The Leslie Matrix Model For Age-Structured Populations

Kellee Williams

Northern Arizona University
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REU
Advisor: Professor Terence Blows

Introduction

Attempts are currently being made by mathematicians and biologists to produce satisfactory models of populations that also consider the age of the organisms being studied.
One such model that accommodates the use of age analysis for populations is the Leslie matrix model. In dealing with these matrices, the possibilities for truncating the matrices, pooling age classes of organisms, and comparing the use of post-breeding and pre-breeding models are being considered and are the focus of this paper.

The Leslie Matrix Model

In order to make progress towards understanding these topics of study, it is first necessary to understand the matrices that are to be used. Leslie matrices are of the general form

$$\begin{pmatrix} m_1p_0 & m_2p_1 & m_3p_2 & \cdots & m_{w+1}p_w & 0 \\ p_0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & 0 & \cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & p_w & 0 \end{pmatrix} \text{ or } \begin{pmatrix} m_1p_0 & m_2p_0 & m_3p_0 & \cdots & m_{w+1}p_0 \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix}$$

as determined by the use of either a pre-breeding or a post-breeding model. In a post-breeding model the number of organisms in each age class is counted right after they have given birth while in a pre-breeding model, the count is taken right before the organisms have produced their offspring. Leslie matrices are square and have positive, real entries. The m_i's represent the *maternity rates* of the organisms in a particular age class. These maternity rates are the average number of female offspring produced by a female in that age class. The p_i's in the matrix refer to the probability that an individual from a particular age class survives to the next age class. For example, p_0 is interpreted as the probability that a newborn survives to the age class of organisms that are one year old. This probability of survival is often called *survivorship*. It should be noted that while the p_i's range between 0 and 1, the m_i's do not have this restriction.

The differences noted in the entries in the post-breeding and pre-breeding matrices are a result of the time at which the headcount is taken. In the post-breeding model, because the count is performed right after the young are produced, the probability of a newborn, one-year-old, two-year-old, etc. surviving until the next count is taken is expressed as p_0, p_1, p_2, etc. However, in the pre-breeding model, because the organisms are counted at the end of that particular age class rather than at the beginning right after having entered the age class, the newborns, one-year-olds, two-year-olds etc. have a survivorship of p_1, p_2, p_3, etc. because, for example, in a very short period of time the newborns will be living in the one-year old class although they will not be counted as this age until right before they turn two. The fecundities expressed in the top row of both matrices is a product of the probability that an organism in that age class will survive to be counted in the next one, the number of offspring it will have and the probability that those offspring survive to be counted. For the post-breeding model the survivorship of the individuals of that age is given by p_0, p_1, p_2, etc. since they are counted right as they enter that age class and have the whole age class to survive through before being counted next. Then the number of offspring produced is accounted for, but the survivorship of the newborns at the different stages in this model is 1 since they are counted right after birth and so have a very brief time to survive before the counting occurs. In the pre-breeding model, the survivorship of the individuals is 1 since they are counted right before crossing over to the next age class and so have only a brief time to survive before being in the next age class. That leaves only the number of offspring produced and the probability that they survive, which is p_0 each time.

The Leslie matrix is considered a projection matrix in that it allows one to calculate the number of organisms in the different age classes for next year (time t+1) given the Leslie matrix and the population vector at time t in this way:

$$\underline{N}_{t+1} = L\underline{N}_t$$

where $\mathbf{N}_{t+1} = \begin{pmatrix} N_{t+1}^0 \\ N_{t+1}^1 \\ N_{t+1}^2 \\ \cdots \\ N_{t+1}^w \end{pmatrix}$ and $\mathbf{N}_t = \begin{pmatrix} N_t^0 \\ N_t^1 \\ N_t^2 \\ \cdots \\ N_t^w \end{pmatrix}$. When the post-breeding model is examined, it is seen

that the number of organisms in next year's age classes, one-year olds and beyond, is given by the following set of equations:

$$N_{t+1}^1 = p_0 N_t^0$$
$$N_{t+1}^2 = p_1 N_t^1$$
$$N_{t+1}^3 = p_2 N_t^2$$
$$\vdots$$
$$N_{t+1}^w = p_{w-1} N_t^{w-1}$$

Calculating the number of newborns next year is slightly more complicated but looks like

$$N_{t+1}^0 = m_1 N_{t+1}^1 + m_2 N_{t+1}^2 + \ldots + m_w N_{t+1}^w$$
$$= m_1 p_0 N_t^0 + m_2 p_1 N_t^1 + \ldots + m_w p_{w-1} N_t^{w-1}$$

Several important values can be calculated from the Leslie matrix. The characteristic equation of the matrix yields several eigenvalues. The largest, positive eigenvalue found is called the *Perron root*, λ, and is significant because this number represents the *stable growth rate* for the population. The stable growth rate is the rate at which the population is increasing when it converges to the carrying capacity. The right eigenvector associated with the Perron root is called the *stable age of distribution.* When scaled to 1, the components of this vector yield the percentage of individuals in each age class at the time when the stable growth rate is achieved. The left eigenvector of the Perron root is called the *reproductive value* and provides the relative contributions of organisms in each age class to the future population.

Two important matrices can be derived from the Leslie matrix, a matrix of sensitivities and one of elasticities. *Sensitivity* provides a means of determining how the stable growth rate changes depending upon changes in the components of the Leslie matrix and *elasticity* exhibits the

Age Class Truncation

Perhaps one of the simplest concerns to address is the truncation of a Leslie matrix that is the result of the elimination of the last column of all zeros and the last row of the matrix.

Theorem 1: *Let* A *be the* $(n+1)\text{x}(n+1)$ *matrix* $A=\begin{pmatrix} b_1 & b_2 & b_3 & \dots & b_n & 0 \\ p_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & p_2 & 0 & \dots & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_n & 0 \end{pmatrix}$.

Then A *can be reduced to the matrix* $B=\begin{pmatrix} b_1 & b_2 & b_3 & \dots & b_n \\ p_1 & 0 & 0 & \dots & 0 \\ 0 & p_2 & 0 & \dots & 0 \\ 0 & 0 & p_3 & \dots & 0 \\ 0 & 0 & 0 & \dots & 0 \end{pmatrix}$ *so that the stable growth rate remains the same and the stable age distribution is the same except for the last term, which is missing.*

Proof: Examining the determinant of A it is seen that

$$|A| = \begin{vmatrix} b_1-\lambda & b_2 & b_3 & \dots & b_n & 0 \\ p_1 & -\lambda & 0 & \dots & 0 & 0 \\ 0 & p_2 & -\lambda & \dots & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & 0 & -\lambda \end{vmatrix} = -\lambda \begin{vmatrix} b_1-\lambda & b_2 & b_3 & \dots & b_n \\ p_1 & -\lambda & 0 & \dots & 0 \\ 0 & p_2 & -\lambda & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & -\lambda \end{vmatrix}$$

Now $\lambda = 0$ is not the Perron root of A since it is not of positive value. Thus the Perron root is given by the characteristic equation of this smaller determinant. The determinant of B is

$$|B| = \begin{vmatrix} b_1-\lambda & b_2 & b_3 & \dots & b_n \\ p_1 & -\lambda & 0 & \dots & 0 \\ 0 & p_2 & -\lambda & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & -\lambda \end{vmatrix}$$ which will yield the same Perron root as A, so the stable

growth rates of A and of B are the same.
Let λ'be the Perron root of A and of B. Then

$$\begin{pmatrix} b_1-\lambda' & b_2 & b_3 & \dots & b_{n-1} & b_n & 0 \\ p_1 & -\lambda' & 0 & \dots & 0 & 0 & 0 \\ 0 & p_2 & -\lambda' & \dots & 0 & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_{n-1} & -\lambda' & 0 \\ 0 & 0 & 0 & \dots & 0 & p_n & -\lambda' \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ \dots \\ x_{n-1} \\ x_n \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ \dots \\ 0 \\ 0 \end{pmatrix}$$

will provide the stable age distribution vector **x** of A. Now all of the first n - 1 elements of the eigenvector can be found without making use of the n^{th} row's equation since there are $n-1$ equations and $n-1$ unknowns as a result of the zeros in the last column. Then the n^{th} element of the eigenvector can be found in terms of the element above it. Therefore the last row of A has no effect on the first $n-1$ elements of the eigenvector. Note that to find the stable age distribution vector **y** of B the same $n-1$ set of equations are used as when finding **x**.

$$\begin{pmatrix} b_1-\lambda' & b_2 & b_3 & \dots & b_{n-1} & b_n \\ p_1 & -\lambda' & 0 & \dots & 0 & 0 \\ 0 & p_2 & -\lambda' & \dots & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_{n-1} & -\lambda' \end{pmatrix} \begin{pmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ \dots \\ y_{n-1} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ \dots \\ 0 \end{pmatrix}$$

Thus the stable age distributions of A and B only differ by the presence of the n^{th} element in the one for A.

Another potential condition to examine is the case where after a certain age, the adult classes of the population no longer breed, creating a Leslie matrix model with zeros along the top row after the last breeding age is listed. It may be possible to truncate such a matrix so that the final entry in the top row is the fecundity of the last reproductive class.

Theorem 2*: Let* A *be the matrix*

$$A = \begin{pmatrix} b_1 & b_2 & \dots & b_k & 0 & \dots & 0 & 0 \\ p_1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & p_k & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{k+1} & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \dots & p_{k+n} & 0 \end{pmatrix}.$$

Then the matrix

$$B = \begin{pmatrix} b_1 & b_2 & \dots & b_{k-1} & b_k \\ p_1 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & p_{k-1} & 0 \end{pmatrix}$$

has the same stable growth rate and almost the same stable age distribution as A, in that all of the vector components are the same except for the $n+1$ last components which are absent.

Proof: Using Theorem 1, matrix A can be reduced as follows:

$$\begin{pmatrix} b_1 & b_2 & \dots & b_k & 0 & \dots & 0 & 0 \\ p_1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & p_k & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{k+1} & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \dots & p_{k+n} & 0 \end{pmatrix} \approx \begin{pmatrix} b_1 & b_2 & \dots & b_k & 0 & \dots & 0 & 0 \\ p_1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & p_k & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{k+1} & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \dots & p_{k+n-1} & 0 \end{pmatrix}$$

$$\approx \begin{pmatrix} b_1 & b_2 & \dots & b_k & 0 & \dots & 0 & 0 \\ p_1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & p_k & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & p_{k+1} & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & \dots & p_{k+n-2} & 0 \end{pmatrix}$$

This process of eliminating one column and row at a time to receive an equivalent matrix can be performed repeatedly until the matrix $\begin{pmatrix} b_1 & b_2 & \ldots & b_{k-1} & b_k \\ p_1 & 0 & \ldots & 0 & 0 \\ 0 & p_2 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & \ldots & p_{k-1} & 0 \end{pmatrix}$ is reached.

By Theorem 1, at each stage of simplification the Perron roots of the comparative matrices are the same and the stable age distributions differ only by the last element in the vector of the larger matrix. Thus when the final matrix is derived, the Perron roots are the same and the eigenvectors of A and B are the same except for the additional elements found in A.

It should be noted that the motivation for truncating matrices and pooling age classes is to produce smaller matrices with which to work. Some species are quite long-lived and may be represented by unwieldy matrices that are more complicated to analyze. The possibility of reducing the size of the matrices at the cost of some small error due to made approximations is enticing.

Age Class Pooling

The next path of investigation leads to the discovery of a technique to pool age classes that exhibit the same fecundity and survivorship values into one class so that the matrix

$\begin{pmatrix} b_0 & b & b & b & \ldots & 0 \\ p_0 & 0 & 0 & 0 & \ldots & 0 \\ 0 & p & 0 & 0 & \ldots & 0 \\ 0 & 0 & p & 0 & \ldots & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & 0 & p & 0 \end{pmatrix}$ is approximated by $\begin{pmatrix} b_0 & b' \\ p_0 & p' \end{pmatrix}$ where $b_j = m_{j+1}p_j$.

Consider the following equation for the number of newborns next year:

$$\begin{aligned} N_{t+1}^{0} &= b_0N_0 + bN_1 + bN_2 + \ldots + bN_{w-1} \\ &= b_0N_0 + b(N_1 + N_2 + \ldots + N_{w-1}) \\ &= b_0N_0 + b'(N_1 + N_2 + N_3 + \ldots) \end{aligned}$$

Then $\quad b' = \dfrac{b(N_1 + N_2 + \ldots + N_{w-1})}{N_1 + N_2 + N_3 + \ldots}$.

We can write $N_2 = pN_1$

$$N_3 = pN_2 = p^2N_1$$
$$N_4 = pN$$
$$\vdots$$
$$N_{w\text{-}1} = p^{w\text{-}2}N_{w\text{-}2}$$

so we have $N_1 + N_2 + \ldots + N_{w\text{-}1} = N_1 + pN_1 + p^2N_1 + \ldots + p^{w\text{-}2}N_1$
$= (1 + p + p^2 + \ldots + p^{w\text{-}2})N_1$

and $N_1 + N_2 + N_3 + \ldots = (1 + p + p^2 + \ldots)N_1 = \left(\dfrac{1}{1-p}\right)N_1.$

If we let $S = 1 + p + p^2 + \ldots + p^{w\text{-}2}$ and $pS = p + p^2 + p^3 + \ldots + p^{w\text{-}1}$

then $pS - S = p^{w\text{-}1} - 1$ so $S = \dfrac{1-p^{w-1}}{1-p}$.

Then after substituting, $b' = b\dfrac{1}{1-p^{w-1}}$.

Similarly, to find the new p value, let $b = pm$ in the newborn equation

$$N_{t+1}^{\ 0} = b_0N_0 + pm(N_1 + N_2 + \ldots + N_{w\text{-}1}) = b_0N_0 + p'm(N_1 + N_2 + \ldots)$$

Then $p' = p\left(\dfrac{N_1 + N_2 + \ldots N_{w-1}}{N_1 + N_2 + \ldots}\right) = p\left(\dfrac{1}{1-p^{w-1}}\right)$

Now the new b and p values have been calculated, it remains to be seen if they will provide a somewhat close approximate to the original matrix Perron root. The numerical examples ahead show the original matrix, the pooled matrix using the above method, and a truncated matrix that uses the b and p given in the matrix without any modifications along with the error found in the calculated Perron roots.

Example 1

$$\begin{pmatrix} .521 & .834 & .834 & .834 & .834 & 0 \\ .27 & 0 & 0 & 0 & 0 & 0 \\ 0 & .62 & 0 & 0 & 0 & 0 \\ 0 & 0 & .62 & 0 & 0 & 0 \\ 0 & 0 & 0 & .62 & 0 & 0 \\ 0 & 0 & 0 & 0 & .62 & 0 \end{pmatrix} \qquad \lambda = 1.0133$$

$$\begin{pmatrix} .521 & .634 \\ .27 & .4712 \end{pmatrix} \qquad \lambda = 0.910588 \qquad \text{Error: } 11\%$$

$$\begin{pmatrix} .521 & .834 \\ .27 & .62 \end{pmatrix} \qquad \lambda = 1.04761 \qquad \text{Error: } 3.4\%$$

Example 2

$$\begin{pmatrix} .36 & .714 & .714 & 0 \\ .698 & 0 & 0 & 0 \\ 0 & .416 & 0 & 0 \\ 0 & 0 & .416 & 0 \end{pmatrix} \qquad \lambda = 1.03503$$

$$\begin{pmatrix} .36 & .543 \\ .698 & .316 \end{pmatrix} \qquad \lambda = 0.954034 \qquad \text{Error: } 8\%$$

$$\begin{pmatrix} .36 & .714 \\ .698 & .416 \end{pmatrix} \qquad \lambda = 1.09451 \qquad \text{Error: } 5.7\%$$

Example 3

$$\begin{pmatrix} .836 & .522 & .522 & .522 & .522 & .522 & .522 & 0 \\ .93 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & .381 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & .381 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & .381 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & .381 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & .381 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & .381 & 0 \end{pmatrix} \qquad \lambda = 1.34128$$

$$\begin{pmatrix} .836 & .397 \\ .93 & .29 \end{pmatrix} \qquad \lambda = 1.22914 \qquad \text{Error: } 9\%$$

$$\begin{pmatrix} .836 & .522 \\ .93 & .381 \end{pmatrix} \qquad \lambda = 1.34145 \qquad \text{Error: } 0.01\%$$

It seems from these examples that pooling is less effective than truncation as it is providing a greater error.

Two outstanding investigations involve the pooling of adult classes in which the fecundities and survivorships differ across age classes and also the pooling of non-breeding juvenile classes. The first problem seems possible. A similar approach to the last is currently in progress and the pooling of various numbers of age classes has been attempted. Once a working modification method has been found, the Perron roots will be compared and the errors established. Attempts at creating a modifying equation for the pooling of juveniles have not yielded results and is a difficult problem to pursue and may not even be possible.

Pre-Breeding and Post-Breeding Model Comparisons

It is now desirable to look at post-breeding and pre-breeding matrices to determine if the pre-breeding matrix really does model the post-breeding matrix. Before proving some general cases, let's examine a more simple example. Consider these post-breeding and pre-breeding matrices:

$$\begin{pmatrix} 0 & m_2 p_1 & 0 \\ p_0 & 0 & 0 \\ 0 & p_1 & 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} 0 & m_2 p_0 \\ p_1 & 0 \end{pmatrix}.$$

Calculating the Perron roots for these matrices shows them to be the same, namely

$$\lambda = \sqrt{p_0 p_1 m_2}$$

The respective stable age distributions are

$$\mathbf{v} = \begin{pmatrix} x \\ \dfrac{\sqrt{p_0 p_1 m_2}}{p_1 m_2} x \\ \dfrac{1}{m_2} x \end{pmatrix} \quad \text{and} \quad \mathbf{v}' = \begin{pmatrix} x \\ \dfrac{\sqrt{p_0 p_1 m_2}}{p_0 m_2} x \end{pmatrix}$$

At first glance, the two stable age distributions appear to be close to equal in their second components, but this creates a problem in explaining why they only differ slightly. A more careful look reveals that in actuality, it is the first component in $\mathbf{v}'$ that is equal to the second component in $\mathbf{v}$ and the second component in $\mathbf{v}'$ that is equal to the third component in $\mathbf{v}$. This is due to the fact that the organisms being counted as newborns in the pre-breeding model are counted at the end of their time as newborns and right before they breed and enter the one-year-old category. This makes them closer in age to the one-year-old organisms in the post-breeding model since they have been sampled right after they entered this age class. Similarly, the one-year-olds in the pre-breeding model are compared to the two-year-olds in the post-breeding model. This can be checked by substituting $\dfrac{\sqrt{p_0 p_1 m_2}}{p_1 m_2} x$ for x in the second component of the pre-breeding matrix. The result is $\dfrac{1}{m_2} x$, which is the number of two-year-olds in the post breeding model.

An interesting relationship is apparent in the elasticity matrices for the post-breeding and pre-breeding models. To calculate the sensitivities and elasticities of some of these matrices, it is necessary to use the following equations:

$$\text{Sensitivity } (s_{ij}) = \frac{v_i x_j}{\mathbf{vx}} \qquad\qquad \text{Elasticity } (e_{ij}) = \frac{s_{ij}L_{ij}}{\lambda}$$

Where **vx** is the product of the reproductive value and the stable age distribution vectors, v_i and x_j are components of these two vectors, and L_{ij} is a component in the Leslie matrix itself. Now contemplate these examples of elasticity matrices for post-breeding and pre-breeding models.

Example 1

Original Matrix (Post)

$$\begin{pmatrix} 0 & 2.3 & 0 \\ .26 & 0 & 0 \\ 0 & .44 & 0 \end{pmatrix}$$

Elasticity Matrix

$$\begin{pmatrix} 0 & .5 & 0 \\ .499999 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

Original Matrix (Pre)

$$\begin{pmatrix} 0 & 1.35909 \\ .44 & 0 \end{pmatrix}$$

Elasticity Matrix

$$\begin{pmatrix} 0 & .500001 \\ .499999 & 0 \end{pmatrix}$$

Example 2

Original Matrix (Post)

$$\begin{pmatrix} 0 & 1.755 & 0 \\ .43 & 0 & 0 \\ 0 & .65 & 0 \end{pmatrix}$$

Elasticity Matrix

$$\begin{pmatrix} 0 & .5 & 0 \\ .5 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

Original Matrix (Pre)

$$\begin{pmatrix} 0 & 1.161 \\ .65 & 0 \end{pmatrix}$$

Elasticity Matrix

$$\begin{pmatrix} 0 & .5 \\ .5 & 0 \end{pmatrix}$$

Looking at these two examples it is interesting to see that the pre-breeding elasticity matrices appear to be truncated versions of the post-breeding elasticity matrices. This pattern still needs to be examined more closely and proved for pre-breeding and post-breeding models in general.

A connection between the pre-breeding and post-breeding Leslie matrix models has been illustrated by the above discussions. Let us now look at the general forms of these models to convince ourselves further of their relationship.

Theorem 3: *A post-breeding matrix* A *of the form*
$$\begin{pmatrix} m_1p_0 & m_2p_1 & m_3p_2 & \dots & m_{k+1}p_k & 0 \\ p_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_k & 0 \end{pmatrix}$$

can be modeled by a pre-breeding matrix B *of the form*
$$\begin{pmatrix} m_1p_0 & m_2p_0 & \dots & m_kp_0 & m_{k+1}p_0 \\ p_1 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & p_k & 0 \end{pmatrix}$$

when compared over a long enough period of time.

Proof: Let us proceed by using math induction. Let $k = n$. Then by Theorem 1,

$$\begin{pmatrix} m_1p_0 & m_2p_1 & m_3p_2 & \dots & m_{n+1}p_n & 0 \\ p_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_n & 0 \end{pmatrix} \approx \begin{pmatrix} m_1p_0 & m_2p_1 & m_3p_2 & \dots & m_np_{n-1} & m_{n+1}p_n \\ p_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_{n-1} & 0 \end{pmatrix}$$

whose characteristic equation yields the Perron root. Assume that the characteristic equation is given by

$$(-1)^{n+1}[\lambda^{n+1} - p_0m_1\lambda^n - p_0p_1m_2\lambda^{n-1} - p_0p_1p_2m_3\lambda^{n-2} - \dots - p_0p_1 \dots p_nm_{n+1}] = 0$$

Now let $k = n+1$ and examine the matrix

$$\begin{pmatrix} m_1p_0 & m_2p_1 & m_3p_2 & \dots & m_{n+1}p_n & m_{n+2}p_{n+1} & 0 \\ p_0 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & p_1 & 0 & \dots & 0 & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & 0 & p_{n+1} & 0 \end{pmatrix} \approx \begin{pmatrix} m_1p_0 & m_2p_1 & m_3p_2 & \dots & m_{n+1}p_n & m_{n+2}p_{n+1} \\ p_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_n & 0 \end{pmatrix}$$

whose characteristic equation is found to be

$$\begin{vmatrix} m_1p_0-\lambda & m_2p_1 & m_3p_2 & \dots & m_{n+1}p_n & m_{n+2}p_{n+1} \\ p_0 & -\lambda & 0 & \dots & 0 & 0 \\ 0 & p_1 & -\lambda & \dots & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & & -\lambda \end{vmatrix}=0$$

$$\Rightarrow -\lambda\begin{vmatrix} m_1p_0-\lambda & m_2p_1 & m_3p_2 & \dots & m_{n+1}p_n \\ p_0 & -\lambda & 0 & \dots & 0 \\ 0 & p_1 & -\lambda & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & -\lambda \end{vmatrix} - (-1)^{n+2}m_{n+2}p_{n+1}\begin{vmatrix} p_0 & -\lambda & 0 & 0 & \dots & 0 \\ 0 & p_1 & -\lambda & 0 & \dots & 0 \\ 0 & 0 & p_2 & -\lambda & \dots & 0 \\ 0 & 0 & 0 & p_3 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & 0 & \dots & p_n \end{vmatrix}=0$$

$$\Rightarrow -\lambda(-1)^{n+1}[\lambda^{n+1} - p_0m_1\lambda^n - p_0p_1m_2\lambda^{n-1} - p_0p_1p_2m_3\lambda^{n-2} - \dots - p_0p_1\dots p_nm_{n+1}]$$
$$- (-1)^{n+2}m_{n+2}p_{n+1}p_0\begin{vmatrix} p_1 & -\lambda & 0 & \dots & 0 \\ 0 & p_2 & -\lambda & \dots & 0 \\ 0 & 0 & p_3 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_n \end{vmatrix}=0$$

$$\Rightarrow (-1)^{n+2}[\lambda^{n+2} - p_0m_1\lambda^{n+1} - p_0p_1m_2\lambda^n - p_0p_1p_2m_3\lambda^{n-1} - \dots - p_0p_1\dots p_nm_{n+1}\lambda]$$
$$- (-1)^{n+2}m_{n+2}p_{n+1}p_0p_1p_2\dots p_n = 0$$

$$\Rightarrow (-1)^{n+2}[\lambda^{n+2} - p_0m_1\lambda^{n+1} - p_0p_1m_2\lambda^n - p_0p_1p_2m_3\lambda^{n-1} - \dots - p_0p_1\dots p_nm_{n+1}\lambda - p_0p_1p_2\dots p_np_{n+1}m_{n+2}] = 0$$

Thus for all $k = n$, the Perron root of A is given by

$$(-1)^{k+1}[\lambda^{k+1} - p_0m_1\lambda^k - p_0p_1m_2\lambda^{k-1} - p_0p_1p_2m_3\lambda^{k-2} - \dots - p_0p_1\dots p_km_{k+1}] = 0$$

Allow $k = n$ and assume the characteristic equation for $\begin{pmatrix} m_1p_0 & m_2p_0 & \dots & m_np_0 & m_{n+1}p_0 \\ p_1 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & p_n & 0 \end{pmatrix}$ is

$$(-1)^{n+1}[\lambda^{n+1} - p_0m_1\lambda^n - p_0p_1m_2\lambda^{n-1} - p_0p_1p_2m_3\lambda^{n-2} - \dots - p_0p_1\dots p_nm_{n+1}] = 0$$

Then the characteristic equation for $\begin{pmatrix} m_1p_0 & m_2p_0 & m_3p_0 & \ldots & m_{n+1}p_0 & m_{n+2}p_0 \\ p_1 & 0 & 0 & \ldots & 0 & 0 \\ 0 & p_2 & 0 & \ldots & 0 & 0 \\ 0 & 0 & p_3 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_{n+1} & 0 \end{pmatrix}$ is

$$\begin{vmatrix} m_1p_0-\lambda & m_2p_0 & m_3p_0 & \ldots & m_{n+1}p_0 & m_{n+2}p_0 \\ p_1 & -\lambda & 0 & \ldots & 0 & 0 \\ 0 & p_2 & -\lambda & \ldots & 0 & 0 \\ 0 & 0 & p_3 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_{n+1} & -\lambda \end{vmatrix} = 0$$

$$\Rightarrow -\lambda \begin{vmatrix} m_1p_0-\lambda & m_2p_0 & m_3p_0 & \ldots & m_np_0 & m_{n+1}p_0 \\ p_1 & -\lambda & 0 & \ldots & 0 & 0 \\ 0 & p_2 & -\lambda & \ldots & 0 & 0 \\ 0 & 0 & p_3 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_n & -\lambda \end{vmatrix} - (-1)^{n+2} m_{n+2}p_0 \begin{vmatrix} p_1 & -\lambda & 0 & \ldots & 0 \\ 0 & p_2 & -\lambda & \ldots & 0 \\ 0 & 0 & p_3 & \ldots & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_{n+1} \end{vmatrix} = 0$$

$$\Rightarrow -\lambda(-1)^{n+1}[\lambda^{n+1} - p_0m_1\lambda^n - p_0p_1m_2\lambda^{n-1} - p_0p_1p_2m_3\lambda^{n-2} - \ldots - p_0p_1\ldots p_nm_{n+1}]$$

$$- (-1)^{n+2} m_{n+2}p_0p_1 \begin{vmatrix} p_2 & -\lambda & 0 & \ldots & 0 \\ 0 & p_3 & -\lambda & \ldots & 0 \\ 0 & 0 & p_4 & \ldots & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_{n+1} \end{vmatrix} = 0$$

$$\Rightarrow (-1)^{n+2}[\lambda^{n+2} - p_0m_1\lambda^{n+1} - p_0p_1m_2\lambda^n - p_0p_1p_2m_3\lambda^{n-1} - \ldots - p_0p_1\ldots p_nm_{n+1}\lambda] - (-1)^{n+2} m_{n+2}p_0p_1\ldots p_{n+1} = 0$$

$$\Rightarrow (-1)^{n+2}[\lambda^{n+2} - p_0m_1\lambda^{n+1} - p_0p_1m_2\lambda^n - p_0p_1p_2m_3\lambda^{n-1} - \ldots - p_0p_1\ldots p_nm_{n+1}\lambda - p_0p_1\ldots p_{n+1}m_{n+2}] = 0$$

Thus for all $k = n$ the Perron root of B can be found from the equation

$$(-1)^{k+1}[\lambda^{k+1} - p_0m_1\lambda^k - p_0p_1m_2\lambda^{k-1} - p_0p_1p_2m_3\lambda^{k-2} - \ldots - p_0p_1\ldots p_km_{k+1}] = 0$$

Since both matrices A and B have the same characteristic equation, they contain the same Perron root. Therefore for long-term use of these matrices, matrix B may be used to model matrix A.

Theorem 4: *A post-breeding matrix of the form* $A = \begin{pmatrix} m_1 p_0 & m_2 p_1 & m_3 p_2 & \dots & m p_k & m s \\ p_o & 0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_k & s \end{pmatrix}$ *can*

be modeled by a pre-breeding matrix of the form $B = \begin{pmatrix} m_1 p_0 & m_2 p_0 & \dots & m p_0 & m p_0 \\ p_1 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & p_k & s \end{pmatrix}$

where m represents a maternity rate that is the same for the last two age classes and s is a pooled probability of survival resulting from the truncation of several adult age classes that continue to have the same probability of coming back the next year.

I will prove a more specialized case of this Theorem where all of the maternity rates past the first age class are the same.

Proof: Consider the two following matrices:

$$P = \begin{pmatrix} m_1 p_0 & m p_1 & m p_2 & \dots & m p_k & m s \\ p_o & 0 & 0 & \dots & 0 & 0 \\ 0 & p_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_k & s \end{pmatrix} \text{ and } P' = \begin{pmatrix} m_1 p_0 & m_2 p_0 & \dots & m p_0 & m p_0 \\ p_1 & 0 & \dots & 0 & 0 \\ 0 & p_2 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & p_k & s \end{pmatrix}.$$

We proceed with an inductive proof.

Assume that for $k = n$ the characteristic equation of P is

$$-\lambda[(-1)^{n+1}[\lambda^{n+1} - (p_0 m_1 + s)\lambda^n - (p_o p_1 m - p_0 m_1 s)\lambda^{n-1} - (p_0 p_1 p_2 m - p_0 p_1 m s)\lambda^{n-2} \\ - \dots - p_0 p_1 \dots p_n m + p_0 p_1 \dots p_{n-1} m s]] = 0$$

Now consider the determinant when $k = n+1$. Then

$$\begin{vmatrix} m_1p_0-\lambda & mp_1 & mp_2 & \ldots & mp_n & mp_{n+1} & ms \\ p_0 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & p_1 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & p_2 & \ldots & 0 & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_n & -\lambda & 0 \\ 0 & 0 & 0 & \ldots & 0 & p_{n+1} & s-\lambda \end{vmatrix} = 0$$

$$\Rightarrow -\begin{vmatrix} m_1p_0-\lambda & mp_1 & mp_2 & \ldots & mp_n & ms & mp_{n+1} \\ p_0 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & p_1 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & p_2 & \ldots & 0 & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_n & 0 & -\lambda \\ 0 & 0 & 0 & \ldots & 0 & s-\lambda & p_{n+1} \end{vmatrix} = 0$$

$$\Rightarrow -\begin{vmatrix} m_1p_0-\lambda & mp_1 & mp_2 & \ldots & mp_n & ms & mp_{n+1} \\ p_0 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & p_1 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & p_2 & \ldots & 0 & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_n & s-\lambda & p_{n+1}-\lambda \\ 0 & 0 & 0 & \ldots & 0 & s-\lambda & p_{n+1} \end{vmatrix} = 0$$

Expanding about the last column we get

$$\begin{aligned} &-(-\lambda[p_{n+1}[(-1)^{n+1}[\lambda^{n+1}-(p_0m_1+s)\lambda^n-(p_0p_1m-p_0m_1s)\lambda^{n-1}-\ldots-p_0p_1\ldots p_nm \\ &+p_0p_1\ldots p_{n-1}ms]]+(-1)^{n+2}mp_{n+1}[p_0p_1\ldots p_n(s-\lambda)]-(p_{n+1}-\lambda)[ms(0) \\ &+(s-\lambda)[(-1)^{n+1}(\lambda^{n+1}-p_0m_1\lambda^n-p_0p_1m\lambda^{n-1}-\ldots-p_0p_1\ldots p_nm]])=0 \end{aligned}$$

$$\begin{aligned} &\Rightarrow -((-1)^{n+1}[-p_{n+1}\lambda^{n+2}+p_{n+1}(p_0m_1+s)\lambda^{n+1}+p_{n+1}(p_0p_1m-p_0m_1s)\lambda^n \\ &+\ldots+p_0p_1\ldots p_np_{n+1}m\lambda-p_0p_1\ldots p_{n-1}p_{n+1}ms\lambda]-(-1)^{n+1}mp_{n+1}(p_0p_1\ldots p_ns-p_0p_1\ldots p_n\lambda) \\ &-(p_{n+1})(-1)^{n+1}(s\lambda^{n+1}-p_0m_1s\lambda^n-p_0p_1ms\lambda^{n-1}-\ldots-p_0p_1\ldots p_nms-\lambda^{n+2}+p_0m_1\lambda^{n+1} \\ &+p_0p_1m\lambda^n+\ldots+p_0p_1\ldots p_nm\lambda))=0 \end{aligned}$$

$$\Rightarrow -((-1)^{n+1}[-p_{n+1}\lambda^{n+2} + p_{n+1}(p_0m_1 + s)\lambda^{n+1} + p_{n+1}(p_0p_1m - p_0m_1s)\lambda^n$$
$$+ \ldots + p_0p_1\ldots p_np_{n+1}m\lambda - p_0p_1\ldots p_{n-1}p_{n+1}ms\lambda] - (-1)^{n+1}[p_0p_1\ldots p_np_{n+1}ms - p_0p_1\ldots p_np_{n+1}m\lambda]$$
$$-(-1)^{n+1}(p_{n+1}s\lambda^{n+1} - p_{n+1}p_0m_1s\lambda^n - p_{n+1}p_0p_1ms\lambda^{n-1} - \ldots - p_{n+1}p_0p_1\ldots p_nms - p_{n+1}\lambda^{n+2} + p_{n+1}p_0m_1\lambda^{n+1}$$
$$+ p_{n+1}p_0p_1m\lambda^n + \ldots + p_{n+1}p_0p_1\ldots p_nm\lambda - s\lambda^{n+2} + p_0m_1s\lambda^{n+1} + p_0p_1ms\lambda^n + \ldots + p_0p_1\ldots p_nms\lambda + \lambda^{n+3} - p_0m_1\lambda^{n+2}$$
$$- p_0p_1m\lambda^{n+1} - \ldots - p_0p_1\ldots p_{n-1}m\lambda^2]) = 0$$

$$\Rightarrow -((-1)^{n+1}[-p_{n+1}\lambda^{n+2} + p_0p_{n+1}m_1\lambda^{n+1} + p_{k+1}s\lambda^{n+1} + p_0p_1p_{n+1}m\lambda^n - p_0p_{n+1}m_1s\lambda^n + \ldots + p_0p_1\ldots p_{n+1}m\lambda$$
$$- p_0p_1\ldots p_{n-1}p_{n+1}ms\lambda - p_0p_1\ldots p_{n+1}ms + p_0p_1\ldots p_{n+1}m\lambda - p_{n+1}s\lambda^{n+1} + p_0p_{k+1}m_1s\lambda^n + p_0p_1p_{n+1}ms\lambda^{n-1}$$
$$+ \ldots + p_0p_1\ldots p_{n+1}ms + p_{n+1}\lambda^{n+2} - p_0p_{n+1}m_1\lambda^{n+1} - p_0p_1p_{n+1}m\lambda^n - \ldots - p_0p_1\ldots p_{n+1}m\lambda + s\lambda^{n+2}$$
$$- p_0m_1s\lambda^{n+1} - p_0p_1ms\lambda^n - \ldots - p_0p_1\ldots p_nms\lambda - \lambda^{n+3} + p_0m_1\lambda^{n+2} + p_0p_1m\lambda^{n+1} + \ldots + p_0p_1\ldots p_nm\lambda^2]) = 0$$

$$\Rightarrow -(-\lambda(-1)^{n+1}[\lambda^{n+2} - p_0m_1\lambda^{n+1} - s\lambda^{n+1} - p_0p_1m\lambda^n + p_0m_1s\lambda^n - \ldots - p_0p_1\ldots p_{n+1}m + p_0p_1\ldots p_{n+1}ms]) = 0$$

$$\Rightarrow -\lambda[(-1)^{n+2}[\lambda^{n+2} - (p_0m_1 + s)\lambda^{n+1} - (p_0p_1m - p_0m_1s)\lambda^n - \ldots - p_0p_1\ldots p_{n+1}m + p_0p_1\ldots p_nms]] = 0$$

Since the Perron root of a matrix is positive, for all $k = n$, the Perron root for P can be found with

$$(-1)^{n+1}[\lambda^{n+1} - (p_0m_1 + s)\lambda^n - (p_0p_1m - p_0m_1s)\lambda^{n-1} - (p_0p_1p_2m - p_0p_1ms)\lambda^{n-2}$$
$$- \ldots - p_0p_1\ldots p_nm + p_0p_1\ldots p_{n-1}ms] = 0$$

It remains to be shown that the Perron root of P' is given by the same characteristic equation. So assume that the characteristic equation of P' for $k = n$ is given by

$$(-1)^{n+1}[\lambda^{n+1} - (p_0m_1 + s)\lambda^n - (p_0p_1m - p_0m_1s)\lambda^{n-1} - (p_0p_1p_2m - p_0p_1ms)\lambda^{n-2}$$
$$- \ldots - p_0p_1\ldots p_nm + p_0p_1\ldots p_{n-1}ms] = 0$$

and consider the determinant of P' when $k = n+1$. Then

$$\begin{vmatrix} m_1p_0 - \lambda & mp_0 & mp_0 & \ldots & mp_0 & mp_0 & mp_0 \\ p_1 & -\lambda & 0 & \ldots & 0 & 0 & 0 \\ 0 & p_2 & -\lambda & \ldots & 0 & 0 & 0 \\ 0 & 0 & p_3 & \ldots & 0 & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & 0 & \ldots & p_n & -\lambda & 0 \\ 0 & 0 & 0 & \ldots & 0 & p_{n+1} & s-\lambda \end{vmatrix} = 0$$

$$\Rightarrow -\begin{vmatrix} m_1p_0-\lambda & mp_0 & mp_0 & \dots & mp_0 & mp_0 & mp_o \\ p_1 & -\lambda & 0 & \dots & 0 & 0 & 0 \\ 0 & p_2 & -\lambda & \dots & 0 & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_n & 0 & -\lambda \\ 0 & 0 & 0 & \dots & 0 & s-\lambda & p_{n+1} \end{vmatrix} = 0$$

$$\Rightarrow -\begin{vmatrix} m_1p_0-\lambda & mp_0 & mp_0 & \dots & mp_0 & mp_0 & mp_o \\ p_1 & -\lambda & 0 & \dots & 0 & 0 & 0 \\ 0 & p_2 & -\lambda & \dots & 0 & 0 & 0 \\ 0 & 0 & p_3 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & p_n & s-\lambda & p_{n+1}-\lambda \\ 0 & 0 & 0 & \dots & 0 & s-\lambda & p_{n+1} \end{vmatrix} = 0$$

$$\Rightarrow -(p_{n+1}(-1)^{n+1}[\lambda^{n+1} - (p_0m_1 + s)\lambda^n - (p_0p_1m - p_0m_1s)\lambda^{n-1} - \dots - p_0p_1\dots p_nm + p_0p_1\dots p_{n-1}ms]$$
$$+ (-1)^{n+1}mp_0[p_1p_2\dots p_n(s-\lambda)] - (p_{n+1}-\lambda)[mp_0(0) + (s-\lambda)[(-1)^n(\lambda^n - p_0m_1\lambda^{n-1} - p_0p_1m\lambda^{n-2}$$
$$- \dots - p_0p_1\dots p_{n-1}m]]) = 0$$

$$\Rightarrow -((-1)^{n+1}[p_{n+1}\lambda^{n+1} - p_0p_{n+1}m_1\lambda^n - p_{n+1}s\lambda^n - p_0p_1p_{n+1}m\lambda^{n-1} + p_0p_{n+1}m_1s\lambda^{n-1} - \dots - p_0p_1\dots p_np_{n+1}m$$
$$+ p_0p_1\dots p_{n-1}p_{n+1}ms] + (-1)^{n+1}[p_0p_1\dots p_nms - p_0p_1\dots p_nm\lambda] + (p_{n+1}-\lambda)(-1)^{n+1}[s\lambda^n - p_0m_1s\lambda^{n-1}$$
$$- p_0p_1ms\lambda^{n-2} - \dots - p_0p_1\dots p_{n-1}ms - \lambda^{n+1} + p_0m_1\lambda^n + p_0p_1m\lambda^{n-1} + \dots + p_0p_1\dots p_{n-1}m\lambda]) = 0$$

$$\Rightarrow -((-1)^{n+1}[p_{n+1}\lambda^{n+1} - p_0p_{n+1}m_1\lambda^n - p_{n+1}s\lambda^n - p_0p_1p_{n+1}m\lambda^{n-1} + p_0p_{n+1}m_1s\lambda^{n-1} - \dots - p_0p_1\dots p_np_{n+1}m$$
$$+ p_0p_1\dots p_{n-1}p_{n+1}ms] + (-1)^{n+1}[p_0p_1\dots p_nms - p_0p_1\dots p_nm\lambda] + (-1)^{n+1}[p_{n+1}s\lambda^n - p_0p_{n+1}m_1s\lambda^{n-1}$$
$$- p_0p_1p_{n+1}ms\lambda^{n-2} - \dots - p_0p_1\dots p_{n-1}p_{n+1}ms - p_{n+1}\lambda^{n+1} + p_0p_{n+1}m_1\lambda^n + p_0p_1p_{n+1}m\lambda^{n-1}$$
$$+ \dots + p_0p_1\dots p_{n-1}p_{n+1}m\lambda - s\lambda^{n+1} + p_0m_1s\lambda^n + p_0p_1ms\lambda^{n-1} + \dots + p_0p_1\dots p_{n-1}ms\lambda + \lambda^{n+2} - p_0m_1\lambda^{n+1}$$
$$- p_0p_1m\lambda^n - \dots - p_0p_1\dots p_{n-1}m\lambda^2]) = 0$$

$$\Rightarrow -((-1)^{n+1}[p_{n+1}\lambda^{n+1} - p_0p_{n+1}m_1\lambda^n - p_{n+1}s\lambda^n - p_0p_1p_{n+1}m\lambda^{n-1} + p_0p_{n+1}m_1s\lambda^{n-1} - \dots - p_0p_1\dots p_np_{n+1}m$$
$$+ p_0p_1\dots p_{n-1}p_{n+1}ms + p_0p_1\dots p_nms - p_0p_1\dots p_nm\lambda + p_{n+1}s\lambda^n - p_0p_{n+1}m_1s\lambda^{n-1}$$
$$- p_0p_1p_{n+1}ms\lambda^{n-2} - \dots - p_0p_1\dots p_{n-1}p_{n+1}ms - p_{n+1}\lambda^{n+1} + p_0p_{n+1}m_1\lambda^n + p_0p_1p_{n+1}m\lambda^{n-1}$$
$$+ \dots + p_0p_1\dots p_{n-1}p_{n+1}m\lambda - s\lambda^{n+1} + p_0m_1s\lambda^n + p_0p_1ms\lambda^{n-1} + \dots + p_0p_1\dots p_{n-1}ms\lambda + \lambda^{n+2} - p_0m_1\lambda^{n+1}$$
$$- p_0p_1m\lambda^n - \dots - p_0p_1\dots p_{n-1}m\lambda^2]) = 0$$

$$\Rightarrow (-1)^{n+2}[\lambda^{n+2} - (p_0 m_1 + s)\lambda^{n+1} - (p_0 p_1 m - p_0 m_1 s)\lambda^{n} - (p_0 p_1 p_2 m - p_0 p_1 m s)\lambda^{n-1} - \ldots - p_0 p_1 \ldots p_{n+1} m + p_0 p_1 \ldots p_n m s] = 0$$

Thus the pre-breeding matrix possesses the same characteristic equation and so the same Perron root as the post-breeding matrix. Therefore the post-breeding model can be modeled by the pre-breeding model over a long enough period of time.

Concluding Comments

Clearly the topics presented here will be pursued for quite some time. The difficulties with pooling age classes, adult and juvenile alike, are yet present and will with any skill and luck be resolved shortly. The mysterious workings of the elasticity matrices will no doubt likewise be revealed and the modeled populations will continue to age, survive, and breed, oblivious to the manipulation of their data.

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