

An Application of Linear Algebra in Population Biology

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1 Introduction

While interesting in its own right, linear algebra is also quite useful in a variety of real-world applications, including population biology. A population can be defined as “a group of plants, animals, or other organisms, all of the same species, that live together and reproduce” (Gotelli, 1995). Population biology, then, is the branch of ecology which is concerned with the study of how distinct populations change over time and how they interact with both biotic and abiotic factors in their environment. These environmental factors will affect the birth rates, death rates, and even fecundity of the population in question.

In studying these questions, it becomes extremely useful to use mathematics as a tool for modeling changes in population structure and composition over time. The simplest form of population model is the exponential growth model, which assumes that the population is growing exponentially with no limits placed on its growth. While exponential growth models work well for certain organisms like bacteria that continually grow and divide, they become less accurate when we consider other organisms that go through different stages as they age. With these species, it can be biologically relevant to consider population dynamics in an age-structured manner, and it is here that linear algebra comes into play.

2 Background Biological Information

First, we should mention that for simplicity of modeling, we sort individuals into discrete age classes, denoted n_i . We further simplify our modeling by assuming that there is an approximately 50:50 male to female ratio, and that there is demographic dominance of females (i.e. the number of offspring per year depends primarily on the number of females). Therefore, we only consider the females present in the population.

To look at how a given population is structured, we examine a **cohort life table**. This is a table which shows us how many individuals all born at approximately the same time (cohorts) will survive to a given age, and the average number of offspring they will produce each year of their life.

Now that we understand the biological underpinnings, on to the mathematics!

3 Terms and Notation

To start our examination of how linear algebra can be used to model changes in age-structured populations, we need to provide certain definitions and commonly used notation.

In mathematical modeling of populations, we use the terminology:

$n_i(t)$ = number of females of age i in year t

p_i = probability that a female of age i will survive to age $i + 1$

m_i = average number of female offspring produced by a female of age i (the **maternity function**)

f_i = number of offspring surviving to age 1 (the **fertility function**)

We say that i ranges from 0 to ω , where ω is the maximum lifespan. The time period t and the age class interval i can be defined as days, months, years, etc., whichever is most appropriate for the organism of interest. However, while this is up to the researcher's discretion, the interval t should be equal to i .

The number of individuals in a given age class i at time $t + 1$ is thus dependent on the number and survival rate of individuals in the age class $i - 1$ at t . Then, for any $1 < i \leq \omega$

$$n_i(t + 1) = p_{i-1}n_{i-1}(t)$$

The exception is the first age class, which is composed of newly born individuals. The number of individuals in the first age class at $t + 1$ is thus the number of offspring born to older individuals in the original population at t

$$n_1(t + 1) = \sum_{k=1}^{\omega} f_k n_k(t)$$

We can now combine all of the $n_i(t)$ terms into a column vector $\mathbf{n}(t)$ of size ω . This is called our **population vector**, and describes the number of individuals in each age class at time t .

4 Leslie Matrix/Projection Matrix

The projection matrix, often called the Leslie matrix after Patrick Holt Leslie, combines fertility and survivorship information for an age-structured population. Based on empirical data from the cohort life table, the Leslie matrix is constructed with the fertility values (f_i) in the first row, and the survivorship probabilities (p_i) along the subdiagonal, with zeros everywhere else. Thus we can write the Leslie matrix,

$$L = \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & f_{\omega-1} & f_{\omega} \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & p_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{\omega-1} & 0 \end{pmatrix}$$

Now that we have the Leslie matrix L , and the column vector $\mathbf{n}(t)$ representing the current population, this notation allows us to describe population growth as matrix multiplication between matrix L and column vector $\mathbf{n}(t)$. We can now see that

$$\begin{aligned} L\mathbf{n}(t) &= \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & f_{\omega-1} & f_{\omega} \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & p_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & p_{\omega-1} & 0 \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ \vdots \\ n_{\omega}(t) \end{pmatrix} \\ &= \begin{pmatrix} f_1(n_1(t)) + f_2(n_2(t)) + f_3(n_3(t)) + \cdots + f_{\omega-1}(n_{\omega-1}(t)) + f_{\omega}(n_{\omega}(t)) \\ p_1(n_1(t)) + 0(n_2(t)) + 0(n_3(t)) + \cdots + 0(n_{\omega-1}(t)) + 0(n_{\omega}(t)) \\ 0(n_1(t)) + p_2(n_2(t)) + 0(n_3(t)) + \cdots + 0(n_{\omega-1}(t)) + 0(n_{\omega}(t)) \\ 0(n_1(t)) + 0(n_2(t)) + p_3(n_3(t)) + \cdots + 0(n_{\omega-1}(t)) + 0(n_{\omega}(t)) \\ \vdots \\ 0(n_1(t)) + 0(n_2(t)) + 0(n_3(t)) + \cdots + p_{\omega-1}(n_{\omega-1}(t)) + 0(n_{\omega}(t)) \end{pmatrix} \\ &= \begin{pmatrix} f_1(n_1(t)) + f_2(n_2(t)) + f_3(n_3(t)) + \cdots + f_{\omega-1}(n_{\omega-1}(t)) + f_{\omega}(n_{\omega}(t)) \\ p_1(n_1(t)) + 0 + 0 + \cdots + 0 + 0 \\ 0 + p_2(n_2(t)) + 0 + \cdots + 0 + 0 \\ 0 + 0 + p_3(n_3(t)) + \cdots + 0 + 0 \\ \vdots \\ 0 + 0 + 0 + \cdots + p_{\omega-1}(n_{\omega-1}(t)) + 0 \end{pmatrix} \\ &= \begin{pmatrix} f_1(n_1(t)) + f_2(n_2(t)) + f_3(n_3(t)) + \cdots + f_{\omega-1}(n_{\omega-1}(t)) + f_{\omega}(n_{\omega}(t)) \\ p_1(n_1(t)) \\ p_2(n_2(t)) \\ p_3(n_3(t)) \\ \vdots \\ p_{\omega-1}(n_{\omega-1}(t)) \end{pmatrix} \\ &= \begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ \vdots \\ n_{\omega}(t+1) \end{pmatrix} \\ &= \mathbf{n}(t+1) \end{aligned}$$

So by this we see that

$$\mathbf{n}(t + 1) = L\mathbf{n}(t)$$

Then, we can find

$$\begin{aligned}\mathbf{n}(t + 2) &= L\mathbf{n}(t + 1) \\ &= L(L\mathbf{n}(t)) \\ &= L^2\mathbf{n}(t)\end{aligned}$$

So more generally, it follows by induction that for each time $t + x$,

$$\mathbf{n}(t + x) = L^x\mathbf{n}(t)$$

We now see that projecting into the future becomes a process of computing high matrix powers. One simple way to obtain a reasonable approximation of these high powers is to use the spectral decomposition, which reveals certain interesting connections between the equilibrium population structure and eigenvectors/eigenvalues. The spectral decomposition is very similar to our rank one decomposition (Beezer, 2007).

5 Spectral Decomposition

Theorem 1:

There exists a spectral decomposition of a matrix A such that

$$A = \sum_{k=1}^{\omega} \lambda_k T_k$$

Where $T_k = \mathbf{e}_k \otimes \epsilon_k$, the outer product of the right and left eigenvectors.

Proof:

Our proof is constructive. To prove that the spectral decomposition exists, we start by creating a matrix R whose columns are the right eigenvectors for the matrix A . The right eigenvector (\mathbf{e}) is a usual eigenvector as we have used before, where $A\mathbf{e} = \lambda\mathbf{e}$.

We also create the matrix L whose columns are the left eigenvectors for matrix A . A left eigenvector (ϵ) is defined as the vector for which $\epsilon A = \lambda\epsilon$, so is a “normal”, right eigenvector for A^T . However, we scale the vectors in L so that $\langle \mathbf{e}_i, \epsilon_i \rangle = 1$. Since right and left eigenvectors for different eigenvalues are orthogonal, $\langle \mathbf{e}_i, \epsilon_j \rangle = 0$. Thus, $RL = I$, and $L = R^{-1}$.

Then

$$AR = [A\mathbf{e}_1 | A\mathbf{e}_2 | \dots | A\mathbf{e}_\omega] = [\lambda_1\mathbf{e}_1 | \lambda_2\mathbf{e}_2 | \dots | \lambda_\omega\mathbf{e}_\omega]$$

We can also construct a diagonal matrix D with the eigenvalues of A as its diagonal entries, with zeros everywhere else. Then, we can write

$$RD = \left[R \begin{pmatrix} \lambda_1 \\ 0 \\ \vdots \\ 0 \end{pmatrix} \mid R \begin{pmatrix} 0 \\ \lambda_2 \\ \vdots \\ 0 \end{pmatrix} \mid \dots \mid R \begin{pmatrix} 0 \\ 0 \\ \vdots \\ \lambda_\omega \end{pmatrix} \right] = [\lambda_1 \mathbf{e}_1 \mid \lambda_2 \mathbf{e}_2 \mid \dots \mid \lambda_\omega \mathbf{e}_\omega]$$

We now see that

$$\begin{aligned} AR &= RD \\ ARR^{-1} &= RDR^{-1} \\ AI &= RDL \end{aligned}$$

$$\begin{aligned} A &= RDL \\ &= \sum_{k=1}^{\omega} \mathbf{e}_k \lambda_k \epsilon_k \\ &= \sum_{k=1}^{\omega} \lambda_k \mathbf{e}_k \otimes \epsilon_k \end{aligned}$$

We now see that there is indeed a spectral decomposition

$$A = \sum_{k=1}^{\omega} \lambda_k T_k$$

6 Asymptotic Growth and Equilibrium Population

Now that we are convinced this decomposition exists, we can consider the biological significance of the equation. An important characteristic of the matrix T_k is that $T_k T_k = T_k$ and $T_j T_k = 0$ when $j \neq k$. We can see a proof of these by considering $T_j T_k$.

$$\begin{aligned} T_j T_k &= (e_j \otimes \epsilon_j)(e_k \otimes \epsilon_k) \\ &= e_j \otimes \epsilon_k \langle \epsilon_j, e_k \rangle \end{aligned}$$

When $j \neq k$, e and ϵ are eigenvectors for different eigenvalues, so their inner product equals 0. When $j = k$, then e and ϵ are eigenvectors for the same eigenvalue, and we have scaled them such that their inner product equals 1. Thus,

$$\begin{aligned} T_k T_k &= e_k \otimes \epsilon_k (1) \\ &= T_k \end{aligned}$$

$$\begin{aligned} T_j T_k &= e_k \otimes \epsilon_k (0) \\ &= 0 \end{aligned}$$

Now that we understand these two characteristics of T , we can easily find a high matrix power for the Leslie matrix L where

$$L^p = \sum_{k=1}^{\omega} \lambda_k^p T_k$$

For a Leslie matrix, there is one and only one real, positive eigenvalue, which is the dominant eigenvalue (i.e. eigenvalue of largest magnitude). We prove this by considering the characteristic polynomial $p = \det(L - \lambda I)$. If we define matrix $A = L - \lambda I$, then we see that

$$\det(A) = \begin{vmatrix} f_1 - \lambda & f_2 & f_3 & \dots & f_{\omega-1} & f_{\omega} \\ p_1 & -\lambda & 0 & \dots & 0 & 0 \\ 0 & p_2 & -\lambda & \dots & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{\omega-1} & -\lambda \end{vmatrix}$$

When we expand around the first row, we find

$$\det(A) = [A_{11}]|A_{11}| - [A_{12}]|A_{12}| + \dots \pm [A_{1\omega}]|A_{1\omega}|$$

Each minor looks something like

$$|A_{12}| = \begin{vmatrix} p_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & -\lambda & 0 & \dots & 0 & 0 \\ 0 & p_3 & -\lambda & \dots & 0 & 0 \\ 0 & 0 & p_4 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & p_{\omega-1} & -\lambda \end{vmatrix}$$

and can easily be converted to a diagonal matrix using type 3 row operations. For example, $(\lambda/p_3) \times r_3 + r_2$, $(\lambda/p_4) \times r_4 + r_3$, etc. These types of row operations do not change the determinant, so each minor is simple the produce of its diagonal elements. Thus, we see that

$$\det(A) = (f_1 - \lambda)(-\lambda)^{\omega-1} - p_1 f_2 (-\lambda)^{\omega-2} + p_1 p_2 f_3 (-\lambda)^{\omega-3} - \dots \pm p_1 p_2 \dots p_{\omega-1} f_{\omega}$$

If we let $l_x = p_1 p_2 \dots p_{x-1}$, then we can write

$$\begin{aligned} \det(A) &= (f_1 - \lambda)(-\lambda)^{\omega-1} - p_1 f_2 (-\lambda)^{\omega-2} + p_1 p_2 f_3 (-\lambda)^{\omega-3} - \dots \pm p_1 p_2 \dots p_{\omega-1} f_{\omega} \\ &= (-1)^{\omega} (\lambda^{\omega} - l_1 f_1 \lambda^{\omega-1} - l_2 f_2 \lambda^{\omega-2} - \dots - l_{\omega} f_{\omega}) \end{aligned}$$

If we set the characteristic polynomial equal to zero and divide by λ , we find that the eigenvalues are the roots of the equation

$$0 = \sum_{x=1}^{\omega} \lambda^{-x} l_x f_x - 1$$

If we call this equation $g(\lambda)$, then when $\lambda > 0$, $g(\lambda)$ is a decreasing function of λ . Therefore, there it has a unique positive real root (denoted λ_1) and all others are negative or complex. This eigenvalue (λ_1) will dominate the spectral decomposition, so asymptotically, we find that we can reasonably estimate

$$A^p \cong \lambda_1^p T_1$$

Thus, we see that this eigenvalue gives us the asymptotic growth rate for the population. At equilibrium, the proportions of individuals belonging to each age class will remain constant, and the absolute number of individuals will increase by λ_1 times each year.

Perhaps unsurprisingly, the right and left eigenvalues corresponding to λ_1 are also of biological significance. The right eigenvalue (\mathbf{e}_1) gives the stable age distribution. If this is scaled to sum 1, then each entry will provide the % of the population that will be in each age class at equilibrium.

Meanwhile, the left eigenvalue (ϵ_1) gives you the reproductive values for each age class. For example, if

$$\epsilon_1 = \begin{pmatrix} 1 \\ 1.6 \\ \vdots \end{pmatrix}$$

this tells us that a 2-year-old female will have 1.6 times as many descendants in the distant future than will a 1-year-old female.

The one exception to the above conclusions regarding λ_1 , \mathbf{e}_1 , and ϵ_1 occurs when the Leslie matrix is periodic. A periodic matrix is one in which the females in the population breed only at certain ages, so there is some common denominator > 1 for all ages at which females are reproducing. Because of this, different cohorts are considered distinct. Such a population would not be able to be characterized by the intrinsic growth rate, nor would it move toward a steady-state equilibrium, since the different cohorts would be independent of each other. In essence, each cohort would be a single reproductively isolated population.

It would be instructive to consider a concrete example. This type of periodic Leslie matrix is characteristic of many semelparous species, where individuals reproduce only once in their lifetime. For example, we can consider the scarlet gilia. At first, this plant lives in a vegetative, growth state consisting only of a rosette of basal leaves. Then, after several years the plant sends up a flowering stalk, reproduces, and dies at the end of the growing season. A simplistic model in which we take the average age at reproduction, say 4 years, and assume that every plant flowers at age 4, then dies, would result in a periodic Leslie matrix. The cohorts from each seed set would in turn grow for 4 years, then reproduce and die. Each cohort would be the seeds from a cohort exactly 4 years older than they themselves, and would not really interact with individuals from other cohorts on their own 4-year cycles.

Alternatively, we could consider other plants who often reproduce biennially. Thus, about half the population is reproducing in the odd years, while the other half is reproducing in the even years. There would therefore be a common denominator (2) of the ages at which the plants reproduce, again creating a periodic Leslie matrix. The two reproductively isolated populations would behave differently, thereby preventing us from accurately describing the overall population change by use of powers and eigenvectors of the Leslie matrix.

7 Conclusion

We now see that not only can matrices provide an excellent way to keep track of changes in age-structured populations, but the application of linear algebra techniques reveals certain biologically relevant characteristics. The unique properties of the Leslie matrix, with its specific form, enable us to find a single positive, real eigenvalue, and a useful spectral decomposition of the matrix. The dominant eigenvalue then provides us with the intrinsic growth rate, while the right and left eigenvectors provide the age distribution and relative reproductive values of a population in equilibrium. Thus, we see that linear algebra allows us to better model real-world populations, illuminating certain properties of the population itself.

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