Further Mathematical Methods (Linear Algebra) 2002

Lecture 8: Age-Specific Population Growth

The first application of diagonalisation which we shall consider is a simple model of how ‘populations’ change over time. For example, we may want to predict how many animals of a certain species will be alive in a few years time, or how rapidly a progressive disease will spread throughout a given population. The model is called *age-specific* because it is sophisticated enough to take into account the fact that the likelihood of an animal reproducing (or succumbing to a progressive disease) is dependent on its age. We shall develop the model for the case of population growth because it is less grim. Further discussion of this topic may be found on pp. 754-64 of the textbook *Elementary Linear Algebra: Applications Version* (7th edition, Wiley, 1994) by H. Anton and C. Rorres.

8.1 The model

Here, we shall develop a model which can be used to describe the female population of a species. The assumption here is that as females actually give birth, they are more essential to the propagation of a species than the male. This makes sense as one male can fertilise the eggs of many females and once this has been done each female will gestate for some period of time. Obviously, the female will not be in a position to be fertilised again until this gestation period has elapsed. So, the rate at which offspring are produced is determined by parameters that describe the female population.

Suppose that the maximum age of a female of the species is L. We shall divide the interval $[0, L]$ into n age classes,

$$\left[0, \frac{L}{n}\right), \left[\frac{L}{n}, \frac{2L}{n}\right), \ldots, \left[\frac{(n-1)L}{n}, L\right].$$

We are interested in the number of females in each age class and how this grows with time. We assume that the population in each of these age classes is measured at time intervals of L/n; that is, at times

$$t_0 = 0,\ t_1 = \frac{L}{n},\ t_2 = \frac{2L}{n}, \ldots,\ t_k = \frac{kL}{n}, \ldots.$$

Now, for $1 \leq i \leq n$, let $x_i^{(k)}$ be the population in the ith age class C_i where

$$C_i = \left[\frac{(i-1)L}{n}, \frac{iL}{n}\right),$$

as measured at time $t_k = kL/n$. We consider two demographic parameters which determine how these age-specific populations change:

- for $i = 1, 2, \ldots, n$, a_i will be the average number of daughters born to a female in age class C_i,
- for $i = 1, 2, \ldots, n-1$, b_i will denote the fraction of females in age class C_i expected to survive for the next L/n years (and hence enter class C_{i+1}).

We further assume that $a_i \geq 0$ and $0 < b_i \leq 1$. If for any i we find that $a_i > 0$, we call the age class C_i *fertile.*

The number of daughters born between successive population measurements at times t_{k-1} and t_k is

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

and this quantity must be exactly $x_1^{(k)}$. So, equating these we get:

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

Also, for $i = 1, 2, \ldots, n-1$, we have

$$x_{i+1}^{(k)} = b_i x_i^{(k-1)}.$$

Writing this in matrix form we find that,

$$\begin{bmatrix} x_1^{(k)} \\ x_2^{(k)} \\ \vdots \\ x_n^{(k)} \end{bmatrix} = \begin{bmatrix} a_1 & a_2 & a_3 & \cdots & a_{n-1} & a_n \\ b_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & b_{n-1} & 0 \end{bmatrix} \begin{bmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ \vdots \\ x_n^{(k-1)} \end{bmatrix},$$

or, indeed,

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

where L is called the *Leslie Matrix.*

For example: Suppose that the maximum age of a female of a certain species is 45 years and that we consider the three age classes $[0, 15), [15, 30), [30, 45]$. If the demographic parameters defined above are such that

$$a_1 = 0, a_2 = 4, a_3 = 3, b_1 = 1/2 \quad \text{and} \quad b_2 = 1/4,$$

then the Leslie matrix for this species is

$$\mathsf{L} = \begin{bmatrix} 0 & 4 & 3 \\ 1/2 & 0 & 0 \\ 0 & 1/4 & 0 \end{bmatrix}.$$

Now, if the initial population in each age class is 1000, then

$$\mathbf{x}^{(0)} = \begin{bmatrix} 1000 \\ 1000 \\ 1000 \end{bmatrix},$$

which implies that after one time period (i.e. 15 years), the population in each age class will be given by

$$\mathbf{x}^{(1)} = \mathsf{L}\mathbf{x}^{(0)} = \begin{bmatrix} 7000 \\ 500 \\ 250 \end{bmatrix},$$

after two time periods (i.e. 30 years), the population in each age class will be given by

$$\mathbf{x}^{(2)} = \mathsf{L}\mathbf{x}^{(1)} = \begin{bmatrix} 2750 \\ 3500 \\ 125 \end{bmatrix},$$

and after three time periods (i.e. 45 years), the population in each age class will be given by

$$\mathbf{x}^{(3)} = \mathsf{L}\mathbf{x}^{(2)} = \begin{bmatrix} 14375 \\ 1375 \\ 875 \end{bmatrix}.$$

Obviously we can repeat this process to find the population in each age class after r time periods (i.e. $15r$ years). ♣

It is natural to ask what the *long-term* population distribution will be, and to find this, we need eigenvalues and eigenvectors.

8.2 Eigenvalues and long-term behaviour

We have found that the population distribution in the kth time period can be found from the population distribution in the $(k-1)$th time period using the formula

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

and so clearly, we can relate the population distribution in the kth time period to the initial population distribution by using the formula

$$\mathbf{x}^{(k)} = \mathsf{L}^k \mathbf{x}^{(0)}.$$

So, to understand what happens in the long run, we need to be able to find L^k for suitably large k and the easiest way to do this is to use *diagonalisation*.

Consequently, assuming that the Leslie matrix L is diagonalisable, we can find an invertible matrix P such that

$$\mathsf{P} = \begin{bmatrix} | & | & & | \\ \mathbf{v}_1 & \mathbf{v}_2 & \cdots & \mathbf{v}_n \\ | & | & & | \end{bmatrix},$$

where the vectors $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n$ are the eigenvectors corresponding to the eigenvalues $\lambda_1, \lambda_2, \ldots, \lambda_n$ (with multiplicity) of L and

$$\mathsf{P}^{-1}\mathsf{L}\mathsf{P} = \mathsf{D} = \text{diag}[\lambda_1, \lambda_2, \ldots, \lambda_n].$$

On re-arranging we find that $\mathsf{P}\mathsf{D}\mathsf{P}^{-1} = \mathsf{L}$ and so if we were to multiply L by itself k times we would find that

$$\mathsf{L}^k = (\mathsf{P}\mathsf{D}\mathsf{P}^{-1})^k = \underbrace{(\mathsf{P}\mathsf{D}\mathsf{P}^{-1})(\mathsf{P}\mathsf{D}\mathsf{P}^{-1})\cdots(\mathsf{P}\mathsf{D}\mathsf{P}^{-1})}_{k \text{ times}} = \mathsf{P}\mathsf{D}^k\mathsf{P}^{-1}.$$

This, in turn, gives

$$\mathsf{L}^k = \mathsf{P}\,\text{diag}[\lambda_1^k, \lambda_2^k, \ldots, \lambda_n^k]\mathsf{P}^{-1},$$

since the matrix D is diagonal. Clearly, this drastically simplifies the task of finding the population distribution in the kth time period. However, if we are concerned with suitably large values of k we can further simplify the problem.

To see why, consider the following fact,

Fact: The characteristic polynomial, $p(\lambda) = |\mathsf{L} - \lambda\mathsf{I}|$, of the Leslie matrix L is given by

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

We know that the eigenvalues of the Leslie matrix are the solutions of the equation $p(\lambda) = 0$, and so given this fact, it can be seen that

$$p(\lambda) = 0 \iff q(\lambda) = 1,$$

where $q(\lambda)$ is given by

$$q(\lambda) = \frac{a_1}{\lambda} + \frac{a_2b_1}{\lambda^2} + \cdots + \frac{a_nb_1b_2\ldots b_{n-1}}{\lambda^n}.$$

You should convince yourself that $q(\lambda)$ has the following three properties:

- $q(\lambda)$ is a decreasing function for $\lambda > 0$,
- as $\lambda \to 0^+$, $q(\lambda) \to \infty$,
- as $\lambda \to \infty$, $q(\lambda) \to 0$.

Consequently, we can conclude that there is a unique positive real solution of the equation $q(\lambda) = 1$. That is, L has a unique positive real eigenvalue, and we shall call this λ_1. Further, an eigenvector corresponding to this eigenvalue is given by

$$\mathbf{v}_1 = \begin{bmatrix} 1 \\ b_1/\lambda_1 \\ b_1b_2/\lambda_1^2 \\ \vdots \\ b_1b_2\ldots b_{n-1}/\lambda_1^{n-1} \end{bmatrix},$$

and all of the entries in this vector are positive.[1] (You will have a chance to verify that $\mathbf{v}_1$ is an eigenvector of L corresponding to λ_1 in Problem Sheet 4.)

We now consider another fact,

> **Fact:** If two successive entries of the Leslie matrix L (say a_i and a_{i+1}) are both non-zero, then for any eigenvalue λ of L other than λ_1,
>
> $$|\lambda| < \lambda_1.$$
>
> In other words, if there are two successive fertile classes, then the eigenvalue λ_1 is *dominant.*

So, let us suppose that there are two successive fertile classes and that L is [still] diagonalisable. We let λ_1 be the dominant eigenvalue of L and take $\mathbf{v}_1$ as given above to be the eigenvector that corresponds to it. Now, denoting the other eigenvalues of L and their corresponding eigenvectors by $\lambda_2, \ldots, \lambda_n$ and $\mathbf{v}_2, \ldots, \mathbf{v}_n$ respectively, we recall our earlier result, namely,

$$\mathsf{L}^k = \mathsf{P}\,\mathrm{diag}[\lambda_1^k, \lambda_2^k, \ldots, \lambda_n^k]\mathsf{P}^{-1},$$

where the matrix P is given by,

$$\mathsf{P} = \begin{bmatrix} | & | & & | \\ \mathbf{v}_1 & \mathbf{v}_2 & \cdots & \mathbf{v}_n \\ | & | & & | \end{bmatrix}.$$

Hence, as the population distribution in the kth time period is related to the initial population distribution by the formula,

$$\mathbf{x}^{(k)} = \mathsf{L}^k\mathbf{x}^{(0)},$$

we can write

$$\mathbf{x}^{(k)} = \mathsf{P}\,\mathrm{diag}[\lambda_1^k, \lambda_2^k, \ldots, \lambda_n^k]\mathsf{P}^{-1}\mathbf{x}^{(0)},$$

and dividing both sides by λ_1^k we get

$$\frac{\mathbf{x}^{(k)}}{\lambda_1^k} = \mathsf{P}\,\mathrm{diag}\left[1, \left(\frac{\lambda_2}{\lambda_1}\right)^k, \ldots, \left(\frac{\lambda_n}{\lambda_1}\right)^k\right]\mathsf{P}^{-1}\mathbf{x}^{(0)},$$

But, since λ_1 is dominant, we know that $|\lambda_i/\lambda_1| < 1$ for $i = 2, 3, \ldots, n$, and this means that the diagonal entries of the form $(\lambda_i/\lambda_1)^k \to 0$ as $k \to \infty$. Consequently, we find that

$$\lim_{k\to\infty} \frac{\mathbf{x}^{(k)}}{\lambda_1^k} = \lim_{k\to\infty} \mathsf{P}\,\mathrm{diag}\left[1, \left(\frac{\lambda_2}{\lambda_1}\right)^k, \ldots, \left(\frac{\lambda_n}{\lambda_1}\right)^k\right]\mathsf{P}^{-1}\mathbf{x}^{(0)} = c\mathbf{v}_1,$$

where the constant c is the first entry of the vector given by $\mathsf{P}^{-1}\mathbf{x}^{(0)}$. Thus, for large values of k, we have the approximation

$$\mathbf{x}^{(k)} \simeq c\lambda_1^k\mathbf{v}_1,$$

and this tells us that the *proportion* of the population lying in each age class is, in the long run, constant. From this we can also deduce that

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

which tells us that the population in each age class grows by a factor of λ_1 every time period (i.e. every L/n years).

[1] It turns out that this eigenvalue is of multiplicity one, i.e. $(\lambda - \lambda_1)$ is a factor of $p(\lambda)$, but $(\lambda - \lambda_1)^2$ is not. Consequently, the eigenspace of L corresponding to this eigenvalue is one-dimensional, and so any eigenvector corresponding to it will be some multiple of $\mathbf{v}_1$.

For example: Returning to the earlier example we find that the characteristic polynomial of the Leslie matrix

$$\mathsf{L} = \begin{bmatrix} 0 & 4 & 3 \\ 1/2 & 0 & 0 \\ 0 & 1/4 & 0 \end{bmatrix},$$

is given by

$$p(\lambda) = -\lambda^3 + 2\lambda + \frac{3}{8}.$$

As L has two successive positive entries in its top row, we have two successive fertile classes. Consequently, we expect a dominant eigenvalue, and this turns out to be $\lambda_1 = 3/2$. Using the formula above, the eigenvector $\mathbf{v}_1$ corresponding to this eigenvalue is,

$$\mathbf{v}_1 = \begin{bmatrix} 1 \\ b_1/\lambda_1 \\ b_1 b_2/\lambda_1^2 \end{bmatrix} = \begin{bmatrix} 1 \\ (1/2)/(3/2) \\ (1/2)(1/4)/(3/2)^2 \end{bmatrix} = \begin{bmatrix} 1 \\ 1/3 \\ 1/18 \end{bmatrix}.$$

Thus, for large k, our approximation gives

$$\mathbf{x}^{(k)} \simeq c \left(\frac{3}{2}\right)^k \begin{bmatrix} 1 \\ 1/3 \\ 1/18 \end{bmatrix},$$

and so this tells us that the *proportion* of the population lying in each age class is, in the long run, constant and given by the ratio $1 : 1/3 : 1/18$. From this we also deduce that,

$$\mathbf{x}^{(k)} \simeq \frac{3}{2}\mathbf{x}^{(k-1)},$$

which tells us that the population in each age class grows by a factor of 3/2 (i.e. increases by 50%) every time period, which in this case is every 15 years. ♣