Leslie Matrices

We are going to describe an application of linear algebra to *discrete population dynamics .* Generally speaking, we are talking about the population of a certain species (of people, plants, animals etc.) that is divided into a discrete number of age groups.

These groups may be labelled, for example, as young, middle aged and old. In general, we may have to deal with more than three age groups. For example, official US census data are usually broken down into 18 age groups:
$0-4; 5-9; 10-14; \ldots; 75-79; 80-84; \geq 85.$ However, in most examples we will restrict ourselves to three or four age groups.

Given the different age groups, we can describe the population by a vector $\mathbf{n}^t = (n_1, n_2, \ldots, n_k)$ here t stands for transposed, $\mathbf{n}$ should be a column. We assume that we have divided the whole population $\mathbf{n}$ into k distinct age groups, which are the components of $\mathbf{n}$. Of course, $n_i \geq 0.$ The size $[\mathbf{n}]$ of the population is the sum of the populations in the different age groups. It is conveniently calculated as a dot product:

$$[\mathbf{n}] = (1, 1, \ldots 1) \cdot \mathbf{n}$$

In general, the population changes over time. We assume that time is divided into periods of equal length, like days, months, years etc. Our fundamental assumption is that change progresses linearly. That is, if at time period i the population is given by the vector $\mathbf{n}^i,$ then at $i+1$ the population $\mathbf{n}^{i+1}$ is given by a formula

$$\mathbf{n}^{i+1} = \mathbf{P}\mathbf{n}^i$$

where $\mathbf{P}$ is a fixed $k \times k$ – matrix.

In order to be specific, let us assume that $k = 3$. Then the *population dynamics* is given by three linear equations:

$$\begin{aligned} n_1^{i+1} &= P_{11}n_1^i + P_{12}n_2^i + P_{13}n_3^i \\ n_2^{i+1} &= P_{21}n_1^i + P_{22}n_2^i + P_{23}n_3^i \\ n_3^{i+1} &= P_{31}n_1^i + P_{32}n_2^i + P_{33}n_3^i \end{aligned}$$

As we said, the matrix $\mathbf{P}$ is fixed, it does not depend on time.

Exercise *If we start with an initial population*

$$\mathbf{n}^0 = \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}$$

at $i = 0,$ then at time $i = j,$ we have that

$$\mathbf{n}^j = \mathbf{P}^j\mathbf{n}^0$$

Thus our discrete population model is assumed to be *deterministic*. If we have a count $\mathbf{n}^i$ of the population at any time i, then we know the population at any future time $i+k$.

We now can simplify the notation by dropping the superscript $i,$ and instead of $i+1$use $+$. Thus we describe the change from $\mathbf{n}$ to the population $\mathbf{n}^+$ at the next time period by:

$$\begin{aligned} n_1^+ &= P_{11}n_1 + P_{12}n_2 + P_{13}n_3 \\ n_2^+ &= P_{21}n_1 + P_{22}n_2 + P_{23}n_3 \\ n_3^+ &= P_{31}n_1 + P_{32}n_2 + P_{33}n_3 \end{aligned}$$

We are working with three age groups. We may think that n_1 stands for the number of newborns, the group where the age is bigger than 0 but less than $1,$ n_2 is the population where the age is at least 1 but less than $2,$ and n_3 is the the number of individuals where the age is at least 2 but less than 3. We also may think that there is no population of age ≥ 3. The equation:

$$n_1^+ = P_{11}n_1 + P_{12}n_2 + P_{13}n_3$$

tell us how the first age group has changed within a year. We interpret P_{11}, P_{12}, P_{13} as fertility rates. For example, if 50% of all individuals in the third age group give birth to one newborn, then P_{13} should be 0.5. Of course, P_{13} can be larger than 1. But none of the birth rates, or *fecundities,* can be negative. But they can be 0. We re-write the first equation as:

$$n_1^+ = f_1n_1 + f_2n_2 + f_3n_3$$

Now we look at the second equation

$$n_2^+ = P_{21}n_1 + P_{22}n_2 + P_{22}n_3$$

The term $P_{21}n_1$ may be interpreted as the survival rate of the newborns. P_{21} is the percentage of the newborns who survived their first year and made it to the second year. P_{21} should be between 0 and 1. One year later, the elements of the second group are no longer in the second group. They are either dead or in the third group. And of course, elements in the third age group cannot get younger. So $P_{22} = P_{23} = 0$. We set $P_{21} = P_1$ and get the second equation as:

$$n_2^+ = P_1n_1$$

For the third equation

$$n_3^+ = P_{31}n_1 + P_{32}n_2 + P_{33}n_3$$

we argue similarly. Only individuals of the second group can a year later be in the third group. Thus $P_{31} = P_{33} = 0,$ and P_{32} is the percentage of two year olds, who a year later are in the third group.

Thus the third equation reduces to:

$$n_3^+ = P_2n_2$$

Thus the population dynamics is given by the following three equations:

$$\begin{aligned} n_1^+ &= f_1n_1 + f_2n_2 + f_3n_3 \\ n_2^+ &= P_1n_1 \\ n_3^+ &= P_2n_2 \end{aligned}$$

The matrix of this linear system is

$$\mathbf{L} = \begin{pmatrix} f_1 & f_2 & f_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}$$

and is called a *Leslie* matrix, named after P.H. Leslie who published 1945 a paper "*On the use of Matrices in Certain Population Mathematics",* Biometrika , Vol. 32., pp. 183-212.

Example *Assume that a certain species, say fish, reproduces only during the third year and then dies. Assume that we have an initial population of* $\mathbf{n}^0 = \mathbf{n} = (1000, 0, 0)$, *that is of* 1000 *newborns, and no other fishes. Assume that during the first year,* 25% *survived and then* 50% *of those make it to reproduction age. The Leslie matrix for this situation is*

$$\mathbf{L} = \begin{pmatrix} 0 & 0 & f_3 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix}$$

Example *After one year, we have only* 250 *fishes left. And then* 125 *have reached their reproduction rate. If we set* $f_3 = 8,$ *then we are back to* $\mathbf{n} = (1000, 0, 0)$*: We see that* $\mathbf{n}^1 = (0, 250, 0), \mathbf{n}^2 = (0, 0, 125), \mathbf{n}^3 = (1000, 0, 0)$

Exercise *Write down the Leslie matrix for the previous example and calculate for various choices of* $\mathbf{n}$ *the population vectors* $\mathbf{n}^i$*. What do you observe?*

Exercise *Show that you can find some* $\mathbf{n}$ *such that* $\mathbf{n}^+ = \mathbf{L}\mathbf{n} = \mathbf{n}.$ *If* $\mathbf{n} = (a, b, c)$ *then* $\mathbf{n}^+ = (8c, 0.25a, 0.5b).$ *Then* $(a, b, c) = (8c, 0.25a, 0.5b)$ *determines a unique stable distribution* $\mathbf{n}$ *amongst the age groups.* $\mathbf{n}$ *itself is unique up to a factor.*

Exercise *Now change* $f_3 = 8$ *to numbers smaller as well as larger than* 8*, say* 6 *and* 10*. Then calculate again for various choices of* $\mathbf{n}$ *the population vectors* $\mathbf{n}^i$*. Can you still find some* $\mathbf{n}$ *such that* $\mathbf{n}^+ = \mathbf{n}$?

Exercise *Calculate some powers of* $\mathbf{L} = \begin{pmatrix} 0 & 0 & f_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}$*, say* $\mathbf{L}^2, \mathbf{L}^3$ *and* $\mathbf{L}^4$*. What do you observe?*

Exercise *Calculate some powers of* $\mathbf{L} = \begin{pmatrix} 0 & 0 & 0 & f_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix}$*, say* $\mathbf{L}^2, \mathbf{L}^3$ *and* $\mathbf{L}^4$*. What do you observe?*

Exercise *What happens if one of the* P_i *is* 0? *Of course, it is easy to guess the outcome.*

Exercise *Now choose as the only positive birthrate not the one for the last age group. In order to be specific, let*

$$\mathbf{L} = \begin{pmatrix} 0 & 4 & 0 \\ 0.5 & 0 & 0 \\ 0 & 0.2 & 0 \end{pmatrix}$$

and compute the first eight powers. What kind of regularity do you observe?

The situation is quite different when not only the last fecundity is positive. For example in

$$\mathbf{L} = \begin{pmatrix} 0 & f_2 & f_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}$$

the last two age groups have a positive fertility rate.

Exercise *Now compute the first few powers. Do the same for*

$$\mathbf{L} = \begin{pmatrix} f_1 & 0 & f_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}$$

Definition *An $n \times n$ –matrix is non-negative, $\mathbf{A} \geq \mathbf{0}$, if all entries $A_{ij} \geq 0$. Similarly, positive matrices are defined.*

Exercise *Assume that $\mathbf{A}$ is a non-negative matrix for which some power $\mathbf{A}^k$ is positive. Then all following powers are positive.*

Exercise ***Let $k \leq 4$ and L be any Leslie matrix where not only f_k is positive but also f_i for some $i < k$. Then for which choices of i is $L^n > 0$ for some n.***

Let's look again at the Leslie matrix

$$\mathbf{L} = \begin{pmatrix} 0 & 0 & 8 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix}$$

We could solve $\mathbf{Ln} = \mathbf{n}$, because $\mathbf{1}$ is an **eigenvalue** for $\mathbf{L}$. We can redo the problem using SNB to find eigenvalues and eigenvectors :

$$\begin{pmatrix} 0 & 0 & 8 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix}, \text{ eigenvectors: } \left\{ \begin{pmatrix} 0.96309 \\ 0.24077 \\ 0.12039 \end{pmatrix} \right\} \leftrightarrow 1.0,$$

Exercise *How does this eigenvector differ from what you got before through simple hand calculation?*

Square matrices where all entries are real positive numbers have many applications. For such matrices one has the following

Theorem *Let $\mathbf{A}$ be a positive $n \times n$ matrix. Then the following holds:*

1. *The eigenvalue λ_1 of $\mathbf{A}$ with largest modulus is **unique**, **real** and **positive**. It is called the dominant eigenvalue.*
2. *The dimension of the eigenspace $E = E_{\lambda_1}$ for $\lambda = \lambda_1$ is one.*
3. *The coordinates of a base vector for E are all non-zero and have the same sign. Thus there is a unique eigenvector $\mathbf{m}$ for $\lambda = \lambda_1$ where all coordinates are positive and the sum of coordinates is 1.*
4. *Let $\mathbf{u}$ be any non-zero vector in $\mathbb{R}^n$ with non-negative entries. Put $\mathbf{u}^i = \mathbf{A}^i\mathbf{u}$. Then $\mathbf{v} = \lim \mathbf{u}^i$ is an eigenvector for λ_1. Thus $\frac{1}{[\mathbf{v}}]\mathbf{v} = \mathbf{m}$.*

The modulus of an eigenvalue is its length in the complex number plane. For example let $\mathbf{L} = \begin{pmatrix} 0 & 0 & 8 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix}$. We have already observed that $\mathbf{L}^3 = \mathbf{I}_3$. Using SNB, we calculate

for
$\begin{pmatrix} 0 & 0 & 8 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix}$, eigenvalues: $1.0, -0.5 + 0.86603i, -0.5 - 0.86603i$ which are the third roots of 1.

Exercise *Check this statement. Also,* $\|-0.5 + 0.86603i\| = 1.0$ *That is, all eigenvalues have the same modulus. Why?*

Of course, our $\mathbf{L}$ is not positive. It is only non-negative. Now lets look at
$\mathbf{L} = \begin{pmatrix} 0 & 3 & 8 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix}$. We already know because of an earlier exercise that a power of $\mathbf{L}$ is positive.

Now we get eigenvalues: $1.246, -0.62301 - 0.64375i, -0.62301 + 0.64375i$. We have one positive eigenvalue and two conjugate complex eigenvalues. The modulus of $\|-0.62301 - 0.64375i\| = 0.89585$, thus we have one positive eigenvalue of largest modulus. For the 4×4 – Leslie matrix $\mathbf{L} = \begin{pmatrix} 0 & 0 & 3 & 8 \\ 0.4 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{pmatrix}$ we have the eigenvalues: $1.0, -0.23371 - 0.83453i, -0.23371 + 0.83453i, -0.53258$. There is one positive eigenvalue, namely 1, one negative eigenvalue of absolute value < 1, and two conjugate complex eigenvalues of modulus less than 1 : $\|-0.23371 - 0.83453i\| = 0.86664$.

If λ is a positive eigenvalue of the Leslie matrix $\mathbf{L}$ and $\mathbf{n}$ any eigenvector, that is $\mathbf{Ln} = \lambda\mathbf{n}$, then $\mathbf{n}^+ = \lambda\mathbf{n}$ tells us, for example, that $[\mathbf{n}^+] = \lambda[\mathbf{n}]$. If we have for $\mathbf{L}$ also the properties **2**, **3** and **4** of the theorem, more can be said. Namely, that all eigenvectors $\mathbf{n}$ for the dominant eigenvalue λ_1 are multiples of the unique normalized eigenvector $\mathbf{m}$ and where all coordinates are positive. While of course the total population will change over time according to $[\mathbf{m}^+] = \lambda[\mathbf{m}]$, the ratios of the populations in the various age groups remain the same. This is because all $\mathbf{n}$ for λ_1 are multiples of $\mathbf{m}$. And $\mathbf{m}$ can be found, or better approximated, by iterations of $\mathbf{L}$. Start with any non-negative population vector $\mathbf{n}$ and calculate $\mathbf{L}^i\mathbf{n}$ for $i = 1, 2, \ldots$ To check the progress of convergence, compare $\frac{[\mathbf{n}^{i+1}]}{[\mathbf{n}^i]}$ with $\frac{[\mathbf{n}^{i+2}]}{[\mathbf{n}^{i+1}]}$. In case that $\frac{[\mathbf{n}^{i+1}]}{[\mathbf{n}^i]} \approx \frac{[\mathbf{n}^{i+2}]}{[\mathbf{n}^{i+1}]}$ then $\frac{[\mathbf{n}^{i+1}]}{[\mathbf{n}^i]} \approx \lambda_1$ and $\frac{1}{[\mathbf{n}^i]}\mathbf{n}^i \approx \mathbf{m}$.

Definition *A non-negative $n \times n$ matrix $\mathbf{A}$ is called a Frobenius matrix if it has the property*

1. The eigenvalue λ_1 of $\mathbf{A}$ with largest modulus is **unique**, **real** and **positive**. It is called the *dominant* eigenvalue.

The following is a central

Theorem *Any Frobenius matrix shares with positive matrices the properties*

2. The dimension of the eigenspace $E = E_{\lambda_1}$ for $\lambda = \lambda_1$ is one.

3. The coordinates of a base vector for E are all non-zero and have the same sign. Thus there is a unique eigenvector $\mathbf{m}$ for λ where all coordinates are positive and the sum of coordinates is 1.
4. Let $\mathbf{u}$ be any non-zero vector in $\mathbb{R}^n$ with non-negative entries. Put $\mathbf{u}^i = \mathbf{A}^i\mathbf{u}$. Then $\mathbf{v} = \lim \mathbf{u}^i$ is an eigenvector for λ_1. Thus $\frac{1}{[\mathbf{v}}]\mathbf{v} = \mathbf{m}$.

From this theorem follows easily the

Corollary *Any Leslie matrix* $\mathbf{L}$ *for which* $\mathbf{L}^i > \mathbf{0}$ *holds for some i is a Frobenius matrix.*

Proof The eigenvalues for $\mathbf{L}^k$ are the powers μ^k where μ is an eigenvalue for $\mathbf{L}$. Now $\mathbf{L}^i$ is as a positive matrix Frobenius. Thus $\mathbf{L}^i$ has a dominant eigenvalue of the form $\lambda^i > 0$. Then $\lambda > 0$ because $\mathbf{L}^{i+1}$ is according to a previous exercise also positive and therefore the powers of λ don't change signs.

The importance of Leslie matrices which are Frobenius matrices lies in the fact that any given population converges over time to a stable age distribution. Only periodic processes are the exception.

Exercise *Find* λ_1 *and* $\mathbf{m}_1$ *for the Leslie matrices* $\mathbf{L} = \begin{pmatrix} 0 & 3 & 8 \\ 0.25 & 0 & 0 \\ 0 & 0.5 & 0 \end{pmatrix}$ *and*

$\mathbf{L} = \begin{pmatrix} 0 & 0 & 3 & 8 \\ 0.4 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.25 & 0 \end{pmatrix}$ *through iterations. These are Frobenius matrices because they have positive powers.*

Express the stable age distribution in terms of percentages. In the long term, is the population increasing or decreasing? Express your answer in terms of percentages.

Exercise *The matrices* $\mathbf{L}_1 = \begin{pmatrix} 2 & 0 & 3 & 0 \\ 0.2 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.1 & 0 \end{pmatrix}$ *and* $\mathbf{L}_1 = \begin{pmatrix} 0 & 2 & 3 & 0 \\ 0.2 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0 \\ 0 & 0 & 0.1 & 0 \end{pmatrix}$ *do not have positive powers. All powers have last column zero. Investigate these matrices as before for stable long-term behavior.*

The following example is taken from Edward Kellers article *"Population Projection"* which is contained in **UMAP Modules 1980** , **Tool for Teaching**. This article contains a table provided by Keyfitz and Flieger of the 1967 Female US Population. As usual, the table breaks down the population in five year increments. It assumes that females of 50 years and older can no longer give birth. Here is this table as a $10x10$ Leslie Matrix.

$$\begin{pmatrix} 0.00000 & 0.00105 & 0.08203 & 0.28849 & 0.37780 & 0.26478 & 0.14055 & 0.05857 & 0.01344 & 0.00081 \\ 0.99694 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.99842 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.99785 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.99671 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.99614 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.99496 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.99247 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.98875 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.98305 & 0 \end{pmatrix}$$

The 10 columns may be labelled as $0, 5, 10, 15, 20, 25, 30, 35, 40, 45$. The first column stands for ages $0 - 4$, the second column for ages $5 - 10$, the last column for ages $45 - 49$.

Exercise *What is the percentage by which the population of females under* 50 *increases every five years? Provided that there is no change in birth and death rates. Expressed in percentages, what is the stable distribution of the* 10 *age groups amongst females under* 50*?*

There is a vast literature on Leslie matrices. You should feel encouraged to browse the internet for similar projects or professional presentations. Some of those deal with real life data in order to substantiate recommendations for environmental policies. While certainly a highly specialized population model, Leslie matrices provide more than academic exercises.