The Leslie Matrix

Math 45 — Linear Algebra

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Abstract

The Leslie Model is a powerful tool used to determine the growth of a population as well as the age distribution within a population over time. *Prerequisites: Matrix multiplication. Some familiarity with Matlab's indexing methods.*

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Population Modeling Using the Leslie Matrix

This lab focuses on the use of the Leslie Matrix to determine the growth of a population, as well as the age distribution within the population over time. The model used here was described by P. H. Leslie in 1945.[1] This model has been used to describe the population dynamics of a wide variety of organisms including: brook trout, rabbits, lice, beetles, pine trees, buttercups, killer whales, and humans. We will apply the Leslie model to find the population and population distribution of a species of salmon that has been recently introduced into the area.

Discussion

The Leslie model uses the following assumptions:

- We consider only the females in the salmon population.
- The maximum age attained by any individual salmon is three years.
- The salmon are grouped into three one-year age classes.
- An individual salmon's chances of surviving from one year to the next is a function of its age.
- The survival rate P_i of each age group is known.
- The reproduction (fecundity) rate F_i for each age group is known.
- The initial age distribution is known.

[1] *On the Use of Matices in Certain Population Mathematics*, Leslie, P.H., *Biometrika*, Volume XXXIII, November 1945, pp. 183–212

From these assumptions it is possible to construct a deterministic model by using matrices. Since the maximum age attained by any salmon is three years, the entire population can be broken up into three one-year age classes. Class 1 contains all salmon in their first year, class 2 contains all salmon in their second year, and class 3 contains all salmon in their third and last year of life.

Suppose we know the number of females in each of the three age classes at some time $t = t_0$. Let there be $x_1^{(0)}$ females in the first age class, $x_2^{(0)}$ females in the second age class, and $x_3^{(0)}$ females in the third age class. With these three numbers we form the column vector $\mathbf{x}^{(0)}$.

$$\mathbf{x}^{(0)} = \begin{pmatrix} x_1^{(0)} \\ x_2^{(0)} \\ x_3^{(0)} \end{pmatrix}$$

We call $\mathbf{x}^{(0)}$ the *initial age distribution vector* or the age distribution vector at time $t = t_0$.

As time progresses, the number of females in each of the three age classes changes because of three biological processes: birth, death, and aging. By describing these three processes quantitatively, we shall see how to project the initial age distribution vector into the future.

We will observe the population at discrete one year time intervals defined as $t_0, t_1, t_2, t_3, \ldots$. The birth and death processes between two successive observation times may be described by the means of defining parameters called the *average reproduction rate* and the *net survival rate*.

Let F_1 be the average number of females born to a single female in the first age class, F_2 is the average number of females born to a single female in the second age class, and F_3 is the average number of females born to a single female in the third age class. Each F_i is average reproduction rate of a single female in the ith age group.

Let P_1 be the fraction of females in the first age class that survive the year to live on into the second age class. Let P_2 be the fraction of females in the second age class that survive the year to live on into the third age class. There is no P_3. After the third year, all the salmon die after spawning, so none survive to live on into a fourth age class. In general,

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F_i	is the average reproduction rate of a female in the ith age class,
P_i	is the survival rate of females in the ith age class.

By their definitions, $F_i \geq 0$ since the number of offspring produced cannot be negative. In the case of this salmon population, $F_1 = 0$ and $F_2 = 0$ because the salmon only produce offspring in their last year of life. Thus, only F_3 has a positive value. Also, $0 < P_i \leq 1$ for $i = 1, 2$, since we assume that some of the salmon must survive into the next age class. This is true except for the last age class, when all the salmon die after spawning.

We next define the age distribution $\mathbf{x}^{(k)}$ at time t_k by

$$\mathbf{x}^{(k)} = \begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \end{pmatrix},$$

where $x_i^{(k)}$ is the number of female salmon in the i-th age class at time t_k. Now, at time t_k, the number of salmon in the first age class $x_1^{(k)}$, are just those salmon born between time t_{k-1} and t_k. The number of offspring produced by each age class can be calculated by multiplying the reproductive rate for the age class times the number of females in the age class. The sum of all these values gives the total number of offspring produced. Thus, we can write

$$x_1^{(k)} = F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + F_3 x_3^{(k-1)} \tag{1}$$

which says that the number of females in age class 1 equals the number of daughters born to females in age class 1 between times t_k and t_{k-1}, plus the number of daughters born to females in age class 2 between times t_k and t_{k-1}, plus the number of daughters born to females in age class 3 between times t_k and t_{k-1}. In this example, since salmon only produce offspring in their last year of life, $F_1 = 0$ and $F_2 = 0$, so we get the equation

$$x_1^{(k)} = 0x_1^{(k-1)} + 0x_2^{(k-1)} + F_3 x_3^{(k-1)}. \tag{2}$$

The number of females in the second age class at time t_k are those females in the first age class at time t_{k-1} who are still alive at time t_k, or mathematically $x_2^{(k)} = P_1 x_1^{(k-1)}$, the number of

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females in the third age class at time t_k are those females in the second age class at time t_{k-1} who are still alive at time t_k, or mathematically $x_3^{(k)} = P_2 x_2^{(k-1)}$. We end up with the following system of linear equations.

$$\begin{aligned} x_1^{(k)} &= F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + F_3 x_3^{(k-1)} \\ x_2^{(k)} &= P_1 x_1^{(k-1)} \\ x_3^{(k)} &= P_2 x_2^{(k-1)} \end{aligned} \tag{3}$$

We can use matrices to rewrite this system of equations as

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \end{pmatrix},$$

and even more compactly as

$$\mathbf{x}^{(k)} = L\mathbf{x}^{(k-1)}, \tag{4}$$

where

$$\mathbf{x}^{(k)} = \begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \end{pmatrix}$$

is the age distribution vector at time t_k, and

$$\mathbf{x}^{(k-1)} = \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \end{pmatrix}$$

is the age distribution vector at time t_{k-1}, and

$$L = \begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \tag{5}$$

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is called the *Leslie Matrix.*

Finally, because $F_1 = F_2 = 0$, we get

$$L = \begin{pmatrix} 0 & 0 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}. \tag{6}$$

We can now generate a sequence of matrix equations to find the age distribution vector at any time t_k.

$$\begin{aligned} \mathbf{x}^{(1)} &= L\mathbf{x}^{(0)} \\ \mathbf{x}^{(2)} &= L\mathbf{x}^{(1)} = L(L\mathbf{x}^{(0)}) = L^2\mathbf{x}^{(0)} \\ \mathbf{x}^{(3)} &= L\mathbf{x}^{(2)} = L(L^2\mathbf{x}^{(0)}) = L^3\mathbf{x}^{(0)} \\ &\vdots \\ \mathbf{x}^{(k)} &= L\mathbf{x}^{(k-1)} = L(L^{k-1}\mathbf{x}^{(0)}) = L^k\mathbf{x}^{(0)} \end{aligned} \tag{7}$$

Thus, if we know the initial age distribution vector

$$\mathbf{x}^{(0)} = \begin{pmatrix} x_1^{(0)} \\ x_2^{(0)} \\ x_3^{(0)} \end{pmatrix}$$

and the Leslie matrix L, we can determine the female age distribution vector at any later time by multiplying an appropriate power of the Leslie matrix with the initial age distribution vector $\mathbf{x}^{(0)}$.

An Example Using MATLAB

Suppose there are 1,000 females in each of the three age classes, so

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$$\mathbf{x}^{(0)} = \begin{pmatrix} x_1^{(0)} \\ x_2^{(0)} \\ x_3^{(0)} \end{pmatrix} = \begin{pmatrix} 1,000 \\ 1,000 \\ 1,000 \end{pmatrix}.$$

Suppose further that the survival rate for salmon in the first age class is 0.5%, the survival rate for salmon in the second age class is 10%, and that each female in the third age class produces 2,000 female offspring. Then $P_2 = 0.005$, $P_3 = 0.10$, and $F_3 = 2,000$. The corresponding Leslie matrix for this system is

$$L = \begin{pmatrix} 0 & 0 & 2000 \\ .005 & 0 & 0 \\ 0 & .10 & 0 \end{pmatrix}.$$

To find the age distribution vector after one year, we use the equation $\mathbf{x}^{(1)} = L\mathbf{x}^{(0)}$. We can use MATLAB to find $\mathbf{x}^{(1)}$. First, enter the initial age distribution vector and the Leslie matrix.

```
>> x0=[1000;1000;1000];
>> L=[0 0 2000;0.005 0 0;0 .10 0]
L =
  1.0e+003 *
         0          0    2.0000
    0.0000          0         0
         0     0.0001         0
```

Note that Matlab is using scientific notation. The `1.0e+003 *` prior to the display of the matrix indicates that you should multiply each entry of the resulting matrix by 1.0×10^3, effectively moving each decimal point three places to the right. Let's try a different format for our output (Type `help format` to get a complete list of Matlab's formatting possibilities).

```
>> format short g
>> L=[0 0 2000;0.005 0 0;0 0.10 0]
L =
```


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```
            0             0          2000
        0.005             0             0
            0           0.1             0
```

The command `format short g` prompts Matlab to use the best of fixed or floating point format, making a decision on each entry of the matrix, rather than applying one format to the entire matrix. Now, compute $x^{(1)}$ in the following manner.

```
>> x1=L*x0
x1 =
     2000000
           5
         100
```

The age distribution vector $\mathbf{x}^{(1)}$ shows that after the first year there are 2,000,000 salmon in the first age class, 5 in the second age class, and 100 in the third age class. Use MATLAB to find the age distribution vector $\mathbf{x}^{(2)}$ after two years.

```
>> x2=L*x1
x2 =
        2e+005
         10000
           0.5
```

You can produce exactly the same result with

```
>> x2=L^2*x0
x2 =
        2e+005
         10000
           0.5
```

The age distribution vector $\mathbf{x}^{(2)}$ shows that after two years there are 200,000 salmon in the first age class, 10,000 in the second age class, and 0.5 in the third age class. In real life it is not possible to have 1/2 of a salmon. However, let's postpone this issue for a moment and continue with the computation of the population after three years.

```
>> x3=L*x2
x3 =
         1000
         1000
         1000
```

Again, rather than proceeding with consecutive iterations, one can proceed directly to the answer with

```
>> x3=L^3*x0
x3 =
         1000
         1000
         1000
```

Note that the salmon population has returned to its original configuration, with 1,000 fish in each age category. Use Matlab to perform at least four more iterations; i.e., find $x^{(4)}$, $x^{(5)}$, $x^{(6)}$, and $x^{(7)}$. What pattern do you see?

The Graph of the Age Distribution Vector

One of the best ways to examine trends in population growth is to sketch the graph of the age distribution vector versus time. Also, it's often desirable to track a population for more than three or four years.

Using For Loops

Iterating the equation $x^{(k)} = Lx^{(k-1)}$ in the manner above is inefficient. If you know ahead of time the precise number of times that you wish to perform the iteration, then using a `for` loop in Matlab is the most efficient method.

First, load your Leslie Matrix and the initial age distribution vector.

```
>> L=[0 0 2000;0.005 0 0;0 0.10 0];
>> x0=[1000;1000;1000];
```

Let's iterate the equation $x^{(k)} = Lx^{(k-1)}$ a total of 24 times which will produce 24 generations of the age distribution vector. The makers of Matlab recommend that you plan ahead and reserve space in the memory of your computer to store your results. Let's follow this recommendation and reserve space for the results of 24 iterations by creating a 3×24 matrix of zeros: three rows because each age distribution vector contains three rows, twenty four columns because we will generate 24 age distribution vectors.

```
>> X=zeros(3,24)
```

Next, place the initial age distribution vector in the first column of the matrix X.

```
>> X(:,1)=x0
```

Recall that the Matlab index notation, `X(:,1)`, is read "every row, first column." Consequently, the command `X(:,1)=x0` places the initial conditions, contained in `x0`, into the first column of the matrix `X`.

Calculate the second through twenty-fourth columns of the matrix X by iterating the equation $x^{(k)} = Lx^{(k-1)}$ for k-values ranging from two through twenty four.

```
>> for k=2:24, X(:,k)=L*X(:,k-1); end
```


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When the number of iterations needed are known in advance, Matlab's `for` loop is the ideal construct. Recall that `2:24` produces a row vector, starting at 2 and proceeding in increments of 1 until it reaches the number 24. Therefore, the command `for k=2:24` begins the loop with a k-value equal to 2. The next time through the loop a k-value of 3 is used. Iteration continues and the last time through the loop, a k-value of 24 is used. Note that the `end` command signals the end of the loop.

The command `X(:,k)=L*X(:,k-1)` warrants explanation. Recall that `X(:,k)` is read "matrix `X`, every row, kth column." Similarly, the command `X(:,k-1)` is read "matrix `X`, every row, $k-1$st column." Consequently, the command `X(:,k)=L*X(:,k-1)` forms the product of the Leslie matrix L and the $k-1$st column of matrix `X` and stores the result in the kth column of matrix `X`, precisely the iteration we need (recall that $\mathbf{x}^{(k)} = L\mathbf{x}^{(k-1)}$).[2]

Once the iteration is complete, you can display the contents of the matrix `X` by entering `X` at the Matlab prompt and pressing the Enter key.

```
>> X =
  Columns 1 through 6
       1000      2e+006      2e+005        1000      2e+006      2e+005
       1000           5       10000        1000           5       10000
       1000         100         0.5        1000         100         0.5
  Columns 7 through 12
       1000      2e+006      2e+005        1000      2e+006      2e+005
       1000           5       10000        1000           5       10000
       1000         100         0.5        1000         100         0.5
  Columns 13 through 18
       1000      2e+006      2e+005        1000      2e+006      2e+005
       1000           5       10000        1000           5       10000
       1000         100         0.5        1000         100         0.5
  Columns 19 through 24
```

[2]We have suppressed output during the iteration of the for loop, but it is instructive to remove the semicolon after `X(:,k)=L*X(:,k-1)`.

1000	2e+006	2e+005	1000	2e+006	2e+005
1000	5	10000	1000	5	10000
1000	100	0.5	1000	100	0.5

Type `help plot` at the Matlab prompt and read the resulting helpfile. Pay particular attention to the following lines.

```
>> help plot

 PLOT   Plot vectors or matrices.
    PLOT(Y) plots the columns of Y versus their index.
```

However, the first *row* of the matrix X contains the numbers of female salmon in the first age class (juveniles), the second *row* contains the second age class (subadults), and the third *row* contains the number of female salmon in the third and final age class (adults). We want to plot the *rows* of X versus the index but `plot(X)` plots the *columns* of X versus the index.[3] The solution: plot the *transpose* of X.

The following command will produce an image similar to that in **Figure 1**.

```
>> plot(X')
```

If the command `plot(X')` is supposed to plot each of the three columns of the matrix `X'`, then where are the graphs of the remaining two columns in **Figure 1**? If you look closely you can see a little activity near the x-axis in **Figure 1**. Note that the upper limit on the y -axis in Figure 1 is 2×10^6. When there is such a wide range in the data (values as small as 1/2 and as large as 2,000,000) you can get a better picture by plotting the natural logarithm of the salmon populations versus the time. The following command produces an image similar to that in **Figure 2**.

---

[3]The following experiment is instructive. Enter and execute `Y=[1 2 3 4 5;2 3 4 5 1]` at the Matlab prompt. Then enter `plot(Y,'*-'), figure, plot(Y','*-')` and compare and contrast the differences between the two plots.

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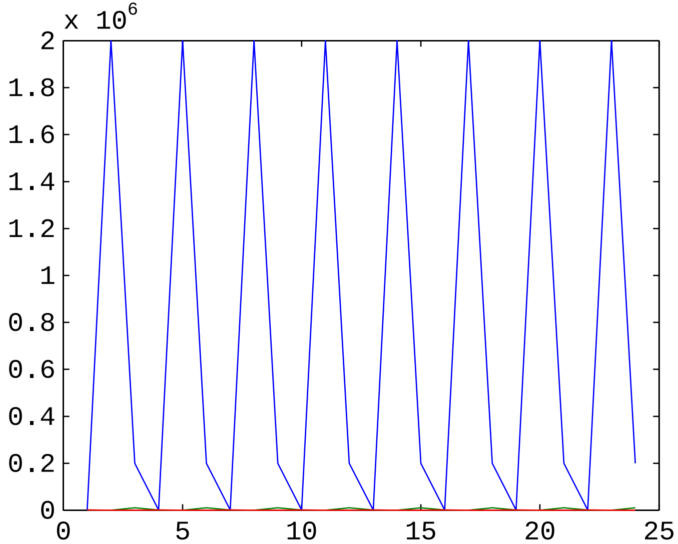

Figure 1 The salmon population over time.

```
>> semilogy(X')
```

It is helpful to place a legend on your graph. The following command will produce an image similar to that in **Figure 3**.

```
>> legend('Juveniles','Subadults','Adults')
```

It is clear from the graph in **Figure 3** that each age division of the salmon population is oscillating with period 3.

Extra for Experts. The actual graph in **Figure 3** was produced using Matlab's handle graphics capabilities. If you are interested, try the following commands.

```
>> h=semilogy(X')
h =
```

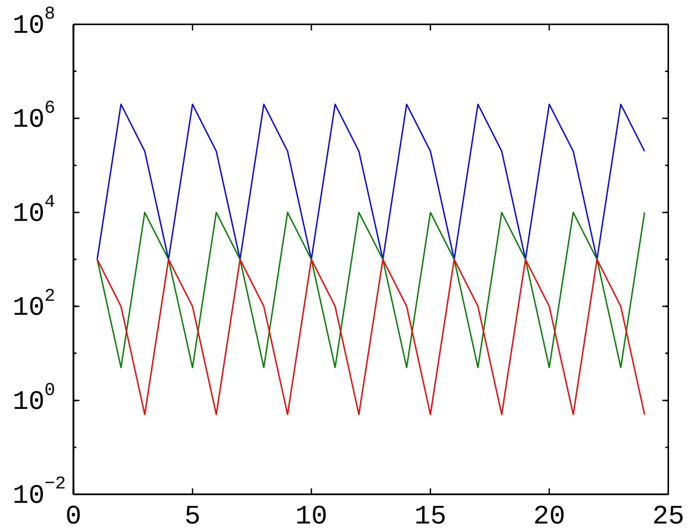

Figure 2 Semilog plot of salmon population over time.

```
        9.0011
        12.001
        13.001
>> set(h(1),'LineStyle','--')
>> set(h(2),'LineStyle',':')
>> legend('Juveniles','Subadults','Adults')
>> grid off
```

In the latest release of Matlab, version 5.3, Release 11, you can change linestyles interactively by enabling plot editing, then right clicking a line with the mouse. A popup menu provides choices for linestyles, colors, and a host of other properties.

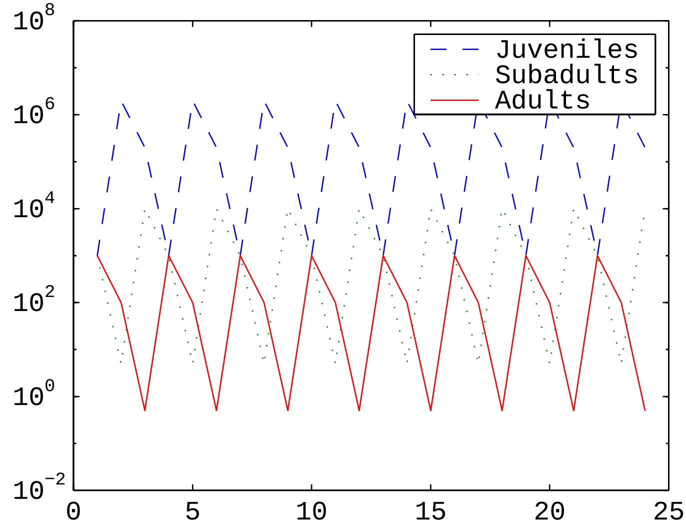

Figure 3 Providing a legend.

Homework

Instructions. For each of the following questions use the printer to produce a hardcopy image of the required graph.

1. Suppose a particular species of salmon lives to *four* years of age. In addition, suppose that the survival rate of salmon in their first, second, and third years is 0.5%, 7%, and 15%, respectively. You also know that each female in the fourth age class produces 5,000 female offspring. The other age classes produce no offspring.

   a. Find the Leslie matrix for this population.

   b. If 1,000 female salmon in each of the four age classes are introduced into the system, find the initial age distribution vector.

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c. Use a `for` loop to iterate the Leslie equation 25 times. Use MATLAB to plot the natural logarithm of each age class of salmon versus time. What is the eventual fate of this salmon population?

d. Calculate the salmon population on the 50th iteration, without calculating the preceding 49 iterations.

2. Suppose another species of salmon lives to *four* years of age. In addition, the survival rate of salmon in their first, second, and third years is 2%, 15%, and 25%, respectively. You also know that each female in the fourth age class produces 5,000 female offspring. The other age classes produce no offspring.

   a. Find the Leslie matrix for this population.

   b. If 1,000 female salmon in each of the four age classes are introduced into the system, find the initial age distribution vector.

   c. Use a `for` loop to iterate the Leslie equation 25 times. Use MATLAB to plot the natural logarithm of each age class of salmon versus time. What is the eventual fate of this salmon population?

   d. Calculate the salmon population on the 50th iteration, without calculating the preceding 49 iterations.

3. Suppose a third species of salmon lives to *four* years of age. In addition, the survival rate of salmon in their first, second, and third years is 1%, 10%, and 2%, respectively. You also know that each female in the fourth age class produces 5,000 female offspring. The other age classes produce no offspring.

   a. Find the Leslie matrix for this population.

   b. If 1,000 female salmon in each of the four age classes are introduced into the system, find the initial age distribution vector.

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c. Use a `for` loop to iterate the Leslie equation 25 times. Use MATLAB to plot the natural logarithm of each age class of salmon versus time. What is the eventual fate of this salmon population?

d. Calculate the salmon population on the 50th iteration, without calculating the preceding 49 iterations.

Discussion

Although **equation 7** gives the age distribution of the population at any time, it does not immediately give a general picture of the dynamics of the growth process. To study the limiting behavior of the population growth we will need to learn about the eigenvalues and eigenvectors of the Leslie matrix. We will return to this problem later in the course.