CONSTRUCTION AND ANALYSIS OF LESLIE MATRIX POPULATION MODEL FOR AMBOSELI ELEPHANTS

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Declaration

I the undersigned declare that this dissertation is my original work and has not been presented for a degree in any other university.

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Date:.................................

This dissertation has been submitted for examination with my approval as the university supervisor

Supervisor:Dr. Charles Nyandwi

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Dedication

This dissertation is dedicated to my parents Mr. and Mrs. Josphat Kiplagat,my siblings Susan, Jackson, Jane, Peter and Nicholas for their support and prayers throughout my studies..

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Abstract

In this study, construction of a density independent Leslie matrix used for projecting Amboseli elephant population is discussed, where the only factors that determine the population dynamics are survivorship and fertility rates. Only the female population is considered and elephant population are grouped into age classes comprising of individuals with similar characteristics. All elephants population in a certain age class move to the next age class during the next time step. Properties of the matrix relevant to population growth rate and stable population is highlighted and discussed.Transient and asymptotic population dynamics are analysed.Perturbation methods have also been discussed. It is noted that in the lower age classes, change in survival rates have more effect to the asymptotic growth rate than change in fertility rates while in the older population,change in fertility rates bring greater effect to the asymptotic growth rate than change in survivorship. The eigenvalues of the Leslie matrix are calculated and the dominant eigenvalue is found to represent the long run growth rate.Its corresponding right and left eigenvectors represent stable age structure and reproductive value respectively.Attempt to incorporate density dependence into the model is made with density as the total number of population. Model analysis shows that population increases in all the age classes.

Contents

Chapter 1

Introduction

Studies in population dynamics have been carried out solely to predict future characteristics of a population when the past or present is known. Various models have been derived to predict future population size. These models can be broadly classified as calculus or matrix models.

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

Calculus model describing the growth of a population is given by

$$N(t) = N_0 e^{rt} \tag{1.1}$$

where

$$N(t) is\ the\ population\ size\ at\ time\ t$$

$$N_0\ is\ the\ initial\ \ population\ \ size$$

$$r\ \ is\ the\ intrinsic\ rate\ of\ natural\ increase$$

The above type of model is only applicable for a short term projection when resources are abundantly available.For a long-term projection, we need an improved model. A good example is the Logistic population model given by the equation

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0)e^{-r_0 t}} \tag{1.2}$$

where
r_0 is some initial growth rate
K is the carrying capacity of the population

Matrix population models are as a result of studies by Bernadelli (1941), P.H Leslie (1945, 1948) and Lewis (1942). They provide a good basis on which to analyse population dynamics using the theory of matrix algebra. In his 1945 paper, Leslie expressed the basic age-specific projection equations in matricial form and applied matrix analysis to determine the stable age distribution. In his second paper in 1948, he extended the use of matrix models by studying their connection with logistic population growth and predator-prey interactions.

Leslie matrix model ,named after P.H Leslie due to his discovery,generally makes use of age specific rates of fertility and mortality of a population. The matrix form of the model makes it flexible and mathematically easy to study and perform analysis. The basic model forms a strong base for projecting and describing population dynamics of animals and plants. As a fairly recent innovation in mathematics , the Leslie model is widely used to project the present state of a population into the future as a way of forecasting the age distribution by considering survival and fecundity parameters.

1.1 Model Structure

In its simplest form, Leslie matrix model only considers female population. This assumption is from the fact that there will always be enough males to fertilize the females. The female population is then divided into several categories by age or by size. If the grouping is by age, the group intervals may be uniform or non-uniform.The grouping is done following characteristics and features shared by animals (or plants). Animals or plants with similar characteristics are put in the same age group. The group length can be 1 unit of time (e.g. second, day, year etc.) or more than 1. For example, it may be 5 years for human and 2 years for large whales. We assume that the fecundity and survival rates of each group do not vary with time and are therefore not dependent on population density.

In calculus model, data is extracted from life tables. Below,are life table functions.

1.2 Life tables

Life table functions are indexed by x in continuous time.

Definition 1 *Survivorship schedule* (l_x)

This describes the probability of surviving through each age class. Survivorship from birth to age class x is denoted l_x and given by

$$l_x = \frac{N_x}{N_0} \tag{1.3}$$

where N_x is the number of individuals of age x and N_0 is the number of individuals at birth.

Age specific survival is denoted s_x or P_x and given by

$$s_x = \frac{N_{x+1}}{N_x} = \frac{l_{x+1}}{l_x} \tag{1.4}$$

Definition 2 *Fecundity schedule* (m_x)

This is the expected number of offspring (female) per female individual of age x at a unit time.

Definition 3 *Gross reproductive rate:* $\sum m_x$

This is the total lifetime reproduction in the absence of mortality. It is the average lifetime reproduction of an individual that lives to senescence and is useful in considering potential population growth if all the ecological limits were removed from a population.

Definition 4 *Net reproductive rate* $R_0 = \sum l_x m_x$

This is the average number of offspring produced by an individual in its lifetime taking into account normal mortality. $l_x m_x$ is the average number of offsprings produced by individuals of age x. If summed across all ages, we have the average lifetime reproduction.

R_0 is also called the replacement rate.

$R_0 < 1 \Longrightarrow$ individuals not fully replacing themselves and thus population shrinks

$R_0 = 1 \Longrightarrow$ individuals exactly replacing themselves and thus population size remains stable

$R_0 > 1 \Longrightarrow$ individuals more than replacing themselves and thus population grows

Definition 5 *Generation time:* T

This is defined as the mean age of a female when each of her children was born and is expressed as

$$T = \frac{\sum x l_x m_x}{\sum l_x m_x} \tag{1.5}$$

If most offsprings are produced when mothers are young T will be short. T will be long if most offsprings are produced when mothers are old.

In a stable population,$R_0 = 1$ and therefore the denominator has no effect on generation time.

Definition 6 *Intrinsic rate of increase (r)*

This is expressed as

$$r \sim \frac{\ln R_0}{T} \tag{1.6}$$

This equation only gives accurate results when $R_0 \sim 1$ (*or* $r \sim 0$). The exact solution comes from Euler's equation below

$$1 = \sum e^{-rx} l_x m_x \tag{1.7}$$

1.3 Projection Matrix functions

Even if data are collected in continuous time, the construction of the life table requires a discretization of age to form age classes.Here population is arranged in age classes.

Survival rate P_i and fertility rate F_i are the common projection matrix functions. They are indexed by age class in discrete time.

Survival rates P_i is the probability of survival from time t to $t+1$ of age class i

Fertility rates F_i is the number of offspring born by a single parent in age group i per unit time.

1.3.1 Objectives of the study

- To demonstrate how Leslie matrix model is constructed
- To build a mathematical model to predict the population size and age structure of Amboseli elephants in the future
- To calculate Amboseli elephants growth rates in the long run
- To calculate the elasticity and sensitivity of the growth rate with respect to different parameters.
- To incorporate density dependence into the model

Chapter 2

Literature review

Since its discovery, several studies have been done on the basic Leslie matrix population model. Over the years, major contributions have been made in order to sophisticate the model.

- In his paper in 1945, Leslie expressed the basic age-specific equations in matrix form and applied the usual methods of analyzing matrix to determine stable age population. In 1948, he extended the use of matrix models by studying their relationship to logistic growth and predator-prey interactions.

- Usher in 1966 developed further the Leslie matrix model by considering size instead of age for forest trees.

- Skyles in 1969 showed that the Leslie matrix is irreducible and Brauer in 1962 called it unreduced matrix.

- Lefkovitch (1965,1966, 1967) built a stage structured matrix model for insect using four stages, namely: eggs, larvae, pupae and adult and later in 1967, he investigated the effect of harvesting in the development structure of the population.

  In stage-classified model, there is a possibility of an individual of a group i moving backwards to the previous group, forward to the next group or staying in the same group at next time period. This occurs to organisms that grow in stages.

- Lefkovitch showed that a population projection matrix modeled on stage classifications rather than on age classification is in the form shown below

$$A = \begin{bmatrix} F_{11} & F_{12} & F_{13} & F_{14} & \cdot & \cdot & \cdot & F_{1\ ,n-1} & F_{1\ ,n} \\ P_{21} & P_{22} & P_{23} & 0 & \cdot & \cdot & \cdot & 0 & 0 \\ 0 & P_{32} & P_{33} & P_{34} & \cdot & \cdot & \cdot & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & & & & \cdot & 0 \\ \cdot & \cdot & & \cdot & & & & \cdot & 0 \\ \cdot & \cdot & \cdot & & & & & \cdot & 0 \\ 0 & \cdot & \cdot & \cdot & 0 & 0 & P_{n-1,\ n-2} & P_{n-1\ ,n-1} & P_{n-1,\ n} \\ 0 & \cdot & \cdot & \cdot & & & 0 & P_{n\ ,n-1} & P_{n\ ,n} \end{bmatrix} \tag{2.1}$$

- Leslie looked at time-lag in his model and he discovered that it showed oscillatory solution.
- Usher in 1966 and Goodman (1969) together showed that the Leslie basic model can be written as

$$A = F + P$$

where

$$F = \begin{bmatrix} F_1 & F_2 & \cdot & \cdot & \cdot & F_n \\ 0 & 0 & \cdot & \cdot & \cdot & 0 \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ 0 & 0 & \cdot & \cdot & \cdot & 0 \end{bmatrix}$$

and

$$P = \begin{bmatrix} 0 & 0 & \cdot & \cdot & \cdot & 0 \\ P_1 & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & P_2 & \cdot & \cdot & \cdot & 0 \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ 0 & \cdot & \cdot & \cdot & P_{n-1} & 0 \end{bmatrix}$$

- Lewis independently considered a group of individuals whose breeding occur at regular intervals. He showed that if the individuals filled the n age groups, then the age frequency distribution after the nth breeding class would be the nth power of the projection matrix. According to him, the age distribution will generally display no periodicity but tends to a stable distribution depending on the dominant eigenvalue of the matrix.

- Bernadelli in 1948 focussed on the intrinsic oscillations on population structure. By observing oscillations in the age structure of human population, he developed a projection matrix and further showed numerically ,that this gave rise to permanent oscillations in the age structure.

- If age and size are both important and significant interactions exist between the two, then we will need to formulate a two dimensional model.Yu in1990 showed that developmental stages are useful as age classes. He used stage-classified model to study population dynamics of corn earthworm (CEW). He divided the CEW into five stages and split the first stage into four age groups, the second, third and fourth stages into six age groups, while the last stage he considered as a single group. His projection matrix was of order 23.

- For large mammals and birds, we only consider age classification and therefore end up with the Leslie matrix model.

- Wen-Ching Li (1994) applied Leslie matrix model to wild turkey populations. He considered three classes,namely: poults,yearlings and adults. He ended up with a matrix of order three. Only yearlings and adults are productive.

- G. C Smith and R.C Trout used Leslie matrices to determine wild rabbit population growth and the potential for control. To examine the rate of population growth under various control policies, two age categories of rabbits were defined:young and old categories. A survival rate of 0.95 for young rabbits and 0.05 for old rabbits was used. It was found out that as the maximum age of young rabbits increased, the variation of the rate of growth with timing of the control increased. Also, overall λ is greatest between late April to early september and λ is least between the periods November to January.

- Neon and Sauer studied population models for passerine birds. They recommended an after birth-pulse censuring for population of passerine birds because the rates of population change for these birds are highly sensitive to fecundity and/or first year survival rate.

Chapter 3

Development of Leslie model

The Model is a powerful tool (named after P.H Leslie) and is used to determine the growth of a population as well as the age distribution within a population.To be able to develop this model, we make use of the following assumptions:

- We consider only the females in the population
- The maximum age attained by any individual is n years
- The population is grouped into age classes
- An individual chance of surviving from one age class to the next is a function of its age.
- The survival rate P_i of each age group is known
- The reproduction rate F_i for each age group is known
- The initial age distribution is known

We will put a superscript on the upper right of quantities to signify the point in time to which the symbol refers and a subscript on the lower right of the quantity to signify the name of the age class.

Define

$x_i^{(k)}$ =the number of females alive in the group i at time t_k

P_i=the probability that a female of group i at time t_k will be alive in group $i+1$ at time t_{k+1}

F_i=the number of daughters born per female in group i from time t_k to time t_{k+1}

We define the age distribution $x^{(k)}$ at time t_k by

$$x^{(k)} = \begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ . \\ . \\ . \\ x_n^{(k)} \end{pmatrix} \tag{3.1}$$

where $x_i^{(k)}$ is the number of females in the ith age class at time t_k.

At time t_k ,the number of females in the first age class, $x_1^{(k)}$, are those daughters born between time t_{k-1} and t_k. The number of offsprings produced by each age class can be calculated by multiplying the reproductive rate by the number of females in that particular age class. The sum of all these values gives the total number of offsprings produced. Mathematically, we have

$$x_1^{(k)} = F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + ... + F_n x_n^{(k-1)} \tag{3.2}$$

The number of females in the second age class at time t_k are those in the first age class at time t_{k-1} who are still alive at time t_k. Mathematically, this becomes

$$x_2^{(k)} = P_1 x_1^{(k-1)} \tag{3.3}$$

The number of females in the third age class at time t_k are those females in the second age class at time t_{k-1} who are still alive at time t_k. Mathematically, we have

$$x_3^{(k)} = P_2 x_2^{(k-1)} \tag{3.4}$$

In genaral, the number of females in the nth age class at time t_k are those females in the age class $(n-1)$ at time t_{k-1} who are still alive at time t_k , i.e

$$x_n^{(k)} = P_{n-1} x_{n-1}^{(k-1)} \tag{3.5}$$

We end up with the following system of linear equations:

$$x_1^{(k)} = F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + ... + F_n x_n^{(k-1)}$$

$$x_2^{(k)} = P_1 x_1^{(k-1)}$$

$$\begin{aligned} x_3^{(k)} &= P_2 x_2^{(k-1)} \\ &. \\ &. \\ &. \end{aligned}$$

$$x_n^{(k)} = P_{n-1} x_{n-1}^{(k-1)}$$

In matricial form, we rewrite the above system of equations as

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ . \\ . \\ . \\ x_n^{(k)} \end{pmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & . & . & . & F_{n-1} & F_n \\ P_1 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & P_2 & 0 & . & . & . & 0 & 0 \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ 0 & 0 & 0 & . & . & . & P_{n-1} & 0 \end{bmatrix} \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \\ . \\ . \\ . \\ x_n^{(k-1)} \end{pmatrix} \tag{3.6}$$

The above matricial form can be compactly written as

$$x^{(k)} = L x^{(k-1)} \tag{3.7}$$

where

$$x^{(k)} = \begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ . \\ . \\ . \\ x_n^{(k)} \end{pmatrix} \textit{ is the age distribution vector at time } t_k$$

$$x^{(k-1)} = \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \\ . \\ . \\ . \\ x_n^{(k-1)} \end{pmatrix} \textit{is the age distribution vector at time } t_{k-1}$$

$$L = \begin{bmatrix} F_1 & F_2 & F_3 & . & . & . & F_{n-1} & F_n \\ P_1 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & P_2 & 0 & . & . & . & 0 & 0 \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ 0 & 0 & 0 & . & . & . & P_{n-1} & 0 \end{bmatrix} \textit{is the Leslie Matrix}$$

Matrix population models can be classified by the nature of the projection matrix L. In the simplest case, the matrix L is a constant. The resulting model is as given above. This model is linear and time invariant.

If L is not constant, it may vary because of external factors e.g weather. A variable enviroment leads to linear, time-varying model as shown below

$$x^{(k)} = L_k \; x^{(k-1)} \tag{3.8}$$

where each of L_k may be a function of time.

Variation due to the population yields the non-linear model

$$x^{(k)} = L_x \; x^{(k-1)} \tag{3.9}$$

where each of L_x may be a function of the population vector x .These models are what are normally referred to as density dependent models.

It is possible to combine environmental variation and density dependence to yield a system of other non-linear equations shown below

$$x^{(k)} = L_{x,k}\ x^{(k-1)} \tag{3.10}$$

From equation (3.7) above,

$$x^{(1)} = Lx^{(0)}$$

$$x^{(2)} = Lx^{(1)} = L(Lx^{(0)}) = L^2x^{(0)}$$

$$x^{(3)} = Lx^{(2)} = L(L^2x^{(0)}) = L^3x^{(0)}$$

$$\vdots$$

$$x^{(k)} = Lx^{(k-1)} = L^kx^{(0)} \tag{3.11}$$

Thus if we know the initial age distribution vector

$$x^{(0)} = \begin{pmatrix} x_1^{(0)} \\ x_2^{(0)} \\ x_3^{(0)} \\ . \\ . \\ . \\ x_n^{(0)} \end{pmatrix}$$

we can determine the age distribution vector at any later time.

The Leslie matrix

$$L = \begin{bmatrix} F_1 & F_2 & F_3 & . & . & . & F_{n-1} & F_n \\ P_1 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & P_2 & 0 & . & . & . & 0 & 0 \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ 0 & 0 & 0 & . & . & . & P_{n-1} & 0 \end{bmatrix}$$

$$0 < Pi < 1, \ F_i \geq 0$$

is a non-negative , square matrix of order n with all the elements zero except those that are in the first row and in the subdiagonal immediately below the principal diagonal. L is based on age classifications.

We have already seen that the Leslie matrix L is a non-negative matrix. This leads us to a brief study of non-negative matrices in order to understand the properties of the Leslie matrix L.

Chapter 4

Nonnegative matrices and Perron Frobenius theorem

$A \in \mathbb{R}^{m\times n}$ is said to be a non-negative matrix whenever $a_{ij} \geq 0$ and this is denoted by writing $A \geq 0$. In general $A \geq B$ means that $a_{ij} \geq b_{ij}$ where a_{ij} is an element in A and b_{ij} is an element in B. Similarly, A is a positive matrix when each $a_{ij} > 0$ and is denoted by writing $A > 0$. More generally, $A > B$ means that each $a_{ij} > b_{ij}$

Since non-negative matrices have numerous applications, it is natural to investigate their properties and we do so in this chapter. A primary issue concerns the extent to which the properties $A > 0$ *or* $A \geq 0$ translate to spectral properties e.g. to what extent does A have positive (or non-negative) eigenvalues and eigenvectors.

Here we will focus on matrices $A_{n\times n}$ and investigate the extent to which this property (non-negativity) is inherited by the eigenvalues and eigenvectors of A.

First we notice that

$$A > 0 \Longrightarrow \rho(A) > 0 \text{ where } \rho(A) \text{ is the spectral radius of } A$$

We also note the following

$$\begin{aligned} P &> 0, X \geq 0, X \neq 0 \Longrightarrow PX > 0 && (4.1) \\ N &\geq 0, u \geq v \geq 0 \Longrightarrow Nu \geq Nv && (4.2) \\ N &\geq 0, z > 0, Nz = 0 \Longrightarrow N = 0 && (4.3) \\ N &\geq 0, N \neq 0, u > v > 0 \Longrightarrow Nu > Nv && (4.4) \end{aligned}$$

where P and N are $n \times n$ matrices while u, v and z are vectors of dimension n

Statement If $A_{n\times n} > 0$, then the following statements are true

- $\rho(A) \in \sigma(A)$
- $\rho(A)$ is the only eigenvalue of A on the spectral circle and is termed as the Perron root, latent root or the dominant eigenvalue.

A vector corresponding to this value ($\rho(A)$) is referred to as Perron vector.

While eigenvalues of $A \geq 0$ other than $\rho(A)$ may or may not be positive, it turns out that no eigenvectors other than positive multiples of the Perron vector can be positive or even non-negative. Infact, there are no non-negative eigenvectors for $A_{n\times n} \geq 0$ other than the Perron vector and its multiples.

Perron's Theorem

If $A_{n\times n} > 0$ with $r = \rho(A)$, then the following statements are true:

- $r > 0$
- $r \in \sigma(A)$ (r is called the Perron root)
- There exists an eigenvector $x > 0$ such that

$$Ax = rx \tag{4.5}$$

The Perron vector is the unique vector defined by

$$Ap = rp \ , \ p > 0 \ \text{ and } \ \| \, p \, \|_1 = 1$$

Except for positive multiple of p , there are no other non-negative eigenvectors for A, regardless of the eigenvalue.r is the only eigenvalue on the spectral circle of A

Now we seek to include zero and investigate the extent to which Perron's results generalize to non-negative matrices containing at least one zero entry.

For $A_{n\times n} \geq 0$ with $r = \rho(A)$, the following statements are true:

- $r \in \sigma(A)$
- $Az = rz$ for some $z \in \mathbb{R}^n$

4.0.2 Reducibility

$A_{n\times n}$ is said to be reducible matrix when there exists a permutation matrix P such that

$$P^T AP= \begin{bmatrix} X & Y \\ 0 & Z \end{bmatrix}$$

where X and Z are both square.

Otherwise, A is said to be an irreducible matrix

A reducible matrix can always be arranged by numbering the stages , into normal form:

$$\begin{bmatrix} B & O \\ C & D \end{bmatrix} \tag{4.6}$$

where the square submatrices B and D are either irreducible or can themselves be divided to eventually yield a series of irreducible diagonal blocks (Gantmacher 1959).

An irreducible matrix always has a real positive latent root λ_1 that is distinct. The absolute values of all other roots are less than or equal to λ_1 and in practice the other roots are either complex or else negative.

Corresponding to λ_1 is an eigenvector whose entries are non-negative. No other eigenvector of non-negative elements exists, disregarding multiples of the eigenvector.

4.0.3 Primitive Matrices

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

$$\lambda^* = \lambda_1$$

$$then$$

$$\lambda_1 = \mid \lambda_2 \mid = \ldots = \mid \lambda_h \mid$$

If $h = 1$,the matrix A is called primitive , that is, a non-negative irreducible matrix A having only one eigenvalue , $r = \rho(A)$, on its spectral circle is said to be a primitive matrix.

If $h > 1$, the matrix A is called imprimitive and h is called the index of imprimitivity.

We next state without proof a sufficient condition for primitivity.

Corollary 7 *If a non-negative irreducible matrix A has at least one positive diagonal element, then A is primitive.*

Below is a statement to show how powers of a non-negative matrix determine whether or not the matrix is primitive

Lemma 8 *Frobenius test for Primitivity*

$A \geq 0$ is primitive iff $A^m > 0$ for some $m > 0$

This is to say that an irreducible non-negative matrix A is primitive if it becomes positive when raised to sufficiently high powers. A reducible matrix cannot be primitive because when the matrix (4.6) above is raised to powers , the upper-right block remains zero.

4.0.4 Evaluating irreducibility and primitivity numerically

Evaluating irreducibility and primitivity of large matrices can be very difficult. Horn and Johnson (1985) summarize several theorems that provide numerical methods that enable one to quickly evaluate irreducibility and primitivity of matrices. Suppose A is a nonnegative $n \times n$ matrix. Then

- A is irreducible iff
$$(I + A)^{n-1} > 0 \tag{4.7}$$

- A is primitive iff
$$A^{n^2-2n+2} > 0 \tag{4.8}$$

Theorem of Perron-Frobenius

Let A be a square matrix with non-negative elements only , and such that all elements of A^n are positive for some integer n (we say that A is primitive). Then A has a positive eigenvalue of algebraic multiplicity 1, which correspond to a right eigenvector V_1 and to a left eigenvector U_1 both of which have only positive elements. This eigenvalue is greater in absolute size than any other eigenvalue of A

The summary of this theorem is as follows:

Primitive matrices:If A is primitive , then there exists a real, positive eigenvalue λ_1 that is simple root of the characteristic equation. This eigenvalue is strictly greater in magnitude than any other eigenvalue. The right and left eigenvectors V_1 and U_1 corresponding to λ_1 are real and strictly positive. There may be other real eigenvalues besides λ_1, but λ_1 is the only eigenvalue with nonnegative eigenvectors.

i.e.

$$\begin{aligned}
\lambda_1 &> 0 \\
U_1 &> 0 \\
V_1 &> 0 \\
\lambda_1 &> |\lambda_i|\,,\ i > 1
\end{aligned}$$

Irreducible but imprimitive matrices: If A is an irreducible matrix but imprimitive , with index of imprimitivity h, then there exists a real positive eigenvalue λ_1 which is a simple root of the characteristic equation. The associated right and left eigenvectors are positive. The dominant eigenvalue λ_1 is greater than or equal to in magnitude to any of the other eigenvalues

i.e.

$$\begin{aligned}
\lambda_1 &> 0 \\
U_1 &> 0 \\
V_1 &> 0 \\
\lambda_1 &= |\lambda_i|\,,\ i = 2, ..., h \\
\lambda_1 &> |\lambda_i|\,,\ i > h
\end{aligned}$$

Reducible matrices: If A is reducible, there exists a real eigenvalue $\lambda_1 \geq 0$ with corresponding right and left eigenvectors $V_1 \geq 0$ and $U_1 \geq 0$. This eigenvalue $\lambda_1 \geq |\lambda_i|\,,\ i > 1$

We have just shown that an irreducible non-negative matrix always has a real positive latent root λ_1 . The absolute values of all other roots are less than or equal to λ_1.Second, corresponding to λ_1 are eigenvectors whose elements are positive . There is no other eigenvector of non-negative elements , disregarding multiples of these eigenvectors .

4.1 Properties of the basic matrix L

Leslie matrix L derived above is a square matrix of order n. If $i = s < n$ is the last age group within which reproduction occurs, F_s is the last F_i which is not equal to zero. We can therefore partition matrix L as follows:

$$L = \begin{bmatrix} A & 0 \\ B & C \end{bmatrix} \tag{4.9}$$

where

A is square of order s

B is of order $(n-s) \times s$

C is square of order $n - s$

0 is of order $s \times (n-s)$

A matrix of the above nature is said to be reducible. To study the properties of the matrix L , it is sufficient to study matrix A which consists of reproductive individuals.

$$L^k = \begin{bmatrix} A^k & 0 \\ f(A, B, C) & C^k \end{bmatrix} \tag{4.10}$$

C^k is of the type such that $C^{n-s} = 0$, so that L^k, $k \geq n - s$ will have all its last $n - s$ columns consisting of zeros. This is from the fact that individuals alive in the post-reproductive classes will eventually contribute nothing after they are dead. This affirms why matrix A will be of interest in such a case.

Matrix A is nonsingular since

$$\det A = (-1)^{s+1}(P_1 P_2 ... P_{s-1} F_s) \neq 0 \tag{4.11}$$

If the entire population is productive, then matrix A will be the entire matrix and we say in this case that $A = L$ is irreducible.

We will later show that the Leslie matrix L used in elephants demography falls in a restricted subclass of irreducible non-negative matrices called primitive matrices. From the Perron- Frobenius theory, L has a unique root λ_1 which is larger in magnitude than any other root (eigenvalue) of L. Corresponding to λ_1 is a eigenvector which is positive and no other non-negative eigenvector will exist for matrix L.

4.1.1 Parameter estimation

Survival probability P_i

The values of P_i is usually obtained from a life table or experiments. It is usually assumed that (Leslie 1945,Caughley 1977:87)

$$P_i = \frac{l_{i+1}}{l_i} \tag{4.12}$$

P_i is assumed to be constant over a unit of time.

Fecundity rates F_i

F_i is determined not only by the average number of female births per mother per time period , m_i in the life table , but also including infant survival rates (Leslie 1945). We divide populations into two breeding systems: birth-flow and birth-purse populations.

Birth-flow breeding Here reproduction is continuous. Estimation of F_i involves integration of fertility and infant mortality functions over the continuous time interval.

Birth-pulse breeding Populations in this system reproduce during a short period of time per year. In this system , it is important to know the exact breeding period with respect to the time step . Estimation of F_i will be influenced by way of census. Census before reproduction or after reproduction give rise to different value of F_i.

Since births occur during the next birthday of an individual, the probability of surviving for a fraction $1-p$ is P_i^{1-p}. For the individual to be counted in $n_1(t+1)$, it must survive a fraction p of a time unit , and that probability is determined by $l(p)$.

Thus the fertility of a population is calculated as:

$$F_i = l(p)P_i^{1-p}m_i = \left\{ \begin{array}{c} P_i m_{i+1} \text{ postbirth-pulse sampling } (p \to 0) \\ \\ l_1 m_i \text{ prebirth-pulse sampling } (p \to 1) \end{array} \right\} \tag{4.13}$$

F_i is assumed to be constant and not dependent on density.

Chapter 5

Eigensystem

5.1 Eigenvalues and corresponding eigenvectors

Consider the system

$$x^{(k)} = Lx^{(k-1)}$$

We apply linear algebra techniques to the above model to interpret several biological phenomena.

If L has the formula

$$LV_i = \lambda_i V_i \tag{5.1}$$

then λ_i ; $i = 1, 2, ..., n$ are the eigenvalues of L. For the above system

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

V_i are the corresponding linearly independent eigenvectors.

The eigenvalues are arrived at by solving the system

$$|L - \lambda I| = 0 \tag{5.2}$$

that is

$$\begin{vmatrix} F_1 - \lambda & F_2 & F_3 & \cdot & \cdot & \cdot & F_n \\ P_1 & -\lambda & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & P_2 & -\lambda & \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & & & & & \cdot & \cdot \\ \cdot & & & & & \cdot & 0 \\ 0 & 0 & \cdot & \cdot & \cdot & P_{n-1} & -\lambda \end{vmatrix} = 0$$

To each an eigenvalue , there corresponds an eigenvector. The eigenvectors are linearly independent and are achieved by solving for V in the following equation

$$LV = \lambda V$$

V is commonly referred to as the right eigenvector corresponding to the eigenvalue λ of matrix L.

In demographic applications, the roots λ_i are always distinct. In particular, the root λ_1 of largest magnitude compared to λ_i $i \geq 2$ is of much interest. It is referred to as the dominant eigenvalue or the latent root or the Perron root.

The dominant eigenvalue describes the growth rate of a population in the long run.

$$
\begin{aligned}
\lambda_1 &= 1, \text{ the population is stationary} \\
\lambda_1 &> 1, \text{ over population will be experienced.} \\
\lambda_1 &< 1, \text{ the population diminishes.}
\end{aligned}
$$

For $\lambda_1 > 1$, one may think of harvesting as an option in order to keep the population stable.

For the system

$$x^{(k)} = Ax^{(k-1)} \qquad (5.1.3)$$

where A is an arbitrary matrix,

The system (5.1.3) is said to be asymptotically stable iff the eigenvalues of A have magnitude less than 1, that is, $|\lambda_i| < 1$ for every i . The vector $x^{(k)}$ will tend to an equilibrium point for any initial condition if the system is asymptotically stable. Once the system state vector is equal to an equilibrium point, it will remain equal to it for all time in the future.

The system (5.1.3) is said to be marginally stable if the magnitude of the eigenvalues are less or equal to 1. If 1 is an eigenvalue of A, then the corresponding eigenvector is an equilibrium point. If 1 is not an eigenvalue of A , the origin is the only equilibrium of the system.

Each eigenvalue defines a characteristic growth as well as a characteristic frequency of oscillation. For a discrete-time system, we do not have oscillations if the eigenvalues are positive. Oscillations are only derived from negative or complex eigenvalues.

5.2 Vertical Stable Vectors

From the Perron-Frobenius theorem, the Leslie matrix which is non-negative, has a positive dominant eigenvalue which is simple. Thus a population based on Leslie matrix will in the long run have a growth factor. That is , from some year on, next year's population will be a multiple of this year's. Therefore, after some time, the population in the age-classes will grow proportionally. The proportions of populations in the age classes will be constant. This age composition is called a stable-age distribution.

Mathematically, we have

$$x^{(k+1)} = \lambda_1 x^{(k)} \tag{5.3}$$

where the factor λ_1 is the dominant eigenvalue of the Leslie matrix L. If V_1 is the associated right eigenvector,we can obtain the stable-age distribution from V_1.

Let

$$V_1 = \begin{bmatrix} v_1 \\ v_2 \\ v_3 \\ \cdot \\ \cdot \\ \cdot \\ v_n \end{bmatrix}$$

and

$$C = v_1 + v_2 + \cdots + v_n$$

Then the stable-age distribution ,S_1, is expressed as

$$S_1 = \begin{bmatrix} \frac{v_1}{C} \\ \frac{v_2}{C} \\ \frac{v_3}{C} \\ \cdot \\ \cdot \\ \cdot \\ \frac{v_n}{C} \end{bmatrix} \tag{5.4}$$

The sum of the elements of S is unity.

The right eigenvectors are linearly independent. This means that there exists no nonzero constant b_i such that

$$b_1V_1 + b_2V_2 + ... + b_nV_n = 0$$

If the right eigenvectors V_i ; $i = 1, 2, ..., n$ are arranged side by side to constitute a matrix V below

$$V = [V_1 \ V_2 \ \cdots V_n] = \begin{bmatrix} a_{11} & a_{12} & \cdot & \cdot & \cdot & a_{1n} \\ a_{21} & a_{22} & \cdot & \cdot & \cdot & a_{21} \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ a_{n1} & a_{2n} & \cdot & \cdot & \cdot & a_{nn} \end{bmatrix} \tag{5.5}$$

then using the fact that the columns of the matrix V are V_i and that

$$LV_i = \lambda_i V_i$$

we have

$$LV = V\Lambda \tag{5.6}$$

where Λ is the diagonal matrix

$$\Lambda = \begin{bmatrix} \lambda_1 & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & \lambda_2 & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & 0 \\ 0 & \cdot & \cdot & \cdot & 0 & \lambda_n \end{bmatrix} \tag{5.7}$$

that is

$$\begin{bmatrix} F_1 & F_2 & . & . & F_{n-1} & F_n \\ P_1 & 0 & . & . & 0 & 0 \\ 0 & P_2 & . & . & 0 & 0 \\ . & . & & & . & . \\ . & . & & & . & . \\ 0 & 0 & . & . & P_{n-1} & 0 \end{bmatrix} \begin{bmatrix} a_{11} & a_{12} & \cdot & \cdot & a_{1,n} \\ a_{21} & a_{22} & \cdot & \cdot & a_{2,n} \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ a_{n,1} & a_{2,n} & \cdot & \cdot & a_{n,n} \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} & \cdot & \cdot & a_{1,n} \\ a_{21} & a_{22} & \cdot & \cdot & a_{2,n} \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ \cdot & & & & \cdot \\ a_{n,1} & a_{n,2} & \cdot & \cdot & a_{n,n} \end{bmatrix} \begin{bmatrix} \lambda_1 & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & \lambda_2 & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & 0 \\ 0 & \cdot & \cdot & \cdot & 0 & \lambda_n \end{bmatrix}$$

From

$$LV = V\Lambda$$

we have

$$L = V\Lambda V^{-1} \tag{5.8}$$

thus

$$\begin{aligned} L^2 &= \left(V\Lambda V^{-1}\right)\left(V\Lambda V^{-1}\right) = V\Lambda\left(V^{-1}V\right)\Lambda V^{-1} \\ &= V\Lambda^2 V^{-1} \end{aligned}$$

Repeating the multiplication gives

$$L^k = V\Lambda^k V^{-1} \qquad ; \quad k > 0 \textit{ is an integer} \tag{5.9}$$

But

$$x^{(k)} = L^k x^{(0)}$$

This means

$$x^{(k)} = V\Lambda^k V^{-1} x^{(0)} \tag{5.10}$$

or

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ \cdot \\ \cdot \\ \cdot \\ x_n^{(k)} \end{pmatrix} = \begin{bmatrix} a_{11} & a_{12} & \cdot & \cdot & \cdot & a_{1,n} \\ a_{21} & a_{22} & \cdot & \cdot & \cdot & a_{2,n} \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ a_{n,1} & a_{n,2} & \cdot & \cdot & \cdot & a_{n,n} \end{bmatrix} \begin{bmatrix} \lambda_1^k & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & \lambda_2^k & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & \cdot \\ \cdot & & & & & 0 \\ 0 & \cdot & \cdot & \cdot & 0 & \lambda_n^k \end{bmatrix} \begin{bmatrix} d_1 \\ d_2 \\ \cdot \\ \cdot \\ \cdot \\ d_n \end{bmatrix} \tag{5.11}$$

where

$$\vec{d} = \begin{bmatrix} d_1 \\ d_2 \\ \cdot \\ \cdot \\ \cdot \\ d_n \end{bmatrix} = V^{-1}x^{(0)} \tag{5.12}$$

From equation (5.11), we have

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ \cdot \\ \cdot \\ \cdot \\ x_n^{(k)} \end{pmatrix} = \begin{bmatrix} a_{11}\lambda_1^k & a_{12}\lambda_2^k & \cdot\ \cdot\ \cdot & a_{1n}\lambda_n^k \\ a_{21}\lambda_1^k & a_{22}\lambda_2^k & \cdot\ \cdot\ \cdot & a_{2n}\lambda_n^k \\ \cdot & & & \\ \cdot & & & \\ \cdot & & & \\ a_{n1}\lambda_1^k & a_{n2}\lambda_2^k & & a_{nn}\lambda_n^k \end{bmatrix} \begin{bmatrix} d_1 \\ d_2 \\ \cdot \\ \cdot \\ \cdot \\ d_n \end{bmatrix} \tag{5.13}$$

or

$$x_1^{(k)} = a_{11}d_1\lambda_1^k + a_{12}d_2\lambda_2^k + \cdots + a_{1n}d_n\lambda_n^k \tag{5.14}$$

$$x_2^{(k)} = a_{21}d_1\lambda_1^k + a_{22}d_2\lambda_2^k + \cdots + a_{2n}d_n\lambda_n^k \tag{5.15}$$

$$\cdot$$

$$\cdot$$

$$\cdot$$

$$x_n^{(k)} = a_{n1}d_1\lambda_1^k + a_{n2}d_2\lambda_2^k + \cdots + a_{nn}d_n\lambda_n^k \tag{5.16}$$

For large time t_k, although the influence of $\lambda_2, \lambda_3, ..., \lambda_n$ does not necessarily disappear, the first term with the dominant eigenvalue will grow faster than the others. That is, the population at time t_k will approach closer and closer to $d_1\lambda_1^k V_1$

That is

$$x^{(k)} \simeq d_1\lambda_1^k V_1 \tag{5.17}$$

V_1 is the right eigenvector corresponding to the dominant eigenvalue λ_1

This property is commonly referred to as the *ergodic property* in demography, that is the tendency of a population to forget its initial age distribution.

5.3 Horizontal stable vector

We can pre-multiply matrix L by a new set of vectors U_i, this time horizontal, to have

$$U_i L = \lambda U_i \tag{5.18}$$

Condition of consistency still remains as below

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

For each eigenvalue λ_i, we find the vectors U_i, which are commonly referred to as the left eigenvectors.

Again, the dominant eigenvalue λ_1 will be of much interest. The corresponding left eigenvector U_1 tell us about the reproductive potential of a population.

Let $U_1 = [u_{11}\ u_{12}\ \cdots\ u_{1n}]$
Let $\omega = u_{11} + u_{12} + \cdots + u_{1n}$
Then

$$T_1 = \frac{1}{\omega}\left[u_{11}\ u_{12}\ \cdots\ u_{1n}\right] \tag{5.19}$$

is said to be the horizontal stable vector. It represents the reproductive value of each of the age classes .

Reproductive value is the total prospective number of female children that would be born taking into account mortality. Aggregate reproductive value is got by multiplying the reproductive value with a state vector, for example, if $X^{(0)}$is the initial state vector , then aggregate reproductive value will be

$$U_1 X^{(0)} \tag{5.20}$$

5.4 Properties of the left and right eigenvectors

For each latent root λ_i,we find $U_i = [u_{i1}\ u_{i2}\ u_{i3}...u_{in}]$ from the set of linear equations below

$$[u_{i1}\ u_{i2}\ u_{i3}...u_{in}]\begin{bmatrix} F1 & F2 & \cdot & \cdot & \cdot & Fn \\ P1 & & & & & 0 \\ \cdot & P2 & & & & \cdot \\ \cdot & & \cdot & & & \cdot \\ \cdot & & & \cdot & & \cdot \\ 0 & \cdot & \cdot & 0 & Pn & 0 \end{bmatrix} = \lambda_i\,[u_{i1}\ u_{i2}\ u_{i3}...u_{in}]$$

or $U_iL{=}\lambda_iU_i$

We have n horizontal vectors and can be arrayed one beneath the other to have the vector U as shown below;

$$U = \begin{bmatrix} U_1 \\ U_2 \\ \cdot \\ \cdot \\ \cdot \\ U_{n-1} \\ U_n \end{bmatrix} \tag{5.21}$$

where each U_i is a row vector
The stable vectors posses an orthogonality property by which if $i \neq j$, then

$$U_iV_j = 0 \tag{5.22}$$

where

$$LV_j = \lambda_j V_j \tag{5.23}$$

(5.4.2) is from the fact that if we premultiply (5.4.3) by U_i, we get

$$\begin{aligned} U_iLV_j &= U_i\lambda_j V_j \\ &= \lambda_j U_i V_j \end{aligned} \tag{5.24}$$

It is also true to have

$$U_iL = \lambda_i U_i \tag{5.25}$$

Multiplying (4) on the right by V_j, we get

$$U_i L V_j = \lambda_i U_i V_j \tag{5.26}$$

Now (5.4.4) and (5.4.6) gives

$$0 = (\lambda_j - \lambda_i) U_i V_j \quad , \lambda_j \neq \lambda_i$$

which gives

$$U_i V_j = 0 \quad \text{for } i \neq j$$

In demography, the vector U_1 corresponding to the dominant eigenvalue λ_1 is the one of much interest. It represents the left eigenvector corresponding to the dominant eigenvalue and tells us about the reproductive potential of a population.

The equation above can be rewritten as

$$UL = \Lambda U$$

where Λ is a diagonal matrix of order n whose diagonal elements are the various eigenvalues of matrix L

The above equation can also be written as

$$L = U^{-1} \Lambda U \tag{5.27}$$

We also noted earlier that if V is the matrix of right eigenvectors, then

$$L = V \Lambda V^{-1}$$

so that

$$U^{-1} \Lambda U = V \Lambda V^{-1} \tag{5.28}$$

Now normalising U_i by the dividing it with $U_i V_i$, we have

$$\overline{U}_i = \frac{U_i}{U_iV_i} \qquad (5.4.9) \tag{5.29}$$

This gives

$$\begin{aligned} \overline{U}_iV_j &= 1 \text{ for } i = j \\ &= 0 \text{ for } i \neq j \end{aligned} \tag{5.30}$$

The above helps us express an observed age distribution, say the state vector $X^{(0)}$ as a sum of the stable vectors each multiplied by a constant, that is,

$$X^{(0)} = c_1V_1 + c_2V_2 + ... + c_nV_n \tag{5.31}$$

To find c_i, premultiply (5.31) by the normalised $\overline{U}_i$ and have

$$\overline{U}_iX^{(0)} = c_1\overline{U}_iV_1 = c_2\overline{U}_iV_2 + ... + c_n\overline{U}_iV_n \tag{5.32}$$

This gives

$$\overline{U}_iX^{(0)} = c_i$$

or

$$c_i = \frac{U_iX^{(0)}}{U_iV_i} \tag{5.33}$$

Premultiplying (5.31) by L gives;

$$\begin{aligned} LX^{(0)} &= c_1LV_1 + c_2LV_2 + ... + c_nLV_n \\ &= \lambda_1c_1V_1 + \lambda_2c_2V_2 + ... + \lambda_nc_nV_n \end{aligned} \tag{5.34}$$

This shows that after k steps, the population will be

$$L^k X^{(0)} = \lambda_1^k c_1 V_1 + \lambda_2^k c_2 V_2 + ... + \lambda_n^k c_n V_n \tag{5.35}$$

After a long time has passed, only the first term in (5.35) counts and we write

$$X^{(k)} = L^k X^{(0)} = \lambda_1^k c_1 V_1 \tag{5.36}$$

$$c_1 = \frac{U_1 X^{(0)}}{U_1 V_1} \qquad \text{is termed as the stable equivalent population} \tag{5.37}$$

5.4.1 Effects of eigenvalues

The long term behavior of a population depends on the eigenvalues λ_i as they are raised to high powers.

- If $\lambda_i > 1$, λ_i^k produces exponential growth
- If $\lambda < 1$, we have exponential decay
- If $-1 < \lambda_i < 0$, then λ_i^k exhibits damped oscillations.

- If $\lambda_i < -1$,then λ_i^k produces diverging oscillations.
- Complex eigenvalues produce oscillations.

If $\lambda = a + bi = |\lambda| (\cos\theta + i \sin\theta)$, complex conjugate is $\overline{\lambda} = a - bi$. Thus raising λ to k th power yields

$$\lambda^k = |\lambda|^k (\cos\theta k + i \sin\theta k)$$

The solution to the projection equation will thus contain terms of the form

$$\lambda^k + \overline{\lambda}^k = |\lambda|^k \, 2\cos\theta k \tag{5.38}$$

Thus ,as a complex eigenvalue raised to higher and higher powers , its magnitude $|\lambda|^k$ increases /decreases exponentially , depending on whether $|\lambda|$ is greater or less than 1.

5.4.2 The damping ratio

We want to study the oscillations produced by the subdiagonal eigenvalue during convergence. This rate of convergence to the stable age distribution is referred to as the damping ratio. It is governed by the eigenvalue(s) with the second largest magnitude.The damping ratio ρ is defined as

$$\rho = \frac{\lambda_1}{|\lambda_2|} \tag{5.39}$$

where λ_1 is the dominant eigenvalue and λ_2 is the eigenvalue with the second largest magnitude.

5.4.3 The period of oscillation

When complex eigenvalues are raised to powers, they produce oscillations in the distribution. Here, the period of oscillation is given by

$$\eta_i = \frac{2\pi}{\theta_i} = \frac{2\pi}{\tan^{-1}(\frac{\mathrm{Im}(\lambda_i)}{\mathrm{Re}(\lambda_i)})} \tag{5.40}$$

where θ_i is the angle formed by λ_i in the complex plane, $\mathrm{Im}(\lambda_i)$ and $\mathrm{Re}(\lambda_i)$ are the imaginary and real parts of λ_i respectively.

The longest-lasting of the oscillatory components is that associated with λ_2. In age-classified models, η_2 is approximately equal to the mean age of childbearing in the stable population (Lotka 1945, Coale 1972)

5.4.4 Sensitivity

We start from the general matrix population model

$$Av = \lambda v$$

We then change a single element of A and analyse the effect of this change to the dominant eigenvalue of A. Thus, the basic formula for the sensitivity of the dominant eigenvalue to a small change in element a_{ij} is given by the following equation

$$S_{ij} = \left(\frac{\partial \lambda}{\partial a_{ij}}\right) \tag{5.41}$$

And the sensitivity matrix S, is thus expressed as

$$S = \left(\frac{\partial \lambda}{\partial a_{ij}}\right)$$

To find an explicit expression of eigenvalue sensitivity, we proceed as follows:

We begin by the equations defining the eigenvalues and the right and left eigenvectors, V_i and U_i respectively.

$$\begin{aligned} LV_i &= \lambda_i V_i \qquad (5.42) \\ U_i L &= \lambda_i U_i \end{aligned}$$

Taking differential on both sides of (5.42) and suppressing the subscript i gives

$$L(dV) + (dL)V = \lambda\,(dV) + (d\lambda)\,V \tag{5.43}$$

where $dL = da_{ij}$

Forming scalar product on both sides of (5.43) with the left eigenvector U_1, we get:

$$\langle L(dV), U\rangle + \langle (dL)V, U\rangle = \lambda \left\langle (dV), U\right\rangle + \left\langle (d\lambda) V, U\right\rangle \tag{5.44}$$

Expanding the scalar products in (5.44) and cancelling like terms gives

$$\frac{d\lambda}{dL} = \frac{\langle V, U\rangle}{\langle V, U\rangle} = \frac{U * V}{U * V} \tag{5.45}$$

Suppose that only one element,a_{ij}, is changed. Then dL contains only one nonzero entry,da_{ij}, which is in row i and column j. Thus we have (5.45) becoming

$$\frac{d\lambda}{da_{ij}} = \frac{\overline{U}_i * V_j}{\langle V, U\rangle} \tag{5.46}$$

$\overline{U}_i$ is the complex conjugate of U_i

5.4.5 Elasticity

This is another measure of the change in a matrix given a small change in an element of the matrix.

The elasticity of λ with respect to a_{ij} is given by the expression

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial \log \lambda}{\partial \log a_{ij}} \tag{5.47}$$

An important property of elasticities is that they sum up to 1, i.e

$$\sum_{ij} e_{ij} = 1 \tag{5.48}$$

5.5 Some theorems and proofs for the Leslie Matrix models

5.5.1 Theorem1

The eigenvalues of Leslie matrix L are given by the solutions to an equation of the form

$$1 = \sum_x \lambda^{-x} l_x m_x \tag{5.49}$$

Proof
we have

$$0 = \begin{bmatrix} F_1 - \lambda & F_2 & F_3 & . & . & . & F_k \\ P_1 & -\lambda & 0 & . & . & . & 0 \\ 0 & P_2 & -\lambda & . & . & . & 0 \\ 0 & 0 & P_3 & . & . & . & 0 \\ . & . & & . & & & . \\ . & . & & & . & & . \\ . & . & & & & . & . \\ 0 & 0 & 0 & . & . & P_{k-1} & 0 \end{bmatrix}$$

$$= (F_1 - \lambda) \begin{bmatrix} -\lambda & 0 & . & . & . & 0 \\ P_2 & -\lambda & . & . & . & 0 \\ . & & . & & & . \\ . & & & . & & . \\ . & & & & . & . \\ 0 & . & . & . & P_{k-1} & -\lambda \end{bmatrix} - (F_2) \begin{bmatrix} P_1 & 0 & . & . & . & 0 \\ 0 & -\lambda & . & . & . & 0 \\ . & & . & & & . \\ . & & & . & & . \\ . & & & & . & . \\ 0 & . & . & . & P_{k-1} & 0 \end{bmatrix} + ...$$

$$= (F_1 - \lambda)(-\lambda)^{k-1} + (-1)F_2[P_1(-\lambda)^{k-2}] + ...$$

$$= (F_1 - \lambda)(-1)^{k-1}\lambda^{k-1} - F_2P_1(-1)^{k-2}\lambda^{k-2} + F_3P_1P_2(-1)^{k-3}\lambda^{k-3} - ...$$

$$= (-1)^{k-1}[F_1\lambda^{k-1} - \lambda^k + F_2P_1\lambda^{k-2} + F_3P_1P_2\lambda^{k-3} + ...]$$

or

$$F_1\lambda^{k-1} - \lambda^k + F_2P_1\lambda^{k-2} + F_3P_1P_2\lambda^{k-3} + ... = 0$$

or

$$\lambda^k = F_1\lambda^{k-1} + F_2P_1\lambda^{k-2} + F_3P_1P_2\lambda^{k-3} + ... \tag{5.50}$$

dividing both sides by λ^k,we have

$$1 = F_1\lambda^{-1} + F_2P_1\lambda^{-2} + F_3P_1P_2\lambda^{-3} + ... \tag{5.51}$$

replacing F_i by P_im_i , we have

$$1 = P_1m_1\lambda^{-1} + P_1P_2m_2\lambda^{-2} + P_1P_2P_3m_i\lambda^{-3} + ... \tag{5.52}$$

since

$$l_1 = P_1$$

$$l_2 = P_1 P_2$$

$$l_3 = P_1 P_2 P_3$$

we have

$$1 = \sum_x \lambda^{-x} l_x m_x$$

5.5.2 Theorem 2

Equations of the form

$$1 = \sum_{x=1}^{k} \lambda^{-x} l_x m_x$$

have one and only one real positive root $\lambda_1$of algebraic multiplicity 1. The other roots λ_i are either negative or complex in nature and $\lambda_1 >\mid \lambda_i \mid$

Proof

The function of λ

$$f(\lambda) = \sum_x \lambda^{-x} l_x m_x$$

is positive on $[0, \infty]$ and strictly decreasing from ∞ to 0 (since all l_x and m_x are positive). Hence there is only one real positive root of multiplicity 1.

Let λ_i be any other latent root , and write $\lambda_i^{-1} = e^{\alpha + \beta}$,where α and β are real and positive and $\beta \neq 2\pi r$. That is ,λ_i must be negative or complex. We then have

$$\lambda_i^{-n} = e^{\alpha}(\cos\beta + i\sin\beta))^n = e^{n\alpha}(\cos(n\beta) + i\sin(n\beta)) \tag{5.53}$$

substituting for λ_i^{-1} in the equation

$$1 = \sum_{x=1}^{k} \lambda^{-x} l_x m_x \tag{5.54}$$

and equating the real parts of the left hand side and right hand side, we obtain

$$\sum_{x} l_x m_x e^{x\alpha} \cos(\beta x) = 1 \tag{5.55}$$

since $\beta \neq 2\pi r, \cos(\beta x)$ and $\cos((x+1)\beta)$ cannot both be unity, we have either both must be less than unity. A comparison of equation (5.54) and (5.55) shows that e^{α} must be greater than λ^{-1} and we can conclude that

$$\mid \lambda_i \mid < \lambda_1 \quad for \quad all \quad i \neq 1 \tag{5.56}$$

Theorem 3 (Theorem of Perron-Frobenius)

Let T be a square matrix with non-negative elements only , and such that all elements of T^n are positive for some integer n (we say that T is primitive). Then T has a positive eigenvalue of algebraic multiplicity 1, which correspond to a right eigenvector V_1 and to a left eigenvector U_1 both of which have only positive elements. This eigenvalue is greater in absolute size than any other eigenvalues of T

5.5.3 Theorem 4

The general solution to an equation such as

$$N(t) = L^t N(0) \tag{5.57}$$

with L diagonalizable,is

$$n_i(t) = \sum_j c_{ij}\lambda_i^t \tag{5.58}$$

where λ_i are the eigenvalues of L and and c_{ij} are constants whose values depend on the initial population vector.

Proof

$$\begin{aligned} N(t) &= L^t N(0) \\ &= (PDP^{-1})^t N(0) \end{aligned} \tag{5.59}$$

(where P is the eigenvector matrix and D is the diagonal matrix containing the eigenvalues of L denoted λ_i)

$$= (PDP^{-1})(PDP^{-1})(PDP^{-1})...(PDP^{-1})N(0)$$

$$= PD^tP^{-1}N(0)$$

where

$$D^t = \begin{bmatrix} \lambda_1^t & 0 & . & . & . & 0 \\ 0 & \lambda_2^t & . & . & . & 0 \\ . & & . & & & . \\ . & & & . & & . \\ . & & & & . & . \\ 0 & 0 & . & . & . & \lambda_k^t \end{bmatrix} \tag{5.60}$$

now consider any element of $N(t)$, noticing that it is a sum of the various λ_i^t each multiplied by a value reflecting a combination of the elements of P, P^{-1} and

$N(0)$,i.e.

$$n_i(t) = \sum C_{ij}\lambda_j^t$$

where $\{\lambda_j\}$ are the eigenvalues of L and the C_{ij} are constants whose values depend on the initial population vector.

Chapter 6

Application to Amboseli elephants

6.1 Facts about the African elephant

Elephants are the largest living land mammal found in most regions of Africa.They have massive bodies, broad feet, loose skin with large, thin and floppy ears which provide extensive cooling to the body during hot periods. The upper lip and nose are elongated into a flexible trunk reaching nearly to the ground. This is used for picking food and drawing water during feeding.The upper incisor teeth are elongated into tusks valued for ivory. A gland between the eye and the ear often produces a substance called musth. During these periods, the animal is in an excitable, dangerous condition called musth period.

Elephants are browsing animals feeding on leaves ,shoots,tall grasses and fruits. They are relational animals, living and travelling in groups called family units of between 15 and 30 individual composed of a matriarch (female elder) , her daughters and their offsprings. Upto 5 family units associate in bond groups temporarily. Male older than 13 years are generally solitary or live in small groups.

A single calf is born after a gestation period of 22 months and is nursed for approximately 5 years . Elephants reach maturity at between 11-20 years of age with a lifespan of up to 65 years.The African elephant is commonly referred to as *Loxodonta africana* and are generally found at the south of the Sahara. Bulls may reach a shoulder height of 13 ft and weigh upto 8 tons. Cows are slightly smaller with slender tusks.

6.2 Measuring elephant ages

Several equations for measuring elephant ages are available. An example is the shoulder-height equations deduced by Von Bertalanffy (1938). The equations relate shoulder height (h) of elephants ,of different gender, to their ages (x).The equations are given below:

$$male(1-20years) : h(x) = 265(1-e^{-0.114(x+3.95)})cm \tag{6.1}$$

$$male(20-60years) : h(x) = 307(1-e^{-0.166(x-10.48)})cm \tag{6.2}$$

$$female(2-60years) : h(x) = 252(1-e^{-0.099(x+6.00)})cm \tag{6.3}$$

If we want to deduce the age from the height, we use the following equations:

$$male(96-245cm) : x(h) = -\log\frac{(1-\frac{h}{265})}{0.114} - 3.95years \tag{6.4}$$

$$male(245-307cm) : x(h) = -\log\frac{(1-\frac{h}{307})}{0.166} + 10.48years \tag{6.5}$$

$$female(113-252cm) : x(h) = -\log\frac{(1-\frac{h}{252})}{0.099} - 6.00years \tag{6.6}$$

6.2.1

6.2.2 Amboseli elephants

The Amboseli elephants are unusual in Africa because they have been relatively unaffected by human activities for example settlement, poaching and culling as part of Park Management Program. This is because of the following:The land surrounding Amboseli National Park belongs to the Maasai community who have coexisted well with wildlife. Second, the presence of tourists in and around the National Park makes it difficult for poachers to operate. Finally, the presence and monitoring of elephants by researchers has served well in conserving the elephant population.

6.2.3 Structure of the model

An age classified model based on female Amboseli elephants is built. The female elephant population is subdivided into 13 age classes named below

Age class (years)	name
0-4	1
5-9	2
10-14	3
15-19	4
20-24	5
25-29	6
30-34	7
35-39	8
40-44	9
45-49	10
50-54	11
55-59	12
60-65	13

6.2.4 Vital rates to population growth

Fertility

Fertility refers to the number of offspring of a female of age i to $i+1$ in a unit of time t_k that will survive to the next age class. Calving interval (CI) plays a major role in determining the fertility of an elephant.

Survivorship

Survivorship refers to the likelihood or probability that an individual of age i at time t_k will survive to time t_{k+1} when her age will be $i+1$.

Man remains the only predator that has a limiting effect on elephant population. Other predators usually prey on isolated calves.

Mortality depends strongly on age and thus we have age-specific mortality. For Amboseli elephants, mortality is higher during the drought periods.

Reproduction of female elephants starts at age 12 years but a few instances of reproduction starting from as young as 8 years of age have been recorded.

The maximum age of a female population is 65 years.

We model the population of these large mammals by use of Leslie matrix population model.

Let

P_i=the probability that a female elephant of group i at time t_k will be alive in group $i+1$ for $i = 1, 2, ..., 12$

F_i= the number of daughters born per female elephant in group i from time t_k to time t_{k+1} for $i = 1, 2, ..., 13$

The state variables are the number of female elephants at each age class and denoted by

$$x_1^{(k)} = F_1 x_1^{(k-1)} + F_2 x_2^{(k-1)} + ... + F_{13} x_{13}^{(k-1)} \tag{6.7}$$

$$x_2^{(k)} = P_1 x_1^{(k-1)} \tag{6.8}$$

$$.$$

$$.$$

$$.$$

$$x_{13}^{(k)} = P_{12} x_{12}^{(k-1)} \tag{6.9}$$

The system below is derived from the above equations

$$\begin{pmatrix} x_1^{(k)} \\ x_2^{(k)} \\ x_3^{(k)} \\ . \\ . \\ . \\ x_{12}^{(k)} \end{pmatrix} = \begin{bmatrix} F_1 & F_2 & F_3 & . & . & . & F_{12} & F_{13} \\ P_1 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & P_2 & 0 & . & . & . & 0 & 0 \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ 0 & 0 & 0 & . & . & . & P_{12} & 0 \end{bmatrix} \begin{pmatrix} x_1^{(k-1)} \\ x_2^{(k-1)} \\ x_3^{(k-1)} \\ . \\ . \\ . \\ x_{13}^{(k-1)} \end{pmatrix} \tag{6.10}$$

$$L = \begin{bmatrix} F_1 & F_2 & F_3 & . & . & . & F_{12} & F_{13} \\ P_1 & 0 & 0 & . & . & . & 0 & 0 \\ 0 & P_2 & 0 & . & . & . & 0 & 0 \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ 0 & 0 & 0 & . & . & . & P_{12} & 0 \end{bmatrix} \qquad 0 < P_i < 1 \;\; i = 1, 2, ..., 12 \qquad F_i \geq 0 \;\; i = 1, 2, ..., 13$$

Assumptions

We will assume that for Amboseli elephants :

- The individuals in each group always go to the next group from one time step to the next
- The survival and reproductive rates are constant over time within each age class and are therefore not dependent on population density
- The dynamics of the population are determined largely by females. We assume that there will always be enough males to fertilize the females and therefore the bulls do not play a major role in projecting the population
- Territory remains the same and is closed to migration. This implies that no migration of elephants to and out of the park.

6.2.5 Parameter estimation

Data is extracted from a study by Cynthia Moss (2001) on Amboseli elephants.

Amboseli elephants life table is shown below

	Age class (years)	Fecundity rates m_i	Survival rates P_i
1	0-4	0.000	0.917
2	5-9	0.015	0.976
3	10-14	0.600	0.956
4	15-19	1.010	0.939
5	20-24	1.135	0.918
6	25-29	1.150	0.911
7	30-34	1.165	0.890
8	35-39	1.190	0.832
9	40-44	1.075	0.842
10	45-49	0.905	0.844
11	50-54	0.705	0.802
12	55-59	0.515	0.718
13	60 -65	0.109	0

In calculating the fertility rates F_i , i consider the prebirth-pulse sampling, that is,

$$F_i = l_1 m_i \tag{6.11}$$

Here $l_1 = 0.916$

From the table above, we have

Age class (in years)	F_i	Age class (in years)	F_i
0-4	0.000	35-39	1.090
5-9	0.014	40-44	0.985
10-14	0.550	45-49	0.829
15-19	0.925	50-54	0.646
20-24	1.040	55-59	0.472
25-29	1.053	60-65	0.099
30-34	1.067		

The Leslie matrix L is therefore obtained as follows:

$$L =$$
$$\begin{bmatrix}
0.000 & 0.014 & 0.550 & 0.925 & 1.040 & 1.053 & 1.067 & 1.090 & 0.985 & 0.829 & 0.646 & 0.472 & 0.099 \\
0.917 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.976 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.956 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.939 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.918 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.911 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.890 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.832 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.842 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.844 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.802 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.718 & 0
\end{bmatrix}$$

Here, we see that

$$(I + L)^{12} > 0 \tag{6.12}$$

and

$$L^{145} > 0 \tag{6.13}$$

Thus, we conclude that Leslie matrix L is irreducible, primitive matrix.

We thus expect that L will have a simple dominant eigenvalue λ_1 which is positive. The magnitude of all other eigenvalues of L are less than λ_1 .The other eigenvalues are either negative or complex. Corresponding to λ_1 are eigenvectors V_1 and U_1 whose elements are positive.

Chapter 7

Results and analysis

Here, we intend to carry out the following analysis:

a) Transient analysis: This focusses on the short-run behavior

b) Asymptotic analysis: This asks what happens if the life processes operate for a very long time. What is the long-run behaviour of population? Does it grow, decline or remain stationary?

c) Ergodicity : A model is said to be ergodic if its asymptotic dynamics are independent of initial conditions

d) Perturbation analysis: Here, we ask what would happen to some dependent variable if one or more independent variables were to change

7.0.6 Transient analysis

Matlab programming

Matlab programming is used to project future elephant population. First, we run projection for the next 8 time steps to be able to see the trend and thereafter observe population trend in the long run by considering many years. Here, what is of interest is the stable population. This is the behavior of population in the long run where we consider future proportions according to age classes. Population projection are also represented in graphs for easier observation.

First, we follow the changes in the first 7 steps of time. This is done by starting from zero and end with step 8. There are 13 age classes to deal with in each iteration. We begin by inserting the Leslie matrix L , then prepare matlab to accommodate the first seven time steps by inserting a null matrix. The null matrix will have 13 rows to represent each of the 13 age classes and columns columns to accommodate population for the first seven time steps. The first column contains the initial population vector. Population in the year 1990 is taken to be the initial vector

The results are shown in the table below.

Age classes	1994	1999	2004	2009	2014	2019	2024
0-4	280	251	231	337	506	673	874
5-9	29	257	230	212	308	464	617
10-14	31	29	251	224	207	301	453
15-19	31	29	27	240	214	198	288
20-24	30	29	28	25	225	201	185
25-29	29	28	26	25	23	207	184
30-34	29	27	25	24	23	21	188
35-39	29	26	24	22	21	21	19
40-44	27	24	21	20	19	17	17
45-49	27	22	20	18	17	16	15
50-54	27	23	19	17	15	14	13
55-59	25	22	18	15	14	12	11
60-65	23	18	15	13	10	10	9

Figure 7.1: Elephant population over 8 time steps

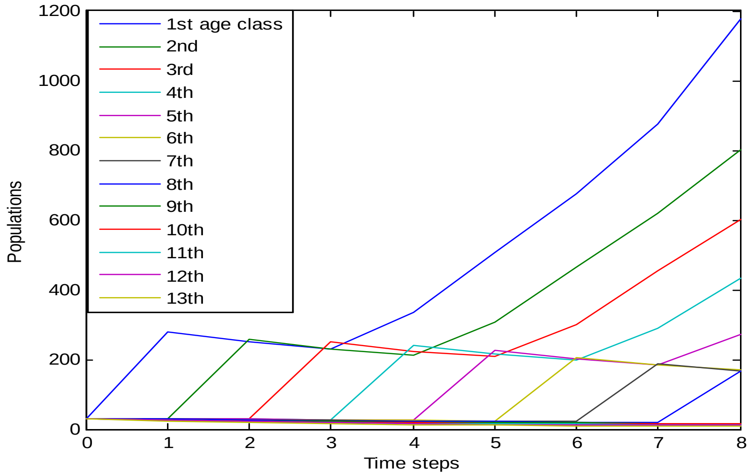

Figure 7.1 shows the graph for population vs time.

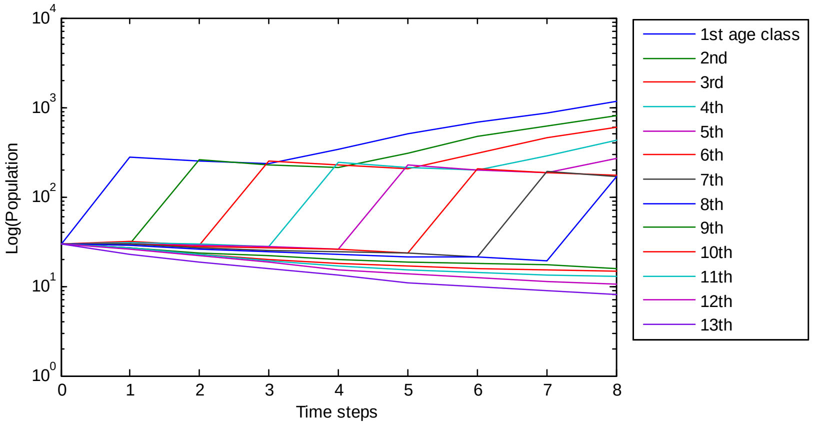

Figure 7.2: Logarithm of populations over 8 time steps

We notice that the number of female elephants generally increases with time but with some oscillatory behaviour. Figure 7.2 shows the plot for the logarithm of the population against time.

7.0.7 Asymptotic analysis

Here, we analyse what happens in the long run.

From the equation

$$X^{(k)} = L^k x^{(0)}$$

we have ;

Population by age classes after 20 time steps, 21st time steps and 22 time steps respectively are shown in the table below

Age classes	Pop. at 20^{th} time step	at 21^{st} time step	at 22^{nd} time step
0-4	19030	25538	34267
5-9	13004	17451	23418
10-14	9459	12691	17032
15-19	6741	9043	12133
20-24	4716	6330	8492
25-29	3224	4329	5811
30-34	2190	2937	3944
35-39	1454	1949	2614
40-44	900	1210	1621
45-49	564	758	1019
50-54	357	476	639
55-59	214	286	382
60-65	112	154	206
Totals	61965	83151	111577

From the table above $\frac{83151}{61965} = \frac{111577}{83151} = 1.3419$

This is to mean that in the long run, population grows with a constant rate (asymptotic growth rate) from one time step to the next. Population at each age class also grows at this rate from one time step to the next.

Normalised population vector at each of the above time steps is given in the table below;

Age classes	20th time step	21st time step	22nd time step
0-4	0.3071	0.3071	0.3071
5-9	0.2099	0.2099	0.2099
10-14	0.1527	0.1527	0.1527
15-19	0.1088	0.1088	0.1088
20-24	0.0761	0.0761	0.0761
25-29	0.0521	0.0521	0.0521
30-34	0.0353	0.0353	0.0353
35-39	0.0234	0.0234	0.0234
40-44	0.0145	0.0145	0.0145
45-49	0.0091	0.0091	0.0091
50-54	0.0057	0.0057	0.0057
55-59	0.0034	0.0034	0.0034
60-64	0.0018	0.0018	0.0018

We can use Matlab to calculate the age distribution vectors in the long run, say the first 20 time steps. Instead of considering the number of individuals in a class, we can choose to consider relative percentages of each age class.

Figure 7.3 shows the plot for the above normalised populations.

Once again, we have found out that in the long run, the population will follow a distribution.

Power method

The dominant eigenvalue and the corresponding eigenvector of Leslie matrix L can be computed using the power method.

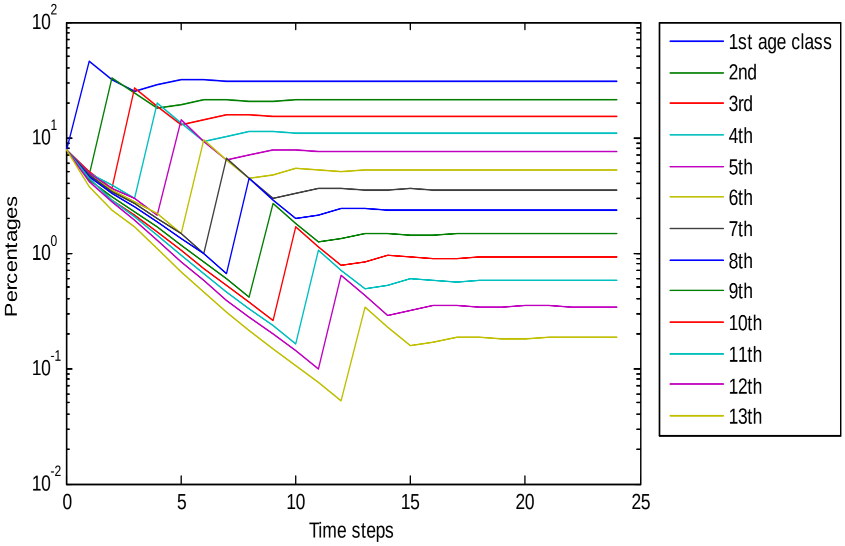

Figure 7.3: Elephant percentages at each iteration showing stable population

Choose an approximation to the eigenvector and label it $\overrightarrow{y}^{(0)}$. Then normalise $\overrightarrow{y}^{(0)}$ by requiring that one component be a particular non-zero, say 1.

Then find $L\overrightarrow{y}^{(0)}$, where

$$L\overrightarrow{y}^{(0)} = \overrightarrow{\gamma}^{(1)} = \lambda^{(1)}\overrightarrow{y}^{(1)} \tag{7.1}$$

where $\overrightarrow{y}^{(1)}$ is normalised the same way $\overrightarrow{y}^{(0)}$ was normalised.

In the same manner,

$$L\overrightarrow{y}^{(1)} = \overrightarrow{\gamma}^{(2)} = \lambda^{(2)}\overrightarrow{y}^{(2)} \tag{7.3}$$

In general,

$$L\overrightarrow{y}^{(k)} = \overrightarrow{\gamma}^{(k+1)} = \lambda^{(k+1)}\overrightarrow{y}^{(k+1)} \tag{7.4}$$

For the Leslie matrix

$L =$

$$\begin{bmatrix}
0.000 & 0.014 & 0.550 & 0.925 & 1.040 & 1.053 & 1.067 & 1.090 & 0.985 & 0.829 & 0.646 & 0.472 & 0.099 \\
0.917 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.976 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.956 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.939 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.918 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.911 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.890 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.832 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.842 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.844 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.802 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.718 & 0
\end{bmatrix}$$

let

$$y^{(0)} = \begin{bmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \tag{7.5}$$

then

$$Ly^{(0)} = \begin{bmatrix} 0 \\ 0.9170 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix} = \overrightarrow{\gamma}^{(1)} = 1 \begin{bmatrix} 0 \\ 0.9170 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix} = \lambda^{(1)} y^{(1)} \tag{7.6}$$

$$Ly^{(1)} = \begin{bmatrix} 0.0128 \\ 0 \\ 0.8950 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix} = \overrightarrow{\gamma}^{(2)} = 0.0128 \begin{bmatrix} 1.0000 \\ 0 \\ 69.9213 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix} = \lambda^{(2)} y^{(2)} \tag{7.7}$$

$$Ly^{(2)} = \begin{bmatrix} 38.4567 \\ 0.9197 \\ 0.0000 \\ 68.8447 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix} = \overrightarrow{\gamma}^{(3)} = 38.4567 \begin{bmatrix} 1.0000 \\ 0.0268 \\ 0.0000 \\ 9.1048 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \\ 0.0000 \end{bmatrix} = \lambda^{(3)} y^{(3)} \tag{7.8}$$

$$\vdots$$

$$Ly^{(20)} = \begin{bmatrix} 1.3416 \\ 0.9170 \\ 0.6670 \\ 0.4749 \\ 0.3323 \\ 0.2277 \\ 0.1546 \\ 0.1022 \\ 0.0633 \\ 0.0401 \\ 0.0251 \\ 0.0148 \\ 0.0080 \end{bmatrix} = \overrightarrow{\gamma}^{(21)} = 1.3416 \begin{bmatrix} 1.0000 \\ 0.6835 \\ 0.4972 \\ 0.3540 \\ 0.2477 \\ 0.1697 \\ 0.1153 \\ 0.0762 \\ 0.0472 \\ 0.0299 \\ 0.0187 \\ 0.0110 \\ 0.0060 \end{bmatrix} = \lambda^{(21)} y^{(21)} \qquad (7.9)$$

$$Ly^{(21)} = \begin{bmatrix} 1.3419 \\ 0.9170 \\ 0.6671 \\ 0.4753 \\ 0.3324 \\ 0.2274 \\ 0.1546 \\ 0.1026 \\ 0.0634 \\ 0.0397 \\ 0.0252 \\ 0.0150 \\ 0.0079 \end{bmatrix} = \overrightarrow{\gamma}^{(22)} = 1.3419 \begin{bmatrix} 1.0000 \\ 0.6833 \\ 0.4971 \\ 0.3542 \\ 0.2477 \\ 0.1694 \\ 0.1152 \\ 0.0765 \\ 0.0472 \\ 0.0296 \\ 0.0188 \\ 0.0112 \\ 0.0059 \end{bmatrix} = \lambda^{(22)} y^{(22)} \tag{7.10}$$

The dominant eigenvalue of L is $\lambda_1 = \lambda^{(22)} = 1.3419$ while its corresponding eigenvector is

$$V_1 = \alpha \begin{bmatrix} 1.0000 \\ 0.6833 \\ 0.4971 \\ 0.3542 \\ 0.2477 \\ 0.1694 \\ 0.1152 \\ 0.0765 \\ 0.0472 \\ 0.0296 \\ 0.0188 \\ 0.0112 \\ 0.0059 \end{bmatrix} \quad \text{where } \alpha \text{ is any real constant} \tag{7.11}$$

To arrive at the eigenvalues and corresponding eigenvectors directly, we use Matlab programming .

The eigenvalues of matrix L are listed below

$$\lambda_1 = 1.3419 \tag{7.12}$$

$$\lambda_2, \lambda_3 = 0.5964 \pm 0.5585i \tag{7.13}$$

$$\lambda_4, \lambda_5 = 0.2692 \pm 0.7524i \tag{7.15}$$

$$\lambda_6, \lambda_7 = -0.0293 \pm 0.8560i \tag{7.16}$$

$$\lambda_8, \lambda_9 = -0.4021 \pm 0.6491i \tag{7.17}$$

$$\lambda_{10} = -0.7471 \tag{7.18}$$

$$\lambda_{11}, \lambda_{12} = -0.6292 \pm 0.3769i \tag{7.19}$$

$$\lambda_{13} = -0.2050 \tag{7.20}$$

The eigenvector corresponding to the eigenvalue $\lambda = 1.3419$ is V_1 below. The normalised eigenvector corresponding to $\lambda = 1.3419$ is $\widetilde{V_1}$ which is also shown below.

$$V_1 = \alpha \begin{bmatrix} 0.7157 \\ 0.4891 \\ 0.3557 \\ 0.2534 \\ 0.1773 \\ 0.1213 \\ 0.0824 \\ 0.0546 \\ 0.0339 \\ 0.0213 \\ 0.0134 \\ 0.0080 \\ 0.0043 \end{bmatrix} \quad , \quad \widetilde{V_1} = \begin{bmatrix} 0.3071 \\ 0.2099 \\ 0.1526 \\ 0.1088 \\ 0.0761 \\ 0.0521 \\ 0.0353 \\ 0.0234 \\ 0.0145 \\ 0.0091 \\ 0.0057 \\ 0.0034 \\ 0.0018 \end{bmatrix} \tag{7.21}$$

We have found out that the long run growth rate is equivalent to the eigenvalue of largest magnitude and the structure of the population is the same as the eigenvector corresponding to the eigenvalue of largest magnitude.

7.0.8 Ergodicity

A population is said to be ergodic if its eventual behavior is independent of its initial state. An understanding of ergodicity relies on a powerful theorem about eigenvalues of non-negative matrices.

We have that

$$x^{(k)} = d_1\lambda_1^k V_1 + d_2\lambda_2^k V_2 + ... + d_{12}\lambda_{12}^k V_{12} + d_{13}\lambda_{13}^k V_{13} \tag{7.22}$$

where the eigenvalues λ_i are numbered in order of decreasing magnitude.

Since λ_1 is greater in magnitude than all the other eleven eigenvalues, we have

$$\frac{x^{(k)}}{\lambda_1^k} = d_1V_1+d_2\left(\frac{|\lambda_2|}{\lambda_1}\right)^k V_2+...+d_{12}\left(\frac{|\lambda_{12}|}{\lambda_1}\right)^k V_{12}+d_{12}\left(\frac{|\lambda_{13}|}{\lambda_1}\right)^k V_{13} \tag{7.23}$$

As

$$\frac{|\lambda_i|}{|\lambda_1|} < 1 \qquad \text{for} \quad i = 2, 3, ..., 12 \tag{7.24}$$

it follows that

$$\left(\frac{|\lambda_i|}{\lambda_1}\right)^k \longrightarrow 0 \quad \text{as} \quad k \to \infty \quad i = 2, 3, ..., 12 \tag{7.25}$$

We then take limit as $k \to \infty$ on both sides of (7.25) and have

$$\lim_{k \longrightarrow \infty} \left\{\frac{x^{(k)}}{\lambda_1^k}\right\} = d_1V_1 \tag{7.26}$$

So for large values of k, we approximate $x^{(k)}$ by

$$x^{(k)} \approx d_1\lambda_1^k V_1 \tag{7.27}$$

that is

$$x^{(k)} \approx d_1(1.3419)^k \begin{bmatrix} 0.7157 \\ 0.4891 \\ 0.3557 \\ 0.2534 \\ 0.1773 \\ 0.1213 \\ 0.0824 \\ 0.0546 \\ 0.0339 \\ 0.0213 \\ 0.0134 \\ 0.0080 \\ 0.0043 \end{bmatrix} \qquad (7.28)$$

Result (7.28) is known as the strong ergodic theorem. It shows that if a nonnegative matrix is primitive, the long-term dynamics of the population are described by the population growth rate λ_1 and the stable population structure V_1 .

7.0.9 Pertubation analysis: Sensitivities and Elasticities

Eigenvalue sensitivity

Here, we seek to perturb λ_1 by increasing/decreasing $a_{ij} \in L$ by a small component. We then see the effect of this change to the dominant eigenvalue. This is referred to as sensitivity of the dominant eigenvalue to a small change in a_{ij}.We further seek to identify which parameter is the most sensitive. This is helpful in management purposes where one requires to identify which age category needs to be taken care of in order to prevent the overall population from being extinct. It also serves to know which elephant category to avoid hunting in an event where hunting is legally allowed. On the other hand,in an event of explosion in population, sensitivity analysis may give information on which elephant category (with respect to age) should be removed during harvesting in order to check on the population growth.

The formula for eigenvalue sensitivity is

$$S = \left(\frac{\partial \lambda_1}{\partial a_{ij}}\right) \tag{7.29}$$

Eigenvalue elasticity

Survival probabilies does not exceed 1 but fertility rates have no restriction ,that is, not bounded above. If the differences between survival rates and fertility rates are too big, then sensitivity analysis may not give a very reliable information. Here it will be useful to consider the effect of a proportional change of parameters to the dominant eigenvalue. For example how much change to the dominant eigenvalue will be caused by increasing fertility or survival rates by some proportion. The proportional response to a proportional perturbation is known as elasticity.

The elasticities of λ with respect to the element $a_{ij} \in L$ are often interpreted as the contributions of each of the a_{ij} to λ .

Eigenvalue elasticity is expressed as

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} \tag{7.30}$$

The table below shows sensitivities and elasticities of the dominant eigenvalue of matrix L $(\lambda_1 = 1.3419)$ to a small change in different parameters:

Parameters	Sensitivity	Elasticity
P_1	0.2844	0.1943
P_2	0.2653	0.1930
P_3	0.2153	0.1534
P_4	0.1514	0.1059
P_5	0.1003	0.0686
P_6	0.0630	0.0428
P_7	0.0376	0.0249
P_8	0.0208	0.0129
P_9	0.0098	0.0061
P_{10}	0.0041	0.0026
P_{11}	0.0014	0.0008
P_{12}	0.0002	0.0001
F_2	0.1328	0.0014
F_3	0.0966	0.0396
F_4	0.0688	0.0474
F_5	0.0482	0.0374
F_6	0.0330	0.0259
F_7	0.0224	0.0178
F_8	0.0148	0.0120
F_9	0.0092	0.0068
F_{10}	0.0058	0.0036
F_{11}	0.0036	0.0017
F_{12}	0.0022	0.0008
F_{13}	0.0012	0.0001

The sensitivity of the dominant eigenvalue λ_1 to fertility F_i is a strictly decreasing function of age. The sensitivity of the dominant eigenvalue λ_1 to survival P_i also decreases with age. We also note that λ_1 is more sensitive to survival than to fertility at lower age classes but the inequality is reversed at older age classes. This is to say that at older age classes, λ_1 is more sensitive to fertility than to survival. Infact a change in survival rates in the last two age classes has very little effect to the dominant eigenvalue λ_1.

From the above results, we conclude that the dominant eigenvalue is more sensitive to survival of lower age classes of elephants than to fertility of these age classes. This shows the importance of juvenile survivorship in determining future elephant population.

Sensitivity of the damping ratio

The damping ratio $\rho = \frac{\lambda_1}{|\lambda_2|}$ where λ_1 is the dominant eigenvalue and $|\lambda_2|$ is the modulus of the second largest eigenvalue, gives the rate of convergence to the stable population. Here $\lambda_2 = 0.5964 + 0.5585i$ is a complex eigenvalue and $|\lambda_2| = 0.8171$.

We want to investigate which parameter affects the damping ratio the most.

Sensitivity of ρ to a_{ij} is denoted by

$$S_\rho = \left(\frac{\partial \rho}{\partial a_{ij}}\right) \tag{7.31}$$

while elasticity of ρ to a_{ij} is

$$e_\rho = \frac{a_{ij}}{\rho}\frac{\partial \rho}{\partial a_{ij}} \tag{7.32}$$

Thus the damping ratio is $\rho = \frac{1.3419}{|0.5964+0.5585i|} = 1.6423$

Here, we seek to perturb ρ by increasing/decreasing a_{ij} by small components.We then see the effect of this change to the damping ratio. This is referred to as sensitivity of the damping ratio to a small change in a_{ij} . We will do so by adding 10% to the fertility rates F_i

The table below shows some elasticity of the damping ratio of matrix L to 10% change in different parameters:

Parameter	damping ratio	elasticity
F_2	1.6424	0.0714
F_3	1.6479	0.1018
F_4	1.6557	0.1438
F_6	1.6604	0.1719
F_8	1.6353	-0.0642
F_{12}	1.6450	0.0572
F_{13}	1.6437	0.1414

Increasing F_i in the middle age classes reduces ρ while increasing F_i in the lower and higher age classes increases ρ . The effects of survival changes to the damping ratio are similar to those of fertility changes.

7.0.10 Reproductive value and stable equivalent

The table below shows reproductive value per Amboseli elephant born and aggregate reproductive value. The stable equivalent is $c_1 = 75$

Reproductive value	Aggregate reproductive value
0.1781	6
0.2606	8
0.3557	11
0.3968	13
0.3917	12
0.3708	12
0.3403	11
0.2997	10
0.2500	8
0.1901	6
0.1274	4
0.0697	2
0.0131	0

The annual rate of increase of Amboseli elephants is $r=\ln(1.3419)=0.294$ and the mean child-bearing age (generation time) is 30 years.

Chapter 8

Incorporating density dependence into the Leslie matrix model

A case of density independent Leslie matrix model has been considered above and the general trend is that the elephant population increases with time and in the long run population dynamics is an increment with a constant factor from one time step to the next. This is basic model that seeks to get the overall trend of population dynamics.

Due to limitation of Amboseli National park in terms of resources and competition among elephants, the population will not grow indefinately with time and thus there is a need to incorporate density dependence into the model.This will ensure that in the long run, elephant population will not grow indefinately. Any incorporation of density dependence decreases the vital rates.

There are several ways of incorporating density dependence and hereby, one way is discussed. We consider density as the sum of all individuals in the population irrespective of their ages. Let this sum be $x^{(k)}$, where

$$x^{(k)} = \sum_i x_i^{(k)} \quad \text{where} \quad x_i^{(k)} \text{ is the number of individuals at age class } i \text{ during time step } k \tag{8.1}$$

Now, let P_i and F_i be variables and not costants because they will be affected by the density. As the population increases, the survival rate P_i will decrease. This is because of increased competition of resources among elephants. To ensure that this is true, we define a quantity q such that P_i is a decreasing function.

Let

$$q = 1 + \alpha x^{(k)} \tag{8.2}$$

where $\alpha = \frac{\lambda - 1}{K}$ is a density parameter. λ is the asymptotic growth rate considering density independence, K is the carrying capacity of the park.

Arrange the quantity q such it forms the diagonal element of an $n \times n$ matrix Q, that is,

$$Q = \begin{bmatrix} q_1(t) & o & \cdot & \cdot & \cdot & 0 \\ 0 & q_2(t) & 0 & \cdot & \cdot & 0 \\ \cdot & & \cdot & & & \cdot \\ \cdot & & & \cdot & & \cdot \\ \cdot & & & & \cdot & 0 \\ 0 & 0 & \cdot & \cdot & 0 & q_n(t) \end{bmatrix} \tag{8.3}$$

We divide matrix L by this quantity Q and have that at time at time k+1,

$$x^{(k+1)} = LQ^{-1}x^{(k)} \tag{8.4}$$

This means that the new Leslie matrix will have its vital rates divided by the quantity q.

8.1 Analysis of the density parameter α

If $\alpha = 0$, then $q = 1$ and thus we have density independence as discussed earlier.

If $\alpha < 0$, then $q < 1$ with necessarily no lower bound. This will lead to negative entries in the vital rates of the new Leslie matrix. This will invalidate the model because ordinarily, projection matrices are supposed to be non-negative.

The only viable option is to have $\alpha > 0$. This means that $q(t) > 1$

After several projections,the population will reach stability say at time τ .Thus, from $q = 1 + \alpha x^{(k)}$, we have

$$\begin{aligned} q &= 1 + (\frac{\lambda - 1}{K})x^{(k)} \\ &= 1 + (\frac{\lambda - 1}{K})K \\ &= 1 + (\lambda - 1) \\ &= \lambda \end{aligned} \tag{8.5}$$

and the new Leslie matrix becomes

$$L = \begin{bmatrix} \frac{F_1}{\lambda} & \frac{F_2}{\lambda} & \frac{F_3}{\lambda} & . & . & . & \frac{F_{12}}{\lambda} & \frac{F_{13}}{\lambda} \\ \frac{P_1}{\lambda} & 0 & 0 & . & . & . & 0 & 0 \\ 0 & \frac{P_2}{\lambda} & 0 & . & . & . & 0 & 0 \\ . & . & . & & & & . & . \\ . & . & . & & & & . & . \\ . & . & . & & & . & . & . \\ 0 & 0 & 0 & . & . & . & \frac{P_{12}}{\lambda} & 0 \end{bmatrix} \tag{8.6}$$

$0 < P_i < 1 \quad i = 1, 2, ..., 12$

$F_i \geq 0 \quad i = 1, 2, ..., 13$

8.2 Results

This model shows that elephant population increases with up to a certain time where the population becomes constant, that is, with no growth rate. This is where the park has attained its carrying capacity and will therefore not accommodate more elephants. Infact, the dominant eigenvalue of the new Leslie matrix is 1 .

Chapter 9

Findings and recommendations

9.1 Findings

The Leslie matrix L largely depends on two vital rates: fertility and survival rates. This matrix is used to describe the population dynamics of Amboseli elephants by calculating its eigenvalues and corresponding eigenvectors.

A time-invariant and density independent system was first considered. Here, the Leslie matrix elements are considered to be constant over time. The elephant population is grouped into uniform age classes where individuals in the same age class are assumed to have almost similar characteristics. Each individual in a particular age class is considered to have the same chance of surviving from its current age class to the next. All populations are considered to move to the next age class during the next time interval.

It is noted that all elephants age classes, except the first one, are productive. The extreme age classes however, have lower productivity. The most productive age classes are those in the middle.

Four types of analysis are carried out.

Transient analysis: Here, short-run behaviour of Amboseli elephants is observed.

The population is observed to be generally on the increase with oscillatory motion.

In order to visualise this well, a graph of population with time is sketched.

Asymptotic analysis: Long-run population dynamics is analysed. It is noted that the population of Amboseli elephants increase with time in all the age classes. A close look at the behaviour of increment shows that from one time interval to the next, the population in all the age classes increases with a constant factor. This constant factor is what is referred to as asymptotic growth rate. In an attempt to find out what this growth rate would mean with respect to the matrix L, the eigenvalues of the matrix were calculated.

Since L is a nonnegative, irreducible matrix, it will possess (using Perron Frobenius theorem) an eigenvalue which is greatest in magnitude compared to all the other eigenvalues. This eigenvalue is termed as the dominant eigenvalue of matrix L. A famous method of calculating this dominant eigenvalue is called power method. The dominant eigenvalue is found to be 1.3419 . The other 12 eigenvalues were got by programming using Matlab software. They are either negative or complex. It is noted that the asymptotic growth rate is indeed the dominant eigenvalue of matrix L .

Another feature of the long-run population dynamics is the stable age distribution.The population is observed to grow proportionally in the long run. That is, the percentages of elephants in each and every age class is constant. Once again, these proportions are the same as the right eigenvector corresponding to the dominant eigenvalue of matrix L .

Ergodicity: It is found out that the long run population dynamics does not depend on the initial population vector but only on the dominant eigenvalue and its corresponding eigenvector. The fact that we can use any population vector as the initial vector and still arrive at stable population is an important thing to note in population modelling.

Perturbation analysis: It is noted that the sensitivity of the dominant eigenvalue to fertility rates F_i is a decreasing function. The sensitivity of the dominant eigenvalue to survival rates P_i is also a decreasing function. This is to say that the growth rate is more sensitive to changes in survival and fertility rates at younger age classes than older age classes of Amboseli elephants. A small change in F_i and P_i at younger age classes will cause greater impact to the asymptotic growth rate than when the change is applied to older age classes. If one needs to cause some bigger changes to the growth rate, then it should be applied to the lower age classes. The asymptotic growth rate is also more sensitive to survival rates than fertility rates at younger age classes but is more sensitive to fertility rates than survival rates at older age classes. Damping ratio ρ refers to the rate of convergence to the stable population. Increasing Fi in the lower and higher age classes of Amboseli elephants increases the rate of convergnce to the stable population. Increasing Fi in the middle age classes reduce the rate of convergence to the stable population. An explanation of this is that increasing Fi at the middle age classes would begin to make fertility periodic with respect to age, which will slow down convergence to the stable population. Effects of changing survival rates are similar to those of fertility changes.

Incorporation of density dependence was also considered. Density was defined to be the total population of individuals irrespective of their age classes. Incorporation of density dependence was found to decrease the vital rates and hence the asymptotic growth rate. Once the population attains an equilibrium (carrying capacity of the park), the population in all the age classes remain constant at any time thereafter.

9.2 Recommendation

In this study, we have mostly concentrated on density independent Leslie matrix model and later incorporated some density dependence with respect to total population. As an extension to this study, i intend to fully incorporate density dependence by also including effects of different climatic conditions to population dynamics of Amboseli elephants. Interraction between elephants and the environment (vegetation in the park) and competition of resources among elephants will also be considered. The model analysed was to a higher extent linear.The effects of nonlinear terms have not been addressed. This needs to be incorporated in order to make the model more realistic.

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APPENDIX

1.Transient analysis

```
>> % Leslie matrix L
>> L=[0,0.014,0.550,0.925,1.040,1.053,1.067,1.090,0.985,0.829,0.646,0.472,0.099;0.917,0,0,0
0 0 0 0 0 0 0 0 0;0 0.976 0 0 0 0 0 0 0 0 0 0 0;0 0 0.956 0 0 0 0 0 0 0 0 0 0;0 0 0 0.939
0 0 0 0 0 0 0 0 0;0 0 0 0 0.918 0 0 0 0 0 0 0 0;0 0 0 0 0 0.911 0 0 0 0 0 0 0;0 0 0 0 0 0
0.890 0 0 0 0 0 0;0 0 0 0 0 0 0 0.832 0 0 0 0 0;0 0 0 0 0 0 0 0 0.842 0 0 0 0;0 0 0 0 0
0 0 0 0 0.844 0 0 0;0 0 0 0 0 0 0 0 0 0 0.802 0 0;0 0 0 0 0 0 0 0 0 0 0 0.718 0];
>> %Initial population vector
>> x0=[32;32;32;32;32;32;32;32;32;32;32;32;32];
>> %Preparing matlab to accommodate population vectors for the first 8 time
steps
>> X=zeros(13,9);
>> %The initial population vector occupies the first column of X
>> X(:,1)=x0;
>> % Population for the next 8 time steps
>> for k=2:9,X(:,k)=L*X(:,k-1);end
>> format short g
>> X;
```

Graph

```
>> t=0:8;
>> plot(t,X’)
>> xlabel(’Time steps’)
>> ylabel(’Populations’)
>> legend(’1st age class’,’2nd’,’3rd’,’4th’,’5th’,’6th’,’7th’,’8th’,’9th’,’10th’,’11th’,’12th’,’13th’)
```

Logarithm of population

```
>> t=0:8;

>> semilogy(t,X’)
```

```
>> xlabel(’Time steps’)
>> ylabel(’Log(Population’)
>> legend(’1st age class’,’2nd’,’3rd’,’4th’,’5th’,’6th’,’7th’,’8th’,’9th’,’10th’,’11th’,’12th’,’13th’)
```

2. Asymptotic analysis

```
>> %Considering population percentages
>> X=zeros(13,25);
>> x0=[30;30;30;30;30;30;30;30;30;30;30;30;30];
>> X(:,1)=x0;
>> for k=2:25,X(:,k)=L*X(:,k-1);end
>> Y=zeros(13,25);
>> for k=1:25,Y(:,k)=(X(:,k)/sum(X(:,k)))*100;end
>> t=0:24;
>> semilogy(t,Y’)
>> xlabel(’Time steps’)
>> ylabel(’Log(Percentages’)
>> legend(”1st age class’,’2nd’,’3rd’,’4th’,’5th’,’6th’,’7th’,’8th’,’9th’,’10th’,’11th’,’12th’,’13th’)
```

3. Eigenvalues and eigenvectors

```
>> [V,D]=eig(L);%Right eignvectors V and eigenvalues in Matrix D
>> [U,D]=eig(L.’); U=conj(U) % Left eigenvector U and eigenvalues in D
```

4. Sensitivity matrix

```
>> [V,D]=eig(L);
>> D=diag(D);
>> imax=find(D==max(D));
>> W=conj(inv(V));
>> v=V(:,imax);
>> w=real(W(imax,:)).’;
>> senmat=w*v’
```