A Note on the Eigenvalues and Eigenvectors of Leslie matrices.

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1. Vectors and Matrices.

A size n ***vector***, $\mathbf{v}$, is a list of n numbers put in a column:

$$\mathbf{v} := \begin{bmatrix} v_1 \\ v_2 \\ \vdots \\ v_n \end{bmatrix}.$$

When for the values $n = 2$ and $n = 3$ this looks like

$$\mathbf{v} = \begin{bmatrix} v_1 \\ v_2 \end{bmatrix}, \qquad \mathbf{v} = \begin{bmatrix} v_2 \\ v_2 \\ v_3 \end{bmatrix}.$$

where v_1, v_2, v_3 are numbers (often called ***scalars*** when also talking about vectors). Examples of size 2, 3 and 4 vectors are

$$\begin{bmatrix} 3 \\ -2 \end{bmatrix}, \qquad \begin{bmatrix} 4 \\ 1 \\ 9 \end{bmatrix}, \qquad \begin{bmatrix} -5.2 \\ 31.7 \\ 4.6 \\ 9.1 \end{bmatrix}.$$

For use a ***matrix***, $\mathbf{A}$, is an $n \times n$ array of numbers[1] Thus 2×2 and 3×3 matrices look like

$$\begin{bmatrix} a_{1\,1} & a_{1\,2} \\ a_{2\,1} & a_{2\,2} \end{bmatrix}, \qquad \begin{bmatrix} a_{1\,1} & a_{1\,2} & a_{1\,3} \\ a_{2\,1} & a_{2\,2} & a_{2\,3} \\ a_{3\,1} & a_{3\,2} & a_{3\,3} \end{bmatrix}$$

where the entries $a_{i\,j}$ are scalars.

The formula for multiplying a matrix $\mathbf{A}$ with a vector $\mathbf{v}$ in the cases $n = 2$ and $n = 3$ is

$$\begin{bmatrix} a_{1\,1} & a_{1\,2} \\ a_{2\,1} & a_{2\,2} \end{bmatrix} \begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = \begin{bmatrix} a_{1\,1}v_1 + a_{1\,2}v_2 \\ a_{2\,1}v_1 + a_{2\,2}v_2 \end{bmatrix}$$

[1] The general definition of a matrix is an $m \times n$ array, as we will only be working with the case of square matrices it seems pointless to complicate things with the more general rectangular matrices.

$$\begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} v_1 \\ v_2 \\ v_3 \end{bmatrix} = \begin{bmatrix} a_{11}v_1 + a_{12}v_2 + a_{13}v_3 \\ a_{21}v_1 + a_{22}v_2 + a_{23}v_3 \\ a_{31}v_1 + a_{32}v_2 + a_{33}v_3 \end{bmatrix}.$$

Thus a matrix times a vector yields a vector.

We can also multiply two matrices together. If $\mathbf{A}$ and $\mathbf{B}$ are 2×2 matrices then let

$$\mathbf{B} = \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = \begin{bmatrix} B_1, B_2 \end{bmatrix}$$

where $\mathbf{B}_1 = \begin{bmatrix} b_{11} \\ b_{21} \end{bmatrix}$ and $\mathbf{B}_2 = \begin{bmatrix} b_{12} \\ b_{22} \end{bmatrix}$ are the columns of $\mathbf{B}$. Note these columns are vectors and thus we can multiple them by the matrix $\mathbf{A}$ to get $\mathbf{AB}_1$ and $\mathbf{AB}_2$. Then the product $\mathbf{AB}$ is

$$\mathbf{AB} = \begin{bmatrix} \mathbf{AB}_1, \mathbf{AB}_2 \end{bmatrix}.$$

That is $\mathbf{AB}$ is the matrix whose columns are the result of multiplying the columns of $\mathbf{B}$ by $\mathbf{A}$. In full detail this is

$$\mathbf{AB} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = \begin{bmatrix} a_{11}b_{11} + a_{12}a_{21} & a_{11}b_{12} + a_{12}a_{22} \\ a_{21}b_{11} + a_{22}a_{21} & a_{21}b_{12} + a_{22}a_{22} \end{bmatrix}.$$

In the 3×3 case this is in terms of the columns of $\mathbf{B}$:

$$\mathbf{AB} = \mathbf{A} \begin{bmatrix} \mathbf{B}_1, \mathbf{B}_2, \mathbf{B}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{AB}_1, \mathbf{AB}_2, \mathbf{AB}_3 \end{bmatrix}.$$

The full blown, and fully hideous, formula is

$$\begin{aligned} \mathbf{AB} &= \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} b_{11} & b_{12} & b_{13} \\ b_{21} & b_{22} & b_{23} \\ b_{31} & b_{32} & b_{33} \end{bmatrix} \\ &= \begin{bmatrix} a_{11}b_{11} + a_{12}b_{21} + a_{13}b_{31} & a_{11}b_{12} + a_{12}b_{22} + a_{13}b_{32} & a_{11}b_{13} + a_{12}b_{23} + a_{13}b_{33} \\ a_{21}b_{11} + a_{22}b_{21} + a_{23}b_{31} & a_{21}b_{12} + a_{22}b_{22} + a_{23}b_{32} & a_{21}b_{13} + a_{22}b_{23} + a_{23}b_{33} \\ a_{31}b_{11} + a_{32}b_{21} + a_{33}b_{31} & a_{31}b_{12} + a_{32}b_{22} + a_{33}b_{32} & a_{31}b_{13} + a_{32}b_{23} + a_{33}b_{33} \end{bmatrix} \end{aligned}$$

We can also define powers $\mathbf{A}^n$ of a matrix. So $\mathbf{A}^2 = \mathbf{AA}$, $\mathbf{A}^3 = \mathbf{AAA}$, $\mathbf{A}^4 = \mathbf{AAAA}$ etc. Fortunately we can have the calculator multiply and take powers of a matrices.

2. Eigenvectors and Eigenvalues of Matrices.

Let $\mathbf{A}$ be a square matrix (that is $\mathbf{A}$ has the same number of rows and columns). Let $\mathbf{v}$ be a vector and λ a number. Then $\mathbf{v}$ and λ number is an ***eigenvector*** of $\mathbf{A}$ with ***eigenvalue*** λ iff

$$\mathbf{Av} = \lambda \mathbf{v}.$$

For a 2×2 matrix

$$\mathbf{A} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

the eigenvalues are the roots of the ***characteristic equation***

$$\begin{aligned}\det(xI - \mathbf{A}) &= \det\begin{bmatrix} x-a & -b \\ -c & x-d \end{bmatrix} \\ &= (x-a)(x-d) - cd \\ &= x^2 - (a+d)x + (ad - bc) = 0.\end{aligned}$$

(If you don't know what det and I are in the above, don't worry, in the cases we consider these will not be important.)

3. Eigenvalues and Eigenvectors of Leslie matrices.

Assume we have a population of organisms where we will count their numbers of each age once during progressive time periods of the same length (which to be concrete we assume to be a year). Let $\mathbf{m}$ be the maximum reproductive age of the organism. For each x with $1 \le x \le \mathbf{m}$, let

$$\mathbf{n}_x(t) = \text{number of females that have age } x \text{ during the census year } t.$$

Let $\mathbf{n}(t)$ be the vector which keeps track of all the ages in the year t, that is

$$\mathbf{n}(t) = \begin{bmatrix} \mathbf{n}_1(t) \\ \mathbf{n}_2(t) \\ \vdots \\ \mathbf{n}_{\mathbf{m}}(t) \end{bmatrix}.$$

For example of the $\mathbf{m} = 4$ (so that only females of age at most 4 are reproductively active) we would have

$$\mathbf{n}(t) = \begin{bmatrix} \mathbf{n}_1(t) \\ \mathbf{n}_2(t) \\ \mathbf{n}_3(t) \\ \mathbf{n}_4(t) \end{bmatrix}$$

To be a little more specific, $\mathbf{n}_1(t)$ is the number of females that were born in the year before the census year t *and* survived until the time of the census (which is different from the number of births), $\mathbf{n}_2(t)$ is the number of two year olds at the time of the year t census, and in general $\mathbf{n}_x(t)$ the number of x-year olds at the time of the year t census. For $1 \le x \le \mathbf{m} - 1$ let p_x be the proportion of the age x organisms from the year t census that survive until the year $t+1$ census. This means that

$$\mathbf{n}_{x+1}(t+1) = p_x \mathbf{n}_x(t) \qquad \text{for} \qquad 1 \le x \le \mathbf{m} - 1.$$

If b_x is the net fecundity (which can also be thought of as the per capita birth rate) of females of age x, that is the number average number of females offsprings of an age x female that survive until the next census, then

$$\mathbf{n}_1(t+1) = p_1\mathbf{n}_1(t) + p_2\mathbf{n}_2(t) + \cdots + p_{\mathbf{m}}\mathbf{n}_{\mathbf{m}}(t).$$

(In most realistic cases $p_1 = 0$, but there is no reason to rule it out mathematically.) In the case that $\mathbf{m} = 4$ and $b_1 = 0$ all this can summarized by saying the given the vector

$$\mathbf{n}(t) = \begin{bmatrix} \mathbf{n}_1(t) \\ \mathbf{n}_2(t) \\ \mathbf{n}_3(t) \\ \mathbf{n}_4(t) \end{bmatrix}$$

which records the number of females of age 1, 2, 3 and 4 in the census year t that we find ages in the next year by use of the loop diagram:

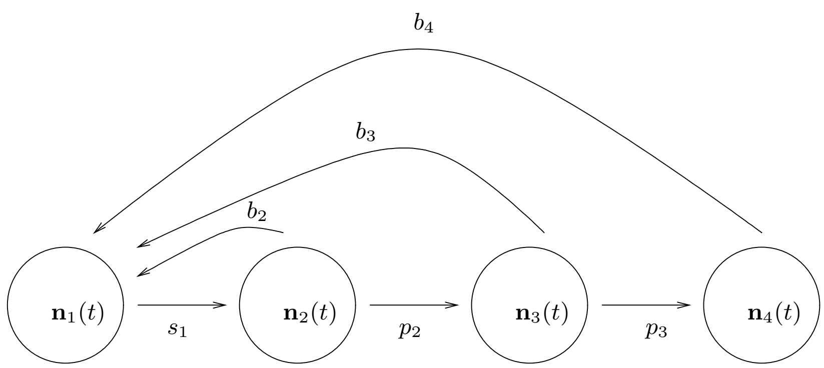

FIGURE 1

For most of the rest of these notes we will simplify notation and assume that $\mathbf{m} = 4$. Then from either the loop diagram or the equations preceding it

$$\begin{aligned} \mathbf{n}_1(t+1) &= b_1\mathbf{n}_1(t) + b_2\mathbf{n}_2(t) + b_3\mathbf{n}_3(t) + b_4\mathbf{n}_4(t) \\ \mathbf{n}_2(t+1) &= p_1\mathbf{n}_1(t) \\ \mathbf{n}_3(t+1) &= p_2\mathbf{n}_2(t) \\ \mathbf{n}_4(t+1) &= p_3\mathbf{n}_3(t). \end{aligned} \tag{1}$$

We rewrite this as a matrix equation. Let

$$n_t := \begin{bmatrix} \mathbf{n}_1(t) \\ \mathbf{n}_2(t) \\ \mathbf{n}_3(t) \\ \mathbf{n}_4(t) \end{bmatrix}, \qquad \text{and} \qquad \mathbf{A} := \begin{bmatrix} b_1 & b_2 & b_3 & b_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix}.$$

The vector $\mathbf{n}_t$ gives the age distribution of females at the year t census, and $\mathbf{A}$ is the ***Leslie matrix***. Then the system (1) of four scalar equations can be written as the single matrix equation:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t. \tag{2}$$

Our next goal is to find eigenvectors for $\mathbf{A}$. That is vector $\mathbf{v}$ for some scalar λ

$$\mathbf{A}\mathbf{v} = \lambda\mathbf{v}.$$

If we have such an eigenvector, then

$$\mathbf{n}_t = \lambda^t\mathbf{v}$$

is a solution to the matrix equation (2). To see this note if $\mathbf{n}_t = \lambda^t\mathbf{v}$

$$\mathbf{n}_{t+1} = \lambda^{t+1}\mathbf{v} = \lambda^t\lambda\mathbf{v} = \lambda^t\mathbf{A}\mathbf{v} = \mathbf{A}(\lambda^t\mathbf{v}) = \mathbf{A}\mathbf{n}_t,$$

where we have used that $\mathbf{A}\mathbf{v} = \lambda\mathbf{v}$. Also note that if $\mathbf{v}$ is an eigenvector and c is a scalar, then $c\mathbf{v}$ is also an eigenvector. (Exercise: Show this.) Therefore given an eigenvector with first element v_1 we can multiple by the scalar $c = v_1^{-1}$ and get a new eigenvector $c\mathbf{v}$ where the first entry is 1. That is we assume we have an eigenvector of the form

$$\mathbf{v} = \begin{bmatrix} 1 \\ v_2 \\ v_3 \\ v_4 \end{bmatrix}.$$

Then computing $\mathbf{A}\mathbf{v}$ and $\lambda\mathbf{v}$ and setting them equal we get

$$\mathbf{A}\mathbf{v} = \begin{bmatrix} b_1 + b_2v_2 + b_3v_3 + b_4v_4 \\ p_1 \\ p_2v_2 \\ p_3v_3 \end{bmatrix} = \lambda\mathbf{v} = \begin{bmatrix} \lambda \\ \lambda v_2 \\ \lambda v_3 \\ \lambda v_4 \end{bmatrix}. \tag{3}$$

Comparing the last three entries of these vectors gives the equations

$$p_1 = \lambda v_2, \quad p_2v_2 = \lambda v_3, \quad p_3v_3 = \lambda v_4.$$

We can solve successively for v_2, v_3, and v_4 to get

$$v_2 = \lambda^{-1}p_1, \quad v_3 = \lambda^{-1}p_2v_2 = \lambda^{-2}p_1p_2, \quad v_4 = \lambda^{-1}p_3v_3 = \lambda^{-3}p_1p_2p_3.$$

Using these values in (3) gives

(4)

$$\mathbf{A}\mathbf{v} = \begin{bmatrix} b_1 + b_2\lambda^{-1}p_1 + b_3\lambda^{-2}p_1p_2 + b_4\lambda^{-3}p_1p_2p_3 \\ p_1 \\ \lambda^{-1}p_2 \\ \lambda^{-2}p_1p_2p_3 \end{bmatrix} = \lambda\mathbf{v} = \begin{bmatrix} \lambda \\ p_1 \\ \lambda^{-1}p_1p_2 \\ \lambda^{-2}p_1p_2p_3 \end{bmatrix}.$$

So for $\mathbf{v}$ to be an eigenvector the only condition left is make the first entries agree. That is

$$b_1 + b_2\lambda^{-1}p_1 + b_3\lambda^{-2}p_1p_2 + b_4\lambda^{-3}p_1p_2p_3 = \lambda. \tag{5}$$

For x from 1 to $\mathbf{m}$ let $\ell_1 = 1$ and for $2 \le x \le \mathbf{m}$ Let ℓ_x be the product of p_1, p_2, up to p_{x-1}:

$$\ell_x = p_1 \cdots p_{x-1}, \qquad \text{that is} \qquad \ell_x = \prod_{j=1}^{x-1} p_j.$$

In our case of $\mathbf{m} = 4$ we have

$$\ell_1 = 1,\ \ell_2 = p_1,\ \ell_3 = p_1p_2,\ \ell_4 = p_1p_2p_3.$$

Then ℓ_x the proportion of one year olds that survive to the beginning of the x-th year. Using this notation we can rewrite (5) as

$$b_1\ell_1 + b_2\ell_2\lambda^{-1} + b_3\ell_3\lambda^{-2} + b_4\ell_4\lambda^{-3} = \lambda. \tag{6}$$

Now divide this by λ to get

$$b_1\ell_1\lambda^{-1} + b_2\ell_2\lambda^{-2} + b_3\ell_3\lambda^{-3} + b_4\ell_4\lambda^{-4} = 1. \tag{7}$$

This is the ***Lotka-Euler equation***. Note if we write it in summation notation it becomes

$$\sum_{x=1}^{\mathbf{m}} b_x\ell_x\lambda^{-x} = 1. \tag{8}$$

Just to be specific about the dependence of the Lotka-Euler equation on the survival rates p_x we note it can be written as

$$\lambda^{-1}b_1 + b_2\lambda^{-2}p_1 + b_3\lambda^{-3}p_1p_2 + b_4\lambda^{-4}p_1p_2p_3 = 1, \tag{9}$$

which in the general case looks like

$$\sum_{x=1}^{\mathbf{m}} b_xp_1p_2\cdots p_{x-1}\lambda^{-x} = 1$$

If we multiple (5) by λ move all the terms of the result to one side of the equation we get

$$\lambda^4 - b_1\lambda^3 - b_2p_1\lambda^2 - b_3p_1p_2\lambda - b_4p_1p_2p_3 = 0. \tag{10}$$

which is the ***characteristic equation*** (that is the equation $\det(\lambda\mathbf{I} - \mathbf{A}) = 0$ which is the equation for λ to be an eigenvalue of the matrix $\mathbf{A}$, see any text on linear algebra) of the Leslie matrix $\mathbf{A}$. This can be rewritten in terms of the ℓ_x's as

$$\lambda^4 - b_1\ell_1\lambda^3 - b_2\ell_2\lambda^2 - b_3\ell_3\lambda - b_4\ell_4 = 0. \tag{11}$$

(And this can also be derived by multiplying (7) by λ^4 and rearranging a bit.)

Note that as the characteristic equation (11) results from the Lotka-Euler equation by just multiplying by λ^4 the two equation have the same collection of non-zero roots. As both equations only have one positive root (this is not really quite elementary, but can be shown without too much trouble) we have:

Proposition. *The Lotka-Euler equation has exactly one positive root. We call it the **dominate eigenvalue** of Leslie matrix.*

Finally we note that when λ is a solution to the Lotka-Euler equation then (4) becomes

$$\mathbf{A}\mathbf{v} = \lambda\mathbf{v} \qquad \text{where} \qquad \mathbf{v} = \begin{bmatrix} 1 \\ \lambda^{-1}p_1 \\ \lambda^{-2}p_1p_2 \\ \lambda^{-3}p_1p_2p_3 \end{bmatrix}.$$

Therefore

$$\mathbf{v} = \begin{bmatrix} 1 \\ \lambda^{-1}p_1 \\ \lambda^{-2}p_1p_2 \\ \lambda^{-3}p_1p_2p_3 \end{bmatrix} \tag{12}$$

gives the stable age distribution normalized so that $n_1(t) = 1$. Written in terms of the ℓ_x's this is

$$\mathbf{v} = \begin{bmatrix} 1 \\ \lambda^{-1}\ell_2 \\ \lambda^{-2}\ell_3 \\ \lambda^{-3}\ell_4 \end{bmatrix}. \tag{13}$$

To be explicit about the general case (that is for general values of $\mathbf{m}$, not just $\mathbf{m} = 4$) the Leslie matrix is

$$\mathbf{A} = \begin{bmatrix} b_1 & b_2 & b_3 & \cdots & b_{\mathbf{m}-1} & b_{\mathbf{m}} \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & p_{\mathbf{m}-1} & 0 \end{bmatrix} \tag{14}$$

The characteristic equation is

$$\lambda^{\mathbf{m}} - b_1\ell_1\lambda^{\mathbf{m}-1} - b_2\ell_2\lambda^{\mathbf{m}-2} - \cdots - b_{\mathbf{m}-1}\ell_{\mathbf{m}-1}\lambda - b_{\mathbf{m}}\ell_{\mathbf{m}} = 0$$

which in summation notation is

$$\lambda^{\mathbf{m}} - \sum_{k=0}^{\mathbf{m}-1} b_{\mathbf{m}-k}\ell_{\mathbf{m}-k}\lambda^k = 0.$$

(Dividing by $\lambda^{\mathbf{m}}$ and rearranging gives the Lotka-Euler equation (8).) It has exactly one positive root (the others are negative or complex) and this positive root is the dominate eigenvalue of $\mathbf{A}$. The stable age distribution, normalized so that $n_1(t) = 1$, is given by the column vector

$$\mathbf{v} = \begin{bmatrix} 1 \\ \lambda^{-1}\ell_2 \\ \lambda^{-2}\ell_3 \\ \vdots \\ \lambda^{-(\mathbf{m}-2)}\ell_{\mathbf{m}-1} \\ \lambda^{-(\mathbf{m}-1)}\ell_{\mathbf{m}} \end{bmatrix}.$$