

The Leslie Matrix Part II

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 eigenvalues and eigenvectors and Matlab's indexing methods.*

1 Introduction

This is the second lab that focuses on the use of the Leslie Model to determine the growth of a population. In the first lab, we introduced the Leslie Matrix model. Recall that the Leslie model uses the following assumptions:

- We consider only the females in the population.
- The maximum age attained by any individual is n years.
- The population is grouped into n one-year age classes.
- An individual'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 rate F_i for each age group is known.
- The initial age distribution is known.

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

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

where $x_i^{(k)}$ is the number of females in the i th age class at time t_k . Now, at time t_k , the number of females in the first age class, $x_1^{(k)}$, are just those daughters born between time t_{k-1} and t_k . The number of offspring produced by

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each age class can be calculated by multiplying the reproductive rate by the number of females in that particular age class. The sum of all these values gives the total number of offspring produced. Thus, we can write

$$x_1^{(k)} = F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + \dots + F_n x_n^{(k-1)}.$$

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 . In symbols, $x_2^{(k)} = P_1 x_1^{(k-1)}$. The number of 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 . In symbols, $x_3^{(k)} = P_2 x_2^{(k-1)}$. In general, the number of females in the n th age class at time t_k are those females in the $(n-1)$ st age class at time t_{k-1} who are still alive at time t_k . In symbols, $x_n^{(k)} = P_{n-1} x_{n-1}^{(k-1)}$. We end up with the following system of linear equations.

$$\begin{aligned} x_1^{(k)} &= F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + \dots + F_n x_n^{(k-1)} \\ x_2^{(k)} &= P_1 x_1^{(k-1)} \\ x_3^{(k)} &= P_2 x_2^{(k-1)} \\ &\vdots \\ x_n^{(k)} &= P_{n-1} x_{n-1}^{(k-1)} \end{aligned}$$

We can use matrices to rewrite this system of equations as

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ \vdots \\ x_n^{(k)} \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 & \dots & F_{n-1} & F_n \\ P_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & P_2 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \dots & P_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \\ \vdots \\ x_n^{(k-1)} \end{pmatrix},$$

or even more compactly as

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

where

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

is the age distribution vector at time t_k ,

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

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

$$L = \begin{pmatrix} F_1 & F_2 & F_3 & \cdots & F_{n-1} & F_n \\ P_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & P_{n-1} & 0 \end{pmatrix}$$

is called the *Leslie Matrix*.

We can iterate **equation 1** to find the age distribution vector at any time t_k as follows.

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

Thus, if we know the initial age distribution vector

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

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

2 An Example Using Matlab

Suppose a population has three age classes. In addition, suppose that females in the second and third age classes produces 4 and 3 offspring, respectively, every iteration. Suppose further that 50% of the females in the first age class live on into the second age class and 25% of the females in the second age class live on into the third age class. The Leslie matrix for this population is

$$L = \begin{pmatrix} 0 & 4 & 3 \\ .5 & 0 & 0 \\ 0 & .25 & 0 \end{pmatrix}.$$

Suppose that the initial population vector is

$$\mathbf{x}^{(0)} = \begin{pmatrix} 10 \\ 10 \\ 10 \end{pmatrix}.$$

Load the Leslie matrix and initial age distribution vector with these Matlab commands.

```
>> L=[0 4 3;.5 0 0;0 .25 0]
>> x0=[10;10;10]
```

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We will follow the changes in the population over a 10-year period. We start with year zero and end with year eleven. There are three age classes to deal with on each iteration. We begin by initializing a matrix to contain the population data. The matrix will have three rows, each row containing data for one of three age classes. The matrix will contain eleven columns, the first of which will contain the initial age distribution vector. The remaining ten columns will contain the age distribution vectors at each stage of the iteration (years one through ten).

```
>> X=zeros(3,11)
```

We store the initial age distribution vector in the first column of matrix X .

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

We now use [equation 1](#) to compute the age distribution vector over the next 10 years. These ten age distribution vectors will be stored in columns two through eleven of matrix X . At the k th step, we compute the k th age distribution vector by multiplying the $(k - 1)$ st age distribution vector by the Leslie matrix L . We encase this command in a for loop.

```
>> for k=2:11, X(:,k)=L*X(:,k-1); end
```

We can view the results by simply entering the variable containing the data.

```
>> X
```

X =

1.0e+003 *

Columns 1 through 8

0.0100	0.0700	0.0275	0.1437	0.0813	0.2978	0.2164	0.6261
0.0100	0.0050	0.0350	0.0138	0.0719	0.0406	0.1489	0.1082
0.0100	0.0025	0.0013	0.0088	0.0034	0.0180	0.0102	0.0372

Columns 9 through 11

0.5445	1.3333	1.3238
0.3130	0.2722	0.6667
0.0271	0.0783	0.0681

Note the prefix to the output, $1.0e+003 *$. This means that you must multiply each number in the output by 1×10^3 . This is scientific notation. For the remainder of the activity, we will use a friendlier format.

```
>> format short g
```

```
>> X
```

X =

Columns 1 through 6

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10	70	27.5	143.75	81.25	297.81
10	5	35	13.75	71.875	40.625
10	2.5	1.25	8.75	3.4375	17.969

Columns 7 through 11

216.41	626.09	544.49	1333.3	1323.8
148.91	108.2	313.05	272.25	666.67
10.156	37.227	27.051	78.262	68.062

The population distribution for each year is shown as one of the column vectors of matrix X. The graph of population vs time, as shown in **Figure 1**, can be produced by entering the following commands.

```
>> t=0:10;
>> plot(t,X')
>> xlabel('Time')
>> ylabel('Population')
```

Adding a legend is helpful.

```
>> legend('First age class', 'Second age class', 'Third age class')
```

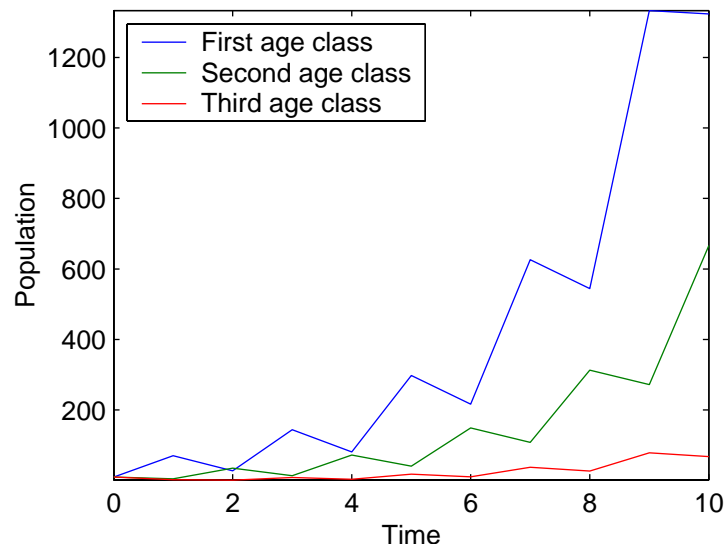


Figure 1 Salmon population over 10 years.

Notice that the number of females in each age group in Figure 1 generally increases over time, with some oscillatory behavior. We can plot the log of the population over time, as shown in **Figure 2**, by entering the following commands.

```
>> t=0:10;
>> semilogy(t,X')
>> xlabel('Time')
>> ylabel('Log(Population)')
>> legend('First age class', 'Second age class', 'Third age class')
```

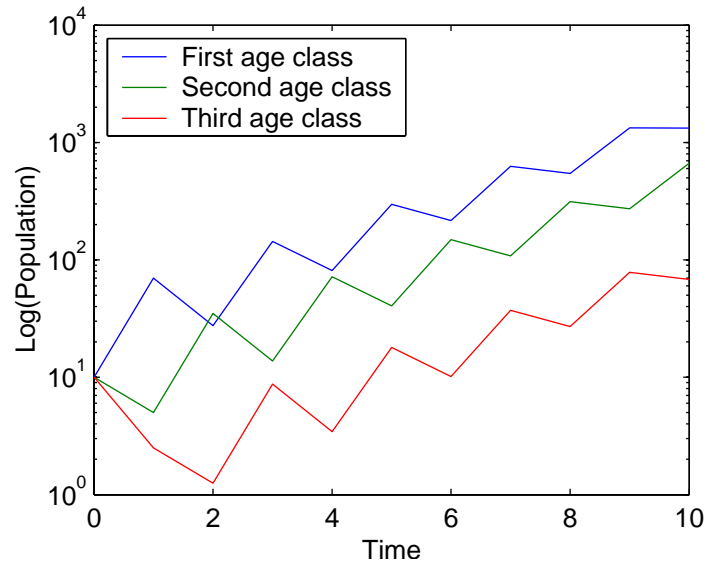


Figure 2 Logarithm of the salmon population over 10 years.

We can use Matlab to compute the age distribution vector for any particular year by multiplying the initial age distribution vector by an appropriate power of the Leslie matrix. For example, the age distribution vector in year ten is $\mathbf{x}^{(10)} = L^{10}\mathbf{x}^{(0)}$.

```
>> x0=[10;10;10]
x0 =
    10
    10
    10

>> x10=L^10*x0
x10 =
  1323.8
   666.67
   68.062
```

Notice that x10 is the same vector as column 11 in the matrix X above. Try multiplying x0 by other powers of L to verify that $\mathbf{x}^{(k)} = L^k\mathbf{x}^{(0)}$ for any positive integer k .

3 Limiting Behavior

In *The Leslie Matrix, Part I*, we examined several examples of the Leslie Model applied to different populations of salmon. In some cases, the population went into extinction, in some cases the population exploded with growth, and in some cases the population exhibited a periodic behavior. To understand why these cases occur, we will have to investigate the eigenvalues and eigenvectors of the Leslie matrix. The eigenvalues of the Leslie matrix L are found by finding the zeros of the characteristic polynomial $p(\lambda) = \det(L - \lambda I)$.

Suppose the Leslie matrix L is $n \times n$ with n distinct eigenvalues, $\lambda_1, \lambda_2, \dots$, and λ_n . In this case, it can be shown that there are n linearly independent eigenvectors, $\mathbf{v}_1, \mathbf{v}_2, \dots$, and \mathbf{v}_n , so that

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$$L\mathbf{v}_i = \lambda_i \mathbf{v}_i,$$

for $i = 1, 2, \dots, n$. If we let

$$V = \begin{pmatrix} \mathbf{v}_1 & \mathbf{v}_2 & \dots & \mathbf{v}_n \end{pmatrix},$$

then

$$\begin{aligned} LV &= L \begin{pmatrix} \mathbf{v}_1 & \mathbf{v}_2 & \dots & \mathbf{v}_n \end{pmatrix} \\ &= \begin{pmatrix} L\mathbf{v}_1 & L\mathbf{v}_2 & \dots & L\mathbf{v}_n \end{pmatrix} \\ &= \begin{pmatrix} \lambda_1 \mathbf{v}_1 & \lambda_2 \mathbf{v}_2 & \dots & \lambda_n \mathbf{v}_n \end{pmatrix} \\ &= \begin{pmatrix} \mathbf{v}_1 & \mathbf{v}_2 & \dots & \mathbf{v}_n \end{pmatrix} \begin{pmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n \end{pmatrix} \\ &= V\Lambda \end{aligned}$$

Because the columns of V are independent, V is invertible and we can *diagonalize* matrix A . That is,

$$A = V\Lambda V^{-1},$$

where V contains the eigenvectors of L as its columns and

$$\Lambda = \begin{pmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n \end{pmatrix}.$$

Powers of the Leslie matrix are now easily calculated.

$$L^k = (V\Lambda V^{-1})^k = (V\Lambda V^{-1})(V\Lambda V^{-1}) \dots (V\Lambda V^{-1}) = V\Lambda^k V^{-1},$$

It is a simple matter to raise a diagonal matrix to a power. Readers can check that

$$\Lambda^k = \begin{pmatrix} \lambda_1^k & 0 & \dots & 0 \\ 0 & \lambda_2^k & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n^k \end{pmatrix}.$$

Thus,

$$L^k = V \begin{pmatrix} \lambda_1^k & 0 & 0 & \dots & 0 \\ 0 & \lambda_2^k & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & 0 & \lambda_n^k \end{pmatrix} V^{-1}$$

for $k = 1, 2, \dots$. For any initial age distribution vector $\mathbf{x}^{(0)}$ we can find the age distribution vector $\mathbf{x}^{(k)}$ after k years by finding $L^k \mathbf{x}^{(0)}$. In this case,

$$\mathbf{x}^{(k)} = L^k \mathbf{x}^{(0)} = V \begin{pmatrix} \lambda_1^k & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2^k & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & 0 & \lambda_n^k \end{pmatrix} V^{-1} \mathbf{x}^{(0)}. \quad (2)$$

We define the vector $V^{-1} \mathbf{x}^{(0)}$ to be

$$V^{-1} \mathbf{x}^{(0)} = \begin{pmatrix} c_1 \\ c_2 \\ \vdots \\ c_n \end{pmatrix}.$$

Inserting this result in [equation 2](#),

$$\mathbf{x}^{(k)} = [\mathbf{v}_1, \mathbf{v}_2, \dots, \mathbf{v}_n] \begin{pmatrix} \lambda_1^k & 0 & 0 & \cdots & 0 \\ 0 & \lambda_2^k & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & 0 & \lambda_n^k \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \\ \vdots \\ c_n \end{pmatrix}.$$

Multiplying the diagonal matrix and the vector $(c_1, c_2, \dots, c_n)^T$,

$$\mathbf{x}^{(k)} = [\mathbf{v}_1, \mathbf{v}_2, \dots, \mathbf{v}_n] \begin{pmatrix} c_1 \lambda_1^k \\ c_2 \lambda_2^k \\ \vdots \\ c_n \lambda_n^k \end{pmatrix},$$

and

$$\mathbf{x}^{(k)} = c_1 \lambda_1^k \mathbf{v}_1 + c_2 \lambda_2^k \mathbf{v}_2 + \cdots + c_n \lambda_n^k \mathbf{v}_n. \quad (3)$$

Remark 1

Notice that this is similar to the equation that was derived for the closed form solution of a first order difference equation!

Now suppose λ_1 is greater in absolute value than every other eigenvalue (we say λ_1 is a *strictly dominant eigenvalue*). Divide each side of [equation 3](#) by λ_1^k .

$$\frac{1}{\lambda_1^k} \mathbf{x}^{(k)} = \frac{\lambda_1^k}{\lambda_1^k} c_1 \mathbf{v}_1 + \frac{\lambda_2^k}{\lambda_1^k} c_2 \mathbf{v}_2 + \cdots + \frac{\lambda_n^k}{\lambda_1^k} c_n \mathbf{v}_n \quad (4)$$

Now if $|\lambda_1| > |\lambda_i|$ for $i = 2, 3, \dots, n$, then $|\lambda_i|/|\lambda_1| < 1$ for $i = 2, 3, \dots, n$. It follows that

$$\left(\frac{\lambda_i}{\lambda_1} \right)^k \rightarrow 0 \quad \text{as} \quad k \rightarrow \infty,$$

for $i = 2, 3, \dots, n$. Using this fact, we can take the limit of both sides of the [equation 4](#) to get

$$\lim_{k \rightarrow \infty} \left\{ \frac{1}{\lambda_1^k} \mathbf{x}^{(k)} \right\} = c_1 \mathbf{v}_1.$$

So for large values of k , we can approximate $\mathbf{x}^{(k)}$ by

$$\mathbf{x}^{(k)} \approx c_1 \lambda_1^k \mathbf{v}_1. \quad (5)$$

Remark 2

This means that for large values of time, the age distribution vector is a scalar multiple of the eigenvector associated with the largest eigenvalue of the Leslie matrix. Consequently the proportion of females in each of the age classes becomes a constant, and these limiting proportions can be determined from the eigenvector \mathbf{v}_1 associated with the largest eigenvalue λ_1 .

4 More Examples using Matlab

Using the Leslie matrix

$$L = \begin{pmatrix} 0 & 4 & 3 \\ .5 & 0 & 0 \\ 0 & .25 & 0 \end{pmatrix},$$

we can use Matlab to find the eigenvalues and eigenvectors of L .

```
>> L=[0 4 3;.5 0 0;0 .25 0]
L =
      0      4.0000      3.0000
  0.5000      0      0
      0      0.2500      0
```

```
>> [V,D]=eig(L)
V =
  0.9474    0.9320    0.2259
  0.3158   -0.3560   -0.5914
  0.0526    0.0680    0.7741
```

```
D =
  1.5000      0      0
      0   -1.3090      0
      0      0   -0.1910
```

The Matlab command `[V,D]=eig(L)` stores the eigenvalues of L in a diagonal matrix D , and the eigenvectors associated with each eigenvalue are stored in the columns of matrix V . In this example, Matlab calculates $\lambda_1 = 1.5$, and the associated eigenvector

$$\mathbf{v}_1 = \begin{pmatrix} 0.9474 \\ 0.3158 \\ 0.0526 \end{pmatrix}$$

is stored in the first column of matrix V . Also, $\lambda_2 = -1.3090$, and the associated eigenvector

$$\mathbf{v}_2 = \begin{pmatrix} 0.9320 \\ -0.3560 \\ 0.0680 \end{pmatrix}$$

is stored in the second column of matrix V . Finally, $\lambda_3 = 0.1910$, and the associated eigenvector

$$\mathbf{v}_3 = \begin{pmatrix} 0.2259 \\ -0.5914 \\ 0.7741 \end{pmatrix}$$

is stored in the third column of V . We can use the following commands to show that $L = VDV^{-1}$.

```
>> V*D*inv(V)
ans =
    0.0000    4.0000    3.0000
    0.5000    0.0000    0.0000
    0.0000    0.2500    0.0000
```

Note that this result is identical to the Leslie matrix L .

Note that the dominant eigenvalue is $\lambda_1 = 1.5$ and its associated eigenvector \mathbf{v}_1 is stored in the first column of matrix V . Recall that any scalar multiple of an eigenvector is also an eigenvector. In our analysis, it will be useful to divide each entry of the eigenvector \mathbf{v}_1 by the sum of all the entries in the vector. First, strip \mathbf{v}_1 from the first column of matrix V .

```
>> v1=V(:,1)
v1 =
    0.94737
    0.31579
    0.052632
```

Next, divide each entry in \mathbf{v}_1 by the sum of the entries in \mathbf{v}_1 .

```
>> v1=v1/sum(v1)
v1 =
    0.72
    0.24
    0.04
```

Notice that the sum of the entries of this new eigenvector is now 1, and that the first element is 72% of the total sum, the second is 24% of the total, and the last element is 4% of the total. These are the same relative proportions for each entry in the original eigenvector \mathbf{v}_1 . However, these values will help us determine the relative proportion of females in each age class after a long period of time.

From [equation 3](#), we know that

$$\mathbf{x}^{(k)} = c_1 \lambda_1^k \mathbf{v}_1 + c_2 \lambda_2^k \mathbf{v}_2 + c_3 \lambda_3^k \mathbf{v}_3.$$

Substituting the eigenvalues and eigenvectors into this equation we get

$$\mathbf{x}^{(k)} = c_1 (1.5)^k \begin{pmatrix} 0.9474 \\ 0.3158 \\ 0.0526 \end{pmatrix} + c_2 (-1.3090)^k \begin{pmatrix} 0.9320 \\ -0.3560 \\ 0.0680 \end{pmatrix} + c_3 (-0.1910)^k \begin{pmatrix} 0.2259 \\ -0.5914 \\ 0.7741 \end{pmatrix}.$$

Because $\lambda_1 = 1.5$ is the dominant eigenvalue, for large values of k the population age distribution vector $\mathbf{x}^{(k)}$ will be a scalar multiple of the eigenvector \mathbf{v}_1 . This eigenvector gives the long-term structure of the population age distribution. For large values of time, the population will be distributed in the ratios of the entries of the eigenvector \mathbf{v}_1 . We can check this in Matlab.

```
>> L=[0 4 3;.5 0 0;0 .25 0]
L =
      0      4.0000      3.0000
    0.5000      0      0
      0      0.2500      0
```

```
>> x0=[10;10;10]
x0 =
    10
    10
    10
```

```
>> x100=L^100*x0
x100 =
  1.1555e+019
  3.8516e+018
  6.4194e+017
```

```
>> x=x100/sum(x100)
x =
    0.72
    0.24
    0.04
```

The command $x=x100/\text{sum}(x100)$ divides the vector $x100$ by the sum of the entries of $x100$. This calculation shows that after 100 years the population has a distribution where 72% of the females are in the first age class, 24% of the females are in the second age class, and 4% of the females are in the third age class. Also note that this is same vector we obtained by dividing the eigenvector v_1 by the sum of its entries.

We can use Matlab to calculate the age distribution vectors for the first 100 years.

```
>> X=zeros(3,101);
>> X(:,1)=[10;10;10] ;
>> for k=2:101, X(:,k)=L*X(:,k-1); end
```

We can also calculate the relative percentages of each of the age classes over time by dividing each column by its sum.

```
>> G=zeros(3,101);
>> for k=1:101, G(:,k)=X(:,k)/sum(X(:,k)); end
```

The plot of these “normalized” populations is interesting.

```
>> t=0:100;
>> plot(t,G')
>> xlabel('Time')
>> ylabel('Percentages')
>> legend('First Age Class','Second Age Class','Third Age Class')
```

The plot is shown in **Figure 3**. After a long period of time the percentage of organisms in each of the three age classes approaches 74%, 24%, and 4%.

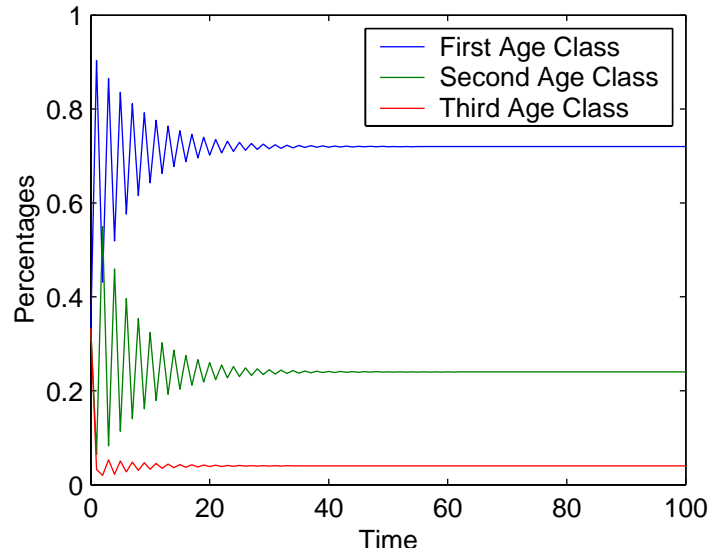


Figure 3 Percentages at each iteration.

The dominant eigenvalue $\lambda_1 = 1.5$ tells us how the population vector is changing from one year to the next. Enter in the following commands in Matlab.

```
>> x99=L^99*x0
x99 =
    7.7033e+018
    2.5678e+018
    4.2796e+017

>> x100./x99
ans =
    1.5
    1.5
    1.5
```

The command `x100./x99` divides each entry of the population vector `x100` by the corresponding entry of the vector `x99`. In this case we see that the number of females in each age class after 100 years is 1.5 times the number of females in each age class after 99 years. So, after a long period of time, the number of females in each age class increases by about 50% per year. In general, after a long period of time $\mathbf{x}^{(k)} \approx \lambda_1 \mathbf{x}^{(k-1)} \approx 1.5 \mathbf{x}^{(k-1)}$. This formula can be derived from [equation 5](#) as follows. First, by [equation 5](#), we write

$$\mathbf{x}^{(k)} \approx c_1 \lambda_1^k \mathbf{v}_1.$$

Similarly, we write

$$\mathbf{x}^{(k-1)} \approx c_1 \lambda_1^{k-1} \mathbf{v}_1,$$

or, equivalently,

$$\mathbf{v}_1 \approx \frac{1}{c_1 \lambda_1^{k-1}} \mathbf{x}^{(k-1)}.$$

Thus,

$$\mathbf{x}^{(k)} \approx c_1 \lambda_1^k \mathbf{v}_1 \approx c_1 \lambda_1^k \frac{1}{c_1 \lambda_1^{k-1}} \mathbf{x}^{(k-1)} \approx \lambda_1 \mathbf{x}^{(k-1)}.$$

5 Summary

The Leslie model is given by the equation $\mathbf{x}^{(k)} = L^k \mathbf{x}^{(0)}$, where $\mathbf{x}^{(0)}$ is the initial population distribution vector and $\mathbf{x}^{(k)}$ is the population distribution vector at time k . If L is diagonalizable, then $L = VDV^{-1}$, where D is a diagonal matrix whose diagonal entries are the eigenvalues of L . The columns of V are the corresponding eigenvectors. In this case, the equation for the Leslie model can be written as

$$\mathbf{x}^{(k)} = c_1 \lambda_1^k \mathbf{v}_1 + c_2 \lambda_2^k \mathbf{v}_2 + \cdots + c_n \lambda_n^k \mathbf{v}_n,$$

where λ_i and \mathbf{v}_i are the associated eigenvalues and eigenvectors of L . If λ_1 is a *strictly dominant eigenvalue* of L , then for large values of time,

$$\mathbf{x}^{(k)} \approx c_1 \lambda_1^k \mathbf{v}_1,$$

and the proportion of females in each of the age classes becomes a constant. These limiting proportions can be determined by the entries of the eigenvector \mathbf{v}_1 . Finally, the dominant eigenvalue λ_1 determines how the population vector is changing from one year to the next. Because

$$\mathbf{x}^{(k)} \approx \lambda_1 \mathbf{x}^{(k-1)}$$

for large values of k , the population vector at time k is a scalar multiple of the population vector at time $k - 1$, with the scalar being the dominant eigenvalue. If $\lambda_1 > 1$, then the population will grow, and the population will go to extinction if $\lambda_1 < 1$.

6 Homework

1. Suppose the survival rate of females in their first and second years is 60% and 25%. Each female in the second age class produces 4 female offspring, and each female in the third age class produces 3 female offspring.
 - a. Find the Leslie matrix for this population.
 - b. If there are 10 females in each of the three age classes, find the initial age distribution vector. Use Matlab to find the population age distribution vectors for each of the first 100 years, and plot the age distribution vectors using the plot and semilogy commands.
 - c. Use Matlab to find the eigenvalues and eigenvectors of the Leslie Matrix. What happens to this population over time?
 - d. After 100 years, what is the relative number of females in each of the three age classes?
 - e. After a long period of time, by what percentage is the population growing or shrinking?
2. Suppose the survival rate of females in their first and second years is 20% and 25%. Each female in the second age class produces 4 female offspring, and each female in the third age class produces 3 female offspring.
 - a. Find the Leslie matrix for this population.
 - b. If there are 10 females in each of the three age classes, find the initial age distribution vector. Use Matlab to find the population age distribution vectors for each of the first 100 years, and plot the age distribution vectors using the plot and semilogy commands.
 - c. Use Matlab to find the eigenvalues and eigenvectors of the Leslie Matrix. What happens to this population over time?
 - d. After 100 years, what is the relative number of females in each of the three age classes?
 - e. After a long period of time, by what percentage is the population growing or shrinking?
3. Suppose a population of salmon live to three years of age. Each adult salmon produces 800 offspring. The probability of a salmon surviving the first year to live on to the second year is 5%, and the probability of a salmon surviving the second year to live on to the third year is 2.5%.
 - a. Find the Leslie matrix for this population.
 - b. If there are 10 females in each of the three age classes, find the initial age distribution vector. Use Matlab to find the population age distribution vectors for each of the first 100 years.
 - c. Use Matlab to find the eigenvalues and eigenvectors of the Leslie Matrix. Is there a strictly dominant eigenvalue?
 - d. Describe what happens to this population of salmon over time?
4. Suppose the population of the United States is broken up into ten 5-year age classes. The values for the reproduction rates F_i and the survival rates P_i for each age class are shown in the table below.

The Leslie Matrix Part II

i	F_i	P_i
1	0	0.99670
2	0.00102	0.99837
3	0.08515	0.99780
4	0.30574	0.99672
5	0.40002	0.99607
6	0.28061	0.99472
7	0.15260	0.99240
8	0.06420	0.98867
9	0.01483	0.98274
10	0.00089	0

Table 1 Fecundities and survival rates.

- a. Find the Leslie matrix for this population.
 - b. If there are 10 females in each of the ten age classes, find the initial age distribution vector. Use Matlab to find the population age distribution vectors for each of the first 100 years, and plot the age distribution vectors using the plot and semilogy commands.
 - c. Use Matlab to find the eigenvalues and eigenvectors of the Leslie Matrix. What happens to this population over time?
 - d. After a long period of time, what is the relative number of females in each of the ten age classes?
 - e. After a long period of time, by what percentage is the population growing or shrinking?
5. Show that if L is the 3×3 matrix

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

then the characteristic polynomial is

$$p(\lambda) = \det(\lambda I - L) = \lambda^3 - F_1\lambda^2 - F_2P_1\lambda - F_3P_1P_2.$$

6. Show that if L is a 4×4 matrix

$$L = \begin{pmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix},$$

then the characteristic polynomial is

$$p(\lambda) = \det(\lambda I - L) = \lambda^4 - F_1\lambda^3 - F_2P_1\lambda^2 - F_3P_1P_2\lambda - F_4P_1P_2P_3.$$

7. Given the Leslie matrix

$$L = \begin{pmatrix} F_1 & F_2 & \cdots & F_{n-1} & F_n \\ P_1 & 0 & \cdots & 0 & 0 \\ \vdots & P_2 & \cdots & \vdots & \vdots \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & P_{n-1} & 0 \end{pmatrix},$$

try to find a formula for the characteristic polynomial of L .

7 Internet Links

Here are a number of references on the internet that may be of interest.

- A population ecology lab experiment. Virginia Tech University.
<http://www.gypsymoth.ento.vt.edu/sharov/PopEcol/lab5/lab5.html>
- Materials for Linear Algebra. Duke University. University.
<http://www.math.duke.edu/education/modules2/materials/linalg/leslie/contents.html>

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