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RESEARCH ARTICLE

FLUCTUATIONS IN LESLIE MATRIX PARAMETERS, AND THEIR EFFECT ON THE STABLE POPULATION STRUCTURE

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ABSTRACT

Matrix population models, which are as a result of studies by Bernadelli (1941), Leslie (1945,1948), and Lewis (1942), have provided a good basis on which to analyse population dynamics, using the algebraic theory of matrices, with populations divided into age-classes. Of particular importance is how the stable population structure looks like and this is found by a computation of the dominant eigenvalue of the Leslie matrix, whose eigenvector describes the stable age structure. In this paper, an analysis of how changes in the Leslie matrix entries affect population growth is considered. In particular, we investigate how changes in fertility rates and transition probabilities at different stages affect population growth. We compare the population parameters so as to determine which one among them would impact more on the population growth factor.

1.0. INTRODUCTION

Early studies on matrix population models were done by Bernadelli (1941), Leslie (1945,1948) and Lewis (1942). In his work, Bernadelli focused on the intrinsic oscillations on population structure. By observing oscillations in the age structure of a given population of humans, he developed a projection matrix and further showed, numerically, that this gave rise to permanent oscillations in the age structure. Lewis independently studied the lower biological populations. In his paper, he considered a group of individuals born at some epochs $(t \to 0)$ and whose breeding occurs at regular intervals $z, 2z, \dots nz.$ He showed that if the individuals filled the n age groups $y_1, y_2, \dots y_n$, then the age frequency distribution after the n^{th} breeding epoch would be the n^{th} power of the projection matrix. According to Lewis, the age distribution will generally display no periodicity, but tends to a stable distribution depending on the dominant Eigen value of the matrix $A.$ The model could be generalized by relaxing the conditions of interaction between groups; or incorporating the time changes in fertility and survival rates. In his 1945 paper, Leslie expressed the basic age-specific projection equations in matrix form, and applied the usual methods of matrix analysis to determine the stable age distribution.

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In the second paper (Leslie, 1948), he extended the use of matrix models by studying their relationship to logistic population growth and predator-prey interactions. Many human demographers and ecologists have adopted Leslie's Model in their studies and applied it to different biological populations. In his model, Leslie divided a population of females into age groups, and expressed the basic age-specific projection equations into matrices. The equations form a difference equation of the form $Y_{i+1} = f(y_i)$. A special form of these iteration equations is considered, taking into account the fact that reproduction takes place only in certain age groups. The vector equations are expressed as

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ \dots \\ \dots \\ \dots \\ x_n(t+1) \end{bmatrix} = \begin{bmatrix} f_1(x(t)) \\ f_2(x(t)) \\ \dots \\ \dots \\ \dots \\ f_n(x(t)) \end{bmatrix} \tag{1.1}$$

In situations where the population is divided into age-classes and basing on discrete time and age-scale, then this gives the

Leslie matrix model

2.0. Basic Concepts and Notation

The following basic concepts and notations are found to be useful in this study;

(a) Non-negative matrix: A matrix is said to be non-negative if all its elements are greater than or equal to zero.

(b) Irreducibility: A non-negative matrix is said to be irreducible if its life cycle graph contains at least one stage that cannot contribute, via any path, to any other stage.

(c) Primitivity: A non-negative matrix is primitive if it becomes positive when raised to sufficiently high powers.

(d) $x_i(t)$: The number of individuals in age class i at time t, $(i-1,2,\ldots n, t-1,2,\ldots)$.

(e) p_i: The portion of individuals in age class i who survive to age class $i+1$.

(f) f_i: The number of offspring per individual of age class i per unit time.

3.0. The Leslie Matrix Model

Given the fecundity and the survival rates of a population of females at some unit of time, a system of $n+1$ linear equations can be set up, where n to $n+1$ is the last age group that is considered.

We will let

$$x(t) = \begin{bmatrix} x_1(t) \\ x_2(t) \\ \cdots \\ \cdots \\ \cdots \\ x_n(t) \end{bmatrix} \qquad (3.1)$$

be the vector representing the population's age structure at time t. An individual in the age bracket i to $i+1$ is described as being of age i, and since n to $n+1$ is the last age group, then no one can live to be older than n. The continuous age variable x is therefore partitioned into discrete age classes where age class i corresponds to ages $i-1<x<i, i=1,2,3,\ldots,n$. We further define survival rates as p_i and fertility rates as f_i so that the individuals in any age class other than the first at time $t+1$ must have survived the previous age class at time t, that is

$$\begin{aligned} x_2(t+1) &= p_1x_1(t) \\ x_3(t+1) &= p_2x_2(t) \\ x_4(t+1) &= p_3x_3(t), \\ &\vdots \\ x_{i+1}(t+1) &= p_ix_i(t) \end{aligned} \qquad (3.2)$$

The first age-class at time $t+1$ consists of those individuals born during the time interval $(t, t+\delta t)$ so that;

$$x_1(t+1) = f_1x_1(t) + f_2x_2(t) + \cdots = \qquad (3.3)$$

These equations are formulated with the assumption that individuals move exactly to the next age group after each unit of time.

In matrix notation therefore, the equations become,

$$\begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ \vdots \\ x_n \end{bmatrix}(t+1) = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_n \\ p_1 & 0 & 0 & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & \cdots & 0 & p_{n-1} & 0 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ \vdots \\ x_n \end{bmatrix} \qquad (3.4)$$

Hence,

$$x(t+1) = Mx(t) = \cdots = M^{t+1}x(0) \qquad (3.5)$$

Where $x(0)$ is the initial age distribution, and the matrix M is a population projection matrix, also referred to as the Leslie projection matrix. The Leslie matrix is a non-negative matrix, since it is a population projection matrix. By the theorem of Perron and Frobenius, the matrix obeys the following properties;

(a) If M is non-negative and primitive, then there exists a real valued Eigen value $\lambda > 0$, which is a simple root of the characteristic equation. This Eigen value is strictly greater in magnitude than any other Eigen value of M.

(b) If M is irreducible, but not primitive with index of imprimitivity d, then there exists a real Eigen value $\lambda_1 > 0$, which is a simple root of the characteristic equation. This eigen value satisfies the conditions in (a), but there are $d-1$ complex Eigen values equal in magnitude to λ_1.

(c) If M is irreducible, there exists a real valued Eigen value $\lambda_1 \geq 0$ with right and left eigenvectors $\overrightarrow{\omega_1} \geq 0$ and $\overrightarrow{v_1} \geq 0$.

Generally, these properties are based on the notion that an irreducible, non-negative matrix M of order $n \times n$ always has a positive Eigen value λ_1 which is a simple root of the characteristic equation. It is the dominant Eigen value, and it determines the ergodic properties of population growth. The matrix M is non-negative and primitive, and has a real-valued Eigen value, given by $\lambda > 0$, which is a simple root of the characteristic equation. This Eigen value is strictly greater in magnitude than any other Eigen value of M. It has been shown that the latent root of a matrix given by λ is equal to e^r, where r is the intrinsic rate of natural increase in the Lotka (1925) equation. For a stable population $\lambda = 1$, for a constantly increasing population $\lambda > 1$ and for a constantly decreasing population $\lambda < 1$. Thus λ, which is the dominant Eigen value, gives insight into the population growth rate.

4.0. Sensitivity Analysis of a Leslie Matrix

Sensitivity analysis is defined as a technique for systematically changing parameters in a model, to determine the effects of such changes. In our situation, we will look at how growth rate responds to changes in fertility rates and transition probabilities, also referred to here as survival rates. We consider a biological population that exhibits three age classes, 1, 2 and 3, with respective sizes n_1, n_2, n_3. The age-specific fertilities are f_1, f_2, f_3,and the transition probabilities are p_1, p_2. Assuming that there's no reproduction initially, that is $f_1 = 0$,the projection matrix is given as;

$$M = \begin{bmatrix} 0 & f_2 & f_3 \\ p_1 & 0 & 0 \\ 0 & p_2 & 0 \end{bmatrix} \quad (4.1)$$

The Eigen values of this projection matrix are given by the solution of the equation

$$|\lambda I - M| = 0$$

such that

$$\lambda^3 - \lambda p_1 f_2 - f_3 p_1 p_2 = 0 \quad (4.2)$$

The largest positive root of (4.2) will give the dominant Eigen value $\lambda_1$of the matrix M. We will investigate the sensitivity of λ_1 with respect to changes in the fertilities f_2, f_3 and the transition probabilities p_1, p_2.

Lemma 4.1

A marginal increase or decrease in $f_2$produces a similar change in ë$_1$

Proof

Let $\lambda_1$be the dominant eigenvalue, then $\lambda_1$is a solution to (4.2) , so that

$$\lambda_1^3 - \lambda_1 p_1 f_2 - f_3 p_1 p_2 = 0 \quad (4.3)$$

Case 1:

Here, we increase f_2 by a small margin to f_2^* such that

$$f_2^* = f_2 + \delta, \delta > 0$$

So, now from (4.3) we have that

$$\lambda_1^3 - \lambda_1 p_1 f_2^* - f_3 p_1 p_2 < 0 \quad (4.4)$$

Further, let λ_2 be the dominant Eigen value of (4.3), then

$$\lambda_2^3 - \lambda_2 p_1 f_2^* - f_3 p_1 p_2 = 0 \quad (4.5)$$

From (4.3) and (4.5) we can now deduce that

$$\lambda_2^3 - \lambda_2 p_1 f_2^* - f_3 p_1 p_2 > \lambda_1^3 - \lambda_1 p_1 f_2^* - f_3 p_1 p_2 \quad (4.6)$$

and

$$\lambda_2 > \lambda_1$$

Thus increasing f_2 to f_2^* results in an increase in λ_1 to λ_2 which implies a higher population growth rate.

Case 2:

Suppose f_2 is now decreased by a small margin to f_2', then

$$f_2' = f_2 - \delta, \delta > 0$$

so that now we have,

$$\lambda_1^3 - \lambda_1 f_2' p_1 - f_3 p_1 p_2 > 0 \quad (4.7)$$

And if λ_2' is the dominant Eigen value of (4.7), then

$$\lambda_2'^3 - \lambda_2' f_2' p_1 - f_3 p_1 p_2 = 0 \quad (4.8)$$

And therefore

$$\lambda_2'^3 - \lambda_2' f_2' p_1 - f_3 p_1 p_2 < \lambda_1^3 - \lambda_1 f_2' p_1 - f_3 p_1 p_2 \quad (4.9)$$

which implies that

$$\lambda_2' < \lambda_1$$

Hence decreasing f_2 by δ leads to a decrease in the population growth rate.

Lemma 4.2

A marginal increase or decrease in $f_3$leads to a similar change in λ_1.

Proof:

We shall prove only the case where f_3 is increased to f_3^*. The other case will follow from the previous lemma.

Now, let

$$f_3 + \delta = f_3^*, \delta > 0$$

Then,

$$\lambda_1^3 - \lambda_1 f_2 p_1 - f_3^* p_1 p_2 < 0 \quad (4.10)$$

If λ_3 is the dominant latent root of (4.10), then

$$\lambda_3^3 - \lambda_3 f_2 p_1 - f_3^* p_1 p_2 = 0 \quad (4.11)$$

We deduce from (4.10) and (4.11) that,

$$\lambda_3^3 - \lambda_3 f_2 p_1 - f_3^* p_1 p_2 > \lambda_1^3 - \lambda_1 f_2 p_1 - f_3^* p_1 p_2 \quad (4.12)$$

So that now

$$\lambda_3 > \lambda_1$$

Hence an increment in f_3 will result in an increase in the population growth rate.

Lemma 4.3

A marginal change in the transition probabilities p_1 will result in a similar change in the population growth rate.

Proof :

We look at the case where p_1 is increased by a small margin $\delta > 0$. The other case follows from earlier results. Let

$$p_1^* = p_1 + \delta$$

Then

$$\lambda_1^3 - \lambda_1 f_2 p_1^* - f_3 p_1^* p_2 < 0 \quad (4.13)$$

Further, let λ'_1 be the new dominant latent root, then

$$\lambda_1'^3 - \lambda'_1 f_2 p_1^* - f_3 p_1^* p_2 - 0 \quad (4.14)$$

So that,

$$\lambda_1'^3 - \lambda'_1 f_2 p_1^* - f_3 p_1^* p_2 > \lambda_1^3 - \lambda_1 f_2 p_1^* - f_3 p_1^* p_2 \quad (4.15)$$

And this implies that

$$\lambda'_1 > \lambda_1$$

An increment in the transition probabilities p_1 will result in an increased population growth rate. We will note here that increasing p_2 produces the same effect as increasing f_3, hence the proof will follow from the earlier lemma. These results can be explained from the point of view that, since f_i was defined as the number of offspring per given individual, then adding a factor δ implies an additional offspring, and as such, the population increases. Also, an individual whose survival in enhanced, has its lifespan prolonged. Since there's no decline in the population size, any small increment will definitely lead to an addition in the size of the population.

Theorem 4.1

The dominant eigenvalue is more sensitive to changes in f_2 than in f_3 If $\lambda > p_2$ and is more sensitive to changes in f_3 than f_2 if $\lambda < p_2$.

Proof :

The characteristic equation of the matrix M from (4.2) was given as

$$f(\lambda) = \lambda^3 - \lambda p_1 f_2 - f_3 p_1 p_2$$

The gradient of this function is

$$f'(\lambda) = 3\lambda^2 - p_1 f_2 \quad (4.16)$$

We also had that

$$f_2^* = f_2 + \delta$$

And

$$f_3^* = f_3 + \delta, \delta > 0$$

The shift created in $f(\lambda)$ when f_2 is replaced by f_2^* is given by

$$\Delta_2 = (\lambda^3 - \lambda p_1 f_2 - f_3 p_1 p_2) - (\lambda^3 - \lambda p_1 f_2^* - f_3 p_1 p_2)$$

$$= \lambda \delta p_1 \quad (4.17)$$

Let

$$f^*(\lambda) = \lambda^3 - \lambda p_1 f_2^* - f_3 p_1 p_2$$

be the new characteristic equation, then the change in λ due to a change in f_2 will now be given as a fraction of Δ_2 and the gradient, that is

$$\frac{\lambda \delta p_1}{f'^*(\lambda)} = \frac{\lambda \delta p_1}{3\ ⍰^2 - p_1 f_2^*} \quad (4.18)$$

Similarly, the change in λ due to a change in f_3 will be given as,

$$\frac{\delta p_1 p_2}{3\lambda^2 - p_1 f_2} \quad (4.19)$$

So the condition for λ to be more sensitive to changes in f_2 than in f_3 is that (4.18) must be greater than (4.19) so that

$$\frac{\lambda \delta p_1}{3\lambda^2 - p_1 f_2^*} > \frac{\delta p_1 p_2}{3\lambda^2 - p_1 f_2} \quad (4.20)$$

Now suppose $\delta > 0$, then we have that

$$3\lambda^2 - p_1 f_2 > 3\lambda^2 - p_1 f_2^* \quad (4.21)$$

And the following inequality will ensure that condition (4.20) ;

$$\frac{\lambda \delta p_1}{3\lambda^2 - p_1 f_2^*} > \frac{\lambda \delta p_1}{3\lambda^2 - p_1 f_2} > \frac{\delta p_1 p_2}{3\lambda^2 - p_1 f_2} \quad (4.22)$$

Which clearly implies that

$$\lambda > p_2$$

Now suppose again that $\delta < 0$, then we shall have that,

$$\lambda \delta p_1 > \delta p_1 ⍰_2 \frac{3\lambda^2 - p_1 f_2^*}{3\lambda^2 \quad p_1 f_2} \quad (4.23)$$

But

$$\frac{3\lambda^2 - p_1 f_2^*}{3\lambda^2 - p_1 f_2} > 1$$

Hence

$$\lambda\delta p_1 > \delta p_1 p_2 \tag{4.24}$$

So that once more

$$\lambda > p_2$$

We note that λ will be more sensitive to changes in f_2 than f_3 for an increasing population, since $\lambda > 1.$

Another Proof:

We will also try to prove that λ is more sensitive to changes in f_3 than in f_2 if $\lambda < p_2$;

From (4.18) and (4.19) we have that the condition for λ to be more sensitive to f_3 than f_2 is that;

$$\frac{\lambda\delta p_1}{3\lambda^2 - p_1 f_2^*} < \frac{\delta p_1 p_2}{3\lambda^2 - p_1 f_2} \tag{4.25}$$

If we increase f_2 to f_2^*, then

$$3\lambda^2 - p_1 f_2^* < 3\lambda^2 - p_1 f_2 \tag{4.26}$$

And therefore;

$$\frac{\lambda\delta p_1}{3\lambda^2 - p_1 f_2^*} < \frac{\lambda\delta p_1}{3\lambda^2 - p_1 f_2} < \frac{\delta p_1 p_2}{3\lambda^2 - p_1 f_2} \tag{4.27}$$

Hence

$$\lambda < p_2$$

Alternatively, if the fertility coefficients were decreased, that is $\delta < 0$, then we have that,

$$\lambda\delta p_1 < \delta p_1 p_2 \frac{3\lambda^2 - p_1 f_2^*}{3\lambda^2 - p_1 f_2} \tag{4.28}$$

And since

$$\frac{3\lambda^2 - p_1 f_2^*}{3\lambda^2 - p_1 f_2} < 1 \tag{4.29}$$

Then it follows that,

$$\lambda\delta p_1 < \delta p_1 p_2 \tag{4.30}$$

Which clearly implies that

$$\lambda < p_2$$

Hence the proof.

Theorem 4.2

The dominant eigenvalue λ will be more sensitive to changes in p_1 than p_2 if $p_1 < p_2 + \frac{\lambda f_2}{f_3}$ and to p_2 than p_1, if the inequality is reversed.

Proof :

The transition probabilities are changed by a factor $\delta > 0$, such that

$$p_1^* = p_1 + \delta$$

And

$$p_2^* = p_2 + \delta$$

The new characteristic equation when p_1 is changed to p_1^* will now be

$$f^*(\lambda) = \lambda^3 - \lambda p_1^* f_2 - p_1^* p_2 f_3 \tag{4.31}$$

The shift created by this replacement is given by,

$$\Delta_1 = \delta\lambda f_2 + \delta f_3 p_2$$

And similarly, the shift when p_2 is replaced by p_2^* is

$$\Delta_2' = \delta f_3 p_1$$

The rate of change in λ due to a change in p_1 is

$$\frac{\delta\lambda f_2 + \delta f_3 p_2}{3\lambda^2 - f_2 p_1^*} \tag{4.32}$$

While the rate of change due to a change in p_2 is,

$$\frac{\delta f_3 p_1}{3\lambda^2 - f_2 p_1} \tag{4.33}$$

λ will be more sensitive to changes in p_1 than in p_2 if

$$\frac{\delta\lambda f_2 + \delta f_3 p_2}{3\lambda^2 - f_2 p_1^*} > \frac{\delta f_3 p_1}{3\lambda^2 - f_2 p_1} \tag{4.34}$$

But, for $\delta > 0$ we have that

$$\frac{\delta\lambda f_2 + \delta f_3 p_2}{3\lambda^2 - f_2 p_1^*} > \frac{\delta\lambda f_2 + \delta f_3 p_2}{3\lambda^2 - f_2 p_1} > \frac{\delta f_3 p_1}{3\lambda^2 - f_2 p_1} \tag{4.35}$$

Clearly

$$\lambda f_2 + f_3 p_2 > f_3 p_1$$

So

$$\frac{\lambda f_2}{f_3}+p_2>p_1$$

Alternatively, if $\delta<0$, the we now have that,

$$\delta\lambda f_2+\delta f_2 p_2>\delta f_3 p_1\frac{3\lambda^2-f_2p_1^*}{3\lambda^2-f_2p_1} \tag{4.36}$$

But since

$$3\lambda^2-f_2p_1^*>3\lambda^2-f_2p_1$$

Then

$$\frac{3\lambda^2-f_2p_1^*}{3\lambda^2-f_2p_1}>1 \tag{4.37}$$

Hence,

$$\delta\lambda f_2+\delta f_3 p_2>\delta f_3 p_1$$

And therefore

$$\frac{\lambda f_2}{f_3}+p_2>p_1$$

Another Proof:

Again, the condition for the dominant Eigen value to be more sensitive to changes in p_2 than in p_1 is that;

$$\frac{\delta\lambda f_2+\delta f_3p_2}{3\lambda^2-f_2p_1^*}<\frac{\delta f_3p_1}{3\lambda^2-f_2p_1} \tag{4.38}$$

Suppose $\delta>0$, then

$$3\lambda^2-f_2p_1^*<3\lambda^2-f_2p_1$$

Then,

$$\frac{\delta\_f_2+\delta f_3p_2}{3\lambda^2-f_2p_1^*}<\frac{\delta f_3p_1}{3\lambda^2-f_2p_1^*} \tag{4.39}$$

So that

$$\frac{\lambda f_2}{f_3}+p_2<p_1$$

Alternatively, if $\delta<0$ then

$$\delta\lambda f_2+\delta f_3 p_2<\delta f_3 p_1\frac{3\lambda^2-f_2p_1^*}{3\lambda^2-f_2p_1} \tag{4.40}$$

But since $3\lambda^2-f_2p_1^*>3\lambda^2-f_2p_1$,

then

$$\frac{3\lambda^2-f_2p_1^*}{3\lambda^2-f_2p_1}>1 \tag{4.41}$$

Therefore

$$\delta\lambda f_2+\delta f_3 p_2<\delta f_3 p_1$$

Hence

$$\frac{\lambda f_2}{f_3}+p_2<p_1$$

Which clearly proves our theorem.

5.0. The Generalised Leslie Process

We will now define the Leslie process in a more generalised form. The matrix is expressed as follows:

$$A=\begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_m & \cdots & \cdots & f_n \\ p_1 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & p_2 & 0 & \cdots & \cdots & \cdots & 0 & 0 \\ \vdots & \ddots & \ddots & \vdots & \vdots & \vdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & p_{m-1} & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & p_{n-1} & 0 \end{bmatrix} \tag{5.1}$$

The characteristic equation of the matrix is given by a solution of
$$|A-\lambda I|=0$$

We will let
$$p_1p_2p_3\ldots\ldots p_n=p(n) \tag{5.2}$$
So that the characteristic equation can be expanded to give
$$f(\lambda)=\lambda^n-f_1\lambda^{n-1}-p(1)f_2\lambda^{n-2}-\cdots-p(k)f_{r+1}\lambda^{n-r-1}-p(k-1)f_n \tag{5.3}$$
Equation (5.3) gives a polynomial in λ which can be solved to give the n roots of $f(\lambda)$. The equation can also be expressed in a condensed form as,
$$f(\lambda)=k_0\lambda^n-k_1\lambda^{n-1}-k_2\lambda^{n-2}\ldots\ldots-k_{n-1}\lambda-k_n \tag{5.4}$$
Where
$$k_i=p(i-1)f_i, i=1,2,3\ldots n, k_0=1$$
We will then solve for λ, such that

$$k_o\lambda^n-k_1\lambda^{n-1}-k_2\lambda^{n-2}\ldots-k_{n-1}\lambda-k_n=0 \tag{5.5}$$

The largest positive real root of (5.5) is the dominant Eigen value of a population structure given by the matrix A. We will now look at the sensitivity of λ to small changes in the matrix elements. In particular, we seek to show that increasing or decreasing $k_i,(i=0,1,2,\ldots,n)$ results in changes in the dominant Eigen value λ, and thus, the rate of population growth. We illustrate in the following lemma:

Lemma 5.1

A marginal increase or decrease in $k_i, (i = 0,1,2,\dots,n)$, leads to a similar change in λ.

Proof:

Let λ be the dominant eigenvalue, then λ is a solution of (5.5).

That is

$$\lambda^n - k_1\lambda^{n-1} - k_2\lambda^{n-2} \dots\dots - k_{n-1}\lambda - k_n = 0 \qquad (5.6)$$

Suppose k_i is increased to k_i^*, such that

$$k_i^* = k_i + \delta$$

Where δ is a small positive real number, and k_i is as defined earlier

Then from (5.6),

$$\lambda^n - k_1\lambda^{n-1} - \dots - k_i^*\lambda^{n-i} \dots - k_{n-1}\lambda - k_n < 0 \quad (5.7)$$

λ^* is the dominant eigenvalue of equation (5.7) such that

$$\lambda^{*n} - k_1\lambda^{*n-1} - \dots - k_i^*\lambda^{*n-i} \dots - k_{n-1}\lambda^* - k_n = 0 \qquad (5.8)$$

This clearly shows from (5.6) and (5.7) that,

$$\lambda^{*n} - k_1\lambda^{*n-1} - \dots - k_i^*\lambda^{*n-i} \dots - k_n > \lambda^n - k_1\lambda^{n-1} - \dots - k_{n-1}\lambda - k_n \qquad (5.9)$$

If we suppose that $\lambda^* < \lambda$

From above, we have that

$$\lambda^{*n-1} - k_1\lambda^{*n-2} - \dots - k_i^*\lambda^{*n-i-1} \dots > \lambda^{n-1} - k_1\lambda^{n-2} - \dots - k_i^*\lambda^{n-i-1} \dots \qquad (5.10)$$

So that

$$\lambda^*(\lambda^{*n-i} - k) > \lambda(\lambda^{n-i} - k_i^*) \qquad (5.11)$$

and therefore, $\lambda^* > \lambda$, which contradicts our earlier assumption. Increasing k_i to k_i^* implies an increase in the population growth rate. Alternatively, we can decrease the value of k_i, so that now we have that

$$k_i^* = k_i - \delta$$

δ is as defined earlier.

So now we have that

$$\lambda^{*n} - k_1\lambda^{*n-1} - \dots - k_i^*\lambda^{*n-i} \dots - k_n < \lambda^n - k_1\lambda^{n-1} - \dots - k_n \qquad (5.12)$$

$$\lambda^*(\lambda^{*n-1} - k_1\lambda^{*n-2} - \dots - k_i^*\lambda^{*n-i-1} \dots) < \lambda(\lambda^{n-1} \quad k_1\lambda^{n-2} \quad \dots \quad k_i^*\lambda^{n-i-1} \dots) \qquad (5.13)$$

This therefore implies that

$$\lambda^*(\lambda^{*n-i} - k_i) < \lambda(\lambda^{n-i} - k_i) \qquad (5.14)$$

and clearly $\lambda^* < \lambda$.

Decreasing k_i by a small quantity δ is likely to lead in a decrease in population growth rate. We will now present two theorems that that will seek to show the effects on λ, due to small increments in the fertility coefficients f_i and the transition probabilities p_i.

Theorem 5.1

The sensitivity of λ to fertility changes is a strictly decreasing function of age, if $\lambda > 1$

Proof :

From earlier results, we had that
$f(\lambda) = \lambda^n - f_1\lambda^{n-1} - p_1f_2\lambda^{n-2} \dots$
The gradient of this function is,

$$f'(\lambda) = n\lambda^{n-1} - (n-1)f_1\lambda^{n-2} - (n-2)p_1f_2\lambda^{n-3} - \dots \qquad (5.15)$$

Let Δ_{f_i} represent the shift in $f(\lambda)$ when f_i is replaced by $f_i^*(f_i^* = f_i + \delta)$

If $f^*(\lambda)$ is the new characteristic equation as a result of this change, then the change in λ as a result of a decrease or increase in f_i is given by,

$$\Delta_i = \frac{\Delta_{f_i}}{f'^*(\lambda)}$$

$$\Delta_1 = \frac{\delta\lambda^{n-1}}{n\lambda^{n-1} - (n-1)f_1\lambda^{n-2} - (n-2)p_1f_2\lambda^{n-3} - \dots}$$

$$\Delta_{i-1} = \frac{p(i-2)\delta\lambda^{n-(i-1)}}{n\lambda^{n-1} - (n-1)f_1\lambda^{n-2} - \dots - (n-(i-1))p_{i-2}f_{i-1}^*\lambda^{n-(i-2)} - \dots}$$

$$\Delta_i = \frac{p(i-1)\delta\lambda^{n-i}}{n\lambda^{n-1} - (n-1)f_1\lambda^{n-2} - \dots - (n-i)p_{i-1}f_i^* \;{}^{-n-(i-1)} - \dots} \qquad (5.16)$$

λ will therefore be more sensitive to f_{i-1} than f_i if

$$\Delta_{i-1} > \Delta_i \qquad (5.17)$$

If we now further define $f'^{(i-1)}(\lambda)$ and $f'^{(i)}(\lambda)$ as the gradients of the new functions resulting from changes in f_{i-1} and f_i respectively,

Then Suppose $\delta > 0$, then,

$f'^{(i-1)}(\lambda) > f'^{(i)}(\lambda) > f'^{(i+1)}(\lambda)$

The condition (5.17) will be satisfied by the following inequality;

$$\frac{p(i-2)\delta\lambda^{n-(i-1)}}{f'^{(i-1)}(\lambda)} > \frac{p(i-1)\delta\lambda^{n-i}}{f'^{(i-1)}(\lambda)}$$

And therefore

$$\lambda^{n-i} > p_i\lambda^{n-(i-1)}\ \lambda > p_i$$

Hence λ will be more sensitive to changes in f_i than in f_{i+1} for the condition $\lambda > p_i$, and obviously if $\lambda > 1$, then this is implied.

Again, if $\delta < 0$, then

$$p(i-2)\delta\lambda^{n-(i-1)} > p(i-1)\delta\lambda^{n-i}\frac{f'^{(i-1)}(\lambda)}{f'^{(i)}(\lambda)}$$

In this situation we have that

$f'^{(i-1)}(\lambda) < f'^{(i)}(\lambda)$, therefore

$\frac{f'^{(i-1)}(\lambda)}{f'^{(i)}(\lambda)} < 1$ So that

$p(i-2)$ [illegible] $\lambda^{n-(i-1)} > p(i-1)\delta\lambda^{n-1}$

Hence

$$\lambda > p_i$$

Using a similar argument, it can be shown that λ is more sensitive to changes in f_{i+1} than in f_i if the reverse condition is met.

Theorem 5.2

The sensitivity of λ with respect to marginal changes in the transition probabilities is monotonically decreasing if $\lambda \geq 1$ and $p_{i+1} \geq p_i$

Proof:

We will let Δ_{p_i} represent the shift created in $f(\lambda)$ due to a replacement of p_i by $p_i^*(p_i^* = p_i + \delta)$.

Define also, the gradients of the functions resulting from changes in p_i and p_{i+1} as $f'^{(*)}(\lambda)$ and $f'^{(**)}(\lambda)$. If we let Δ be the change in λ as a result of these shifts, then

$$\Delta_i = \frac{\delta(f_{n-(i+1)}\lambda^{n-(i+1)} + p_{n-(i+1)}f_{n-(i-1)}\lambda^{n-(i-1)} + \cdots + p_{n-(i+1)}p_{n-(i-1)}f_n)}{f'^{(*)}(\lambda)}$$

$$\Delta_{i+1} = \frac{\delta(f_{n-(i+2)}\lambda^{n-(i+2)} + p_{n-(i+2)}f_{n-i}\lambda^{n-i} + \cdots + p_{n-(i+2)}p_{n-i}f_n)}{f'^{(**)}(\lambda)} \tag{5.18}$$

λ will be more sensitive to changes in p_i than in p_{i+1} if $\Delta_i > \Delta_{i+1}$.

Suppose that $\delta > 0$,

then

$$f'(\lambda) > f'^{(*)}(\square) > f'^{(**)}(\lambda)$$

and

$$\frac{\delta\lambda f_{n-i} + \delta f_n p_{i+1}}{f'^{(*)}(\lambda)} > \frac{f_n p_i}{f'^{(*)}}$$ Therefore,

$$\frac{\lambda f_{n-i}}{f_n} + p_{i+1} > p_i \tag{5.19}$$

Alternatively, we can let $\delta < 0$, then we can have that

$$\lambda f_{n-i} + f_n p_{i+1} > f_n p_i \frac{f'^{(*)}(\lambda)}{f'^{(**)}(\lambda)} \tag{5.20}$$

And since for this situation

$f'(\lambda) < f'^{(*)}(\lambda) < f'^{(**)}(\lambda)$ then

$$\lambda f_{n-i} + f_n p_{i+1} > f_n p_i$$

Hence the dominant eigenvalue λ will be more sensitive to changes in p_i than in p_{i+1} if

$$\frac{\lambda f_{n-i}}{f_n} + p_{i+1} > p_i$$

The converse is also true for all values of i.

6.0. DISCUSSION

The results of the analysis indicate that an increase or decrease in either fertility or survival rates has an effect on the growth of a population, depending on the value of the dominant eigenvalue. The sensitivity of the growth rate factor to fertilities is found to be a decreasing function of age, for exponentially increasing populations. The sensitivity to survival decreases monotonically provided $\lambda \geq 1$ and $p_{i+1} \geq p_i$. If survival was age-dependent, then the sensitivity of λ to changes in survival would decrease monotonically with age as long as $\lambda > 1$. For a further comprehensive analysis, however, it may be necessary to provide an extension of this model, so as to include developmental stages among the species. Another possible extension of the Leslie matrix would be to accommodate the migrating populations whose survival is dependent on regions. In this case, a new parameter, namely migration rate is incorporated; hence the resulting sensitivity would not necessarily be as in the normal Leslie matrix.

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