OPTIMAL HARVESTING IN MATRIX POPULATION MODELS

BY

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

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CONTENTS

ABSTRACT

The use of matrix models in population mathematics has drawn much interest in recent times. The growth, survival and harvesting of lower species of animals have been modelled using the algebraic theory of matrices.

In this project we develop a matrix model for a harvesting policy or method which maximises the harvest of a population without altering its age-structure. The model thus developed is applied in harvesting a poultry population with the objective of maximising the egg production (or a function of it).

CHAPTER ONE

INTRODUCTION.

1.1:Introduction

The study of population dynamics has drawn the interest of both the biologist and the mathematician over the last few decades. This has been attributed mainly to the importance attached to the population distributions of pests, parasites and other destructive lower animal species. Governments have also found it desirable to be able to predict future human population numbers and other resources as far as planning is concerned.

For the ecological populations like those of insect pests, for instance,the scientist would be interested in establishing a control policy aimed at eliminating the pest at its most destructive age or stage. This demands a thorough understanding of the dynamics of the pest population. A clearer grasp of the dynamics of such a population is achieved through modelling its growth and survival.

Since an accurate mathematical model for the growth of a population has been so useful to have,much of the work on population mathematics has been on modelling.Matrices have been extensively used in most models, resulting in the so-called <u>matrix population models</u> (Lewis[1942]; Leslie[1945,1948]).These are <u>deterministic</u> (Keyfitz[1968]).Yet there are other models with chance effects, referred to as <u>stochastic population models</u> (Bartlett[1960]).

In this project we are going to deal with the matrix population model. The main interest would be in harvesting a given population. Further, we would be concerned with biological populations with short life-spans for accuracy in determining the matrix elements and their validity.

Ecological populations can either be <u>structured</u> according to age or stage as in animals, or size as in plants. By <u>structure</u> we mean the population is grouped into classes, each class consisting of individuals of the same age, size or stage as the case may be. We shall base this study on the Leslie matrix model (Leslie[1945,1948]) and apply it on an age-structured population, where it is most appropriate.

1.2 : Objective and significance of study.

In this study we aim at developing a matrix model for the optimal harvesting policy(or method) of a poultry population, which will maximise the egg production (or minimise a value attached to it,e.g cost of feeds). We would ultimately result with an optimisation problem solvable by linear programming techniques.

The harvesting model thus developed would be beneficial to the poultry farmer,who is interested in maximising the exploitation of his flock.He could as well adopt it as a management policy for the business whereby the portion harvested is transferred to another site. The wildlife manager could use it to control the population of wildlife in the park,given that often he has to strike a compromise between tourism promotion and maintaining the numbers that can be sustained by the environment.Indeed, the model would be useful to any resource-manager.

1.3 : Brief Literature Review.

The use of matrices in population mathematics was pioneered by Lewis(1942) and Leslie(1945,1948). Each independently developed the basic matrix model that could be used to predict the future age-structure of a population given the initial age-structure and age-specific fecundity and survival rates. Lewis considered the age-structure of a group of individuals belonging to a lower biological population generated by individuals born at the same time and used the matrix to obtain the numerical history after the nth breeding period, n>=1.

Leslie classified a biological population of females and used the matrix to obtain the stable population structure. However,the model is only applicable to populations with several developmental stages (e.g insect populations) after some modifications (Söndgerath and Ritcher[1990]).

Lefkovitch(1965) extended the use of matrices to the case whereby the population is divided into unequal stage groups, commonly in ecological studies. He applied the model on the cigarette beetle.Shortly after, Usher (1966) applied the model to the management of a Scots spine forest (a rewable resource) grouped according to size and predicted the stable structure of the resource.His version of the basic matrix consisted as elements the percentage recruitment of plants from one class to the class above, comparable to the survival rate in the Leslie matrix ,and data on regeneration of young trees.

Sykes(1969) showed that the basic matrix was irreducible and primitive. He attributed the two properties to the limiting behaviour of its powers.

Matrix population models have not only been used to model population growth and survival but also harvesting. Among the early harvesting models are Lefkotvitch[1967] and Williamson(1967) who considered the case whereby the population size and age-structure was restored after each harvesting, which was presumably done after reproduction had taken place. Lefkotvitch also independently studied harvesting a population of fish and that of the cigarette beetle. Later, Bosch(1971) applied the harvesting model in harvesting California redwoods.

Beddington and Taylor(1973) investigated the problem of maximising the sustainable yield from a population of fixed size by changing the age composition of a harvest. Rorres and Fair(1975) also considered the same problem when subjected to the population vector satisfying a general linear constraint. Rorres(1976) investigated the case of more than one linear constraint.Other harvesting models include Mendelssohn(1976), Reed(1980) and Harley and Manson(1981) which introduced the concept of intermediate harvesting policies.

In the next chapter we treat optimal age-specific harvesting to some depth basing on the Leslie matrix model. The properties of the projection matrix which make it appropriate for use are also investigated.

CHAPTER TWO

OPTIMAL HARVESTING IN MATRIX POPULATION MODELS

2.1 : Introduction.

Under normal circumstances the growth of a population of an animal species is affected by its size at a particular time.When the individuals are free to interact, with time they would multiply.A method would therefore have to be devised for controlling the growth if population explosion is to be avoided. Harvesting is one method most commonly used to regulate population growth. Through harvesting the size of the population can be maintained or controlled as per the resources available to sustain it.

A simple growth law is obtained by supposing there are $b\delta t$ births and $d\delta t$ deaths per individual in time interval $(t,t+\delta t)$ where $b,d>=0$ are the per capita birth and death rates. If $N(t)$ is the population size at time $t>=0$,then

$$N(t+\delta t)=N(t)+N(t)b\delta t-N(t)d\delta t \tag{2.1.1}$$

Upon rearranging and taking the limit $\delta t \to 0$, it follows that

$$\frac{dN}{dt}=(b-d)N,\ t>0 \tag{2.1.2}$$

This differential equation is popularly called the Malthusian growth law. Its solution is obtained as

$$N(t)=N(0)\exp(b-d)t \tag{2.1.3}$$

Thus once N(0) is specified, N(t) can be determined for all t>0. The Malthusian growth model is the most commonly used calculus model in population mathematics. In the sequel we discuss the matrix population model as the subject of interest.

2.2 : Basic concepts of a matrix population model

The growth, survival and harvesting of a population structured according to age, size or stage can be described by matrix models, once the specific fecundity and survival rates are known. In growth models the relationship between the initial structure and the structure in the distant future is of prime interest.

Age-structured population growth models.

An age-structured model is deterministic and forecasts the age-structure of a population of females given the present structure or structure at some previous epoch and the age-specific survival and fertility rates. The model assumes that:

(i) the age-specific rates remain constant over the period of time between consecutive births.

(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) there is no immigration.

Suppose we have a population of females that is grouped into age-classes 0 to 1, 1 to 2, 2 to 3,---, m-1 to m units of time, assuming that none can live to be older than m. Let

$n_i(t)$ = the number of females in the age class (i-1) to i at time t (i=1,2,---,m) or age i next birthday.

Then the age-distribution of the population at time t can be expressed as

$\{n_1(t),\ n_2(t),---,n_m(t)\}$

Or, in matrix notation,

$$\mathbf{n}'(t) = (n_1(t),\ n_2(t),---,n_m(t)). \tag{2.2.1}$$

Further, let

$f_i(t) = f_i$ = the fertility rate of the females in the i-th age-group(i.e the number of daughters born in a unit of time to a female aged i that survive into the next age-group (i=1,2,...,m).

$s_i(t) = s_i$ = the probability that an individual in the i-th age-group at time t will be alive in the (i+1)-th age-group at time t+1

Then the age-distribution of the individuals at the end of a unit's time is given by

$$\sum_{i=1}^{m} f_i n_i(t) = n_1(t+1)$$

$$\begin{aligned}
s_1 n_1(t) &= n_2(t+1)\\
s_2 n_2(t) &= n_3(t+1)\\
&\cdot\\
&\cdot\\
&\cdot\\
s_{m-1} n_{m-1}(t) &= n_m(t+1)
\end{aligned} \tag{2.2.2}$$

assuming that individuals move exactly to the next age-group after each unit of time. In matrix notation,

$$\mathbf{n}(t+1) = P\mathbf{n}(t) \qquad (2.2.3)$$

where

$$P = \begin{bmatrix} f_1 & f_2 & . & . & . & f_{m-1} & f_m \\ s_1 & 0 & . & . & . & 0 & 0 \\ 0 & s_2 & . & . & . & 0 & 0 \\ . & . & . & . & . & . & . \\ 0 & 0 & . & . & . & s_{m-1} & 0 \end{bmatrix}$$

(2.2.4)

Since $f_i >= 0$ ($i = 1,2,...,m-1$), $f_m > 0$ and $0 < s_i =< 1$ ($i = 1,2,...,m-1$), P is a non-negative square matrix of order m.(2.2.2) shows that P is a population projection matrix. Unless the females are reproductive until the end of their lifespan,some of the elements in the first row of P towards the right-hand end may be zero,coinciding with their post-reproductive stages. We shall assume that the females are sterile in the last (m-k) age-groups. Then

$$P = \begin{bmatrix} f_1 & f_2 & . & . & . & f_{k-1} & f_k & 0 & . & . & . & 0 & 0 \\ s_1 & 0 & . & . & . & 0 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & s_2 & . & . & . & 0 & 0 & 0 & . & . & . & 0 & 0 \\ . & . & . & . & . & . & . & . & . & . & . & . & 0 \\ 0 & 0 & . & . & . & s_{k-1} & 0 & 0 & . & . & . & 0 & 0 \\ . & . & . & . & . & . & . & . & . & . & . & . & . \\ 0 & 0 & . & . & . & 0 & 0 & 0 & . & . & . & s_{m-1} & 0 \end{bmatrix} = \begin{bmatrix} M & O \\ B & C \end{bmatrix}$$

(2.2.5)

It follows that

$$P^t = \begin{bmatrix} M^t & O \\ f(MBC) & C^t \end{bmatrix}$$

(2.2.6)

where f(MBC) is a function of the product MBC . For t > (m-k),

$C^t = O$ being strictly triangular. Thus P^t has only zeroes in its last (m-k) columns. It is worthy therefore to consider only the reproductive age-groups of the population of females i.e sub-matrix M only, which is of dimension (kxk). Now

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

$$P\mathbf{n}(t+1) = \mathbf{n}(t+2) = P^2\mathbf{n}(t)$$

and in general,

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

Confining ourselves to the reproductive age-groups only would imply that

$$\mathbf{n}(t+x) = M^x\mathbf{n}(t) \qquad (2.2.7)$$

That is , the age-distribution after x units of time interval may be found by pre-multiplying $\mathbf{n}(t)$, the age-distribution at the initial time t, by M^x. As x becomes large, the age-distribution of the population stabilises. We then obtain the stable age-structure.

2.3 : Stable Population Theory.

If M is primitive, the proportional age-distribution of a population whose growth is governed by M would approach a limiting distribution as x becomes large,irrespective of the initial form of the age-distribution. This limiting distribution is known as the stable age-distribution.

At the stable age-distribution the proportion of individuals alive in a particular age-group bears a simple ratio to the corresponding proportion at the initial time.The stable age-distribution is proportional to the eigenvector associated with the maximal eigenvalue, λ, of M. Thus

$$\lim_{x \to \infty} M^x n(0) \propto n(s)$$

(2.3.1)

The elements of the stable age-distribution vector **n**(s) are proportional to the sizes of the age-classes when the age-distribution is stable. Once the stability of the age-distribution has been attained,

$$\mathbf{n}(s+1) = M\mathbf{n}(s) = \lambda_1 \mathbf{n}(s) \qquad (2.3.2)$$

Since M is non-negative and can be decomposed such that

$$KMK^{-1} = \begin{bmatrix} X & O \\ Y & Z \end{bmatrix}$$

(2.3.3)

where X and Z are square sub-matrices and K a <u>permutation matrix</u>, M is an <u>irreducible</u> non-negative matrix. Thus the following Perron-Frobenius theorem applies to M.

<u>Theorem 2.1 (Perron-Frobenius theorem)</u>

A population projection matrix M

(i) has a positive eigenvalue λ_1 which is simple (i.e of multiplicity one)

(ii) is such that if λ_j is another eigen-value, $|\lambda_j|<\lambda_1$ i.e λ_1 is the dominant eigen-value, and

(iii) the eigenvector corresponding to λ_1 is strictly positive.

<u>Proof.</u>

The characteristic equation of M is given by

$$|M-\lambda I| = 0 \qquad (2.3.4)$$

Let $s_1 s_2 \ldots s_r = s(r)$. Then (2.3.4) can be expanded to give

$$\lambda^k - f_1\lambda^{k-1} - s(1)f_2\lambda^{k-2} - \ldots - s(r)f_{r+1}\lambda^{k-r+1} - \ldots - s(k-1)f_k = 0$$

(2.3.5)

By the Descartes' rule of signs for positive roots,the number of positive roots of the characteristic equation equals the number of changes of sign,which is at most one.Since there is at least such a root for an irreducible non-negative matrix, there is only one positive root for M. Hence, result (i).

Results (ii) and (iii) follow if M is primitive.

Now

$$M = \begin{bmatrix} f_1 & f_2 & \ldots & f_{k-1} & f_k \\ s_1 & 0 & \ldots & 0 & 0 \\ . & . & \ldots & . & . \\ 0 & 0 & \ldots & s_{k-1} & 0 \end{bmatrix}$$

(2.3.6)

with $f_i >= 0$ (i = 1,2,...,k-1), $f_k > 0$ and $0 < s_i =< 1$ (i = 1,2,...,k-1).This implies that $f_i >= 0$ and $f_{i+1} >= 0$ for all i. Thus for some integer h, M^h is positive (all entries greater than zero). Since $M^h > 0$,M is primitive (Lopez[1961]).

We now examine the limiting behaviour of M^t. This requires the result given in Theorem 2.2 whose proof is in Gantmatcher[1979]:

<u>Theorem 2.2.</u>

For a primitive population projection matrix M with the dominant eigenvalue λ and associated eigenvalue **z**,

$$\lim_{t\to\infty} \frac{M^t}{\lambda^t} = S$$

(2.3.7)

where S is a matrix whose columns are positive multiples of **z** and the eigenvalues are assumed to be distinct. The matrix model was given as

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

In particular, if the initial time t=0, then

$$M^x\mathbf{n}(0) = \mathbf{n}(x) \tag{2.3.8}$$

By Theorem 2.2,

$$\lim_{x\to\infty}\frac{n(x)}{\lambda^x} = \lim_{x\to\infty}\left(\frac{M^x}{\lambda^x}\right)n(0) = Sn(0) \tag{2.3.9}$$

where S = $(\alpha_1\mathbf{z},\alpha_2\mathbf{z},\ldots,\alpha_m\mathbf{z})$. Consider any non-negative vector $\mathbf{v}>=0$. If

$$w = Sv = (\alpha_1 z,\alpha_2 z,\ldots,\alpha_k z)v' = z\sum_{l=1}^{k}\alpha_l v_l \tag{2.3.10}$$

where $\mathbf{w} = (w_1,w_2,\ldots,w_k)'$ with

$$w_i = z_i\sum_{l=1}^{k}\alpha_l v_l,\; i = 1,2,\ldots,k \tag{2.3.11}$$

so that

$$\frac{w_i}{\sum_{j=1}^{k} w_j} = \frac{z_i(\sum_{l=1}^{k}\alpha_l v_l)}{\sum_{j=1}^{k} z_j(\sum_{l=1}^{k}\alpha_l v_l)} = \frac{z_i}{\sum_{j=1}^{k} z_j} \tag{2.3.12}$$

implying that w_i is independent of **v**. Likewise $S\mathbf{n}(0) = c\Theta$ is independent of **n**(0), where c is a constant depending on M and **n**(0) i.e Θ is independent of **n**(0). Now let

$$\delta(x) = \frac{n(x)}{\sum_{i=1}^{k} n_i(x)}$$

(2.3.13)

Since

$$\lim_{x\to\infty} \frac{n(x)}{\lambda^x} = Sn(0) = c\Theta$$

(2.3.14)

$$\lim_{x\to\infty}\delta(x) = \lim_{x\to\infty} \frac{n(x)}{\sum_{i=1}^{k} n_i(x)} = Tn(0) = k\Theta$$

(2.3.15)

where k is a constant depending on M and $\mathbf{n}(0)$. Clearly $k\Theta$ is independent of $\mathbf{n}(0)$. Hence the age-distribution $\delta(x)$ tends to a limiting value Θ irrespective of the initial age-distribution $\mathbf{n}(0)$. The limiting vector Θ is called the <u>stable age-structure</u> with respect to M. It is the eigenvector corresponding to the dominant eigenvalue λ of M i.e

$$M\Theta = \lambda\Theta \tag{2.3.16}$$

Thus successive stable age-structures satisfy (2.3.2).

Once this stable form is attained for a population, it would thereafter increase without bound if $\lambda>1$, decrease if $\lambda<1$ and remain constant in size if $\lambda=1$. The harvesting strategy that would be adopted for the population would presume such a form to have been attained. The major problem would be to obtain the equilibrium population which maximises the harvest under this strategy.

Stochastic matrices.

These are a special kind of non-negative matrices. A non-negative matrix P is said to be stochastic iff the vector $(1,1,\ldots,1)'$ is its eigenvector that corresponds to the eigenvalue 1. For a stochastic matrix, every row-sum equals unity. Since the dominant eigenvalue always lies between the largest and smallest row-sums, the dominant eigenvalue of every stochastic matrix is one.

If $A = ((a_{ij}))$ be a non-negative square matrix of order n and r be a positive eigenvalue of A with the corresponding eigenvector $\mathbf{y} = (y_1, y_2, \ldots, y_n)$ that is positive, then

$$A\mathbf{y} = r\mathbf{y} \tag{2.3.17}$$

This implies that

$$\sum_{j=1}^{n} a_{ij} y_j = r y_i \,, \quad i = 1, 2, \ldots, n \tag{2.3.18}$$

If $Y = \mathrm{diag}(y_1, y_2, \ldots, y_n)$, then $P = ((p_{ij}))$ can be expressed as

$$P = r^{-1} Y^{-1} A Y \tag{2.3.19}$$

By the definition of P, p_{ij} are non-negative, i.e

$$p_{ij} = r^{-1} y_i^{-1} a_{ij} y_j \geq 0 \,, \quad i = 1, 2, \ldots, n \tag{2.3.20}$$

By (2.3.20) we have the relation

$$\sum_{j=1}^{n} p_{ij} = 1 \,, \quad i = 1, 2, \ldots, n \tag{2.3.21}$$

Thus we have established the following result:

A non-negative matrix A with a positive eigenvalue r and corresponding eigenvector **y** is similar to the product of r by some stochastic matrix P, i.e

$$A = Y(rP)Y^{-1} \tag{2.3.22}$$

(2.3.22) provides the relationship between stochastic matrices and non-negative matrices.

The matrix of transitional probabilities for a homogeneous Markov chain is stochastic; conversely any stochastic matrix may be taken to be the matrix of transitional probabilities of some homogeneous Markov chain. The theorem below gives the relationship between finite Markov chains and irreducible and primitive stochastic matrices.

<u>Theorem 2.3.</u>

Let P be a transition matrix of a finite Markov chain. If P is primitive and irreducible then the chain is <u>ergodic</u> and conversely; in this case

$$\lim_{n\to\infty} p^{(n)}_{ij} = \pi_j > 0 \tag{2.3.23}$$

where

$$\sum_{j=1}^{n} \pi_j = 1 \tag{2.3.24}$$

the limit being approached geometrically fast and uniformly for all i and j.

<u>Proof.</u>

Suppose P is irreducible and primitive. Since P is stochastic, its dominant eigenvalue, λ_1, equals unity. This root is simple and all the other eigenvalues are strictly less than unity in modulus.

Thus by the Perron-Frobenius theorem(thm2.1) there exists a positive row-vector π' satisfying $\pi' P = \pi'$, which can be normalised so that (2.3.24) holds. If (2.3.23) holds, then all the states are <u>aperiodic</u> and, by the limit theorem for Markov chains, <u>recurrent</u>. Hence the chain is ergodic. Conversely, suppose that the chain is ergodic. Then there exists a positive probability distribution $\pi = (\pi_j)$ such that

$$\lim_{n\to\infty} P^n = 1\pi' \qquad (2.3.25)$$

It follows that π is an eigenvector of P corresponding to the eigenvalue 1. Now $P^n > 0$ implies that $P^n > 0$ for sufficiently large n and so P is irreducible; otherwise

$$P = \begin{bmatrix} B & O \\ C & D \end{bmatrix} \qquad (2.3.26)$$

and the zero sub-matrix will recur through all powers of P. If P has any other eigenvalues of modulus 1, then P^n cannot be non-negative for all n. Consequently P is primitive. Thus P is primitive and irreducible.

2.4 : Harvesting strategies

The eigenvector corresponding to the dominant eigenvalue of M, λ_1, gives the stable age-structure. Successive stable age-structures satisfy

$\mathbf{n}(s+1) = M\mathbf{n}(s) = \lambda_1 \mathbf{n}(s)$

When $\lambda_1 > 1$, the population grows and an equal fraction $(\lambda_1 - 1)/\lambda_1$ of each age-group can be harvested from $\mathbf{n}(s+1)$ thereby returning the population to $\mathbf{n}(s)$. This is referred to as <u>proportional</u>

<u>harvesting</u> and leads to the linear programming problem

maximise $H = \mathbf{1}'(M\mathbf{x}-\mathbf{x})$

subject to $M\mathbf{x}>=\mathbf{x}$

and $\mathbf{x}>=\mathbf{0}$ (2.4.1)

where H is the harvest and **x** the unknown equilibrium-population. The solution to (2.4.1) is unbounded if there is no further constraint imposed. The use of the normalising restriction

$$\sum_{i=1}^{k} x_i = 1 \qquad (2.4.2)$$

and the constraint $x_0 = 1$ (2.4.3)

independently leads to feasible solutions for **x**.

<u>Remark</u>.

By using a general vector **c'** of weights instead of **1'**, different harvests from each age-group can be obtained whilst retaining the equilibrium-property that the population be restored.

Each combination of (2.4.1) with (2.4.2) and (2.4.1) with (2.4.3) constitutes a harvesting strategy.

In order to ensure that the parameters in the model remain valid we suggest that the population predicted using M after a small number of time-periods, say two, should act as a bound on the equilibrium-population. This is due to the fact that the parameters in the model remain valid for only short periods of time(Beddington[1974]). Thus (2.4.1) and the above constraint, $\mathbf{x}<=\mathbf{n}(2)$, also constitute a harvesting strategy.

We shall therefore consider the following harvesting strategies:

$$\begin{array}{ll} \textit{maximise} & H = c'(Mx-x) \\ \textit{subject} & Mx \ge x,\ x \ge 0 \\ \textit{with} & \sum_{i=1}^{k} x_i = 1 \end{array}$$

(2.4.4)

$$\begin{array}{ll} \textit{maximise} & H = c'(Mx-x) \\ \textit{subject} & Mx \ge x,\ x \ge 0 \\ \textit{with} & x_1 = 1 \end{array}$$

(2.4.5)

and finally

$$\begin{array}{ll} \textit{maximise} & H = c'(Mx-x) \\ \textit{subject} & Mx \ge x,\ x \ge 0 \\ \textit{with} & x = < n(2) \end{array}$$

(2.4.6)

(2.4.4),(2.4.5) and (2.4.6) are solvable by the matrix form of the simplex method.

2.5 : The matrix form of the simplex method.

The simplex method is essentially the Gauss-Jordan reduction procedure modified to account for the fact that the objective is merely not to solve a system of equations, but rather to solve a system of equations and maximise the objective variable.

A flow chart for the simplex method is in Appendix II.

C H A P T E R T H R E E

APPLICATION OF THE MODEL

3.1 : Introduction

We shall apply the model to an age-structured poultry population kept for egg production. The major aims would be to:

i) determine the intrinsic rate of growth, r.

ii) find the stable age-structure of the population, $\mathbf{n}_s$.

iii) determine the equilibrium-population and harvesting strategy that maximises egg production.

Crucial to the above is the knowledge of λ_1, the dominant eigenvalue of the projection matrix M.

<u>Determination of the dominant eigenvalue</u>.

One of the mostly used techniques is the power method. In its simplest form the method assumes an arbitrary initial vector $\mathbf{n}_o$ and produces a sequence of vectors $\mathbf{n}_i$ defined by

$$\mathbf{n}_{i+1} = M\mathbf{n}_i = \lambda_1 \mathbf{n}_i \qquad i = 0,1,2,---$$

We wish therefore to solve the above equation for λ_1. Under certain conditions it is possible to prove that this sequence converges to the eigenvalue of M with the largest modulus. The following theorem will prove to be useful.

<u>Theorem3.1.</u>

Let M be a kxk matrix with eigenvalues λ_i and linearly independent eigenvectors $\mathbf{x}_i$. If

$$\|\lambda_1\| > \|\lambda_2\| \geq \|\lambda_3\| \geq --- \geq \|\lambda_n\|$$

(3.1.1)

and

$$n_o = \sum_{j=1}^{k} \alpha_j x_j$$

(3.1.2)

for some scalars α_j with α_1 non-zero, then

$$n_i \rightarrow (\lambda_1^i \alpha_1) x_1$$

(3.1.3)

x_1 corresponding to the dominant eigenvalue, λ_1.

Proof.

From the definition of an eigenvector,

$$M\mathbf{x}_i = \lambda_i \mathbf{x}_i \qquad (3.1.4)$$

So $\mathbf{n}_1 = M\mathbf{n}_o = M(\alpha_1\mathbf{x}_1 + \alpha_2\mathbf{x}_2 + --- + \alpha_n\mathbf{x}_n)$

$= \alpha_1 M\mathbf{x}_1 + \alpha_2 M\mathbf{x}_2 + --- + \alpha_n M\mathbf{x}_n$

$= \alpha_1\lambda_1\mathbf{x}_1 + \alpha_2\lambda_2\mathbf{x}_2 + --- + \alpha_n\lambda_n\mathbf{x}_n$ (3.1.5)

Similarly,

$\mathbf{n}_2 = M\mathbf{n}_1 = \alpha_1\lambda_1^2\mathbf{x}_1 + \alpha_2\lambda_2^2\mathbf{x}_2 + --- + \alpha_n\lambda_n^2\mathbf{x}_n$

Proceeding in a like manner yields

$\mathbf{n}_s = \alpha_1\lambda_1^s\mathbf{x}_1 + \alpha_2\lambda_2^s\mathbf{x}_2 + --- + \alpha_n\lambda_n^s\mathbf{x}_n$.

This can be expressed as

$$n_s = \lambda_1^s [\alpha_1 x_1 + \alpha_2 (\frac{\lambda_2}{\lambda_1})^s x_2 + --- + \alpha_n (\frac{\lambda_n}{\lambda_1})^s x_n]$$

(3.1.6)

It can be noticed that all the terms except the first in the square brackets converge to the null vector as $s \rightarrow \infty$, since

$$\|\lambda_1\| > \|\lambda_j\|,\ j \neq 1$$

(3.1.7)

Hence

$\mathbf{n}_s \rightarrow (\lambda_1{}^s \alpha_1)\mathbf{x}_1.$

Remark.

If $\|\lambda_1\| > 1$, the elements of $\mathbf{n}_s$ increase boundlessly, resulting in computer overflow.Likewise, if $\|\lambda_1\| < 1$,the elements of $\mathbf{n}_s$ decrease to zero,leading to a loss of significant figures. Thus for computational purposes it is much more convenient to rescale at each stage so that the largest element of $\mathbf{n}_s$ is unity, the interest being in the ratio of the elements of an eigenvector.In practice, therefore ,it is better to compute the sequence of vectors defined by

$$\mathbf{p}_{s+1} = M\mathbf{n}_s$$

$$\mathbf{n}_{s+1} = \mathbf{p}_{s+1}/\max(\mathbf{p}_{s+1})$$

where $\max(\mathbf{p}_{s+1})$ denotes the element of $\mathbf{p}_{s+1}$ of largest modulus.(3.1.6) is unaffected by this modification and can be replaced by

$$n_s = k_s \lambda_1^s [\alpha_1 x_1 + \alpha_2 (\frac{\lambda_2}{\lambda_1})^s x_2 + \ldots + \alpha_n (\frac{\lambda_n}{\lambda_1})^s x_n]$$

(3.1.8)

where

$$k_s = \frac{1}{[\max(p_1)\max(p_2)\ldots\max(p_s)]}$$

(3.1.9)

Remark.

The above description shows why the power method works.

Clearly, $\mathbf{n}_s$ converges to a multiple of $\mathbf{x}_1$ as previously,where $\mathbf{x}_1$ is the eigenvector corresponding to the eigenvalue λ_1. Hence

$M\mathbf{n}_s \rightarrow \lambda_1\mathbf{n}_s$ i.e $\mathbf{p}_{s+1} \rightarrow \lambda_1\mathbf{n}_s$. Consequently, the scaling factors $\max(\mathbf{p}_{s+1})$ converge to the dominant eigenvalue λ_1 since the largest component of $\mathbf{n}_s$ is unity. An easier procedure of estimating λ_1 when programming the power method is derived from Theorem 3.1.

If we replace s by (s+1) in Theorem 3.1 we get

$\mathbf{n}_{s+1} \approx \lambda_1\mathbf{n}_s$. Thus $\mathbf{n}_s'\mathbf{n}_{s+1} \approx \lambda_1\mathbf{n}_s'\mathbf{n}_s$, implying that

$$\lambda_1 \approx n'_s n_{s+1} \tag{3.1.10}$$

Alternatively, if the largest component of $\mathbf{n}_s$ is the i-th one, then dividing this into the corresponding element of $\mathbf{n}_{s+1}$ gives an estimate of λ_1 i.e

$$\lambda_1 \approx \frac{1'_i n_{s+1}}{1'_i n_s} \tag{3.1.11}$$

where 1_i is the i-th unit-vector. Thus λ_1 can be generally estimated from the sequence of constants $\{\tau_s\}$ from the equation

$$\tau_s = \frac{m' n_{s+1}}{m' n_s} \tag{3.1.12}$$

where $\mathbf{m}$ is $\mathbf{n}_s$ or $\mathbf{1}_i$.

The power method algorithm therefore is as follows:

(a) Choose an arbitrary initial vector $\mathbf{u}_0$ such that $\mathbf{u}_0'\mathbf{u}_0 = 1$

(b) Let $\mathbf{v}_i = M\mathbf{u}_{i-1}$, $i = 1,2,\ldots$

(c) Set $\tau_i = \mathbf{v}_i'\mathbf{u}_{i-1}$

(d) Let $\beta_i = \surd(\mathbf{v}_i'\mathbf{v}_i)$

(e) Set $\mathbf{u}_i = \mathbf{v}_i/\beta_i$

(f) Return to (b) if $\mathbf{u}_i$ and $\mathbf{u}_{i-1}$ are not approximately equal or output τ_i and $\mathbf{u}_i$ if they are equal.A computer program for this is given in Appendix I.

<u>Remark.</u>

If $\lambda_1 = \lambda_2$ and $\|\lambda_1\| > \|\lambda_3\| >= \ldots >= \|\lambda_n\|$, then τ_i still converges to λ_1 (multiple eigenvalues still work with the power method). If $\lambda_1 = -\lambda_2$ and $\|\lambda 1\| > \|\lambda 3\| >= \ldots >= \|\lambda n\|$, then τ_i would show some periodicity. In this case $\mathbf{m}'\mathbf{n}_{s+2}/\mathbf{m}'\mathbf{n}_s$ would give an estimate for λ^2_1.

3.2 : Application

The following assumptions are made:

i) the model is an age-structured population model. The age-classification criterion considers the age of the individual next birthday.

ii) the parameters in the model are valid only for few time-periods so that an extended use of M is likely to produce an unrealistic estimate of the population.

iii) individuals move exactly one class up after each unit of time.

3.2.1 : <u>Determination of the intrinsic rate</u>

In poultry farming,the birds are kept either for egg or meat production. At the Egerton University poultry farm,where the data for this study was sourced,the birds are kept for egg production.The data was extracted from the information supplied by the attendants at the farm.The birds kept for egg production (all females) are normally classified according to age thus:

(i) from (egg) 0 weeks to 9 weeks : chicks

(ii) from 10 weeks to 20 weeks : growers

(iii) from 21 weeks to 30 weeks: layers

(iv) from 31 weeks to 40 weeks(and beyond):overmature layers.

After the 40-th week the birds are culled,as it becomes uneconomical to keep them. The peak laying week is the 28-th week. Egg-laying begins at the 21-st week at the rate of five eggs per week. The death rate for chicks is 2%. Thus the survival probability is 0.98. For growers, the death rate is 5%, implying that their survival probability is 0.95.Since 10% of the birds die during the process of growth from eggs to layers, 90% survive. Assuming that the new chicks are <u>born</u> to the layers, the fertility rate for the layers becomes 1.11 (or 100%/90%). Thus

$$M = \begin{bmatrix} 0.00 & 0.00 & 1.11 & 1.11 \\ 0.98 & 0.00 & 0.00 & 0.00 \\ 0.00 & 0.95 & 0.00 & 0.00 \\ 0.00 & 0.00 & 0.95 & 0.00 \end{bmatrix} \tag{3.2.1}$$

Let the initial age-distribution be

$\mathbf{n}_o = (344,276,214,166)'$,

assuming an initial arbitrary total population of 1000.The model used is therefore given by

$M^t\mathbf{n}_o = \mathbf{n}_t \quad ,t = 1,2,...$

That M is non-negative and irreducible is easy to see. The characteristic equation of M is obtained as

$\lambda^4 - 1.03341\lambda - 0.98174 = 0$

The index of primitivity, h , is the greatest common divisor of the differences of the consecutive indices of λ i.e G.C.D of {4-1,1-0}. In this case h = 1, implying that M is primitive and therefore has a dominant eigenvalue, λ_1, which is positive and (2.3.7) holds. Using the Pascal program for the power method in Appendix I, $\lambda_1 = 1.22433$. Thus the intrinsic rate of growth, r, is $r = \ln\lambda_1 = 0.20239$.

3.2.2 : <u>Generating the stable-population structure.</u>

According to (2.2.8), the elements of $\mathbf{n}_s$ are proportional to the sizes of the age-classes when the age-distribution is stable.

Once the stability of the age-distribution has been reached, we can write

$$\mathbf{n}_{s+1} = M\mathbf{n}_s = \lambda_1\mathbf{n}_s \qquad (3.2.2)$$

Let $s_1 s_2 \ldots s_r = s(r)$, r = 1,2,3. Then

$$\mathbf{n}_1 = (1,\ s(1)/\lambda_1,\ s(2)/\lambda_1^2,\ s(3)/\lambda_1^3\ )'$$

$$= (1, 0.800435829, 0.621084327, 0.481919633)'$$

$$\lambda_1\mathbf{n}_1 = (1.224333, 0.98, 0.760414037, 0.539003011)' \qquad (3.2.3)$$

$$M\mathbf{n}_1 = (1.2243344, 0.98, 0.760414037, 0.539003011)' \qquad (3.2.4)$$

Equality of (3.2.3) and (3.2.4) shows that $\mathbf{n}_1$ is the eigenvector of M corresponding to λ_1. The stable population vector, $\mathbf{n}_s$, is obtained as

$$\mathbf{n}_s = \mathbf{n}_1/\mathbf{1}'\mathbf{n}_1$$

$$= (0.34441, 0.27568, 0.21391, 0.16598)' \text{ (5 s.f)} \qquad (3.2.5)$$

Since $\lambda_1 > 1$, a positive harvest is possible.

<u>Remark</u>.

The value of λ_1 (the finite rate of natural increase of the population) and the given stable age vector ($\mathbf{n}_s$) do not uniquely determine a population's projection matrix, M. Two different projection matrices can have the same λ_1 and the same $\mathbf{n}_s$ even though they differ in some of their non-zero elements. The following numerical example, with k = 3 , illustrates this fact.

Consider two projection matrices X and Y where

$$X = \begin{bmatrix} 0.3 & 1.6 & 6.0 \\ 0.5 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.0 \end{bmatrix}$$

(3.2.6)

and

$$Y = \begin{bmatrix} 0.7 & 1.9 & 1.5 \\ 0.5 & 0.0 & 0.0 \\ 0.0 & 0.5 & 0.0 \end{bmatrix}$$

(3.2.7)

Both have the same dominant eigenvalue, λ_1 = 1.5, and both have the same stable vector

$$n_s \propto (9/13, 3/13, 1/13)'$$

(3.2.8)

Let both populations start with the same initial age-structure

$$n_o = (1/3, 1/3, 1/3)'$$

(3.2.9)

That the two populations would not be of the same total size at time t, however large it becomes, is attributed to their different growth behaviour.

3.2.3 : Determination of the equilibrium-population and optimal harvesting strategy.

A linear programming package, LINDO(Linear, Interactive, Discrete Optimizer), is employed in solving the optimization problems (2.4.4),(2.4.5) and (2.4.6). Using (2.4.4) with $\mathbf{c}' = (1,1,1,1)$, we find that $\mathbf{x} = (0.263473369, 0.258203902, 0.245293706, 0.233029021)'$ giving a harvest of 0.26747 per member of the population.This implies that 66 layers and 62 overmature layers are harvested (culled),thereby resulting in a yield of 1260 eggs per week from the remaining birds. (2.4.5) gives $\mathbf{x} = (1, 0.98, 0.931, 0.88445)'$ with a harvest of 1.01520 per member of the population,which implies that 94 layers and 90 overmature layers are harvested.The resulting yield is 980 eggs per week. Finally, applying the upper bound technique of the simplex algorithm in (2.4.6) gives $\mathbf{x} = (0.4216779, 0.413244342, 0.32064571, 0.2488012)'$ and a harvest of 0.33816 per member of the population,yielding 940 eggs per week. When $\mathbf{x} = \mathbf{n}_s = (0.34441, 0.27568, 0.21391, 0.16598)'$ is used,the harvest is 0.22433 per member of the population with a yield of 1480 eggs per week. In order to maintain the age-structure and size of the population we harvest a proportion

$$(\lambda_1 - 1)/\lambda_1 = 0.18323$$

from each age-group of the population (or 18.3%).

<u>Remark</u>.

It is noteworthy that egg production is maximised by minimising the number of layers culled.Evidently, working with the stable population results in the largest harvest. However,strategy (2.4.6) gives the most useful harvest of all,since the harvesting is done before the population grows to be very large .Thus it is the optimal strategy. The same harvest will be taken each time-period thereafter returning the population to the equilibriumstate until some change in policy is decided upon.

3.3 : Conclusion

The population growth model $\mathbf{n}(t+1) = M\mathbf{n}(t)$ reduces to $\mathbf{n}(t+1) = \lambda_1\mathbf{n}(t)$ after stability has been attained. Thereafter the population grows geometrically. However, as long as (λ_i/λ_1) approximates zero $(i = 1,2,..,k)$ the population will grow approximately geometrically.

The projections obtained using this classical model indicate the future course of population growth if the current trends in the vital rates are maintained. The model is only useful for predicting growth in discrete time.

So long as $\lambda_1 > 1$ harvesting is possible. In real life, the poultry farmer does not deal with a normalised equilibrium-population, $\mathbf{x}$, but with an age-stable population, $\mathbf{n}_0$. In order to maximise the harvest he should aim at the equilibrium-population, as obtained using strategy (2.4.6). The problem usually is how to obtain the equilibrium-population starting from the age-stable population. Intermediate harvesting strategies have been tried in solving this; however some of these strategies result in large or oscillating intermediate populations, both being features considered undesirable. A smooth progression from $\mathbf{n}_0$ to $\mathbf{x}$ is achieved by imposing a componentwise constraint on the intermediate populations (Harley and Mansion[1981]). This would enable him to monitor the effects of the gradual changes in the population so as to decide best on the population distribution to aim at for maximum harvest. This harveting model can also be applied in poultry farms where birds are kept for meat production as well as in any other situations where optimal use of resources is desired.

By introducing variability in the age-specific rates,the deterministic models becomes stochastic. Hence the parameters(rates) are estimable using statistical techniques. Future research in harvesting in matrix population models should focus on this aspect.

The failures of the age-structured matrix models derive from the non-uniformity in length of the age-classes, sizes of the age-classes and the general lifespan of the population under study. Modifications of the basic matrix model, the Leslie model, has helped in overcoming these to some extent.However,in general, the models do exhibit robustness as opposed to the calculus models.

In practice, therefore, the matrix models have to be applied with a number of assumptions from the data.This is due to their deterministic nature which hardly conforms to the natural processes of birth and death.

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APPENDIX I

```
{
 1. Specify a matrix (4 by 4)
 2. Pick any vector u0
 3. Multiply with  matrix M
 4. Call this product vi, i=1,2,...
 5. Set τi equal to the scalar product of vi and ui-1
 6. Let ßi equal the norm of vi
 7. Set ui equal the quotient of vi by ßi
 8. Find the difference between ui and ui-1
 9. If zero-vector then output the τi and ui
    else repeat 3.
 }
 Program Domeig;
 Type
 OneByFour = Array[1..4] of Real;  {Vector type definition}
 FourByFour= Array[1..4] of OneByFour; {Matrix type
             definition}
 Const
 Matrix : FourByFour =
          ((0.00,0.00,1.11,1.11),
           (0.98,0.00,0.00,0.00),
           (0.00,0.95,0.00,0.00),
           (0.00,0.00,0.95,0.00));
 Tolerance =   1.0e-5;
 Maximum : Word= 100;
 Var
 UZero,U0,
```

```
 UOne  ,
VOne   : OneByFour;
Vlarge : Real;
Row,Col,Count,
i,j,n  : Integer;
Function Generator(var cv:byte;var sum:Real):Real;
var ss : Real;
    counter : Byte;
  Begin
   Inc(cv);
   counter := 0;
   If cv = 4 then
   Generator := sqrt(1-Sum)
   else
   begin
   Inc(Maximum,cv);
   repeat
   Randomize;
   inc(counter);
    ss := (Random(Maximum))/(Maximum);
    if (counter > 15) and (sqr(ss)+sum > 1) then ss:=0;
    Until (Sqr(ss) + sum) <= 1;
    generator := ss;
    end;
   end;

 Procedure Generate;
 Var
```

```
 cv : Byte;
 Sum: Real;
 Begin
  cv:=0;
  Sum:=0;
  Fillchar(Uzero,Sizeof(uone),0);
  For col := 1 to 4 do
  Begin
  Uzero[col]:=Generator(cv,sum);
  Sum:=sum+sqr(Uzero[col]);
  end;
 end;

Procedure GetVector;
 Begin
  Generate;
 {Supply vector values/Generate}
  U0 := Uzero;
  end;

Procedure Vmultiply;
  var Hld : Real;
 Begin
  FillChar(VOne,Sizeof(VOne),#0);
  For Row := 1 to 4 do
   begin
    Hld:=0;
   For col := 1 to 4 do
```

```
    Hld:=Hld + (Matrix[Row,col] * Uzero[Row]);
    VOne[Row]:=Hld;
   end;
  end;

Function GetScalpro(MM:OnebyFour):real ;
var     Prod:real;
begin
FillChar(Vone,Sizeof(Vone),0);
FillChar(Uzero,Sizeof(Uzero),0);
For col:= 1 to 4 do
 begin
 Prod:=0;
 Prod:= Prod + (Vone[col]*Uzero[col]);
 GetScalpro:= Prod;
 Vlarge:= Prod:
end;
end;

Function GetMax(MM:OneByFour):Real;
 var Max : Real;
  Begin
   Max:=0;
  For col := 1 to 4 do
  Max := Max + Sqr(Vone[Col]);
  Max := sqrt(Max);
  GetMax:=Max;
   end;
```

```
Procedure VDiv(var VD : OneByFour;Var Max:Real);
  Begin
   Max := GetMax(vd);
    For Row := 1 to 4 do
     Uone[Row] := Vd[Row] / Max;
   end;

Function Vsub:Boolean;
var
ll      : Boolean;
Maximum : Real;
Hold: OneByFour;
 Begin
  VDiv(Vone,Maximum);
  ll := True;
  For Row := 1 to 4 do
   Begin
    VOne[Row] := Uone[row]-Uzero[row];
    ll := ll and (Abs(Vone[Row])<=Tolerance);
   end;
  Vsub := ll;
  if not ll then Uzero := Uone;
 end;
 Begin
 FillChar(Uzero,Sizeof(Uzero),0);
 FillChar(UOne,Sizeof(Uzero),0);
 For i := 1 to 25 do
 Writeln;
```

```
n:=0;
Count := 0;
Getvector;
Repeat
Vmultiply;
Write('Iteration : ',count,^M);
inc(count);
Until Vsub;
Writeln('Initial Arbitrary          Limiting
Projection');
Writeln('Vector of Unit Norm        Vector of Unit Norm
Matrix');
For col := 1 to 4 do
Writeln(U0[col]:7:5,'':18,Uone[col]:5:5,'':16,Matrix[col,1]:6:
2,Matrix[col,2]:6:2, Matrix[col,3]:6:2,Matrix[col,4]:6:2);
Writeln;
Writeln('Dominant Eigenvalue is : ',Vlarge:7:5);
Writeln('Number of iterations for the limiting vector :
',Count);
Writeln('Convergence due to tolerance (',Tolerance:2,')');
end.
```

OUTPUT FILE

Initial Arbitrary Vector of unit norm	Limiting Vector of unit norm	Projection Matrix
0.67041	0.34441	0.00 0.00 1.11 1.11
0.60364	0.27568	0.98 0.00 0.00 0.00
0.21571	0.21391	0.00 0.95 0.00 0.00
0.37369	0.16598	0.00 0.00 0.95 0.00

Number of Iterations for the Limiting Vector: 7

Dominant Eigenvalue is 1.224333

Convergence due to Tolerance

THE SIMPLEX METHOD FOR AN L P MAXIMIZATION PROBLEM.

(APPENDIX II)