"AN AGE STRUCTURED POPULATION MODEL"

BY

KIPCHIRCHIR ISAAC CHUMBA

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degree of Master of Science in Mathematical Statistics in
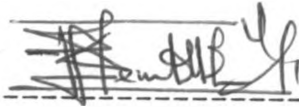the Department of Mathematics*

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DECLARATION

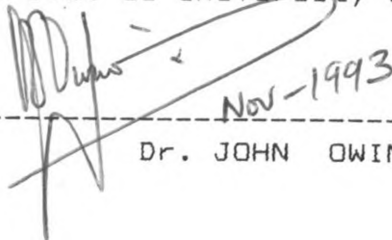This dissertation is my original work and has not been presented for a degree in any other University.

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KIPCHIRCHIR ISAAC CHUMBA

This dissertation has been submitted for examination with my approval as University Supervisor.

Nov-1993

Dr. JOHN OWINO

Department of Mathematics
University of Nairobi
P.O. Box 30197
NAIROBI
KENYA.

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CHAPTER.1. INTRODUCTION

1.1 Introduction.

Studies in population dynamics have been carried out solely to predict future characteristics of a population when the past or the present is known.

One such characteristic is the population size which will be discussed in the sequel. Various models have been derived to predict future population size given the present/past.

These models can further be classified as:

(i) Calculus models

(ii) Matrix models

In calculus models the population parameters are assumed to be continuous on time scale whereas in matrix models they are assumed to be discrete.

The notable calculus model describing the growth of a population is

$$n_t = n_o e^{rt} \qquad\qquad (1.1.1)$$

where n_t is the population size at time t, n_o is the initial population size(i.e. at time t=o) and r is the intrinsic rate of natural increase and often referred to as "Lotka's r". (1.1.1) is also called the Malthusian model (Malthus (1798)) and studied by Lotka (1925).

Remark.

r>o will result in an indefinite population growth and r<o

will result in extinction of the population. These two cases are not applicable hence this type of model is only suitable for short term projection.

An improved model yields the logistic equation (so-called Verhulst-Pearl logistic equation, (Verhulst (1838)); Pearl (1927)).

$$n_t = \frac{n_o K}{n_o + (K - n_o) \, e^{-r_o t}}$$

(1.1.2)

where n_t and n_o are as defined for the exponential growth equation given by (1.1.1.). r_o is some initial growth rate and can be estimated using the available data and K is the carrying capacity of the population.

Remark

The logistic equation has an advantage of long term projection.

In arriving at the above equations the assumptions taken were;

(i) Birth and death rates were independent of age or that population growth occured in such away that the age distribution remained unaltered.

(ii) Density dependence i.e. a decrease in birth rate and an increase in death rate as the population become larger.

The study of population dynamics concepts has demonstrated the complexity of calculus and the simplicity of matrices. In reversing the above assumptions we have the

following:

(i) An individual's chances of reproducing and dying are a function of its age.

(ii) These chances are unaffected by the size of the population in which it finds itself, perhaps because the population numbers never rise so high that density dependence begins to exert any influence.

This latter set of assumptions characterizes the matrix models. The need to employ the matrix models rather than the calculus models is because the calculus models merely predict the size of the population after a lapse of time, given the initial size, but matrix models have an added advantage that it also gives the age structure(distribution).

Other inherent advantages of matrix models over the calculus models are:

(i) Matrix processes are assumed to take place in discrete time units whilst the very nature of calculus implies continuous process taking place in infinitesimally small time intervals. It would appear then that the matrix approach is more reminiscent of biological process of birth and death with which we are concerned with when modelling.

(ii) Matrices are relatively dealt with by numerical rather than algebraic techniques. This is a feature of importance when simulation of populations is required.

The Leslie Matrix model or the Age-Structured Model is

deterministic. It predicts the age structure of a population of female animals, given the age-structure at some past/present time and given the age-specific survival and fecundity rates.

Instead of the differential and integral calculus, matrix algebra is used, a step which leads to a great economy in the use of symbols and consequently to equations which are more easily handled. Moreover, many quite complicated arithmetical problems can be solved with great ease by manipulating the matrix which represents the given system of age specific rates (fecundity and survival rates).

But the question then arises whether these advantages mentioned may not be offset by a greater degree of inaccuracy in the results as compared with those obtained from the previous methods of computation. It is not easy, however, to settle this point satisfactorily at the moment and requires investigation.

The study shall be based on data of a Gorilla species, Gorilla Berengei (Mountain Gorilla).

The data compiled from several sources including:-
*Harcourt A. H, D.Fossey, and J.Sabater-Pi. 1981.
 Demography of Gorilla *J. Zool.*, **195**, 215-233.
*Webber, A.W., and A.Veder. 1983 Population Dynamics of the
 Virunga gorillas:1959-1978 *Biol. Conser.*, **26**, 341-346.

1.2 Objective and Significance of the study.

Concerned to predict the size and age structure of a population after a lapse of time (or at successive intervals of time) given the age-specific rates of fecundity and survival.

To employ matrix algebra and numerical methods to determine the latent vector of the stable age distribution and the intrinsic rate of natural increase.

More precisely, if A is the matrix describing the model then

$$\lim_{t \to \infty} A^t n_0 \propto n_s \qquad (1.2.1)$$

where n_o is the initial age distribution and n_s is the age distribution at time s. The elements of n_s are proportional to the sizes of the age groups when the age distribution is stable. We shall establish that when the population has stabilized

$$n_{s+1} = A\, n_s = \lambda\, n_s \qquad (1.2.2)$$

where λ is a dominant eigenvalue of A.

If the population size increases from n to λn over one period of time, we shall show that the harvest that can be taken is given by

$$H = 100(\lambda-1)/\lambda \qquad (1.2.3)$$

where H is expressed as a percentage of total population. A constant population size is maintained if the harvest is spread proportionately over all of the age groups. However, if the exploitation is aimed at only one age group then an

enhanced exploitation can be taken.

If there is no harvesting the model predicts that the population size continues to increase at a constant rate, namely by a multiplicative factor of λ every period of time. The model thus closely approximates the calculus model describing exponential growth of population given by (1.1.1). Assuming stability the matrix model is described by the equation

$$n_t = \lambda\, n_{t-1} \qquad\qquad (1.2.4)$$

and by induction

$$n_t = \lambda^t\, n_o \qquad\qquad (1.2.5)$$

where λ is the dominant eigenvalue of A. These two models in population dynamics can be related by the equation

$$r = \log_e \lambda \qquad\qquad (1.2.6)$$

It is remarkable to note that the matrix model takes into consideration the age structure of the population.

The essence of predicting the size and age structure of a population at some given time in future is to be utilized in economic and social planning with respect to the population under study.

In human populations, in particular, the classes are usually the quinquennial (or other) age groups 0-4, 5-9, ..., 85 and over, and once the number of individuals in an age group has been predicted one can plan for the requirements appropriate for that age group. The requirements being referred to above are schools, hospitals,

infrastructure, recreation facilities, employment opportunities, housing, food e.t.c.

The system of age specific rates can also be used to model the dynamics of a wide variety of ecological populations e.g. Forests, Wildlife, Insects e.t.c. In populations of pupating insects the classes might be the three stages larvae, pupae and adults.

The results of the study also provide information on harvesting. Harvesting here refers to removal of some individuals from a given age group for consumption or otherwise. Often the harvest is not spread proportionately over all age groups but is taken chiefly from some subset of the age groups.

Finally the results of the study will provide reading and reference material for further researches/investigations by scientists both in Physical/Biological sciences and Social Sciences. The study is also useful to Biostatisticians in their research activities.

1.3 Brief literature review.

Since Leslie(1945, 1948) first put their use on a firm footing, projection matrices have proved exceedingly valuable in ecological and human demography. Further research still continues to expand their use in many directions. A very similar model had, independently been described earlier by Bernardelli (1941) and Lewis (1942).

Herebelow is a brief review on the use of the Leslie's

Matrix Model and its developments.

(i) Polard (1966) showed that the predictions based on the model are not markedly affected by changes in the time interval. Thus he compared two estimates of the rate of increase per annum of Australian human females and showed that the estimates were very close, regardless of whether the age classes were one year or five years long. The error introduced by altering the time interval appears to be small.

(ii) When a projection matrix is used it is normally assumed that the age intervals are of equal length. However, Lefkofitch (1965) has generalized Leslie's model by considering unequal age groupings as characterized by the insect populations. The structure of these populations can most simply be in terms of the four developmental stages - eggs, larvae, pupae and adults. The lengths of time occupied by each of these four stages are in general not equal and hence one of the premises of the basic model, namely that an animal moves up by exactly one class is no longer tenable. Lefkofitch demonstrated the usefulness of his model in studies of the growth of experimental populations of the cigarette beetle, Lasioderma Serricone (Fabricus).

(iii) A modified projection matrix for the two sex situation has been explored by Williamson (1959). A considerable extension of the basic model for the two sex situation has

been made by Goodman (1969). He applies his model to the structure of human populations of the United States. His model records not the actual population age structure at time t but rather how many female descendants aged under five that a female alive in the ith age group will have. From such studies Goodman is able to predict the eventual age structure of the United States, exactly analogous to the Stable age structure predicted by the basic model.

(iv) Forest trees are generally classified according to their size rather than their age. Usher (1966) developed the basic Leslie model for selection forests, these forests which contain an uneven age and size structure of the trees and in which there is no regeneration phase. In a similar manner to the development for the insect populations, trees can either remain in the same size class during the period of time over which the matrix operates or they move to a larger class. Usher (1966, 1967/68, 1969) has assumed that the period of time over which the matrix operates is sufficiently small for a tree not to move up by more than one size class. The major difficulty for the forest model concerns the analogue to the fecundity terms of the model. Usher (1972) has applied the model to forest management on pine trees.

(v) Stochastic versions have been described by Sykes (1969b) and Polard (1966/73). In particular, Polard (1966) has developed a stochastic form of Leslie's basic model, giving

for each integral point of time the mean and variance of the female population of Australia, showing that after 250 periods of time (in this case one year) the ratio of the numbers in the age groups gives a very close approximation to the latent root.

(vi) Keifitz (1964) has applied the model to human demography. In particular, he discussed empirically the approach to stability and illustrated several different ways of calculating the intrinsic rate of natural increase, and examined how these calculations are related to one another.

(vii) Polard (1966) has described some deterministic extensions which allow for immigration, namely:-

(a) It is assumed that each year a constant immigration vector **b** is added to the population. Then

$$n_{t+1} = A \, n_t + b \qquad\qquad (1.3.1)$$

(b) It is assumed that, instead, a population vector proportional to the actual population vector is added to the population each year. That is

$$n_{t+1} = (A + \alpha I) \, n_t \qquad\qquad (1.3.2)$$

(c) It is assumed that immigration may be represented by a combination of the following three factors:-

* An immigration vector whose elements are proportional to those in the population.

* A constant immigration vector; and

* An immigration vector whose elements grow exponentially at the same rate with time.

Mathematically the model may be represented by the recurrence equation

$$n_{t+1} = A\ n_t + \alpha\ n_t + b + \beta^{t+1}\ c \qquad (1.3.3)$$

1.4 Eigenvalues and Eigenvectors.

Generally, we shall be concerned with the exposition and proof of results of the eigenvalue/eigenvector problem.

Defn.1. characteristic root/vector

If A is an nxn matrix and λ is a scalar the characteristic polynomial of A is defined as

$$f(\lambda) = |\ A - \lambda I\ | \qquad (1.4.1)$$

and when it is expanded it produces an nth degree polynomial in λ. $f(\lambda)=0$ is called the characteristic equation of A i.e.

$$\lambda^n + k_1\ \lambda^{n-1} + k_2\ \lambda^{n-2} + \ldots + k_{n-1}\ \lambda + k_n = 0 \qquad (1.4.2)$$

and it factors out linearly as $f(\lambda) = (\lambda - \lambda_1)\ (\lambda - \lambda_2)\ \ldots (\lambda - \lambda_n)$ and the n roots λ_1, λ_2, $\ldots$, λ_n of $f(\lambda)$ are called the characteristic roots of A (also called latent roots, proper roots, secular roots, eigenvalues).   The set { λ_1, λ_2, $\ldots$, λ_n } is called the spectrum of A.   Although an n x n matrix always has n characteristic roots, they need not be distinct.

If u is a non-zero column vector such that

$$A\ u = \lambda\ u \qquad (1.4.3)$$

for some scalar λ, u is called a characteristic vector of A corresponding to λ (other names latent vector, proper vector, eigenvector).   Clearly u is any non-trivial solution

of the homogeneous system of linear equations

$(A - \lambda I)u = o$.   Such a system has a non-trivial solution

iff $| A - \lambda I | = 0$, thus iff λ is a characteristic root of A.

Defn.2. Diagonal matrix

A square matrix $A=(a_{ij})$ of order n is called diagonal if

its elements off the diagonal are all zero i.e. $a_{ij} = 0 \; \forall$

$i \neq j$ and is denoted by

$$A = \text{diag}(a_{11}, a_{22}, \ldots, a_{nn}) \qquad (1.4.4)$$

Theorem.1.

A and A′ (A   transpose) have the same characteristic

equation.

Proof.

We note that $| A| = | A′|$ and $I′ = I$

Let $f(\lambda)=0$, $f^*(\lambda)=0$ be the characteristic equations of A

and A′ respectively. We show that $f(\lambda) = f^*(\lambda)$.

$f(\lambda)= | A - \lambda I | = | A′ - \lambda I′ | = | A′ - \lambda I | = f^*(\lambda)$

Theorem.2.

If λ is an eigenvalue of A corresponding to u then $1+\lambda$ is an

eigenvalue of I+A corresponding to the same eigenvector u.

Proof.

$A u = \lambda u$ by definition.

$(I+A)u = u+Au = u+\lambda u = (1+\lambda)u$ and by definition the proof is

complete .

Corr.

$(1+\lambda)^{n-1}$ is an eigenvalue of $(I+A)^{n-1}$ corresponding to u.

Defn.3. Similarity.

Two n x n matrices A and B are called similar if

$$B = P^{-1} A P \qquad (1.4.5)$$

where P is an arbitrary non-singular n x n matrix.

Theorem.3.

Similar matrices have the same characteristic equation(and hence same eigenvalues).

Proof.

Let A and B be similar matrices and $f(\lambda)=\emptyset$, $f^*(\lambda)=\emptyset$ be their characteristic equations respectively. we show that $f(\lambda)=f^*(\lambda)$

$$f(\lambda)= |\ B - \lambda I\ | = |\ P^{-1}\ (A-\lambda I)\ P\ |$$

$$= |\ P^{-1}|\ |A-\lambda I|\ |P|\ = |\ A-\lambda I|\ = f^*(\lambda)$$

since $|P^{-1}| = 1 / |P|$

Remark.

If two matrices do not have the same characteristic equation, then we can say categorically that they are not similar, however, if two matrices have the same characteristic equations, they may or may not be similar.

Defn.4.

Let u_i denote the eigenvector corresponding to the eigenvalue λ_i then for i=1,2,..., n

$$Au_i = \lambda_i u_i \qquad (1.4.6)$$

Arrange the column vectors u_i side by side to form the n x n matrix U. Let D be a diagonal matrix whose elements are the characteristic roots of A. We note that the

characteristic roots may be made to appear on the diagonal of D in any desired order by suitable choice of U. Then

$$U^{-1} A U = D \qquad\qquad (1.4.7)$$

Proof.

Given that λ_1, $\lambda_2, \ldots, \lambda_n$ are the eigenvalues of A and u_1, $u_2, \ldots, u_n$ are the corresponding eigenvectors, provided that λ_1's are distinct then the eigenvectors u_1's are linearly independent, then $|U| \neq 0$ and U^{-1} exits where $U = [u_1, u_2, \ldots, u_n]$. Using (1.4.6) we have

$$A U = U D \qquad\qquad (1.4.8)$$

which reduces to (1.4.7) on premultiplying both sides by U^{-1}. U is called a *modal* matrix for A, and D is called a *spectral* matrix for A. The similarity transformation (1.4.7) of A into D is called *diagonalization* and has many important applications.

Remark.1.

A matrix is diagonalizable if it is similar to a diagonal matrix.

Remark.2.

Any suitable vectors, u_1 will do. There is no need to use normalized eigenvectors. It should be noted that if some of the λ's are repeated then A is similar to the diagonal matrix D only if A possesses n linearly independent eigenvectors.

Remark.3.

A matrix will have n linearly independent eigenvectors if all the eigenvalues are distinct or, depending upon the matrix, even if some or all of the eigenvalues are equal. A priori, therefore, we place no restrictions on the multiplicities of the eigenvalues.

Similar results can be obtained for matrices which are not diagonalizable. We begin by generalizing the concept of the eigenvector. It will follow that every matrix A has n linearly independent *generalized* eigenvectors and hence similar to an "almost diagonal" matrix.

Defn.5.

A vector u_m is a generalized eigenvector of rank m corresponding to the matrix A and the eigenvalue λ if

$$(A-\lambda I)^m u_m = o \quad \text{and} \quad (A-\lambda I)^{m-1} u_m \neq o \quad (1.4.9)$$

Defn.6.

Let u_m be a generalized eigenvector of rank m corresponding to the matrix A and the eigenvalue λ. The chain generated by u_m is a set of vectors $\{u_m, u_{m-1},...,u_1\}$ given by

$$u_j = (A-\lambda I)^{m-j} u_m = (A-\lambda I)u_{j+1} \quad (1.4.10)$$

for j=1,2,..., m-1.

Remark.1.

u_j given by (1.4.10) is a generalized eigenvector of rank j corresponding to the eigenvalue λ.

Remark.2.

A Chain is a linearly independent set of vectors.

Remark.3.

A generalized eigenvector of rank 1 is in fact an eigenvector.

Theorem.4. (without proof).

Every n x n matrix A possesses n linearly independent generalized eigenvectors, abbreviated liges. Generalized eigenvectors corresponding to distinct eigenvalues are linearly independent. If λ is an eigenvalue of A of multiplicity μ, then A will have μ liges corresponding to λ.

Defn.7.

A set of n liges is a canonical basis if it is composed entirely of chains.

We now generalize the concept of a modal matrix yielding the following defnition.

Defn.8.

Let A be an n x n matrix. A *generalized modal* matrix M for A is an n x n matrix whose columns, considered as vectors, form a canonical basis for A and appear in M according to the following rules.

(i) All chains consisting of one vector appear in the first columns of M.

(ii)Each chain appears in M in order of increasing rank(i.e. the generalized eigenvector of rank 1 appears before the generalized eigenvector of rank 2 of the same chain, which appears before the generalized eigenvector of rank 3 of the same chain, e.t.c.)

Defn.9. Jordan canonical matrix

A square matrix J   is in Jordan canonical form if it is a
diagonal matrix or can be expressed in either one of the
following two partitioned forms.

$$
\begin{bmatrix}
D & 0 & . & . & . & . & 0 \\
0 & J_1 & 0 & . & . & . & 0 \\
0 & 0 & J_2 & 0 & . & . & 0 \\
. & . & . & . & . & . & . \\
0 & 0 & 0 & . & . & 0 & J_q
\end{bmatrix}
$$

(1.4.11)

or

$$
\begin{bmatrix}
J_1 & 0 & . & . & . & . & 0 \\
0 & J_2 & 0 & . & . & . & 0 \\
0 & 0 & J_3 & 0 & . & . & 0 \\
. & . & . & . & . & . & . \\
0 & 0 & 0 & . & . & 0 & J_q
\end{bmatrix}
$$

(1.4.12)

where D is a diagonal matrix, $\emptyset$'s are null matrices and
J_k (k=1,2,...,q) is given by

$$
J_k =
\begin{bmatrix}
\lambda_k & 1 & 0 & . & . & . & 0 & 0 \\
0 & \lambda_k & 1 & 0 & . & . & 0 & 0 \\
. & . & . & . & . & . & . & . \\
0 & 0 & 0 & . & . & 0 & \lambda_k & 1 \\
0 & 0 & 0 & . & . & . & 0 & \lambda_k
\end{bmatrix}
$$

(1.4.13)

Remark.

Here k represents some +ve integer and has no direct bearing
on the order of J_k. A matrix in Jordan canonical form has

non-zero elements on the superdiagonal and the main
diagonal, and that the elements on the superdiagonal are
restricted to be either zero or one. In particular, a
diagonal matrix is a matrix in Jordan canonical form that
has all its superdiagonal elements equal to zero.

Theorem.5.

Every n x n matrix A is similar to a matrix in Jordan
canonical form.

Proof.

If $\{u_m, u_{m-1}, \ldots, u_1\}$ is a chain generated by u_m, then
rewriting (1.4.10) we have

$$Au_{j+1} = \lambda u_{j+1} + u_j \qquad (1.4.14)$$

for $j = 1, 2, \ldots, m-1$. Next, each complete chain of more than
one vector in length that goes into composing M Will give
rise to a J_k submatrix in J. The order of J_k is identical
to the length of the chain. The chains consisting of only
one vector give rise collectively to the D submatrix in J.
The elements on the diagonal of D would be the eigenvalues
corresponding to the one element chains. Analogously to
(1.4.8) we have

$$A M = M J \qquad (1.4.15)$$

Noting that $|M| \neq 0$ (see thm.4.), we postmultiply (1.4.15)
by M^{-1} yielding

$$A = M J M^{-1} \qquad (1.4.16)$$

CHAPTER.2: AGE STRUCTURED MATRIX POPULATION MODEL

2.1. Basic Concepts of Matrix Population Model

Introduction.

We shall now explore the basic concepts associated with the matrix population models.   These concepts shall be discussed under a special class of matrices viz the Non-negative matrices.

We shall be devoted to the exposition and proof of results concerning the eigenvalues and eigenvectors of Non-negative matrices. We will, in particular, be interested in the existence of a non-negative or strictly positive eigenvector and of a positive largest eigenvalue.

Non-negative matrices

Defn.1. Non-negative matrix

A matrix A with real elements $A=(a_{ij})$ $(i=1,2,\ldots,m;j=1,2,\ldots,n)$ is said to be non-negative denoted $(A\geq 0)$ or positive denoted $(A>0)$, if all the elements of the matrix A are non-negative (respectively positive): $a_{ij}\geq 0$ (respectively $a_{ij}>0$).

Corr.

If $A\geq 0$, $B>0$, $AB=0$ then $A=0$

If $A\geq 0$ then $A^m\geq 0$ for a finite integer m.

If $A>0$ then $A^m>0$ for a finite integer m.

Defn.2. Permutation matrix.

An n x n Permutation matrix P is one in which there is a

single element equal to 1 in every row and column, all other elements being zero. In other words, the rows of P consists of a permutation of the rows of I_n. Premultiplying any n x m matrix A by P has the effect of applying the same permutation to the rows of A. Similarly regarding the columns of P as a (different) permutation of the columns of I_n, then postmultiplying an m x n matrix by P performs this permutation on its columns. We remark that $P' = P^{-1}$ for a permutation matrix.

Defn.3. Reducible matrix.

An n x n matrix A is reducible (or decomposable) if there exists a permutation matrix P such that

$$P'AP = \begin{bmatrix} A_1 & 0 \\ A_2 & A_3 \end{bmatrix} \qquad or \qquad \begin{bmatrix} A_1 & A_2 \\ 0 & A_3 \end{bmatrix}$$

$$(2.1.1)$$

where A_1 and A_3 are square submatrices. 0 is a rectangular null submatrix and A_2 is a rectangular submatrix. If A is not reducible it is called *irreducible* (or indecomposable).

Lemma.

Let $Z(x)$ denote the number of zero components of the vector **x**. Then, if A is non-negative and irreducible, and $x \geq 0$, $x \neq 0$ then

$$Z[(I+A)x] < Z(x) \qquad (2.1.2)$$

Proof.

Put $y = (I+A)x$. It is clear that $Z(y) \leq Z(x)$ (Since $Ax \geq 0$ and $y=(I+A)x$, any coordinate of y will be positive if the corresponding coordinate of the vector x is positive). Suppose that $Z(y) = Z(x)$, i.e the zero components of y are the same as those of x. Without lose of generality, it can be supposed that the column vectors y and x have the form

$$y = \begin{bmatrix} y_1 \\ 0 \end{bmatrix} \quad ; \quad x = \begin{bmatrix} x_1 \\ 0 \end{bmatrix}$$

where x_1, y_1, have the same dimension and are strictly positive. Corresponding to the above subdivision, we set

$$A = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix}$$

where A_{ij}, $(i,j=1,2)$ are submatrices and in particular A_{11} are square.

$$\begin{bmatrix} y_1 \\ 0 \end{bmatrix} = \begin{bmatrix} I+A_{11} & A_{12} \\ A_{21} & I+A_{22} \end{bmatrix} \begin{bmatrix} x_1 \\ 0 \end{bmatrix}$$

$y_1 = (I+A_{11})x_1$ implies $0 = A_{21}x_1$. These requires $A_{21}=0$, since $x_1>0$, which contradicts the assumption of irreducibility. Therefore the number of zero components of y is strictly less than those of x.

Corr.

If A is non-negative, and irreducible of order n, then

$$(I+A)^{n-1} > 0 \qquad (2.1.3)$$

Proof.

If we take any non-negative vector x and apply the lemma

repeatedly, then $(I+A)^{n-1}$ x can have no zero components. As x is arbitrary we must have $(I+A)^{n-1} > 0$.

Theorem.1. Due to Perron.

An nxn positive matrix $A = (a_{ij})$ always has an eigenvalue r which is real and positive, which is a simple root of the characteristic equation, and which exceeds in modulus all other eigenvalues. To this dominant (or maximal) eigenvalue there corresponds an eigenvector of the matrix A with positive coordinates.

Remark.

A positive matrix is a special case of a non-negative matrix. Frobenius generalized the theorem of Perron in an investigation of the spectral properties of irreducible non-negative matrices.

Theorem.2. Due to Frobenius.

An irreducible non-negative matrix A of order nxn always has a positive eigenvalue r, which is a simple root of the characteristic equation. The moduli of all the other eigenvalues are at most r. In the special case when A is positive then r is strictly greater than the modulus of any other eigenvalue.

Remark.

Since the theorem of Perron is a special case of the theorem of Frobenius, it suffices to give a proof of the latter.

Proof.

Define a number $r(\mathbf{v}^*)$ associated with the matrix A and

demonstrating its properties. The number is defined by

$$r(v^*) = Max_{v \in S} \{ \min_{1 \le i \le n} \frac{(Av)_i}{v_i} \}$$

<div align="right">(2.1.4)</div>

for i=1,2,...,n; where

$$S = \{v \ / \ v \ge 0, \ \sum_{i=1}^{n} v_i = 1\}$$

$(Av)_i$ is the ith component of the vector Av and v^* is the vector for which the maximum occurs. In words $r(v^*)$ is found by taking weighted sums of the rows of A and choosing the row i with the lowest ratio of this weight to the weight for the ith element of each row (i.e. the ith column); then we maximize this value over all possible weightings. Now since A $\ge$ 0, v $\ge$ 0, we can easily show that $r(v^*) \ge 0$(strictly positive if at least one element of each row and column is strictly positive).

Let v = u =(1/n,1/n,...,1/n) $\in$ S. Then

$$r(u) = \min_i \frac{(Au)_i}{u_i} = \min_i (1/n) \frac{(A\,1)_i}{(1/n)} = \min_i \sum_{j=1}^{n} a_{ij} \ge 0$$

Since A $\ge$ 0. By definition

<div align="center">

$r(v^*) \ge r(u) \ge 0$ (2.1.5)

</div>

Thus, we see that $r(v^*)$ is greater or equal to the minimum row sum of the matrix. We now show that $r(v^*)$ gives us the maximum value which might be taken by an eigenvalue of A; in

other words $r(\mathbf{v}^*)$ is the *largest* number satisfying the
inequality :

$$A\ \mathbf{v} \geq r\ \mathbf{v}$$

The kth component of the inequality gives

$$\frac{(A\mathbf{v})_k}{v_k} \geq r \qquad i.e. \qquad r \leq \min_k \frac{(A\mathbf{v})_k}{v_k}$$

Clearly for a maximum of r we will have the equality with
$r=r(\mathbf{v}^*)$. If this is not an equality, then

$$[A\mathbf{v}^* - r(\mathbf{v}^*)\mathbf{v}^*] \geq \emptyset$$

(i.e.is a non-negative vector).   We multiply it by the
strictly positive matrix $(I+A)^{n-1}$ (see (2.1.3)) to obtain
$(I+A)^{n-1}[A\mathbf{v}^* - r(\mathbf{v}^*)\mathbf{v}^*] > \emptyset$.
Noting that $(I+A)^{n-1}A = A(I+A)^{n-1}$ and putting
$\mathbf{y} = (I+A)^{n-1}\mathbf{v}^*$ we get

$$A\ \mathbf{y} - r(\mathbf{v}^*)\mathbf{y} > \emptyset.$$

However, this contradicts the fact that $r(\mathbf{v}^*)$ is the maximum
over all r, so that we must have equality in $A\ \mathbf{v}^* \geq r(\mathbf{v}^*)\mathbf{v}^*$
i.e. in other words $r(\mathbf{v}^*)$ is an eigenvalue of A and $\mathbf{v}^*$ the
associated eigenvector, more precisely

$$A\ \mathbf{v}^* = r(\mathbf{v}^*)\mathbf{v}^* \qquad\qquad (2.1.6)$$

If $r(\mathbf{v}^*)$ is an eigenvalue of A, $1+r(\mathbf{v}^*)$ must be an
eigenvalue of I+A (see thm.2, sec.1.4), and thus
$[1+r(\mathbf{v}^*)]^{n-1}$ will be an eigenvalue of $(I+A)^{n-1}$ with $\mathbf{v}^*$ as
the eigenvalue in each case.

Since $(I+A)^{n-1}$ is strictly positive we have

$[1+r(v^*)]^{n-1}v^* = (I+A)^{n-1}v^* > \emptyset$ and using (2.1.5) we have

$$v^* > \emptyset \qquad (2.1.7)$$

Now consider any other eigenvalue λ with eigenvector x so that $Ax = \lambda x$. Take the absolute values and put $x^+ = (|x_1|, |x_2|, ..., |x_n|)$ so that we get

$$|\lambda| x^+ \leq |\lambda x| = |Ax| = Ax^+$$

(Since $|a||b| \leq |ab|$ for any real numbers a and b and $|Ax| = Ax^*$ by the non-negativity of A). But $r(v^*)$ is the largest number satisfying this inequality.

Therefore $|\lambda| x^+ \leq r(v^*)x^+ \leq Ax^+$. Hence

$$r(v^*) \geq |\lambda| \qquad (2.1.8)$$

for every eigenvalue of A, we will call $r(v^*)$ the *dominant* root of A and denote it by λ^*.

Further it is clear that λ^* *cannot* be a repeated eigenvalue. Suppose not, so that there was another vector x^* which would have to be strictly positive by the above argument and not equal to v^* such that $Ax^* = \lambda^* x^*$. Now we can choose x^* such that $\Sigma_i x^*_i = 1$, so that since $x^* \neq v^*$ for some i, $x_1^* > v_1^*$. Subtracting the two eigenvector equations we get

$$A(v^* - x^*) = \lambda^*(v^* - x^*) \qquad (2.1.9)$$

In other words the vector $(v^* - x^*)$, which must have a negative element, is another eigenvector associated with λ^*. This contradicts the demonstration that the vector associated with λ^* must be strictly positive (see (2.1.6) & (2.1.7)). Hence λ^* cannot be a repeated eigenvalue.

If A is a strictly positive matrix we can show that $\lambda^* > |\lambda|$ for all $\lambda \neq \lambda^*$. Suppose not, so that $\lambda^* = -\lambda_1$. Consider $B = A - \delta I$ with two of its eigenvalues $\lambda^* - \delta$, $\lambda_1 - \delta$. Since $A > 0$, for small enough δ, $B > 0$ so that its largest eigenvalue is $\lambda^* - \delta$ (see thm.2, sec. 1.4). But $|\lambda_1 - \delta| = |-\lambda^* - \delta| > |\lambda^* - \delta|$, which contradicts the fact that $\lambda^* - \delta$ is the dominant root of B. This shows that, if α is the smallest element in A, then $\lambda^* - \alpha \geq \lambda$ for any $\lambda \neq \lambda^*$ i.e. $\lambda^* \geq |\lambda| + \alpha$ and hence

$$\lambda^* > |\lambda| \qquad (2.1.10)$$

for all $\lambda \neq \lambda^*$.

Defn.4. Primitive Matrix

Let $A \geq 0$ be an irreducible matrix, and let the dominant eigenvalue be λ^*. Suppose there are exactly h eigenvalues of modulus λ^*, say $\lambda^* = \lambda_1$ then $\lambda_1 = |\lambda_2| = \ldots = |\lambda_h|$. If h=1, the matrix is called *primitive*. If h>1, the matrix is called *imprimitive* and the number h is called the *index of imprimitivity*. The index of imprimitivity can be quickly calculated if all the non-zero coefficients of the characteristic equation

$$\lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + \ldots + a_{n-2}\lambda^2 + a_{n-1}\lambda + a_n = 0$$

of the matrix are known. More precisely, we suppose that $a_i > 0$ for $(i = \alpha_1, \alpha_2, \ldots, \alpha_{q-1}; q \leq n)$ and n where $\alpha_1 < \alpha_2 < \ldots < \alpha_{q-1} < n$. The exponents of λ appearing in the characteristic equation are then n, $n-\alpha_1$, $n-\alpha_2$, ..., $n-\alpha_{q-1}$, 0 and considering the differences $\alpha_1, \alpha_2 - \alpha_1, \ldots, \alpha_{q-1} - \alpha_{q-2}$, $n - \alpha_{q-1}$;

A is primitive iff the g.c.d. of these
differences is one. i.e. h=1 where

$$h = g.c.d\{a_1, a_2-a_1, \ldots, a_{q-1}-a_{q-2}, n-a_{q-1}\} \qquad (2.1.11)$$

This is also a necessary and sufficient condition for
primitivity.

The following theorem gives an important property of
primitive matrices.

Theorem.3.

A non-negative matrix A≥0 is primitive iff there is a power
of A which is positive i.e. $A^p > 0$ for some integer p.

Defn.5. Change in sign

Given a polynomial $f(\lambda)$ of degree n, a change in sign is
said to occur if two successive terms have opposite signs,
missing terms being ignored. On the other hand a
continuation is said to occur whenever the signs of two
consecutive terms are the same.

Defn.6. Descarte´s rule of signs

(i) The number of positive roots cannot exceed the number of
changes in sign of $f(\lambda)$.

(ii)The number of negative roots cannot exceed the number of
changes in sign of $f(-\lambda)$.

Remark.

Whilst Descarte´s rule does not give the exact number of
real roots in an equation, it has the merit of simplicity.
It still leaves an uncertainty as to the exact number of
real roots in an equation, it only gives an upper limit to

them.

Defn.6. Companion matrix

An nxn Companion matrix C is defined as

$$
C = \begin{bmatrix}
k_1 & k_2 & k_3 & . & . & . & k_{n-2} & k_{n-1} & k_n \\
1 & 0 & 0 & . & . & . & 0 & 0 & 0 \\
0 & 1 & 0 & . & . & . & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & . & . & 0 & 0 & 0 \\
. & . & . & . & . & . & . & . & . \\
0 & 0 & 0 & . & . & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & . & . & . & 0 & 1 & 0
\end{bmatrix}
$$

(2.1.12)

The nth degree polynomial

$$f(\lambda)=\lambda^n -k_1\lambda^{n-1} -k_2\lambda^{n-2} - \ldots -k_{n-1}\lambda -k_n \qquad (2.1.13)$$

is associated with the Companion matrix or more precisely the characteristic equation of C is

$$| \lambda I_n - C| \qquad (2.1.14)$$

and when expanded yields (2.1.13). The first row of C consists of coefficients of $f(\lambda)$ (except leading coefficient which is unity) with opposite signs. The polynomial $f(\lambda)$ is called *monic*, since its leading coefficient is one.

Remark.

Companion matrix is a basic tool which enables polynomial problems to be handled using matrices.

Defn.7. Leslie matrix

An nxn Leslie matrix L is defined as

$$L = \begin{bmatrix} f_1 & f_2 & f_3 & . & . & . & f_{n-1} & f_n \\ p_1 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & p_2 & 0 & . & . & . & 0 & 0 \\ . & . & . & . & . & . & . & . \\ 0 & 0 & . & . & . & 0 & p_{n-1} & 0 \end{bmatrix}$$

(2.1.15)

where $f_i \geq 0$ and $0 < p_i \leq 1$ ($i=1,2,\ldots,n$).

Remark.

If $p_i = 1$ for all $i=1,2, \ldots, n-1$; then L reduces to a Companion matrix C where $k_i = f_i$.

Defn.8. Vandermonde matrix

Given an nxn matrix A, having distinct eigenvalues $\lambda_1, \lambda_2, \ldots, \lambda_n$; the corresponding Vandermonde matrix has the form

$$V = \begin{bmatrix} \lambda_1^{n-1} & \lambda_2^{n-1} & . & . & . & \lambda_n^{n-1} \\ \lambda_1^{n-2} & \lambda_2^{n-2} & . & . & . & \lambda_n^{n-2} \\ . & . & . & . & . & . \\ \lambda_1^2 & \lambda_2^2 & . & . & . & \lambda_n^2 \\ \lambda_1 & \lambda_2 & . & . & . & \lambda_n \\ 1 & 1 & . & . & . & 1 \end{bmatrix}$$

(2.1.16)

Remark.

If λ_i is an eigenvalue of C then an associated eigenvector is

$$v_i = [\lambda_i^{n-1}, \lambda_i^{n-2}, \ldots, \lambda_i^2, \lambda_i, 1]' \qquad (2.1.17)$$

which is the ith column of the Vandermonde matrix.

Similarity between C and L.

Define a transformation matrix

$\Lambda = diag(p_1 p_2 \ldots p_{n-1}, \; p_2 p_3 \ldots p_{n-1}, \; p_3 p_4 \ldots p_{n-1}, \; \ldots, \; p_{n-1}, 1)$

and let $p_{(i)} = p_1 p_2 p_3 \ldots p_i$; $i = 1, 2, \ldots, n-1$ then we have

$$\Lambda L \Lambda^{-1} = \begin{bmatrix} f_1 & f_2\, p_{(1)} & f_3\, p_{(2)} & \cdots & f_{n-1}\, p_{(n-2)} & f_n\, p_{(n-1)} \\ 1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 1 & \cdots & 0 & 0 \\ \cdot & \cdot & \cdot & \cdots & \cdot & \cdot \\ 0 & 0 & 0 & \cdots & 1 & 0 \end{bmatrix}$$

(2.1.18)

we note that $\Lambda L \Lambda^{-1} = C$ where $k_1 = f_1$ and $k_i = f_i p_{(i-1)}$, $i = 2, 3, \ldots, n$. We conclude that L and C are similar (see defn.4, sec.1.4) and therefore they must have the same characteristic equation given by

$$\lambda^n - f_1 \lambda^{n-1} - f_2 p_{(1)} \lambda^{n-2} - f_3 p_{(2)} \lambda^{n-3} - \ldots \ldots - f_{n-1} p_{(n-2)} \lambda - f_n p_{(n-1)} = 0$$

(2.1.19)

Theorem.4.

Given that the ith column of V is an eigenvector of C corresponding to λ_1, then the ith column of $\Lambda^{-1} V$ is an eigenvector of L corresponding to λ_1.

Proof:

Let λ_i, $i = 1, 2, \ldots, n$ be distinct eigenvalues of a Companion matrix C and v_i their corresponding eigenvectors where v_i is given by (2.1.17).

$C v_i = \lambda_i v_i$ $i = 1, 2, \ldots, n$ and in matrix form

$\quad C \, [v_1, v_2, \ldots, v_n] = [v_1, v_2, \ldots, v_n] \, D$

where $D = \text{diag}(\lambda_1, \lambda_2, \ldots, \lambda_n)$.

From (2.1.16), (2.1.17) & (2.1.18) we have $CV = VD$ and $\Lambda L\Lambda^{-1} = VDV^{-1}$ which yields

$$L(\Lambda^{-1}V) = (\Lambda^{-1}V)D \qquad\qquad (2.1.20)$$

Therefore the columns of $\Lambda^{-1}V$ constitute the eigenvectors of L. In particular if v_1 is the eigenvector of C then $u_1 = \Lambda^{-1}v_1$ is the eigenvector of L corresponding to λ_1 in each case and

$$u_1 = [1, p_1/\lambda_1, p_1p_2/\lambda_1^2, p_1p_2p_3/\lambda_1^3, \ldots, p_1p_2p_3\ldots p_{n-1}/\lambda_1^{n-1}]'$$

$$(2.1.21)$$

Determining dominant eigenvalue.

Basically the application of the model which will be discussed in the next section will require the determination of the positive real root with maximum modulus and its corresponding eigenvector. One of the most widely used procedure is the power method.

The Power method.

Our basic assumptions are that A is a real nxn matrix, its eigenvalues satisfy

$$|\lambda_1| > |\lambda_2| \geq |\lambda_3| \geq \ldots \geq |\lambda_n| \qquad\qquad (2.1.22)$$

and that A has n linearly independent eigenvectors u_i, $i = 1, 2, \ldots, n$ where

$$A u_1 = \lambda_1 u_1 \qquad\qquad (2.1.23)$$

λ_1 is the *dominant* eigenvalue.

Since corresponding eigenvectors $u_1, u_2, \ldots, u_n$ are linearly independent they form a basis, so any arbitrary

column n-vector x_0 can be uniquely expressed as a linear combination of the basis vectors.

$$x_0 = a_1u_1 + a_2u_2 + \ldots + a_nu_n \qquad (2.1.24)$$

where a_i's are constants not all zero. If $x_1 = A\, x_0$, then from (2.1.23) we have

$$x_1 = a_1Au_1 + a_2Au_2 + \ldots + a_nAu_n = a_1\lambda_1u_1 + a_2\lambda_2u_2 + \ldots + a_n\lambda_nu_n$$

Similarly if $x_2 = Ax_1$, $x_3 = Ax_2$ e.t.c. we have

$$x_k = a_1\lambda_1^ku_1 + a_2\lambda_2^ku_2 + \ldots + a_n\lambda_n^ku_n, \qquad k = 1,2,\ldots \qquad \text{or}$$

equivalently

$$x_k/\lambda_1^k = a_1u_1 + a_2(\lambda_2/\lambda_1)^ku_2 + \ldots + a_n(\lambda_n/\lambda_1)^ku_n \qquad (2.1.25)$$

Since $|\lambda_1/\lambda_i| < 1$ for $i > 1$, it follows that as $k \to \infty$ the terms $(\lambda_1/\lambda_1) \to 0$, so that as $k \to \infty$

$$x_k/\lambda_1^k \to a_1u_1 \qquad (2.1.26)$$

i.e. x_k/λ_1^k tends to a multiple of the eigenvector u_1. However, as k increases the elements of x_k are growing quite large, so to avoid this it is preferable to scale x_k at each step so that its largest element is unity in order to keep within computational limits. We therefore define a modified sequence $x_1, x_2, \ldots$ as follows (i.e. 2.1.27/28/29)

$$y_{k+1} = A\, x_k \qquad k = 0,1,2,\ldots \qquad (2.1.27)$$

Let β_{k+1} = element of y_{k+1} having largest modulus (2.1.28)

$$x_{k+1} = y_{k+1}/\beta_{k+1} \qquad (2.1.29)$$

as k tend to ∞ we will have x_k tending to some multiple of u_1, so we can write

$$x_k \to mu_1 \qquad (2.1.30)$$

and then using (2.1.23), (2.1.27) & (2.1.30) we have

y_k tend to $A(mu_1)=m(Au_1)=m(\lambda_1 u_1)= \lambda_1(mu_1)$ and using (2.1.30) again we have

$$y_k \rightarrow \lambda_1 x_k \qquad (2.1.31)$$

as $k \rightarrow \infty$.

Because the largest element of x_k is unity and using (2.1.28) & (2.1.29), it follows that the element of y_k having largest modulus approaches λ_1, as k tend to ∞. Thus β_k and x_k defined by (2.1.27/28/29) respectively provide successively better approximations to λ_1 and u_1 and the process is terminated when x_{k+1} and x_k are sufficiently close or equivalently when β_{k+1} and β_k are sufficiently close.

We wish to be fairly careful about the description of the power method, for this description has two parts, namely the "practical" part which shows how the method is actually carried out, and the "theoretical" part (described above) which shows why the method works.

Power method "practical".

Recalling (2.1.25), it is natural to write x_k as

$$x_k = \lambda_1^k \{a_1 u_1 + a_2(\lambda_2/\lambda_1)^k u_2 + \ldots + a_n(\lambda_n/\lambda_1)^k u_n\} \qquad (2.1.32)$$

so that for large k, the approximation

$$x_k \approx \lambda_1^k(a_1 u_1) \qquad (2.1.33)$$

should be good because of (2.1.22).

In order to estimate λ_1 we replace k by k+1 in (2.1.31) to obtain

$$x_{k+1} \approx \lambda_1 x_k \qquad (2.1.34)$$

This suggests a number of ways to approximate λ_1. For example $x_k'x_{k+1} \approx \lambda_1 x_k'x_k$ and thus

$$\lambda_1 \approx x_k'x_{k+1}/x_k'x_k \qquad (2.1.35)$$

Another common procedure is to divide the largest component of x_k into the corresponding element of x_{k+1}. If the largest component is the jth, then this amounts to

$$\lambda_1 \approx e_j'x_{k+1}/e_j'x_k \qquad (2.1.36)$$

where e_j is the jth unit-vector. The estimates of λ_1 can be found by generating the sequence of scalars $\{\beta_k\}$ from the equation

$$\beta_k = v'x_{k+1}/v'x_k \qquad (2.1.37)$$

where v is usually x_k or e_j.

When programming the power method, it is a little easier to generate the estimate β_k from (2.1.35) than (2.1.36) which includes a test at each step to determine the maximum component of x_k (moreover the program will execute faster). The advantage in finding the maximum component of x_k is that round-off errors will tend to be reduced.

Finally, as k increases, the vectors x_k are usually growing quite large if $|\lambda_1| > 1$ (or quite small if $|\lambda_1| < 1$); It is desirable to "scale" or "normalize" x_k to keep within computational limits. This can be done by dividing x_k by $\|x_k\|$ at each step. The process is terminated when β_k and β_{k+1} are *sufficiently close*.

Power method program algorithm.

First an initial (arbitrary) vector $x_\emptyset$ is chosen where

$x_\emptyset' x_\emptyset = 1$ (i.e. $\|x_\emptyset\|_2 = 1$). The power method then proceeds for $i = 1, 2, \ldots$ as follows

(a) Let $y_i = Ax_{i-1}$ (b) Set $\beta_i = y_i' x_{i-1}$ (c) Let $\eta_i = \sqrt{(y_i' y_i)}$

(d) Set $x_i = y_i/\eta_i$ and return to step a. We note that β_i is the approximation to λ_1 and that each x_i is an approximate eigenvector.

Remark.

If $\lambda_1 = \lambda_2$, and $|\lambda_1| > |\lambda_3| \geq \ldots \geq |\lambda_n|$, then the β_i still converge to λ_1 (that is, multiple eigenvalues do not affect the power method). If $\lambda_1 = -\lambda_2$ and $|\lambda_1| > |\lambda_3| \geq \ldots \geq |\lambda_n|$, then the β_i would exhibit a periodic behaviour while $v' x_{i+2}/v' x_i$ would provide an estimate for $(\lambda_1)^2$. Dominant complex eigenvalues cause the most problems.

2.2 Age-Structured Model

Introduction.

In the sequel we shall introduce and discuss a discrete time model with a discrete age scale viz, the age-structured model put forward by Leslie (1945). The model is deterministic and predicts the age structure of a population of female animals, given the age structure at some past time (or present) and given the age-specific survival and fecundity rates.

Assumptions.

(i) The age-specific rates remain constant over a period of time.

(ii) Age groups are of equal length.

(iii)The same unit of age is adopted as that of time i.e.
time intervals have the same duration as the age
intervals.

(iv) No migration.

Formulation of the Matrix Projection Model.

Given any arbitrary age distribution at time t the
female population in one unit time, can be expressed in the
form of m+1 linear equations, where m to m+1 is the last age
group considered. Let

$$u_t = (u_{0t}, u_{1t}, \ldots, u_{mt})' \qquad (2.2.1)$$

be a column vector representing the population's age
structure at time t, where u_{it} is the number of females
alive in the age group i to i+1 at time t. A female in the
age group i to i+1 is described as of age i and since m to
m+1 is the last age group considered, none can live to be
older than m. The m+1 elements in the vector (2.2.1)
represent m+1 different age groups. u_{t+1} is a column vector
similar to u_t, but representing the age structure at time
t+1.

Age-specific rates.

Let

p_i=the probability that a female aged i to i+1 at time t
will be alive in the age group i+1 to i+2 at time t+1. $0 <$
$p_i \leq 1$ for i=0,1,2,...,m-1. These values are termed as the
survival rates.

f_i=the average number of daughters who will be alive at

time t+1 in the age group 0-1 born in the interval t to t+1
to each female who was in the age group i to i+1 at time t.
$f_i \geq 0$ for i = 0,1,2, ..., m and until the first unit of
time has passed their ages will be 0. These values are
termed as the *fecundity* rates.

Now, given the age distribution at time t=0

$$u_0 = (u_{00}, u_{10}, u_{20}, ..., u_{m0})' \qquad (2.2.2)$$

the age distribution at the end of one unit's interval

$$u_1 = (u_{01}, u_{11}, u_{21}, ..., u_{m1})' \qquad (2.2.3)$$

is obtained as follows:-

The total number of daughters who will be alive in the
age group 0-1 at time t=1 born by females who were alive in
the age group i to i+1 at time t=0 (i=0,1, ..., m) is given
by

$$u_{i0} \, f_i \qquad (2.2.4)$$

By definition of u_{01} we have

$$u_{01} = \sum_{i=0}^{m} u_{i0} \, f_i$$

$$(2.2.5)$$

The number of individuals who were in the age group i
to i+1 at t=0 who will be alive in the age group i+1 to i+2
at t=1 for i=0,1,2, ..., m is given by

$$u_{i+1,1} = p_i u_{i0} \qquad (2.2.6)$$

Thus

$$u_1 = \left[\sum_{i=0}^{m} u_{10}\, f_i \;,\; p_0\, u_{00},\; p_1\, u_{10},\; \cdots \;,\; p_{m-1}\, u_{m-1,0}\right]$$

$$u_1 = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_{m-1} & f_m \\ p_0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & p_2 & 0 \cdots & 0 & 0 \\ \cdot & \cdot & \cdot & \cdots & \cdot & \cdot \\ 0 & 0 & 0 & \cdots 0 & p_{m-1} & 0 \end{bmatrix} \begin{bmatrix} u_{00} \\ u_{10} \\ u_{20} \\ \cdot \\ \cdot \\ u_{m0} \end{bmatrix}$$

(2.2.7)

$$u_1 = M\, u_0 \tag{2.2.8}$$

where in general the $(m+1) \times (m+1)$ matrix M describes the transition of the population from one age structure to another over one period of time. The matrix M is called the *Projection matrix*, and often referred to as *Leslie matrix* (cf.(2.1.15)). (2.2.8) defines the *Projection Matrix Model* or the *Age-Structured Model*.

$$u_2 = M\, u_1 = M(M\, u_0) = M^2\, u_0 \tag{2.2.9}$$

and in general for $t = 0,1,2,\ldots$

$$u_t = M^t\, u_0 \tag{2.2.10}$$

Properties of the Basic matrix M.

The matrix M is square of order $m+1$; it is not necessary, however, in what follows to consider this matrix as a whole. For if $i=k$ is the largest age within which reproduction occurs, or rather females are sterile in the last $m-k$ age groups, f_k is the last f_i figure which is not equal to zero.

The matrix M can now be partitioned as follows

$$M = \begin{bmatrix} A & 0 \\ B & C \end{bmatrix}$$

(2.2.11)

The submatrix A is square of order k+1, B is of order (m-k) x (k+1), C is square of order m-k with only non-zero elements in the subdiagonal immediately below the principle diagonal. The remaining submatrix is null and of order (k+1) x (m-k). On investigating the powers of M it is found that

$$M^t = \begin{bmatrix} A^t & 0 \\ f(ABC) & C^t \end{bmatrix}$$

(2.2.12)

where

$$f(ABC) = \sum_{j=0}^{t-1} C^j B A^{t-j-1}$$

(2.2.13)

$C^0 = A^0 = I$ and since $C^{m-k} = 0 \rightarrow C^t = 0 \ \forall \ t \geq m-k$ (2.2.14)

In biological terms this is merely an expression of the obvious fact that individuals alive in the post-reproductive ages contribute nothing to the population. The terms of f(ABC) are zero for j>m-k-1, and so f(ABC) has only m-k terms, each of which is readily computed if we know the powers of A.

$\lim_{t \to \infty} f(ABC) = \lim_{t \to \infty} (BA^{t-1} + CBA^{t-2} + \ldots + C^{m-k-1} BA^{t-(m-k)})$

$\qquad\qquad = (I + C + \ldots + C^{m-k-1}) \ B \ \lim_{t \to \infty} A^t$

$$= (I-C)^{-1}(I-C^{m-k}) \ B \ \lim_{t \to \infty} A^t$$

$$= (I-C)^{-1} \ B \ \lim_{t \to \infty} A^t \qquad (2.2.15)$$

so that if $\lim_{t \to \infty} A^t$ is known, $\lim_{t \to \infty} M^t$ is easy to find.

It is a submatrix A of M which is principally of interest, and in mathematical discussion which follows, attention is focused entirely on it and on age distributions confined to the pre-productive and reproductive age groups.

The matrix A is of order $(k+1)x(k+1)$ where $i=k$ is the last age group in which reproduction occurs, and written in full,

$$A = \begin{vmatrix} f_0 & f_1 & f_2 & . & . & . & f_{k-1} & f_k \\ p_0 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & p_1 & 0 & . & . & . & 0 & 0 \\ . & . & . & . & . & . & . & . \\ 0 & 0 & . & . & . & 0 & p_{k-1} & 0 \end{vmatrix}$$

$$(2.2.16)$$

Therefore we shall only consider the reduced model

$$u_{t+1} = A \ u_t \qquad (2.2.17)$$

for $t=0,1,2,...$ where

$$u_t = (u_{0t}, u_{1t}, ..., u_{kt}) \qquad (2.2.18)$$

is of course now taken to be $(k+1)$-dimensional. We shall from now henceforth treat the population under study only that part of the total population that is of reproductive age, i.e. we consider A only.

Repeated premultiplication by A of the column vector u_0 permits prediction of the future growth and age distribution of the reproducing part of the population made up of females

aged k or less, i.e.

$$u_t = A^t u_\emptyset \qquad (2.2.19)$$

Contribution to future population.

Moreover, it will be seen that with the help of the $(j+1)^{th}$ column of A^t we can predict the contribution of some one particular age group, i.e. those of age j at time t=0 say, to the population at some future time t. This can be obtained as follows.

Let the population projection matrix be A and $A^t=(a_{ij})$ i,j=0,1,2,...,k. Then using (2.2.19) we have

$$\begin{bmatrix} a_{00} & a_{01} & \cdot & \cdot & \cdot & a_{0k} \\ a_{10} & a_{11} & \cdot & \cdot & \cdot & a_{1k} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a_{k0} & a_{k1} & \cdot & \cdot & \cdot & a_{kk} \end{bmatrix} \begin{bmatrix} u_{00} \\ u_{10} \\ \cdot \\ u_{k0} \end{bmatrix} = \begin{bmatrix} u_{0t} \\ u_{1t} \\ \cdot \\ u_{kt} \end{bmatrix}$$

Showing only those contributions to the elements in u_t that come from the elements $u_{j\emptyset}$ of $u_\emptyset$ we have

$$\begin{bmatrix} \cdot & \cdot & + & a_{0j}\,u_{j0} & + & \cdot & \cdot \\ \cdot & \cdot & + & a_{1j}\,u_{j0} & + & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & & \cdot & \cdot \\ \cdot & \cdot & + & a_{kj}\,u_{j0} & + & \cdot & \cdot \end{bmatrix} = \begin{bmatrix} u_{0\,t} \\ u_{1\,t} \\ \cdot \\ u_{k\,t} \end{bmatrix}$$

$$(2.2.20)$$

At time t, provided t>k, every element in u_t has some contribution from the $u_{j\emptyset}$ individuals that were of age j at the start. At time t the number of living individuals contributed to the total population at time t by this particular age group for j=0,1,2,...,k is

$$u_{j0} \sum_{i=0}^{k} a_{ij}$$

<div align="right">(2.2.21)</div>

which is the product of the number in the age group j to j+1
(referred to as of age j) at time t=0 and the sum of the
elements in the $(j+1)^{th}$ column of A^t. The age group j to
j+1 is the ancestral age group we are concerned with in
knowing the number of individuals it will contribute to the
total population at time t. Moreover, it is noticeable that
for i=0,1,2,...,k the number contributed to u_{it} in
particular, is given by

<div align="center">$a_{ij} u_{j0}$ (2.2.22)</div>

i.e. the product of the $(i,j)^{th}$ element of A^t and the number
in the age group j to j+1 at time t=0.

Backward Projection.

The matrix A is non-singular, since the determinant

$$| A | = (-1)^{k+2} (p_0 p_1 p_2 ... p_{k-1} f_k) \neq 0 \qquad (2.2.23)$$

and therefore there exists an inverse of A.

In order to discover the age composition of a population
prior to the time say t at which it came under observation
provided we concern ourselves only with reproducing part of
the population, having a projection matrix of the form A
there is no difficulty since A^{-1} exits. The backward
projection is described by the backward series $A^{-1}u_0$, $A^{-2}u_0$,
$A^{-3}u_0$, ... e.t.c.

Remark.

Whereas the forward series can be continued indefinitely into the future given any initial age distribution, the backward series can only be performed so long as $u_{1t} \geq 0$, since biologically a negative number of individuals in an age group is meaningless.

Algebraic Properties of the Matrix A.

A is square matrix of order k+1. A is a non-negative matrix, a characteristic of projection matrices. A is non-singular (see (2.2.23)).

We shall now show that A is irreducible so that the Perron-Frobenius theorem (see P-F thm. sec. 2.1)applies to this matrix. A can be expressed as the sum of two matrices A_s and A_f as follows:

$A = A_s + A_f$ i.e.

$$A = \begin{bmatrix} 0 & 0 & . & . & 0 & 0 \\ p_0 & 0 & . & . & 0 & 0 \\ 0 & p_1 & . & . & 0 & 0 \\ . & . & . & . & . & . \\ 0 & 0 & . & . & p_{k-1} & 0 \end{bmatrix} + \begin{bmatrix} f_0 & f_1 & . & . & f_{k-1} & f_k \\ 0 & 0 & . & . & 0 & 0 \\ 0 & 0 & . & . & 0 & 0 \\ . & . & . & . & . & . \\ 0 & 0 & . & . & 0 & 0 \end{bmatrix}$$

$$(2.2.24)$$

Without loss of generality, we may restrict ourselves to matrix A_s with $f_0 = f_1 = ... = f_{k-1} = 0$ and $f_k > 0$, since we can easily show that if A_s is irreducible, then so is a more general matrix A, where A_f can have non-zero elements only in the first row.

Suppose that A_s is irreducible and A is reducible, then

there exist a permutation matrix P (see defn.3, sec.2.1) such that

$$P'AP = P'(A_g + A_f)P = P'A_g P + P'A_f P = \begin{bmatrix} A_1 & 0 \\ A_2 & A_3 \end{bmatrix}$$

(2.2.25)

where A_1 and A_3 are square. Since $A_f \geq 0$ then $P'A_fP \geq 0$ and $P'A_gP$ is not of the required form by hypothesis. Hence A is irreducible, since the addition of the non-negative matrix to the matrix not already of the required form cannot result in a sum of that form.

Using (2.1.19), the characteristic equation of A is

$$\lambda^{k+1} - f_0\lambda^k - f_1 p_0\lambda^{k-1} - f_2 p_0 p_1\lambda^{k-2} - \ldots - f_{k-1}p_0 p_1 \ldots p_{k-2}\lambda - f_k p_0 p_1 \ldots p_{k-1} = 0$$

(2.2.26)

We can now assert that the matrix A has *exactly one* positive real root say λ_1 since on applying Descarte's rule of signs (see defn.6, sec. 2.1) to the characteristic equation (2.2.26) we find that the number of positive real roots is *at most one*, and since A is non-negative and irreducible, the Perron-Frobenius theorem tells us there is *at least one*. Hence the remaining roots of A are negative or complex.

Also by Perron-Frobenius theorem the moduli of these remaining roots are at most λ_1. λ_1 is referred to as the *dominant root* and a characteristic vector u_1 say, corresponding to λ_1 is positive (see pf of P.F.thm.sec.2.1)

A is primitive iff the index of primitivity is one. In particular, if $f_i > 0$ for all $i=1,2, \ldots, k+1$, $h=1$ and hence A is primitive. If $h>1$ then A is imprimitive (see defn.4, sec.2.1).

We remark that if a projection matrix A is primitive the powers A^t approach a limiting form. In fact A^t (and hence u_t) will behave periodically if A is imprimitive with period equal to the index of imprimitivity. Pure periodicity is displayed when the initial age distribution u_0 is repeated periodically. We suppose that $h=k+1$ such that

$$A^{k+1} = nI \qquad (2.2.27)$$

i.e. nu_0 will be repeated periodically with period $k+1$. Cayley Hamilton theorem says that every square matrix satisfies its own characteristic equation therefore from the characteristic equation of A.

$$A^{k+1}-f_0 A^k-f_1 p_0 A^{k-1}- \ldots -f_{k-1}p_0 p_1 \ldots p_{k-2}A-f_k p_0 p_1 \ldots p_{k-1}I = 0$$
$$(2.2.28)$$

and for (2.2.27) to be satisfied we must have

$$f_0 = f_1 = \ldots = f_{k-1} = 0 \qquad (2.2.29)$$

and

$$f_k p_0 p_1 \ldots p_{k-1} = n \qquad (2.2.30)$$

Expression (2.2.29) results in the special case of the matrix A having only a single non-zero element in the first row. Whenever $n=1$ in (2.2.30) pure periodicity will be displayed.

The question of approximation to case of pure

periodicity may be of practical importance, for some lower animals with few age groups whose individuals are fertile for only a short period right at the end of their lives e.g. some locust species.

An interesting example of a case in which the requirement of primitivity is not met is provided by a hypothetical insect population(such as beetle), which lives for only three years and which propagates in the third year of life, considered by Bernardelli (1941) and referred to by Leslie (1945). The system of survival and fecundity rates is given by

$$A = \begin{bmatrix} 0 & 0 & 6 \\ 1/2 & 0 & 0 \\ 0 & 1/3 & 0 \end{bmatrix}$$

(2.3.31)

Biologically this can be interpreted as each female in the age group 2-3 produces, on the average, 6 new living females.

The matrix A above is clearly not primitive and the dominant root is not larger than the moduli of all other roots. In fact roots of this matrix are of the same modulus. Any initial age distribution repeats itself regularly every three years.

In the next section we shall particularly be concerned with primitive projection matrices and investigate on their limiting behaviour.

2 .3. Stable Population Theory.

Introduction.

Formally it was remarked that if a projection matrix A is primitive then the powers A^t approach a limiting form. In this section we are concerned with the behaviour of the sequence $\{u_t\}$ over long periods of time or the stable population theories in discrete version.

Theorem.1.

Let A be a primitive population projection matrix with dominant eigenvalue λ_1 and associated(right) positive eigenvector u_1. Then

$$\lim_{t \to \infty} (A/\lambda_1)^t = H_1 \qquad (2.3.1)$$

exists, where H_1 is a matrix whose columns are positive multiples of u_1. (H_1 is of rank 1).

Remark.

The requirement that A be primitive ensures that λ_1 is the only eigenvalue of maximum modulus. To establish the above result (i.e. (2.3.1)) we shall assume that the remaining eigenvalues λ_1, (i=2,3,..., k+1) of A are distinct and then show that they need not be distinct in order for the above limit to exist.

Proof.

Suppose that λ_1, (i=2,3,...,k+1) are distinct then A is diagonalizable and is similar to a diagonal matrix $D=\text{diag}(\lambda_1,\lambda_2,...,\lambda_{k+1})$. Since complex roots occur in conjugate pairs, the moduli of these eigenvalues need not be

distinct.

Let U be a matrix whose columns constitute the eigenvectors of A. The eigenvalues may be made to appear on the diagonal of D in any desired order by suitable choice of U(see defn.4, sec. 1.4). Suppose they are arranged in order of decreasing modulli, i.e. $|\lambda_1| > |\lambda_2| \geq |\lambda_3| \geq \ldots \geq |\lambda_{k+1}|$.

$$A = U \, D \, U^{-1} \tag{2.3.2}$$

and for the tth power of A we have

$$A^t = U \, D^t \, U^{-1}$$

$$= U \begin{bmatrix} \lambda_1^t & 0 & . & . & . & 0 \\ 0 & \lambda_2^t & 0 & . & . & 0 \\ . & . & . & . & . & . \\ 0 & 0 & . & . & 0 & \lambda_{k+1}^t \end{bmatrix} U^{-1}$$

$$\tag{2.3.3}$$

and dividing both sides by λ_1^t we have

$$\frac{A^t}{\lambda_1^t} = U \begin{bmatrix} 1 & 0 & . & . & . & 0 \\ 0 & (\frac{\lambda_2}{\lambda_1})^t & 0 & . & . & 0 \\ . & . & . & . & . & . \\ 0 & 0 & . & . & 0 & (\frac{\lambda_{k+1}}{\lambda_1})^t \end{bmatrix} U^{-1}$$

$$\tag{2.3.4}$$

But $|\lambda_i/\lambda_1| < 1$ for i=2,3,...,k+1 so that

$$\lim_{t \to \infty} \frac{A^t}{\lambda_1^t} = U \begin{bmatrix} 1 & 0 & . & . & 0 \\ 0 & 0 & . & . & 0 \\ . & . & . & . & . \\ 0 & 0 & . & . & 0 \end{bmatrix} U^{-1} = H_1$$

(2.3.5)

H_1 is a square matrix of rank 1. Moreover, columns of H_1 are *positive multiples* of u_1. The fact that columns of H_1 are positive multiples will be made clear later.

Suppose now that the remaining eigenvalues λ_i, i=2,3, ..., k+1 are not distinct. Let the distinct roots be λ_1 and λ_i, i=2,3,...,q < k+1 and if λ_i has multiplicity n_i then A is similar to a matrix J in Jordan canonical form i.e. there exists a generalized modal matrix M for A (see defn.8 and thm.5,sec. 1.4) such that

$$A = M \ J \ M^{-1}$$

$$= M \begin{bmatrix} J_1 & 0 & . & . & . & 0 & 0 \\ 0 & J_2 & 0 & . & . & 0 & 0 \\ . & . & . & . & . & . & . \\ 0 & 0 & . & . & . & 0 & J_q \end{bmatrix} M^{-1}$$

(2.3.6)

where J_i, i=1,2,..., q; is given by (1.4.12) is an $n_i \times n_i$ square matrix with diagonal elements λ_i, 1's on the superdiagonal and zeros elsewhere. The tth power of A is

$$A^t = M \begin{bmatrix} J_1^t & 0 & . & . & . & 0 \\ 0 & J_2^t & 0 & . & . & 0 \\ . & . & . & . & . & . \\ 0 & 0 & . & . & 0 & J_q^t \end{bmatrix} M^{-1}$$

(2.3.7)

J_1 can be expressed as

$$J_1 = \lambda_1 I_n + B_n \qquad (2.3.8)$$

where I_n is the identity matrix of order n_1 and B_n is a $n_1 \times n_1$ square matrix whose elements are zero everywhere except for ones on the superdiagonal. Noting that $IB=BI$ and for $x \geq n_1$

$$B^x = \emptyset \qquad (2.3.9)$$

Using binomial theorem and (2.3.9) (dropping subscript n_1 for convenience) the expansion of $J_1{}^t$ is given by

$$J_1{}^t = (\lambda_1 I + B)^t$$

$$= \sum_{x=0}^{t} \binom{t}{x} (\lambda_1 I)^x B^{t-x}$$

$$= \sum_{y=0}^{n_1-1} \binom{t}{t-y} (\lambda_1 I)^{t-y} B^y$$

$$(2.3.10)$$

Since A is primitive, $J_1 = \lambda_1$ and first column of M is u_1, (see defn.8, sec. 1.4 and defn.4, sec.2.1) so that

$$\lim_{t \to \infty} (J_1/\lambda_1)^t = 1 \qquad (2.3.11)$$

For $i \neq 1$

$$\lim_{t \to \infty} \left(\frac{J_i}{\lambda_1}\right)^t = \sum_{y=0}^{n_1-1} \left\{ \lim_{t \to \infty} \binom{t}{t-y} \left(\frac{\lambda_1 I}{\lambda_1}\right)^t \right\} \left(\frac{B}{\lambda_1}\right)^y$$

$$(2.3.12)$$

We note that

$$1/y!\{t(t-1) \ldots (t-(y-1))\} < t^y \qquad (2.3.13)$$

and for $\lambda_1 > \lambda_1$

$$\theta_i = \log_e \lambda_1 - \log_e \lambda_1 = \log_e(\lambda_1/\lambda_1) > \emptyset \qquad (2.3.14)$$

$$\therefore \; (\lambda_1/\lambda_1)^t = \exp(-\theta_1 t) \tag{2.3.15}$$

Using (2.3.13/14/15) we have

$$\lim_{t \to \infty} (J_1/\lambda_1)^t = \emptyset \tag{2.3.16}$$

and finally using (2.3.11/16)

$$\lim_{t \to \infty} \frac{A^t}{\lambda_1^t} = M \begin{bmatrix} 1 & 0 & . & . & . & 0 \\ 0 & 0 & . & . & . & 0 \\ . & . & . & . & . & . \\ 0 & 0 & . & . & . & 0 \end{bmatrix} M^{-1} = H_1$$

$$(2.3.17)$$

Therefore, regardless of λ_1, i=2,3,..., k+1 being not distinct, A^t/λ_1^t still converges to H_1.

On investigation it is found that

$$H_1 = u_1 v_1' \tag{2.3.18}$$

where u_1 is the right positive eigenvector and v_1' is the left positive eigenvector of A both corresponding to λ_1. Consequently, since v_1' is a positive vector then the columns of H_1 are *positive multiples* of u_1.

This result will be established through a lemma but first we shall examine

$$\lim_{t \to \infty} A^t z \tag{2.3.19}$$

where z is an arbitrary k+1 vector. Suppose that the eigenvalues of A are λ_1, the corresponding eigenvectors u_1, i=1,2,..., k+1 and u_1 form a basis for R^{k+1}. Then we can write

$$z = \sum_{i=1}^{k+1} \alpha_i u_i$$

$$(2.2.20)$$

where α_1 are constants not all zero.

Clearly as t gets large this sum will be dominated by the term involving the eigenvalue with the largest absolute value(modulus), provided that the associated coefficient is not zero. Let us assume that this eigenvalue has the index i=1, so that we can write for large t

$$A^t\ z \approx \alpha_1\lambda_1{}^t u_1 \qquad (2.3.21)$$

or equivalently

$$\lim_{t\to\infty} A^t z = \alpha_1\lambda_1{}^t u_1 \qquad (2.3.22)$$

Lemma.

Let A be an nxn matrix, x an n-vector, and α, λ real numbers. Then for all $z \in R^n$

$$\lim_{t\to\infty} A^t z = \alpha\lambda^t x \qquad (2.3.23)$$

iff

$$\lim_{t\to\infty} A^t = \lambda^t xy' \qquad (2.3.24)$$

$y \in R^n$ is arbitrary and $\alpha=y'z$

Proof.

Since z is independent of t

$$\lim_{t\to\infty} A^t z = (\lim_{t\to\infty} A^t)z$$

$$= (\lambda^t xy')z \qquad \text{using (2.3.24)}$$

$$= \lambda^t x\ y'z$$

$$= \alpha\lambda^t x$$

conversely

$$\lim_{t\to\infty} A^t z = \alpha\lambda^t x \qquad \text{where}\quad \alpha=y'z$$

$$= \lambda^t x\alpha$$

$$= \lambda^t xy'z$$

$$= (\lambda^t xy')z$$

so that

$$\lim_{t \to \infty} A^t = \lambda^t xy'$$

which proves sufficiency.

Now suppose that

$$\lim_{t \to \infty} A^t = \lambda^t xy' + E \qquad (2.3.25)$$

where $E \neq 0$ is an nxn matrix then

$$\lim_{t \to \infty} A^t z = (\lambda^t xy' + E)z$$

$$= a\lambda^t x + Ez \qquad (2.3.26)$$

for arbitrary z we must therefore have $E=0$, which proves necessity.

We can now use the lemma to establish (2.3.8) where A is a primitive population projection matrix with dominant eigenvalue λ_1 and associated positive right eigenvector u_1. Noting that A and A' have the same eigenvalues(see thm.1, sec.1.4). Let

$$z = \sum_{i=1}^{k+1} \beta_i v_i$$

$$(2.3.27)$$

where v_1' are the right eigenvectors of A' corresponding to λ_1 or equivalently v_1' are the left eigenvectors of A. β_1's are constants not all zero.

Using (2.3.22) we have

$$\lim_{t \to \infty}(A')^t z = \beta_1 \lambda_1^t v_1 \qquad (2.3.28)$$

and using lemma

$$\lim_{t \to \infty} (A')^t = \lambda_1{}^t v_1 w' \qquad (2.3.29)$$

$w \in R^{k+1}$ is arbitrary and $\beta_1 = w'z$ and since $(A')^t = (A^t)'$ we have

$$\lim_{t \to \infty} (A')^t = (\lim_{t \to \infty} A^t)' \qquad (2.3.30)$$

From (2.3.22) and lemma

$$(\lim_{t \to \infty} A^t)' = (\lambda_1{}^t x u_1)' \qquad (2.3.31)$$

where $x \in R^{k+1}$ is arbitrary and $\alpha_1 = x'z$.

Using (2.3.29/30/31) we can take $x = v_1$ and $w = u_1$ so that

$$\lim_{t \to \infty} = \lambda_1{}^t u_1 x' = \lambda_1{}^t u_1 v_1' \qquad (2.3.32)$$

or equivalently

$$\lim_{t \to \infty} A^t / \lambda_1{}^t = u_1 v_1' \qquad (2.3.33)$$

where u_1, v_1' are respectively the right (left) positive eigenvectors of A both corresponding to the dominant eigenvalue λ_1. Using (2.3.5/33) then (2.3.18) follows.

Considering the spectral representation of the diagonalizable matrix A demonstrated by (2.3.18) we have

$$A = \sum_{i=1}^{k+1} \lambda_i\, u_i v_i'$$

$$(2.3.34)$$

where u_1, v_1' are respectively the right(left) eigenvectors of A both corresponding to the eigenvalue λ_1, (i = 1,2,...,k+1) so that

$$H_1 = u_1 v_1' \qquad (2.3.35)$$

Using (2.3.35) we can write (2.3.34) as

$$A = \sum_{i=1}^{k+1} \lambda_i H_i$$

(2.3.36)

and model (2.2.19) can be rewritten as

$$u_c = \lambda_1^c \sum_{i=1}^{k+1} \left(\frac{\lambda_i}{\lambda_1}\right)^c H_i u_0$$

(2.3.37)

i.e. the population is growing *approximately geometrically* so long as $(\lambda_i/\lambda_1)^t$ is close to zero.

Theorem.2.

For any non-negative vector **x** the relative values of the components of

$$y = H_1 x$$

(2.3.38)

are independent of **x**.

Proof.

$$y = H_1 x$$

$$= (m_1 u_1, m_2 u_1, \ldots, m_{k+1} u_1) x$$

$$= u_1 m' x$$

(2.3.39)

where $m = (m_1, m_2, \ldots, m_{k+1})'$.

The relative values of the components of **y** in vector form is given by

$$y(1'y)^{-1} = u_1 m' x (1' u_1 m' x)^{-1}$$

$$= u_1 m' x (m' x)^{-1} (1' u_1)^{-1}$$

$$= u_1 (1' u_1)^{-1}$$

(2.3.40)

which is independent of x and hence the result.

Applying theorem 1 to (2.2.19) we note that

$$\lim_{t \to \infty} u_t/\lambda_1^t = (\lim_{t \to \infty} A^t/\lambda_1^t) \, u_\emptyset$$

$$= H_1 \, u_\emptyset \qquad\qquad (2.3.41)$$

$$= c \, \zeta \qquad\qquad (2.3.42)$$

The age distribution vector $\zeta_t = u_t(1'u_t)^{-1}$ approaches a limiting value ζ which is independent of the initial population $u_\emptyset$, depending only on the matrix A and satisfies

$$1'\zeta = 1 \qquad\qquad (2.3.43)$$

A determines $\lim_{t \to \infty} u_t$ to within a scalar c which depends on both $u_\emptyset$ and A.

$$\lim_{t \to \infty} u_t/\lambda_1^t(1'u_t/\lambda_1^t)^{-1} = \lim_{t \to \infty} u_t(1'u_t)^{-1} = \zeta \qquad (2.3.44)$$

Applying theorem 2 to (2.3.41)

$$\lim_{t \to \infty} u_t/\lambda_1^t(1'u_t/\lambda_1^t)^{-1} = u_1(1'u_1)^{-1} \qquad\qquad (2.3.45)$$

From (2.3.44) & (2.3.45)

$$\zeta = u_1(1'u_1)^{-1} \qquad\qquad (2.3.46)$$

and clearly satisfies (2.3.43).

The limiting vector ζ is called the *stable age distribution* or *stable population vector* corresponding to A, and the fact that it is independent of $u_\emptyset$ is known as the ergodic property for population growth (i.e. it forgets its past).

It is observed that as t gets large the matrix A^t displays a very interesting property i.e. the ratio of an element in A^{n+1} to the corresponding element in A^n will for large n tend to λ_1 and when the population has stabilized

this ratio is λ_1.

From (2.2.19), this is equivalent to saying that when the population has stabilized

$$u_{t+1} = \lambda_1 u_t \qquad (2.3.47)$$

and by the definition of the model (2.2.17) we conclude that

$$A\, u_t = \lambda_1\, u_t \qquad (2.3.48)$$

which has non-trivial solution iff

$$|A - \lambda_1 I| = 0 \qquad (2.3.49)$$

or equivalently iff the characteristic equation of A has dominant root λ_1.

We can now establish (2.3.47) by supposing that it holds and show that the characteristic equation of A has dominant root λ_1.

Proof.

Let $Y_0, Y_1, Y_2, \ldots, Y_k$ be a set of frequencies such that

$$u_t = (Y_0, Y_1, Y_2, \ldots, Y_k)' \qquad (2.3,50)$$

and by hypothesis

$$u_{t+1} = (\lambda_1 Y_0, \lambda_1 Y_1, \lambda_1 Y_2, \ldots, \lambda_1 Y_k)' \qquad (2.3.51)$$

Using model (2.2.17)

$$u_{t+1} = [\Sigma_i f_i Y_i, p_0 Y_0, p_1 Y_1, \ldots, p_{k-1} Y_{k-1}]' \qquad (2.3.52)$$

It is clear from (2.3.51) & (2.3.52) that

$$\lambda_1 Y_0 = f_0 Y_0 + f_1 Y_1 + f_2 Y_2 + \ldots + f_k Y_k \qquad (2.3.53)$$

and for $i = 1, 2, \ldots, k$

$$Y_i = p_0 p_1 p_2 \ldots p_{i-1} Y_0 / \lambda_1^i$$

On substituting Y_i, $i = 1, 2, \ldots, k$ into (2.3.53) we obtain

$$\lambda_1^{k+1} - f_0 \lambda_1^k - f_1 p_0 \lambda_1^{k-1} - f_2 p_0 p_1 \lambda_1^{k-2} - \ldots - f_{k-1} p_0 p_1 \ldots p_{k-1} = 0$$

$$(2.3.54)$$

which is the characteristic equation of A given by (2.2.26) in dominant root λ_1 and hence the result.

It is clear from the established relation (2.3.47) that the dominant root λ_1 gives the rate of increase of the population in a single step; so that the population grows *geometrically*. It is related to Lotka's r(intrinsic rate of natural increase) by expression (1.2.6). λ_1 is also called population *finite* rate of natural increase.

If the dominant root λ_1 is greater than unity implies that the population is capable of increasing. If λ_1 is less than unity then the population is capable of decreasing. If λ_1 is unity then the population remains constant and is often referred to as *stationary* population.

2.4. Harvesting in Matrix Population Models.

Introduction.

Before we focus specifically on harvesting we wish to briefly study or rather examine stochastic matrices and establish a relationship with a non-negative matrix. The relationship will be utilized in a proof of a theorem on positive harvesting. We shall consider harvesting problem in terms of matrix algebra with the intention of maximizing yields subject to maintaining a constant population size and age structure after each time period.

Stochastic matrices.

Defn.1.

A square matrix, $P=(p_{ij})$ of order n is called stochastic if the matrix P is non-negative and if every row sum is equal to 1.

Thus, the matrix of transitional probabilities for a homogeneous markov chain is stochastic; and conversely, an *arbitrary stochastic* matrix may be taken to be the matrix of *transition probabilities* of some homogeneous markov chain.

A stochastic matrix is a special case of a non-negative matrix. Special addition properties of a stochastic matrix are the following. It follows from the definition, that such a matrix has characteristic root 1, to which the positive characteristic vector $z=(1,1,\dots,1)'$ corresponds. Conversely, it is clear that if the corresponding characteristic root is 1, then the matrix P is stochastic. Further, the root 1 is the dominant characteristic root of every stochastic matrix, since the dominant characteristic root always *lies between the largest and smallest row sums and each row sum is 1*. These facts are restated yielding definition 2 of a stochastic matrix.

Defn.2.

A non-negative matrix P (≥ 0) is stochastic iff the vector $(1,1,\dots,1)'$ is a characteristic vector of P, with corresponding characteristic root 1. For a stochastic matrix, *1 is the dominant characteristic root*.

Now we establish a representation for certain non-negative matrices. Let $A=(a_{ij})$ be a non-negative square

matrix of order n; let the positive root r (>0) be a characteristic root of A, and let the corresponding characteristic vector $z=(z_1,z_2,\ldots,z_n)'$ (>0) be positive.

$$A \, z = r \, z \qquad (2.4.1)$$

so that for $i=1,2,\ldots,n$

$$\sum_{j=1}^{n} a_{ij} \, z_j = r \, z_i$$

$$(2.4.2)$$

We define diagonal matrix Z by

$$Z = \text{diag}(z_1,z_2,\ldots,z_n) \qquad (2.4.3)$$

and the matrix $P=(p_{ij})$ by

$$P = r^{-1}Z^{-1}AZ \qquad (2.4.4)$$

The elements p_{ij} of P are clearly non-negative:

$$p_{ij} = r^{-1}z_i^{-1}a_{ij}z_j \geq 0 \qquad (2.4.5)$$

for $i,j=1,2,\ldots,n$ and using (2.4.2.) we have the relation

$$\sum_{j=1}^{n} p_{ij} = 1$$

$$(2.4.6)$$

for $i=1,2,\ldots,n$.

We have established the following definition,

Defn.3.

If A (≥0) is a non-negative matrix which has a positive dominant characteristic root, to which there corresponds a positive characteristic vector $z=(z_1,z_2,\ldots,z_n)'>0$, it is similar to the product rP of r by some stochastic matrix P.

$$A = Z(rP)Z^{-1} \qquad\qquad (2.4.7)$$

where Z is given by (2.4.3).

Remark.1.

If $r = 1$ then A is similar to a stochastic matrix P.

Remark.2.

If A is primitive then P is also primitive.

Defn.4.

We call a stochastic matrix P and the corresponding homogeneous markov chain proper if the matrix P has no characteristic roots ($\neq 1$) of modulus 1, and call a matrix of chain regular if it is proper and if 1 is a simple characteristic root (simple root of the characteristic equation) of P.

Remark.

A homogeneous markov chain is called aperiodic if the corresponding stochastic matrix P is primitive.

If P is the matrix of transition probabilities of a homogeneous markov chain, then the matrix P^{∞} of limiting probabilities exists iff the chain is proper.

$$P^{\infty} = \lim_{m \to \infty} P^m \qquad\qquad (2.4.8)$$

Remark.

The rows of the matrix P^m add to unity, and as they contain a fixed number of elements it is impossible that $p_{ij}^m \to 0 \quad \forall$ pairs i,j (see Feller Vol.1, Pg. 392).

Harvesting.

Under favourable conditions, natural animal populations

have a tendency to increase in numbers. It is, however, possible to remove some animals and maintain a constant population size. If the population is divided into groups by age, different proportions of the various groups can be harvested subject to the condition that a fixed population size and age structure is maintained after every time interval.

The problem of harvesting was introduced to matrix population theory by Lefkovitch and Williamson in 1967. If the population is distributed by ages according to the stable age distribution ζ, the latent vector corresponding to λ_1 then

$$A \zeta = \lambda_1 \zeta \qquad (2.4.9)$$

and it is possible to remove the vector

$$(\lambda_1 - 1) \zeta \qquad (2.4.10)$$

from the population after it *has reproduced*, restoring the initial age structure and population size. This corresponds to harvesting equal fractions $(\lambda_1-1)/\lambda_1$ from each age group or equivalently $100(\lambda_1-1)/\lambda_1$ % of the total population. This is called *uniform* harvesting.

It is required that the *population size* and *age structure* be restored after each time period(this is referred to as *sustainable* harvesting). Subject to this constraint, an age structure and harvesting policy may be chosen to maximize some value attached to the harvest (the number of animals harvested, the biomass harvested,e.t.c.)

Both authors enquired whether some harvesting policy other than harvesting equal proportions from each group might produce a higher yield. Neither author attempted to solve the problem generally, but Williamson demonstrated that the above mentioned harvesting procedure is not always best(optimal).

He considers the matrices

$$A_1 = \begin{bmatrix} 0 & 9 & 12 \\ 1/3 & 0 & 0 \\ 0 & 1/2 & 0 \end{bmatrix} \quad \& \quad A_2 = \begin{bmatrix} 0 & 3 & 36 \\ 1/3 & 0 & 0 \\ 0 & 1/2 & 0 \end{bmatrix}$$

$$(2.4.11)$$

A_1 and A_2 both have $\lambda_1=2$. The stable age structure for both is $\zeta = 1/29(24,4,1)'$. The yield

$$1'(A u - u) \qquad (2.4.12)$$

is 1 per member of the population when $u = \zeta$. However if $u = 1/9(6,2,1)'$ is used instead of ζ a yield of 8/3 per member of the population is possible for A_1 and a yield of 4 per member for A_2.

Harvesting problem in terms of matrix algebra.

For harvesting after reproduction, it is required to find a non-negative column vector u and a non-negative diagonal matrix

$$R = \text{diag}(r_1, r_2, \ldots, r_n) \qquad (2.4.13)$$

such that

$$R A u = u \qquad (2.4.14)$$

and

$$c'(I - R) A u \qquad (2.4.15)$$

is maximized over u and R. u is the *chosen distribution* of ages, the diagonal elements of R are the proportions of various groups *remaining* in the population after harvesting, $c'=(c_1,c_2,\ldots,c_n)$ is the set of weights given to the groups, (2.4.14) is the requirement that the initial age structure and population size be restored at the end of each cycle of reproduction and harvesting.

For harvesting before reproduction the value of the harvest is

$$c'(I - R) u \qquad (2.4.16)$$

and the initial age distribution and population structure is restored by the constraint

$$A R u = u \qquad (2.4.17)$$

Intuitively, it seems obviously better to harvest after rather than before reproduction. Without loss of generality the total population size can be constrained by the relation

$$1'u = 1 \qquad (2.4.18)$$

so that the problem can be restated as that of maximizing (2.4.15) subject to (2.4.14),(2.4.18) and $Au-u \geq 0$, where $u \geq 0$ or equivalently we are maximizing

$$c'(A u - u) \qquad (2.4.19)$$

for

$$A u - u \geq 0, \quad u \geq 0 \text{ and } 1'u = 1 \qquad (2.4.20)$$

This is a linear programming problem which can be solved by the simplex method.

Since it is possible in some cases to increase the yield by not choosing $u = \zeta$ (demonstrated by (2.4.11)), we may ask whether it is necessary that $\lambda_1 > 1$ for a positive harvest to be possible. If A is primitive (some power of A has positive entries)(see thm 3, sec. 2.1) then it is necessary that $\lambda_1 > 1$. However, if $\lambda_1 = 1$ and A is not primitive a positive harvest may be possible. An example is any Leslie matrix A with a zero fertility in the last age group. The last age group can be harvested completely in this case with $u = \zeta$ in the remaining components.

Theorem.

If the dominant root, λ_1, of A is less than 1, no positive harvest is possible. If $\lambda_1 = 1$ and A is primitive, no positive harvest is possible.

Proof. (By contradiction).

For a positive harvest to be possible there must exist a $u \geq \mathbf{0}$ such that $A\,u \geq u$ and strict inequality holds for at least one component. It follows that

$$A^m\, u \geq u \qquad (2.4.21)$$

for any positive integer m.

(i) If $\lambda_1 < 1$ then $A^m \to \mathbf{0}$ as $m \to \infty$ (all entries tend to zero). Therefore, there is no non-zero u satisfying $A\,u \geq u$ and no positive harvest is possible.

(ii) If $\lambda_1 = 1$ and A is primitive, then u_1 is strictly positive. Also A is similar to a primitive stochastic matrix P (see rem.1 of defn.3, sec.2.4).

$$A = Z P Z^{-1} \qquad (2.4.22)$$

where Z is a diagonal matrix whose diagonal elements are the components of u_1.

Since P is primitive (regular in markov chains, or aperiodic in homogeneous markov chains)(see rem.2 of defn.3, sec. 2.4)

$$\lim_{m \to \infty} P^m = P^\infty \qquad (2.4.23)$$

exists and has all entries positive(see rem. of (2.4.8)). Therefore

$$\lim_{m \to \infty} A^m = Z \,(\lim_{m \to \infty} P^m)\, Z^{-1} = Z \, P^\infty \, Z^{-1} \qquad (2.4.24)$$

also exists and has *all entries positive*.

For any u,

$$\lim_{m \to \infty} A^m(A\, u - u) = \lim_{m \to \infty} A^{m+1}\, u - \lim_{m \to \infty} A^m\, u$$
$$= 0 \qquad (2.4.25)$$

But if Au-u has at least one positive component, then

$$\lim_{m \to \infty} A^m \,(A\, u - u) > 0 \qquad (2.4.26)$$

i.e. is *strictly* positive. Therefore no positive harvest is possible.

Remark.

For the special case when $u = \zeta$ i.e. harvesting equal proportions of $(\lambda_1-1)/\lambda_1$ from each age group(uniform harvesting), it is quite clear that a positive harvest is not possible whenever $\lambda_1 \le 1$.

In the next chapter we shall consider practical applications of the model we have described.

CHAPTER.3. APPLICATION OF THE MODEL

3.1 Introduction

We shall apply the model to a population of a gorilla species (Mountain gorilla)(see last paragraph of sec. 1.1 for source of data). The central problem is to determine the stable population vector, the intrinsic rate of natural increase and the harvest that can be taken subject to the condition that a fixed population size and age-structure is maintained after every time interval. With knowledge of λ_1, the dominant root of the matrix A, all the above three are readily obtainable from the appropriate formulae; namely

(i) The stable vector is given by

$$\zeta = u_1(1'u_1)^{-1} \qquad (3.1.1)$$

where

$$u_1 = (1, p_\emptyset/\lambda_1, p_\emptyset p_1/\lambda_1^2, \ldots, p_\emptyset p_1 \ldots p_{k-1}/\lambda_1^k)' \qquad (3.1.2)$$

is the eigenvector corresponding to λ_1.

(ii) The intrinsic rate r of natural increase (Lotka's r) is given by

$$r = \log_e \lambda_1 \qquad (3.1.3)$$

(iii)The harvest that can be taken so that a constant population vector is maintained after every time interval is given by

$$H = 100(\lambda_1-1)/\lambda_1 \qquad (3.1.4)$$

where H is expressed as a percentage of the total population i.e. harvesting a proportion of $(\lambda_1-1)/\lambda_1$ from each age

group. It is remarkable to note that this harvesting policy may or may not be optimal. If it is not optimal we can alternatively maximize (2.4.19) subject to (2.4.20).

3.2. Application to generate and maintain ζ

The general information includes the assumption that

(a) There is

    (i) No migration, (ii) No density dependence

(b) Age-specific rates remain constant over a period of time.

(c) Same unit of age is adopted as that of time.

The sex ratio is 0.500 and the population is partitioned into 5-yr age groups and a maximum age of 6 will be considered i.e. we shall have 7 age groups. The initial age distribution and the age-specific rates are as tabulated below.

Age	Initial	Fecundity	Surviva
0	80	0.00	0.682
1	57	0.00	0.896
2	46	1.15	0.730
3	34	1.15	0.730
4	25	1.15	0.730
5	19	1.15	0.730
6	14	1.15	0.730

so that the initial age distribution is given by

$$u_0 = (80, 57, 46, 34, 25, 19, 14)' \qquad (3.2.1)$$

and the projection matrix A is given by

$$A = \begin{bmatrix} 0 & 0 & 1.15 & 1.15 & 1.15 & 1.15 & 1.15 \\ 0.682 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.896 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.730 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.730 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.730 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.730 & 0 \end{bmatrix}$$

$$(3.2.2)$$

Thus, the model is described by

$$u_t = A^t u_0 \qquad (3.2.3)$$

for t=1,2,3, ...

The non-negativity of A is obvious. The irreducibility of A follows as already proved for a general matrix. It only remains to find the index of imprimitivity of A. The characteristic equation of A is given by (2.2.26) for k+1=7 i.e.

$$\lambda^7 - 0.7027328\lambda^4 - 0.512994944\lambda^3 - 0.374486309\lambda^2 - 0.273375005\lambda -$$
$$0.199563754 = 0 \qquad (3.2.4)$$

The index of imprimitivity h is the g.c.d. of the differences {7-4, 4-3, 3-2, 2-1, 1-0}. Here h=1, hence A is primitive which implies that the dominant root λ_1 of A is greater than the moduli of all other roots and

$$\lim_{t \to \infty} A^t/\lambda_1^t \qquad (3.2.5)$$

exists. In other words there exist a stable population vector ζ.

The power method procedure is used to determine the dominant root λ_1. The algorithm is on page 34 and a fortran program utilizing this method is in the appendix. The dominant root is found to be

$$\lambda_1 = 1.1856588 \qquad (3.2.6)$$

Letting $p(i) = p_0 p_1 p_2 \ldots p_i$, $\quad i = 0,1,2,3,4,5.$ we have

$u_1 = (1, p(0)/\lambda_1, p(1)/\lambda_1^2, p(2)/\lambda_1^3, p(3)/\lambda_1^4, p(4)/\lambda_1^5, p(5)/\lambda_1^6)'$

$\quad = (1, 0.575207639, 0.43468327, 0.26630778, 0.164777985,$

$\qquad 0.10152398, 0.062463375)' \qquad (3.2.7)$

$\lambda_1 u_1 = (1.1856588, 0.681999999, 0.515386044, 0.317318787,$

$\qquad 0.195370468, 0.120287928, 0.07406025)' \qquad (3.2.8)$

$A u_1 = (1.185658977, 0.682, 0.515386044, 0.317318787,$

$\qquad 0.195370467, 0.120287929, 0.07406025)' \qquad (3.2.9)$

(3.2.7) & (3.2.8) confirms that u_1 is an eigenvector of A corresponding to λ_1. The stable population vector is

$\quad \zeta = u_1/(1'u_1)$

$\quad\quad = u_1/2.606215445$

$\quad\quad = (0.383698132, 0.220706097, 0.166787158, 0.102689429,$

$\qquad 0.063225005, 0.038927095, 0.02396708)' \qquad (3.2.10)$

and satisfies

$$1'\zeta = 1 \qquad (3.2.11)$$

The intrinsic rate of natural increase r is

$\quad r = \log_e(1.1856588)$

$\quad\quad = 0.170298569$

$\quad\quad \approx 0.1703 \qquad (3.2.12)$

Noting that $\lambda_1 > 1$ a positive harvest is possible.

Subject to the condition of maintaining a constant population size and age-structure after each time period we can harvest a proportion of

$$(\lambda_1-1)/\lambda_1 = 0.156587038$$

$$\approx 0.1566 \tag{3.2.13}$$

from each age group i.e 15.66% of the tatal population. This harvesting policy is equivalent to using (2.4.19) by taking $c'=(1,1,\ldots,1)$, $u = \zeta$ so that the yield is

$$c'(Au-u) = 1'(A\zeta-\zeta)$$

$$= (\lambda_1-1)1'\zeta$$

$$= \lambda_1-1 \text{ (using 3.2.11)}$$

$$= 1.1856588-1$$

$$= 0.1856588 \tag{3.2.14}$$

per member of the population.

Carrying out the above harvesting policy after reproduction will restore the stable population vector ζ after each time period.

3.3 Concluding Remarks.

We have established that when the population has stabilized the model $u_t = A \ u_{t-1}$ reduces to $u_t = \lambda_1 \ u_{t-1}$ where λ_1 is the dominant eigenvalue of the projection matrix A, so that the population grows geometrically. Moreover, the eigenvector u_1 of A corresponding to the eigenvalue λ_1 is a function of the survival rates p_1 (i=0,1,..., k-1) and λ_1.

It is also found that when the population has not

stabilized the population grows *approximately geometrically* so long as $(\lambda_i/\lambda_1)^t$ is close to zero$(i=2,3,...,k+1)$

For the Gorilla data λ_1 = 1.1856588 > 1 i.e. the population is capable of increasing at a constant rate of 1.1856588 in a single step and a positive harvest is possible. To maintain the stable population vector ζ after every time period we should harvest a proportion of $(\lambda_1 - 1)/\lambda_1$ = 0.1566 from each age group after reproduction.

The model we have considered is often referred to as the classical (traditional) model. The projections are intended only to indicate the future course of population growth if the present trends in vital rates continue. The predictions are therefore not exact if time intervals are long, however, for short intervals of time the approximations are good.

The matrix is defined as operating over a period of time, and thus the model can take the structure of the ecosystem at time t, and predict the new structures at times t+1, t+2, t+3, e.t.c. There is no way of using the model to predict what the structure would be at time t+(1/2), or any non-integer value of time. However, many biological processes occur in discrete periods of time and are not continuous in their operations.

It has been observed in practise that population growth is a highly variable process and that the projections using classical models are quickly invalidated. Any results

obtained using this model are only as valid as the underlying assumptions made.

Models should incorporate insight into the biological mechanisms involved as well as being sufficiently general for the model to be applicable in a variety of situations merely by changes in the parameters or modifications of the underlying assumptions. Such models are called *robust* models.

If there is reason to suspect a violation of any of the postulates inherent in the construction of the model, or if sufficient information to judge their validity is not available then a more general model which includes *variable factors* is desirable (refer litrature review, (sec. 1.3)).

It is possible to develop models which represent specific growth events with a certain degree of precision but it is much more difficult to develop models with a general range of applicability, however, the extentions of the classical model (refer litrature review, (sec. 1.3)) has demonstrated its robustness.

APPENDIX

```
PROGRAM DEVALU

DIMENSION A(20,20), X(20)

REAL LAMBDA

OPEN( UNIT = 5, FILE = 'INPUT.', STATUS = 'OLD')

OPEN( UNIT = 2, FILE = 'OUTPUT', STATUS = 'NEW')

READ(5,10) ((A(I,J),I = 1,7),J = 1,7)

READ(5,20) (X(I), I = 1,7)

10    FORMAT(7F5.3)

15    FORMAT(/,7F8.3)

20    FORMAT(7F9.7)

25    FORMAT(7(F13.10/)//)

30    FORMAT(5X,' INITIAL ARBITRARY  VECTOR OF UNIT NORM'/)

35    FORMAT(5X,' PROJECTION MATRIX A')

40    FORMAT(5X,'LIMITING VECTOR OF UNIT NORM'/)

45    FORMAT(4X,'*****************************************
    ***************')

    TOL = 1E-10

    N    = 7

    M    = 10000

    WRITE(*,30)

    WRITE(*,25)(X(I),I=1,7)

    WRITE(2,30)

    WRITE(2,45)
```

```
      WRITE(2,25)(X(I),I=1,7)

      WRITE(*,35)

      WRITE(*,15)((A(I,J), I= 1,7),J= 1,7)

       CALL POWERM(A,X,LAMBDA,TOL,N,M,ITERM)

50    FORMAT(/,'   DOMINANT EIGENVALUE IS   ',F15.12///)

      WRITE(2,45)

      WRITE(2,35)

      WRITE(2,15) ((A(I,J),I=1,7),J=1,7)

      WRITE(*,50) LAMBDA

      WRITE(2,45)

      WRITE(2,50) LAMBDA

      WRITE(*,40)

      WRITE(2,40)

      WRITE(*,25)(X(I),I=1,7)

      WRITE(2,25)(X(I),I=1,7)

      IF(ITERM.EQ.2) GO TO 60

      WRITE(2,55)

55    FORMAT(5X,'CONVERGENCE DUE TO TOLERANCE')

      GO TO 70

60    WRITE(2,65)M

65    FORMAT(5X,' CONVERGENCE AFTER',I4,'ITERATIONS')

70    STOP

      END
```

```
      SUBROUTINE POWERM(A,X,LAMBDA,TOL,N,M,ITERM)
      REAL LAMBDA
      DIMENSION A(20,20),X(20),Y(20)
C
C     SUBROUTINE POWERM USES THE POWER METHOD WITH
C     SCALING TO ESTIMATE THE DOMINANT EIGENVALUE OF A MATRIX
C     A . THE CALLING PROGRAM MUST SUPPLY THE MATRIX A, AN
C     INITIAL VECTOR X OF EUCLIDEAN LENGTH 1, A TOLERANCE
C      TOL,  AN INTEGER N(WHERE A IS (NXN)) AND AN INTEGER M=
C     MAXIMUM  NUMBER OF POWER ITERATIONS DESIRED. THE
C     SUBROUTINE RETURNS WHEN THE DIFFERENCE OF TWO
C     SUCCESSIVE ESTIMATES IS LESS THAN TOL IN ABSOLUTE VALUE
C     OR WHEN M ITERATIONS  HAVE BEEN EXECUTED. IN  THE FIRST
C     CASE, A FLAG, ITERM IS  SET TO 1 AND IN THE SECOND CASE
C     ITERM IS SET TO 2.  THE  APPROXIMATE EIGENVALUE IS
C     RETURNED AS LAMDA AND AN   APPROXIMATE EIGENVECTOR   AS
C     X. LAMBDA MUST BE DECLARED  REAL IN THE CALLING
C     PROGRAM.
C
      ITR=1
C
C     CALCULATE THE INITIAL EIGEN VALUE APPROXIMATION
C
      DO 1 I=1,N
      Y(I)=0.
      DO 1 J=1,N
```

```
  1 Y(I)=Y(I)+A(I,J)*X(J)
    TEMP=0.
    YSCALE=0.
    DO 2 I=1,N
    TEMP=TEMP+Y(I)*X(I)
  2 YSCALE=YSCALE+Y(I)*Y(I)
    YSCALE=SQRT(YSCALE)
    ESTOLD=TEMP
C
C     POWER METHOD ITERATION WITH SCALING
C
  3 ITR=ITR+1
    DO 4 I=1,N
  4 X(I)=Y(I)/YSCALE
    DO 5 I=1,N
    Y(I)=0.
    DO 5 J=1,N
  5 Y(I)=Y(I)+A(I,J)*X(J)
    TEMP = 0.
    YSCALE=0.
    DO 6 I=1,N
    TEMP=TEMP+Y(I)*X(I)
  6 YSCALE=YSCALE+Y(I)*Y(I)
    YSCALE=SQRT(YSCALE)
    ESTNEW=TEMP
C
```

```
C     TEST FOR TERMINATION OF THE POWER METHOD ITERATION
C

      IF(ABS(ESTNEW-ESTOLD).LE.TOL) GO TO 7

      IF(ITR.GE.M) GO TO 8

      ESTOLD=ESTNEW

      GO TO 3

    7 ITERM=1

      LAMBDA=ESTNEW

      RETURN

    8 ITERM=2

      LAMBDA=ESTNEW

      RETURN

      END
```

OUTPUT FILE

INITIAL ARBITRARY VECTOR OF UNIT NORM

****
```
                            0.3779644966
                            0.3779644966
                            0.3779644966
                            0.3779644966
                            0.3779644966
                            0.3779644966
                            0.3779644966
```

****
PROJECTION MATRIX A

0.000	0.000	1.150	1.150	1.150	1.150	1.150
0.682	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.896	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.730	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.730	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.730	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.730	0.000

****

DOMINANT EIGENVALUE IS   1.185658812523

LIMITING VECTOR OF UNIT NORM

```
                            0.2175698429
                            0.3782458007
                            0.5005250573
                            0.4702009261
                            0.4209486246
                            0.3409535885
                            0.2110264301
```

CONVERGENCE DUE TO TOLERANCE

REFERENCES

(1)Andrews J.G. & McLeone R.R. (1976). *Mathematical Modelling.* Butherworths (Publishers) Inc.

(2)Aitken A.C.(1956). *Determinants and Matrices.* Interscience Publishers, Inc. New York.

(3)Barnett S. (1990). *Matrices: Methods of applications.* Clarendon Press Oxford.

(4)Bellman R.E. (1970). *Introduction to Matrix analysis.* McGraw-Hill Book Company.

(5)Bernardelli H.(1941) Population waves. *J. Burma Res. Soc.* 31, no. 1, 1-18.

(6)Bronson R.(1970). *Matrix Methods, An introduction.* Academic Press, Inc. (London) Ltd.

(7)Butler R. & Kerr E.(1962). *An Introduction to Numerical methods.* The Pitman Press, Bath. London.

(8)Caswell H. (1989). *Matrix Population Models* (Woods Hole, Massachusetts).

(9)Dorn W.S. & McCracken D.D.(1972). *Numerical methods with Fortran IV case Studies.* John Wiley & Sons, Inc.

(10)Doubleday W.G.(1975) Harvesting in matrix population models. *Biometrics*, 31, 189-200.

(11)Ellis T.M.R.(1980). *Structured Fortran.* Published by the University of Sheffield Computing Services.

(12)Feller, W.,(1957). *An Introduction to probability Theory and Its Applications,* Vol.1, 2nd ed. Wiley.

(13)Gantmacher F.R.(1959). *Application of the theory of*

matrices. Interscience Publishers, Inc; New York.

(14)Heal G.M.(1974). *Linear Algebra and Linear Economics*. The Macmillan Press Ltd.

(15)Horn R.A. and Johnson C.R.(1985). *Matrix analysis*. Cambridge University Press.

(16)Johnson L.W. & Riess R.D.(1977). *Numerical Analysis*. Addison-Wesley Publishing Company. U.S.A.

(17)Keifitz N. (1964) The intrinsic rate of Natural Increase and the Dominant Root of the Projection Matrix. *Population Studies*, **18**, 293-308.

(18)Lefkovitch L. P. (1965) The study of population growth in organisms grouped by stages. *Biometrics*, **21**, 1-18.

(19)Leslie P.H.(1945) On the use of matrices in certain population mathematics. *Biometrika*, **33**, 183-212.

(20)Leslie P.H.(1948). Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**, 213-245

(21)Lewis E.G.(1942) On the generation and growth of a population. *The Indian Journal of Statistics-Sankhya* **6**, 93-96.

(22)Lotka A.J. and Louis I.D (1925) On the true rate of natural increase. *JASA*, **20**, 305-339 .

(23)Macduffee C.C. (1946). *The Theory of Matrices*. Chelsea Publishing Company, Ney York.

(24)Ogden J. and Neal E.(1979) Applications of transition matrix models in forest dynamics, *Australian*

Journal of Ecology, **4**, 3-23.

(25)Perlis, S.(1952). *Theory of Matrices*. Addison-Wesley
Publishing Company, Inc. U.S.A.

(26)Pielou E.C.(1969). *Mathematical Ecology*. A Wiley
Interscience Publication. John Wiley & Sons. New York.

(27)Polard J.H. (1966) On the use of the direct matrix
product in analysing certain stochastic population
models. *Biometrika*, **53**, 397-415.

(28)Polard J.H.(1973). *Mathematical Models for the growth
of human populations*. Cambridge University Press.

(29)Sykes Z.M. (1969a) On the discrete Stable population
theory. *Biometrics* **25**, 285-293.

(30)Turnbull H.W.(1952). *Theory of Equations*, Oliver &
Boyd. New York: Interscience Publishers, Inc.

(31)Usher M. B.(1966) A matrix approach to the management
of renewable resources, with special reference to
selection forests. *Journal of Applied Ecology*, **3**, 355-
367.

(32)Usher M.B.(1969) A matrix model for forest management.
Biometrics, **25**, 309-367.

(33)Usher M.B.(1972). Developments in the Leslie Matrix
Model In: *Mathematical Models in Ecololy*(Ed. by J.N.R.
Jeffers). Blackwell Scientific Publications,
Oxford.

(34)Watson W.A., Philipson T.& Oates P.J.(1981). *The
mathematics of computing* 2nd edition. Edward

Anorid(Publishers) Ltd.   London.