Leslie Population Models

One of the most common models of population growth is the so–called **Leslie population model**. Developed in the 1940's, this model describes the growth of the female portion of an animal population. In this lab we describe how this model is developed and introduce some programs for computing with it.

The Leslie population model

In this model the females are divided into age groups of equal duration. Suppose the maximum age attained by any female in the population is L years. We divide the female population into n age groups, each age group then being $T = L/n$ years long. We'll label the age groups as indicated below.

Age Group	Ages
1	$0 \leq Age < T$
2	$T \leq Age < 2T$
3	$2T \leq Age < 3T$
$\vdots$	$\vdots$
$n-1$	$(n-2)T \leq Age < (n-1)T$
n	$(n-1)T \leq Age < nT = L$

Suppose we know the number of females in each age group at some initial time t_0; say, the first age group contains $x_1^{(0)}$ females, the second group contains $x_2^{(0)}$ females, and so on. We form the following *initial age distribution vector*.

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

The aging process is described by observing the population at discrete time periods, say, $t_0, t_1, t_2, \ldots,$ by, for example, taking a census every few years. In the Leslie model we suppose these observation times to be separated by the length of the age interval, that is we put

$$\begin{aligned} t_0 &= 0 \\ t_1 &= LT \\ t_2 &= 2T \\ &\vdots \\ t_k &= kT \\ &\vdots \end{aligned}$$

This assumption leads to the following important observation.

All females in the $(i+1)$–st age group at time t_{k+1} were in the i–th age group at time t_k.

As time goes on the number of females in each of the n age groups changes due to three biological processes: birth, death, and aging. We now describe these three processes quantitatively in order to project the initial age distribution into the future.

The birth and age processes between two successive observation times can be described by means of the following parameters.

a_i	*The average number of daughters born to a female during the time she is in the i–th age group.*
b_i	*The fraction of females in the i–th age group that can be expected to survive and pass into the $(i+1)$–st age group.*

Note that a_i is defined for $i = 1, 2, \ldots, n$ and b_i is defined for $i = 1, 2, \ldots, n-1$. Furthermore, it is clear that

$$\begin{array}{lll} \text{(i)} & a_i \geq 0 & \text{for } i = 1, 2, \ldots, n \\ \text{(ii)} & 0 < b_i \leq 1 & \text{for } i = 1, 2, \ldots, n-1 \end{array}$$

Notice that we don't allow any b_i to be equal to zero. We will also assume that at least one of the a_i is not zero.

We let $x_i^{(k)}$ denote the number of females in the i–th age group at time t_k. We'll call the following vector $\mathbf{x}^{(k)}$ the *age distribution vector* at time k.

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

Now, at time t_k the females in the first age group are just those daughters born between times t_{k-1} and t_k. Thus we can write

$$\left\{\begin{array}{c} \textit{number of} \\ \textit{females} \\ \textit{in age group 1} \\ \textit{at time } t_k \end{array}\right\} = \left\{\begin{array}{c} \textit{number of} \\ \textit{daughters} \\ \textit{born to} \\ \textit{females in} \\ \textit{age group 1} \\ \textit{between times} \\ t_{k-1} \textit{ and } t_k \end{array}\right\} + \left\{\begin{array}{c} \textit{number of} \\ \textit{daughters} \\ \textit{born to} \\ \textit{females in} \\ \textit{age group 2} \\ \textit{between times} \\ t_{k-1} \textit{ and } t_k \end{array}\right\} + \cdots + \left\{\begin{array}{c} \textit{number of} \\ \textit{daughters} \\ \textit{born to} \\ \textit{females in} \\ \textit{age group } n \\ \textit{between times} \\ t_{k-1} \textit{ and } t_k \end{array}\right\},$$

or,

$$x_1^{(k)} = a_1 x_1^{(k-1)} + a_2 x_2^{(k-1)} + \cdots + a_n x_n^{(k-1)}. \tag{1}$$

The females in the $(i+1)$–st age group $(i = 1, 2, \ldots, n-1)$ at time t_k are those females in the i–th age group at time t_{k-1} who survive to reach time t_k. Thus,

$$\left\{\begin{array}{c}\textit{number of}\\ \textit{females}\\ \textit{in age group } i+1\\ \textit{at time } t_k\end{array}\right\} = \left\{\begin{array}{c}\textit{fraction of}\\ \textit{females in}\\ \textit{age group } i\\ \textit{who survive}\\ \textit{and pass into}\\ \textit{age group } i+1\end{array}\right\} \cdot \left\{\begin{array}{c}\text{number of}\\ \text{females}\\ \text{in age group } i\\ \text{at time } t_{k-1}\end{array}\right\}$$

or,

$$x_{i+1}^{(k)} = b_i x_i^{(k-1)}, \qquad i = 1, 2, \ldots, n-1. \tag{2}$$

Now, equations (1) and (2) are both linear equations in the variables $x_1^{(k-1)}, x_2^{(k-1)}, \ldots, x_n^{(k-1)}$ with coefficients $a_1, a_2, \ldots, a_n$ and $b_1, b_2, \ldots, b_{n-1}$. Using matrix notation equations (1) and (2) can be written

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ x_4^{(k)} \\ \vdots \\ x_n^{(k)} \end{pmatrix} = \begin{pmatrix} a_1 & a_2 & a_3 & a_4 & \ldots & a_{n-1} & a_n \\ b_1 & 0 & 0 & 0 & \ldots & 0 & 0 \\ 0 & b_2 & 0 & 0 & \ldots & 0 & 0 \\ 0 & 0 & b_3 & 0 & \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \ldots & b_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \\ x_4^{(k-1)} \\ \vdots \\ x_n^{(k-1)} \end{pmatrix}$$

or, more compactly,

$$\mathbf{x}^{(k)} = L\mathbf{x}^{(k-1)}, \qquad k = 1, 2, 3, \ldots \tag{3}$$

where L is the **Leslie matrix**

$$L = \begin{pmatrix} a_1 & a_2 & a_3 & a_4 & \ldots & a_{n-1} & a_n \\ b_1 & 0 & 0 & 0 & \ldots & 0 & 0 \\ 0 & b_2 & 0 & 0 & \ldots & 0 & 0 \\ 0 & 0 & b_3 & 0 & \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \ldots & b_{n-1} & 0 \end{pmatrix} \tag{4}$$

From equation (3) it follows that

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

We have the important relationship

$$\boxed{\mathbf{x}^{(k)} = L^k\mathbf{x}^{(0)}} \tag{5}$$

We see that in order to determine the female population distribution at any future time it is enough to know the initial population distribution and the powers of the Leslie matrix, L^k.