatrix} 3 \\ 3 \end{bmatrix} = 3\mathbf{v}.$$

We say that $\mathbf{v}$ is an eigenvector with **eigenvalue** $\lambda = 3$. Explain why $5\mathbf{v}$ is also an eigenvector with eigenvalue $\lambda = 3$. For what choice of c is $c\mathbf{v}$ not an eigenvector of B with eigenvalue $\lambda = 3$?

Exercise 10: Notice that the equation $B\mathbf{v} = \lambda\mathbf{v}$ can be rewritten as

$$(B - \lambda I)\mathbf{v} = 0.$$

Since we require $\mathbf{v}$ is nonzero, this can only happen when $\det(B - \lambda I) = 0$.

For our Leslie matrix A, this equation is

$$\det\begin{bmatrix} \frac{1}{8} - \lambda & 6 \\ \frac{1}{5} & -\lambda \end{bmatrix} = 0$$

which is a quadratic equation in λ. Write down the equation. What are its roots? We will call these roots λ_1 and λ_2, with λ_1 being the largest of the two in absolute value. These are the eigenvalues. For each of λ_1 and λ_2, find an eigenvector, i.e. a nonzero solution of

$$A\mathbf{v}_i = \lambda_i\mathbf{v}_i.$$

for $i = 1$ and $i = 2$. Do one of these computations by hand and include it with your lab.

Exercise 11: In fact Matlab can compute eigenvalues and eigenvectors. The magic words are

```
[E D] = eig(A)
```

The columns of matrix `E` will be eigenvectors, while `D` will be a diagonal matrix with the corresponding eigenvalues on the diagonal, so that `A*E` will be the same as `E*D`. Use Matlab to verify the computations you did in the previous problem. Record the resulting matrices `E` and `D`.

Exercise 12: Let $\mathbf{v}_1$ and $\mathbf{v}_2$ be the two eigenvectors you discovered in the previous exercises. For maximal accuracy, you should extract these eigenvectors out of E. Generate a graph of the populations over 25 generations starting from $\mathbf{v}_1$. Then do the same for $\mathbf{v}_2$. Sketch the resulting populations below.

(Don't worry that that a negative population size is not physical; we're just trying to understand the mathematics of the model at this stage).

Exercise 13: If $\mathbf{p}_0 = \mathbf{v}_1$, what is the exact value of $\mathbf{p}_{121}$? Don't use Matlab to answer this question; I'm looking for an analytical answer.

Exercise 14: Suppose A has eigenvalue λ and you produce a population graph starting at a corresponding eigenvector. For each of the values of λ below, sketch by hand what you would expect the graph to look like.

- $\lambda = 1.3$

- $\lambda = .7$

- $\lambda = -0.7$

- $\lambda = -1.3$

Exercise 15: The initial vector $\mathbf{p}_0 = (10, 10)$ can be written as a linear combination of $\mathbf{v}_1$ and $\mathbf{v}_2$. Use Matlab to determine the coefficients of this combination. Record the Matlab commands you used and the values of the coefficients.

Exercise 16: Starting from $\mathbf{p}_0 = (10, 10)$, use your answer to the previous question to write down an explicit formula for the population size of the form

$$\mathbf{p}_n = x_1 \lambda_1^n \mathbf{v}_1 + x_2 \lambda_2^n \mathbf{v}_2.$$

Everything on the right-hand side of this equation except for n should be a number or a vector of numbers.

Exercise 17: How does your expression from the previous problem explain the original graph you made in Exercise 3 in terms of the graphs in Exercise 12. How does the fact that any vector can be written as a linear combination of the basis $\mathbf{v}_1$ and $\mathbf{v}_2$ explain what you saw in Exercise 4?

Exercise 18: Which of the eigenvalues λ_1 and λ_2 are related to the graphs you saw in exercise 6? Why is this eigenvalue, and not the other one, the one that controls the long-term growth rate? We call this eigenvalue the **intrinsic growth rate** of the population. Why is it important to know if this number is greater or less than one?

Exercise 19: Suppose A turned out to have eigenvalues $\lambda_1 = 0.7$ and $\lambda_2 = -0.2$. For almost all initial populations, how would you expect the population to behave over time. Explain in a way that makes clear the effect of *both* eigenvalues. Sketch a graph of the population sizes with the right qualitative features.

Exercise 20: The eigenvector corresponding to the largest eigenvalue of A is called the **stable age distribution** for the model. To see why, with λ_1 the intrinsic growth rate, rewrite your answer to Exercise 16 in the form

$$\frac{1}{\lambda_1^n} \mathbf{p}_n = x_1 \mathbf{v}_1 + x_2 \left(\frac{\lambda_2}{\lambda_1} \right)^n \mathbf{v}_2.$$

Write down this equation with no symbols on the right-hand side except for n.

Note $|\lambda_2/\lambda_1| < 1$. This equation should be interpreted as follows: If we account for the main growth trend of the population by dividing by λ_1^t, then the rescaled population will tend to the vector $\mathbf{v}_1$, the stable age distribution.

Explain how you can predict the long term ratio c_n/a_n. Compare this prediction with your answer to Exercise 8.

Exercise 21: Now that you understand the principles involved in analyzing a Leslie model, let's vary the model. Consider

$$\mathbf{p}_{n+1} = \begin{bmatrix} 0 & 6 \\ \frac{1}{5} & \frac{1}{4} \end{bmatrix} \mathbf{p}_n.$$

Now we're allowing $\frac{1}{4}$ of the adults at each time step to survive to the next time step, but no immatures remain immature. Track this model graphically with a few different initial vectors. Draw a representative sketch.

Exercise 22: What is the intrinsic growth rate for the model of the last problem?

What is the stable age distribution?

How are both eigenvalues of the matrix reflected in the graph you sketched?

Exercise 23: For each of the following matrices, use Matlab to compute eigenvectors and eigenvalues. For each, record 1) the intrinsic growth rate and the other eigenvalue, and 2) the stable age distribution. Also *without using Matlab to do a population simulation*, sketch a likely graph of the way such a population would behave over time.

a) $\begin{bmatrix} 0 & 6 \\ \frac{1}{6} & 0 \end{bmatrix}$ b) $\begin{bmatrix} 0 & 6 \\ \frac{1}{7} & 0 \end{bmatrix}$ c) $\begin{bmatrix} 0 & 6 \\ \frac{1}{6} & \frac{1}{4} \end{bmatrix}$ d) $\begin{bmatrix} 0 & 6 \\ \frac{1}{12} & \frac{1}{4} \end{bmatrix}$

Exercise 24: The data in the following table (taken from Keyfiz's *Introduction to the Mathematics of Population*) applies to women in the United States in 1964.

Age	Fertility	Survivorship	Population (in millions)
0-5	0.00000	0.99661	10.136
5-10	0.00103	0.99834	10.006
10-15	0.08779	0.99791	9.065
15-20	0.34873	0.99682	8.045
20-25	0.47607	0.99605	6.546
25-30	0.33769	0.99474	5.614
30-35	0.18333	0.99229	5.632
35-40	0.07605	0.98866	6.193
40-45	0.01744	0.98304	6.345
45-50	0.00096	-	5.796

Fertility is the number of infants born on average to each woman in a five year time span. Survivorship is the fraction of individuals that survive from one age class to the next over a five year timespan. We stop tracking at age 50 since there are no births to women over the age of 50 and hence these individuals do not impact the population dynamics. This data is available as `survivorship64`, `fertility64`, `population64` in the file `lab3data.mat` on the course web page. From them, assemble a Leslie matrix. Record the Matlab commands you used to do this. Hint: you might find the

Matlab command `diag` to be useful. Type `help diag` for information on how to use it; you'll want the two-argument version.

Exercise 25: How many women would you predict there will be in the 35-40 age group in 2004? **Be careful about the time step size.**

Exercise 26: What is the total number of women of age 50 or less in the United States in 1964? Hint: Matlab has a `sum` command.

Exercise 27: If you only had the fertility and survivorship data from the table in Exercise 24, along with your answer to Exercise 26, what would you predict for the number of women in each age class? Record the Matlab commands you used to generate this answer, and then graph your prediction alongside the true population sizes.

Exercise 28: Discuss the possible reasons why the actual population in 1964 differs from your predictions. Your discussion should be specific to the data you are observing, not a general discussion of why differences may occur.

Remark: The Leslie matrix you construct in Exercise 24 will have some complex eigenvalues and eigenvectors. Don't let this bother you too much! One can show that for Leslie matrices, the eigenvalue of largest magnitude will be real and positive, and its associated eigenvector will be real and its entries will be non-negative. So the intrinsic growth rate and stable age distributions still make sense. You should, however, be intrigued by those complex eigenvalues and eigenvectors. They lead to oscillations more complicated than the ones you saw earlier in the lab. I'll discuss this material a little later when we discuss eigenvectors and eigenvalues in more detail.