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Relationships between Elements of Leslie Matrices and Future Growth of the Population

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RELATIONSHIPS BETWEEN ELEMENTS OF LESLIE MATRICES AND FUTURE GROWTH OF THE POPULATION

By

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ABSTRACT

Leslie matrices have been used for years to model and predict the growth of animal populations. Recently, general rules have been applied that can relatively easily determine whether an animal population will grow or decline. My mentor, Dr. Justin Brown and I examine, more specifically, whether there are relationships between certain elements of a population and the dominant eigenvalue, which determines growth. Not only do we consider the general *3x3* Leslie matrix, but also we looked into modified versions for incomplete data and migration models of Leslie matrices. We successfully found several connections within these cases; however, there is much more research that could be done.

Keywords: Leslie matrix, migration, eigenvalue, dominant eigenvalue, characteristic equation, net reproduction rate, population growth

INTRODUCTION

Leslie matrices are named for Patrick Holt Leslie (1900-1972), who created them after researching rodent populations under Charles Elton at Oxford (Bacaër, 2011, p. 117). In 1945, Leslie published his article in *Biometrika* detailing his findings concerning population models (Leslie, 1945, p. 183-212). Leslie matrices are used in mathematical ecology to determine how populations are affected by characteristics such as survival and fertility rates. Specifically, Leslie matrices are used in mathematical ecology to predict how populations of animals grow or decline. Using formulas, the eigenvalues of the Leslie matrices are found, including the dominant eigenvalue (see section labeled "Eigenvalue" for definition). If the dominant eigenvalue and, hence, all the eigenvalues are less than 1, then the population will decline. If the dominant eigenvalue is greater than one, regardless of the values of the other eigenvalues, the population will grow. In the most generic cases, 3×3 Leslie matrices are of the form

$$\begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix}$$

where a, b, c, and d represent non-negative real numbers such that $0 \le c, d \le 1$.

SUMMARY OF PRELIMINARY RESEARCH

Suppose there is a population of dogs divided into three age classes- young, middle aged, and old. It is also known that each dog will progress into the next age class in one time period (Burks, Lindquist, & McMurran, 2008, p. 76). If we know the survival and fertility rates for each age class, it is then possible to deduce a number of characteristics about this population using Leslie matrices.

Properties

A Leslie matrix is a square matrix with m rows and columns, where m represents the number of age classes and is equal to the number of time intervals (Allen, 2007, p. 19). In order to simplify the models, only the female population is modeled in the matrix. The male population and, thus, the total populatio, can be figured from knowing the ratio of female to male for the species (Allen, 2007, p. 19). The Leslie matrix is shown in Figure 1.

$$\begin{bmatrix} F_0 & F_1 & F_2 & \dots & F_{m-1} & F_m \\ P_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & P_2 & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & P_{m-1} & \dots & 0 \end{bmatrix}$$

Figure 1: The Leslie Matrix

In the Leslie matrix, there are entries on the subdiagonal directly below the main diagonal and in the first row. Every other element in this form of matrix is zero (Leslie, 1945, p. 184). The entries on the subdiagonal describe the survival probabilities for each age class (Allen, 2007, p. 19). This survival probability P_i is the chance that a female in age class *i* survives for one time interval to age *i+1* (Caswel, 2001, p. 9). The entries in the first row represent the fertilities F_i for each age class (Allen, 2007, p. 19), which is described by the number of individuals in age class 1 after one time interval (at time t+1) per individual in age class *i* during the original interval, or at

time *t* (Caswell, 2001, p. 10). Lastly, the initial state population vector is a vector where each entry represents the number of individuals in each age group at time *t*. (Caswell, 2001, p. 10; Leslie, 1945, p. 183). Thus *t+1* is the age class one interval after the original time.

Projection

Knowing the properties of the Leslie matrix listed above and the initial population, it is possible to project the population. To begin, the initial population values are placed into a vector. This is then multiplied by the Leslie matrix that is raised to the power of the number of time intervals projected (Allen, 2007, p. 19). Projection is expressed using the formula $X(t)=L^tX(0)$, where X(t) is the projection matrix, t is the desired number of time intervals of projection, and X(0) is the initial population vector.

Eigenvalues

Eigenvalues are one of the more important properties to consider when looking at Leslie matrices because they give an idea of how the population will change over time. To find eigenvalues, the characteristic equation $det(A-\lambda I)=0$ is solved for lambda. In other words, subtract λ times the identity matrix I from the original matrix A, then find the determinant and set this equal to 0. For each Leslie matrix, there will then be a dominant eigenvalue that has a value greater than the absolute value of any other eigenvalue (Anton & Rorres, 1994, p. 759). The value of the eigenvalue describes the change in population in the future- if $|\lambda|$ is less than one, the population will decrease and if $|\lambda|$ is greater than one, the population will increase.

Net Reproduction Rate

Net reproduction rate is another statistic that can be found using the Leslie matrix. The net reproduction rate is simply the expected number of children a female will bear during her lifetime by taking the sum of each survival probability multiplied by all previous fertility rates. This rate is represented by the expression

$$R=F_0+F_1P_1+F_2P_1P_2+\ldots+F_NP_1P_2\ldots P_{n-1}.$$

This shows that a population has zero value population growth if and only if its net reproduction rate is 1 (Anton & Rorres, 1994, p.763).

Example

In the example of the dog population, the population is divided into three age classes and each dog will move forward one age class for each time period. Suppose it is also known that each middle-aged dog will have a litter of three puppies each time period and an old dog will have one puppy each time period. Lastly, assume the survival probability of surviving to become a middle-aged dog is forty percent and the probability of a middle-aged dog surviving to become an old dog is thirty percent (Burks, Lindquist, & McMurran, 2008, p. 76). With this information, we can construct a Leslie matrix as follows:

$$\begin{bmatrix} 0 & 3 & 1 \\ .4 & 0 & 0 \\ 0 & .3 & 0 \end{bmatrix}$$

Figure 2: Leslie Matrix for Dog Population

It is also possible to project the population into the future if the current values of the dog population are known. Say that there are twenty young dogs, thirty middle-aged dogs, and ten old dogs and that the population projection is desired for 25 time intervals into the future (Burks, Lindquist, & McMurran, 2008, p. 76). The formula for calculating this projection is to raise the Leslie matrix by the desired number of years of projection and multiply that by the initial population vector. The projection for the dog population is as follows:

$$\begin{bmatrix} 0 & 3 & 1 \\ .4 & 0 & 0 \\ 0 & .3 & 0 \end{bmatrix}^{25} \begin{bmatrix} 20 \\ 30 \\ 10 \end{bmatrix} = \begin{bmatrix} 1632.4 \\ 498.98 \\ 151.95 \end{bmatrix}$$

Figure 3: Projection

Thus, in twenty-five years, there will be approximately 1,623 young dogs, 499 middle-aged dogs, and 152 old dogs in the population.

The eigenvalues of the matrix are found by solving *det(A-λI)x=0*. To begin, we find the characteristic equation (Lay, 2006, p. 310-1).

$$\begin{bmatrix} 0 & 3 & 1 \\ .4 & 0 & 0 \\ 0 & .3 & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 & 0 \\ 0 & \lambda & 0 \\ 0 & 0 & \lambda \end{bmatrix} = \begin{bmatrix} -\lambda & 3 & 1 \\ 0.4 & -\lambda & 0 \\ 0 & 0.3 & -\lambda \end{bmatrix}$$

$$\det L = (-\lambda^3 + 0 + 0.12) - (0 + 0 + 1.2\lambda) = -\lambda^3 + 1.2\lambda + 0.12$$

This equation can then be solved by plugging values into a formula for solving cubic equations, and the solutions give the eigenvalues (Lay, 2006, p. 310-1).

$$0 = -\lambda^3 + 1.2\lambda + 0.12 \ ,$$

Solution is: $\{[\lambda = -1.0415], [\lambda = 1.1424], [\lambda = -0.10085]\}$

Thus the eigenvalues of the Leslie matrix are approximately 1.142, -1.042, and -0.101. Because the dominant eigenvalue equals 1.142, which is greater than one, the population is increasing. Keyfitz and Caswell (2005) explain that, as long as the dominant eigenvalue is positive there is exponential growth.

METHODOLOGY

In the most generic cases, 3×3 Leslie matrices are of the form

$$\begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix}$$

where *a*, *b*, *c*, and *d* represent non-negative real numbers such that $0 \leq c, d \leq 1$. We will begin by looking at the relationships between the entries *a* and *c* in the matrix that imply that the matrix has an eigenvalue greater than one. In the later proofs, we have expanded from upon this statement in order to discover and prove other statements related to the various matrices. Next, we examine the results of matrices obtained by replacing zeroes in the matrix above with non-zero numbers. Many researchers have studied the general *nxn* case of Leslie matrices and have found rules that are very vague concerning the eigenvalues and population growth.

In our research, we provide new information by finding rules that apply to the matrix above and its variations in more detail. Taking rules previously proven by past mathematicians, we work to provide a more streamlined process for predicting future growth or decline of an animal population. Through original proofs, we provide evidence for all patterns we found to be true for different cases of Leslie matrices.

RESULTS

In our research, we looked at several different cases of Leslie matrices. To begin, in the first few proofs we looked at matrices that had information for the last two fertility rates and the first two survival rates. By the end of the third age class, the individuals of a population all die so that there is a 0 survival rate for the last age class.

Proof 1: If $ac = 1$, then the population is increasing.

In other words, if $ac = 1$, then $\lambda \geq 1$

Suppose we are given a Leslie Matrix

$$A = \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} \qquad \text{where } a,b > 0 \text{ and } 0 \leq c,d \leq 1$$

To find the eigenvalues, we solve for the determinant of $|A - \lambda I|$ set equal to 0.

$$\det|A - \lambda I| = \det\left\| \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 & 0 \\ 0 & \lambda & 0 \\ 0 & 0 & \lambda \end{bmatrix} \right\|$$

$$= \det\left\| \begin{bmatrix} -\lambda & a & b \\ c & -\lambda & 0 \\ 0 & d & -\lambda \end{bmatrix} \right\|$$

$$= (-\lambda^3 + 0 + bcd) - (0 + 0 - ac\lambda)$$

$$= -\lambda^3 + ac\lambda + bcd$$

From the given condition, we know $ac = 1$, so

$$\det|A - \lambda I| = -\lambda^3 + \lambda + bcd$$

We also know that *bcd≥0* by the conditions of the Leslie matrix.

Case 1: $bcd = 0$

If $bcd = 0$ then the characteristic equation is

$$\det\left|A - \lambda I\right| = -\lambda^3 + \lambda$$

Setting this equal to 0 and solving yields

$$-\lambda^3 + \lambda = 0$$

$$\lambda(-\lambda^2 + 1) = 0$$

$$\lambda = 0, \pm 1$$

Thus, the dominant eigenvalue is 1, showing that the population is growing.

Case 2: $bcd > 0$

From above, we have a characteristic equation

$$\det\left|A - \lambda I\right| = -\lambda^3 + \lambda + bcd$$

Let $f(x) = -x^3 + x$ and $m = bcd$

Also, let $h(x) = f(x) + m$

At $f(1)$, the root is $x = 1$. Therefore, adding bcd will cause the function to shift up.

Because the function is decreasing, this causes the root to increase.

Thus, the dominant eigenvalue $\lambda > 1$

Therefore, the population is increasing.

It has been shown that if $ac = 1$ then $\lambda \geq 1.$ Thus, if $ac = 1$, then the population is growing.

Using the characteristic polynomial and conditions of the Leslie matrix, namely *bcd≥0*, we have proven that the population will grow if the product of the fertility rate of the second class and the survival rate of the first class are greater than one for a general Leslie matrix.

Proof 2: If the net reproduction rate of a population is greater than one, then the population is increasing. In other words, if $R > 1$, then $\lambda > 1$.

Suppose we are given a Leslie Matrix

$$A = \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} \qquad \text{where } a, b > 0 \text{ and } 0 \le c, d \le 1$$

The net reproduction rate is $R = 0 + ac + bcd$.

Based on the conditions of the Leslie matrix, $ac \geq 0$ and $bcd \geq 0$.

Also, based on the given conditions, $R > 1$ so $ac + bcd > 1$.

Case 1: $ac = 1$

With this condition, the net reproduction rate can be rewritten as

$$1 + bcd - 1 > 0$$

$$bcd > 0$$

By Proof 1, if $ac = 1$ and $bcd > 0$, then $\lambda > 1$.

Therefore, the population is increasing.

Case 2: $ac > 1$

From the hypothesis, we know that $R > 1$.

The characteristic equation of the Leslie matrix is

$$-\lambda^3 + ac\lambda + bcd = 0$$

Start with $-\lambda^3 + ac\lambda = 0$

$$-\lambda(\lambda^2 - ac) = 0$$

$$-\lambda(\lambda + \sqrt{ac})(\lambda - \sqrt{ac}) = 0$$

The dominant eigenvalue of this equation is $\lambda = \sqrt{ac}$. Because $ac > 1$, $\sqrt{ac} > 1$

Adding bcd , we get

$$-\lambda(\lambda + \sqrt{ac})(\lambda - \sqrt{ac}) + bcd = 0$$

The root of this equation is greater than $\sqrt{ac}$, because bcd causes an upward shift.

Case 3: $ac < 1$

Note: this serves as the general case. After proving this case, we realized we did not use the fact that *ac<1*, so this also covers Case 1 and Case 2.

Let *f(* λ *)=-* λ^3*+ac* λ *+bcd*

From the hypothesis, we know that *R=* $ac + bcd$ *= f(1) + 1*

f(1)= $ac + bcd$ *-1 > 0*

$f(\lambda)$ is decreasing because the $\lim f(\lambda)$ as $\lambda \to \infty$ is $-\infty$.

The function $f(\lambda) = -\lambda(\lambda^2 - ac)$ has a root at $\lambda = 1$ such that $f(\lambda) > 0$.

Because we know that the $\lim f(\lambda)$ as $\lambda \to \infty$ is $-\infty$ and *f* is continuous, it can be shown that there is some Q between $(1, \infty)$ such that $-Q^3 + acQ + bcd = 0$.

Because of the above, we can conclude that there is some *q>1* such that the function at *q* equals 0.

Therefore, it has been shown that if $R > 1$ then $\lambda > 1$.

Thus, if the net reproduction rate is increasing, then the population is growing.

In three cases, we have shown that the net reproduction rate and the dominant eigenvalue of a general Leslie matrix are related. For *ac=1, ac>1,* and *ac<1*, when the net reproduction rate is greater than 1, then the dominant eigenvalue is greater than 1 and thus the population is growing.

Proof 3: If the population is increasing, then the net reproduction rate is greater than one. In other words, if $\lambda > 1$, then $R > 1$.

Suppose we are given a Leslie Matrix

$$A = \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} \qquad \text{where } a, b > 0 \text{ and } 0 \le c, d \le 1$$

The net reproduction rate is $R = 0 + ac + bcd$.

The characteristic polynomial is

$$\det\left|A - \lambda I\right| = \det\left\| \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 & 0 \\ 0 & \lambda & 0 \\ 0 & 0 & \lambda \end{bmatrix} \right\|$$

$$= \det\left\| \begin{bmatrix} -\lambda & a & b \\ c & -\lambda & 0 \\ 0 & d & -\lambda \end{bmatrix} \right\|$$

$$= (-\lambda^3 + 0 + bcd) - (0 + 0 - ac\lambda)$$

$$= -\lambda^3 + ac\lambda + bcd$$

Thus, we have $-\lambda^3 + ac\lambda + bcd = 0$ for some $\lambda > 1$

Let $f(\lambda) = -\lambda^3 + ac\lambda + bcd$

Then, $f'(\lambda) = -3\lambda^2 + ac$

$$-3\lambda^2 + ac = 0$$

$$3\lambda^2 = ac$$

$$\lambda = \pm\sqrt{\frac{ac}{3}}$$

At $\lambda = \sqrt{\frac{ac}{3}}$, there is a shift in direction. There are no other shifts of direction for $\lambda > 0$

Then, for any $\lambda > 1$,

$$-1 + ac + bcd > 0$$

$$ac + bcd > 1$$

Therefore, it has been shown that if $\lambda > 1$ then $R > 1$.

Thus, if the population is increasing, then the net reproduction rate is greater than one.

In a general Leslie matrix, we have proven that if the population is growing, indicated by a dominant eigenvalue greater than 1, then the net reproduction rate is also greater than 1. This was shown by looking at the graphical representation of the characteristic equation and the shifts it undergoes.

Therefore, it can be said that the net reproduction rate is greater than one if and only if the population is increasing. In other words, $R > 1$ if and only if $\lambda > 1$.

Proof 4: If $\lambda = 1$ then the net reproduction rate is derived from the characteristic polynomial.

3x3 Matrices

$$\begin{bmatrix} a & b & c \\ d & 0 & 0 \\ 0 & e & 0 \end{bmatrix} \rightarrow \begin{bmatrix} a-\lambda & b & c \\ d & -\lambda & 0 \\ 0 & e & -\lambda \end{bmatrix}$$

Determinant: $f(\lambda) = -\lambda^3 + a\lambda^2 + bd\lambda + cde$

$$f(1) = -1 + a + bd + cde$$

$$f(1) = a + bd + cde > 1$$

$$R = a + bd + cde > 1$$

4x4 Matrices

$$\begin{bmatrix} a & b & c & d \\ e & 0 & 0 & 0 \\ 0 & f & 0 & 0 \\ 0 & 0 & g & 0 \end{bmatrix} \rightarrow \begin{bmatrix} a-\lambda & b & c & d \\ e & -\lambda & 0 & 0 \\ 0 & f & -\lambda & 0 \\ 0 & 0 & g & -\lambda \end{bmatrix}$$

Determinant: $f(\lambda) = \lambda^4 - a\lambda^3 - be\lambda^2 - cfe\lambda - dfge$

$$f(1) = 1 - a - be - cfe - dfge$$

$$f(1) = a + be + cfe + dfge > 1$$

$$R = a + be + cef + defg > 1$$

5x5 Matrices

$$\begin{bmatrix} a & b & c & d & e \\ f & 0 & 0 & 0 & 0 \\ 0 & g & 0 & 0 & 0 \\ 0 & 0 & h & 0 & 0 \\ 0 & 0 & 0 & i & 0 \end{bmatrix} \rightarrow \begin{bmatrix} a-\lambda & b & c & d & e \\ f & -\lambda & 0 & 0 & 0 \\ 0 & g & -\lambda & 0 & 0 \\ 0 & 0 & h & -\lambda & 0 \\ 0 & 0 & 0 & i & -\lambda \end{bmatrix}$$

Determinant: $f(\lambda) = -\lambda^5 + a\lambda^4 + bf\lambda^3 + cfg\lambda^2 + dfgh\lambda + ifghe$

$$f(1) = -1 + a + bf + cfg + dfgh + ifghe$$

$$f(1) = a + bf + cfg + dfgh + ifghe > 1$$

$$R = a + bf + cfg + dfgh + efghi > 1$$

nxn Matrices

$$\begin{bmatrix} a_1 & a_2 & a_3 & a_4 & \ldots & a_{n-2} & a_{n-1} & a_n \\ b_1 & 0 & 0 & 0 & \ldots & 0 & 0 & 0 \\ 0 & b_2 & 0 & 0 & \ldots & 0 & 0 & 0 \\ 0 & 0 & b_3 & 0 & \ldots & 0 & 0 & 0 \\ 0 & 0 & 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . & . & . \\ 0 & 0 & 0 & 0 & \ldots & b_{n-2} & 0 & 0 \\ 0 & 0 & 0 & 0 & \ldots & 0 & b_{n-1} & 0 \end{bmatrix} \rightarrow \begin{bmatrix} a_1-\lambda & a_2 & a_3 & a_4 & \ldots & a_{n-2} & a_{n-1} & a_n \\ b_1 & -\lambda & 0 & 0 & \ldots & 0 & 0 & 0 \\ 0 & b_2 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & 0 & b_3 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . & . & . \\ 0 & 0 & 0 & 0 & \ldots & b_{n-2} & -\lambda & 0 \\ 0 & 0 & 0 & 0 & \ldots & 0 & b_{n-1} & -\lambda \end{bmatrix}$$

Determinant (see work below): $f(\lambda) = \lambda^n - a_1\lambda^{n-1} - a_2 b_1 \lambda^{n-2} -$

$$\ldots - a_{n-1} b_{n-2} b_{n-3} \ldots b_2 b_1 \lambda - a_n b_{n-1} b_{n-2} b_{n-3} \ldots b_2 b_1$$

$$f(1) = 1 - a_1 - a_2 b_1 - \ldots - a_{n-1} b_{n-2} b_{n-3} \ldots b_1 - a_n b_{n-1} b_{n-2} b_{n-3} \ldots b_1$$

$$f(1) = a_1 + a_2 b_1 + \ldots + a_{n-1} b_{n-2} \ldots b_1 + a_n b_{n-1} b_{n-2} \ldots b_1 > 1$$

$$R = a_1 + a_2 b_1 + \ldots + a_{n-1} b_{n-2} b_{n-3} \ldots b_1 + a_n b_{n-1} b_{n-2} b_{n-3} \ldots b_1 > 1$$

Determinant of the nxn Leslie Matrix

$$\begin{bmatrix} a_1 & a_2 & a_3 & a_4 & \ldots & a_{n-2} & a_{n-1} & a_n \\ b_1 & 0 & 0 & 0 & \ldots & 0 & 0 & 0 \\ 0 & b_2 & 0 & 0 & \ldots & 0 & 0 & 0 \\ 0 & 0 & b_3 & 0 & \ldots & 0 & 0 & 0 \\ 0 & 0 & 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . & . & . \\ 0 & 0 & 0 & 0 & \ldots & b_{n-2} & 0 & 0 \\ 0 & 0 & 0 & 0 & \ldots & 0 & b_{n-1} & 0 \end{bmatrix} \rightarrow \begin{bmatrix} a_1 - \lambda & a_2 & a_3 & a_4 & \ldots & a_{n-2} & a_{n-1} & a_n \\ b_1 & -\lambda & 0 & 0 & \ldots & 0 & 0 & 0 \\ 0 & b_2 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & 0 & b_3 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . & . & . \\ 0 & 0 & 0 & 0 & \ldots & b_{n-2} & -\lambda & 0 \\ 0 & 0 & 0 & 0 & \ldots & 0 & b_{n-1} & -\lambda \end{bmatrix}$$

The determinant of an nxn matrix can be found using cofactors and expanding the matrix. To find the determinant of the second matrix above, I proceeded as follows:

$$\det = (a_1 - \lambda) \begin{bmatrix} -\lambda & 0 & 0 & \ldots & 0 & 0 & 0 \\ b_2 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & b_3 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . & . \\ 0 & 0 & 0 & \ldots & b_{n-2} & -\lambda & 0 \\ 0 & 0 & 0 & \ldots & 0 & b_{n-1} & -\lambda \end{bmatrix} - (b_1) \begin{bmatrix} a_2 & a_3 & a_4 & \ldots & a_{n-2} & a_{n-1} & a_n \\ b_2 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & b_3 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . & . \\ 0 & 0 & 0 & \ldots & b_{n-2} & -\lambda & 0 \\ 0 & 0 & 0 & \ldots & 0 & b_{n-1} & -\lambda \end{bmatrix}$$

$$= (a_1 - \lambda)(-\lambda) \begin{bmatrix} -\lambda & 0 & \ldots & 0 & 0 & 0 \\ b_3 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . \\ 0 & 0 & \ldots & b_{n-2} & -\lambda & 0 \\ 0 & 0 & \ldots & 0 & b_{n-1} & -\lambda \end{bmatrix} - (b_1)(a_2) \begin{bmatrix} -\lambda & 0 & \ldots & 0 & 0 & 0 \\ b_3 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & b_4 & \ldots & 0 & 0 & 0 \\ . & . & . & . & . & . \\ 0 & 0 & \ldots & b_{n-2} & -\lambda & 0 \\ 0 & 0 & \ldots & 0 & b_{n-1} & -\lambda \end{bmatrix} -$$

$$(b_1)(-b_2)\begin{bmatrix} a_3 & a_4 & \dots & a_{n-2} & a_{n-1} & a_n \\ b_3 & -\lambda & \dots & 0 & 0 & 0 \\ 0 & b_4 & \dots & 0 & 0 & 0 \\ . & . & . & . & . & . \\ 0 & 0 & \dots & b_{n-2} & -\lambda & 0 \\ 0 & 0 & \dots & 0 & b_{n-1} & -\lambda \end{bmatrix}$$

$$=(\lambda^2 - a_1\lambda)(-\lambda)\begin{bmatrix} -\lambda & \dots & 0 & 0 & 0 \\ b_4 & \dots & 0 & 0 & 0 \\ . & . & . & . & . \\ 0 & \dots & b_{n-2} & -\lambda & 0 \\ 0 & \dots & 0 & b_{n-1} & -\lambda \end{bmatrix} - (b_1 a_2)(-\lambda)\begin{bmatrix} -\lambda & \dots & 0 & 0 & 0 \\ b_4 & \dots & 0 & 0 & 0 \\ . & . & . & . & . \\ 0 & \dots & b_{n-2} & -\lambda & 0 \\ 0 & \dots & 0 & b_{n-1} & -\lambda \end{bmatrix} +$$

$$(b_1)(b_2)(a_3)\begin{bmatrix} -\lambda & \dots & 0 & 0 & 0 \\ b_4 & \dots & 0 & 0 & 0 \\ . & . & . & . & . \\ 0 & \dots & b_{n-2} & -\lambda & 0 \\ 0 & \dots & 0 & b_{n-1} & -\lambda \end{bmatrix} + (b_1)(b_2)(-b_3)\begin{bmatrix} a_4 & \dots & a_{n-2} & a_{n-1} & a_n \\ b_4 & \dots & 0 & 0 & 0 \\ . & . & . & . & . \\ 0 & \dots & b_{n-2} & -\lambda & 0 \\ 0 & \dots & 0 & b_{n-1} & -\lambda \end{bmatrix}$$

$$=(-\lambda^3 + a_1\lambda^2)(-\lambda)\begin{bmatrix} \dots & 0 & 0 & 0 \\ . & . & . & . \\ \dots & b_{n-2} & -\lambda & 0 \\ \dots & 0 & b_{n-1} & -\lambda \end{bmatrix} + (b_1 a_2 \lambda)(-\lambda)\begin{bmatrix} \dots & 0 & 0 & 0 \\ . & . & . & . \\ \dots & b_{n-2} & -\lambda & 0 \\ \dots & 0 & b_{n-1} & -\lambda \end{bmatrix} +$$

$$(b_1 b_2 a_3)(-\lambda)\begin{bmatrix} \dots & 0 & 0 & 0 \\ . & . & . & . \\ \dots & b_{n-2} & -\lambda & 0 \\ \dots & 0 & b_{n-1} & -\lambda \end{bmatrix} - (b_1 b_2 b_3)(a_4)\begin{bmatrix} \dots & 0 & 0 & 0 \\ . & . & . & . \\ \dots & b_{n-2} & -\lambda & 0 \\ \dots & 0 & b_{n-1} & -\lambda \end{bmatrix} -$$

$$(b_1b_2b_3)(-b_4)\begin{bmatrix} \ldots & a_{n-2} & a_{n-1} & a_n \\ . & . & . & . \\ \ldots & b_{n-2} & -\lambda & 0 \\ \ldots & 0 & b_{n-1} & -\lambda \end{bmatrix}$$

If n is odd:

$$\det = -\lambda^n + a_1\lambda^{n-1} + a_2b_1\lambda^{n-2} + \ldots + a_{n-1}b_{n-2}\ldots b_2b_1\lambda + a_nb_{n-1}b_{n-2}\ldots b_2b_1$$

If n is even:

$$\det = \lambda^n - a_1\lambda^{n-1} - a_2b_1\lambda^{n-2} - \ldots - a_{n-1}b_{n-2}\ldots b_2b_1\lambda - a_nb_{n-1}b_{n-2}\ldots b_2b_1$$

In either case, when $\lambda = 1$ then the net reproduction rate is derived from the characteristic polynomial, as shown above.

For the general Leslie matrix where all classes have a fertility rate and all but the last class have a survival rate in the matrix, the net reproduction rate is related to the characteristic equation. We began with a *2x2* matrix and showed this property held true up through the *nxn* Leslie matrix by using cofactors to find the determinants of the matrices and thus the characteristic equation.

For the following proof, we will use mathematical induction to show that the net reproduction rate is derived from the characteristic polynomial.

Proof 5: For an nxn matrix, if $\lambda = 1$ then the net reproduction rate is derived from the characteristic polynomial

To begin, let $n = 2$, so that the matrix is

$$A = \begin{bmatrix} a_1 & a_2 \\ b_1 & 0 \end{bmatrix}$$

The net reproduction rate for this matrix is $R = a_1 + a_2b_1 > 1$

The characteristic polynomial is found by finding the determinant of $A - \lambda I$

$$\det|A-\lambda I| = \det\begin{bmatrix} a_1-\lambda & a_2 \\ b_1 & -\lambda \end{bmatrix}$$

$$=[-\lambda(a_1-\lambda)]-[a_2b_1]$$

$$=\lambda^2 - a_1\lambda - a_2b_1$$

When $\lambda = 1$

$$\det = 1 - a_1 - a_2b_1$$

$$\Rightarrow a_1 + a_2b_1 = 1$$

The characteristic equation is equal to the net reproduction rate when $\lambda = 1$ for a $n = 2$

Assume that this holds for all $n = k$ such that the net reproduction rate

$$R = a_1 + a_2b_1 + a_3b_2b_1 + \ldots + a_kb_{k-1}b_{k-2}\ldots b_2b_1$$

and that the characteristic equation is

$$\det = \pm\lambda^n \mp a_1\lambda^{n-1} \mp a_2b_1\lambda^{n-2} \mp \ldots \mp a_{n-1}b_{n-2}b_{n-3}\ldots b_2b_1\lambda \mp a_nb_{n-1}b_{n-2}b_{n-3}\ldots b_2b_1$$

as shown in the earlier examples

Let $n = k+1$, thus the matrix is

$$\begin{bmatrix} a_1 & a_2 & a_3 & \ldots & a_{k-3} & a_{k-2} & a_{k-1} & a_k & a_{k+1} \\ b_1 & 0 & 0 & \ldots & 0 & 0 & 0 & 0 & 0 \\ 0 & b_2 & 0 & \ldots & 0 & 0 & 0 & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & b_{k-3} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \ldots & 0 & b_{k-2} & 0 & 0 & 0 \\ 0 & 0 & 0 & \ldots & 0 & 0 & b_{k-1} & 0 & 0 \\ 0 & 0 & 0 & \ldots & 0 & 0 & 0 & b_k & 0 \end{bmatrix}$$

The net reproduction rate R is

$$R = a_1 + a_2b_1 + \ldots + a_kb_{k-1}b_{k-2}b_{k-3}\ldots b_2b_1 + a_{k+1}b_kb_{k-1}\ldots b_2b_1 > 1$$

$$|A-\lambda I| = \begin{bmatrix} a_1-\lambda & a_2 & a_3 & \dots & a_{k-3} & a_{k-2} & a_{k-1} & a_k & a_{k+1} \\ b_1 & -\lambda & 0 & \dots & 0 & 0 & 0 & 0 & 0 \\ 0 & b_2 & -\lambda & \dots & 0 & 0 & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & b_{k-3} & -\lambda & 0 & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & b_{k-2} & -\lambda & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & b_{k-1} & -\lambda & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 & b_k & -\lambda \end{bmatrix}$$

Use cofactors to find the determinant

$$\det|A-\lambda I| = (-\lambda)\begin{bmatrix} a_1-\lambda & a_2 & a_3 & \dots & a_{k-3} & a_{k-2} & a_{k-1} & a_k \\ b_1 & -\lambda & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & b_2 & -\lambda & \dots & 0 & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & b_{k-3} & -\lambda & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & b_{k-2} & -\lambda & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & b_{k-1} & -\lambda \end{bmatrix} \pm$$

$$(a_{k+1})\begin{bmatrix} b_1 & -\lambda & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & b_2 & -\lambda & \dots & 0 & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & b_{k-3} & -\lambda & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & b_{k-2} & -\lambda & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & b_{k-1} & -\lambda \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 & b_k \end{bmatrix}$$

The first matrix is simply a kxk Leslie matrix, for which we already know the determinant.

The second matrix is an upper triangular matrix, for which the determinant is the product of the diagonal.

$$\det|A-\lambda I| = (-\lambda)(\lambda^k - a_1\lambda^{k-1} - a_2 b_1 \lambda^{k-2} - \dots - a_{k-1}b_{k-2}b_{k-3}\dots b_2 b_1 \lambda -$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1) \pm (a_{k+1})(b_1 b_2 \dots b_{k-1} b_k)$$

$$= -\lambda^{k+1} + a_1\lambda^k + a_2 b_1 \lambda^{k-1} + \dots + a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda^2 +$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda \pm a_{k+1} b_1 b_2 \dots b_{k-1} b_k$$

If n is even:

$$\det\left|A - \lambda I\right| = (-\lambda)(\lambda^k - a_1 \lambda^{k-1} - a_2 b_1 \lambda^{k-2} - \dots - a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda -$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1) + (a_{k+1})(b_1 b_2 \dots b_{k-1} b_k)$$

$$= -\lambda^{k+1} + a_1 \lambda^k + a_2 b_1 \lambda^{k-1} + \dots + a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda^2 +$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda + a_{k+1} b_1 b_2 \dots b_{k-1} b_k$$

When $\lambda = 1$:

$$\det\left|A - \lambda I\right| = -1 + a_1 + a_2 b_1 + \dots + a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 +$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 + a_{k+1} b_1 b_2 \dots b_{k-1} b_k$$

If n is odd:

$$\det\left|A - \lambda I\right| = (-\lambda)(-\lambda^k + a_1 \lambda^{k-1} + a_2 b_1 \lambda^{k-2} + \dots + a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda +$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1) - (a_{k+1})(b_1 b_2 \dots b_{k-1} b_k)$$

$$= \lambda^{k+1} - a_1 \lambda^k - a_2 b_1 \lambda^{k-1} - \dots - a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda^2 -$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 \lambda - a_{k+1} b_1 b_2 \dots b_{k-1} b_k$$

When $\lambda = 1$:

$$\det\left|A - \lambda I\right| = 1 - a_1 - a_2 b_1 - \dots - a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 -$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 - a_{k+1} b_1 b_2 \dots b_{k-1} b_k$$

Both determinants can be rearranged so that

$$\det\left|A - \lambda I\right| = a_1 + a_2 b_1 + \dots + a_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 +$$

$$a_k b_{k-1} b_{k-2} b_{k-3} \dots b_2 b_1 + a_{k+1} b_1 b_2 \dots b_{k-1} b_k = 1$$

Thus the net reproduction rate can be derived from the characteristic polynomial when $\lambda = 1$ for $n = k+1$

Thus, the net reproduction rate can be derived from the characteristic polynomial for nxn matrices for all $n \geq 2$.

For the general Leslie matrix where all classes have a fertility rate and all but the last class have a survival rate in the matrix, the net reproduction rate is related to the characteristic equation. We began with a *2x2* matrix and showed this property held true up through the *nxn* Leslie matrix by using an inductive proof. Because the property was true for the first matrix, the *2x2* matrix, and we have shown that for any *P(k): kxk* matrix that followed this property implies *P(k+1): (k+1)x(k+1)* matrix is true, then we can use induction to show that this property holds for an *P(n): nxn* matrix.

For the following proofs, we allow individuals to survive past the third age class so that there is a variable m representative of the last survival rate.

Proof 6: If the net reproduction rate of a population is greater than one, then the population is increasing. In other words, if $R > 1$, then $\lambda > 1$.

Suppose we are given a Leslie Matrix

$$A = \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & m \end{bmatrix} \qquad \text{where } a, b > 0 \text{ and } 0 \leq c, d, m \leq 1$$

The net reproduction rate is $R = ac + bcd + m - acm > 1$.

Based on the conditions of the Leslie matrix, $ac > 0$, $acm > 0$, and $bcd > 0$.

Let $f(\lambda) = -\lambda^3 + m\lambda^2 + ac\lambda - acm + bcd$

Let $g(\lambda) = -\lambda^3 + m\lambda^2 + ac\lambda - acm$

Thus, $f(\lambda) = g(\lambda) + bcd$

The function $f(\lambda)$ is decreasing because the $\lim f(\lambda)$ as $\lambda \to \infty$ is $-\infty$

Case 1: $ac = 1$

$$m + ac - acm + bcd - 1 > 0$$

$$m + (1-m)ac + bcd - 1 > 0$$

$$m + 1 - m + bcd - 1 > 0$$

Therefore, $bcd > 0$.

Now let us find λ such that *g(λ)=0*.

$$-\lambda^3 + m\lambda^2 + ac\lambda - acm = 0$$

$$-\lambda^3 + m\lambda^2 + ac(\lambda - m) = 0$$

$$-\lambda^3 + m\lambda^2 + 1(\lambda - m) = 0$$

$$-\lambda^2(\lambda - m) + 1(\lambda - m) = 0$$

$$-\lambda^2(\lambda - m) + 1(\lambda - m) = 0$$

$$(\lambda - m)(-\lambda^2 + 1) = 0$$

$$(\lambda - m)(1-\lambda)(1+\lambda) = 0$$

$$\lambda = \pm 1, m$$

Thus, *g(1)=0.*

Because *f(λ)=g(λ)+bcd,* adding bcd will cause an upward shift. Thus *f(1)>0.* Because the function $f(\lambda)$ is decreasing, the dominant eigenvalue $\lambda \geq 1$

Case 2: $ac > 1$

$$m + ac + bcd - acm > 1$$

When $ac > 1$ then $R > 1$

Using limits, we know that the function $g(\lambda)$ is decreasing

$$-\lambda^3 + m\lambda^2 + ac\lambda - acm = 0$$

$$-\lambda^2(\lambda - m) + ac(\lambda - m) = 0$$

$$(-\lambda^2 + ac)(\lambda - m) = 0$$

$$(-\lambda^2 + ac)(\lambda - m) = 0$$

$$\lambda = \pm\sqrt{ac}, m$$

Because $ac > 1$, it is shown that $\sqrt{ac} > 1$

Because *f(λ)=g(λ)+bcd,* adding bcd will cause an upward shift. Thus *f(1)>0.* Because the function $f(\lambda)$ is decreasing, the dominant eigenvalue $\lambda \geq 1$

Case 3: $ac < 1$

Note: this serves as the general case. After proving this case, we realized we did not use the fact that *ac<1*, so this also covers Case 1 and Case 2.

Let $f(\lambda) = -\lambda^3 + m\lambda^2 + ac\lambda - acm + bcd$

From the hypothesis *R>1*, we know that *f(1)=* $m + ac + bcd - acm$ *-1 > 0*

$f(\lambda)$ is decreasing because the $\lim f(\lambda)$ as $\lambda \to \infty$ is $-\infty$.

Because we know that the $\lim f(\lambda)$ as $\lambda \to \infty$ is $-\infty$ and *f(λ)* is continuous, it can be shown that there is some Q between $(1, \quad \infty)$ such that

$$-Q^3 + mQ^2 + acQ + bcd - acm = 0$$

Therefore, it has been shown that if $R > 1$ then $\lambda > 1$.

Thus, if the net reproduction rate is increasing, then the population is growing for a Leslie matrix with a population that survives past the last age class.

In three cases, we have shown that the net reproduction rate and the dominant eigenvalue of a modified Leslie matrix are related. For *ac=1, ac>1,* and *ac<1*, when the net reproduction rate is greater than 1, then the dominant eigenvalue is greater than 1 and thus the population is growing.

Proof 7: If the population is increasing, then the net reproduction rate is greater than one. In other words, if $\lambda > 1$, then $R > 1$.

Suppose we are given a Leslie Matrix

$$A = \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & m \end{bmatrix} \qquad \text{where } a, b > 0 \text{ and } 0 \le c, d \le 1$$

The net reproduction rate is $R = m + ac + bcd - acm$

The characteristic polynomial is

$$\det|A - \lambda I| = \det\left\| \begin{bmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & m \end{bmatrix} - \begin{bmatrix} \lambda & 0 & 0 \\ 0 & \lambda & 0 \\ 0 & 0 & m-\lambda \end{bmatrix} \right\|$$

$$= \det\left[\begin{bmatrix} -\lambda & a & b \\ c & -\lambda & 0 \\ 0 & d & m-\lambda \end{bmatrix}\right]$$

$$= -\lambda^3 + m\lambda^2 + ac\lambda + bcd - acm$$

Thus, we have $-\lambda^3 + m\lambda^2 + ac\lambda + bcd - acm = 0$ for some $\lambda > 1$

$$bcd - acm = \lambda^3 - m\lambda^2 - ac\lambda$$

$$bcd - acm = \lambda(\lambda^2 - m\lambda - ac)$$

The reciprocal of two equal statements are also equal, so

$$\frac{1}{bcd - acm} = \frac{1}{\lambda(\lambda^2 - m\lambda - ac)}$$

$$\frac{\lambda}{bcd - acm} = \frac{1}{\lambda^2 - m\lambda - ac}$$

Because λ *>1*, $\frac{1}{k} < \frac{\lambda}{k}$ for some constant *k.*

$$\frac{1}{bcd - acm} < \frac{1}{\lambda^2 - m\lambda - ac}$$

Taking the reciprocal in an inequality reverses the direction of the sign.

$$bcd - acm > \lambda^2 - m\lambda - ac$$

$$ac + bcd - acm > \lambda^2 - m\lambda$$

$$ac + bcd - acm > \lambda(\lambda - m)$$

Once again, we take the reciprocal of the inequality and reverse the sign so the following statement holds true:

$$\frac{1}{ac+bcd-acm} < \frac{1}{\lambda(\lambda\ -m)}$$

$$\frac{\lambda}{ac+bcd-acm} < \frac{1}{\lambda\ -m}$$

$$\frac{1}{ac+bcd-acm} < \frac{1}{\lambda\ -m}$$

Because $0 \le m < 1$, $\lambda\ -m$ *>0.* Thus, both sides of the following inequality are positive and the proof can be finished.

$$ac+bcd-acm > \lambda\ -m$$

$$ac+m+bcd-acm > \lambda\ > 1$$

Therefore, it has been shown that if $\lambda > 1$ then $R > 1$.

Thus, if the population is increasing, then the net reproduction rate is greater than one.

In a modified Leslie matrix, we have proven that if the population is growing, indicated by a dominant eigenvalue greater than 1, then the net reproduction rate is also greater than 1. This was shown using inequalities stemming from the characteristic population.

Therefore, it can be said that the net reproduction rate is greater than one if and only if the population is increasing. In other words, $R > 1$ iff $\lambda > 1$.

For the following proofs, we introduce the variable m as representing the fertility rates of the first age class. Thus, individuals can reproduce in the youngest age class.

Proof 8: If the net reproduction rate of a population is greater than one, then the population is increasing. In other words, if $R > 1$, then $\lambda > 1$.

Suppose we are given a Leslie Matrix

$$A = \begin{bmatrix} m & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} \qquad \text{where } a, b > 0 \text{ and } 0 \le c, d, m \le 1$$

The net reproduction rate is $R = ac + bcd + m > 1$.

Based on the conditions of the Leslie matrix, $ac > 0$ and $bcd > 0$.

Let $f(\lambda) = -\lambda^3 + m\lambda^2 + ac\lambda + bcd$

Let $g(\lambda) = -\lambda^3 + m\lambda^2 + ac\lambda$

Thus, $f(\lambda) = g(\lambda) + bcd$

The function $f(\lambda)$ is decreasing because the $\lim f(\lambda)$ as $\lambda \to \infty$ is $-\infty$

$$\lim f(\lambda \to \infty) = -\infty^3 + m\infty^2 + ac\infty + bcd$$

The $-\infty^3$ is the dominant term and causes the limit to be $-\infty$

$$\lim(g(\lambda)) \to -\infty \text{ as } \lambda \to \infty$$

Case 1: $ac = 1$

We will find λ such that $g(\lambda)=0$.

$$-\lambda^3 + m\lambda^2 + ac\lambda = 0$$

$$-\lambda^3 + m\lambda^2 + \lambda = 0$$

$$-\lambda(\lambda^2 - m\lambda + 1) = 0$$

$$\lambda = 0, \frac{m \pm \sqrt{m^2 + 4}}{2}$$

By the given conditions, $m > 0$

Therefore, $\lambda = \frac{m + \sqrt{m^2 + 4}}{2} > 0$

When $m = 0$, then $\lambda = 1$, and, when $m > 0$, then $\lambda > 1$

Adding bcd will cause an upward shift. In other words, *f(λ)* is an upward shift of *g(λ).* Because the function $f(\lambda)$ is decreasing, the dominant eigenvalue $\lambda \geq 1$.

Case 2: $ac > 1$

$m + ac + bcd > 1$ because $ac > 1$

$$-\lambda^3 + m\lambda^2 + ac\lambda + bcd = 0$$

$$-\lambda(\lambda^2 - m\lambda - ac) + bcd = 0$$

We will find λ such that *g(λ)=0.*

$$-\lambda(\lambda^2 - m\lambda - ac) = 0$$

$$\lambda = 0, \frac{m \pm \sqrt{m^2 + 4ac}}{2}$$

When $m = 0$, then $\lambda = \sqrt{ac}$

Because $ac > 1$, $\lambda = \sqrt{ac} > 1$ and, when $m > 0$, then $\lambda > 1$.

Adding bcd will cause an upward shift. In other words, *f(λ)* is an upward shift of *g(λ).* Because the function $f(\lambda)$ is decreasing, the dominant eigenvalue $\lambda \geq 1$.

Case 3: $ac < 1$

Note: this serves as the general case. After proving this case, we realized we did not use the fact that *ac<1*, so this also covers Case 1 and Case 2.

Let $f(\lambda) = -\lambda^3 + m\lambda^2 + ac\lambda + bcd$.

From the hypothesis *R>1*, we know that *f(1)=* $ac + bcd + m - 1 > 0$.

Because we know that the $\lim f(\lambda)$ as $\lambda \to \infty$ is $-\infty$, it can be shown that there is some Q between $(1, \infty)$ such that $-Q^3 + mQ^2 + acQ + bcd = 0$

Therefore, it has been shown that if $R > 1$ then $\lambda > 1$.

Thus, if the net reproduction rate is increasing, then the population is growing for a Leslie matrix where the first age class bears children.

In three cases, we have shown that the net reproduction rate and the dominant eigenvalue of a modified Leslie matrix are related. For *ac=1, ac>1,* and *ac<1*, when the net reproduction rate is greater than 1, then the dominant eigenvalue is greater than 1 and thus the population is growing.

Proof 9: If the population is increasing, then the net reproduction rate is greater than one.

In other words, if $\lambda > 1$, then $R > 1$.

Suppose we are given a Leslie Matrix

$$A = \begin{bmatrix} m & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} \qquad \text{where } a, b > 0 \text{ and } 0 \le c, d \le 1$$

The net reproduction rate is $R = m + ac + bcd - acm$

The characteristic polynomial is

$$\det|A - \lambda I| = \det\left|\begin{bmatrix} m & a & b \\ c & 0 & 0 \\ 0 & d & 0 \end{bmatrix} - \begin{bmatrix} m-\lambda & 0 & 0 \\ 0 & \lambda & 0 \\ 0 & 0 & -\lambda \end{bmatrix}\right|$$

$$= \det\left[\begin{bmatrix} m-\lambda & a & b \\ c & -\lambda & 0 \\ 0 & d & -\lambda \end{bmatrix}\right]$$

$$= -\lambda^3 + m\lambda^2 + ac\lambda + bcd$$

Thus, we have $-\lambda^3 + m\lambda^2 + ac\lambda + bcd = 0$ for some $\lambda > 1$

Because *λ>1,* adding multiples of λ to the left side will increase its value. Thus,

$$-\lambda^3 + m\lambda^2 + ac\lambda^2 + bcd\lambda^2 > 0$$

$$-\lambda^3 + \lambda^2(m + ac + bcd) > 0$$

$$\lambda^2(m + ac + bcd) > \lambda^3$$

$m + ac + bcd > \lambda > 1$ for some *λ>1*

$$m + ac + bcd > 1$$

Therefore, it has been shown that if $\lambda > 1$ then $R > 1$.

Thus, if the population is increasing, then the net reproduction rate is greater than one.

In a modified Leslie matrix, we have proven that if the population is growing, indicated by a dominant eigenvalue greater than 1, then the net reproduction rate is also greater than 1. This was shown by comparing inequalities stemming from the characteristic equation.

Therefore, it can be said that the net reproduction rate is greater than one if and only if the population is increasing. In other words, $R > 1$ if and only if $\lambda > 1$.

DISCUSSION

Leslie matrices have a wide variety of practical applications in and of themselves. Using the Leslie matrix, as discussed above with projection and eigenvalues, it is possible for ecologists and animal behaviorists to predict how a set number of individuals in a species will grow or decline in total. With our research, we have found several shortcuts in this prediction process. We take known facts from previous rules about Leslie matrices and streamline them to make the process of predicting future growth or decline easier.

Through our research, we have successfully found associations between elements of a Leslie matrix and the future growth or decline of the corresponding population. For instance, we have discovered that knowing the survival probability of the first class and the reproductive behavior of the second class is enough to determine whether the population will grow. As long as these values, when multiplied together, are greater than or equal to 1, then the population will grow. Also, we have found connections between the net reproduction rate and the characteristic polynomial. The population is growing if and only if the net reproduction rate is greater than 1. With this information, it is not necessary to solve for the eigenvalues of a Leslie matrix in order to determine the future prospects of a population's survival.

Not only have we looked at the general *3x3* case of the Leslie matrix, but we also modified this case for incomplete data. By inserting variables into the first or last entry of the Leslie matrix, we simulated the case where there is either no information on the beginning stage(s) of a population or no information on the end stage(s) of a population, respectively. Through this, we have discovered that there are relations amongst the elements and the dominant eigenvalue of the matrix that can help predict the future growth or decline with more ease.

Conclusion

The relationships between the various elements within Leslie matrices are extremely interesting and make it much easier to determine information about a population. While there has been research in this area, the results have been general and do not give many options as to which elements are observed. With this paper, we hope to encourage more research into the area of determining relationships between elements of the Leslie matrix and future growth of a population. While the current research is an extension of previous work, there is much more to discover with future research.

Direction of Further Research

While we have had positive results in looking for connections between future growth of a population and elements of said population's Leslie matrix, there are many possibilities for research that have not been considered yet. For example, in the Leslie matrix, it would be possible to work with more incomplete data so that there would be values for the entry in the first row and first column along with values for the entry in the last row and last column. This would give a different characteristic polynomial and net reproduction rate and further research could tell whether the relationships we have discussed transfer over to this new case as well. There are also other variations of the Leslie matrix to consider, such as the migration model.

Migration Models

In order to model a more varied population, it is necessary to organize data in different ways. One such model is the migration model, which is shown in Figure 3.

$$\left[\begin{array}{ccc|ccc} 0 & a & b & 0 & 0 & 0 \\ c & 0 & 0 & r & 0 & 0 \\ 0 & d & 0 & 0 & s & 0 \\ \hline 0 & 0 & 0 & 0 & f & g \\ m & 0 & 0 & h & 0 & 0 \\ 0 & n & 0 & 0 & j & 0 \end{array}\right]$$

Figure 3: Migration Model

The upper left quadrant is the Leslie matrix representative of population 1 and the lower right quadrant is the Leslie matrix describing the second population. The two remaining quadrants are used to show the migration patterns between these two populations (Marland, 2008, p. 90). The entire matrix is read counterclockwise to find the migration patterns. For example, the percentage of the first age class from population 1 that migrates into the second age class of population 2 is *m.* It is important to note when using this model, however, that space in the matrix does not necessarily mean death but that parts of the population may have migrated (90). Lastly, the dominant eigenvalue is found by computing the eigenvalues for both Leslie matrices separately and taking the maximum (p. 90).There are restrictions currently for finding the dominant eigenvalue, such as that one must go through the process of finding the eigenvalue for both Leslie matrices. Also, how do eigenvalues and growth change for populations with only one way migration instead of both ways? Further research could specify certain migration patterns that result in future growth as well as which age class' reproduction behaviors might affect the future of the population.

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