Age-specific population growth I

Leslie model: An age-specific model of population growth accounts for how birth rates, death rates, and reproductive capacities vary across different age groups rather than treating all individuals as identical. The model is called age-specific because it accounts for the fact that an animal's likelihood of reproducing or succumbing to disease depends on its age. One of the most common models of age-specific population growth is the so-called "Leslie model". This model describes the growth of the female portion of a human or animal population. In this model, the females are divided into age classes of equal duration. To be specific, suppose the maximum age attained by any female in the population is L units (which may be years or some other unit). We divide the population into n age classes, each of duration $\frac{L}{n}$. We label the age classes according to the following table:

Age class	Age interval
1	$[0, \frac{L}{n})$
2	$[\frac{L}{n}, \frac{2L}{n})$
3	$[\frac{2L}{n}, \frac{3L}{n})$
$\vdots$	$\vdots$
n-1	$[\frac{(n-2)L}{n}, \frac{(n-1)L}{n})$
n	$[\frac{(n-1)L}{n}, L]$

Suppose we know the number of females in each of the n classes at time $t = 0$. Thus, $x_i^{(0)}$ $(i = 1, 2, \cdots, n)$ is the number of females in class i at time $t = 0$. This can be written compactly using a vector $\boldsymbol{x}^{(0)}$ as

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

This is called the initial stage distribution vector. Over time, the number of females in each of the n classes changes due to birth, death, and ageing processes. By describing these three processes mathematically, we examine how the initial age distribution changes over time.

We study the ageing process by observing the (female) population at discrete times $t_0, t_1, \cdots, t_k, \cdots$. The Leslie model stipulates that the duration between any two successive observation times must equal the duration of the age intervals. Thus, we take $t_0 = 0$, $t_1 = \frac{L}{n}$, $t_2 = \frac{2L}{n}, \cdots, t_k = \frac{kL}{n}, \cdots$. Consequently, all the females in the class $(i+1)$ at time t_{k+1} were in the class i at time t_k.

The birth and death processes between two successive observation times are described by means of the following demographic parameters:

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i. The average number of female daughters born to a single female is a_i $(i = 1, 2, \cdots, n)$ during the time she is in the class i. From the definition, it is clear that $a_i \geq 0$ for $i = 1, 2, \cdots, n$. We also assume that at least one a_i is positive so that some births occur. An age class for which the corresponding a_i is positive is called a fertile class.

ii. The fraction b_i $(i = 1, 2, \cdots, n-1)$ of females in the age class i survives and transitioned to the age class $(i+1)$. Clearly, $0 < b_i \leq 1$ for $i = 1, 2, \cdots, n-1$. Note that we do not allow b_i to be zero, because otherwise no female will survive beyond class i.

Now, we define age distribution vector $\boldsymbol{x}^{(k)}$ at time t_k by

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

where $x_i^{(k)}$ is the number of females in the age class i at time t_k. We note that the females in the first age class at time t_k are those daughters that were born between times t_{k-1} and t_k:

Number of females in age class 1 at time t_k	=	Number of daughters born to females in age class 1 between times t_{k-1} and t_k	+	Number of daughters born to females in age class 2 between times t_{k-1} and t_k	$+\cdots+$	Number of daughters born to females in age class n between times t_{k-1} and t_k

Equivalently,

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

Further, the number of females in the age class $i+1$ $(i = 1, 2, \cdots, n-1)$ at time t_k is the number of females in the age class i at time t_{k-1} who are still alive at time t_k. Thus,

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

Using matrix and vector notation, we write the above two in the following form:

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ \vdots \\ x_n^{(k)} \end{pmatrix} = \begin{pmatrix} a_1 & a_2 & a_3 & \cdots & a_{n-1} & a_n \\ b_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & b_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \\ \vdots \\ x_n^{(k-1)} \end{pmatrix} \quad \text{equivalently} \quad \boldsymbol{x}^{(k)} = \mathcal{L}\boldsymbol{x}^{(k-1)}, \quad k = 1, 2, \cdots,$$

where $\mathcal{L}$ is the Leslie matrix:

$$\mathcal{L} = \begin{pmatrix} a_1 & a_2 & a_3 & \cdots & a_{n-1} & a_n \\ b_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & b_{n-1} & 0 \end{pmatrix}$$

Thus, it follows that

$$\boldsymbol{x}^{(1)} = \mathcal{L}\boldsymbol{x}^{(0)},\ \boldsymbol{x}^{(2)} = \mathcal{L}\boldsymbol{x}^{(1)} = \mathcal{L}^2\boldsymbol{x}^{(0)},\ \boldsymbol{x}^{(3)} = \mathcal{L}\boldsymbol{x}^{(2)} = \mathcal{L}^3\boldsymbol{x}^{(0)}, \cdots, \boldsymbol{x}^{(k)} = \mathcal{L}\boldsymbol{x}^{(k-1)} = \mathcal{L}^k\boldsymbol{x}^{(0)}$$

Consequently, if we know the initial age distribution $\boldsymbol{x}^{(0)}$ and the Leslie matrix $\mathcal{L}$, we can find the age distribution of the female population at any subsequent time.

Example: Suppose the maximum age of females of a certain species is 15 years, and we consider three equal age classes. Average number of female offspring per female in age groups 1, 2 and 3 are 0, 2 and $\frac{1}{2}$ respectively. Proportion of females survival from age group 1 to age group 2 is $\frac{6}{10}$, and that from age group 2 to age group 3 is $\frac{3}{10}$. Suppose the initial number of females in each age group is 100.

From the given data, we find

$$\mathcal{L} = \begin{pmatrix} 0 & 2 & \frac{1}{2} \\ \frac{6}{10} & 0 & 0 \\ 0 & \frac{3}{10} & 0 \end{pmatrix} \quad \text{and} \quad \boldsymbol{x}^{(0)} = \begin{pmatrix} 100 \\ 100 \\ 100 \end{pmatrix}.$$

From the data, we find

$$\boldsymbol{x}^{(1)} = \mathcal{L}\boldsymbol{x}^{(0)} = \begin{pmatrix} 250 \\ 60 \\ 30 \end{pmatrix},\ \boldsymbol{x}^{(2)} = \mathcal{L}\boldsymbol{x}^{(1)} = \begin{pmatrix} 135 \\ 150 \\ 18 \end{pmatrix},\ \boldsymbol{x}^{(3)} = \mathcal{L}\boldsymbol{x}^{(2)} = \begin{pmatrix} 309 \\ 81 \\ 45 \end{pmatrix}, \quad \text{and so on.}$$

Thus, we conclude that the number of females in 15 years' time will be 309, 81, and 45 for the age groups 1, 2, and 3, respectively. Obviously, we can repeat this process to find the distribution of the female population in any year that is a multiple of 5.

Long-term behaviour: It is important to know what the long-term distribution of the female population will be. Here, we show that this can be answered from the eigenvalues and eigenvectors of the Leslie matrix. We know that

$$\boldsymbol{x}^{(k)} = \mathcal{L}\boldsymbol{x}^{(k-1)} = \mathcal{L}^k\boldsymbol{x}^{(0)}.$$

Hence, to know what happens in the long run, we need to find $\mathcal{L}^k$ for suitably large k. This can be easily done if the Leslie matrix $\mathcal{L}$ is diagonalisable. We assume that the Leslie matrix is diagonalisable. Then, we can find an invertible matrix $\mathcal{P}$ such that

$$\mathcal{L} = \mathcal{P}\mathcal{D}\mathcal{P}^{-1},$$

where

$$\mathcal{P} = \begin{pmatrix} \boldsymbol{v}_1 & \vdots & \boldsymbol{v}_2 & \vdots & \boldsymbol{v}_3 & \vdots & \cdots & \vdots & \boldsymbol{v}_n \end{pmatrix} \quad \text{and} \quad \mathcal{D} = \operatorname{diag}(\lambda_1, \lambda_2, \lambda_3, \cdots, \lambda_n).$$

Here, $\boldsymbol{v}_1, \boldsymbol{v}_2, \cdots, \boldsymbol{v}_n$ are the eigenvectors corresponding to eigenvalues $\lambda_1, \lambda_2, \cdots, \lambda_n$ (counting multiplicity) of $\mathcal{L}$. Now

$$\mathcal{L}^k = \left(\mathcal{P}\mathcal{D}\mathcal{P}^{-1}\right)^k = \underbrace{\left(\mathcal{P}\mathcal{D}\mathcal{P}^{-1}\right)\left(\mathcal{P}\mathcal{D}\mathcal{P}^{-1}\right)\cdots\left(\mathcal{P}\mathcal{D}\mathcal{P}^{-1}\right)}_{k \text{ times}} = \mathcal{P}\mathcal{D}^k\mathcal{P}^{-1}$$

Consequently

$$\mathcal{L}^k = \mathcal{P}\text{diag}(\lambda_1^k, \lambda_2^k, \lambda_3^k, \cdots, \lambda_n^k)\mathcal{P}^{-1}$$

Clearly, this simplifies the problem of finding the distribution of the female population in the k-th time period. This can be simplified further if we are interested in the distribution for large k. To see this, we first prove a few results.

Characteristic polynomial of Leslie matrix: The characteristic polynomial $p(\lambda) = |\lambda\mathcal{I} - \mathcal{L}|$ of Leslie matrix $\mathcal{L}$ is given by

$$p(\lambda) = \left(\lambda^n - a_1\lambda^{n-1} - a_2b_1\lambda^{n-2} - \cdots - a_{n-1}b_1b_2\cdots b_{n-2}\lambda - a_nb_1b_2\cdots b_{n-1}\right)$$

Proof: We prove this by induction. For $n = 1$, we find $p_1(\lambda) = \lambda - a_1$. For $n = 2$, we find

$$p_2(\lambda) = \det\begin{pmatrix} \lambda - a_1 & -a_2 \\ -b_1 & \lambda \end{pmatrix} = \lambda^2 - a_1\lambda - a_2b_1$$

Hence, the given relation is true for $n = 1$ and $n = 2$. Let it be true for $n = k$:

$$\begin{aligned} p_k(\lambda) &= \det\begin{pmatrix} \lambda - a_1 & -a_2 & -a_3 & \cdots & -a_{k-1} & -a_k \\ -b_1 & \lambda & 0 & \cdots & 0 & 0 \\ 0 & -b_2 & \lambda & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & -b_{k-1} & \lambda \end{pmatrix} \\ &= \left(\lambda^k - a_1\lambda^{k-1} - a_2b_1\lambda^{k-2} - \cdots - a_{k-1}b_1b_2\cdots b_{k-2}\lambda - a_kb_1b_2\cdots b_{k-1}\right) \end{aligned}$$

For $n = k + 1$, we write

$$p_{k+1}(\lambda) = \det\begin{pmatrix} \lambda - a_1 & -a_2 & -a_3 & \cdots & -a_k & -a_{k+1} \\ -b_1 & \lambda & 0 & \cdots & 0 & 0 \\ 0 & -b_2 & \lambda & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & -b_k & \lambda \end{pmatrix}$$

We expand the determinant using the last column, which leads to

$$p_{k+1}(\lambda) = (-1)^{k+2}(-a_{k+1})\det\begin{pmatrix} -b_1 & \lambda & 0 & \cdots & 0 \\ 0 & -b_2 & \lambda & \cdots & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & 0 & \cdots & -b_k \end{pmatrix} + \lambda\det\begin{pmatrix} \lambda - a_1 & -a_2 & \cdots & -a_{k-1} & -a_k \\ -b_1 & \lambda & \cdots & 0 & 0 \\ 0 & -b_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & \cdots & -b_{k-1} & \lambda \end{pmatrix}$$

Observe that the last determinant is the characteristic polynomial $p_k(\lambda)$. Hence, the expression of $p_{k+1}(\lambda)$ becomes

$$\begin{aligned} p_{k+1}(\lambda) &= (-1)^{k+3}a_{k+1}(-1)^kb_1b_2\cdots b_k + \lambda(\lambda^k - a_1\lambda^{k-1} - a_2b_1\lambda^{k-2} - \cdots - a_{k-1}b_1b_2\cdots b_{k-2}\lambda - a_kb_1b_2\cdots b_{k-1}) \\ &= \lambda^{k+1} - a_1\lambda^k - a_2b_1\lambda^{k-1} - \cdots - a_kb_1b_2\cdots b_{k-1}\lambda - a_{k+1}b_1b_2\cdots b_k \end{aligned}$$

Hence, the result is true for $n = k + 1$. Thus, by induction, we conclude that for an n-dimensional Leslie matrix, the characteristic polynomial $p(\lambda) = |\lambda\mathcal{I} - \mathcal{L}|$ is

$$p(\lambda) = \left(\lambda^n - a_1\lambda^{n-1} - a_2b_1\lambda^{n-2} - \cdots - a_{n-1}b_1b_2\cdots b_{n-2}\lambda - a_nb_1b_2\cdots b_{n-1}\right)$$