

Population models and eigenvectors

In this exercise you will be investigating a type of *structured population model* called a *Leslie model*. The ‘structure’ of the model refers to the fact that rather than treating a population as one big group, it breaks it up into a number of different subgroups by age, or stage of development. Then the impact of the passage of time on each subgroup may depend on the sizes of other groups. We use only linear equations to model how the population changes, so that everything can be formulated in terms of matrices.

Although this exercise focuses on biological examples, similar types of matrix models arise in other fields as well. The biological context is simply a clear one in which to explore how eigenvectors and eigenvalues are the key to understanding such models.

1. Consider a species whose members fall into two groups: immature and adult. Let x_n denote the number of immature individuals at time n , and let y_n denote the number of adults at time n . A reasonable model for how the population changes over time could be given by equations like

$$x_{n+1} = \frac{1}{8}x_n + 6y_n, \quad y_{n+1} = \frac{1}{5}x_n.$$

These mean that at each time step, for every living adult we get six new immatures, while only a fifth of the immature individuals become adults. An eighth of the immature individuals remain immature, and no adults survive. In matrix notation

$$\begin{pmatrix} x \\ y \end{pmatrix}_{n+1} = \begin{pmatrix} \frac{1}{8} & 6 \\ \frac{1}{5} & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}_n.$$

Suppose we begin with $(x, y)_0 = (10, 10)$. (This means we have 10 individuals in each age group, or perhaps, using more realistic units, 10 thousand.) Enter the above the matrix in MATLAB as **A**, and the initial vector as **x**. The MATLAB command **x=A*x** can be entered repeatedly to track the population over many time steps. What appears to be happening? Do the number of individuals in each group get bigger or smaller? Do they oscillate?

2. To investigate the situation graphically, try entering:

```
x=[10 10]'  
xx=x
```

Then repeatedly (say 25 times or so, using the \uparrow key) enter:

```
x=A*x, xx=[xx x]
```

Make sure you understand what this last command is doing before you go on.

Finally, plot the rows of \mathbf{xx} by entering:

```
plot(xx')
```

Sketch your plot here, labeling the lines that represent immatures and adults.

3. Repeat item (2) with the same matrix \mathbf{A} , but with several different choices of an initial vector (say $(19, 1)$, $(1, 19)$, and a few others). Sketch at least 2 of the resulting graphs here.

4. 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?

5. Compute the eigenvectors and eigenvalues of A by entering `[S,D]=eig(A)`. The columns of S are the eigenvectors of A , with the diagonal entries of D being the eigenvalues. You should make sure, by entering the appropriate MATLAB commands to see that $AS=SD$. Record S and D here.

6. Repeat item (3) using as your initial vector first one of the eigenvectors of A , and then the other. (Don't worry about the fact that negative numbers of individuals don't make sense biologically – we're just trying to understand the *model* now.) To begin, $x=S(:,1)$ will pick off the first column of S , and $x=S(:,2)$ picks off the second. Sketch graphs for both initial vectors here.

7. How do the behaviors you see in the graphs from the last question relate to the fact that you are using eigenvectors as your initial vectors? How is the corresponding eigenvalue reflected in the graph? Explain

8. Suppose A had eigenvalue λ , and you produced a graph like in question (6) using the corresponding eigenvector. Sketch what you would expect the graph to look like for each of the following possible values of λ . Be sure you think about the equation $A^n \mathbf{v} = \lambda^n \mathbf{v}$ as you draw your graphs.

$$\lambda = 1.3$$

$$\lambda = .7$$

$$\lambda = -0.7$$

$$\lambda = -1.3$$

9. Return to the initial vector $(x, y)_0 = (10, 10)$. The two eigenvectors of A given in question (5) form a basis for \mathbb{R}^2 , so you can express $(x, y)_0$ as a linear combination of the two eigenvectors. Use MATLAB to do so, and write your expression here.

10. For $(x, y)_0 = (10, 10)$, use your answer to the last question to give a formula for the size of the population at all times of the form

$$\mathbf{x}_t = c_1 \lambda_1^t \mathbf{v}_1 + c_2 \lambda_2^t \mathbf{v}_2.$$

Record your formula here.

11. How does the expression you gave in question (10) explain the graph you sketched in question (2) in relation to the graphs in question (6)? How does the fact that *any* initial vector can be expressed in terms of the eigenvectors explain the how all your graphs in question (3) looked?

12. Why would biologists be most interested in knowing the *largest* eigenvalue of a Leslie matrix? How do expressions like the one you found in (10) show this number is important for the long-term behavior of most initial populations? Why is it reasonable to call it the *intrinsic growth rate* of the population? Why is it important to know whether it is bigger or smaller than 1?

13. 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.

14. 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 question (10) in the form

$$\frac{1}{\lambda_1^t} \mathbf{x}_t = c_1 \mathbf{v}_1 + c_2 \left(\frac{\lambda_2}{\lambda_1} \right)^t \mathbf{v}_2.$$

Record it here.

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.

15. Compute the ratio of immatures to adults in \mathbf{v}_1 , and record it here.

Then, for a few different choices of \mathbf{x}_0 , compute the ratios of immatures to adults in \mathbf{x}_t for some large t . Are they close to the same ratio computed for \mathbf{v}_1 , as the last question indicates they should be?

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

$$\begin{pmatrix} x \\ y \end{pmatrix}_{n+1} = \begin{pmatrix} 0 & 6 \\ \frac{1}{5} & \frac{1}{4} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}_n.$$

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, drawing a representative sketch here.

17. 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?
18. 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.

$$\begin{pmatrix} 0 & 6 \\ \frac{1}{6} & 0 \end{pmatrix}$$

$$\begin{pmatrix} 0 & 6 \\ \frac{1}{7} & 0 \end{pmatrix}$$

$$\begin{pmatrix} 0 & 6 \\ \frac{1}{6} & \frac{1}{4} \end{pmatrix}$$

$$\begin{pmatrix} 0 & 6 \\ \frac{1}{12} & \frac{1}{4} \end{pmatrix}$$

19. It turns out that for 2×2 matrix population models, both eigenvalues are always real. For larger matrices, they may be complex. Although this exercise will not carefully develop all background on complex numbers, it is still instructive to work through one example to see how the ideas you've worked with in the real case carry over to the complex situation.

Consider a species with three age groups: immature, youth, and adult. Denoting the number of individuals in each by x_n , y_n , and z_n , the species might be modeled by

$$\mathbf{x}_{n+1} = \begin{pmatrix} x \\ y \\ z \end{pmatrix}_{n+1} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{4} & 0 & 0 \\ 0 & \frac{1}{2} & \frac{1}{4} \end{pmatrix} \begin{pmatrix} x \\ y \\ z \end{pmatrix}_n = B\mathbf{x}_n.$$

Explain why this might be a reasonable model. In particular, explain the biological meaning of each of the non-zero entries of the matrix B .

20. Picking a few different initial vectors \mathbf{x}_0 , produce plots like those in question (3). Sketch one for $\mathbf{x}_0 = (10, 10, 10)$ here.

21. Compute eigenvectors and eigenvalues of the matrix B . Record them here.

22. To compare the sizes of complex numbers, we compare their absolute values, where $|a + bi| = \sqrt{a^2 + b^2}$. Compute the absolute values of the 3 eigenvalues of B , and record them here. Which eigenvalue is the intrinsic growth rate? What is the stable age distribution?

(It's possible to show that these sorts of population models always have a real number as their intrinsic growth rate.)

23. Complex eigenvalues always produce oscillations in population models – though much more complex oscillations than the ones produced by negative eigenvalues that you've seen earlier. Whether the oscillations grow or decay depends on whether the absolute value of the eigenvalue is > 1 or < 1 . Does your work in the last question suggest the oscillations for this model will grow or decay? Is this consistent with what you saw in question 20?

24. Even if they involve complex numbers, eigenvectors still give a way to separate out different types of behavior in a model. As an example, suppose we begin with an initial vector $(x, y, z)_0 = (10, 10, 10)$. Using complex numbers as coefficients, you can write it as a linear combination

$$(10, 10, 10) = c_1 \mathbf{v}_1 + c_2 \mathbf{v}_2 + c_3 \mathbf{v}_3$$

of the three eigenvectors of B . Use MATLAB to find the c_i and record the linear combination here.

25. Now one of your eigenvectors (say \mathbf{v}_1) is real and so is the scalar that appears next to it (c_1). Since the whole sum is real, then $c_2 \mathbf{v}_2 + c_3 \mathbf{v}_3$ must be real as well, even though the $\mathbf{v}_2, \mathbf{v}_3, c_2, c_3$ individually are not.

Try using $c_2 \mathbf{v}_2 + c_3 \mathbf{v}_3$ as your initial vector and see what happens over time. (If you call that vector \mathbf{x} , type `x=real(x)` to throw away the very small imaginary part which appears only due to numerical round-off errors.) Draw a sketch of the ‘population’ over time.

26. Produce a graph of the population if it is initially given by the stable age distribution, and sketch it here. How does this graph and the one from the last problem relate to the one in question 20?