

Mathematical and Statistical Population Models: Elephants Population Modeling

By

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This thesis is submitted to the University of Nairobi in fulfillment of the Degree of Doctor of Philosophy in Mathematical Statistics at the School of Mathematics.

Declaration

Declaration by Candidate

This Thesis is my original work and has not been presented for examination in any other university.

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This thesis has been submitted for examination for the Degree of Doctor of Philosophy in Mathematical Statistics of the University of Nairobi with our approval as the candidate's supervisors.

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Abstract

Population modeling is an area of interest in mathematics, statistics, population studies and ecological management among others disciplines. Population of wild animals especially those classified as endangered species require to be managed in scientifically verifiably way. In this study emphasis has been put on the application of mathematical and statistical models to the African Elephant (*Loxodonta Africana*) population dynamics. Data from published sources, independent conservation and research organizations, and bodies mandated to conserve the elephant in different countries is used in our study. To be able to conserve African elephant population sustainably and make management decisions in a verifiable way, there is need for better understanding of; i) the current and expected future population trend, ii) the influence of each population vital rates to population dynamics, iii) the role of population demographic structure in population dynamics and management strategies, iv) how to incorporate processes uncertainty, observation error and model uncertainty in population models and forecasts, and, v) how scientific methods can be used to monitor population trends, study population regulation, and determine best management strategies. In the effort to study the elephant population it was noted that the biological, demographic, social processes and ecological characteristics governing the elephant population process are not understood with certainty.

Integrated autoregressive moving average (ARIMA) models, log-linear, bootstrapping, structured population models were used in modeling the elephant population of different ecosystems and for different selected scenarios. The mathematical basis and analytical approach of these methods are given. The derived models were used to project, forecast future population and analyze age specific mortality required for zero population growth. A Bayesian state space modeling framework for unstructured and structured population was discussed. Most simulations and graphics have been done using MATLAB® or R, a statistical environment free ware. ARIMA model were fitted the Amboseli National Park (ANP) total population abundance and the populations' growth rates time series. The log-linear fits indicate that the AENP population has a faster growth than the ANP elephant population. Population predictions and projection acquired from the log-linear models, time series models, and bootstrapping were compared. The populations considered showed increasing total population abundance.

Important properties and analysis techniques of a transition matrix in age structured population models were reviewed. Sensitivity analysis and elasticity analysis showed that population trend and growth rate was more sensitive to calving interval than age sexual maturity or age at reproductive menopause. The survival of animals less than 24 years and the fecundity of animals between ages of 10 to 30 years were found to be the most important to the elephant's population dynamics. The most sensitive transitions were for those classes with age less than 24 years. Different age dependent mortality scheme are necessary to course zero percent growth rate depending on the frequency of occurrence. These age dependent mortality schemes are higher for population with low average calving interval. Populations with average caving interval above 5.5 year tend to stagnate or decline depending on the mortality levels. For population recovery purposes, it is recommended that management strategies that increase survival rates of classes with ages less than 24 years and fecundity of classes between 10 and 30 years would be the most effective. Removal or induced mortality of classes with age less than 30 years produces zero percent growth for lower percentages and shorter time periods.

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DEDICATION

To my Family: A fair and just Kenya will be build on Love, justice, mercy, faithfulness, righteousness, joy, peace and hard work. These are important values in the Kingdom of God and of Christ. To Christ the King: immortal and invisible. Praises!

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ABBREVIATIONS AND ACCRONYMS

AENP: Addo Elephant national Park in South Africa.

AIC: Akaike Information Criterion.

ANP: Amboseli National Park in Kenya.

BIC: Bayesian Information Criterion.

CITES: The Convention on International Trade in Endangered Species of Flora and Fauna.

CRAN: the comprehensive R Achieve Network.

DLM: Dynamic Linear Models.

$E[\]$: the Expected value operator.

IUCN: the International Union for Conservation of Nature

KNP: Kruger National Park in South Africa.

MCMC: Mackov Chain Monte Carlo.

$N(\mu, \sigma^2)$: Normal or Gaussian with mean μ and variance σ^2 .

N_t, X_t, x and y : denote total population abundance,

$n(t), x(t)$ and $y(t)$: denote age/stage-structured population distribution,

$\Re$: Set of real numbers.

SPMs: Structured Population Models.

SSM: State Space Models.

Var: the variance operator.

WWF: the World Wide Fund for Nature,

W_t : Brownian motion or Wiener process,

3-CEPMM: three classes elephant population matrix model,

6-CEPMM: six classes elephant population matrix model,

15-CEPMM: fifteen classes elephant population matrix model.

CHAPTER ONE: INTRODUCTION

1.1 Background

A population is a group of plants, animals, or other organisms, all of the same species, that live together and reproduce” (Gotelli, 2001). Population dynamics is an area of investigation between the fields of population biology and population mathematics. Thus population dynamics can be taken as a balance of biology and mathematics.

Animal population models offer many challenges and interesting modeling problems to solve. These problems allow impetus for application both exciting mathematical and statistical methods or development new methods. Computer and numerical simulation is an example of fast developing area in modeling of both population dynamics and other research areas. Mathematical and statistical models can help solve a growing problem in biological research. As we seek to understand complex patterns of observations in collected data, statistical and mathematical models come in as an important tool.

Elephants and their population have become popularized both by positive and negative human-elephant interaction. Tourism and game viewing are a form of positive interaction whereas spread of infectious livestock diseases, lose of human live, loss of biodiversity, crops and infrastructure as a result of damage by elephants, are a form of negative interaction. They are also large long-lived herbivores that can transform or destroy the landscape. Elephant populations and their management generate passionate debates among ecologist, wildlife conservationist, local wildlife management, international wildlife organizations, stakeholders and the general public. Most of the stakeholders are in agreement on the need to conserve elephant population.

It is estimated that there were 3-5 million African elephants in the 1930s and 1940s in the continent. But a population decline was observed in the 1950s to 1980s. In the 1980s, for example, an estimated 100,000 elephants were being killed per year and up to 80% of herds were lost in some regions according to World Wildlife Fund (WWF). The African elephants were moved from Appendix II to Appendix I of the Convention on International Trade in Endangered Species of Flora and Fauna (CITES), declaring elephants an endangered species in October 1989. The listing of the African elephants in Appendix I of CITES demonstrated the danger faced by the African elephant populations. Appendices I, II and III to the Convention are lists of species afforded different levels

or types of protection from over-exploitation. Appendix I lists species that are the most endangered among CITES-listed animals and plants.

Elephant numbers vary greatly over the 37 range states with some populations remain endangered, while others are now secure according to the International Union for Conservation of Nature (IUCN) African Elephant Specialist Group. Western African populations are still small, with few countries having more than 1000 animals. The southern Africa populations are large and expanding, with more than 300,000 elephants in the sub-region. Table B1 in appendix B gives population estimates of African Elephant in some sub-Saharan African countries. These estimates are based on available published and unpublished source by year 2007 (African elephant database (Barnes et al. 1998) and status reports (Blanc *et al.* 2003)). According to African Elephant Status Report (Blanc et al., 2007) there was an approximately 472,200 African elephant in the across the continent as a whole.

As an example of the concerns on African elephant population, the WWF (2009) have identified five issues that need to be addressed in order to conserve African elephants and diminish the factors that threaten them. These are:

- i. Slowing the loss of natural habitat.
- ii. Strengthening activities against poachers and the illegal ivory trade.
- iii. Reducing conflict between human and elephant populations.
- iv. Determining the status of elephant populations through improved surveys.
- v. Enhancing the capacity of local wildlife authorities to conserve and manage elephants.

While these five issues are necessary to conserve elephant populations they also gives us insight into the need for scientifically verifiable and evidence based population management.

Scholes et. al. (2008) while reporting on an assessment of South African elephant management, gives a wide range of issues that arise in managing African Elephant populations. These include; the history and distribution of elephant populations, elephant population biology and ecology, effects of Elephants on ecosystems and biodiversity, reproductive control of elephants, controlling the distribution of elephants and lethal management of elephants, the economic value of elephants and national and international law among other.

Save the Elephants (STE) in South Africa was started in the late 1990 launched the trans-boundary Elephant program that followed elephant movements across private conservation reserves, Associated Private Nature Reserves (APNR), into the great Kruger National Park (KNP), and over the border into Mozambique. In a report of this project, we single out the classification of elephant males into three main size categories; immature males of one to twelve years, young adults of 12 to 35 years, senior adults older than 35 years. These categories are observed over time and

capture recapture methods used to estimate total population of bulls. The importance of age/class structured model is easily captured in this STE project and study (Henley *et. al.* 2009).

In Kenya, elephant's population conservation has attracted local and international attention through the focused awareness efforts created by the Kenya wildlife Service (KWS) and other stakeholders. Through KWS-STE 2008 report (Thouless *et al.*, 2008) and strategic plan, the KWS plans and creates awareness on status and conservation strategy for elephant population. The KWS conservation and management strategy for the elephant in Kenya 2012 to 2021 (Litoroh *et. al.*, 2012) has both a long term and a ten years goal focused on elephant management.

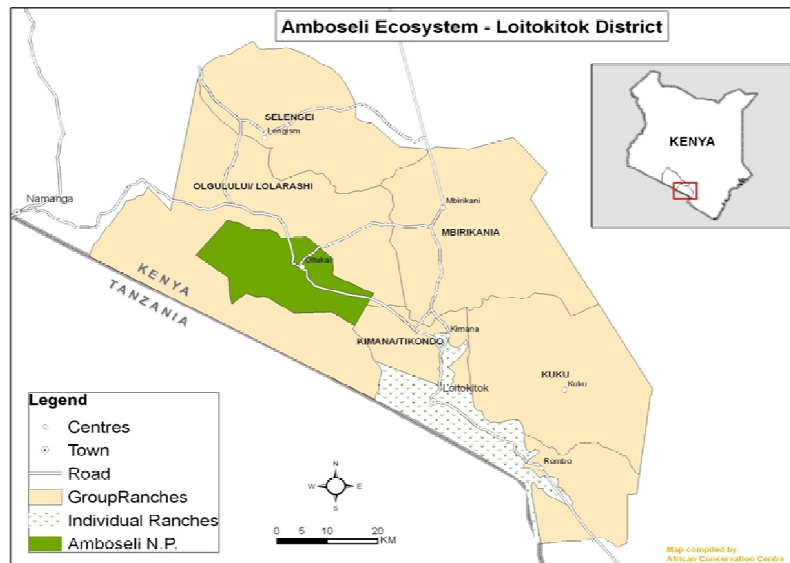
“The long term vision for the strategy is; “A secure future for elephants and their habitats, based on peaceful and beneficial co-existence with people, now and for generations yet to come.

While the overall goal for the next ten years is to “maintain and expand elephant distribution and numbers in suitable areas, enhance security to elephants, reduce human-elephant conflict and increase value of elephants to people and habitat”.

In the KWS-2012 strategy, they do acknowledge the importance of research in conservation of elephants. I quote; “there is still a lot we need to know about elephants for their effective conservation and management and, therefore need more focused research and monitoring in partnership with research organizations and individual researchers”.

One of the elephant's population we used as an example in demonstrating our model is the Amboseli National park elephant population. The Amboseli landscape covers an area of approximately 5,700 Km² stretching between Mt. Kilimanjaro, Chyulu Hills, Tsavo West National Park and the Kenya/Tanzania border. Amboseli ecosystem consists of Amboseli National Park and the surrounding six group ranches namely; Kimana/Tikondo, Kuku, Olgulului/Olalarashi, Imbirikani, Kuku, and Eselenkei cover an area of about 506,329 hectares in Loitokitok district. It also includes the former 48 individual ranches located at the foot slope of Kilimanjaro that are now under crop production, mainly rain fed agriculture (African conservation center, ACC; 2012).

Elephant population has increased over the last two decade in the Samburu District and surrounding ecosystems 2312 in 1990 (Thouless1990), 2969 in 1992 (Thouless 1992), 3436 in 1999 (Kahumbu et al. 1999) and 5447 in 2002 (Omondi et al. 2002) although the total range size may not be same for these counts. There is also mortality figure reported as a result of management actions by the KWS, though the focus of the management was to control troublesome animals (Thouless 2008),



AMBOSELI ECOSYSTEM: AFRICAN CONSERVATION CENTER, (ACC; 2012)

Changes in total elephant population numbers are the basis of many management plans and policies, but the effectiveness of management ought to be weighed response on impact of affected species, ecological processes, elephant range utilisation, and elephant numbers. It is thus important to increase understanding on social, spatial, and demographic profiles of Africa's elephant populations since they affect the distribution and numbers of elephant population.

The demographic factors that affect elephant population include; age at first calving, calving interval, and age at last calving. These traits and any factors that alter them determine how fast a population will grow holding other factors constant. These factors are also the determinant of the total number of calves a single female reproduce, which gives the reproductive number. We note here that the gestation period of an elephants is 22 months (Hodges *et al.*, 1994).

Challenges exist in trying to define the economic value of elephant population. The use and non-use values are driven by perceptions and are influenced by specific contexts. With an optimal way of evaluating the economic value in mind, elephant populations need to be managed in an adaptive and sustainable way. If not managed in an adaptive manner elephant population may lead to environmental degradation and loss of ecological diversity (Blignaut *et al*, 2008).

Human and elephants interaction have intensified and diversified with the growth of human populations, increases in elephant populations and expansion of conservation areas in some regions in Africa. Human–elephant conflict is gaining attention in the eastern and southern Africa, hence the need to manage elephant population in a scientifically verifiable way with consideration given to the benefit of wild life conservation to the local communities. Current human and elephant's

competition for resources, human wildlife conflict, reducing ecological balance and endangered species are indication of the importance of this and other research work in this area.

Population models encompass many factors that are known to determine a population trend. Population growth rate is a unifying parameter that incorporates all the different determinants of population trend. Single cohort population studies consider the animals in the group as being homogeneous, with all the vital parameter and characteristics of the population similar. In chapter four our focus will be on the central role of population growth rate for single population cohort.

We will evaluate the importance of population structure in studying population growth rate and analyzing population management strategies. State space models, also considered, are important for studying structured population dynamics in the presence of process and measurement errors. State space models enable us to incorporate statistical inference in wild population dynamics. The important and indispensable role of mathematical, statistical and simulation principles were demonstrated all through different types of models.

1.2 Statement of the problem

African elephant populations although listed as endangered have shown remarkable recovery in most Eastern and Southern Africa ecosystems. Their increase in number has raised concern of the possible effects of their increased number to the ecological diversity and wildlife human conflict among others. In certain ecosystems where the populations have shown recovery, the optimal population management strategy need to be found and its possible effects evaluated before implementation. There is thus need for scientifically verifiable research on Elephant population trends and an evaluation of whether the populations in different ecosystems are still threatened with extinction.

If a population is classified as recovered, debates exist on whether the population should be left to regulate themselves through density dependent mechanisms or by other strategies such as reproductive control, culling or translocation should be applied. If it is scientifically decided that a population require to be controlled, questions arise as to the best strategies to be applied and what will be the outcome of applying such strategies. A management strategy may aimed at population conservation, maintain a stable population or population control, but in such cases the population managers are interested in evaluating such a strategy before implementation it. The population managers would like to know which of the vital parameters of the elephant population demographics they should focus their management strategy to attain the desired outcome. There is need to evaluate what role population structure plays in developing successful management strategies.

The biological, ecological, social processes and demographic characteristics governing the elephant population process are not fully understood. We are thus unable with absolute certainty determine the future dynamics of a given population. Even if we could learn everything about the population through the observed data, questions arise on how accurate is the data we have and how accurate are surveys conducted on the population under study. Both aerial and ground counts of elephant population have error due to our inability to fully recognize or observe all the animals to be counted. Thus the role of process and measurement errors in any population models used to study or forecast future population arises. Some of the questions or uncertainties that arise include;

- i. What are the expected elephant population trends? Are the population still threatened with extinction in selected ecosystems?
- ii. What certainty level can we attach to population forecast or predicted values using total population figures?
- iii. What is the importance of elephant population demographic structure in population management? And,
- iv. How do we manage process uncertainty, measurement errors and model uncertainty to be certain of the applicability of figures used in the management process?

There is a heated debate as to whether elephant numbers need to be controlled or reduced in east and Southern Africa, and if so, how. Gathering, evaluating, and presenting all the relevant information on the African elephant and continued scientific studies are required to guide all stakeholders in the elephant population management. In this thesis we study explanatory population models, use of field data and simulation methods to model elephant population dynamics. Theoretical foundation and dynamical behavior of the underlying models is given with possible applications.

1.3 Objectives

1.3.1 General objective:

It has been to model elephant population dynamics using time series of population abundance and age structured models, and explore techniques of incorporating multiple sources of uncertainty. With the purpose of being able to; understand the role of demographic variations in population dynamics, monitor and predict future population trend, and evaluate population regulation techniques for better conservation decisions.

Objective population management requires to be done in scientifically verifiable way. Our goal was to be able to model some of the environmental and demographic factors that influence population dynamics of elephant population. This research re-evaluates the key concepts in African

elephant population dynamics models and the use of simulations to inform our understanding of the population. The models need to capture autocorrelation in data, demographic structure, uncertainties in process and data while maintaining simplicity in the models. Emphasis was put on the importance of the models in population management and enhancing decision making in elephant population management.

1.3.2 Specific objectives;

These were to:

- i. Review the dynamical behaviour of difference and differential equation models and give extensions incorporating stochasticity, process variability and observation errors:

As part of the literature review we explored the role per capita growth rate plays in determining density dependence. We simulated the dynamical behaviour of the difference and differential equation models and the resulting computer graphic given to demonstrate different scenarios.

- ii. Explore different methods of modelling the time series of total elephant population abundance for selected conservation areas:

We fitted log-linear and ARIMA models to elephant population data and used them to forecast future population and compare them. Where few data points are available we compared ARIMA results with bootstrapping methods. We derived a Bayesian distribution of the population growth rate and sample from its posterior distribution. Total population models are necessary since population data is mostly presented as total counts without other demographic details.

- iii. Formulate realistic population models for elephant population's dynamics that capture population age structure:

Although determining the exact age of an elephant is not easy unless the population is well monitored, individual animals vital characteristics differ by age. We study structured population models that put into consideration these age dependent characteristics of the population. Leslie's like matrix population models were used and analyzed using the reproductive value, dominant Eigen value, sensitivity and elasticity of the transition matrix. What-if analyses were conducted to demonstrate the effect of the different vital parameters and evaluate natural or artificial changes in these vital rates.

- iv. Demonstrate and model the effect of process, measurement and model uncertainty wild animals population modelling:

The quality of data used to model, project and make management decision is very important in designing conservation goals and evaluating management options. We evaluated the effect

of uncertainty in data, model parameters and the models used in determining elephant population trend, conducting statistical analysis and designing management strategies. We derived models for a population with process and measurement error, in a Bayesian framework. The role of simulation in population modelling and embedding population dynamics models in inference was discussed considering the complexity of the multidimensional integrals involve.

1.4 Significance of the Study

Models are an important abstraction of a real world issue in order gain better understanding. Thus apart from demonstrating the important role that mathematical modelling, statistical tools and simulation play in population modelling, this study is important for the following purposes;

- i. Population prediction: Population forecast play a vital role in predicting population trend and possible effects of population management strategies. Every forecast should be accompanied with a measure of uncertainty that help determine the utility of the forecasts. We evaluate methods of predicting elephant populations in the presence of uncertainty.
- ii. Demographic structure: the study enables one to appreciate how population management can influence by understanding or the demographic structure of the population. The population demographic structure and individual characteristics were evaluated to determine their importance in the population management strategy.
- iii. Data collection strategies and research: Models can also be used to inform population experts and wildlife managers on better data collection strategies. What population characteristics and rate ought to be recorded to enhance monitoring of the selected population? The modular approach in modelling wild population sub-process like birth, survival, ageing and removal requires detailed data and study of the individual processes.
- iv. Population management strategy: establishing the population trend and chances of extinction enables better conservation decision. There is also need to establish the most effective strategy to attain desired population scenario and to evaluate the impact of a selected population management policy.

1.5 Basic population models

1.5.1 Density independence

If a population grows without bound it can be represented using the exponential growth model:

$$\frac{dx}{dt} = rx \quad (1.1)$$

With the solution given by $x(t) = x(0)e^{rt}$. Writing the exponential model as a difference equation we have $X_{t+1} = (1 + R)X_t$ which iteratively give a solution $X_{t+1} = (1 + R)^t X_0$. Here X_t is the population at time t and R is the finite rate of growth.

1.5.2 Density Dependence logistic model

As a differential equation the logistic model is denoted as

$$\frac{dx}{dt} = rx(t) \left[1 - \frac{x(t)}{K} \right]. \quad (1.2)$$

It can be shown that the solution of the equation (1.2) can be written as

$$x(t) = \frac{K}{1 + \left(\frac{K}{x(0)} - 1 \right) e^{-rt}}.$$

where K is the carrying capacity and r is the instantaneous rate of growth. The logistic equation can also be expressed as a difference equation; $X_{t+1} = X_t \left[1 + R(1 - X_t/K) \right]$.

1.5.3 Ricker model

The Ricker model (Ricker, 1954) can be written as a difference equation:

$$X_{t+1} = X_t e^{r_0(1 - X_t/K)}. \quad (1.3)$$

Here $r = r_0(1 - X_t/K)$ is the growth rate for one time step, X_t is the population or quantity at time t , r_0 is the per capita growth rate when $X_0 = 1$ and K the carrying capacity.

1.5.4 Theta Logistic Population Growth Model

The theta-logistic which is a generalization of the standard Logistic equation is defined as

$$\frac{dx}{dt} = rx(t) \left[1 - \left(\frac{x(t)}{K} \right)^\theta \right]. \quad (1.4)$$

The parameter theta θ is the shape parameter determining the form of density dependence.

1.5.5 Leslie Structured Matrix Model

Leslie matrix (Leslie, 1945), which is sometimes referred to as the projection matrix has the following form:

$$X(t+1) = LX(t)$$

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 & \cdots & F_n \\ P_1 & 0 & 0 & \cdots & 0 \\ 0 & P_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & P_{n-1} & \cdots & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_n(t) \end{pmatrix}, \quad (1.5)$$

where, $x_i(t)$ is population in the i^{th} age class in generation t , F_i = age specific birth rate for the i^{th} age class, P_i is the fraction of the i^{th} age group surviving to the $(i+1)^{st}$ age. $0 < P_i \leq 1$, and the first age group x_1 consists of births from all age groups. The number in the i^{th} age group that survives to age $i+1$ is $x_{i+1}(t+1) = P_i x_i(t)$. The Leslie model is simply the following difference equations,

$$x_1(t+1) = \sum_{i=1}^n F_i x_i(t), \quad i=1,$$

$$x_{i+1}(t+1) = P_i x_i(t), \quad i=2, 3, \dots, n. \quad (1.6)$$

1.5.6 McKendrick-Von Forester Equation

The McKendrick–von Forster equation is a partial differential equation in which both time and age are continuous variable. The standard McKendrick-Von Forester age-structured population equation has the form,

$$\frac{\delta n(x, t)}{\delta t} + \frac{\delta n(x, t)}{\delta x} = -\mu(x)n(x, t),$$

$$n(0, t) = \int_0^{\infty} b(x)n(x, t)dx, \quad (1.7)$$

where $n(x, t)$ is the population aged x at time t , $-\mu(x)$ is the age dependent death rate, $n(0, t)$ is the total new births at time t and $b(x)$ is the age dependent birth rate.

1.5.7 Likelihood

If $x_1, x_2, \dots, x_n$ are values of a random sample from a population with the parameter θ , the likelihood function of the sample is given by,

$$L(\theta) = f(x_1, x_2, \dots, x_n; \theta), \quad (1.8)$$

for values of θ within the domain. Here $f(x_1, x_2, \dots, x_n; \theta)$ is the value of the joint density distribution or the joint probability density of the random variables $X_1, X_2, \dots, X_n$ at $X_1 = x_1, X_2 = x_2, \dots, X_n = x_n$.

1.5.8 State space model

Formally, a state space model consists of an $\mathfrak{R}_p$ valued time series $(\theta_t, t=1,2,\dots)$ and an $\mathfrak{R}_p$ valued time series $(Y_t, t=1,2,\dots)$, satisfying the following assumptions.

- i. $\theta_t, t=1,2,\dots$ is a Markov chain,
- ii. Conditionally on $(\theta_t, t=1,2,\dots)$, the $(Y_t, t=1,2,\dots)$'s are independent and Y_t depends on θ_t only.

The consequence of i) and ii) is that a state space model is completely specified by the initial distribution $f(\theta_0)$ and the conditional densities $f(\theta_t | \theta_{t-1})$ and $f(y_t | \theta_t)$ $t \geq 1$.

1.5.9 Dependence structure for a state space model

$$\begin{array}{ccccccccccc}
 \theta_0 & \rightarrow & \theta_1 & \rightarrow & \theta_2 & \rightarrow & \dots & \rightarrow & \theta_{t-1} & \rightarrow & \theta_t & \rightarrow & \theta_{t+1} & \rightarrow & \dots \\
 & & \downarrow & & \downarrow & & & & \downarrow & & \downarrow & & \downarrow & & \\
 & & Y_1 & & Y_2 & & & & Y_{t-1} & & Y_t & & Y_{t+1} & &
 \end{array}$$

The dependence structure can be expressed as follows

$$\begin{aligned}
 f(y_t | \theta_{0:t-1}, y_{1:t-1}) &= f(y_t | \theta_t), \\
 f(\theta_{0:t} | \theta_{0:t-1}, y_{1:t-1}) &= f(\theta_t | \theta_{t-1}).
 \end{aligned} \tag{1.9}$$

The time series $(Y_t)_{t \geq 1} = y_1, y_2, \dots, y_t$ is Markovian if for any $t > 1$,

$$f(y_t | y_{1:t-1}) = f(y_t | y_{t-1}).$$

1.5.10 Dynamic Linear Model (DLM)

An important class of state space models is given by Gaussian linear state space models, also called dynamic linear models. A dynamic linear model (DLM) is specified by a Normal prior distribution for the p -dimensional state vector at time $t = 0$,

$$\begin{aligned}
 \theta_0 &\sim N_p(m_0, C_0), \\
 Y_t &= F_t \theta_t + v_t, \quad v_t \sim N_m(0, V_t), \quad t \geq 1, \\
 \theta_t &= G_t \theta_{t-1} + w_t, \quad w_t \sim N_p(0, W_t), \quad t \geq 1,
 \end{aligned} \tag{1.10}$$

together with a pair of equations for each time $t \geq 1$, where G_t and F_t are known matrices (of order $p \times p$ and $m \times p$ respectively) and $(v_t)_{t \geq 1}$ and $(w_t)_{t \geq 1}$ are two independent sequences of independent Gaussian random vectors with mean zero and known variance matrices $(V_t)_{t \geq 1}$ and $(W_t)_{t \geq 1}$ respectively.

1.5.11 Non-Linear Non-Gaussian State Space Model

The state-space model can be given by the equations,

$$\begin{aligned} x_t &= F_t(x_{t-1}, w_t), \\ y_t &= H_t(x_t, v_t), \end{aligned} \quad (1.11)$$

where F_t and H_t are known functions that may depend on parameters θ and w_t and v_t are white noise processes. The main component of the model is that the states are Markov, and the observations are conditionally independent, but we do not necessarily assume F_t and H_t are linear, or w_t and v_t are Gaussian. If $F_t(x_{t-1}, w_t) = \Phi_t x_{t-1} + w_t$ and $H_t(x_t, v_t) = A_t x_t + v_t$ and w_t and v_t are Gaussian, we have the standard DLM.

1.5.12 Bayes's Theorem:

Bayes's theorem states that;

$$P(H | E) = \frac{P(E | H)P(H)}{P(E)}. \quad (1.12)$$

In Bayesian statistics, H represents the event of interest for the researcher and E an experimental result which she believes can provide information about H.

In general, suppose that $B_1, B_2, \dots, B_k$ is a partition of the sample space Ω such that $B_i \cap B_j = \emptyset$, $i \neq j$ and $B_1 \cup B_2 \cup \dots \cup B_k = \Omega$. For any set A, we have that

$$A = (A \cap B_1) \cup (A \cap B_2) \cup \dots \cup (A \cap B_k),$$

and since $B_1, B_2, \dots, B_k$ are disjoint

$$P(A) = P(A \cap B_1) + P(A \cap B_2) + \dots + P(A \cap B_k) = \sum_{i=1}^k P(A \cap B_i).$$

Therefore, the general Bayes's theorem is given as,

$$P(B_j | A) = \frac{P(A | B_j)P(B_j)}{P(A)} = \frac{P(A | B_j)P(B_j)}{\sum_{i=1}^k P(A \cap B_i)}. \quad (1.13)$$

Bayes's theorem is extremely important because it tells us exactly how to update our beliefs after observing new information. The Bayes's Theorem in equation 1.12 can be expressed as,

$$P(\text{Parameters} | \text{Data}) = \frac{P(\text{Data} | \text{Parameters})P(\text{Parameters})}{P(\text{Data})}. \quad (1.14)$$

Bayes's Theorem tells us how to rationally update the prior beliefs about θ , $p(\theta)$ in light of the data y , to yield posterior beliefs $p(\theta | y)$. It enables us to draw inference directly about the

parameters, θ , or models of interest using the posterior distribution, $P(\text{Parameters} | \text{Data})$, on the left hand side. The posterior probability distribution provides a information of what is known about the each parameter based on the data and the model, together with any prior information known about the parameters, $P(\text{Parameters})$.

Bayesian inference on θ consists of computing its conditional distribution given the sampling results. Suppose that, based on her knowledge of the problem, the researcher can assign a conditional distribution $f(y|\theta)$ for Y given θ , the likelihood, and a prior distribution $f(\theta)$ expressing her uncertainty on the parameter θ . Upon observing $Y = y$, we can use a generalization of the elementary Bayes' theorem, to compute the conditional density of θ given y :

$$f(\theta | y) = \frac{f(y | \theta) f(\theta)}{f(y)}, \quad (1.15)$$

where the marginal distribution of Y is $f(y) = \int f(y | \theta) f(\theta) d\theta$.

1.5.13 Elephant population modeling

A model is an abstraction or representation of reality. The mathematical model describes interactions between biological components. Analysis of the model, via statistical computational, simulations and applied mathematical methods, allows us to deduce the consequences of the interactions.

One of the basic objectives of theoretical ecology research is finding the factors controlling and maintaining the size of a population. For African elephant the important demographic parameters include, age at sexual maturity, calving interval, sex ratio at birth, age-specific reproductive and survival rates, number of individuals per age class, and age at senescence. These vital demographic parameters, ecological factors and management strategies determine how fast the population grows. Evaluation of the sensitivity of an elephant's population to these and other population vital parameters can enable conservation managers to predict the response of populations to various management actions.

CHAPTER TWO: LITERATURE REVIEW

2.1 Modelling approaches

2.1.1 Description of a model

A model is an abstract and partial representation of some aspect or aspects of the world. A population model may be developed for research or policy purposes. Whatever the purpose of the model, all models must be built on good science, be based on good data, and address good problems. Research models are expected to exhibit a higher degree of scientific rigor and to contribute some original theoretical insights. In policy models originality is less of an issue but transparency, manipulability, and the inclusion of key policy variables are especially important.

A more pragmatic approach considers a model as a hypothetical representation of reality, a focused problem-solving tool, whose design depends on the specific objective (Starfield et al, 1991 and Starfield, 1997). In this case the effectiveness of the model is determined by its original purpose and the assumptions or conditions imposed in the light of the objectives of the modeling exercise.

One of the basic objectives of theoretical ecology research is finding the factors controlling and maintaining the size of a population (May, 1974). In designing elephant population models, emphasis will be put on the variables that have a significant effect on the behaviour of the model. Observing how the model is affected by manipulating these variables can give population managers insights to the actual population behaviour. The main goals of the population models will be description, explanation, generalization or prediction.

There are two complementary methodological and theoretical approaches to the study of systems that are useful in our modelling effort. The top-down modeling approach and the bottom-up paradigm are important for model building. In top-down modeling approach, problems can be decomposed into simpler sub-systems, which themselves may be subdivided into even simpler sub-sub-systems, until a level is reached where the component parts may be treated as elementary.

Starting with the objective of a model leads to a top-down modeling approach in which we capture the broad and essential aspects of the dynamics first as opposed to a bottom-up paradigm where start with ecosystem processes. In a top-down approach, further refinement can be added to the model successfully as need arises.

Although population models are important tool for population management, Starfield (1997) gave seven common misconceptions about modeling that act as impediments to wide spread use of models in wildlife management. These are;

- i. A model cannot be built with incomplete understanding of the behavior of a system or population.
- ii. It is not useful to build a model if there are gaps in the data it is likely to need (so the priority is to collect data).
- iii. A model cannot be used in any way or form until it has been validated or been proven to be accurate.
- iv. A model must be as realistic as possible, accounting for all the detailed intricacies of a biological system.
- v. Modeling is a process akin to mathematics; as such it cannot be used or understood by most managers and many field biologists.
- vi. The primary purpose of building models is to make predictions.
- vii. Modeling is time-consuming and expensive; it follows that models must be designed to answer all the questions that have been thought of, or questions that may arise in the future.

Models are useful for informing decision making in ecosystem management even with the concerns and challenges raised by the issues above. A continuum for models that can help appreciate the role of each model is one starting with simple strategic models for description purposes, to tactical models for prediction.

- i. Strategic models: Simple highly abstract models for explanation developed to better understand population processes. Will usually use few parameter estimates and have minimal data requirement. Very general models are poor at making accurate quantitative predictions but can inform or help understand the population general behaviour.
- ii. Tactical models: these are models developed in an attempt to forecast quantitatively the state of a population. Require more parameter estimates and have more data requirement than strategic models (Hassell et al., 1976).

The terms strategic and tactical models are only by preference and different ecological managers and researchers may use different terms. In between the two extreme are different models with different level of abstraction, parameter estimates and data requirement.

2.1.2 Classes of models

The class of models considered in this thesis can be classified as either discrete or continuous time models, or, deterministic or stochastic models. This classification is simply for modeling approaches and is not mutually exclusive;

- i. **Continuous verses Discrete:** In designing a model we may deal with time continuously or in discrete steps. Continuous time models are usually expressed as one or more differential

equations, while discrete models are expressed using difference equations. In a discrete model the time steps are fixed, the length of which is determined by the structure of the model itself. Matrix models considered in this thesis are example of discrete models. The age-structured model given by McKendrick–von Forster equation is a continuous in both time and age.

- ii. **Deterministic verses stochastic;** Deterministic models are those without a random component and the population size in the next time period is entirely determined by the population size at the current time, or, by the previous history of population size in the case of time-delayed models. Stochastic models include one or more random components, so that the population size in the future follows a probability distribution. Both deterministic and stochastic structured models were derived for elephant population for selected ecosystems and used to evaluate the sensitivity of the population dynamics to various vital rates.

Population models seek to approximate the real behaviour of the population dynamics using three features: a deterministic or systematic part, a random element to capture random variations, and a relation between the systematic and stochastic part. Modeller makes effort to construct a model that is parsimonious, robust and mathematically tractable Thomas et al. (2005). Capturing as well as possible the physical system under study while maintain simplicity.

2.2 Non-structured population Modelling

When population is treated as a single homogeneous group, our main interest will be the population rate of growth that captures the characteristics of the population. The annual change in abundance or density of a population is described as the rate of increase. The annual finite rate of increase is defined as $\lambda = N_{t+1}/N_t$ while the annual instantaneous rate of change is defined as $r = \ln(N_{t+1}/N_t)$. The maximum annual population growth rate, r_m , is the maximum increase in numbers that occurs when resources are not limiting and there are no predators (and no population control), parasites or competitors (Sibly & Hone, 2002),

Eberhardt and Simmons (1992) states that: “Virtually all analyses of the dynamics of wild populations involve the concept of a rate of increase”. Their results on estimating r from trend data indicated that the record of trend of an individual population may provide a relatively unbiased estimate of the underlying rate of change, but they discounted on the ability to compare and contrast similar population and the population trend using such an estimate. Eberhardt and Simmons (1992) also identifies that annual fluctuations in λ may result from chance, measurement errors, actual annual fluctuations in birth and death rates, and oscillations generated by any substantial deviations from the stable age structure.

The central role of the population growth rate is well captured by the statement of Sibly & Hones (2002). They stated: “We conclude that population regulation, density dependence, resource and interference competition, the effects of environmental stress and the form of the ecological niche, are all best defined and analysed in terms of population growth rate”. The role population growth rate plays include;

- i. Defining the form of density dependence: The way a populations size changes through time result from the precise relationship between the populations size (N) and its per capita growth rate (pgr). If the population growth rate is not affected by population size then the population is said to be density independent. The per capital growth rate is defined as, $pgr = \frac{1}{N} \frac{dN}{dt}$ where t is time (Silby et al 2005). The fundamental growth curves and models include the exponential, Logistic, theta logistic or generalized logistic and Ricker (1954). Through simulations we illustrate the relationship between population growth rate and population size or density, in section 2.5.
- ii. Population prediction: Population growth rate, r , gives an easy method for forecasting future population trend although the accuracy of the predictions is subject to error in r and may fail to capture expected annual fluctuations, and form of density dependence (Eberhardt and Simmons, 1992).
- iii. Ecological niche: Environmental stressors can be defined as factors that, when first applied to a population, reduce population growth rate. We define an organism’s ecological niche as the set of points in ‘niche space’ where the population growth rate is greater than zero. The axes of niche space are physical or chemical variables such as temperature, food size or pH.
- iv. The response of populations to management can best be evaluated by their growth rates. An important application of the maximum growth rate r_m is the estimation of the maximum proportion of a population that can be removed to stop population growth(p). We study the maximum proportion of animals can remove from and given elephant population in order to reduce population growth zero percent, which is equivalent to $\lambda = 1$ for a structured elephant population.
- v. Silby et. al. (2005) states that the form of the pgr –density relationship has implications beyond population dynamics, and it is used to make predictions and to analyze management options in areas such as conservation, pest management, risk assessment, and disease epidemiology. Population management goals may be summarised in terms of population growth rate (Caughley, 1980);

- a) Population conservation: this include measure intended to increase birth rate or reduce mortality, that is to keep $r > 1$
- b) Sustained yield: equivalent to maintaining the population at a stable level with $r = 1$, and
- c) Population control: to reduce population abundance the growth rate must be maintained at levels less than one ($r < 1$).

Understanding the behaviour and determinants of population growth rate is thus important given its role in population dynamics and management. Different paradigms used to identify the determinants of population growth rate, although it is not easy to separate the effects of the multiple factors that affect it, include;

- i. Focusing on the link between population growth rate and population density gives the density paradigm. We theoretically demonstrate this paradigm in our work in section 2.6 as we lay the foundation of difference and differential equation and their application to population dynamics.
- ii. Exploration of the link between population growth rate and the age-specific life table gives the demographic paradigm. In chapter five, emphases are put on the demographic approach to the study of elephant populations. What if analysis is conducted to establish the importance of each vital parameter in elephant population dynamics
- iii. Looking directly at the link between the causal factors of age-specific population birth and death rate, such as food supply per individual, parasite burdens, predation, environmental stressors and interference competition and the population growth rate gives us mechanistic paradigm.

Hones (1999) describes the expected and observed patterns of population variation using the mean and the frequency distribution of the growth rate for three species, the European rabbit *Oryctolagus cuniculus* L., red fox *Vulpes vulpes* L. and house mouse *Mus domesticus* Ratty in Australia, and examines the implications of the patterns for wildlife management. The frequency distribution of the rate of growth does not show departure from the normal curve. Hone (1999) studied the effect of the three population management goals mentioned above and documents the following;

- i. Conservation: it shifts the distribution of r to the right so that the mean is significantly larger than zero,
- ii. Sustained yield; Stabilize the distribution by reducing extreme high or low rates of increase. This does not shift the distribution either to the right or to the left.

- iii. Control: acts to decrease abundance and hence shift the distribution of the rate of increase to lower or negative levels.

In chapter four we derive Bayesian distribution for elephant population growth rate and use it to compare two different African elephant populations. We link the goals of wildlife management suggested by Hones (1999) and Caughley (1980) to the Bayesian distribution of the rate of increase. We consider the important role of r in population forecasts for elephant population. A Bayesian approach to comparing r for multiple populations is also performed. This gives a method of comparing the dynamics of a population using the distribution of r instead of a single estimate.

Explaining and predicting patterns in stochastic population systems can be captured by the study of the interplay between stochasticity and low dimensional deterministic trends (Henson et. al. 2003). Studies have identified many low-dimensional deterministic phenomena in population data that shape population fluctuation.

In order to be able to use age structured population dynamic and unstructured models we lay a foundation by studying the deterministic skeleton of stochastic model. This is in agreement with ‘deterministic skeleton’ paradigm for analysing the mix of noise and order in population time-series (Chan & Tong 2001). In chapter two we study and illustrate basic deterministic population dynamics and give extension to the basic difference and differential models. These investigative studies offer important information on describing, predicting and generalizing on populations, and thus the need for us to explore them all over.

2.3 Structured population models historical review

2.3.1 Structured population models

Demography is the study of populations with special attention to age or stage structure. Demography is, in part, the study of how demographic rates vary among ages or stages, and the consequences of those differences. The demography of a population is the age (or stage) structure and the survival, fertility, and other demographic rates associated with those ages or life history stages. Age structure is the number or relative abundance of individuals of different ages or age classes. Stage structure is the number or relative abundance of individuals of different stages. Stages are merely useful categories of individuals, such as size classes or life history stages.

Structure or classification can be done by using age, stage, size, physiology, spatial location, behavior, or a combination of these, among others. Stages are particularly useful when, age is difficult to determine, and, when stage is a better predictor of demographic rates (e.g. birth, death, survival) than is age.

Structured population models provide important tools for evaluating conservation strategies and management actions. In a demographic model, that consists of a population projection matrix we are interested in;

- i. The finite rate of increase, λ , which is the asymptotic population growth rate.
- ii. The stable stage distribution, which is the population structure that would emerge if the demographic rates do not change.
- iii. The elasticity, which gives the relative importance of each transition to λ .
- iv. Methods of capturing environmental and demographic stochasticity in a structured model.

Age-dependent population models are basic in population dynamics. Wild animal populations as well as plant and insect populations are age-structured. The analysis of an age-structured population model is of great mathematical and biological interest. An age-structured population at a given time reveals a set of individuals who were born over a range of past times, and whose fertility and probability of survival depend on their age. When the age-structured models for biological species is not considered the individuals are treated as homogeneous with respect to age. The homogeneous assumption is not valid for African Elephant population since the fertility and probability of survival does depend on age (Whitehouse & Hall-Martin, 2009).

Most of the mathematical models that have been developed to account for the dynamic of reproducing populations assume that the ages of individuals are known. When this is true, there are basically two alternatives approaches that can be used. The first is the continuous-time integral equation method pioneered by Sharpe and Lotka (1911). The second uses grouped age intervals and a matrix formulation, and was first proposed independently by Bernardelli (1941), Lewis (1942) and Leslie (1945).

Leslie (1945, 1948) matrix model considers the female population only, at discrete intervals of time $t = 0, 1, 2, \dots$, and break the population into age groups corresponding to the unit intervals of time. Let us assume that we have m age groups. The number of females in age group 1 at time $t + 1$ will then be the sum of the offspring's from different ages. In some cases the first age class is denoted using a zero to emphasize that this class includes the new born. Otherwise the first class is labeled with a one. The Leslie (1945) model is of the form

$$\begin{aligned} x_1(t+1) &= f_1x_1(t) + f_2x_2(t) + \dots + f_mx_m(t), \\ x_{i+1}(t+1) &= s_ix_i(t) \text{ for } i = 2, 3, \dots, m-1. \end{aligned} \tag{2.1}$$

This can be written together as the matrix equation as

$$\underline{x}(t+1) = A\underline{x}(t),$$

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & f_m \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_m(t) \end{pmatrix},$$

where $x_i(t)$ = the number of females in the age group i at time t , s_i is the probability that a female in the age group i at time t will survive to be in the age group $i+1$ at $t+1$, and f_i is the average number of female offspring born to females in age class i that survive to the end of the period. The matrix A , whose elements are the fecundity rates f_i , and the survival probabilities s_i , is usually called the Leslie matrix. The Leslie matrix Model can in general be summarized as,

$$x(t+1) = Lx(t),$$

$$L = \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & f_m \\ P_1 & 0 & 0 & \cdots & 0 \\ 0 & P_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & P_{m-1} & \cdots & 0 \end{pmatrix} \text{ and } x(t) = \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_m(t) \end{pmatrix}. \quad (2.2)$$

Fertility ($F_i \geq 0$) is the number of offspring of a female of age i to $i+1$ in a unit of time t that will survive to the next age class at time $t+1$. Survival ($0 < P_i < 1$) is the probability that an individual of age i at time t will survive to time $t+1$, when her age will be $i+1$. The elements of the square matrix are non-negative, the elements of the first row are greater than or equal to zero, the elements of its main sub-diagonal are positive and less than unity and the remaining elements are zero. We can easily solve equation $x(t+1) = Lx(t)$ to get that $x(t) = L^t x(0)$.

Many extensions and development have occurred over time on the basic Leslie matrix model to enhance the model applicability. The extensions include stochastic transition matrix, density dependence, sex structure and spatial structure among others. Environmental and demographic variability can be incorporated into a Leslie matrix by making the by having the transition matrix to consist of probabilities or random variables.

The major studies and extension of the basic Leslie matrix models are summarized in the Figure 2.1 below. This figure is not exhaustive but captures major developments which are closely related to the initial structured model.

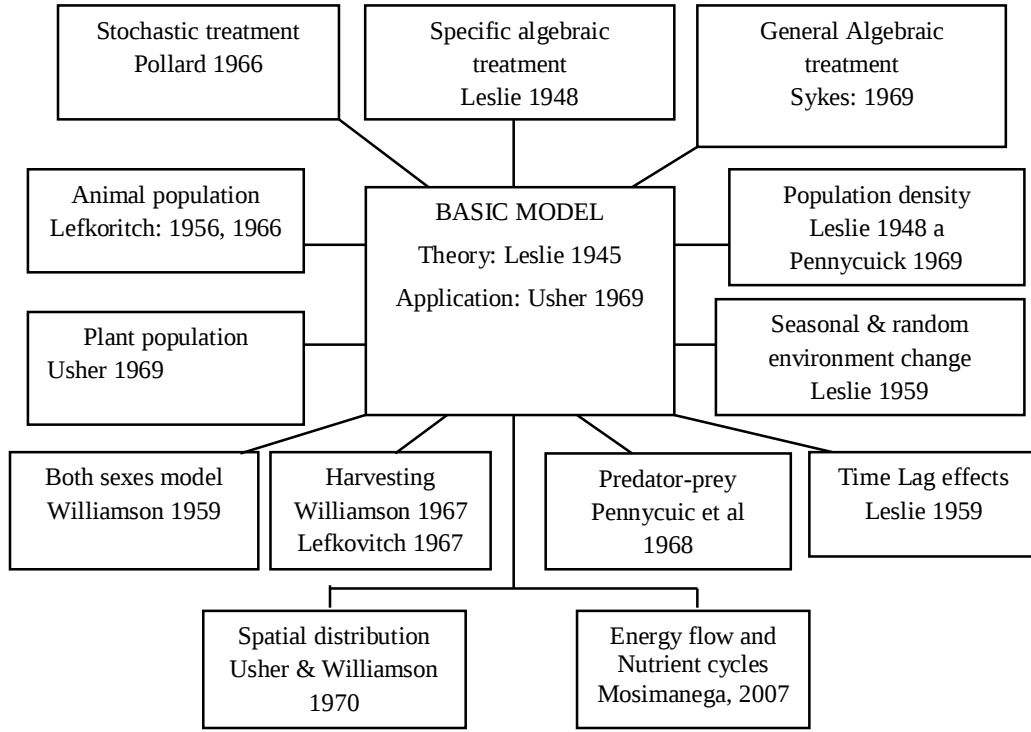


Figure 2.1 Historical development of the basic Leslie matrix model. A graphic representation of the development and sophistication of the Leslie matrix model, (Mosimanegape, 2007).

Lefkovitch (1963, 1964, 1965) modified the Bernardelli-Leslie-Lewis model to allow population to be modeled and to be grouped by life stage rather than by age. Individuals in a given stage are subject to identical growth, survival, and fecundity rates. Lefkovitch (1965) is a more general case where all the transitions between stages are possible. The model becomes,

$$y(t+1) = Ay(t),$$

$$\begin{pmatrix} y_1(t+1) \\ y_2(t+1) \\ y_3(t+1) \\ \vdots \\ y_q(t+1) \end{pmatrix} = \begin{pmatrix} m_{11} & m_{12} & m_{13} & \cdots & m_{1q} \\ m_{21} & m_{22} & m_{23} & \cdots & m_{2q} \\ m_{31} & m_{32} & m_{33} & \cdots & m_{3q} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ m_{q1} & m_{q2} & m_{q3} & \cdots & m_{qq} \end{pmatrix} \begin{pmatrix} y_1(t) \\ y_2(t) \\ y_3(t) \\ \vdots \\ y_q(t) \end{pmatrix}, \quad (2.3)$$

where m_{ij} reflect how the number in stage i at time $t+1$ depends on the number in stage j time t . Which can be put in the form $y_{t+1} = My_t$, so that $y_t = M^t y_0$. There is an implicit assumption with Lefkovitch's model that the age distribution within stages is constant enough to make any variation in the m_{ij} values with time unimportant.

Another common extension of the Leslie matrix model is the Usher (1966, 1969) stage structure population model, where the time interval is such that individuals can only remain in their current stage, transit to the next immediate stage, or exit through death.

$$\begin{aligned}
& x(t+1) = Ux(t), \\
& \begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_{m-1}(t+1) \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 & \dots & F_{m-1} & F_m \\ P_{12} & P_{22} & 0 & \dots & 0 & 0 \\ 0 & P_{23} & P_{33} & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & P_{m-1,m-1} & 0 \\ 0 & 0 & 0 & \dots & P_{m-1,m} & P_{m,m} \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_{m-1}(t) \\ x_m(t) \end{pmatrix}. \quad (2.4)
\end{aligned}$$

Similarly for Usher model population progression is given by the iterations, $x(t+1) = U^t x(0)$. The Usher model results from the Lefkovitch's model, if the time between samples is small so that the possibility of individuals developing through more than one stage in this time can be discounted. The $P_{j,j}$'s give the probability that an individual in class j in time t is still in class j , in time $t+1$. The $P_{j,j+1}$'s give the probability that an individual in class j in time t moves to class $j+1$ class in time $t+1$. The F_i are the fertility values of respective classes.

Usher (1969) was similar to the Leslie model but used size instead of age for forests trees. Leslie (1945), Lefkovitch's (1965) and Usher (1969) are all linear and time invariant matrices for projecting the female population step by step recursively. Usher (1969) and Goodman (1969) together showed that the Leslie basic model can be written as

$$\begin{aligned}
& A = F + T, \\
& A = \begin{pmatrix} f_1 & f_2 & \dots & f_m \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \dots & 0 \end{pmatrix} \text{ and } T = \begin{pmatrix} 0 & \dots & 0 & 0 \\ s_1 & \dots & 0 & 0 \\ \vdots & \ddots & 0 & \vdots \\ 0 & \dots & s_{m-1} & 0 \end{pmatrix}. \quad (2.5)
\end{aligned}$$

Other deterministic extensions to the deterministic Leslie matrix model include;

- i. Immigration models where constant immigration vector e is added to the population such that

$$x_{t+1} = Ax_t + e. \quad (2.6)$$

A negative vector $\underline{e}$ would denote emigration from the population being studied.

- ii. Immigration or emigration models where a population vector proportional to the actual population vector is added to the population. The constant of proportionality is in this case α ,

$$x_{t+1} = (A + \alpha I)x_t, \quad (2.7)$$

- iii. Harvesting can be treated either as an absolute loss from the population as in equation 2.8 or affecting survival of the classes from which harvesting is done as in equation 2.9. Equation 2.8 and 2.9 also has a minor modification that allows individuals in the last class m to

continue in the population even after attaining age m . In animal population models, this allows us to put all animals past a given age in the same class.

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ \vdots \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & \dots & f_m \\ s_1 & 0 & \dots & 0 \\ \vdots & \ddots & & \vdots \\ 0 & 0 & s_{m-1} & s_m \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_m(t) \end{pmatrix} - \begin{pmatrix} h_1 \\ h_2 \\ \vdots \\ h_m \end{pmatrix}, \quad (2.8)$$

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ \vdots \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & \dots & f_m \\ s_1 - h_1 & 0 & \dots & 0 \\ \vdots & \ddots & & \vdots \\ 0 & 0 & s_{m-1} - h_{m-1} & s_m - h_m \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_m(t) \end{pmatrix}. \quad (2.9)$$

Density dependence can be captured in the Leslie model by incorporating density dependent function $q(t)$ in the model such that

$$x(t+1) = AQ^{-1}x(t), \quad (2.10)$$

where $q(t) = 1 + aN(t)$ with $a = 1 - \lambda/K$ representing the density dependence strength, $N(t) = \sum_{i=1}^m x_i(t)$ is the total population, and

$$Q(t) = \begin{pmatrix} q_1(t) & 0 & \dots & 0 \\ 0 & q_2(t) & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & q_m(t) \end{pmatrix}.$$

Variations in $q(t)$ can be done to capture time-lag in density dependence e.g. $q(t) = 1 + aN(t-i-1) + bN(t)$, with a and $b > 0$. Leslie (1948, 1959) discussed density dependence in matrix models. Different recruitment functions which can be adapted are discussed later under basic population models include the logistic, Beverton-Holt and the Ricker.

A model that considers the two sexes in the population is,

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_m(t+1) \\ y_1(t+1) \\ y_2(t+1) \\ y_3(t+1) \\ \vdots \\ y_m(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & \dots & f_{m-1} & f_m & 0 & 0 & \dots & 0 & 0 \\ s_1 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_2 & \dots & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & s_{m-1} & 0 & 0 & 0 & \dots & 0 & 0 \\ f_1' & f_2' & \dots & f_{m-1}' & f_m' & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & s_1' & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 & 0 & s_2' & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & 0 & 0 & 0 & 0 & \dots & s_{m-1}' & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_m(t) \\ y_1(t) \\ y_2(t) \\ y_3(t) \\ \vdots \\ y_m(t) \end{pmatrix}. \quad (2.11)$$

In this model $x_i(t)$ is the population of females in class i at time t , $y_i(t)$ is the population of males in class i at time t , f_i is birth rate of female to females and f'_i is birth rate of male to females, s_i and s'_i the survival rates of females and males respectively. This is essentially equivalent to a one sex (female) model since the eigenvalues of the transition matrix are given by,

$$\lambda^m (\lambda^m - f_1 \lambda^{m-1} - f_2 p_1 \lambda^{m-2} - \dots - f_m s_1 s_2 \dots s_{m-1}).$$

The non-zero eigenvalue are the eigenvalues of the $n \times n$ female's sub-matrices. Due to the fact that the ratio of birth in elephant population are basically in a 1:1 ratio of male to female we will consider only one sex models. Although there is minor variation in the survival of male to female (Moss, 2001) we will assume equal survival for both gender.

A stochastic model takes into account of the randomness in the environment, birth and death processes where as a deterministic model do not. Accordingly, a stochastic age structured model is worth developing and investigating. Different source of variability that can be included in the structured population models (SPM) also known as population projection matrix models can be summarized as in Figure (2.2) below (Caswell 2001).

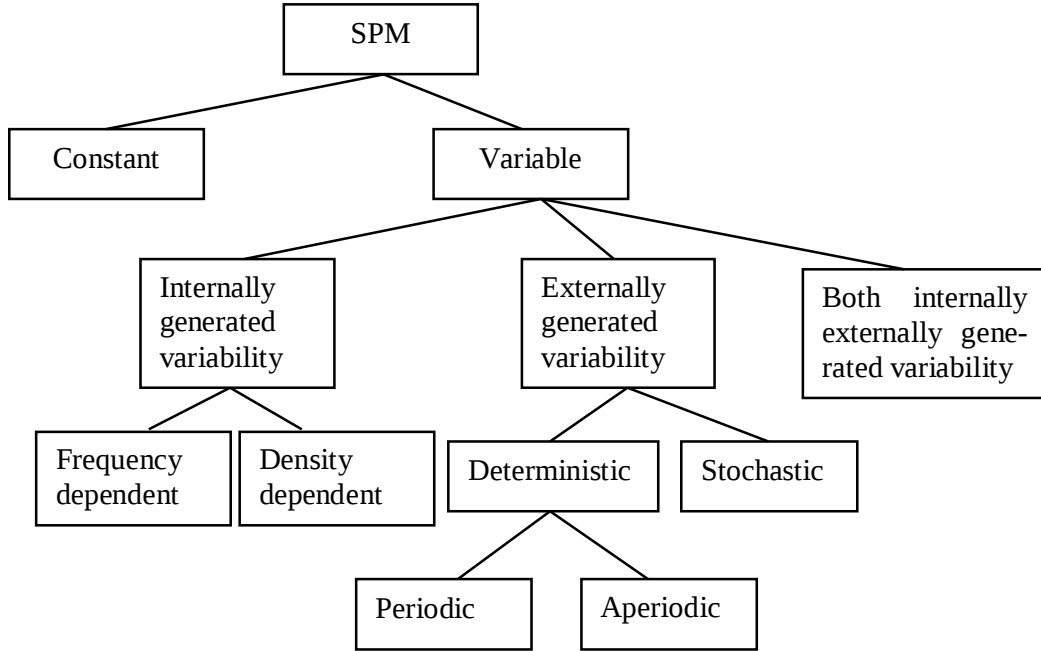


Figure 2.2 Variability in structured population models. A classification of matrix population models according to the variability included in the projection matrix (Caswell 2001).

The different classifications include;

- i. Constant: the projection matrix is constant and does not vary with time and is independent of population size and environmental variation.

- ii. Endogenous factors causing internally generated variability: the projection matrix is dependent population size being either frequency or density dependent. When Endogenous factors causing population dynamics to depend on its own frequency or density are included, the resultant dynamics are non-linear.
- iii. Exogenous factors causing externally generated variability: the projection matrix is dependent on factors external to the population, for example, environmental factors. The external variability may be deterministic (predictable) or stochastic. Environmental variability can be classified further as either occurring with equal and known regularity (periodic) or with unknown and irregular variations.
- iv. Both internally and externally generated variability can be included in the projection matrix.

Models can include other sources of uncertainty due to process and observation errors. Process variability may be due to demographic or environmental variability. An observation error is as a result of error in the measurement process or inability to measure the entire process. Environmental and demographic stochastic variations can be incorporated in a structured model by

$$x(t+1) = A_t x(t) . \quad (2.12)$$

Or by an additive stochastic element such that

$$x(t+1) = Ax(t) + \varepsilon_t . \quad (2.13)$$

Having linked the environment and the vital rates, population projections that captures environmental variation at each time point $t = 1, 2, \dots$ is given by equation, $x(t) = A_{t-1} A_{t-2} \cdots A_0 x(0)$. Precaution must be exercised while selecting the elements of stochastic A_t to ensure that it maintains biological validity. Linear models that are not dependent on population abundance or density can be used if the population is assumed to be below carrying capacity and in a relatively constant environment. Non-linear non-homogeneous models of the form in equation 2.14 will not be considered in the study for the of elephant population.

$$x(t+1) = A_t(x) x(t) . \quad (2.14)$$

In demographic stochasticity the chance of individual in a population transiting from time t to time $t+1$ is a random variable as opposed to deterministic. Even if the vital rates predict positive population growth on the average demographic stochasticity implies that population may go extinct by chance and vice versa. Demographic variation in the elephant population will be incorporated using both a structured matrix model and later using state space model with process and observation error. Analysis of both deterministic and stochastic matrix models will be discussed further in the method for specific case considered for the elephant population.

Matrix population models have become popular tools in research areas as diverse as population dynamics, life history theory, wildlife management, and conservation biology. Transition matrix models are recommended widely as an effective method for evaluating demographic data, especially for calculating population growth rate, extinction probability, and sensitivities (Burgman et al. 1993; Caswell, 2001). The long-term behavior of the population is determined by the dominant eigenvalue of the Leslie matrix for a deterministic. In chapter three we give the theoretical foundation of analysis of structured population models and later apply them in chapter five.

Because matrix models can incorporate observed levels of stochasticity to simulate population dynamics through time, they can be used to calculate the chance of population loss under various conditions. Wildlife resource managers can use this information to determine whether a management action should be taken to benefit a species of concern (Schemske et al. 1994). This type of analysis, therefore, is directly applicable to management and conservation of elephant populations.

In chapter three and five we utilize both deterministic and stochastic structured population models for population dynamics of the African elephant, establishing the dynamics of the population for given assumptions. We also consider a modular approach to processes such as birth, survival, aging and harvesting or removal. Transition matrix then becomes a product of multiple modular processes. Modularizing the processes involved makes it more flexible to study individual processes and hence model these processes using individual distributions. Incorporating process and measurement (or observation) error in these high dimensional models creates a challenge which we discuss using state space models in a Bayesian framework.

2.3.2 Applications of Matrix population models

In this section we give a few examples of recent study and application of matrix population models in modeling wild animal population dynamics. They help us to build on our methodology and review the various themes and objectives in the study of wild animal population.

Li Wen-Ching (1994) uses a generalized Leslie matrix model to study wild turkey populations. Although the turkey population is different from elephant population, the application of matrix model may be useful to this study. The analysis of transition matrix is similar and their approach of determining the stationary population by varying individual matrix elements will be applied to the matrix model for the elephant population. They used their study to predict the future population size, population structure and effect of harvest on the population age structure and

growth. Similar objectives and simulations do have importance in the elephant population dynamics.

Caswell (2001) work on matrix population models gives detailed discussion on construction, analysis and interpretation of such models. He emphasizes on the relationship between the construction, analysis and biological interpretation of the model. A model is constructed to answer a question; its interpretation influences the construction. Models once constructed need to be analyzed and require data to be parameterized. Caswell (2001) is useful in construction, analysis and interpretation of the matrix model for the elephant populations.

Montshiwa (2007) discusses the construction of Leslie matrix population models and gives the mathematics behind the parameters in the matrix model. They reaffirm the importance of fertility and survival rates in a Leslie matrix model. Incorporating density dependence and stochastic variation into the matrix population model is considered.

Wooley et. al. (2008) study models the effect of age-specific mortality on the African elephant populations. They studied the effect of episodic mortality and gave the age specific mortality schemes required for zero percent population growth rate. They established that natural mortality cannot provide regulation for the elephant populations in southern Africa populations. Their model though stochastic was base on the one year model of Wu and Botkin (1980). In this study we consider the use of fewer classifications in a matrix model. Methods for analyzing the matrix model are well established and can be used as an approximation when the population is large.

Schnute (1994) and, Millar and Meyer (2000a, 2000b) discuss the importance of incorporating measurement and process error into a population models, Although Millar and Meyer (2000a, 2000b) considers the construction of fisheries models, techniques for incorporating errors are important for other wild life population models. Recent studies on a framework that allows stochastic structured population dynamics models to be embedded into statistical inference include Buckland *et al.* (2004), Thomas *et al.* (2005) and Newman *et al.* (2006). The Bayesian state space model approach gives a general framework that can be applied to various wild life populations. The modular approach to deterministic and stochastic population sub-processes such as birth, survival, maturation harvesting and movement, adds a useful technique in modelling under multiple sources of uncertainty.

2.4 African Elephant Population Models:

A wide range of factors require to be considered while modeling elephant population. The demographic factors that affect elephant population include; age at first reproduction, inter-calving

interval, and age at senescence, the number of individuals by age and sex class, age- and sex-specific survival (Moss et al. 2011; Van Aarde, 2008; Moss 2001). These traits and any factors that alter them determine how fast a population will grow holding other factors constant. These factors are also the determinant of the total number of calves a single female reproduce, which gives the reproductive number.

Fecundity is determined by age of sexual maturity, age at last calving, calving interval and factors which influence age of sexual maturity, age at last calving and calving interval.

- i. Ages at first calving for African elephant females differ from one population to the other (see table B4 in the appendixes). Mean age at first calving of 9-16 year which are common for populations in South Africa and elsewhere will be adapted for simulation purposes.
- ii. Mean calving interval of between 3-6 year have been observed in different regions with south African population showing shorter calving intervals, and
- iii. Maximum age at last calving will be approximated using 50-60 year depending on the population (Whitehouse & Hall-Martin, 2009, Moss 2001).

Survival probabilities of African Elephant population do not show major variation from one ecosystem to the other. Incidence increased mortality due to predation are low and may not affect the survival of entire population significantly. Mortality of young calves can be affected by low level of predation and drought while the mortality of adults may increase with poaching especially for free roaming animals. Recorded estimates and simulated values will be use for different age classes in this study.

Population dynamics of the African elephant are also affected by immigration and emigration. The dispersal is however limited by barriers and fencing for case of conservation area. Dispersal can also be influenced by provision of resources such as water through digging of dams. In modelling a closed ecosystem we will assume zero movement into and out of the conservation area (Rudi Van Aarde et al. 2008; Blanc et al., 2007; Moss, 2001)

Apart from the stated factors and vital rates, the African elephant is a long-lived species characterized by deferred and intermittent breeding, relatively high adult survivorship and long maximum longevity. The fecundity and mortality of individual animals is dependent on age and time varying processes.

The important question is whether structured population models are applicable in modeling African Elephant population dynamics and if so how reliable are such models? We evaluate the application of structured models for African elephant population and consider why structure is important. Age or stage structure is an essential component in Elephant population management due

to varying demographic characteristics. Management strategies, trophy hunting and poaching, although some of these practices are banned or illegal, affect certain age-stage classes.

In using a Leslie like model to model African elephant population we must put in consideration the following challenges (Wu and Botkin,1980),

- i. The Leslie Matrix model is deterministic where as the vital rates vary for over individual and time.
- ii. The birth and death are dependent on age only and assumptions of extended Leslie model should agree with the population characteristics, and
- iii. Different processes affecting birth and death may occur at different time intervals, and the time interval appropriate may not be explicit.

Monitoring population changes is important for implementing appropriate management options and evaluating their effectiveness. Demographic parameters, such as; sex, age at first calving, calving interval, survival rates and reproductive senescence, which are important for predicting population changes over time, vary over the life time of an elephant. Determining these parameters pose a great challenge, since the age of the elephants in the population ought to be determined accurately.

One reason to consider model with less classes is due to the fact that it is not easily viable to determine the age of each elephant in a wild elephant populations. Methods of determining the chronological ages of elephants include, measuring molar tooth wear and progression, elephant tusk dimensions, back lengths, shoulder height hind foot lengths, and Dung boli diameters.

All these methods rely on the relationship between a particular body structure features and age to determine the age of an individual elephant. The relationships are the best available to assign age for cows up to age 15 and for bulls up to age 25 (Rudi Van Aarde *et al*, 2008). Thus such age estimates are not precise and would better be classified as intervals where individual birth and dates are not tractable.

Woodd (1999) in his study, “A demographic model to predict future growth of Addo elephant population”, used a one year class interval to model the Addo population. But the demographic parameters for the AENP animals show no major differences for animals in certain age classes (Woodd, 1999). His work gives important demographic rates for developing a structured population model for AENP elephants. Addo Elephant National Park (AENP) is a fenced and has a closely monitored population and thus Woodd (1999) model would face challenge if it were to be applied to wild and less monitored population. This model is also deterministic and there is a

challenge if we try to embedding inference into such a model. In chapter five we gives a framework that can be used to model elephant population with an ability to embed inference and study individual population sub-process. We also consider a deterministic structured population model framework with less number of classes that can be used for elephant population that are less monitored, due to their wild nature.

Woodd (1999) while giving the demographic parameters for the Addo elephant population combines certain ages into a single group due to the equality of the parameters, he also assume that there is no difference in fecundity when female elephants attains maturity. This is an indication that elephant population can be modeled using fewer classes especially where populations are less monitored and exact age of individuals is not known. An example is the Tsavo National Park in Kenya where the population is less monitored, the park is not fenced and counts are done using Arial methods.

Population growth rates can be derived from survival and fecundity estimates (e.g., matrix models; Caswell 2001). Identifying the relative contribution of age-specific fecundity and survival to growth may help identify the most important factors influencing population dynamics. Estimates of age-specific fecundity can be derived from age at first reproduction, from intervals between births, and from age of reproductive senescence, but these data are usually difficult to obtain (e.g., Whyte *et al.* 1998, Whyte 2001). Additionally, ages of individual elephants may also be difficult to estimate as stated above, further complicating calculation of fecundity and survival rates (Shrader et al. 2006). Examples of long-term observational studies of known individual elephants that help overcome the inaccuracies of age estimation are Whitehouse and Hall-Martin 2000 and Moss 2001.

Multiple studies that have used structured models for elephant's population dynamics exist. A nonlinear age-class model that captures density dependence in elephant population was developed for Kabalega (formally Murchison Falls National Park) population of elephants in Uganda by Fowler and Smith's (1973). Habitat degradation due to restriction in its range was captured through density dependent calf survival and adult fecundity.

The model by Fowler and Smith's (1973) for elephant dynamics had the following form

$$x(t+1) = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ s_1 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & s_{64} & 0 \end{pmatrix} x(t) + \begin{pmatrix} \phi(y) \\ 0 \\ \vdots \\ 0 \\ 0 \end{pmatrix},$$

where the elements x_i , $i = 0, 1, \dots, 65$ represent the number of female elephants per square mile in age class i . The calf survival function $\phi(y)$ depends on $y = (y_1, y_2)'$, where y_1 is the aggregated breeding population and y_2 is the total density variable given by $y_1(t) = \sum_{i=1}^{65} b_i x_i(t)$ and $y_2(t) = \sum_{i=1}^{65} x_i(t)$. The exact form that Fowler and Smith chose for the calf survival function was $\phi(y) = y_1(1 - 0.03y_2)$ which only applies to population densities below $y_2 = 33.3$ individuals per square mile.

Fowler and Smith's (1973) used comparison of projected population age distribution and observed age distribution to verify their model. This method will be applied where no analytic proves are not given or required. In case where only the total population is available, or a subset of the population vector, the total population is determined by addition of the respective projected population vector. This agrees with the explanation purpose of population modeling. This model gives us a method for capturing density dependence in an elephant population if density dependence is established to be present.

A linear model with 60 age classes that uses the Leslie transition matrix was developed by Croze et al, (1981), for studying elephant populations of Tsavo National Park in Kenya. The survival rates of juveniles and the fecundity rate of young adults in this model were assumed to vary in response to environmental conditions. The model was used to keep track of female population only and was used it to evaluate the effect of time varying parameters on population growth.

Since the gestation period of elephants is just under two years, Wu and Botkin (1980) incorporated three female reproductive stages into the density independent Croze's like model above. The female reproductive stages included susceptible to pregnancy, pregnant less than one year and pregnant more than one year. An illustration of the female reproductive stages and possible transitions for females in the same class is given in Figure (2.3) below.

The model approach of Wu and Botkin (1980), with minor modification, can be represented using columns for; males, immature females, mature females (not pregnant, not lactating), pregnant females in the 1st year of pregnancy, pregnant females in the 2nd year of pregnancy, lactating females in different years of lactation.

Determining the exact age of individual elephants required for Fowler's, Croze's and Botkin's models is a clear challenge (Western, et al. 1983). There is need for models that require less monitoring of the population for use in management of wide-ranging populations. Using an

approach with the similar framework but with fewer classes we simulate structured population model for elephant population where estimates of vital parameters are available.

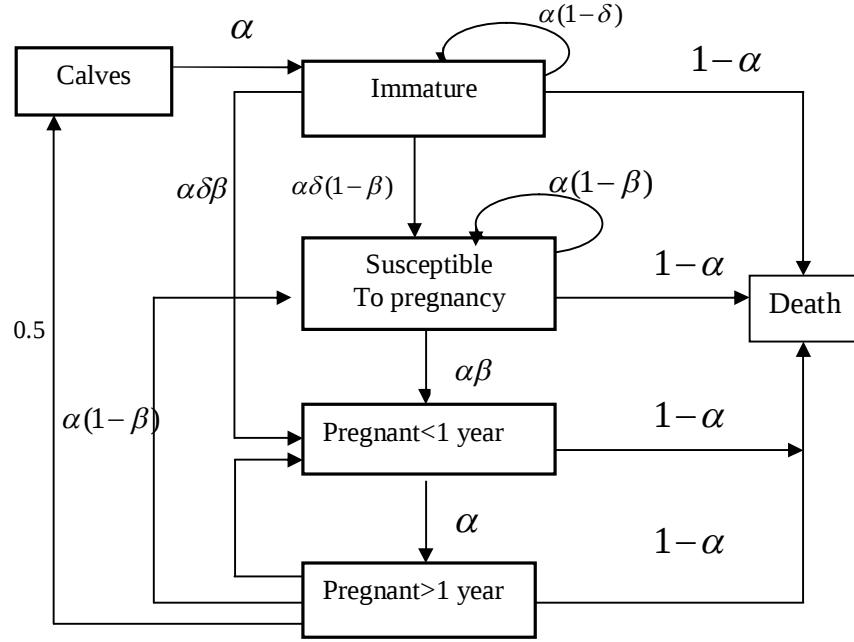


Figure 2.3 Mature female African elephant reproductive life history. Female reproductive stages as in Wu and Botkin (1980) model for African Elephants population. The transition rates corresponding to each arrow in the figure have been omitted.

In our models, fewer classes were used since elephants can be classified using age classes with more homogeneous demographic parameters. In extending the deterministic matrix models to stochastic matrix models we assumed that environmental and climatic variations are capture by individual animal stochastic survival and stochastic recruitments to the first class.

The models for elephant population dynamics will generally have three basic goals, these are prediction, explanation, and generalization;

- i. We may want to predict its future elephant population size given past and current population estimates or population parameters.
- ii. We also want to describe its growth rate and population size in terms of mechanisms that could influence their growth rate. This includes population vital characteristics, management option and other natural phenomenon's.
- iii. We want to compare elephant's population growth and relevant population mechanisms in one ecosystem to those of populations in other ecosystems.

To understand the behaviour of the population of interest and evaluate management options we developed models that incorporate among others, birth process, death process, environmental

stochasticity and population structure. We then perform simulations to determine the required age specific mortality rates scheme required to cause a zero population growth rate.

It was important to note that African elephant live in a well structure and complex social setting. A family unit typically consisting of 1-20 cows, their daughters, and immature male offspring are lead by a female matriarch. Adult male are generally solitary associating with females occasionally. The family unit join with other to form groups, clans, subpopulations, and populations (Rudi Van Aarde *et al*, 2008). Thus, management strategies affecting some age classes in the population may indirectly influence vital rates of other classes in the population. Such indirect inter-relationships of classes' vital rates for elephant society were assumed to be minor and thus were ignored in our models.

2.5 Basic population models

In this section we used simulations to demonstrate the dynamics of basic population models. We reviewed basic phenomena such as bifurcation, attractors and perturbation analysis that relate either to difference equations, differential equations or structured models. We simulated the density independent and density dependent models such as the, exponential, Logistic and theta logistic. Although these models are known to be simplification of reality, they play an important role in our understanding and evaluation of population growth phenomena.

2.5.1 Exponential growth

Deterministic population models are the foundation and skeleton of most extensions in population modelling. In order to evaluate a stochastic model, it's important to study the dynamics of the skeleton deterministic model. We thus reviewed the difference and differential population models for density independence and density dependence, and simulate their dynamics under assumptions or conditions that are natural and easy to relate to their ecological implications.

Difference and differential equation models are the foundation to the study of population studies (Pielous 1976, Gotelli 2001). We reviewed their mathematical properties as a basis to fitting and simulating time series data necessary for illustration. We demonstrated their use in population prediction, explanation and generalization in chapter four.

Simple discrete-time models can often be used to predict the size of certain populations after t discrete-time steps. This class of models works well in modelling densities of populations, where individuals reproduce only during specific breeding periods, or when the populations pass through distinct reproductive cycles.

The major components of population changes include births, immigration, deaths, and emigration. When these vital rates are modeled we acquire BIDE model: $N_{t+1} = N_t + B_t + I_t - D_t - E_t$. Where N_t is the total population, B_t is the number of birth, I_t is the immigration, D_t is the number of death, and E_t is the number of emigration rate at time t . If a population is thought as operating on finite intervals, a difference equation may be derived for the exponential growth:

$$\begin{aligned} N_{t+1} &= N_t + N_t R = N_t(1 + R), \\ N_t &= N_0(1 + R)^t, \quad N_t = N_0 \lambda^t, \quad \lambda = 1 + R. \end{aligned} \quad (2.15)$$

where $\frac{N_{t+1}}{N_t} = 1 + R = \lambda$ is the annual rate of change, and the finite growth rate R is give by: $R = \text{finite birth rate} - \text{finite death rate} + \text{finite immigration rate} - \text{finite emigration rate}$.

The total number of elephant in an area can change due to four reasons: births (b), deaths (d), immigration (i), and emigration (e). The factors that influence births, deaths, immigration, and emigration determine population size and change in numbers over time. The difference equation for change in population size ΔN for a time interval Δt is given by

$$\Delta N = (b - d + i - e)\Delta t. \quad (2.16)$$

A stochastic equation would arise if we allow births, deaths, immigration, and emigration to be functions of time and environmental factors. In a closed environment like a national park where there is no emigration and immigration, and assuming that births (b) and deaths (d) are functions of $N(t - \Delta t)$,

$$\frac{\Delta N}{\Delta t} = b(N(t - \Delta t)) - d(N(t - \Delta t)), \quad (2.17)$$

which as $\Delta t \rightarrow 0$ becomes

$$\frac{dN}{dt} = b(N(t)) - d(N(t)). \quad (2.18)$$

If the functional relation of births (b) and deaths (d) on $N(t)$ is linear we have,

$$b(N(t)) - d(N(t)) = rN(t).$$

This is the same as if the population is thought as changing continually, that is, continuous birth and death results in a differential equation:

$$\frac{dN}{dt} = rN. \quad (2.19)$$

With solution $N_t = N_0 e^{rt}$, $e^r = \lambda = N_{t+1}/N_t$. If again we reintroduce immigration and emigration, the instantaneous rate of growth $r = b - d + i - e$. This is the net value of instantaneous birth and immigration rates less the instantaneous death and emigration rates. Continuous time and instantaneous birth rate is not appropriate for a population with a birth pulse. The percentage population growth rate is given by,

$$(e^r - 1)100\%. \quad (2.20)$$

For the continuous exponential growth case, $N_t = N_0 e^{rt}$, and $\ln(N_t) = \ln(N_0) + rt$. We note that, r is the slope of the linear relation between $\ln(N_t)$ and time t , and $\ln(N_0)$ is the y-intercept. If we fit a straight regression line to log-transformed data, the slope of that line would be r , where $\lambda = e^r$, and $\ln \lambda = r$. In summary the parameters λ and r relate to population growth:

- i. There is no change if $\lambda = 1$, $r = 0$,
- ii. Population grows if $\lambda > 1$, $r > 0$, and
- iii. Population decline if $\lambda < 1$, $r < 0$.

In chapter four, we fitted log-linear models to the transformed data of total population of the ANP and the AENP and use the results to compare and project future populations. Both 95% confidence intervals and confidence limits for each fit are given for the two populations.

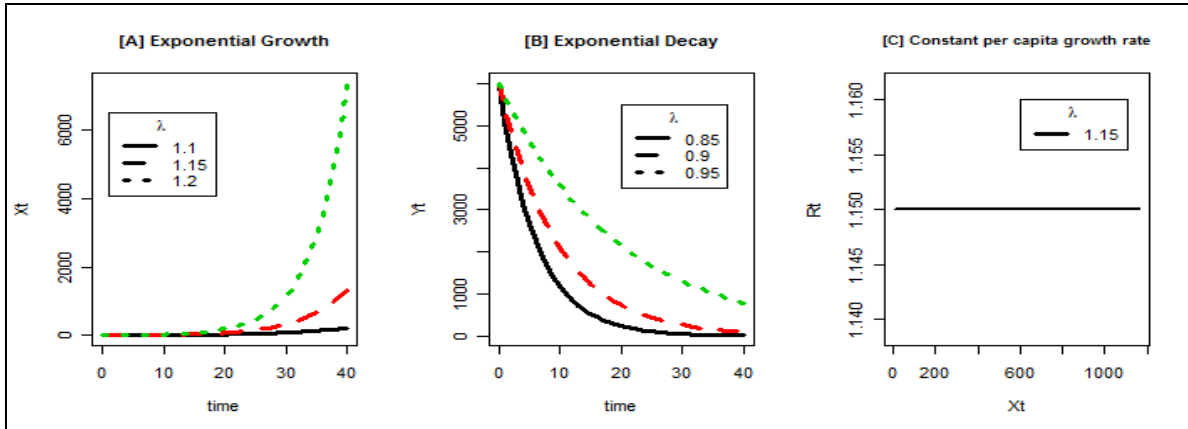


Figure 2.4 Density Independence. Figure a&b shows density independent growth ($\lambda > 1$) and decay ($\lambda < 1$) respectively, for various values λ . Figure c shows constant per-capita growth rate with increasing population a property of density independent growth.

Exponential growth is equivalent to density independence. No matter what the population size, the per capita birth rate and per capita death rate are the same as for all other population sizes (see figure 2.4c). Figure 2.4a illustrates unbounded population growth for $\lambda > 1$ while figure 2.4b gives case of $\lambda < 1$ in which case population decays to extinction. In the case of the exponential growth the per capita growth rate does not depend on density as in Figure 2.4c.

Figure 2.5a show that the exponential growth with different initial population size. In this case, population size remains double the lower level as it is at the initial time as seen in the log scale if Figure 2.5b.

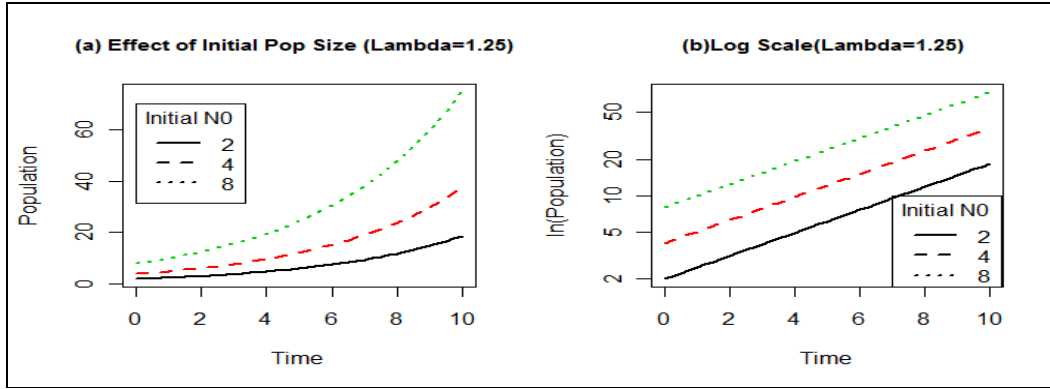


Figure 2.5 Effect of initial population size. Population remains double the size of the lower population as in figure 2.3a. Figure demonstrate the same population levels plotted on the log scale.

2.5.2 Logistic growth

Density-dependent population growth is the case where the per capita population growth rate depends statistically on the density of the population. Negative density-dependence is typically a characteristic of a population undergoing intra-specific competition.

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right). \quad (2.21)$$

We can determine the solution from,

$$\frac{dt}{dx} = \frac{1}{r} \left(\frac{1}{x} + \frac{1}{K-x} \right), \quad \frac{dx}{x(K-x)} = \frac{r}{K} dt, \quad (2.22)$$

$$\int_{x_0}^{x_t} \left(\frac{1}{x} + \frac{1}{K-x} \right) dx = \int_0^t r dt \Rightarrow [\ln(x) - \ln(K-x)]_{x_0}^{x_t} = rt.$$

$$x(t) = \frac{Kx_0 e^{rt}}{K + x_0(e^{rt} - 1)}. \quad (2.23)$$

Letting x represent population size and t represent time, the constant r defines the growth rate and K is the carrying capacity.

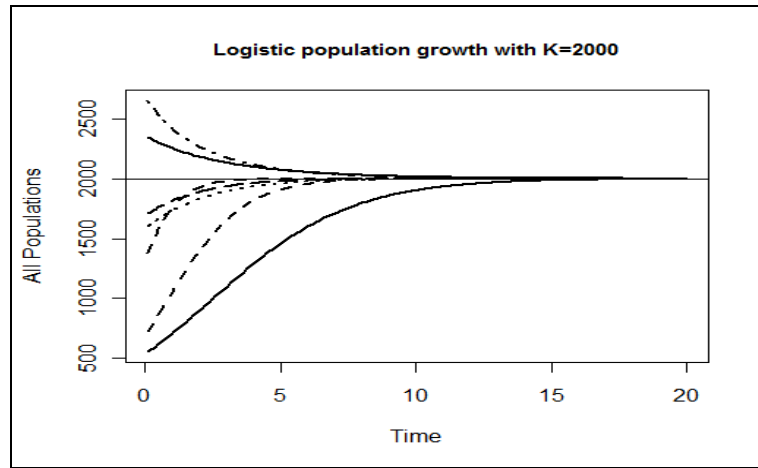


Figure 2.6 Continuous Logistic Growths. Figure 2.6 demonstrate how populations selected between 500 and 2800 approach the attractor $K=2000$ for different values of the growth rate r . The behavior in the region between 0 and K is called Logistic growth.

Figure 2.6 demonstrate a logistic growth with $K = 2000$ as an attractor for different values of r . Figure 2.7 (a) below shows density dependence effect on per capita increase, while Figure 2.7 (b) gives per capita increase as a ratio of total population for equation (2.21) model.

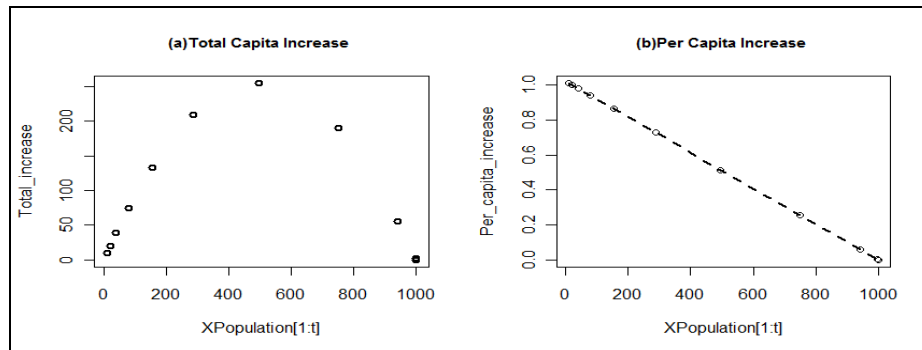


Figure 2.7 Logistic growth density dependence. In a logistic population model the per-capital growth rate reduces linearly with increasing population abundance.

The simulation in Figure 2.6 show that in certain realization density dependence is quickly evident, while in other it take time and one may erroneously conclude that the population does not show any evidence of density dependence. Figure 2.4 gives 15 simulated curves for $K = 1000$ for random N_0 between zero and 1300 individuals, and r randomly selected between 0 and 2. The populations decay with K acting as an attractor. For a logistic population growth, the effects of the varying the initial population size, the carrying capacity K are illustrated in Figure 2.8 below.

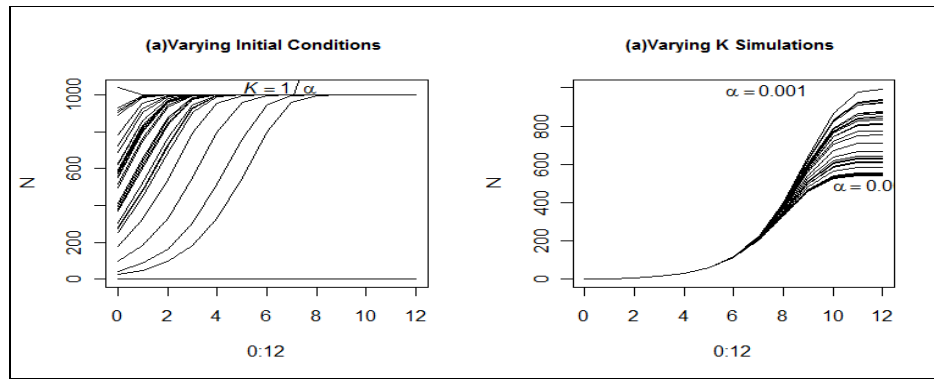


Figure 2.8. Varying initial population N and carrying capacity K . All the population approach the attractor $K=1000$ no matter the initial population size. Figure 2.7b shows the varying the effect of varying K which alters the attractor.

In Figure 2.8a K acts as an attractor no matter the initial size of N , while in Figure 2.8b the attractor varies according to value of K . To fully illustrate the behaviour of the discrete logistic growth we perform bifurcation analysis. The point at which the limit cycle emerges, at $r_d = 2$ (Figure 2.9), is called a bifurcation (Stevens, 2009); it is a splitting of the single attractor into two attractors. As r_d increases the number of attractors will continue to double, growing geometrically. Eventually, we reach a point when there are an infinite number of unique points as in Figure 2.8a below.

Figure 2.9a illustrates discrete logistic bifurcation while 2.9b illustrate sensitivity to initial conditions. With the discrete Logistic model it's important to note we can generate very different trajectories by varying initial conditions slightly. Figure 2.9b shows different trajectories generated for initial populations for $r = 2.7$.

It is important to note that even the simplest deterministic model could create dynamics so complex that we could not distinguish them from random oscillations, (May; 1976). But we can distinguish random dynamics from some chaos-like dynamics, and the hunt for chaos could be very exciting, if most frequently disappointing.

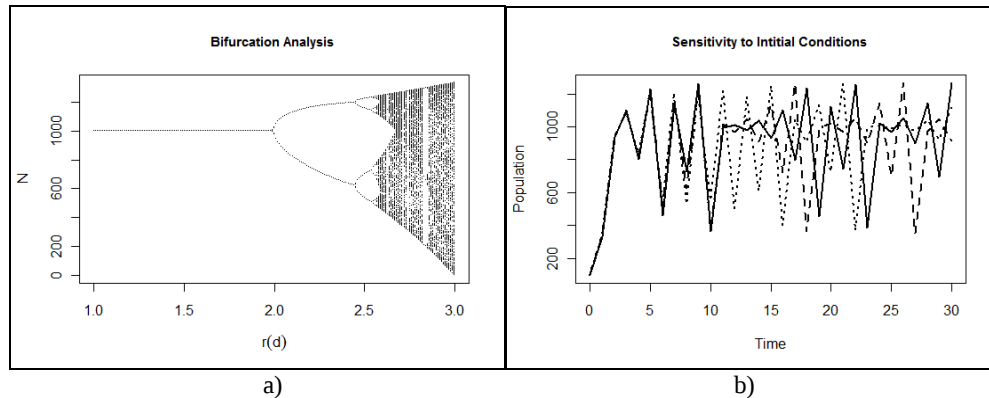


Figure 2.9 Discrete Logistic Bifurcation and sensitivity. The point at which the limit cycle emerges is the bifurcation as shown in figure 2.9a. Figure 2.9b illustrate sensitivity to initial conditions

Chaos implies that the population growth rate exceeds the rate at which the density-dependence feeds back into the process, i.e. the population overcompensates for existing density by either growing too fast or declining too fast, hence overshooting K (Figure 2.10).

The dynamics of a logistic model with τ as the time lag is given by,

$$N_{t+1} = N_t \left[1 + R_0 \left(1 - \frac{N_{t-\tau}}{K} \right) \right]. \quad (2.24)$$

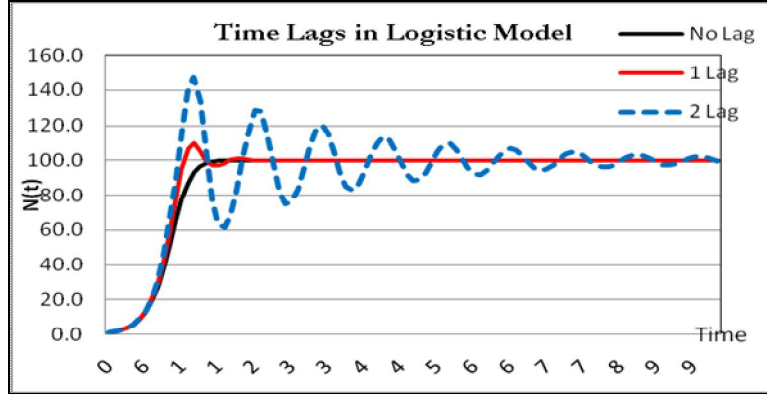


Figure 2.10 Discrete Logistic time lag. The demonstration of the effect of the time lag for the logistic population models

2.5.3 Theta-Logistic Density Dependence

Theta-Logistic population growth is a simple extension of the logistic model that, adds a parameter to increase flexibility and generality (Stevens, 2009).

$$\frac{dN}{dt} = rN \log \left[1 - \left(\frac{N}{K} \right)^\theta \right]. \quad (2.25)$$

When $\theta = 1$, the theta-logistic model reduces to a Logistic population model. The difference in these two models lies in the factor θ which controls how significant the carrying capacity term is. Figure 2.11 illustrates the density dependence (Figure 2.11a), per capita growth rate (Figure 2.11b). The population growth for different values of θ is demonstrated later. For instance, if θ is large ($\theta \gg 1$), then for

- i. $N < K$, the system is going to look like exponential growth for sometime before density dependence sets in.
- ii. $N > K$, the rate of population growth is negative so the population decreases.
- iii. $N = K$, the rate of population growth is zero so the population never remain constant.

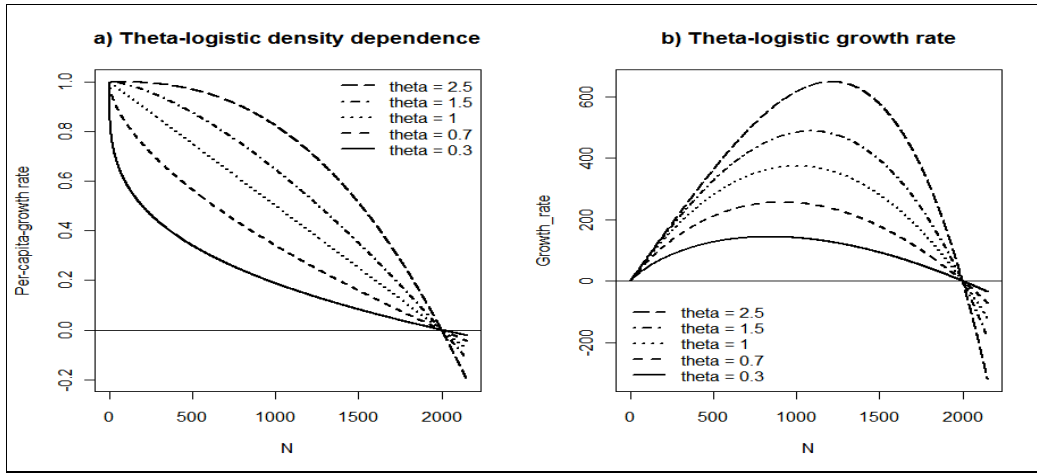


Figure 2.11, The Theta-Logistic population models. The value of θ determines the rate at which density dependence take effect (figure a) and hence affects population growth rate (figure b).

Now, for $\theta \neq 1$, we can find a numerical approximation of the exact solution. We have,

$$\begin{aligned} \frac{N(t+h) - N(t)}{h} &\cong rN(t) \left(1 - (N(t)/K)^\theta\right), \\ N(t+1) - N(t) &\cong rN(t) \left(1 - (N(t)/K)^\theta\right), \\ N(t+1) &\cong N(t) \left(1 + r \left(1 - (N(t)/K)^\theta\right)\right), \end{aligned} \quad (2.26)$$

for $h=1$. Since $e^x = 1 + x + \frac{x^2}{2} + \dots$, it is approximately equal to $1 + x$ by using the Taylor expansion and ignoring terms of order higher than two. Hence,

$$\begin{aligned} N(t+1) &\cong N(t) \exp r \left(1 - (N(t)/K)^\theta\right), \\ N(t+1) &\cong N(t) e^{r \left(1 - (N(t)/K)^\theta\right)}. \end{aligned} \quad (2.27)$$

This gives us a discrete theta-logistic model. If we add a random environmental effect, we have

$$N(t+1) \cong N(t) e^{r \left(1 - (N(t)/K)^\theta\right) + \xi_t}, \quad (2.28)$$

where time series data exist we can determine the kind of density dependence, if any, we can associate with a given wild population dynamics and especially that of the African elephant population. When $\theta > 1$, this weakens density dependence at low N , so the population grows faster than logistic, all else being equal. When $\theta < 1$, this strengthens density dependence at low N , causing the population to grow more slowly than logistic, all else being equal (Figure 2.12).

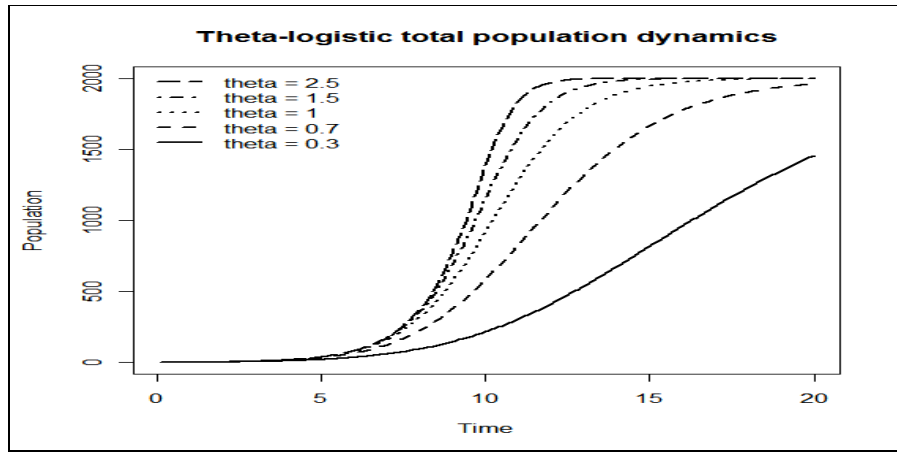


Figure 2.12, Theta Logistic total population dynamics. The shape of the total population growth is determined by the shape parameter θ as evident from figure 2.11, for each of the shape parameter and population growth rate in figure 2.11 above.

Theta-Logistic population growth is a simple extension of the logistic model that, adds a parameter to increase flexibility and generality. To study of population models with process and measurement error we first evaluate if there is any change in the population dynamics by including small variability in the parameters. By introducing an error $\varepsilon \sim N(0,0.125)$ in to a theta logistic population model the dynamics change significantly as demonstrate in Figure (2.13). In this case, the error delays the setting in of density dependence as illustrated in Figure (2.13b) as compared to Figure (2.13a).

$$N_{t+1} = N_t \left(r_0 - (N/K)^\theta \right) + \varepsilon,$$

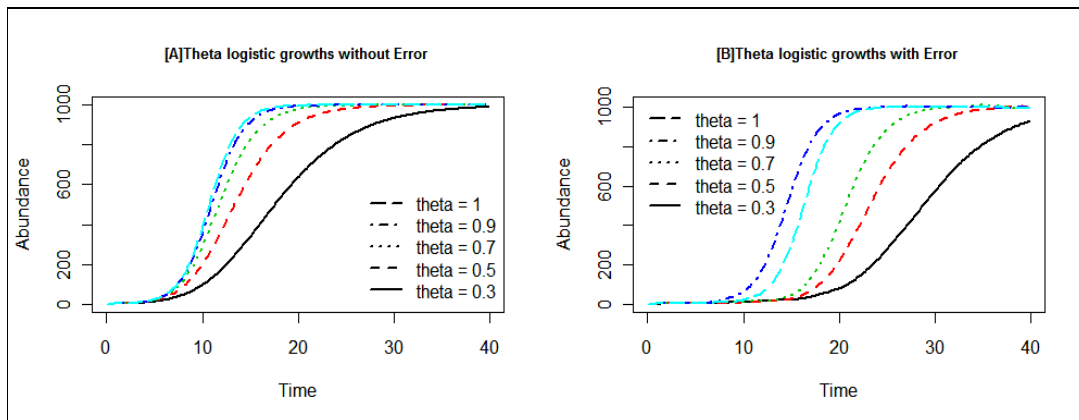


Figure 2.13 Theta logistic with error. Comparison of a theta-logistic population growth models with and without error term.

An example of the application of the Theta-Logistic population growth model is Aanes et al. (2002). They evaluated alternative harvest strategies for a willow ptarmigan (*Lagopus lagopus*) population on a private estate in Sweden. They fitted a theta-logistic model of the form,

$$\log N_{t+1} = \log(N_t - H_t) + \frac{r}{1 - K^{-\theta}} \left[1 - \left(\frac{N_t - H_t}{K} \right)^\theta \right], \quad (2.29)$$

where r is the rate of increase when there is 1 bird in the population, H_t is the harvested proportion and K is carrying capacity.

2.5.4 Ricker Dynamical Model

The Ricker's equation (Ricker 1954) invented this equation to model fishery stocks. It is a discrete population model:

$$N_{t+1} = N_t \exp \left[R_0 \left(1 - \frac{N_t}{K} \right) \right]. \quad (2.30)$$

We note that the density dependence in this model becomes stronger at higher densities, due to the exponential function. The Richards model (e.g. Fowler 1981), the per capita recruitment is

$$R_{t+1} = R_0 \left[1 - \left(\frac{N_t}{K} \right)^m \right], \quad (2.31)$$

with the exponent m changing the shape of the relationship from linear to either concave or convex.

If we substitute $x_t = N_t/K$ in equation $N_{t+1} = N_t \exp(r(1 - N_t/K))$, we obtain the second format.

$$x_{t+1} = g(x_t) = x_t e^{r(1-x_t)}. \quad (2.32)$$

The Ricker model is a limiting case of the Hassell model (Hassel, 1975) which takes the form

$$N_{t+1} = k_1 \frac{N_t}{(1 + k_2 N_t)^c}. \quad (2.33)$$

When $c = 1$, the Hassell model is simply the Beverton–Holt model. In Figure 2.14 we perform comprehensive simulations, and plot the point and periodic attractors. It illustrates of the dynamics of discrete Ricker population model with the attractors shown as a function of growth rate.

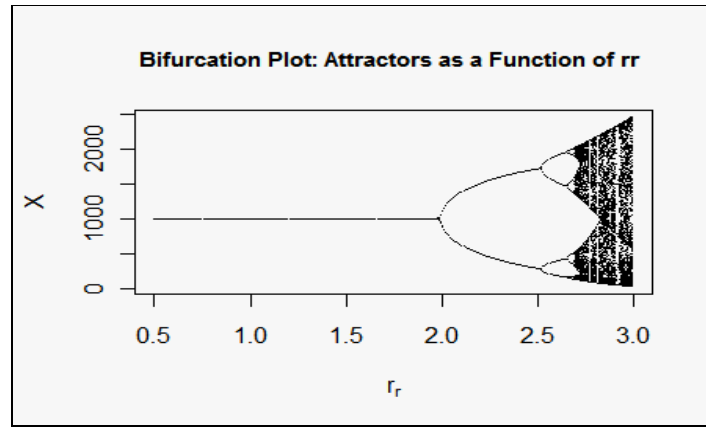


Figure 2.14, Ricker Bifurcation plot. It gives the points at which the limit cycles emerge for a discrete Ricker population model. The figure shows the attractors as a function of growth rate.

The behaviour of many populations cannot be modelled using equation (2.32) alone however, as they are affected by an additional perturbation term u ,

$$x_{t+1} = x_t e^{r(1-x_t)} + u. \quad (2.34)$$

Constant perturbation terms are useful in modelling populations where individuals are either added to or removed from the population at each time step.

- i. $U > 0$, represent immigration to the environment at constant rate, or replenishment in a controlled environment.
- ii. $U < 0$, represent emigration out of the environment at constant rate removal at constant rate, or predation with constant number of predators.

If u_t is a random variable that varies with time due to changes in the environment we acquire a Ricker model with random perturbations

$$x_{t+1} = x_t e^{r(1-x_t)} + u_t. \quad (2.35)$$

A Ricker model with a minor variation to model a declining carrying capacity can be expressed as

$$x_{t+1} = x_t e^{r \left(1 - \frac{x_t}{K(1-\beta)^t} \right)}.$$

Simulated dynamics are illustrated in Figure 2.15 below;

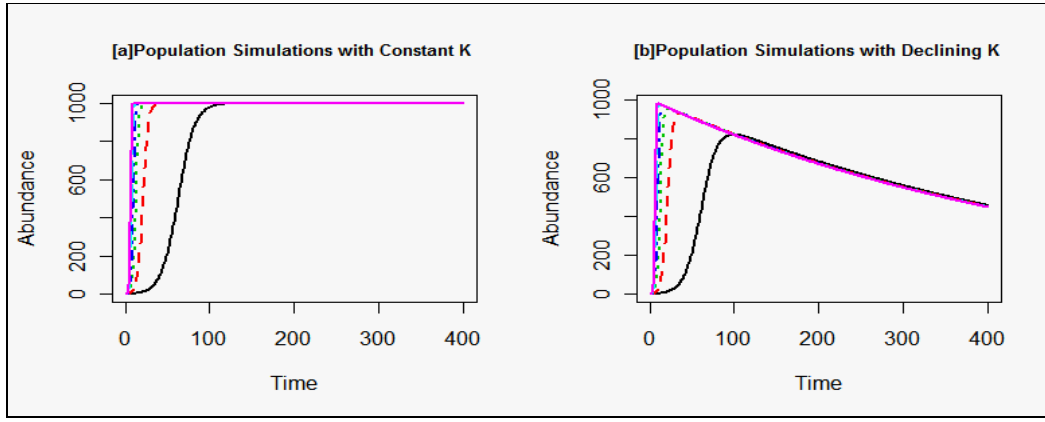


Figure 2.15 A Ricker population model with declining K . Comparison of Ricker population growth models with constant carrying capacity compared with models with declining K .

The modified Ricker model can be used to investigate temporal variation in K the carrying capacity by introducing the parameter β , and a process error, $\varepsilon_p \sim N(0, \sigma_p)$.

$$x_{t+1} = x_t e^{r \left(1 - \frac{x_t}{K(1-\beta)^t} \right) + \varepsilon_p}. \quad (2.36)$$

Simulation of this model dynamics are given in Figure 2.16,

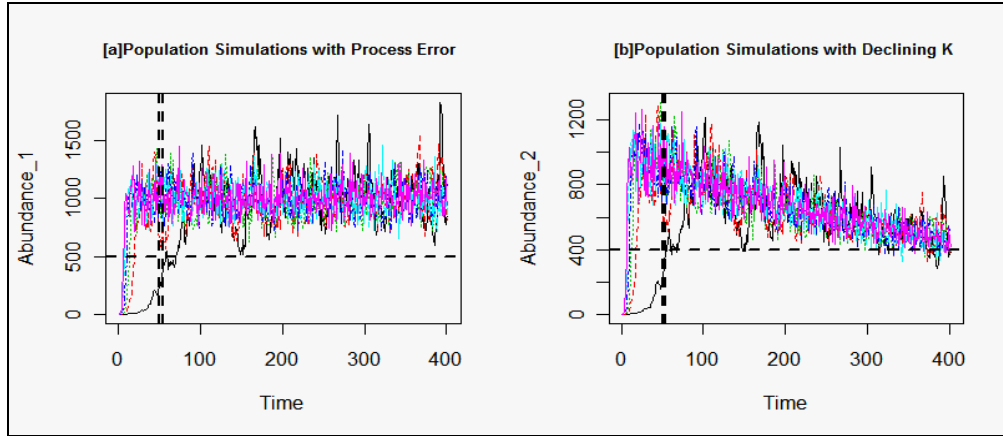


Figure 2.16 Simulated Ricker population models with process error. Figure a shows population growth for Ricker models with process error but constant K while figure b shows the same Ricker models with declining K .

Figure 2.16a) is time series of abundance assuming a process error $\varepsilon_p \sim N(0, 0.125)$ and constant carrying capacity. Figure 2.16b) assumes that, K , the carrying capacity declines at 0.2% per time step. We proceed to add a measurement error to the abundance,

$$x_{t+1} = \left(x_t e^{r \left(1 - \frac{x_t}{K(1-\beta)^t} \right) + \varepsilon_p} \right) e^{\varepsilon_m},$$

where a measurement error $\varepsilon_m \sim N(0, \sigma_m)$ is added to x_t . In this case x_t has a process error as given by equation (2.36) above. We add to x_t a measurement error $\varepsilon_m \sim N(0, 2)$ and generate and plot the new time series in Figure 2.17. The challenge in real data is to quantify and separate process and measurement errors.

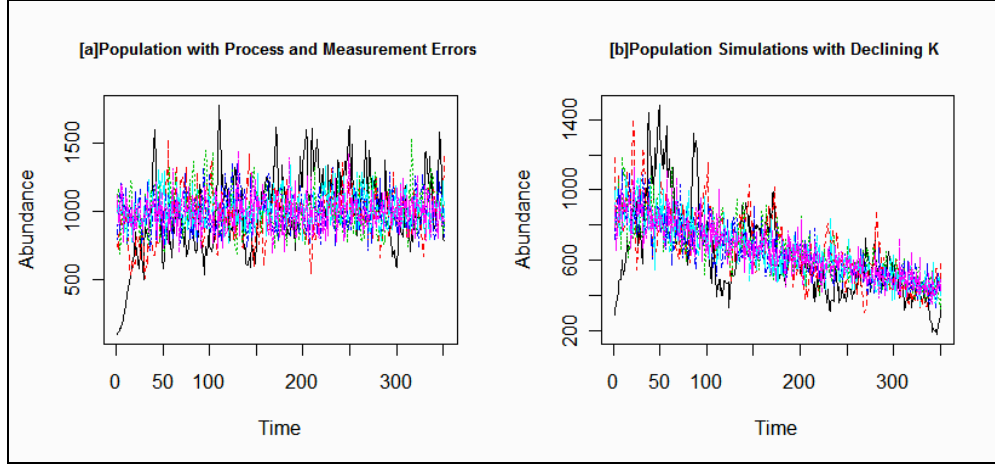


Figure 2.17 Time series with process and measurement errors. Figure a) shows Ricker population growth models with process and measurement error and constant K , while figure b) shows the same Ricker models with declining K .

Process and observation error affect our ability to detect significant temporal trends in the mean population size. As demonstrated by the foregoing simulations of the theta logistic and Ricker model with process and measurement error.

We have also demonstrated the different density independent and density dependent population models by simulating population growths for different parameters. The Per-capita growth rate (pgr) is important in explaining the kind of density dependence of a population dynamics. Knowledge of the shapes of the growth rate and density relationship is required in all areas of population ecology to make projections as to future abundance and population dynamics.

In an exponential growth the growth rate is constant and does not depend on abundance. A more realistic scenario is that of the Logistic growth where the growth rate is a linear function that decreases monotonically with abundance. The relationship between growth rate and N is generally taken to be monotonic and decreasing and can be either concave or convex. Convex relationships $\theta > 1$ in a theta-logistic model imply that growth rate varies little until population size is near carrying capacity, then drops rapidly. Concavity $\theta < 1$ means that growth rate is initially relatively high, so small populations grow quickly, but growth rate then declines rapidly as population size

increases, later flattening out so that the approach to carrying capacity is relatively slow. In the theta-logistic model θ is the parameter determining the curvature.

2.5.5 Differential equation models

Differential equation models of population dynamics were derived by starting from the following simple format

$$\frac{dN(t)}{dt} = \left\{ \begin{array}{l} \text{individual's contribution to} \\ \text{biomass change per unit time} \end{array} \right\} N(t), \quad (2.37)$$

where $N(t)$ denotes the biomass (or population density) of a single species at time t . If the individual's contribution to the change biomass in unit time is denoted by a function say $f(t, N(t))$ defined suitably for all $t > 0$, $N > 0$ then one obtains from (2.37) the Kolmogorov formulation in the form:

$$\frac{dN(t)}{dt} = f(t, N(t))N(t). \quad (2.38)$$

Depending on the population process and ecological assumptions, the form of $f(t, N(t))$ determine the population dynamics. If $f(t, N(t)) \equiv r$ is equivalent to a positive constant r , then we obtain the exponential growth. If $f(t, N(t)) \equiv r - (r/K)N(t)$, we acquire the logistic growth which implies monotonic approach as $t \rightarrow \infty$, of the biomass, to $N(t) = K$, the environmental carrying capacity. If the function $f(t, N(t)) \equiv r - (r/K)N(t - \tau)$, and the delay $\tau > 0$, it leads to Hutchinson's (1948) delay-logistic equation,

$$\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t - \tau)}{K} \right). \quad (2.39)$$

Other forms of $f(t, N(t))$ and delay function assumptions exist which gives non-monotonic dynamics. Volterra's (Volterra, 1926) model of a population which pollutes its environment is given by equation (2.40) below,

$$\frac{dN(t)}{dt} = N(t) \left(r - \frac{rN(t)}{K} - \int_{-\infty}^t H(t-s)F(N(s))ds \right). \quad (2.40)$$

There is an advantage of modelling using the principle of equation (2.37). If the initial conditions are non-negative, the non-negativity of population density $N(t)$ at $t > 0$, follows from the idea that the solution of equation (2.38) is of the form;

$$N(t) = N_0 \exp \left(\int_0^t f(s, N(s))ds \right). \quad (2.41)$$

In modelling elephant population our assumption will be that population change is determined by birth and death, assuming there is no immigration or emigration as in model (2.420).

$$\frac{dN(t)}{dt} = \text{birth rate} - \text{death rate} . \quad (2.42)$$

If for example, there is discrete delay τ in recruitment, equation 2.42 becomes;

$$\frac{dN(t)}{dt} = bN(t - \tau) - dN(t) . \quad (2.43)$$

A continuous distributed where H is the delay kernel would give,

$$\frac{dN(t)}{dt} = b \left(\int_0^\infty H(s)N(t-s)ds \right) - d(N(t)) . \quad (2.44)$$

Some structured population models can be reduced to delay differential equations (Nisbet and Gurney, 1983). There are occasions, however, when this reduction of the structured system does not yield a standard delay differential equation. In such cases, the challenge is to reduce the equation or system of equation into one of the standard forms that can be studied using existing theory.

CHAPTER THREE: METHODOLOGY

3.1 Introduction

In this chapter we give the methods necessary to perform our analysis on population dynamics of elephants. Among the materials discussed include;

- i. Classical time series model: Integrated Autoregressive Moving Average (ARIMA) models with their well established model building procedure are given. An ARIMA model selection criterion is also discussed.
- ii. Structured population models: Methods of analyzing structured population models (SPM) are examined with emphasis on the dominant eigenvalue and eigenvectors, net-productive number, and stable age distribution. The importance of these methods in population management is explained.
- iii. An analytically derivation and application of the filtered, smoothed, and predicted distributions in a Bayesian framework.

We begin with definition of classical time series models whose fitting, diagnosis and forecasting techniques are well established in mathematical literature.

3.2 Time series models

3.2.1 Modeling procedure

Although our model construction adhere to the observation of Thomas et al. (2005) that the process of formulating a model represents an attempt to construct a parsimonious, robust and tractable characterization of the system under study. Effort are made to make the models practical and as representative of the real world as possible. We have made efforts to capture uncertainty in the structure and parameterisation of the model as part of the model fitting. This enables us to capture adequately the nature inherent in the underlying elephant population dynamics. The general modeling procedure used is captured in the following three steps;

- i. Model verification: this is to ensure that the model internal logics work.
- ii. Model calibration: is an attempt to find the best accordance between computed and observed data by verification of the parameters.
- iii. Model validation: consisting of objective test of how well the model fit the data.

For fitting time series model our model building strategy conformed to the Box and Jenkins multistep model-building strategy with iterative three main steps in the process. These steps are, model specification, model fitting, and model diagnostics. In model identification, the classes of models are selected that may be appropriate for a given observed data. We computed different statistics from the data that can be used to evaluate the fit.

In choosing a model, we select the model with the smallest number of parameters that will adequately represent the curve fitted. Model fitting consists of finding the best possible estimates of those unknown parameters within a given model. Model diagnostics is concerned with assessing the quality of the model that one have specified and estimated. How well does the model fit the data? Are the assumptions of the model reasonably well satisfied? If no inadequacies are found, we return to the model specification step. In this way, we cycle through the three steps until, ideally, an acceptable model is found. Model diagnostics will include the analysis of fitted values and the residuals.

3.2.2 ARIMA class of models

Classical time series models have been used in forecasting population growth rate and their volatility. Integrated autoregressive moving average (ARIMA) models with Box et al., (2008) have clear ways of forecasting and quantifying uncertainty in forecasted values. We can consider state space models as part of these models or an extension to cater for specified modelling purposes. Autoregressive moving average $ARMA(p, q)$ processes require the time series to be transformed to a stationary process, but state space models allows for more flexibility.

A time series model can be used to model population dynamics using different approaches including;

- i. Modelling the time series of total population abundance $x_{t+1} = (1 + R_t)x_t$, where R_t is the rate of population change in a time step.
- ii. Modelling the time series of the rate of population change R_t or the change in R_t using $y_t = R_t - R_{t-1}$. The discrete population rates of change, R_t , are approximately equal to the log transformed series $r_t = \ln x_t - \ln x_{t-1}$. The continuous exponential model growth rate is given by r_t .

Time series ARIMA models can be used in each of the two cases. A time series $\{x_t; t = 0, \pm 1, \pm 2, \dots\}$ is $ARMA(p, q)$ if it is stationary and

$$x_t = \phi_1 x_{t-1} + \dots + \phi_p x_{t-p} + \omega_t + \theta_1 \omega_{t-1} + \dots + \theta_q \omega_{t-q}, \quad (3.1)$$

with $\phi_p \neq 0$, $\theta_q \neq 0$ and $\sigma_\omega^2 > 0$. The parameters p and q are called the autoregressive and the moving average orders, respectively. If x_t has a nonzero mean μ , we set $\alpha = \mu(1 - \phi_1 - \dots - \phi_p)$ and write the model as

$$x_t = \alpha + \phi_1 x_{t-1} + \dots + \phi_p x_{t-p} + \omega_t + \theta_1 \omega_{t-1} + \dots + \theta_q \omega_{t-q} \quad (3.2)$$

where, $\{\omega_t; t = 0, \pm 1, \pm 2, \dots\}$ is a Gaussian white noise sequence. In general the parameters in an $ARMA(p, q)$ can be summarized in the vector, $\theta = (\mu, p, q, \phi_1, \phi_2, \dots, \phi_p, \theta_1, \theta_2, \dots, \theta_q, \sigma_\omega^2)'$. An $ARMA(p, q)$ model becomes an autoregressive ($AR(p)$) model or moving average ($MA(q)$) if order $q = 0$ or $p = 0$ respectively. In general the parameters in a $AR(p)$ can be summarized in the vector, $\theta = (\mu, p, \phi_1, \phi_2, \dots, \phi_p, \sigma_\omega^2)'$ with $\phi_p \neq 0$, while the moving average parameters in a $MA(q)$ can be summarized in the vector $\theta = (\mu, q, \theta_1, \theta_2, \dots, \theta_q, \sigma_\omega^2)'$, with $\theta_q \neq 0$.

ARIMA models are useful in modelling series with non-stationary trend component and a zero-mean stationary component. A process x_t is said to be $ARMA(p, q)$ if $\nabla^d x_t = (1 - B)^d x_t$ is $ARMA(p, q)$, and we write the model as

$$\phi(B)(1 - B)^d x_t = \theta(B)\omega_t \quad (3.3)$$

If $E[\nabla^d x_t] = \mu$, we write model as

$$\phi(B)(1 - B)^d x_t = \alpha + \theta(B)\omega_t,$$

where $\alpha = \mu(1 - \phi_1 - \phi_2 - \dots - \phi_p)$. In an $ARIMA(p, d, q)$, p indicates the order of the autoregressive part, d indicates the amount of differencing, and q indicates the order of the moving average part. If the original series is stationary, $d = 0$ and the ARIMA models reduce to the ARMA models. We fit ARIMA and ARMA models to population abundance data and then use the model to forecast future abundance in chapter four.

3.2.3 Steps in the ARIMA model building

Model Identification

The first step is to produce a time-series of X_t against t and examine the plot to identify obvious trends, seasonal components, and outliers. Determine whether the series is stationary or not by considering the graph of sample Autocorrelation Function (ACF).

We can use the graph of the ACF and the sample Partial Autocorrelation Function (PACF) to determine the model which a population time series process can be summarized. The behaviour of the ACF and PACF for causal and invertible ARMA models is as in Table 3.1.

Table 3.1 The behaviour of the ACF and PACF for ARMA models

	$AR(p)$	$MA(q)$	$ARMA(p, q)$
ACF	Tails off	Cuts off after lag q	Tails off
PACF	Cuts off after lag p	Tails off	Tails off

If the series is not stationary, it can often be converted to a stationary series by differencing. That is, the original series is replaced by a series of differences. An ARMA model is then specified for the differenced series. Differencing is done until a plot of the data indicates the series varies about a fixed level, and the graph of ACF either cuts off fairly quickly or dies down fairly quickly. By evaluating the behavior of the ACF and PACF of the data or the differenced series we can select the most appropriate model by use of characteristics given in Table 3.1.

Model Parameter Estimation

Once a tentative model has been selected, the parameters for that model must be estimated. The parameters in ARIMA models are estimated by minimizing the sum of squares of the fitting errors. Once the least squares estimates and their standard errors are determined, p-values can be constructed and used to determine whether a selected parameter is significant or not. Parameters that are judged significantly different from zero are retained in the fitted model while parameters that are not significant are dropped from the model.

Model Checking

In this step, model must be checked for adequacy by considering the properties of the residuals, whether the residuals from an ARIMA model must has the normal distribution and should be random. An overall check of model adequacy is provided by the Ljung-Box Q – statistic (Ljung and Box; 1978). The test statistic Q is,

$$Q_m = n(n+2) \sum_{h=1}^m \frac{r_h^2(e)}{n-h} \sim \chi_{m-h}^2, \quad (3.4)$$

where $r_h(e)$ is the residual autocorrelation at lag h , n is the number of residuals and m is the number of time lags includes in the test. Under the hypothesis of model adequacy, asymptotically ($n \rightarrow \infty$), $Q_m \sim \chi_{m-p-q}^2$. Thus, we would reject the null hypothesis at level α if the value of Q exceeds the $(1-\alpha)^{th}$ quintile of the $Q \sim \chi_{m-p-q}^2$. If the p-value associated with the

Q statistic is small (probability value $< \alpha$), the model is considered inadequate. The analyst should consider a new or modified model and continue the analysis until a satisfactory model has been determined.

Moreover, we can check the properties of the residual with the following techniques:

- i. We can check about the randomness of the residuals by considering the graph of ACF and PACF of the residual. The individual residual autocorrelation should be small and generally within $\pm 2/\sqrt{n}$ of zero.
- ii. Model evaluation criteria can also be performed using calculated values like the Akaike's Information Criterion (AIC);

$$AIC = \ln \hat{\sigma}_k^2 + \frac{n+2k}{n}. \quad (3.5)$$

In the case of regression model with k coefficients (number of parameters in the model), n is the sample size and the maximum likelihood estimator for the variance given by,

$$\sigma_k^2 = \frac{RSS_k}{n}.$$

In this case RSS_k denotes the residual sum of squares under the model with k regression coefficients. Then, Akaike (1973) suggested measuring the goodness of fit of a model by balancing the error of the fit against the number of parameters in the model.

3.2.3.4 Forecasting with the ARIMA Models

When an $ARIMA(p, d, q)$ has been selected and parameters estimated, it can then be used for forecasting. The more accurate the population forecasts are, the more utility is likely to be gained from acting on them.

Although ARIMA models involve differences, forecasts for the original series can be always computed directly from the fitted model. The iterative ARIMA modeling strategy can be captured as in the Figure (3.1) below. The process of fitting ARIMA models can be performed using R software (Venables and Ripley, 2002).

3.3 Bootstrapping

Bootstrapping is useful where the time series of population abundance estimate are few and fitting ARIMA models is not viable. In bootstrapping we calculate the observed parameters of interest with a given model and data. We resample the data or calculated values with replacement to create a large number the parameters and then determine the distribution of the parameters.

In the case of a population modelled using $x_{t+1} = (1 + R_t)x_t$ or $r_t = \ln x_t - \ln x_{t-1}$ we calculate R_t or r_t for the available data. Bootstrapping enables us to create large number of observation of R_t or r_t from a small set of real data.

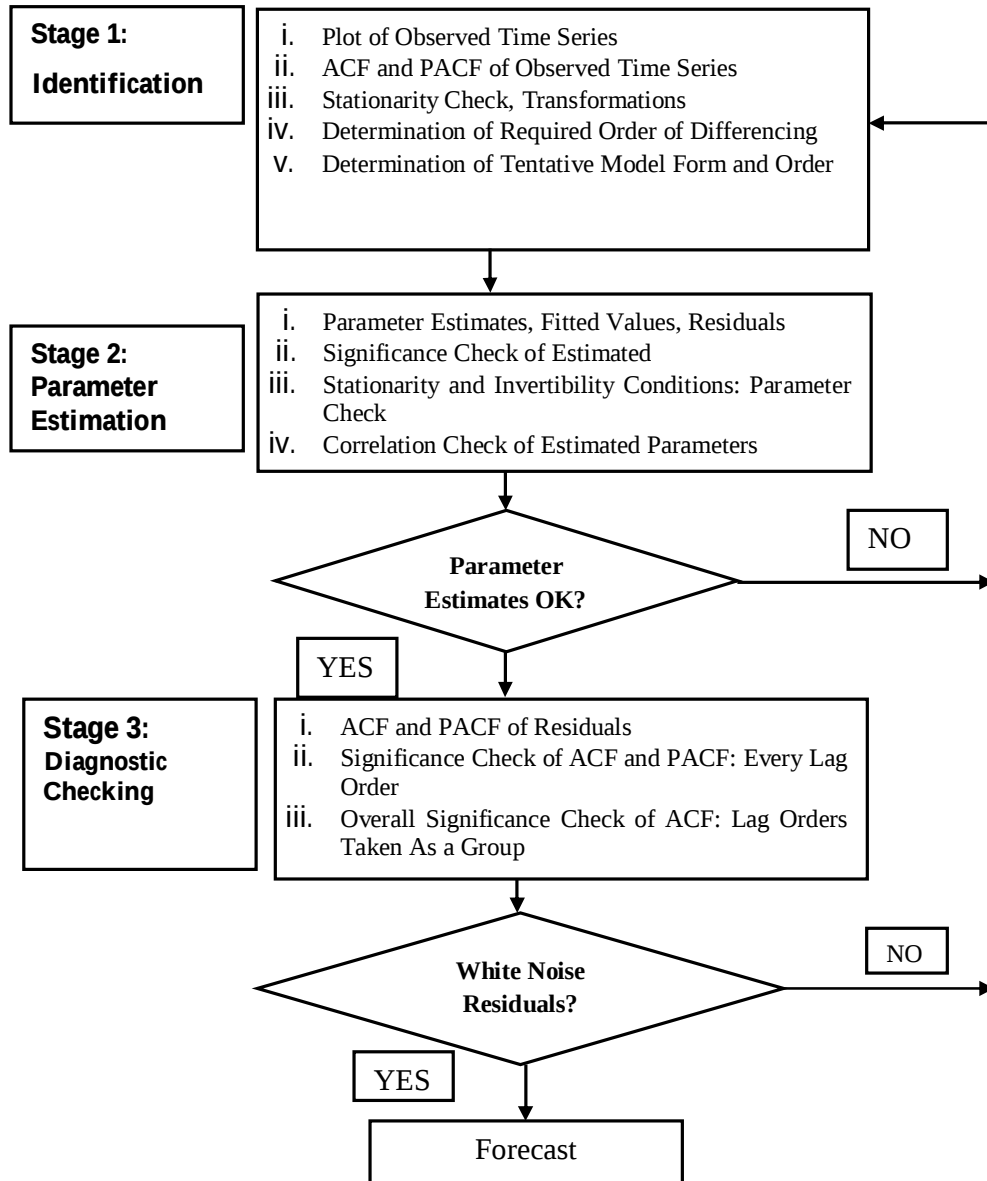


Figure 3.1 Flowchart of the ARIMA methodology. The three steps of fitting a ARIMA model are Model identification, model fitting and model diagnostics.

It is then possible to determine measures of location, spread and a confidence interval for the bootstrapped parameter R_t , r_t or the population projections performed using the values. Population trend predictions acquired through bootstrapping thus presumes that the population vital parameters and the environmental conditions will remain relatively similar to those of the period of the data used.

3.4 Bayesian Inference

In Bayesian approach to statistical models all unknowns, and in particular unknown parameters are considered to be random variables and their probability distributions specify our beliefs about their likely values. Estimation, prediction, model selection, and uncertainty analysis are implemented by using Bayes's theorem to update our beliefs as new data are observed. With the increasing power of computing Bayesian techniques are often the most satisfactory way to compute estimates for complex models. In a time series scenario the vector parameter θ , could include the classical unknown parameters, the white noise parameter and the future values of the series being forecast.

Bayesian inference on θ consists of computing its conditional distribution given the sampling results. Suppose that, based on our knowledge of the problem, we can assign a conditional distribution $f(y_T | \theta)$ for Y_T given θ , the likelihood, and a prior distribution $f(\theta)$, expressing our uncertainty on the parameter θ . The likelihood $f(y_T | \theta)$ is the conditional distribution of the data given θ .

Many good statistical procedures employ values of the population parameters that 'best' explain the observed data. One meaning of best is to select the parameters values that maximize the joint density evaluated at the observations. This technique is called the maximum likelihood estimation, and the maximizing parameters called maximum likelihood estimators.

Suppose we have a series of T observations $y_1, y_2, \dots, y_T$. We label the first t observations as $y_{1:t}$, so subscript t denotes the particular observation of y at time t , and subscript t denotes the series of observations up to and including time T , i.e. $(y_1, y_2, \dots, y_T)$.

The likelihood of a possible choice of parameters θ is defined as the probability that if those were the real parameters, they would have produced the observed data. This is written as

$$L(\theta | y_T) = f(y_T | \theta).$$

Here “ L ” stands for likelihood and “ f ” for probability. The difference between them is that L is viewed as a function of the parameters given the data and f is viewed as a function of the data given the parameters. For a time series, the likelihood can be conveniently expressed recursively as

$$L(\theta | y_T) = f(y_1 | \theta) \prod_{t=2}^T f(y_t | y_{1:t-1}, \theta). \quad (3.6)$$

An important step Bayesian inference is the use of Bayes's theorem to computing the conditional distribution of θ given the data. The posterior distribution combines the prior knowledge about θ with the information in the data. Upon observing $Y_T = y_T$, we can use a generalization of the elementary Bayes' theorem to compute the conditional density of θ given $y_T = \{y_1, y_2, \dots, y_T\}$.

$$f(\theta | y_T) = \frac{f(y_T | \theta) f(\theta)}{f(y_T)}, \quad (3.7)$$

where $f(y_T)$ is the marginal distribution of Y_T ,

$$f(y_T) = \int f(y_T | \theta) f(\theta) d\theta.$$

Bayesian estimation and uncertainty analysis are based upon the posterior. By sampling from the posterior we can acquire estimates of mean and measures of uncertainty. The expectation of the posterior is referred to as posterior expectation is given by

$$E[\theta | y_T] = \int \theta f(\theta | y_T) d\theta = \frac{\int \theta f(\theta) f(y_T | \theta) d\theta}{\int f(\theta) f(y_T | \theta) d\theta}. \quad (3.8)$$

In forecasting we are interested in the value of a future observation Y_s for $s > T$ given the data $\{y_1, y_2, \dots, y_T\}$. The predictive distribution is given by;

$$f(y_s | y_T) = \int f(y_s, \theta | y_T) f(\theta) d\theta = \int f(y_s | y_T, \theta) f(\theta | y_T) d\theta. \quad (3.9)$$

The joint predictive probability distribution of K future values is given by,

$$f(y_{T+1}, y_{T+2}, \dots, y_{T+K} | y_T) = \int f(\theta | y_T) \prod_{k=1}^K f(y_{T+k} | y_{T+K-1}, \theta) d\theta. \quad (3.10)$$

If we are able to specify the probability law of the time series Y_T , we know the joint densities $f(y_1, \dots, y_T)$ for any $T \geq 1$, the one-step-ahead predictive density is,

$$f(y_{T+1} | y_T) = \frac{f(y_{1:T+1})}{f(y_T)}.$$

In practice, specifying the densities $f(y_T)$ directly is not easy, and one finds it convenient to make use of parametric models,

$$f(y_T) = \int f(y_T | \theta) f(\theta) d\theta.$$

In particular, in many applications it is reasonable to assume that $y_1, y_2, \dots, y_T$ are conditionally independent and identically distributed (*iid*) given θ ,

$$f(y_{1:T} | \theta) = \prod_{t=1}^T f(y_t | \theta). \quad (3.11)$$

If $y_1, y_2, \dots, y_T$ are only conditionally independent then the observations $y_1, y_2, \dots, y_T$ provide us information about the unknown value of θ and, through θ , on the value of the next observation y_{T+1} . Thus, y_{T+1} depends, in a probabilistic sense, on the past observations $y_1, y_2, \dots, y_T$. The predictive density

$$\begin{aligned} f(y_{T+1} | y_{1:T}) &= \int f(y_{T+1}, \theta | y_T) d\theta, \\ &= \int f(y_{T+1} | \theta, y_T) f(\theta | y_T) d\theta, \\ &= \int f(y_{T+1} | \theta) f(\theta | y_T) d\theta, \end{aligned} \quad (3.12)$$

the last equality following from the assumption of conditional independence, where $f(\theta | y_T)$ is the posterior density of θ , conditionally on the data $y_1, y_2, \dots, y_T$. As we have seen, the posterior density can be computed by,

$$f(\theta | y_T) = \frac{f(y_T | \theta) f(\theta)}{f(y_T)} \propto \prod_{t=1}^T f(y_t | \theta) f(\theta). \quad (3.13)$$

The marginal density $f(y_T)$ does not depend on θ , having the role of normalizing constant, so that the posterior is proportional to the product of the likelihood and the prior. The posterior distribution can be computed recursively, at time $(T-1)$, the information available about θ is described by the conditional density,

$$\begin{aligned} f(\theta | y_{1:T-1}) &\propto \prod_{t=1}^{T-1} f(y_t | \theta) f(\theta). \\ f(\theta | y_{1:T-1}, y_T) &\propto f(\theta | y_{1:T-1}) f(y_T | \theta) \propto \prod_{t=1}^{T-1} f(y_t | \theta) f(\theta) f(y_T | \theta). \end{aligned} \quad (3.14)$$

The recursive structure of the posterior will play a crucial role when we study state space models and the Kalman filter.

Model uncertainty can be captured by extending equation (3.10) to cater for uncertainty in a set of m models. If model m has θ_m associated vector of parameters, the likelihood for model m is $f(y_T | \theta_m, m)$, the prior distribution for θ_m is $f(\theta_m | m)$ and the posterior distribution is

$$f(\theta_m | y_T, m) = \frac{f(y_T | \theta_m, m) f(\theta_m, m)}{f(y_T | m)}, \quad (3.15)$$

where $f(y_{(T)} | m)$ is normalizing constant known as the marginal likelihood for model m given by

$$f(y_T | m) = \int f(\theta_m | m) f(y_T | \theta_m, m) d\theta. \quad (3.16)$$

The posterior probability of m given data is,

$$f(m | y_T) = \frac{f(y_T | m) f(m)}{f(y_T)}. \quad (3.17)$$

The predictive distribution for population forecasts in the presence of model uncertainty is,

$$\begin{aligned} f(y_{T+1}, y_{T+2}, \dots, y_{T+K} | y_T) &= \sum_{m=1}^M f(m | y_T) f(y_{T+1}, \dots, y_{T+K} | y_T, m), \\ &= \sum_{m=1}^M f(m | y_T) f(\theta_m | y_T, m) \prod_{k=1}^K f(y_{T+K} | y_{T+K-1}, \theta_m, m) d\theta. \end{aligned} \quad (3.18)$$

This is the average of predictive distributions for individual models weighted by their posterior probabilities, $f(m | y_{(T)})$. Simulation techniques such as MCMC help us to compute, for example, the expectations of the posterior and predictive distribution in equation (3.7), (3.10), (3.15) and (3.18), especially when θ is multivariate parameter (Abel, *et al.* 2010).

Results from time series models are given in chapter four of this work. Later in section 3.7 we discuss a Bayesian framework for structured population dynamics which enables us derive the sub-process stochastic matrix model for elephant population in chapter five.

3.5 Filtered, smoothed and predicted recursions.

3.5.1 State space models definitions

Generally the state space model consists of an $\mathfrak{R}_p$ valued time series $\{\theta_t, t = 1, 2, \dots\} \equiv \{\theta_1, \theta_2, \dots\}$ and an $\mathfrak{R}_p$ valued time series $\{Y_t, t = 1, 2, \dots\} \equiv \{y_1, y_2, \dots\}$, satisfying the following assumptions.

- i. $\{\theta_t, t = 1, 2, \dots\}$ is a Markov chain.
- ii. Conditionally on $\{\theta_t, t = 1, 2, \dots\}$, the $\{Y_t, t = 1, 2, \dots\}$ are independent and Y_t depends on θ_t only.

The consequence of i) and ii) is that a state space model is completely specified by the initial distribution $f(\theta_0)$ and the conditional densities $f(\theta_t | \theta_{t-1})$ and $f(y_t | \theta_t)$, $t \geq 1$.

3.5.2 Filtering recursion.

The filtering approach to inference would be appropriate for population monitoring schemes that wish to obtain updated estimates of the current population as soon as new observations are made. The filtering distribution at time t is the conditional distribution of state θ_t given the observations $y_{1:t}$. For a general state space model the following statements hold (Petrus et al., 2009).

- a) The one-step-ahead predictive density for the states can be computed from the filtered density as;

$$\begin{aligned} f(\theta_t | y_{1:t-1}) &= \int f(\theta_{t-1}, \theta_t | y_{1:t-1}) d\theta_{t-1}, \\ &= \int f(\theta_t | \theta_{t-1}, y_{1:t-1}) f(\theta_{t-1} | y_{1:t-1}) d\theta_{t-1}, \\ &= \int f(\theta_t | \theta_{t-1}) f(\theta_{t-1} | y_{1:t-1}) d\theta_{t-1}. \end{aligned} \quad (3.19)$$

- b) The one-step-ahead predictive density for the observations can be computed from the predictive density for the states. Since Y_t is conditionally independent of Y_{t-1} given θ_t .

$$\begin{aligned} f(y_t | y_{1:t-1}) &= \int f(y_t, \theta_t | y_{1:t-1}) d\theta_t, \\ &= \int f(y_t | \theta_t, y_{1:t-1}) f(\theta_t | y_{1:t-1}) d\theta_t, \\ &= \int f(y_t | \theta_t) f(\theta_t | y_{1:t-1}) d\theta_t. \end{aligned} \quad (3.20)$$

- c) The filtering density can be computed from the Bayes' rule and the conditional independence of Y_t and $Y_{1:t-1}$ given θ_t , as

$$f(\theta_t | y_{1:t}) = \frac{f(\theta_t | y_{1:t-1}) f(y_t | \theta_t, y_{1:t-1})}{f(y_t | y_{1:t-1})} = \frac{f(\theta_t | y_{1:t-1}) f(y_t | \theta_t)}{f(y_t | y_{1:t-1})}. \quad (3.21)$$

- d) The k – steps ahead predictive distributions for the state and for the observation is computed recursively by,

$$f(\theta_{t+k} | y_{1:t}) = \int f(\theta_{t+k} | \theta_{t+k-1}) f(\theta_{t+k-1} | y_{1:t}) d\theta_{t+k-1}, \quad (3.22)$$

$$f(y_{t+k} | y_{1:t}) = \int f(y_{t+k} | \theta_{t+k}) f(\theta_{t+k} | y_{1:t}) d\theta_{t+k}. \quad (3.23)$$

Here $f(\theta_t | y_{1:t})$ summarizes the information contained in the past observations $y_{1:t}$, which is sufficient for predicting Y_{t+k} , for any $k > 0$.

3.5.3 Kalman Filter for DLM

Consider the DLM,

$$\begin{aligned}\theta_0 &\sim N_p(m_0, C_0), \\ Y_t &= F_t \theta_t + v_t, \quad v_t \sim N_m(0, V_t), \quad t \geq 1, \\ \theta_t &= G_t \theta_{t-1} + w_t, \quad w_t \sim N_p(0, W_t), \quad t \geq 1.\end{aligned}\tag{3.24}$$

Let $\theta_{t-1} | y_{1:t-1} \sim N(m_{t-1}, C_{t-1})$, then:

- i. The one-step-ahead predictive distribution of θ_t given $y_{1:t-1}$ is Gaussian, with parameters

$$\begin{aligned}a_t &= E(\theta_t | y_{1:t-1}) = G_t m_{t-1}, \\ R_t &= \text{Var}(\theta_t | y_{1:t-1}) = G_t C_{t-1} G_t' + W_t.\end{aligned}$$

- ii. The one-step-ahead predictive distribution of Y_t given $y_{1:t-1}$ is Gaussian, with parameters

$$\begin{aligned}f_t &= E(Y_t | y_{1:t-1}) = F_t a_t, \\ Q_t &= \text{Var}(Y_t | y_{1:t-1}) = F_t R_t F_t' + V_t.\end{aligned}\tag{3.25}$$

- iii. The filtering distribution of θ_t given $y_{1:t}$ is Gaussian, with parameters

$$\begin{aligned}m_t &= E(\theta_t | y_{1:t}) = a_t + R_t F_t' Q_t^{-1} e_t, \\ C_t &= \text{Var}(\theta_t | y_{1:t}) = R_t - R_t F_t' Q_t^{-1} F_t R_t,\end{aligned}$$

where $e_t = Y_t - f_t$ is the forecast error.

For the k -steps-ahead forecasts, since all the forecast distributions are Gaussian, it is enough to compute their means and variances. For $k \geq 1$, define

$$\begin{aligned}a_t(k) &= E(\theta_{t+k} | y_{1:t}), \\ R_t(k) &= \text{Var}(\theta_{t+k} | y_{1:t}), \\ f_t(k) &= E(Y_{t+k} | y_{1:t}), \\ Q_t(k) &= \text{Var}(Y_{t+k} | y_{1:t}).\end{aligned}\tag{3.26}$$

For a DLM, let $a_t(0) = m_t$ and $R_t(0) = C_t$. Then, for $k \geq 1$, the following statements hold.

- i. The distribution of θ_{t+k} given $y_{1:t}$ is Gaussian, with

$$\begin{aligned}a_t(k) &= G_{t+k} a_{t,k-1}, \\ R_t(k) &= G_{t+k} R_{t,k-1} G_{t+k}' + W_{t+k}.\end{aligned}$$

- ii. The distribution of Y_{t+k} given $y_{1:t}$ is Gaussian, with

$$f_t(k) = F_{t+k} a_t(k),$$

$$Q_t(k) = F_{t+k} R_t(k) F'_{t+k} + V_t.$$

For $k > 1$,

$$\begin{aligned} a_t(k) &= E(\theta_{t+k} | y_{1:t}) = E(E(\theta_{t+k} | y_{1:t}, \theta_{t+k-1}) | y_{1:t}), \\ &= E(G_{t+k} \theta_{t+k-1} | y_{1:t}) = G_{t+k} a_{t,k-1}, \\ R_t(k) &= \text{Var}(\theta_{t+k} | y_{1:t}) = \text{Var}(E(\theta_{t+k} | y_{1:t}, \theta_{t+k-1}) | y_{1:t}) \\ &\quad + E(\text{Var}(\theta_{t+k} | y_{1:t}, \theta_{t+k-1}) | y_{1:t}), \\ &= G_{t+k} R_{t,k-1} G'_{t+k} + W_{t+k}. \end{aligned} \quad (3.27)$$

$$\begin{aligned} f_t(k) &= E(Y_{t+k} | y_{1:t}) = E(E(Y_{t+k} | y_{1:t}, \theta_{t+k}) | y_{1:t}), \\ &= E(F_{t+k} \theta_{t+k} | y_{1:t}) = F_{t+k} a_t(k), \\ Q_t(k) &= \text{Var}(Y_{t+k} | y_{1:t}) = \text{Var}(E(Y_{t+k} | y_{1:t}, \theta_{t+k}) | y_{1:t}) \\ &\quad + E(\text{Var}(Y_{t+k} | y_{1:t}, \theta_{t+k}) | y_{1:t}), \\ &= F_{t+k} R_t(k) F'_{t+k} + V_{t+k}. \end{aligned}$$

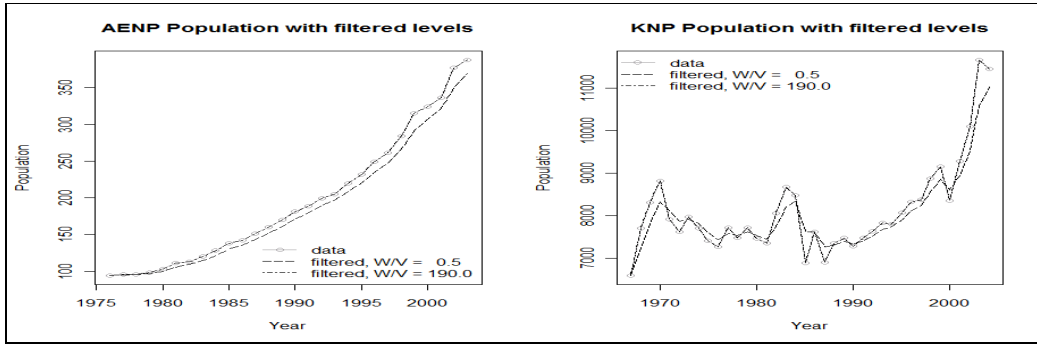


Figure 3.5 Elephant population with filtered values. Determining the unobserved signal x_t given data y_s with $s = t$

If we select a dynamic model with maximum likelihood estimators ratio of $W/V = 0.5$ or $W/V = 190$, the filtered values are almost equal to the observed values for $W/V = 190$. In Figure 3.5 the ratio of W/V determines how sensitive the state prior-to-posterior updating is to unexpected observations.

3.5.4 Smoothing recursion

In time series analysis one often has observations on y_t for a certain period, $t = 0, 1, 2, \dots, T$, and wants to retrospectively reconstruct the behaviour of the system, to study physical phenomenon underlying the observations. In this case, one uses a backward-recursive algorithm to compute the conditional distributions of θ_t given $Y_{1:T}$, for any $t < T$, starting from the filtering distribution $f(\theta_T | Y_{1:T})$ and estimating backward all the states' history.

The smoothing distribution at time $t < T$ is the conditional distribution of $\theta_{0:t}$ given $y_{1:t}$, or sometimes, any of its marginals. Smoothing and the smoothed distribution of past state of the population conditional on all the observed data up to the current time period t is useful when retrospective investigation of a population is the object of inference. For a general state space model;

- a) Conditional on $y_{1:T}$, the state sequence $(\theta_0 \dots \theta_T)$ has backward transition probabilities given by

$$f(\theta_t | \theta_{t+1}, y_{1:T}) = \frac{f(\theta_{t+1} | \theta_t) f(\theta_t | y_{1:t})}{f(\theta_{t+1} | y_{1:t})}.$$

We note that θ_t and $Y_{t+1:T}$ are conditionally independent given θ_{t+1} . Moreover, θ_{t+1} and $Y_{1:t}$ are conditionally independent given θ_t . Using the Bayes formula, one has

$$\begin{aligned} f(\theta_t | \theta_{t+1}, y_{1:T}) &= f(\theta_t | \theta_{t+1}, y_{1:t}), \\ &= \frac{f(\theta_t | y_{1:t}) f(\theta_{t+1} | \theta_t, y_{1:t})}{f(\theta_{t+1} | y_{1:t})}, \\ &= \frac{f(\theta_t | y_{1:t}) f(\theta_{t+1} | \theta_t)}{f(\theta_{t+1} | y_{1:t})}. \end{aligned} \quad (3.28)$$

- b) The smoothing distributions of θ_t given $y_{1:T}$ can be computed according to the following backward recursion in t , starting from $f(\theta_T | y_{1:T})$, as

$$f(\theta_t | y_{1:T}) = f(\theta_t | y_{1:t}) \int \frac{f(\theta_{t+1} | \theta_t)}{f(\theta_{t+1} | y_{1:t})} f(\theta_{t+1} | y_{1:t}) d\theta_{t+1}.$$

Marginalizing $f(\theta_t, \theta_{t+1} | y_{1:T})$ with respect to θ_{t+1} gives,

$$\begin{aligned} f(\theta_t | y_{1:T}) &= \int f(\theta_t, \theta_{t+1} | y_{1:T}) d\theta_{t+1}, \\ &= \int f(\theta_{t+1} | y_{1:t}) f(\theta_t | \theta_{t+1}, y_{1:t}) d\theta_{t+1}, \\ &= \int f(\theta_{t+1} | y_{1:t}) \frac{f(\theta_{t+1} | \theta_t) f(\theta_t | y_{1:t})}{f(\theta_{t+1} | y_{1:t})} d\theta_{t+1}, \\ &= f(\theta_t | y_{1:t}) \int f(\theta_{t+1} | \theta_t) \frac{f(\theta_{t+1} | y_{1:t})}{f(\theta_{t+1} | y_{1:t})} d\theta_{t+1}. \end{aligned} \quad (3.29)$$

Figure 3.6a below illustrates the KNP elephant population abundance with the smoothed levels. Smoothing refers to determining the unobserved signal x_t given data y_s with $s > t$. Figure 3.6b smoothed levels for AENP with 95% confidence intervals plots.

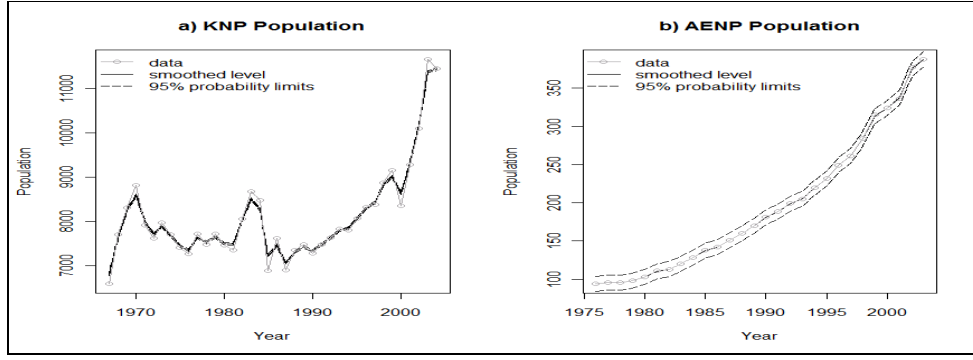


Figure 3.6 Elephant population with smoothing level and 95% confidence. Determining the unobserved signal x_t given data y_s with $s > t$.

Using simulated maximum likelihood estimates of $V = 0.181$ and $W = 5.71$ in a DLM we acquired the smoothed levels as in Figure 3.6.

3.5.5 Forecasting recursion

The goal is to make inference on future states of the population given data up to current state. For a general state space model defined in section 3.5.1 and any $k > 0$,

- i. The k – steps-ahead forecast distribution of the state is

$$f(\theta_{t+k} | y_{1:t}) = \int f(\theta_{t+k} | \theta_{t+k-1}) f(\theta_{t+k-1} | y_{1:t}) d\theta_{t+k-1}.$$

Using the conditional independence of the model:

$$\begin{aligned} f(\theta_{t+k} | y_{1:t}) &= \int f(\theta_{t+k}, \theta_{t+k-1} | y_{1:t}) d\theta_{t+k-1} \\ &= \int f(\theta_{t+k} | \theta_{t+k-1}, y_{1:t}) f(\theta_{t+k-1} | y_{1:t}) d\theta_{t+k-1} \\ &= \int f(\theta_{t+k} | \theta_{t+k-1}) f(\theta_{t+k-1} | y_{1:t}) d\theta_{t+k-1}. \end{aligned} \quad (3.30)$$

- ii. The k – steps-ahead forecast distribution of the observation is

$$\begin{aligned} f(y_{t+k} | y_{1:t}) &= \int f(y_{t+k} | \theta_{t+k}) f(\theta_{t+k} | y_{1:t}) d\theta_{t+k} \\ f(y_{t+k} | y_{1:t}) &= \int f(y_{t+k}, \theta_{t+k} | y_{1:t}) d\theta_{t+k} \\ &= \int f(y_{t+k} | \theta_{t+k}, y_{1:t}) f(\theta_{t+k} | y_{1:t}) d\theta_{t+k} \\ &= \int f(y_{t+k} | \theta_{t+k}) f(\theta_{t+k} | y_{1:t}) d\theta_{t+k}. \end{aligned} \quad (3.31)$$

Figure 3.7 illustrates the AENP and KNP elephant population abundance with the one-step-ahead forecast for different ratios of W and V errors. Forecasting is determining the unobserved signal x_t given data y_s with $s < t$.

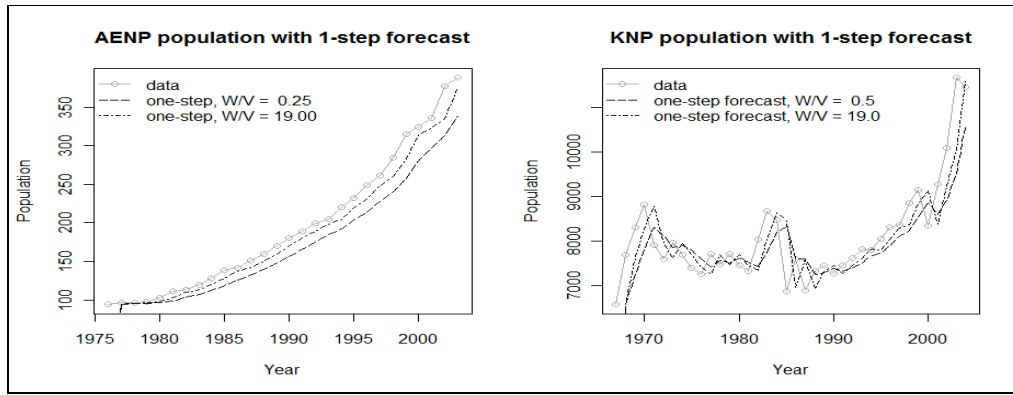


Figure 3.7 AENP and KNP one-step-ahead forecasts. Determining the unobserved signal x_t given data y_s with $s < t$.

In the following section we discuss construction, properties and theorems relating to age structured matrix models. The discussion on how to embed population dynamics into inference using a Bayesian framework is covered thereafter.

3.6 Age Structured Population Models

3.6.1 Population projection matrix Model

Survival and fertility of elephants depend on age of the animal and thus age structured models are useful in the study of their dynamics. Fecundity is defined as the number of female offspring produced per adult female of age i to $i+1$ in a unit of time t that will survive to the next age class at time $t+1$. Survival is the chance of that an individual of age i at time t will survive to age $i+1$ at time $t+1$. A survival curve represents the death rate as a function of age. The structured population model can be built and analyzed by considering the following;

- i. $x = 1, 2, 3, \dots, k$ is the number of age categories,
- ii. P_x is the probability of surviving the interval $(x, x+1)$ class. We have $P_k = 0$ if no animal survives beyond age class k ,
- iii. The fertility function $m(x)$, is the expected number of offspring (female offspring) per individual of age x per unit time. Fertility depends on the distribution of births and deaths in the age class. $m(x)$ is the fecundity or average number of of-spring produced by an individual in age category x while in that age category. For a mature elephant population with calving interval denoted by CI , the number of female offspring in an interval of y years, is approximated using $y/2 * CI$. This approach assumes that the probability of conception per average calving interval is one. A ratio of 1:1 of male to female birth is assumed though out this study (Moss 2001).

- iv. The survivorship $l(x)$ is the proportion of individuals reaching age category x . The survivorship function is the chance of an individual surviving from birth to age x , and it can be rescaled to give a number of survivors from the initial cohort. For a birth-flow population where birth of offspring occurs continuously over the projection interval, survival probability is approximated by,

$$P_x = \frac{l(x+1)}{l(x)},$$

$$l_x = P_1 P_2 \dots P_x = \prod_{i=1}^x P_i, \quad l_0 = 1.$$
(3.32)

- v. Net reproductive rate per generation or the average lifetime number of off-spring produced by a member of the study population is given by,

$$R_0 = \sum_{x=1}^k l(x)m(x).$$

- vi. Mean generation time of the population is,

$$T = \frac{\sum x l(x)m(x)}{\sum l(x)m(x)}.$$

- vii. The Malthusian parameter that measures the reproductive rate per unit time and can be calculated as,

$$r = \frac{\ln(R_0)}{T}.$$

Such that $n(t) = n(0)e^{rt}$ for an exponentially growing population. We can determine the annual growth rate using $g = e^r - 1$.

- viii. In matrix form the female and male population is represented by the vectors

$$n_f(t) = \begin{pmatrix} n_{f1}(t) \\ n_{f2}(t) \\ \vdots \\ n_{fk}(t) \end{pmatrix}, \quad n_m(t) = \begin{pmatrix} n_{m1}(t) \\ n_{m2}(t) \\ \vdots \\ n_{mk}(t) \end{pmatrix},$$

where $N_f(t) = \sum_x n_{fx}(t)$, $N_m(t) = \sum_x n_{mx}(t)$ are the total female and male populations respectively.

- ix. Female population dynamics can be represented as,

$$\begin{pmatrix} n_{f1}(t) = \sum_{x=1} p_0 b_x n_{fx}(t-1) \\ n_{f2}(t) = p_1 n_{f1}(t-1) \\ n_{f3}(t) = p_2 n_{f2}(t-1) \\ \vdots \\ n_{f,k}(t) = p_{k-1} n_{f,k-1}(t-1) \end{pmatrix}. \quad (3.33)$$

These equations can be put in matrix form as,

$$\begin{pmatrix} n_{f1}(t) \\ n_{f2}(t) \\ \vdots \\ n_{fk}(t) \end{pmatrix} = \begin{pmatrix} p_0 b_{f1} & p_0 b_{f2} & p_0 b_{f3} & \cdots & p_0 b_{f,k-1} & p_0 b_{f,k} \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & \cdots & p_{k-2} & 0 & 0 \\ 0 & 0 & \cdots & 0 & p_{k-1} & 0 \end{pmatrix} \begin{pmatrix} n_{f1}(t-1) \\ n_{f2}(t-1) \\ \vdots \\ n_{fk}(t-1) \end{pmatrix},$$

$$n_f(t) = L n_f(t-1),$$

$$n_f(t) = L^t n_f(0).$$

x. The male dynamics can be modelled as

$$\begin{pmatrix} n_{m1}(t) = \sum_{x=1}^k p_0 b_{mx} n_{fx}(t-1) \\ n_{m2}(t) = p_1 n_{f1}(t-1) \\ n_{m3}(t) = p_2 n_{f2}(t-1) \\ \vdots \\ n_{mk}(t) = p_{k-1} n_{f,k-1}(t-1) \end{pmatrix}, \quad (3.34)$$

$$\begin{pmatrix} n_{m1}(t) \\ n_{m2}(t) \\ \vdots \\ n_{mk}(t) \end{pmatrix} = \begin{pmatrix} p_0 b_{f1} & p_0 b_{f2} & p_0 b_{f3} & \cdots & p_0 b_{f,k-1} & p_0 b_{f,k} \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} n_{f1}(t-1) \\ n_{f2}(t-1) \\ \vdots \\ n_{fk}(t-1) \end{pmatrix} + \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & 0 \\ p_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & & \vdots & \vdots \\ 0 & 0 & \cdots & p_{k-2} & 0 & 0 \\ 0 & 0 & \cdots & 0 & p_{k-1} & 0 \end{pmatrix} \begin{pmatrix} n_{m1}(t-1) \\ n_{m2}(t-1) \\ \vdots \\ n_{mk}(t-1) \end{pmatrix}.$$

The ratio of male to female elephants born is approximately 1:1 and no major bias in this ratio has been observed in the case of most Eastern and Southern Africa populations (Moss, 2001). Keeping track of female population is sufficient for such population dynamics.

In general if we define age structure dynamics in terms of difference equations, the Leslie matrix, which is sometimes referred to as the projection matrix has the following form:

$$x(t+1) = Ax(t),$$

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & \cdots & F_{n-1} & F_n \\ P_1 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & P_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_n(t) \end{pmatrix}, \quad (3.35)$$

where, $x_i(t)$ population in the i^{th} age class in generation t , F_i = age specific fecundity rate for the i^{th} age class P_i = fraction of the i^{th} age group surviving to the $(i+1)^{st}$ age. $0 < P_i \leq 1$, and the first age group x_1 consists of births from all age groups:

$$\begin{pmatrix} x_1(t+1) = \sum_{i=1}^n F_i x_i(t), \\ x_2(t+1) = P_1 x_1(t), \\ x_3(t+1) = P_2 x_2(t), \\ \vdots \\ x_n(t+1) = P_{n-1} x_{n-1}(t). \end{pmatrix} \quad (3.36)$$

Two distinctions are usually made for population with a birth-pulse. In a birth-pulse population birth is limited to a short breeding season within the transition interval. Let number in the i^{th} age group that survive to age $i+1$ is $x_{i+1}(t+1) = s_i x_i(t)$. In the first case the animal increment in age, mortality takes place then birth. The population census is after the birth-pulse (post-breeding) and the population is,

$$\begin{pmatrix} x_0(t+1) \\ x_1(t+1) \\ x_2(t+1) \\ \vdots \\ x_{n-1}(t+1) \end{pmatrix} = \begin{pmatrix} s_0 b_1 & s_1 b_2 & \cdots & s_{m-2} b_{m-2} & s_{m-1} b_{m-1} \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_0(t) \\ x_1(t) \\ x_2(t) \\ \vdots \\ x_{n-1}(t) \end{pmatrix}. \quad (3.37)$$

In the second case reproduction takes place then mortality, the census of the population is before the birth-pulse (pre-breeding).

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} b_1 s_0 & b_2 s_0 & \cdots & b_{n-1} s_0 & b_n s_0 \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_n(t) \end{pmatrix}. \quad (3.38)$$

In the after birth-pulse matrix, the top row contains the survival rates of the reproducing animals. In the before birth pulse matrix, the top row contains the survival rate of newborn animals to 1 year of age. If we simply the first row the projection matrix model can be written as,

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & f_m \\ s_1 & 0 & 0 & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & s_{m-1} & \cdots & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_m(t) \end{pmatrix}. \quad (3.39)$$

This is the same as model 3.35 and the transition matrix is in the form of a simple Leslie (1945) matrix. Fertility (f_i) is the number of offspring of a female of age i to $i+1$ in a unit of time t that will survive to the next age class at time $t+1$. Survival is the probability that an individual of age i at time t will survive to time $t+1$, when her age will be $i+1$. The elements of the square matrix are non-negative, the elements of the first row are greater than or equal to zero, the elements of its main sub-diagonal are positive and less than unity and the remaining elements are zero. We can easily solve equation $X(t+1) = AX(t)$ to get that $X(t) = A^t X(0)$.

The principles in the Usher model are used when the time between samples or projection time interval $(t, t+1)$ is small so that not all individuals move from one class/stage to the next (Usher 1966, 1969). The transition matrix is of the form,

$$x(t+1) = Ux(t),$$

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_{n-1}(t+1) \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 & \cdots & F_{n-1} & F_n \\ P_{12} & P_{22} & 0 & \cdots & 0 & 0 \\ 0 & P_{23} & P_{33} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & P_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & P_{n-1,n} & P_{n,n} \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_{n-1}(t) \\ x_n(t) \end{pmatrix}. \quad (3.40)$$

A three classes/stages model using these principles would be of the form in equation (3.41).

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{pmatrix} = \begin{pmatrix} s_1(1-p_1) & F_2 & F_3 \\ s_1 p_1 & s_2(1-p_2) & 0 \\ 0 & s_2 p_2 & s_3(1-p_3) \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{pmatrix}. \quad (3.41)$$

In these models s_i is the chance of an individual surviving in given time interval, p_i is the proportion that develop or age and thus move from class i to $i+1$, $x_i(t)$ is the number of individual in stage i at time t . The first class or stage in model 3.41 is assumed to be of juveniles who have not attained reproductive age. If the time interval is such that all individuals proceed to the next class/stage then $p_i=1$ and the model reduces to the Leslie matrix model. Mathematical representation of population dynamics in matrix format are easy to visualize, analyze and the population projection is also easy to implement. In the next section we discuss important properties and analysis of transition matrix of the forms in model (3.35) and (3.40)

3.6.2 Analysis of Structured Population Models

3.6.2.1 Definitions and properties

The following definitions and properties are important in the build up to the analysis of transition matrices;

- a) Let $A=(a_{ij})$ and $B=(b_{ij})$ be two $n \times m$ matrices then $A \geq B$ if $a_{ij} \geq b_{ij}$ or $A > B$ if $a_{ij} > b_{ij}$ for all $i=1, 2, \dots, n$, $j=1, 2, \dots, m$.
- b) A matrix $A=(a_{ij}) \in \mathfrak{R}^{n \times m}$ is said to be nonnegative if $A \geq 0$, positive if $A > 0$.
- c) A matrix $A=(a_{ij}) \in \mathfrak{R}^{n \times n}$ is said to be reducible if there exists a permutation matrix P such that

$$C = PAP^T = \begin{pmatrix} A_{11} & A_{12} \\ 0 & A_{22} \end{pmatrix},$$

where $A_{11} \in \mathfrak{R}^{m \times m}$, $A_{22} \in \mathfrak{R}^{n-m \times n-m}$ and $A_{12} \in \mathfrak{R}^{m \times n-m}$ for $0 < m < n$.

- d) A matrix $A=(a_{ij}) \in \mathfrak{R}^{n \times n}$ is said to be irreducible if it is not reducible.
- e) Perron-Frobenius theorem: Let $A \geq 0$ be an irreducible $n \times n$ matrix, then:
 - i. A has a positive eigenvalue equal to its spectral radius $\lambda(A)$,
 - ii. To $\lambda(A)$ the corresponds an eigenvector $w > 0$,
 - iii. $\lambda(A)$ increases when any entry a_{ij} of A increases,
 - iv. $\lambda(A)$ a simple eigenvalue of A .
 - v. There is not other nonnegative eigenvector of A deferent from w .
- f) If $A > 0$ is an irreducible matrix, then either

$$\sum_{j=1}^n a_{ij} = \lambda(A) \quad \forall i=1(1)_n \quad \text{or} \quad \min_i \left(\sum_{j=1}^n a_{ij} \right) < \lambda(A) < \max_i \left(\sum_{j=1}^n a_{ij} \right),$$

which relates the row sums and the spectral radius. An analogous result can be stated for the columns of a matrix $A \in \mathbb{R}^{n \times n}$, if it possesses the Perron-Frobenius property.

- g) An irreducible nonnegative matrix A is said to be cyclic of index $k > 1$, if it has k eigenvalues of modulus equal to $\lambda(A)$.
- h) An irreducible nonnegative matrix A is said to be primitive, if the only eigenvalue of A , of modulus $\lambda(A)$ is $\lambda(A)$.
- i) The dominant eigenvalue of a matrix with positive entries is positive and the corresponding eigenvector could be chosen to be positive.
- j) The dominant eigenvalue of an irreducible nonnegative matrix is positive and the corresponding eigenvector could be chosen to be positive. Detailed analyses are given in many matrix analysis texts (see Bellman, 1997).

3.6.2.2 Eigenvalues and eigenvectors analysis;

For the female population model 3.35 above, the eigenvalues of A , the transition or projection matrix, are functions of the transition matrix elements a_{ij} as expressed implicitly by the characteristic equation:

$$|A - \lambda I| = 0. \quad (3.42)$$

The eigenvalues of A are given by the solutions to an equation of the form,

$$1 = \sum_{x=1}^k \lambda^{-x} l(x) m(x). \quad (3.43)$$

A situation in which there is only one positive and dominant eigenvalue. The other eigenvalues are either negative or complex and thus describe population oscillations. The proof of this property is given using the Penrron-Frobenius theorem below.

Consider the discrete homogeneous system $x(t+1) = Ax(t)$ the eigensystem of $Aw = \lambda w$ is such that the eigenvalues $|\lambda_1| \geq |\lambda_2| \geq \dots \geq |\lambda_n|$ and $w_1, w_2, \dots, w_n$ are the corresponding linearly independent enginevectors. The right and left eigenvectors of a matrix A are w_i and v_i^* such that, $Aw_i = \lambda_i w_i$ and $v_i^* A = \lambda_i v_i^*$ respectively, where v_i^* is the complex conjugate of v_i .

The solutions to $x(t+1) = Ax(t)$ have the form (Doucet and Sloep, 1992),

$$\begin{aligned} x_1(t) &= c_{11}\lambda_1^t + c_{12}\lambda_2^t + \dots + c_{1n}\lambda_n^t, \\ x_2(t) &= c_{21}\lambda_1^t + c_{22}\lambda_2^t + \dots + c_{2n}\lambda_n^t, \\ &\vdots \\ x_n(t) &= c_{n1}\lambda_1^t + c_{n2}\lambda_2^t + \dots + c_{nn}\lambda_n^t, \end{aligned} \quad (3.44)$$

where c_{ij} are constants. If the absolute value of $|\lambda_2| \geq |\lambda_3| \geq \dots \geq |\lambda_n|$ are less than one, then $x_i(t)$ is dominated by $c_{i1}\lambda_1^t$ for large t . Each age class eventually will grow exponentially at the rate of the dominant eigenvalue. For the dominant eigenvalue λ_1 we get,

- i. $Aw = \lambda_1 w$ gives the right eigenvector w corresponding to λ_1 . Setting the first element of w to one, $w(1) = 1$, the i^{th} element of w is given by,

$$w(i) = p_1 p_2 \dots p_{i-1} \lambda_1^i.$$

- ii. $v_i^* A = \lambda_1 v_i^*$ gives the left eigenvector v corresponding to λ_1 . If $v(1) = 1$ the $(i+1)^{\text{th}}$ element of v is given by,

$$v(i+1) = \frac{\lambda_1 v(i) - b_i}{p_i}.$$

- iii. The stable age distribution is such that,

$$x(t+1) = Ax(t) = \lambda_1 x. \quad (3.45)$$

If A has distinct eigenvalues $\lambda_1, \lambda_2, \dots, \lambda_n$ we can write $A = Y\Lambda Y^{-1}$ where Λ is the diagonal matrix with elements $\lambda_1, \lambda_2, \dots, \lambda_n$. The matrix Y is the matrix with columns as the right eigenvectors of A . So that $A^t = Y\Lambda^t Y^{-1}$ and $X(t) = Y\Lambda^t Y^{-1}X(0)$. Where

$$\Lambda = \begin{pmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & \dots & 0 \\ \vdots & & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n \end{pmatrix}, \quad \Lambda^t = \begin{pmatrix} \lambda_1^t & 0 & \dots & 0 \\ 0 & \lambda_2^t & \dots & 0 \\ \vdots & & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n^t \end{pmatrix}.$$

Thus we get $x_i(t) = c_{i1}\lambda_1^t + c_{i2}\lambda_2^t + \dots + c_{in}\lambda_n^t$, $i = 1, 2, \dots, n$. Hence, depending on the value of the dominant eigenvalue λ_1 there are following case to consider as $t \rightarrow \infty$;

- i. If $\lambda_1 < 1$ the population will tend to extinction,
- ii. If $\lambda_1 = 1$ the population of all age groups will be asymptotically stationary.
- iii. If $\lambda_1 > 1$ the population of all age groups will grow.

The following eigensystem theorems are important in establishing properties of the Leslie matrices useful in the study of a population. A Leslie matrix has at least one positive real eigenvalue, and if there are at least two consecutive age classes that are fertile, a positive real dominant eigenvalue always exists.

Perron-Frobenius theorem: If $A \geq 0$, the all elements of A^t are strictly positive for some value of t (a positive integer). There exists an eigenvalue λ_1 of A (Perron root) that is positive and larger in magnitude than the remaining $n-1$ eigenvalues. This implies that

- i. There exists one eigenvalue that is greater than or equal to any of the others in magnitude.
- ii. There exists an eigenvector such that its element are non-negative,
- iii. λ_1 is greater or equals to the smallest row sum of A and less or equals to the largest row sum.

Since $A \geq 0$ and its dominant eigenvalue is positive, in order for the equation $Ax = \lambda x$ to hold, the corresponding dominant eigenvector w_1 must have nonnegative elements. The importance of the Perron-Frobenius theorem lies in the fact that for population modeled by the generalized linear model $x(t+1) = Ax(t)$, it guarantees the existence of a stable population structure, w_1 , and growth rate, λ_1 , that determine the ultimate dynamical behavior of the population. That is, as $t \rightarrow \infty$, $x(t)$ aligns itself in the same direction as w_1 and changes in magnitude at a rate that approaches λ_1 .

Let A be a Leslie matrix with at least one pair of consecutive fecundity measures with both elements not zero and with $s_0 b_n \neq 0$, then A has a positive eigenvalue of algebraic multiplicity unity, for which there is a corresponding eigenvector having positive elements and which is greater in absolute value than any other eigenvalue. The eigenvalues of A are the roots of

$$\begin{vmatrix} s_0 b_1 - \lambda & s_0 b_2 & \cdots & s_0 b_{n-1} & s_0 b_n \\ s_1 & -\lambda & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & -\lambda \end{vmatrix} \equiv \begin{vmatrix} f_1 - \lambda & f_2 & \cdots & f_{n-1} & f_n \\ s_1 & -\lambda & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & -\lambda \end{vmatrix} = 0,$$

$$\phi(\lambda) \equiv \lambda^n - f_1 \lambda^{n-1} - f_2 s_1 \lambda^{n-2} + f_3 s_1 s_2 \lambda^{n-3} - \cdots - f_n s_1 s_2 s_3 \cdots s_{n-1} = 0. \quad (3.46)$$

Since $s_1, s_2, s_3, \dots, s_{n-1}$ are all positive and since also $f_n > 0$ we have $\phi(0) < 0$, $\phi(\infty) > 0$, and hence $\phi(\lambda) = 0$ has at least one positive real root.

$$f(\lambda) \equiv f_1 \lambda^{-1} + s_1 f_2 \lambda^{-2} + s_1 s_2 f_3 \lambda^{-3} + s_1 s_2 s_3 f_4 \lambda^{-4} + \cdots + s_1 s_2 s_3 \cdots s_{n-1} f_n \lambda^{-n} = 1, \quad (3.47)$$

which gives

$$f'(\lambda) \equiv -\frac{f_1}{\lambda^2} - \frac{2s_1 f_2}{\lambda^3} - \frac{3s_1 s_2 f_3}{\lambda^4} - \cdots - \frac{ns_1 s_2 \cdots s_{n-1} f_n}{\lambda^{n+1}}.$$

thus, $f'(\lambda) < 0$ when $\lambda > 0$; therefore, $f(\lambda)$ decrease strictly monotonically from ∞ to 0 as λ increase from 0 to ∞ . Hence there is one and only one real positive root of $f(\lambda) = 1$ of multiplicity unity.

$$w = \left[1, \frac{s_1}{\lambda_0}, \frac{s_1 s_2}{\lambda_0^2}, \dots, \frac{s_1 s_2 \dots s_n}{\lambda_0^{n-1}} \right]^T, \quad (3.48)$$

whose components are all positive. Consider a transition matrix model of the form,

$$A = \begin{bmatrix} (1-p_1)s_0 + s_0 f_1 & \dots & s_0 f_{n-1} & s_0 f_n \\ p_1 s_1 & \ddots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \dots & (1-p_{n-1})s_{n-1} & 0 \\ 0 & \dots & p_{n-1}s_{n-1} & s_n \end{bmatrix}.$$

Since this matrix A is nonnegative, the Perron-Frobenius theorem applies. By theory of expanding determinants, the characteristic equation for the eigenvalues associated with the matrix A defined above is the n^{th} order polynomial,

$$\prod_{j=1}^n (\lambda - (1-p_j)s_j) - \sum_{i=1}^n s_0 f_i \prod_{j=1}^{i-1} p_j s_j \prod_{j=i+1}^n (\lambda - (1-p_j)s_j) = 0, \quad (3.49)$$

$$\sum_{i=1}^n \frac{s_0 f_i}{p_i s_i} \prod_{j=1}^i \frac{p_j s_j}{\lambda - (1-p_j)s_j} = 1,$$

which are important for analysis of Leslie matrix model.

3.6.2.3 Stable age distribution.

A population attains a stable age distribution when the proportion of individuals in a particular stage or class does not change from one time interval t to the next time interval $t+1$. Stable age distribution may be used as an aid in predicting growth and anticipating ecological impacts (Fowler & Smith, 1973). It could also indicate stable undisturbed population whereas deviations indicate the impact of disturbance (Sukumar et al. 1988; Wittemyer, 2001).

For the population model $x(t+1) = Ax(t)$ the stable age distribution is such that, $x(t+1) = Ax(t) = \lambda_1 x$. The stable age distribution can be obtained from the eigenvector w_1 , corresponding to λ_1 . If

$$w = \begin{pmatrix} w_1 \\ w_2 \\ \vdots \\ w_n \end{pmatrix} \quad (3.50)$$

and $a = a_1 + a_2 + \dots + a_n$, then the stable age distribution $\hat{x}$ of the population is,

$$\hat{x} = \frac{w}{\sum_{i=1}^n a_i} = \begin{pmatrix} w_1/a \\ w_2/a \\ \vdots \\ w_n/a \end{pmatrix} \quad (3.51)$$

When a population attains a stable age distribution the growth rate is then referred to as intrinsic growth rate. A stable age distribution would basically imply that the vital demographic parameters are the same over time although not necessarily equal across the classes or stage. An equilibrium age structure is attained if the population has attained equilibrium by density regulation and the age structure is stable from one time period to the next.

How fast the population approaches the stable age distribution depends on how much larger $|\lambda_1|$ is than $|\lambda_2| \geq |\lambda_3| \geq \dots \geq |\lambda_n|$. The larger the relative difference, the faster the population moves towards stability.

In using stable age distribution of African elephant, managers would be interested in the time it takes to attain stable age distribution. An evaluation on how a management policy ought to consider the age structure. The expected or projected total population by the time the population attains a stable age distribution, informed by the range size and resource availability can be used to determine the best management strategy.

Reproductive value is the expected contribution of each individual to present and future reproduction. We find each stage's reproductive value by solving for the dominant left eigenvector v , where $vA = \lambda v$. Like the relation between the dominant right eigenvector and the stable age distribution, this vector is actually proportional to the reproductive values. For $v = (v_1, v_2, \dots, v_n)'$ and $b = v_1 + v_2 + \dots + v_n$, the reproductive value is,

$$R_v = \frac{v}{\sum_{i=1}^n v_i} = \begin{pmatrix} v_1/b \\ v_2/b \\ \vdots \\ v_n/b \end{pmatrix} \quad (3.52)$$

The stage structure and reproductive values each in their own way contribute to the importance of each stage in determining λ . The stable age distribution provides the relative

abundance of individuals in each stage. Reproductive value provides the contribution to future population growth of individuals in each stage.

From the fact that $Aw_i = \lambda_i w_i$, where w_i is eigenvector of A ,

$$x(0) = c_1 w_1 + c_2 w_2 + \dots + c_n w_n,$$

where $c = W^{-1}x(0)$. We can recursively find that;

$$\begin{aligned} x(1) &= Ax(0) = \sum_i c_i Aw_i = \sum_i c_i \lambda_i w_i, \\ x(2) &= Ax(1) = \sum_i c_i \lambda_i Aw_i = \sum_i c_i \lambda_i^2 w_i, \\ &\vdots \\ x(t) &= Ax(t-1) = \sum_i c_i \lambda_i^{t-1} Aw_i = \sum_i c_i \lambda_i^t w_i. \end{aligned} \tag{3.53}$$

The dominant eigenvalue λ_1 determine the ergodic properties of the population growth since;

$$x(t) = c_1 \lambda_1^t w_1 + c_2 \lambda_2^t w_2 + c_3 \lambda_3^t w_3 + \dots$$

Assuming the eigenvalues are arranged in order of decreasing magnitude with λ_1 being strictly greater. Dividing all through by λ_1^t we have;

$$\frac{x(t)}{\lambda_1^t} = c_1 w_1 + c_2 \left(\lambda_2/\lambda_1\right)^t w_2 + c_3 \left(\lambda_3/\lambda_1\right)^t w_3 + \dots,$$

$$\lim_{t \rightarrow \infty} \frac{x(t)}{\lambda_1^t} = c_1 w_1.$$

Hence this shows that if A is primitive the long term dynamics of the population are described by the dominant eigenvalue λ , and the stable age distribution w . Let $Aw = \lambda w$, then;

$$\begin{aligned} s_1 w_1 &= \lambda w_2, \\ s_2 w_2 &= \lambda w_3, \\ s_3 w_3 &= \lambda w_4, \\ &\vdots \\ s_{n-1} w_{n-1} &= \lambda w_n. \end{aligned}$$

That is, the eigenvector w has components,

$$w_i = s_i \lambda^{-i+1}.$$

Since we can scale w so that $w_1 = 1$, the stable age distribution with abundance of each age class measured relative to the first class is given by;

$$\begin{pmatrix} w_1 = 1 \\ w_2 = s_1 \lambda^{-1} \\ w_3 = s_1 s_2 \lambda^{-2} \\ \vdots \\ w_n = s_1 s_2 \dots s_{n-1} \lambda^{-n+1} \end{pmatrix},$$

where n is the number of age classes in the structured model.

3.6.2.4 Analysis using net reproductive value

Fertility rates are among the most important vital parameters in population studies. The net reproductive value combines together the age-specific fertility rates and the age-specific rates and gives the expected number of offspring's per individual over its life time. It can be used to characterize the stability of the trivial equilibrium and as a bifurcation parameter in the study of positive equilibrium for linear models (Cushing 1988). The net reproductive value, R_0 for a general class of matrix population models is equal to the expected number of off-spring per individual over its lifetime

Let $x_i(t)$ $i = 1, 2, \dots, m$, denote the number (or density) of individuals in the i th age class at time t , and suppose that the time unit is taken, without loss in generality, to be 1. Let $s_{i+1,i} \in (0,1)$ be the fraction of individuals in age class i that survives to age class $i+1$ after one time unit. Let f_{1i} $i = 1, 2, \dots, m$, be the number of off-springs produced by an individual in age class i that survives to age 1. For the discrete age-structured population model,

$$\begin{aligned} x_1(t+1) &= \sum_{j=1}^m f_{1j} x_j(t), \\ x_i(t+1) &= s_{i+1,i} x_i(t), \quad i = 1, 2, \dots, m, \\ \text{for } t &= t_0, t_0 + 1, t_0 + 2, \dots \end{aligned} \quad (3.54)$$

Given an initial population distribution $x_i(t_0) = x_i^0 \geq 0$, $i = 1, 2, \dots, m$, then the dynamics of the population are uniquely determined by these formulas for all $t > t_0$. In this model the net reproductive value is defined as

$$R_0 = \sum_{i=1}^m f_{1i} \prod_{j=0}^{i-1} s_{j+1,j}, \quad (3.55)$$

or in simply $R_0 = l(x)m(x)$. The number defined by (3.55) has a straightforward biological meaning. The product $\prod_{j=0}^{i-1} s_{j+1,j}$ is the probability that an individual lives to age i and the product

$f_{1i} \prod_{j=0}^{i-1} s_{j+1,j}$ is the number of its offspring. Consequently, n is the expected number of offspring per

individual over its life time.

Let $x(t) = (x_1(t), x_2(t) \dots x_m(t))'$ denote the age-distribution vector at time t . We have following theorem (Cushing, 1988).

Theorem: Reproductive number

For any initial distribution $x_1(t_0) = x^0 > 0 (\neq 0)$,

- i. $R_0 < 1$ implies $\lim_{t \rightarrow \infty} x_i(t) = 0$ for all $i = 1, 2, \dots, m$.
- ii. $R_0 > 1$ implies $\lim_{t \rightarrow \infty} x_i(t) = +\infty$ for all $i = 1, 2, \dots, m$.

If $R_0 = 1$ then there exist positive equilibrium solutions $x = cv$ of the model equations (3.54) where c is an arbitrary positive constant and

$$0 < v = (1, s_{21}, s_{21}s_{32}, s_{21}s_{32}s_{43}, \dots, s_{21}s_{32} \dots s_{m,m-1})'.$$

The theorem above illustrates the role of the net reproductive value R_0 in determining the asymptotic dynamics of the population.

- i. The trivial solution $x = 0$ of equations (3.54) is asymptotically stable if $R_0 < 1$ and is unstable if $R_0 > 1$.
- ii. If $R_0 = 1$, a nontrivial equilibrium exist. Biologically when $R_0 = 1$ an individual produces exactly one offspring to replace itself over its lifetime and, as a result, the whole population maintains itself at a constant level.
- iii. If $R_0 < 1$ means that an individual cannot fully replace itself during its life span and therefore the population decreases.
- iv. In the case $R_0 > 1$, the situation is the opposite, and the population in grows exponentially.

As we noted above the intrinsic rate of increase, r , is given by, $r \cong \ln R_0 / T$, where T is the generation time. The following is also true,

- i. If $R_0 = 1$ or $r = 0$, the population is stationary,
- ii. If $R_0 < 1$ or $r < 0$, the population declines, and
- iii. If $R_0 > 1$ or $r > 0$, the population grows exponentially.

3.6.2.5 Sensitivity and elasticity

In perturbation analysis we ask what would happen to some dependent variable if we change one or more independent variable. Perturbation analysis enables us to predict result of future changes in the vital rates, quantify the effects of past changes, predicting the action of natural selection and designing sampling schemes. In designing sampling schemes we need to understand which vital rate and hence their estimate is λ most sensitive.

Sensitivity and elasticity combine the idea of stable age distribution and reproductive value to tell us the relative importance of each transition in determining λ . Sensitivities of a population projection matrix are the changes in λ given small changes in each element a_{ij} of A . We denote by S the sensitivity matrix giving the sensitivity of λ to all the a_{ij} :

$$\begin{aligned}\frac{\partial \lambda}{\partial a_{ij}} &= \frac{v_{ij} w_{ij}}{v \cdot w}, \\ S &= \left(\frac{\partial \lambda}{\partial a_{ij}} \right) = \frac{\bar{v} w'}{v^* w'}.\end{aligned}\tag{3.56}$$

Elasticities are sensitivities, weighted by the transition probabilities. Sensitivities are large when reproductive value and or the stable age distribution are high, and this makes sense biologically because these factors contribute a lot to λ . The elasticity matrix E and elasticity of λ with respect to a_{ij} are defined as,

$$\begin{aligned}e_{ij} &= \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\delta \log \lambda}{\delta \log a_{ij}}, \\ E &= \left(\frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \right) = \frac{1}{\lambda} S \circ A,\end{aligned}\tag{3.57}$$

where $S \circ A$ is the hadamard product of S and A (see Appendix A). We note that if a transition is not possible it has elasticity equal to zero, because we multiply by the projection matrix itself and that elasticities sum to zero, and so it is easier to compare elasticities among different matrices and different organisms. Sensitivities and elasticities provide us with the predicted effects on λ of a proportional change in demographic rates. This is particularly important in the management of invasive (or endangered) species where we seek to have the maximum impact for the minimum amount of effort and resources. Put in simple terms sensitivity is the slope of λ as a function of the elements of the transition matrix a_{ij} while elasticity is the slope of $\log \lambda$ as a function of $\log a_{ij}$.

3.6.3 Stochastic population dynamics models

Stochastic matrices and integrated autoregressive moving average models (ARIMA) can be used to capture environmental stochasticity. To capture environmental variation using a matrix model, different approaches may be used,

- i. Allowing the elements of the matrix to be independently distributed sequence of random variables. The elements may be selected from a given probability distribution.
- ii. Assuming discrete state Markov chains with finite number of environmental states, then the distribution at t is given by $x(t) = A_t x(t)$, where A_t is a column-stochastic matrix such that $a_{ij} \geq 0, \sum_i a_{ij} = 1$ for all j .

If we incorporate stochastic variations in our matrix dynamics we get,

$$x(t+1) = A(t)x(t),$$

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} F_1(t) & F_2(t) & F_3(t) & \cdots & F_m(t) \\ P_1(t) & 0 & 0 & \cdots & 0 \\ 0 & P_2(t) & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & P_{m-1}(t) & \cdots & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_m(t) \end{pmatrix}, \quad (3.58)$$

where the transition $A(t)$ matrix varies with time.

$$x(t) = A_t A_{t-1} A_{t-2} \cdots A_0 x(0). \quad (3.59)$$

The population size at time t is

$$\begin{aligned} X(t+1) &= \|x(t)\| \\ &= \|A_t A_{t-1} A_{t-2} \cdots A_0 x(0)\|, \end{aligned}$$

where the stochastic population growth rate can be approximated using.

$$\log \lambda_s = \lim_{t \rightarrow \infty} \frac{1}{t} \log \|A_t A_{t-1} A_{t-2} \cdots A_0 X(0)\|. \quad (3.60)$$

The demographic stochasticity can be incorporated in matrix by considering survival P_i and birth F_i rates of class i as though fixed and mutually independent, but allowing an individual's survival and reproduction to be a binomial variables. Survival and birth are then given by $\text{Bin}(x_i(t), P_i)$ and $\text{Bin}(x_i(t), F_i)$ respectively. In this scenario there is variability due to applying probability to a finite sample.

3.6.4 Density dependence

The linear Leslie Matrix formulation is limited because only density-independent population growth with just births and deaths is modeled. The survival for the first age class can be replaced

with a density dependent function, $s_0(x_t) = \beta_0 + \beta_1 N_t$ and survival of other age classes may also be dependent on the total population or other environmental factors (Winkelman, 2009). The matrix model becomes

$$\underline{N}_{t+1} = \begin{bmatrix} b_0(\beta_0 + \beta_1 N_t) & b_1(\beta_0 + \beta_1 N_t) & b_2(\beta_0 + \beta_1 N_t) & \cdots & b_k(\beta_0 + \beta_1 N_t) \\ s_1(N_t) & 0 & 0 & \cdots & 0 \\ 0 & s_2(N_t) & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & s_k(N_t) & 0 \end{bmatrix} \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_k \end{bmatrix}_t$$

Only density-dependence ($s_0(N_t) = \beta_0 + \beta_1 N_t$) in one age class is needed to produce logistic growth. A density dependent form of the Leslie's (1945) model could also be of the form;

$$\underline{N}(t+1) = \begin{pmatrix} b_1 s_0 \phi(N_0(t)) & b_2 s_0 \phi(N_0(t)) & \cdots & b_{n-1} s_0 \phi(N_0(t)) & b_n s_0 \phi(N_0(t)) \\ s_1 & 0 & \cdots & & \\ 0 & s_2 & & & \\ \vdots & & & & \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \\ \vdots \\ N_{n-1}(t) \\ N_n(t) \end{pmatrix}. \quad (3.61)$$

The new born are assumed to experience both density-dependent ($\phi(N_0(t))$) and density-independent (s_0) mortality in their first year of life. In this model we note that

$$N_0(t) = \sum_{i=1}^{\infty} b_i N_i(t), \quad N_1(t+1) = s_0 \phi(N_0(t)) N_0(t). \quad (3.62)$$

If we define $l_i = s_0 s_1 s_2 \cdots s_{i-1}$, which implies that $l_1 = s_0$ and using equations of this model we acquire that,

$$N_i(t) = \frac{l_i}{l_1} N_1(t-i+1).$$

Substituting for $N_0(t)$ using equations (3.62) we have;

$$N_1(t+1) = s_0 \sum_{i=1}^{\infty} b_i N_i(t) \phi \left(\sum_{i=1}^{\infty} b_i N_i(t) \right).$$

We then substitute for $N_i(t) = (l_i/l_1) N_1(t-i+1)$ we get;

$$\begin{aligned} N_1(t+1) &= s_0 \sum_{i=1}^{\infty} b_i \frac{l_i}{l_1} N_1(t-i+1) \phi \left(\sum_{i=1}^{\infty} b_i \frac{l_i}{l_1} N_1(t-i+1) \right), \\ &= \sum_{i=1}^{\infty} b_i l_i N_1(t-i+1) \phi \left(\sum_{i=1}^{\infty} b_i \frac{l_i}{l_1} N_1(t-i+1) \right). \end{aligned}$$

The dynamics of $N_1(t)$ are completely described by the maternity schedules, $b_i l_i$, the value of l_i and the function ϕ . Therefore, since b_i and s_i only appear as a product, high values of adult mortality and fertility could produce the same dynamics as low values of adult mortality and fertility. In this case the reproductive value R_0 is given by,

$$R_0 = \sum_{i=1}^n b_i l_i .$$

If $\underline{N}^*$ is an equilibrium solution then the equilibrium new born level satisfies;

$$N^* \phi(N_0^*) = N_0^* / R_0 .$$

Local stability for the density dependent Leslie model above is assured if the eigenvalues of the population matrix linearized around the equilibrium $\underline{N}^*$ all lie within the unit circle.

3.6.5 Harvesting

We can analyze or study harvesting or destruction using the Leslie model. For example we can use the Leslie matrix model to consider three harvesting strategies;

- i. Harvesting equal proportion $h = h_1, h_2, \dots, h_n$ from all the classes,
- ii. Harvesting equal proportion $h' = h_1, h_2, \dots, h_k, h_{k+1}, h_{k+2}, \dots, h_n = 0$; from all the classes, from the pre-reproductive groups and first reproductive groups,
- iii. Harvest a proportion h'' from some $k'+1$ of the first $k+1$ age groups for $k' < k$.

We remove $H A x(t)$ animals. Thus the population vector after growth and harvesting becomes;

$$A x(t) - H A x(t) = \lambda x \quad (3.63)$$

Where λ is a positive eigenvalue of the matrix $(I - H)A$. If we have $f_1, f_2 \dots f_k = 0$, then;

$$\begin{aligned} \frac{\lambda}{1-h_1} \frac{\lambda}{1-h_2} \dots \frac{\lambda}{1-h_n} &= s_1 s_2 \dots s_k \left(f_{k+1} \frac{\lambda}{1-h_{k+2}} \dots \frac{\lambda}{1-h_n} \right. \\ &\quad \left. + f_{k+2} s_{k+1} \frac{\lambda}{1-h_{k+3}} \dots \frac{\lambda}{1-h_n} + \dots + f_n s_{k+1} s_{k+2} \dots s_{n-1} \right) \end{aligned} \quad (3.64)$$

If $h_1, h_2, \dots, h_n$ satisfy equation (3.63) and $x_1(0), x_2(0), \dots, x_n(0)$ satisfy $|(I - H)A - \lambda I| = 0$ then $A x(t) - H A x(t) = \lambda x$. The population will increase if $\lambda > 1$, decrease if $\lambda < 1$ and remain constant if $\lambda = 1$.

The equations given by equation (3.64) for determining h, h' and h'' as functions of $\lambda < 1$ are:

$$\begin{aligned} \left(\frac{\lambda}{1-h}\right)^n &= s_1 s_2 \dots s_k \left(f_{k+1} \left(\frac{\lambda}{1-h}\right)^{n-k-1} + f_{k+2} s_{k+1} \left(\frac{\lambda}{1-h}\right)^{n-k-2} + \dots + f_n s_{k+1} s_{k+2} \dots s_{n-1}\right), \\ \lambda^{n-k-1} \left(\frac{\lambda}{1-h'}\right)^{k+1} &= s_1 s_2 \dots s_k (f_{k+1} \lambda^{n-k-1} + f_{k+2} s_{k+1} \lambda^{n-k-2} + \dots + f_n s_{k+1} s_{k+2} \dots s_{n-1}), \\ \lambda^{n-k'-1} \left(\frac{\lambda}{1-h''}\right)^{k'+1} &= s_1 s_2 \dots s_k (f_{k+1} \lambda^{n-k-1} + f_{k+2} s_{k+1} \lambda^{n-k-2} + \dots + f_n s_{k+1} s_{k+2} \dots s_{n-1}). \end{aligned}$$

From where we deduce that; $h(\lambda) \leq h'(\lambda) \leq h''(\lambda)$, $h(0) = h'(0) = h''(0) = 0$ and that $h(\lambda)$, $h'(\lambda)$ and $h''(\lambda)$ are monotonically decreasing functions of λ .

In the next section we discuss the Bayesian state space models that are used to study process and measurement error in population time series. Analytical approach of determining general posterior distributions, filtered, smoothed and predicted distributions have been explored.

3.7 Bayesian State space models

3.7.1 State space models Structure and Inference

State-space models describe dynamic systems as consisting of two linked time series processes running in parallel. The state process is the true underlying state of the population at a sequence of successive time steps is defined as n_t ; $t = 0, 1, 2, \dots, T$. It is a vector of states, some of which may be unobservable.

The second time series is the observation process vector y_t ; $t = 1, 2, \dots, T$ which provides a correspondence between the unobserved true state n_t , and the recorded measurement on the population. The observation process is modeled using the probability distribution or process $f(y_t | n_t)$ (Thomas L, 2005; Buckland et al, 2004; Bishop J.R, 2008).

A state space model structure is represented as the sequence,

$$\begin{array}{ccccccc} n_0 & \rightarrow & n_1 & \rightarrow & n_2 & \rightarrow & \dots \rightarrow n_{t-1} \rightarrow n_T \\ & & \downarrow f(\cdot) & & \downarrow & & \downarrow & \downarrow f(\cdot) \\ & & y_1 & & y_2 & & y_{t-1} & y_T \end{array}$$

Important distributions include:

- i. Initial state distribution $g_0(n_0, \Theta)$,
- ii. State process distribution $g_t(n_t | n_{t-1}, \Theta)$,
- iii. Observation process distribution $f_t(y_t | n_{t-1}; \Theta)$,

Where $t = 1, 2, 3, \dots, T$ and Θ is a vector of parameters. The state process is assumed to be first-order Markov, namely,

$$g_t(n_t | n_{t-1}, \dots, n_0; \Theta) = g_t(n_t | n_{t-1}; \Theta).$$

For a state vector n_t and vector of parameters θ , the three probability distributions that are important making inference at include:

- i. Filtering distribution $p(n_t, \theta | y_1, \dots, y_t)$ is used if the purpose of inference is to estimate the current state of the population given all of the data up until the current time period.
- ii. Smoothed distribution $p(n_s, \theta | y_1, \dots, y_t)$, is important when the full series of observations up to time T is used to estimate the state vector at time $s < t$, and
- iii. Predicted distribution $p(n_r, \theta | y_1, \dots, y_t)$, is useful if observations up to year t are used to predict the state vector in year $r > t$.

The joint distribution of the states, n_t , and observations, y_t , is obtained by,

$$P(n_t, y_t | \Theta) = g(n_0, \Theta) \prod_{t=1}^T f_t(y_t | n_t, \Theta) g_t(n_t | n_{t-1}, \Theta), \quad t = 0, 1, \dots, T. \quad (3.65)$$

This is useful in determining the maximum likelihood estimates for Θ . The marginal distribution of y_t , or the likelihood function is,

$$p(y_t | \Theta) = \int \int \dots \int_{n_0 \ n_1 \ n_T} \left\{ \prod_{t=1}^T f_t(y_t | n_t; \Theta) g_t(n_t | n_{t-1}; \Theta) dn_t \right\} g_0(n_0; \Theta) dn_0. \quad (3.66)$$

By the Bayes Theorem the smoothed distribution can be expressed as,

$$p(n_{tT} | y_{1T}, \Theta) = \frac{p(n_{tT}, y_{1T} | \Theta)}{p(y_{1T} | \Theta)}, \quad (3.67)$$

$$p(n_{tT} | y_{1T}, \Theta) = \frac{g_0(n_0; \Theta) \prod_{t=1}^T f_t(y_t | n_t; \Theta) g_t(n_t | n_{t-1}; \Theta) dn_t}{p(y_{1T} | \Theta)}.$$

Using the smoothed distribution, the expectation of the state vector is,

$$E[n_t | y_{1T}; \Theta] = \frac{\int \int \dots \int_{n_0 \ n_1 \ n_T} n_t \left\{ \prod_{t=1}^T f_t(y_t | n_t; \Theta) g_t(n_t | n_{t-1}; \Theta) dn_t \right\} g_0(n_0; \Theta) dn_0}{p(y_{1T} | \Theta)}. \quad (3.68)$$

The posterior distribution of the model parameters Θ conditional on all the observed data $y_{1:T}$ is given by,

$$p(\Theta | y_{1:T}) = \frac{p(y_{1:T} | \Theta)p(\Theta)}{\int_{\Theta} P(y_{1:T} | \Theta)P(\Theta)} = \frac{p(y_{1:T} | \Theta)p(\Theta)}{f(y_{1:T})}. \quad (3.69)$$

Numerator is the product of the prior $p(\Theta)$ and the likelihood $p(y_{1:T} | \Theta)$.

3.7.2 Sub-process Model Structure and Inference

Suppose the population dynamics in a single time interval undergoes sub-processes such as birth, survival, maturation, harvesting and movement, we can model these processes in a modular approach. Suppose there are k sub-processes between time $t-1$ and time t ,

$$\begin{aligned} u_{1t} &\sim g_{1t}(n_{0:t-1}, \Theta), \\ u_{2t} &\sim g_{2t}(n_{0:t-1}, u_{1,t}, \Theta), \\ &\vdots \\ n_t \equiv u_{kt} &\sim g_{kt}(n_{0:t-1}, u_{1,t}, u_{2,t}, \dots, u_{k-1,t}, \Theta), \end{aligned} \quad (3.70)$$

where $g_{i,t}$ is the distribution of the $i^{th} = 1, 2, \dots, k$ sub-process and $u_{i,t}$ is the population state after process $i = 1, 2, \dots, k$. Assuming the sub-process are linear and Markovian, i.e. the state at time t only depends on the state at time $t-1$, and that the sub-process are sequential. The sub-process model would be represented as,

$$\begin{aligned} u_{1t} &\sim g_{1t}(n_{0:t-1}, \Theta), \\ u_{2t} &\sim g_{2t}(u_{1,t}, \Theta), \\ &\vdots \\ n_t \equiv u_{kt} &\sim g_{kt}(u_{k-1,t}, \Theta). \end{aligned} \quad (3.71)$$

In the modular approach, the state probability density function can be written as:

$$g(n_t | n_{0:t-1}, \Theta) = \int \prod_{r=1}^k g_{rt}(n_{0:t-1}, u_{r-1,t}, \Theta) du_{1,k-1,t}. \quad (3.72)$$

If each sub-process is assumed to be first-order Markov the state process distribution can be written as,

$$\begin{aligned} g(n_t | n_{t-1}, \Theta) &= \int \cdots \int_{u_{1,t} \dots u_{k-1,t}} g_{1,t}(u_{1,t} | n_{t-1}, \Theta) \left[\prod_{r=2}^{k-1} g_{rt}(u_{r,t} | u_{r-1,t}, \Theta) \right] \\ &\quad \times g_{k,t}(n_t | u_{k-1,t}, \Theta) du_{1,t}, \dots, du_{k-1,t}. \end{aligned} \quad (3.73)$$

Direct analytical evaluation of $g(n_t | n_{t-1}, \Theta)$ and multidimensional integrals of other equations like (3.66) to (3.69), and (3.72) are not easy. Such integrals become even more complex in the state space model with many sub-processes. MCMC offer computation techniques that make the evaluation of these multidimensional integrals feasible (Gilks and Roberts, 1996).

The modular modelling approach can be considered as an extension of the matrix modelling for the following reasons

- i. Observation model that can be either deterministic or stochastic is explicitly added to the model framework.
- ii. Modular approach: for example birth, survival, movement and maturation are modelled separately and can be either stochastic or deterministic. Each individual sub-process can be modelled separately from the others which allow a greater degree of flexibility in the approach to constructing the models and performing statistical inference. State n_{t-1} evolves to n_t by intermediate sub-processes, the $u_{i,t}$. The observations y_{t-1} and y_t are connected to the corresponding states n_{t-1} and n_t by the observation process probability density functions f_{t-1} and f_t .
- iii. Sub-process matrix representation: each of the sub-process models can be represented in the form of a matrix. For example if each sub-process i is represented by matrix M_i then the progression of a linear Markov process can be estimated by the generalised Leslie model,

$$E[n_t | n_{t-1},] = M_k M_{k-1} \dots M_1 n_{t-1}. \quad (3.74)$$

The state space modelling framework may be used to incorporate multiple sources of uncertainty including, stochastic variation due to the process, model parameters, and measurement error. Alternative management strategies can be investigated with the outputs reflecting the multiple sources of uncertainty (Buckland et. al. 2004). It is also possible to combine either deterministic or stochastic sub-processes into a single model.

CHAPTER FOUR: MODELS FOR TOTAL POPULATION ABUNDANCE

4.1 Introduction

Unstructured models for elephants represent the population abundance with a single variable, aggregating all age classes together. Such models can be kept relatively simple, and the number of parameters required can be kept low. Models requiring few parameters are simple and useful tools for establishing the general population trends and for strategic decision making.

In studying elephant population abundance we may consider a given population in a chosen ecosystem as a single homogeneous group. In such a case the vital rates such as reproductive rate, mortality or survival rates, are considered as uniform for all individuals in population. Models that consider the population age structure are discussed in chapter five.

It is necessary to determine whether the time series of total population abundance data used is for a constant range size. In cases where population counts were done for varying range size it would be more appropriate to study population time series using density estimates. Open population where the animals can migrate into or out of the selected region pose another challenge in fitting models using total population count data, especially where no data on immigration and emigration exist.

Different models can be used to explain observed elephant data and predict future elephant population trends. Log-linear models are used to fit a model using log transformed total population data. The log-linear model is thus, a deterministic model which can be used to project future population.

To capture some of the randomness and autocorrelation in population data a time series model is necessary. Integrated autoregressive moving average (ARIMA) models are used to explain the observed data and give future predictions with a measure of prediction accuracy or forecast error. Due to the relatively few observations available in the population time series, bootstrapping was used to forecast future values and acquire empirical distribution of future populations.

As stated earlier when population is treated as a single homogeneous group, our main interest was the population rate of growth since it captures the characteristics of the population. Due to the central role of the population growth rate (Sibly & Hones, 2002) we derived a method for comparing the distribution of the growth rate using a Bayesian approach.

4.2 Log-linear, ARIMA models and Bootstrapping

4.2.1 Models and modelling challenges

The following challenges arise when fitting both classical time series models and log-linear regression models to elephant's population abundance data;

- i. Only a short lengths of the time series of abundance data is available,
- ii. Missing values and observations collected at unequal intervals in the time series, due to missing observations or irregular sampling, and
- iii. The possibility of process, observation and model uncertainty.

Methods used estimating exponential trend parameters for abundance time series data may be classified by their assumption on process and observation error. They include models that consider;

- i. **Observation error:** Log-linear regression of counts against time, where the slope of the regression gives the population trend (Eberhardt and Simmons1992),
- ii. **Process error:** Population is surveyed without observation error and that variability in abundances is entirely due to process error captured by the growth rate fluctuations. Abundance (on the logarithmic scale) is described by a Brownian motion diffusion process with a constant drift rate.
- iii. **Process and observation error:** Method for estimating trend using a stochastic state-space exponential growth model that assumes both observation error and environmental process noise (Lindley 2003). Such an exponential growth state space model can be written as a linear mixed model and used to accommodate data with missing observations (Staudenmayer and Buonaccorsi, 2006)

4.2.2 Data and exploratory analysis

The elephants population data used is as published by Gough KF (2006) (See Appendix B) and Blanc et. al. (2007), and South Africa National Parks (SANP). The Addo Elephant National Park (AENP) and the Kruger National Park (KNP) elephant populations, both in South Africa, have been monitored and studied by various researchers and organisations (Blanc et. al. 2007; Gough 2006; Woodd 1999, Rude. et al. 1999). The Amboseli National Park population has been monitored and studied by Moss C.J (2011, 2001) and KWS among others.

The time series plot of population abundance (Figure 4.1) showed that all the selected populations indicated recovery. The population of KNP seems to have stagnated between the years 1970 to 1994 as in Figure (4.1c). This is due to the management policy adapted. Our analysis uses KNP elephant population data which include values of population size between 1967 and 1994

when culling was being done to maintain sustainable population size. The policy was to maintain about 7 000 elephants in the park, but fluctuations between 6 000 and 8 000 were deemed to be acceptable. The AENP and ANP population have grown exponentially (Figure 4.2 a and b) with minor fluctuation for the entire period of study.

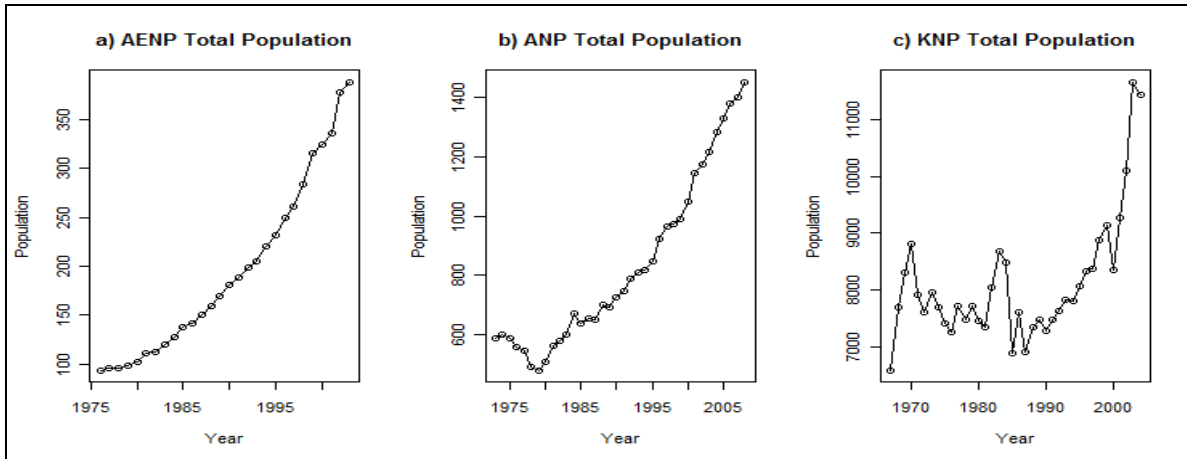


Figure 4.1 Time series plots of total elephant population. Population time series for AENP (figure a) and ANP (figure b) show exponential growth. Figure c show KNP population that stagnated during periods when culling was being done.

For observed time series of population abundance analysis should be preceded by exploratory analysis. For the purpose of illustration, consider the population abundance of African elephants from the ANP and AENP in Kenya and South Africa respectively. The descriptive statistics as in Table 4.1 show that the data is skewed and platykurtic with a negative Kurtosis.

Table 4.1 Descriptive statistics of ANP & AENP

Statistics	Amboseli ANP	Addo ANP
Minimum	481	94
Mean	836.5	195.7
Median	736	175.5
Maximum	1451	388
Skewness	0.724	0.698
Kurtosis	-0.745	-0.665

Both AENP and ANP elephant population data values (figure 4.1a & b) are not stationary in mean value. The Autocorrelation functions (ACF) of the ANP and AENP show the presence of trend as in Figure 4.2 a and b, respectively. We difference twice to get a relatively stationary series for both ANP and AENP as in figure 4.2 c and d, respectively.

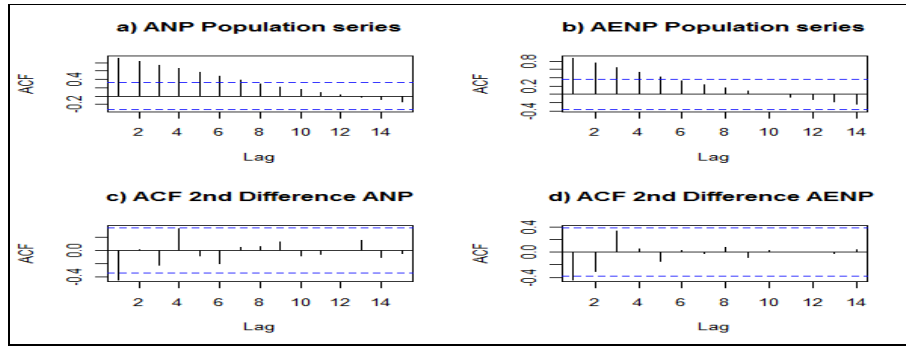


Figure 4.2 ACF of ANP and AENP Population Abundance. Both the ACF of the total abundance for ANP and AENP are not stationary (figure a and b), but the corresponding ACF of the second difference are (figure c and d).

The ACF gives a profile of the linear correlation at all possible lags and shows which values of lag, h , lead to the best predictability. To check for nonlinear relations, it is convenient to display a lagged scatter plot matrix, as in Figure 4.3, that displays values of x_t on the vertical axis plotted against x_{t-h} on the horizontal axis for the AENP. None of the lags show a non-linear relationship between current population and its past size. KNP population show no linear relationship for lags greater than 3, possibly due to the management strategy adopted in 1967 to 1994 that allowed culling.

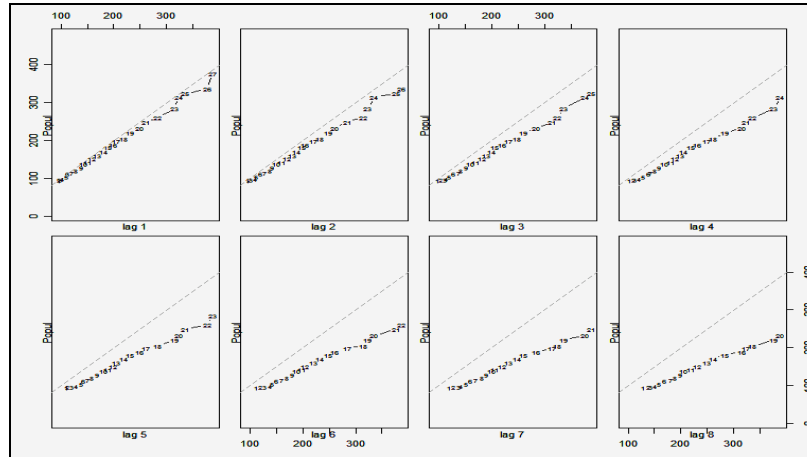


Figure 4.3 Lagged scatter matrix plot for AENP population. The Scatter plots of the lagged values show that there is dependence of the population on past population sizes. Population dependence on past values (i.e. dependence of x_t to its past x_{t-h}) reduces as the lag increases.

4.2.2 Log-linear fit

Assume the population of elephant in a region is affected by births (b), deaths (d), immigration (i), and emigration (e).

$$\Delta n = (b - d + i - e)\Delta t,$$

$$\Rightarrow \frac{dN}{dt} = rN.$$

Consider a deterministic exponential growth model;

$$N(t) = N(0)\lambda^t, \quad (4.1)$$

where λ is the population growth rate per time step. Thus,

$$\log N_t = \log N_0 + t \log \lambda. \quad (4.2)$$

A linear model can be fit to the log transformed data for both discrete and continuous case. For the continuous case the projection model is

$$\begin{aligned} N_t &= N_0 e^{rt}, \\ \log N_t &= \log N_0 + rt. \end{aligned} \quad (4.3)$$

There is a bias in transforming back from logarithm scale to original population count. But transforming back is not necessary if the purpose is comparison. In this section we compare elephant population of ANP in Kenya with that of AENP in South Africa using the slope $\log \lambda$.

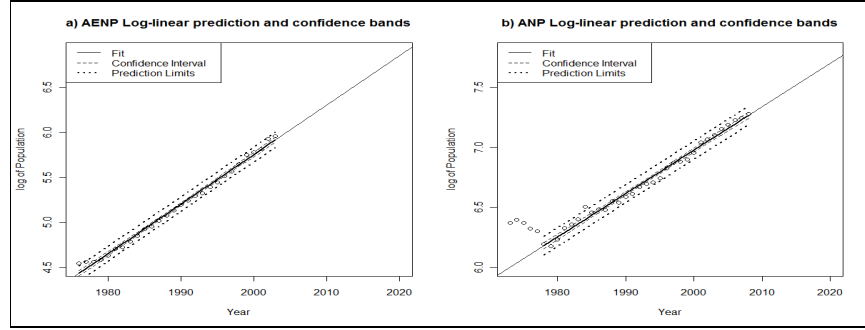


Figure 4.4 Log-linear population fit and projection. Linear fit of the log transform of total population against time with 95% confidence intervals and prediction limits for AENP population (figure a) and ANP (figure b).

Figure 4.4 shows the plot of transformed population data for AENP in South Africa (figure 4.4a) and ANP in Kenya (Figure 4.4b). The prediction bands are wider than the 95% confidence intervals for both cases as we would expect. The narrow bands, confidence bands, reflect the uncertainty about the line itself, while the wide bands, the prediction bands, include the uncertainty about future observations. The models for the two populations are as in Table 4.2 below,

Table 4.2 Log-linear models

National Park	Model	Residuals Standard Error	Degrees of freedom	Multiple R^2	Adjusted R^2	P-value
AENP	$\log N_t = -104.02 + 0.05498t$	0.039	26	0.993	0.9927	$< 2.2e-16$
ANP	$\log N_t = -65.42925 + 0.0362t$	0.0363	29	0.988	0.998	$< 2.2e-16$

All the intercept and slope parameters in the two models are highly significant;

$$\begin{aligned} \text{AENP: } \log N_t &= -104.02 + 0.05498t, \\ \text{ANP : } \log N_t &= -65.43 + 0.0362t. \end{aligned} \quad (4.4)$$

Elephant population in AENP have in general shown higher rate of growth than ANP with $\log \lambda = 0.055$ for AENP and $\log \lambda = 0.0362$ for ANP per annum increase rate on the log scale. If the assumption that the population is undisturbed and there is no catastrophe the population are expected to continue in the upward trend. In chapter five we considered how population structure and corresponding population vital parameter affect population trend and efforts to manage the population of elephants.

4.2.3 ARIMA model fitting and forecasting

The $ARIMA(p, d, q)$ models are useful in modelling series with non-stationary trend component and zero-mean stationary component. We demonstrate the model search for both AENP and ANP series with a similar process also necessary for the KNP population series. In the three classes of models $ARIMA(0, d, q)$, $ARIMA(p, d, 0)$ and $ARIMA(p, d, q)$ the best fitting models using the AIC are:

- $ARIMA(0, 2, 2)$, $ARIMA(3, 2, 0)$ and $ARIMA(1, 2, 1)$ for the ANP total population. The $ARIMA(0, 2, 2)$ is the selected model for it has the least forecasts standard errors and the least AIC (Table 4.3), and
- $ARIMA(0, 2, 2)$, and $ARIMA(1, 2, 2)$ for the AENP total population. The $ARIMA(0, 2, 2)$ is the selected model for it has the least forecasts standard errors and the least AIC (Table 4.3). Another model with is sufficiently low AIC is $ARIMA(2, 2, 2)$ but the psi weights are not small enough for the Ljung-Box tests unless we increase the lag.

Table 4.3 ARIMA Population models.

Region	Model	Parameters	AIC*n	Log likelihood
Amboseli ANP	$ARIMA(0, 2, 2)$	ma1 ma2 -0.7464 -0.0389 s.e. 0.1729 0.1636	9.26575	-163.78
	$ARIMA(3, 2, 0)$	ar1 ar2 ar3 -0.6516 -0.4692 -0.4178 s.e. 0.155 0.1719 0.150	9.285278	-163.13
	$ARIMA(1, 2, 1)$	ar1 ma1 0.0474 -0.7955 s.e. 0.2077 0.1154	9.26584	-163.79
ADDO AENP	$ARIMA(0, 2, 2)$	ma1 ma2 -1.2576 0.6589 s.e. 0.1638 0.1503	6.38704	-86.42,
	$ARIMA(1, 2, 1)$	ar1 ma1 ma2 0.1510 -1.3504 0.7203 s.e. 0.3081 0.2468 0.1942	6.449427	-86.29
	$ARIMA(2, 2, 2)$	ar1 ar2 ma1 ma2 -0.278 -0.803 -0.892 1.00 s.e. 0.134 0.129 0.192 0.3698	6.178897	-81.5

Model diagnosis showed that the residuals are random with mean zero. The ACF of the standardized residuals shows no apparent departure from the model assumptions, and the Ljung-Box-Pierce Q -statistic is never significant at the lags shown for both models. Figure 4.5a & b shows the diagnostics for these models, leading to the conclusion that the models are adequate.).

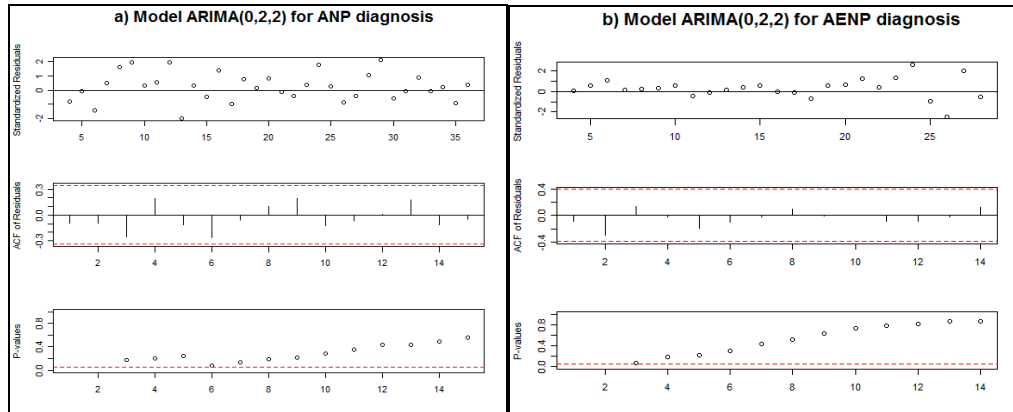


Figure 4.5 ARIMA(0,2,2) models diagnosis for ANP and AENP fits. Diagnosis of the selected models using standardized residuals, ACF of residuals and Ljung-Box-Pierce Q -statistic. The result shows that both models are adequate for the respective data.

Both the models are fairly acceptable since the residual and probability values of the Ljung-Box-Pierce Q -statistics are not significant for the given lags. After diagnosis we proceed to conduct population forecasting assuming the models are a sufficient representation of the population series.

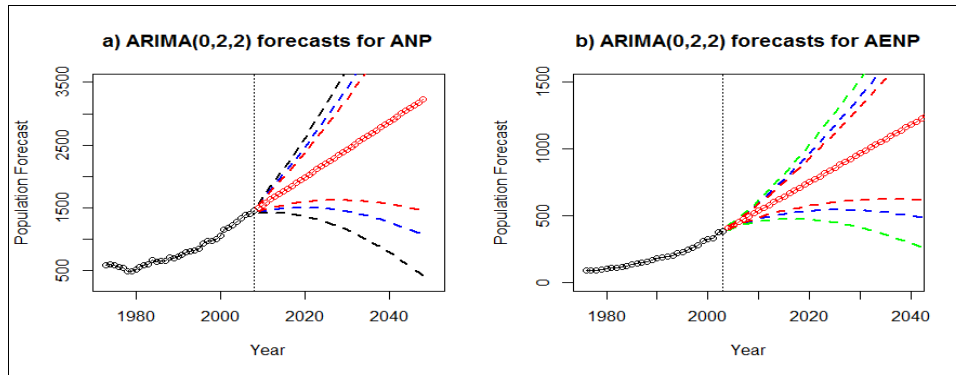


Figure 4.6 ARIMA(0,2,2) forecasts with 90, 95 and 99% confidence interval. ARIMA models for ANP (figure a) and AENP (figure b) with respective forecasts and 95% forecast precision. Forecast show increasing prediction error as the forecast horizon increases.

For $ARIMA(p, d, q)$ models the accuracy of future prediction depends on the memory of the model. The higher the m – steps-ahead forecast, the less accurate is the prediction (see Figure 4.6). Table 4.5 shows the forecasts with the respective forecast's standard error.

In Table 4.4 below, $ARIMA(0, 2, 2)$ forecasts and their corresponding standard errors are given for selected years. Values without standard error are actual observed data values. The $ARIMA(0, 2, 2)$ forecasts shows a much less doubling time for AENP of approximately 15-17 years compare to the ANP population of 22-25 years. This is as expected from other vital parameters as we will see later in chapter five. The AENP elephant population have shown relatively faster recovery than ANP population in Eastern Africa.

We note the growth rate, r_t , series for AENP and ANP have intercept 0.055 (± 0.005) and 0.027 (± 0.0092) respectively. Fitting autoregressive ($AR(p)$) models on the difference in growth rate, $y_t = r_t - r_{t-1}$, for the AENP and ANP give the following (Table 4.4) $AR(p)$ parameter estimates with mean of zero.

Table 4.4 ARIMA Forecasts for population growth rate.

Model	AENP Parameters				ANP Parameters			
	ϕ_1	ϕ_2	ϕ_3	Log L	ϕ_1	ϕ_2	ϕ_3	Log L
AR(1)	-0.55 s.e. 0.18			50.86,	-0.44 s.e. 0.15			54.33
AR(2)	-0.75 s.e. 0.17	-0.59 s.e. 0.18		55.07	-0.53 s.e. 0.17	-0.19 s.e. 0.17		54.95
AR(3)	-0.96 s.e. 0.18	-0.89 s.e. 0.21	-0.44 s.e. 0.20	57.18	-0.59 s.e. 0.16	-0.37 s.e. 0.18	-0.32 s.e. 0.16	56.89

Using the Ljung-Box tests, we select the $ARIMA(2, 1, 0)$ to model the rate of growth. As shown in the figure below, the confidence limits of the predicted growth rate grow wider as we move to the future. The plot shows the 90, 95 and 99 percent confidence limits for the predicted values (Figure 4.7).

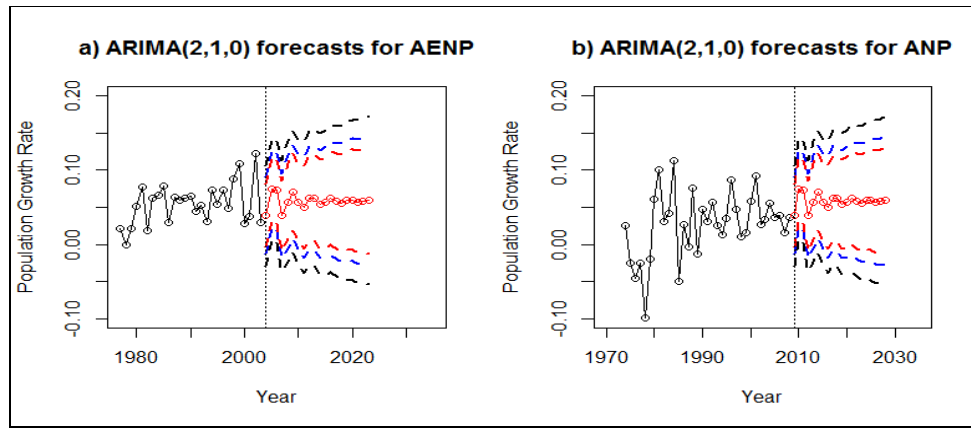


Figure 4.7 ARIMA forecasts for population growth rate. Forecasts for population growth rate with their respective 90, 95 and 99 percent confidence intervals.

Table 4.5 ARIMA Population Forecasts.

Year	ANP Amboseli		AENP Addo	
	Population	Standard Error	Population	Standard Error
2002	1175		377	
2004	1281		412	6
2006	1379		455	11
2008	1451		497	19
2012	1628	81	583	43
2016	1806	155	669	73
2020	1983	239	755	108
2024	2160	334	841	148
2028	2337	438	927	191
2032	2514	551	1012	238
2036	2691	672	1098	289

4.2.4 Predictions using bootstrap

4.2.4.1 AENP and ANP forecasts compared

Bootstrapping is important in estimation of parameter and conducting statistical inference on these parameters. If we do not have enough data to perform statistical inference, bootstrapping is an option that helps us to draw more samples from the available sample and thus enhancing statistical procedures of parameter estimation. After simulating multiple trajectories of population abundance we were able to determine the empirical distribution of the predictions.

Using historical data we calculate $R = (N_{t-1} - N_t) / N_t$ for consecutive years and assume that the conditions in the selected park remain relatively similar. Assuming that these R 's are representative of in the future, and that each is equally likely to occur, we resample the observed values with replacement for each year of the simulation. Bootstrapping results are illustrated in Figure 4.7a and 4.7b, for AENP and ANP respectively.

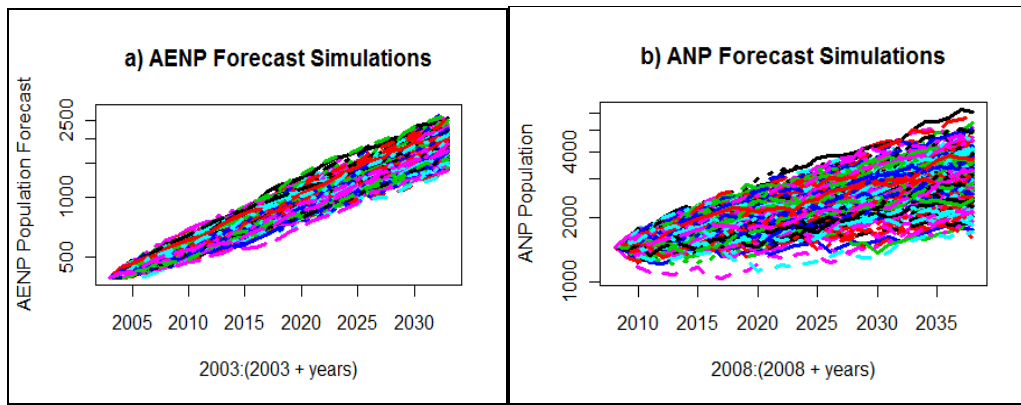


Figure 4.8 Bootstrapping population projections. Population projection plotted on the log scale. Bootstrapping on the rate of growth R shows that AENP population (figure a) shows higher growth rate with less variability compared to the ANP (figure b).

We need to replicate this process a very large number of times (Figure 4.8), and examine the distribution of outcomes, including moments of the distribution such as the mean, median, and confidence interval of eventual outcomes. Plotting on the log scale as in Figure 4.8, helps reveals that the relative population change is independent of population size.

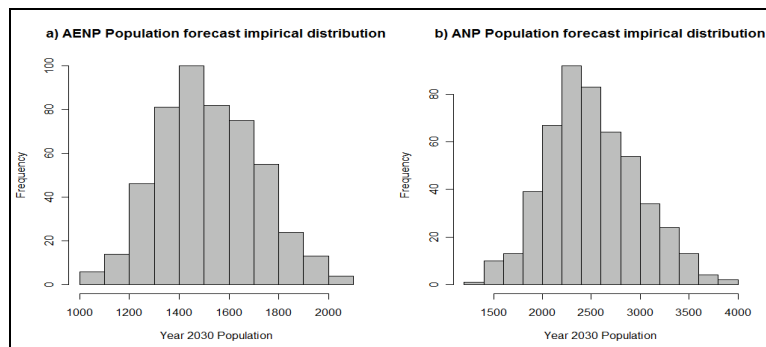


Figure 4.9 Bootstrapping projections distribution. The empirical distribution of the population forecast of year 2030 for AENP (figure a) and ANP (figure b). The population size will grow and there is a zero chance of population extinction if the conditions in the parks remain the same.

Both the histogram in Figure (4.9a) and (4.9b) and the summary statistics of the empirical distribution showed a skewed distribution with mean 1530 and 2592 for AENP and ANP respectively. There is however a zero chance of extinction for both populations. Table 4.6 gives the results for projected populations and summary statistics that help us quantify the level of uncertainty of the projections. The assumption in these projections is no animals are removed or added to the population unless through natural birth or mortality.

Table 4.6 Empirical distribution of bootstrapping projections

Amboseli ANP							ADDO AENP						
Year	Min	Q ₁	Med	mean	Q ₃	Max	Year	Min	Q ₁	Med	mean	Q ₃	Max
2008	1451	1451	1451	1451	1451	1451	2008	436	495	405	506	526	617
2010	1312	1510	1560	1563	1620	1797	2010	458	536	561	564	589	713
2015	1375	1763	1874	1883	3364	2453	2015	572	687	729	734	771	996
2020	1466	2058	2256	2268	2456	3364	2020	684	879	947	956	1028	1341
2025	1569	2432	2694	2723	2985	5001	2025	843	1134	1237	1249	1345	1825
2030	1869	2885	3216	3280	3635	6283	2030	1120	1462	1610	1628	1772	2470
2035	2008	3400	3865	3943	4395	8849	2035	1399	1874	2094	2114	2316	3183
2040	2192	4044	4630	4755	5377	12160	2040	1639	2400	2700	2752	3044	4374

The utility of forecasted values depends on their accuracy or precision error for time series forecasts. The Table (4.7) below shows a comparison of the projected future values for both the ANP and AENP for different models.

Time series forecast are only useful for short forecast horizon. Values projected using a lineal model (straight line fit) do not give any measure of uncertainty as opposed to mean values from bootstrapping that come with a measure of uncertainty.

Table 4.7 Population projections comparison table

Amboseli ANP				Addo AENP			
Year	Linear Model	ARIMA Model	Mean of Bootstraps	Year	Linear Model	ARIMA Model	Bootstrapping
2008	1451	1451	1451	2008	489	497	506
2012	1657	1628	1688	2012	610	583	627
2016	1915	1806	1955	2016	760	669	773
2020	2214	1983	2268	2020	947	755	956
2024	2559	2160	2627	2024	1180	841	1184
2028	2958	2337	3042	2028	1470	927	1465
2032	3419	2514	3224	2032	1832	1012	1807

Using the Table 4.7 above, the linear model gives a population doubling time of about 18 years and 12 years for ANP and AENP respectively. These doubling time are almost equal for the bootstrapping method. The population forecasts obtained from ARIMA models are only useful when the forecasting time horizon is small and become very unreliable as the forecasting time horizon increases, due to the increasing standard error.

4.2.4.2 Evaluating culling effect at KNP using bootstraps

We calculate observed values of the finite growth rate, R , and perform multiple bootstraps to generate trajectories of population forecasts. This is used to compare population projections for values of R calculated with and without culling period. Using KNP data for the period when there was culling and periods with minimal or no culling we obtain the following plot.

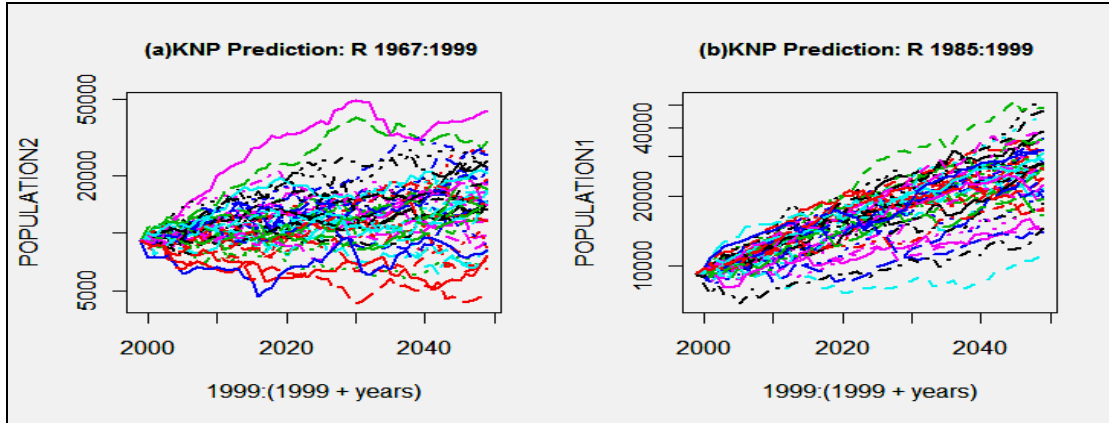


Figure 4.10 50-years population predictions from 2000. Predictions are performed with R re-sampled from the periods 1967-99 (figure a) when there was culling and 1985-99 (figure b) when there was minimal culling. Values are plotted on the log scale.

For the projections in figure 4.10 (b), the minimum=9404, 1st quartile Q_1 = 21306, median=26040, mean=27259, 3rd quartile Q_3 = 32110, and maximum=78186. Giving an empirical confidence of (2.75%, 97.5%) as (14194.49, 45824.95). We might observe Elephant counts anywhere from 12,754 to 45824, where 12,754 and 45824 are equally likely. The forecast gives correct predictions for 2002 to 2006, which by counts done were 10,459 and 12,427.

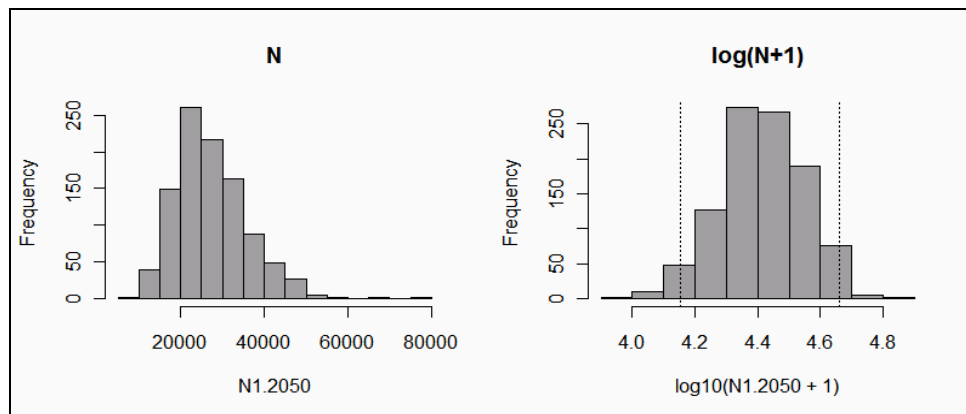


Figure 4.11 Population predictions distribution for R selected from 1985-99: Empirical distribution of KNP elephant population projections with minimal or no culling.

The first histogram show a skewed distribution (Figure 4.11a) which when plotted on the log scale is bell shaped (Figure 4.11b). This is an indication that the predictions have a lognormal

distribution. There is no chance of extinction for that period. If we repeat the same simulations assuming some culling is done occasionally we obtain Figure 4.12.

Similarly for Figure 4.10 (a), the following summaries are obtained: min=3628, 1st quartile $Q_1 = 11069$, median=15410, mean=17280, 3rd quartile $Q_3 = 21716$ and maximum=68156. The 0.0275th and 0.975th quintiles are 6138 and 38793.

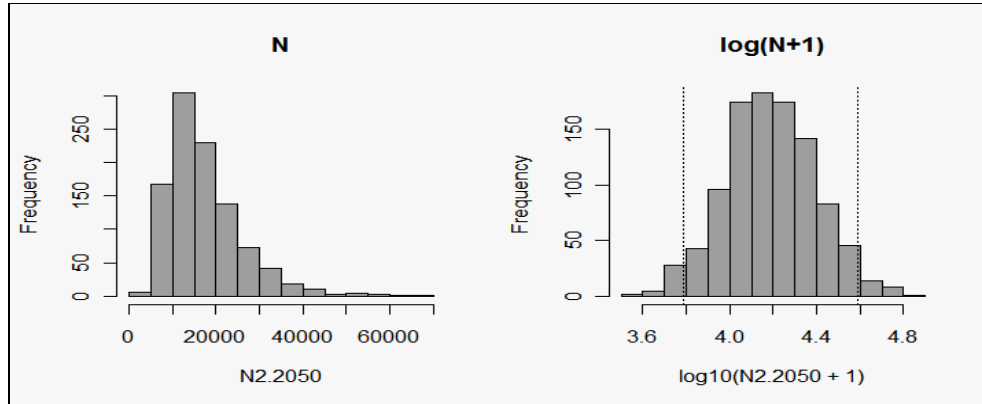


Figure 4.12 Population predictions distribution for R selected from 1967-99: Empirical distribution of KNP elephant population projections with random culling.

Comparing Figures 4.11 and 4.12 shows that we have lower population median and mean while there is random removal. We conclude that random removal will in general reduce population growth although it may not lead to extinction if appropriate strategy is applied. The forecasts give correct predictions for 2002 to 2006, which by counts done were 10,459 and 12,427. Figure 4.13 demonstrate a summary of methods performed above for the KNP.

Using bootstrap on observed finite rate of growth R , the confidence limit for R (between 1985 and 1999) are, (0.994, 1.048), and the confidence limit for R (between 1967 and 1999) are, (0.986, 1.036). This confirms the results observed that the populations are expected be higher when there if reduced culling (Figure 4.13). Simulations using the first R interval (0.994, 1.048), gave (6737, 94756), showing that population will not grow to extinction.

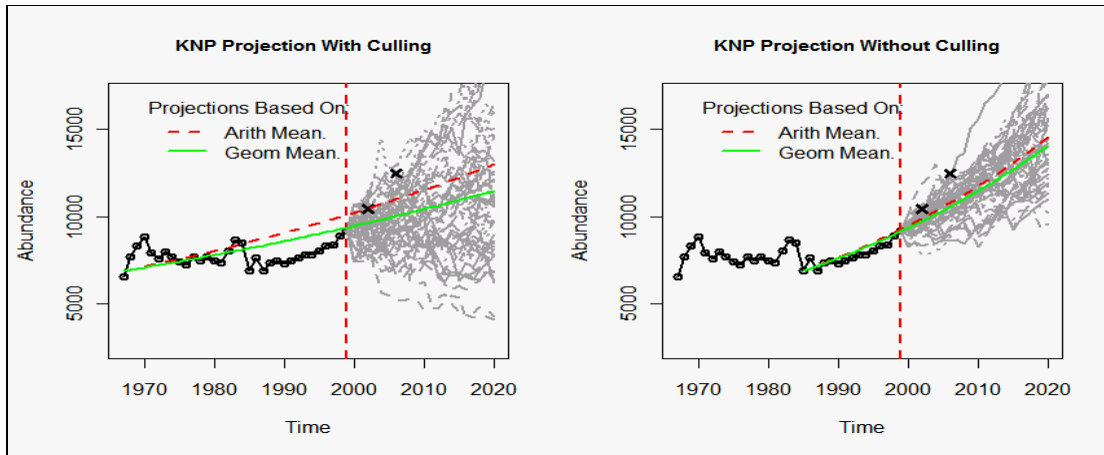


Figure 4.13 Predictions comparison KNP. Population projections with random culling gives lower mean and increase variability (figure a) compared to population projections with minimal or no culling (figure b) which shows higher means and reduced variability.

Simulation using the second R interval, $(0.986, 1.036)$, gave $(4367, 54821)$, showing that population will probably not grow to extinction but the figures are much lower. It important to note that these simulations are based on assumption that, population changes and management policy remain as for the periods between 1967 and 1999.

Using bootstraps of the annual growth rate we have forecasted population growth for two different populations. Value predicted for the KNP agree with observed values for data available as shown in Figure 4.13. It is evident that culling increase the chance of extinction as the time line increases. But population management is necessary for the populations discussed to reduce the high growth predicted and observer during the years there was no culling.

4.3 Bayesian inference on growth rate

4.3.1 Assumption

We define the basic growth rate $r = \ln(N_t/N_{t-1})$ which is also referred to as the annual instantaneous per capita growth rate. The finite rate of growth is given by $\lambda = N_t/N_{t-1}$ where N_t the population size at time t . The relationship between r and population abundance, density or recourses is used to determine population vitality. As already mention in the introduction we seek to study and model r for AENP and KNP and use the derived Bayesian distributions to compare the two populations.

The observed values of r for KNP excluding one outlier and those for AENP do not show departure from the normal distribution (Hones, 1999) as in Figure 4.14. Figure 4.14 shows normal theoretical qq -plots for both KNP and AENP comparing standardized values of r with theoretical normal quantiles. Steven (2009) mentions the need for inference on $\log \lambda = \ln N_t - \ln N_{t-1}$ and uses

the t -distribution due to its pervasive use in statistics and life. While deriving a Bayesian distribution of the rate of growth r in section below, we assumed that the log the transformed data are normally distributed.

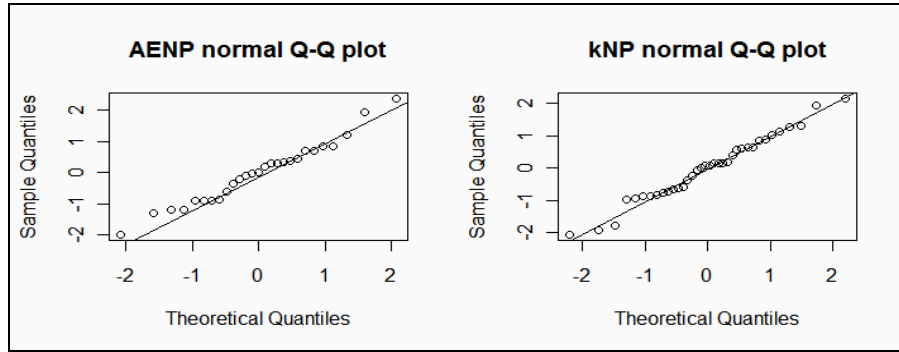


Figure 4.14 Normal theoretical qq -plots for finite population growth rates: testing for the assumption of normality of the observed growth rate using qq -plots. Although the observations are few, they do not depart significantly from the normal assumption.

Using a box plot to compare the KNP and AENP elephant's exponential growth rates (Figure 4.15), we realize that AENP has relatively higher average exponential growth rate (Minimum=0.0, 1st quartile Q_1 = 0.02, Median=0.053, Mean=0.0525, 3rd quartile Q_3 = 0.068, and Maximum=0.115) compared to KNP (Minimum= -0.207, 1st quartile Q_1 = -0.027, Median=0.026, Mean=0.016, 3rd quartile Q_3 = 0.062, Max=0.157). KNP exponential growth rate has higher spread with a standard deviation of 0.073, compared to AENP with standard deviation equal to 0.027. It is important to note that the low values of r and higher spread observed for KNP data was as a result of culling in the years before 1994 when culling took place. The box plots do not show major departure from normality. There is only one outlier in the case of KNP data which correspond to year 1984 when culling was still being done.

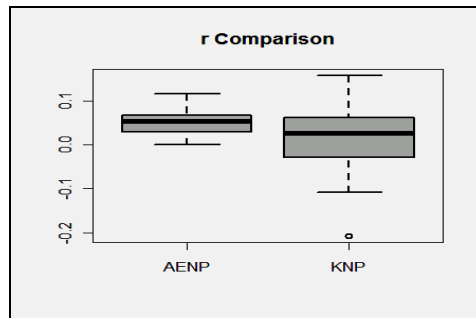


Figure 4.15 Comparison of AENP and KNP growth rates. Box plot of AENP and KNP growth rates show lower mean and wider spread for KNP data.

In classical statistics parameters are assumed to be constant to be estimated, but in a Bayesian approach parameters are regarded as having distributions which provide information about the parameters. The aim of a Bayesian analysis is to estimate the joint posterior distribution of all of the

model parameters. Bayesian methods are data analysis tools that are derived from the principles of Bayesian inference. We use three steps common in Bayesian methodology and given in Hoff (2009) and Albert (2009). For a parameter θ representing an unknown characteristic of the population with entire space Θ , and observed sample data y belonging to the data space Y . Determine the individual yearly r 's observed, $r_1, r_2, \dots, r_n$ form a large sample of independent random variables. By the central limit theorem they are assumed to be normally distributed with mean r and known standard deviation σ . This assumption can be justified by the fact that the sample size is large, hence the central limit theorem applies to the transformed data.

4.3.2 Prior

For $\theta \in \Theta$, the prior distribution $p(\theta)$ describes our belief that θ represents the true population characteristics. This is the prior function $p(r)$ giving the prior knowledge or guess by an expert on the rate of growth. Before collecting data, we assign weights on our belief that the population can increase or decrease with the following percentages:

Percentage	-25%	-20%	-15%	-10%	-5%	0%	5%	10%	15%	20%	25%
Weight	1	2	3	5	7	9	7	5	3	2	1

If we have no prior knowledge we use a non-informative prior or a diffuse prior that assigns equal weights to the possible population percentage changes.

4.3.3 Likelihood

For each $\theta \in \Theta$ and $y \in Y$, our sampling model $p(y|\theta)$ describes the likelihood of observing y given θ to be true. Once we obtain the data y , the last step is to update our beliefs about θ . We start by assuming normality and known constant variance, σ^2 , which does not vary over time in which case the likelihood is given by,

$$L(r) \propto \exp\left(-\frac{n}{2\sigma^2}(r - \bar{r})^2\right), \quad (4.5)$$

where n is the sample size. If the observe annual rate of population growths are $r_1, r_2, \dots, r_n$, act like new data on r .

4.3.4 Posterior

For each numerical value of $\theta \in \Theta$, our posterior distribution $p(\theta|y)$ describes our belief that θ is the true value, having observed dataset y . The posterior distribution is obtained via

$$p(\theta|y) = \frac{p(y|\theta)p(\theta)}{\int_{\Theta} p(y|\tilde{\theta})p(\tilde{\theta})d\tilde{\theta}}. \quad (4.6)$$

The observed data y increases the information we have on θ . Since $\int_{\Theta} p(y|\tilde{\theta})p(\tilde{\theta})d\tilde{\theta}$ does not depend on θ the posterior distribution $p(\theta|data)$ depends on the product of the likelihood $L(\theta) = p(y|\theta)$ and the prior, $p(\theta)$, probability distribution:

$$p(\theta|data) \propto p(\theta)L(\theta). \quad (4.7)$$

The posterior density for r , by Bayes' rule, is obtained, up to a proportionality constant, by multiplying the prior density by the likelihood:

$$p(r|data) \propto p(r)L(r).$$

Later in our analysis we drop the assumption of known variance in which case the joint posterior of the mean and variance (r, σ^2) is given by equation (4.8) assuming a standard non informative prior $p(r, \sigma^2) \propto 1/\sigma^2$ (Albert, 2009) :

$$p(r, \sigma^2 | data) \propto \frac{1}{(\sigma^2)^{n/2+1}} \exp\left(-\frac{1}{2\sigma^2}(S + n(r - \bar{r})^2)\right), \quad (4.8)$$

where $S = \sum_{i=1}^n (r_i - \bar{r})^2$.

We use *R* package, LearnBayes (*R* Development Core Team, 2011), to plot contours and simulate values from the joint posterior. Bayesian methods allow for the relaxing of the normality assumption. If we compute the posterior probabilities of r for the case of AENP, the following weighted posterior is acquired;

r	-.11	-.05	0	.05	.09	.14	.18
Probability	0	0	0.013	0.95	0.033	0	0

It is evident that after data observation we have more information on r and only values in the interval 0 to 10% percent change have a high chance of being observed with probability of 0.99. The posterior probabilities of r for the case of AENP for the diffuse posterior gives:

r	-.11	-.05	0	.05	.09	.14	.18
Probability	0	0	0.009	0.94	0.046	0	0

No major variation in result is realised for either assuming the weighted or diffuse prior probability. The posterior probabilities presented in figure 4.19 represent the discrete posterior by presuming the weighted or diffuse prior distributions. Comparing Figure 4.19a and 4.19c, it shows that the discrete posterior for r will be between 0 and 0.05 and between 0.05 and 0.1 with high probability for KNP and AENP respectively. It is evident the on average r will be high for AENP.

Treating r as a continuous variable, we obtained a posterior distributions illustrated in Figure 4.16 a) and c) for AENP and KNP respectively. Sampling from these posterior distributions we obtained values illustrated using histograms in Figure 4.16 b) and d) for each case.

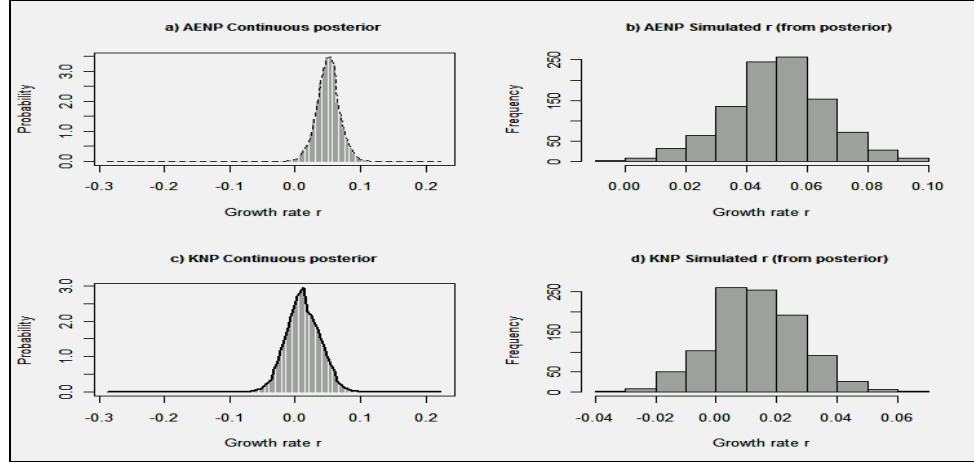


Figure 4.16 Continuous posterior densities and simulated r values. The figure give a continuous approach in determining the distribution of the growth rate with values simulated from the corresponding posterior densities.

Simulating a sample of 1000 values of r from the posterior density we acquire the empirical distribution for r (see figure 4.16 b, c). For 1000 simulated values from each posterior density the minimum= -0.073, 1st quartile Q_1 = -0.005, Median=0.014, Mean=0.013, 3rd quartile Q_3 = 0.031, and maximum=0.094 for KNP and Min=0.004, 1st quartile Q_1 = 0.042, Median=0.052, Mean=0.052, 3rd quartile Q_3 = 0.062 and maximum=0.099 for AENP (figure 4.16). Figure 4.16 a and b are the posterior distribution of r for AENP and KNP respectively, where as 4.16 b and c are the histogram of 1000 simulated values from respective posterior distributions. These values closely agree with the boxplot and summary values in figure 4.15 above. Thus the posterior distribution of r agrees with observed data. This approaches a normal curve as sample size increases. This procedure can also be used to perform predictions and determine the predicted distribution.

We note that practically the simulated values are distributed normally and are concentrated on the values r between 0 and 0.10. The modal class interval of r is 0.05 to 0.06 is in the middle of this empirical distribution of the simulated values for AENP. There is no reason to doubt our Bayesian model since it agrees well with the observed values. To compare the two populations we plot the continuous posterior distributions of r , for the AENP and KNP population assuming a continuous weighted prior. In this case, as in Figure 4.17 below, the posterior distribution of r is higher for AENP taking values larger than 0 and 0.1 compared to lower values of -0.05 and 0.09, for KNP as in figure 4.17.

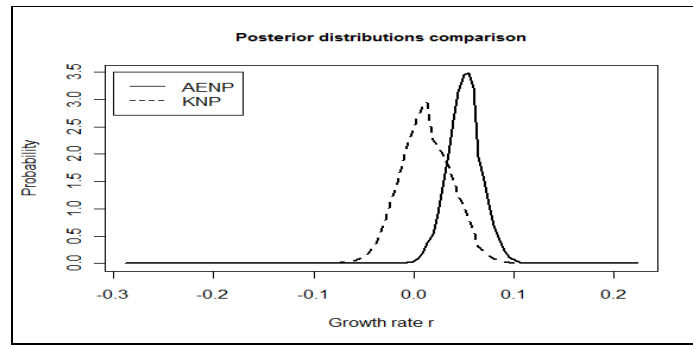


Figure 4.17 Comparison of the Bayesian distributions of r . Figure 4.21 shows comparison of the distribution of the net growth rate for AENP with KNP.

It is evident that posterior r distribution has a higher mean for AENP than for KNP as in Figure 4.17 above. This method of comparing population is desirable, since we are comparing distribution of rate of growth instead of realized values. Culling in these calculations is assumed to increase mortality and thus reduce population growth.

When we drop the known variance assumption, the joint posterior distribution of the mean and variance for growth rate is as in Figure 4.18. AENP shows higher mean and lower dispersion (Figure 4.18b) compared to KNP which has lower mean and higher dispersion (Figure 4.18a).

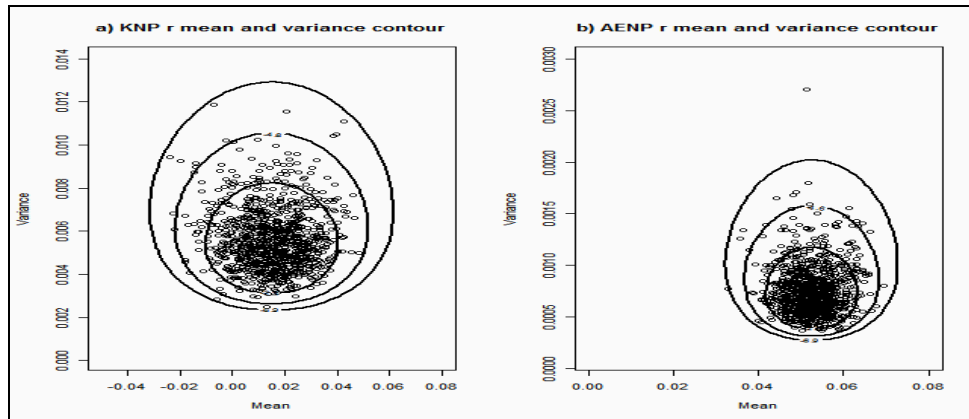


Figure 4.18 Joint posterior distributions for mean and variance. Figure 4.22 shows comparison of the joint distribution of the net growth rate variance and mean for KNP with AENP. The contour lines are drawn at 10%, 1%, and 0.1% of the maximum value of the posterior.

Figure 4.18 gives the contour for joint posterior distribution for mean and variance of r plotted together with 500 simulated points from the joint posterior. The contour lines are drawn at 10%, 1%, and 0.1% of the maximum value of the posterior. Putting the contours and respective points in a single graphic gives a clear and better comparison of the two populations. AENP shows less variance compared to KNP but higher mean value as seen in Figure 4.18.

This analysis shows the effect of culling on elephant population at KNP. Although the KNP elephant population continues to grow exponentially the effect of culling is evident in comparison with AENP population which shows less variation in values of crude population increase, r . These

results hold if we keep in mind the assumption that the log transformed data are normally distributed.

4.4 Concluding remarks

As stated earlier in this chapter, one of the challenges that arise in modeling time series population abundance is the quality of population data available. Total elephant population count data should be accompanied by the range size of the area where the survey or total count was conducted. Population density or its trend, analyzed together with other ecological factors such as resource availability should be used to inform management decisions. Various approaches may be used in the determination of population density among them the crude density or the ecological density (Gaston *et al.*, 1999). These would better replacement of total population when the range size has varied over time. But we should be cautious, since according to Gaston *et al.* (1999) estimates of density are not always independent of the area over which populations are censured.

The two populations considered, the Amboseli National Park (ANP) and the Addo Elephant National Park (AENP) were selected as examples of an open and closed population. The AENP population was about 11 individuals in 1931 and had remained closed to migrants. The range size for the AENP has however, varied due to increase in park size. The model fitted showed a significant exponential growth rate. The ANP elephant population which is an open population was about 480 animals in 1978, the population is much higher today. The model fitted also showed a significant exponential growth.

Another challenge that arises is where the total population counts are not done on regular and equal intervals of time. When the period interval is greater than one year only estimates annual of population growth can be found (Eberhardt and Simmons, 1992). More advance autoregressive models for irregular time series can be applied to such data. The Bayesian distribution of the growth rate approach discussed in section 4.3 offered a way of studying population rate of growth in cases where the population counts have varying range size or irregular time intervals. The Bayesian distribution also offers a method of evaluating the distribution of the growth rate over time and it is possible to sample from the posterior distribution and predictive distribution.

Changes in total elephant population numbers are the basis of many management plans and policies, but the effectiveness of management ought to be weighed response on impact of affected species, ecological processes, elephant range utilisation, and elephant numbers. It is thus important to increase understanding on social, spatial, and demographic profiles of Africa's elephant populations since they affect the distribution and numbers of elephant population.

CHAPTER 5: AGE STRUCTURED MODELING OF ELEPHANTS POPULATIONS

5.1 Introduction

Age-structured models for biological species were traditionally ignored with the assumption that the populations can be treated as homogeneous with respect to age. But many vital population dynamics parameters are age dependent. An age-structured population at a given time reveals a set of individuals who were born over a range of past times, and whose fertility and probability of mortality or survival depend on their age.

Demographic parameters of the elephant population are age dependent. The demographic parameters include, age at reproductive maturity and menopause, calving interval, sex ratio at birth, and age-specific probabilities of conception and survival. We study the importance of these parameters by conducting what-if-analysis. It was established that the optimal strategy of managing structured elephant populations through sensitivity and elasticity analysis of the transition matrices. In this chapter we demonstrate the importance of demographic structure in models used to assess population dynamics of the elephant species. Different structured population models are derived and analysis results given. Main areas considered include

- i. The relationship between different approaches to structured population models: matrix population models, integro-difference equations, delay-differential equations, and partial differential equation,
- ii. Derivation and application of deterministic and stochastic structured elephant population models to evaluate how population trends are affected by vital rates.
- iii. Modular approach to modelling sub-process such as survival, birth, harvesting and aging for a structured population.

There are different types of structured population models, but they can be represented or converted from one form to the other. In the next section we show the formulation of some of the structured population models and discuss their relationship. Structured population models are classified by whether the states are discrete or continuous or whether they project the population in discrete or continuous time.

	<i>Discrete state</i>	<i>Continuous state</i>
<i>Discrete-time</i>	Matrix population models	Integro-difference equation
<i>Continuous-time</i>	Delay differential equation	Partial differential equation

Figure 5.1 Types of structured population models. The different types of structured population models are classified by whether the states are discrete or continuous and whether they project the population in discrete or continuous time.

5.2 Structured population models

5.2.1 The Lotka's renewal equation

The continuous version of the age classified matrix model is given by the McKendrick Foerster equation;

$$\begin{aligned}\frac{\delta n(x,t)}{\delta t} + \frac{\delta n(x,t)}{\delta x} &= -\mu(x)n(x,t), \\ n(0,t) &= \int_0^{\infty} b(x)n(x,t)dx.\end{aligned}\tag{5.1}$$

The boundary condition $n(0,t)$ given by the second equation corresponds to the first row of the Leslie model, gives the births. Note that for the first equation;

$$n(x + \Delta x, t + \Delta t) \cong n(x,t) + \frac{\delta n}{\delta t} \Delta t + \frac{\delta n}{\delta x} \Delta x,$$

Since $\Delta x = \Delta t = h$ for the Leslie model then,

$$\frac{\delta n}{\delta x} + \frac{\delta n}{\delta t} = \frac{n(x+h, t+h) - n(x,t)}{h},$$

and first equation in equation (5.1) becomes a Leslie matrix with survival for a time interval h given by $1 - h\mu(x)$,

$$n(x+h, t+h) = (1 - h\mu(x))n(x,t).\tag{5.2}$$

If we denote the number of births at time t by $B(t)$,

$$B(t) = \int_0^{\infty} b(x)n(x,t)dx.$$

Then $n(x,t) = B(t-x)l(x)$ where $l(x)$ is the survivor function. If we substitute in $B(t)$, we have the renewal equation,

$$B(t) = \int_0^{\infty} b(t-x)l(x)b(x)dx.\tag{5.3}$$

Substituting an exponential solution $B(t) = \exp(rt)$ of the linear function $B(t)$, we have,

$$\begin{aligned}
e^{rt} &= \int_0^{\infty} e^{r(t-x)} l(x) m(x) dx, \\
1 &= \int_0^{\infty} e^{-rx} l(x) m(x) dx.
\end{aligned} \tag{5.4}$$

The Lotka's renewal equation in (5.4) is used to calculate intrinsic rate of increase. Given the functions $l(x)$ and $m(x)$ we tried different values in order to find r , where $m(x)$ is the rate of reproduction at age x .

5.2.2 Delay differential equation

By the principle of causality, the future state of the system is assumed to be independent of the past and is determined solely by the present. This was our assumption in the deterministic and stochastic matrix models but this is an approximation to the true situation. A more realistic model must include some of the past history of the system. For example, an elephant calf, will take around ten years before reaching reproductive maturity inducing a delay in possible models.

Where the age of an animal is not easy to ascertain, we would possibly use size or stage structured models. A delay differential equation model classifies individuals into discrete stages and describes their dynamics in continuous time. A model with juveniles (N_J) and Adults (N_A) as the two stages has the dynamics given by equations;

$$\begin{aligned}
\frac{dN_J}{dt} &= R_J(t) - M_J(t) - D_J(t), \\
\frac{dN_A}{dt} &= R_A(t) - D_A(t),
\end{aligned} \tag{5.5}$$

where $R_J(t)$ and $R_A(t)$ are the recruitment rates, while $D_J(t)$ and $D_A(t)$ are the death rates of the juveniles and adults respectively. If the per-capita rates are given by the equations,

$$\begin{aligned}
D_A(t) &= \mu_A N_A(t), \\
D_J(t) &= \mu_J N_J(t), \\
R_A(t) &= b N_A(t).
\end{aligned}$$

Then noting that maturing juveniles are the survivors of newborn individuals τ time units previously equations (5.5) become,

$$\begin{aligned}
\frac{dN_J}{dt} &= b N_A(t) - b N_A(t - \tau) \exp(-\mu_J \tau) - \mu_J N_J(t), \\
\frac{dN_A}{dt} &= b N_A(t - \tau) \exp(-\mu_J \tau) - \mu_A N_A(t).
\end{aligned} \tag{5.6}$$

The dynamics of such a system are well discussed in Gurney and Nisbet (1983) and Nisbet (1997)

To demonstrate possible application of delay differential equation models for the dynamics of the elephant population, we start with a two stages model. The elephant can be classified as either belonging to either immature juveniles (x_t), aged between zero to around ten year, or mature adults (y_t) above the age of 10. Recruitment into the juvenile stage at any time $t > 0$ is proportional to the existing adult population at a rate b . We then assume that the mortality rate of the juveniles is proportional to the existing juvenile population with proportionality constant μ_j . We assume for the adult population the mortality rate is proportional to the adult population with proportionality constant μ_m . Finally, we assume that those juvenile born at time $t - \tau$ that survive to time t exit from the juvenile population and enter the adult population.

$$\begin{aligned}\frac{dx(t)}{dt} &= by(t) - \mu_j x(t) - be^{-\mu_j \tau} y(t - \tau), \\ \frac{dy(t)}{dt} &= be^{-\mu_j \tau} y(t - \tau) - \mu_m y(t).\end{aligned}\tag{5.7}$$

To capture density dependence and thus consider a more practical model, we assume for the adult population the mortality rate is proportional to the square of adult population with proportionality constant μ_m . The model (5.7) above becomes;

$$\begin{aligned}\frac{dx(t)}{dt} &= by(t) - \mu_j x(t) - be^{-\mu_j \tau} y(t - \tau), \\ \frac{dy(t)}{dt} &= be^{-\mu_j \tau} y(t - \tau) - \mu_m y^2(t).\end{aligned}\tag{5.8}$$

In the case of elephant population the new born and young calves are more likely to be affected by density feedbacks than adult elephant, which are more resilient. A variation on model (5.8) would be;

$$\begin{aligned}\frac{dx(t)}{dt} &= by(t) - \mu_j x(t)y(t) - be^{-\mu_j \tau} y(t - \tau), \\ \frac{dy(t)}{dt} &= be^{-\mu_j \tau} y(t - \tau) - \mu_m y(t).\end{aligned}\tag{5.9}$$

We note that:

- i. For continuity of initial conditions for equation (5.8), we require

$$x(t) = \int_{-\tau}^0 by(\theta)e^{-\mu_j \theta} d\theta,\tag{5.10}$$

the total surviving juvenile population from the observed births on $-\tau \leq t \leq 0$. Assuming that $y(\theta)$ is continuous and nonnegative on $[-\tau, 0]$; then, solutions of system (5.8) exist and are unique for all $t \geq 0$.

- ii. Let $y(0) > 0$, $y(\theta) \geq 0$, on $-\tau \leq \theta \leq 0$. Then the solution of (5.8) with initial condition $y(0)$ and $x(0)$ given by (5.10) is positive for all $t \geq 0$.
- iii. There are two nonnegative steady states in system (5.8), namely, $E_0(0,0)$ and $E^*(x^*, y^*)$ where,

$$x^* = b^2 \mu_m^{-1} \mu_j^{-1} e^{-\mu_j \tau} (1 - e^{-\mu_j \tau}), \quad y^* = b \mu_m^{-1} e^{-\mu_j \tau}.$$

We note that $E_0(0,0)$ is a saddle point in the sense that it has eigenvalues with both positive and negative real parts, and E^* is globally asymptotically (Gurney and Nisbet, 1998 and Nisbet, 1997).

A three class model can be described similarly with elephants aggregated into juveniles from 0 to 9 years, middle-aged from 10 to 39 years and old-aged from 40 to 60 years. Juveniles have not yet reached reproductive maturity while the middle-aged and many of the old-aged elephants are fertile. Such a classification may be represented using delay differential equation. The second stage is chosen such that individuals in this stage have passed the juvenile stage and can thus reproduce.

The delay differential system, which is a deterministic approach, is appropriate for large population, where the stochastic element has a minimal effect in the long run. Delay differential equation models can be applied if the time interval Δx and Δt are not equal ($\Delta x \neq \Delta t$). If the time intervals are equal and population relationship are linear, the model is equivalent to the Leslie (1945) matrix model. A deterministic and stochastic matrix form of the three class model for elephants will be considered later. The delay differential approach was not pursued further in this work.

5.3 Elephants population Model Structure

The population dynamics of the African elephant, which is a long lived species if affected by the age structure of the population since birth and death are age dependent. Individuals in the population have life histories that affect the population dynamics. Birth and death or other transition probabilities are also affected by other sources of variation including time varying processes, such as environmental conditions.

The Leslie matrix model is a simplified discrete approach of modeling the population dynamics of elephant population. The time interval selected determines the form of transition matrix, with small time intervals (less than or equal to 1 year) requiring attention to the individual life history. The three age-classified elephant models derived with a main aim of simplification and mathematical tractability are,

- i. The simplified three age-class model, referred to as the three age-classes elephant's population matrix model. This framework caters for elephants aggregated into juveniles from 0 to 9 years, middle-aged from 10 to 39 years and old-aged from 40 to 60 years. For model simplicity, if the class of middle-aged animals is divided into three classes and the old-age animals are divided into two classes. The resulting model is our next model,
- ii. The six age-classes elephant population matrix model. This model was further grouped into either a ten or one year projection time-scale models.
- iii. The fifteen age-classes elephant population matrix model. This model was further categorized into either a four or one year projection time-scale models.

5.3.1 Three Classes Elephant's Population Matrix Model (3-CEPMM)

These are structured models where the states are discrete and population projection is done on a discrete time steps. For a three-class elephants population model in the Figure 5.2 the dynamics can be described using equation (5.11)

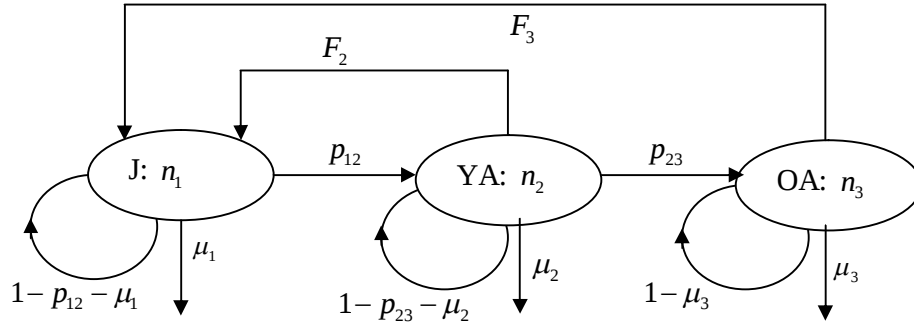


Figure 5.2: Three classes/stage elephant population model. A three age classes or stages model for wild elephant population dynamics. The three classes are n_1 , n_2 and n_3 representing juvenile (ages 0-9), middle-aged (age 10-39) and old-aged (age 40-60).

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \end{pmatrix} = \begin{pmatrix} 1 - \mu_1 - p_{12} & F_2 & F_3 \\ p_{12} & (1 - \mu_2 - p_{23}) & 0 \\ 0 & p_{23} & (1 - \mu_3) \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \end{pmatrix}. \quad (5.11)$$

This is a discrete time scale equivalence of the model in equation (5.11). This model framework is for used in the discussion purposes but further work is required to study the transition matrix parameter estimates.

5.3.2 Six-Classes Elephant Population Matrix Model (6-CEPMM)

Hypothesis: The African elephant population can be modeled using deterministic or stochastic matrix models with six age-classes of 10-years interval.

The Leslie matrix approach can be used to define a basic model for African Elephant population dynamics using 10-years age classes. Consider the life cycle graph below,

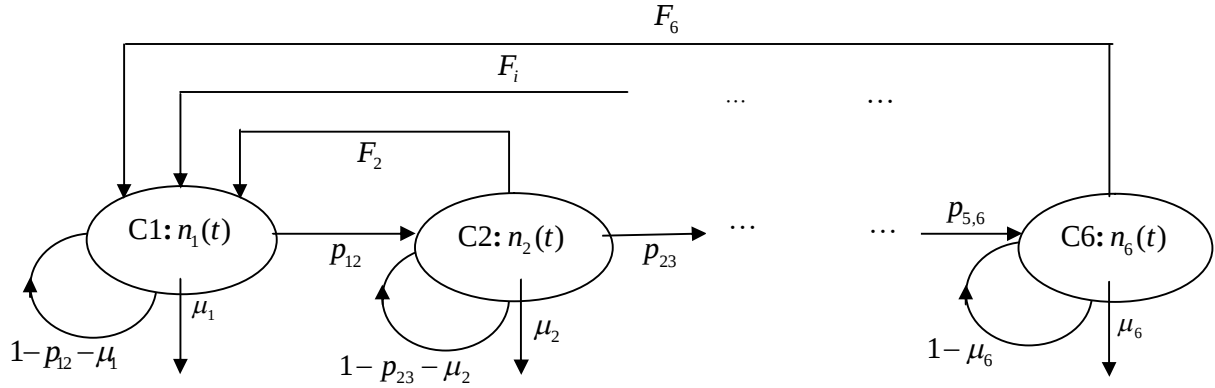


Figure 5.3: The life cycle graph for 6-CEPMM population model framework. A six age class model for wild elephant population dynamics.

The framework in Figure 5.3 is similar to the framework in Figure 5.2 except that in the 6-CEPMM the classes are more. For this model the classes are aged between 0-9, 10-19, 20-29, 30-39, 40-49, and 50-59. If the population projections were done at discrete time scale, less than the age interval, not all individuals progress to the next class.

A 6-CEPMM model with a one year projection timeframe is,

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 1 - \mu_1 - p_{12} & F_2 & F_3 & F_4 & F_5 & F_6 \\ p_{1,2} & 1 - \mu_2 - p_{23} & 0 & 0 & 0 & 0 \\ 0 & p_{2,3} & 1 - \mu_3 - p_{34} & 0 & 0 & 0 \\ 0 & 0 & p_{3,4} & 1 - \mu_4 - p_{45} & 0 & 0 \\ 0 & 0 & 0 & p_{4,5} & 1 - \mu_5 - p_{56} & 0 \\ 0 & 0 & 0 & 0 & p_{5,6} & 1 - \mu_6 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}. \quad (5.12)$$

If the projection timeframe is 10 years, all surviving individuals proceed from their current class to the next class. Then the model reduces to the standard Leslies (1945) matrix model. Each age group was selected to be of length 10 years and population updated using a simple Leslie matrix model. Ten was selected since we can assume elephant's populations attain sexual maturity at ten years. So the fecundity for the first class is equal zero. We also assumed that African Elephant reach

menopause at the age of 60 years (Wu & Botkin, 1980; Woodd, 1999; Moss, 2001), and that the African Elephant do not live beyond the age of 60. The 10-year vital rates are derived from the annual vital rate and population parameters. The resulting model with six age classes is of the form,

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 0 & f_2 & f_3 & f_4 & f_5 & f_6 \\ \phi_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_5 & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}, \quad (5.13)$$

where $f_1 = 0$, $n_{i,t}$ is the number of animals of age i in year t , $i = 1, 2, \dots$, f_i is the number of young produced per unit time, per animal in class i , and ϕ_i is the annual probability of survival of an animal of age i . Simulations were then conducted to investigate the effects of different population parameters that influence population dynamics.

5.3.3 Fifteen-Classes Elephant Population Matrix Model (15-CEPMM)

Hypothesis: The African elephant population can be modeled using a deterministic or a stochastic matrix model with fifteen age classes of 4-years each.

Another Leslie's approach to model definition is a model for African Elephant population with 15 age classes, updated using a simple Leslie (1945) matrix model. Each age group was selected to be of length four years. Four was selected since we can assume approximate age at first calving is twelve years and hence the first three classes that do not reproduce. These three classes include infants (0-3 years), weaned calves (4-7 years) and sub-adults (8-11years). A four year model is also more appropriate since population inter-calving interval can be estimated using an average of four years. The fecundity for the first three classes is equal zero and fecundity of the last classes above 50 years may be reduced to fit the selected population. We also assumed that African Elephant do not live beyond the age of 60 years. Four year vital rates were derived from the annual vital rate and population parameters as is the case with 10-year model above.

In general using a fifteen age-class model, we get a life cycle graph similar to Figure 5.3 but having a total of 15 classes. The 15-CEPMM for a one year projection time frame is of the form,

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ \vdots \\ n_{14,t} \\ n_{15,t} \end{pmatrix} = \begin{pmatrix} 1-\mu_1-p_{12} & 0 & 0 & F_4 & \cdots & F_{15} \\ p_{1,2} & 1-\mu_2-p_{23} & 0 & 0 & \cdots & 0 \\ 0 & p_{2,3} & 1-\mu_3-p_{34} & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & p_{14,15} & 1-\mu_{14}-p_{15,16} & 0 \\ 0 & 0 & 0 & 0 & p_{15,16} & 1-\mu_{15} \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ \vdots \\ n_{15,t-1} \\ n_{16,t-1} \end{pmatrix}. \quad (5.14)$$

It is important to note that even though the animals are classified into fifteen groups of four years each, the progression is done in one year interval resulting in model in equation (5.14). The models parameters must be estimated to fit this scenario. The number of model parameters to be estimated increase with number of classes. If the projection is done on a 4 years time scale then all the animals in one stage proceed to the next. The model is of the form (5.15),

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ \vdots \\ n_{14,t} \\ n_{15,t} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & f_4 & \cdots & f_{13} & f_{14} & f_{15} \\ \phi_1 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_4 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & \phi_{13} & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & \phi_{14} & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ \vdots \\ n_{14,t-1} \\ n_{15,t-1} \end{pmatrix}, \quad (5.15)$$

where $n_{i,t}$ is the number of animals of age i in year t , $i = 1, 2, \dots$, f_i is the mean number of young produced per four-year time unit per animal, and ϕ_i is the per period probability of survival of an animal of age-class i . model parameters in this model were estimated to fit four year projections.

5.3.4 Assumptions

In the matrix population models we incorporate population parameters as follows;

- i. Maximum expected lifespan; the life span of individual elephant is selected to be 60 years and age at sexual menopause ranges from 50 to 60 years,
- ii. Female age at sexual maturity; female age at sexual maturity range from nine to 16 years or more depending on chosen population. Integer values varying from 9 to 15 year were used for simulation. The fifteen classes and the six classes' models assumed an age at sexual maturity of 12 years and 10 years respectively. Age specific parameters estimates can be adjusted for any variation in age at sexual maturity.
- iii. Calving interval of a population; Inter-calving interval or period between consecutive births differs from one population to another and even among individuals in a population.

Simulations are done for values that ranging from 3 to 7 years with an average of 4 years used to study variation in other parameters.

- iv. Age specific survival probabilities; although survival probabilities do not vary much for adult elephants, they are higher for calves and old animals. Induced mortality rates are used to evaluate the mortality level required to reduce population growth rate to zero percent.
- v. A birth sex ratio of 1:1 was used for all the models and although the probability of conception may vary with age and other environmental parameters, deterministic models assume that the probability of conception is one for a period equivalent to the calving interval.

We focus mainly on the density independent models where parameters are not density dependent. In section 5.6 below we evaluated how to incorporate random variations due to model parameters and demographic variability.

5.4 Models parameter estimates

To choose a model with demographic structure, we first extract salient features from the observed data and then choose a model that possesses such features. After estimating parameters we seek to improvements in the model until it fits the data reasonably well.

Demographic analysis in diverse African elephant populations reveal marked differences between elephant in different age classes. Whitehouse & Kerley (2002), for example, reveals difference in mortality for AENP population as in Table 5.1 below.

Table 5.1Demographic structure of AENP population

Age Class	Mortality rate in %	
	Male	Female
0	6.2	6.2
1-9	0.9	0.1
10-19	2.0	0.4
20-29	3.1	0.3
30-44	5.1	1.2
44-59	100	1.6
60-63		100

Natural mortality of free-ranging elephant populations is age-dependent, with the youngest being most susceptible to climatic conditions (Moss, 2001). In addition to drought and senescence other, less common, causes of elephant mortality include disease, injury, and predation by lions and humans. Published natural mortality or survival parameters given in Table 5.2, for different elephant populations were used in our models (Whitehouse & Hall-Martin, 2005, 2009).

Table 5.2 Survival parameters for elephant populations

Population	Age (years)						
	0	1–9	10–19	20–29	30–44	45–60	60+
Addo	0.94	0.99	0.99	0.99	0.99	0.98	0
Kruger	0.97	0.97	0.97	0.97	0.97	0.97	—
Tembe	0.90	0.99	0.99	0.99	0.99	0.99	—
Amboseli	0.94	0.99	0.98	0.99	0.97	0.95	—
Buganga	0.97	0.97	0.97	0.97	0.97	0.97	—
Etosha	0.84	0.87	0.90	0.93	0.92	0.88	0.84
Kasungu	0.94	0.96	0.96	0.94	0.91	0.86	0.67
Luangwa	0.59	0.92	0.89	0.87	0.86	0.50	0
Maputo	0.82	0.94	0.95	0.97	0.97	0.97	—
Mkomazi	0.95	0.95	0.95	0.95	0.95	0.95	—
Murchison	0.97	0.97	0.97	0.97	0.97	0.97	—
Sambura	0.98	0.99	0.98	0.98	0.97	0.97	—
Tsavo	0.95	0.95	0.95	0.95	0.95	0.95	—

We also used published age specific fecundity for selected populations in Africa (Whitehouse & Hall-Martin, 2005) as in Table 5.3.

Table 5.3 Indices of age-specific fecundity for selected elephant populations

Age (yrs)	Kruger Pregnant or lactating	Amboseli Giving birth	Etosha Pregnant or Lactating	Luangwa Pregnant	Murchison Lactating
0–4	0	0	0	0	0
5–9	5.5	0	3.6	0	2.0
10–14	52.0	14.0	32.2	5.2	3.0
15–19	91.0	21.0	76.7	56.6	20.0
20–24	80.5	23.0	94.1	50.6	50.0
25–29	93.0	23.0	98.8	50.6	65.0
30–34	86.5	23.0	89.6	50.0	66.0
35–39	93.7	23.0	93.3	50.0	76.0
40–44	92.9	20.0	100.0	42.1	60.0
45–49	94.7	18.0	93.3	42.1	57.0
50–54	89.3	14.0	86.7	33.3	37.0
55–59	85.7	10.0	56.7	33.3	0
60–64	—	0	—	—	—

Various measures serve as indices of age-specific reproductive output (Table 5.2), which usually is expressed as fecundity. Fecundity is defined as yearly production of female calves per cow of a given age group. Table 5.2 gives the age-specific reproductive rates (given as percentages) as indices of age-specific fecundity for selected elephant populations across southern Africa (Whitehouse & Hall-Martin, 2009).

Other parameters of importance for elephant population include age at first calving (Table 5.4), calving intervals, and age at last calving. The elephant's gestation period is 22 months, the longest of any land animal.

Table 5.4 Elephant age at first calving

Location	Mean	95%CI	Location	Mean	95%CI
Addo	13.3	12.1-15.4	Kasungu	12.8	
Kruger	12.25		Kidepo	11.5	
Mabula	12.3	11.2-13.4	Luangwa	15.8	
Phinda	10.3	9.2-11.4	Maputo	9.8	9.3-10.3
Pilanesberg	9.2	8.8-9.6	Mkomazi	12.2	11.0-13.4
Pongola	8.4	7.3-9.5	Murchison N	16.8	15.5-17.1
Tembe	11.5	10.4-12.5	Murchison S	17.8	16.9-18.6
Amboseli	13.7	12.5-14.6	Tsavo	11.7	10.8-12.6
Augogo	22.4	19.9-24.9	Zambezi	15.5	
Etosha	13.53	11.5-16.2			

A box plot for age at first calving for different African elephant population produced a median of 12.3 years (figure 5.4). Cows in South Africa tend to have their first calves at an average age of 11.3 years. Those elsewhere have their first calves at an age of 14.1 years. Average age at first calving of between 10 to 16 years was studied in our simulations.

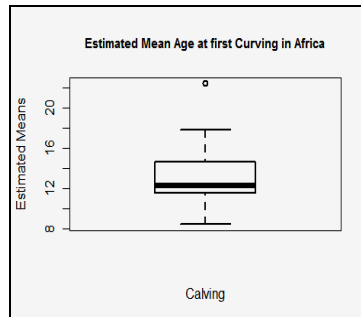


Figure 5.4 African elephant age at first calving. A box-plot of age at first calving for selected locations in Africa.

Matrix population models can thus be used to examine the effects of age-specific fecundity, age-specific mortality, age at first calving and inter-calving intervals, together with other determinants of population growth. We evaluated the effect of these parameters through by simulating different scenarios after deriving appropriate models for different populations. Emphasis being on how much we need to change selected model parameter in order to attain a zero population growth rate (i.e. one dominant eigenvalue, $\lambda_1 = 1$).

5.5 Models simulations results

5.5.1 Six-Classes (6-CEMPP) Structured Population Model

We consider the results attained using the 10-years class model for both the one year projection (5.16) and ten years projection timeframe (5.17).

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 1-\mu_1-p_{12} & F_2 & F_3 & F_4 & F_5 & F_6 \\ p_{1,2} & 1-\mu_2-p_{23} & 0 & 0 & 0 & 0 \\ 0 & p_{2,3} & 1-\mu_3-p_{34} & 0 & 0 & 0 \\ 0 & 0 & p_{3,4} & 1-\mu_4-p_{45} & 0 & 0 \\ 0 & 0 & 0 & p_{4,5} & 1-\mu_5-p_{56} & 0 \\ 0 & 0 & 0 & 0 & p_{5,6} & 1-\mu_6 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}, \quad (5.16)$$

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 0 & f_2 & f_3 & f_4 & f_5 & f_6 \\ \phi_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_5 & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}. \quad (5.17)$$

It is important to note that even though the animals were classified into six groups of ten years each, the progression is done per one year (equation 5.16). All animals do not progress from one class to the next at the end of every. The models parameters must be estimated to fit this scenario.

Result 5.1: The African elephant population can be modeled using deterministic or stochastic matrix models with six classes each of 10-year class interval.

The elephant population life table below (Table 5.5), was developed using data and estimates of vital rates for Amboseli National park, elephant population in Kenya. The following assumptions and parameter estimates were used.

- i. Elephant population attain a maximum age limit of 60 years,
- ii. Average calving interval of 4.6 years (Moss 2001),
- iii. Average age at sexual maturity of $13.7 \cong 14$ years,
- iv. The number b_x is the number of female of-spring produced by an individual in age class x while in that age class. The ratio of male to female to
- v. Survival rates adapted are as in Table 5.2 above.

Table 5.5 Life table for ANP elephant populations

Age in years	P_x	l_x	b_x
0	0.94	0.94	0
1	0.99	0.931	
⋮	⋮	⋮	
9	0.99	0.859	
10	0.98	0.842	0.58
⋮	⋮	⋮	
19	0.98	0.701	
20	0.99	0.695	1.09
⋮	⋮	⋮	
29	0.99	0.635	
30	0.97	0.616	1.09
⋮	⋮	⋮	
39	0.97	0.468	
40-⋮	0.97	0.454	1.09
45	0.95	0.382	
⋮	⋮	⋮	
49	0.95	0.311	
50	0.95	0.295	1.09
⋮	⋮	⋮	
59	0.95	0.186	
60	0	0	0

A matrix model for African Elephant population with 10-years age classes and updated using a simple Leslie matrix model is given by equation (5.18). Each of the vital parameters was estimated for the interval of ten years each. So the fecundity for the first class is equal zero. We also assume that African Elephant reach menopause at the age of 60 years (Wu & Botkin, 1980; Woodd, 1999; Moss, 2001), and that the African Elephant do not live beyond the age of 60. Five year survival rates were derived from the annual survival rate as in Tables 5.4 above.

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 0 & f_2 & f_3 & f_4 & f_5 & f_6 \\ \phi_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_5 & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}, \quad (5.18)$$

where $\phi_6 = 0$, $f_1 = 0$, $n_{i,t}$ is the number of animals of age i in year t , $i = 1, 2, \dots$ $n_{2,t}$ is the number of animals of age ≥ 2 in year t , f_i is the number of young produced per unit time per animal in class i , and ϕ_i is the annual probability of survival of an animal of age i .

We simulate population growth for African elephant for ten-year age classes for the three different scenarios. For the ten-years class model the maximum expected lifespan is 60 years, female age at sexual maturity is assumed to be ten years, average calving interval for the population is take to vary for different ecosystems, age at menopause is estimated to be 60 years, sex ratio of newborns is take to be 1:1, and age-specific probabilities of survival are selected from documented estimates. The numbers of females of different ages were transitioned through a matrix in which the number of individuals of each age was recorded.

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 0 & 0.99 & 1.32 & 1.32 & 1.32 & 0.99 \\ 0.86 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.90 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.90 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.86 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.82 & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}, \quad (5.19)$$

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 0 & 0.67 & 1.11 & 1.11 & 1.11 & 0.56 \\ 0.86 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.82 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.74 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.66 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.60 & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}, \quad (5.20)$$

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 0 & .64 & .91 & .91 & .91 & .91 \\ 0.59 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.60 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.60 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.60 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.60 & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}. \quad (5.21)$$

Equations 5.19, 5.20, and 5.21 were selected to fit the AENP, ANP and Tsavo National park (TNP) scenarios respectively. The dominant eigenvalue of each of the transition matrix are $\lambda_A = 1.50$, $\lambda_L = 1.31$ and $\lambda_T = 1.02$ respectively (see Figure 5.5). These show how each population will increase after every 10-year time interval. The populations were assumed to be made up of an initial female population of 6, 41 and 50 individuals at around 1930 distributed in the six classes. The time selected was to allow the population to attain a stable age structure by the time we investigate effect of increased mortality and calving intervals. To a lesser degree the populations were also selected so as the observed female population in later years is close enough to the model projection.

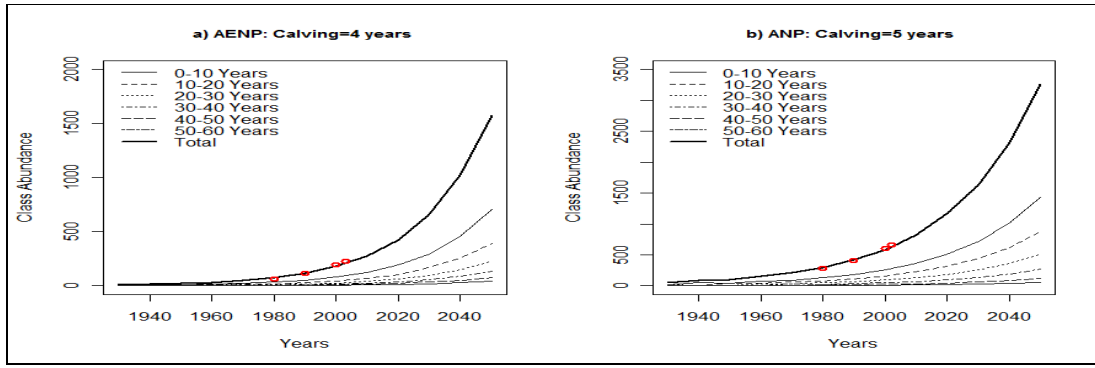


Figure 5.5 Effect of inter-calving interval. Figure 5.5a and b illustrates two different scenarios each corresponding to the parameters selected for AENP and ANP with different calving interval.

For matrix model in equation (5.27) to (5.29), the stable stage distributions are given by;

$$\begin{aligned}\lambda_A &= 1.50, \quad \hat{x}_A = (0.43, 0.25, 0.15, 0.09, 0.05, 0.03)', \\ \lambda_L &= 1.31, \quad \hat{x}_L = (0.41, 0.27, 0.17, 0.09, 0.05, 0.02)', \\ \lambda_T &= 1.023, \quad \hat{x}_T = (0.44, 0.25, 0.15, 0.09, 0.05, 0.03)'. \end{aligned} \quad (5.22)$$

The corresponding reproductive values are,

$$\begin{aligned}RV_A &= (1.0, 1.75, 1.82, 1.58, 1.23, 0.65)', \\ RV_L &= (1.0, 1.52, 1.63, 1.40, 1.08, 0.51)', \\ RV_T &= (1.0, 1.73, 1.89, 1.71, 1.41, 0.89)'. \end{aligned} \quad (5.23)$$

The population with inter-calving interval of 3.8 years would recover faster than the one with inter-calving interval of 4.5 or 5.5 years. After attaining the stable age distribution the populations grows exponentially as in Figure (5.5), if $\lambda > 1$. There are some oscillations before population attains stable class distribution. After a period of time, the population acquires stable age distribution. Figure (5.5) also shows population projections for a period of 40 years. Competition for resources may set in as population increases through increased calving interval.

We note from equations 5.19, 5.20 and 5.21 that the population structure is almost equivalent in the three selected ecosystems, although the population growth rates are different. This is partly due to the survival rates used being almost equal with minor variations. Stochastic variability is bound to course variation from one ecosystem to the other.

$$S_A = \begin{pmatrix} .32 & .18 & .11 & .07 & .04 & .02 \\ .55 & .32 & .19 & .12 & .07 & .04 \\ .58 & .33 & .20 & .12 & .07 & .04 \\ .50 & .29 & .17 & .10 & .06 & .03 \\ .39 & .22 & .13 & .08 & .05 & .03 \\ .20 & .12 & .07 & .04 & .02 & .01 \end{pmatrix}, \quad S_L = \begin{pmatrix} .32 & .21 & .13 & .07 & .04 & .02 \\ .49 & .31 & .20 & .11 & .06 & .03 \\ .52 & .34 & .21 & .12 & .06 & .03 \\ .44 & .29 & .19 & .10 & .05 & .02 \\ .34 & .23 & .14 & .08 & .04 & .02 \\ .16 & .11 & .07 & .04 & .02 & .01 \end{pmatrix}.$$

Performing sensitivity analysis gives the most sensitive transition as that from the juvenile (0-10) to 11-20 for both models in equation (5.19) and (5.20). The next relatively sensitive transition is the transition from 11-19 to 21-29 years. This indicates that management policies that focus on the survival of juvenile and to a lesser extent 10-20 years would be most effective. The sensitivity values are given by matrices S_A and S_L above for the two models respectively.

For the case of ANP, elasticity of the survival of class 0-9 years show the highest values followed by the survival of 10-19 years. Fecundity of class 20-29 years shows the highest value followed by fecundity of class 10-19 years. The Elasticity for the models in equation (5.19) and (5.20) are given by E_A and E_L as below.

$$E_A = \begin{pmatrix} 0 & 0.12 & 0.10 & 0.06 & 0.03 & 0.1 \\ .32 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.20 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.10 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.05 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.01 & 0 \end{pmatrix}, \quad E_L = \begin{pmatrix} 0 & 0.11 & 0.11 & 0.06 & 0.03 & 0.01 \\ .32 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.21 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.10 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.04 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.01 & 0 \end{pmatrix}.$$

To investigate further the sensitivity of model projections to adjustments in mean calving interval, age specific mortality and age at maturity, we varied each of these parameters separately whilst keeping all else constant. We compare multiple scenarios of increased mortality of each group holding all else constant for a population with mean inter calve interval of 4 years. Mortality of classes of age lower than 20 years can be increased by prolonged draught while for classes with greater age by management policies or poaching. We keep the B matrix constant and vary Survival parameters ϕ_i in the survival matrix S, with θ being the unknown vector of parameters $(\lambda, \phi)'$ of the model $E[n_t | n_{t-1}, \theta] = BASn_{t-1}$. By increasing mortality we examined the age-specific mortality levels required to prevent long-term population growth.

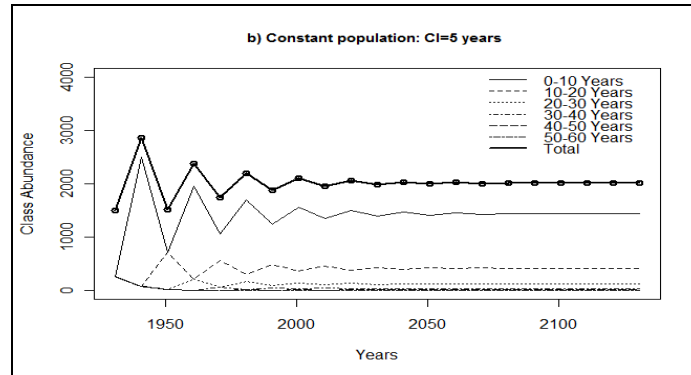


Figure 5.6 Stable population size. Increase mortality rate causes population to stabilize

Figure 5.6 demonstrates the role of mortality in population growth. If a population with calving interval of 4 years and has attained stable age structure (as in Figure 5.4), is exposed to constant population mortality of 0.06 (or annual survival rate of 0.94 for all the classes annually) a constant population growth was observed. This may not be observed in reality, since the probability of a birth per female elephant in every four years varies and was not 1 as the model presumes.

The level of induced mortality required to produce 0% population growth for the 10-year model given in Table (5.6) below,

Table 5.6 10-years mortality required to stabilize population.

Calving interval	All Classes 10-years frequency mortality
3.8	32.2%
4.5	23.2%
5.5	1.2%

For model in equation (5.19), (5.20) and (5.21), the mortality levels required to attain zero percent population growth are 32.2%, 22.2% and 2.2% respectively, all at 10 years frequency. Studying the models in equations 5.19, 5.20 and 5.21 further, we can identify the level of mortality required to stabilize the populations. The percentages reductions in the survival of each group are given in Table (5.7) below. The percentages are class specific and applied at a frequency of ten years and are thus not as large as they appear.

Table 5.7 Increased mortality required for stabilizing population (10 years frequency).

Class or category	3.8 years calving I.	4.5 years calving I	5.5 years CI
0-9	53.7%	42%	3.1%
10-19	64.7%	50.7%	4.2%
20-29	81.7%	59.7%	6.6%
30-39	---	----	12%
40-49	---	---	24%
50-59	---	---	66%

This analysis shows that if natural mortality remains constant;

- i. Population growth is most sensitive to calving interval as compared to age at sexual maturity.
- ii. Total mortality required to stabilize the population is higher for older classes than younger classes.

- iii. Population with larger calving interval can decline for very low induced mortality. six percent mortality (in every 10 years) for a class lower than 30 year causes a population with calving interval of 5.5 years to decline.
- iv. A 100% total mortality for a class above 30 years will not cause a population to stabilize if the calving interval is less than 4.5 years, and
- v. Population stabilizes or is self-regulating if the calving interval is approximately 5.5 to 6.5 years. A population with an average calving interval larger than 6.5 years will most likely decline and will be faced with high chance of extinction.

Using model in equation (5.19) we demonstrated that the effect of initial conditions on population dynamics of a structured model. A hypothetical initial population of six animals was introduced in an ecosystem with 1930 as the initial year. Animals were assumed to either be all juveniles in the first class 1 (as in Figure 5.7a), or aged between 10-19 years and thus in class 2 (as in Figure (5.7b), or aged between 50-59 years and thus in class six (Figure 5.7c). The resulting total female population was compared to expected female population of the ecosystem. Projections in case of Figure 5.7 a) and case c) were lower and took longer to acquire a stable age distribution compared to case b). This, as we would expect, is as a result of the number of reproductive animals and their relative reproductive importance. The case of Figure (5.7b) is favorable due to the high reproductive value of animals in 2nd class interval.

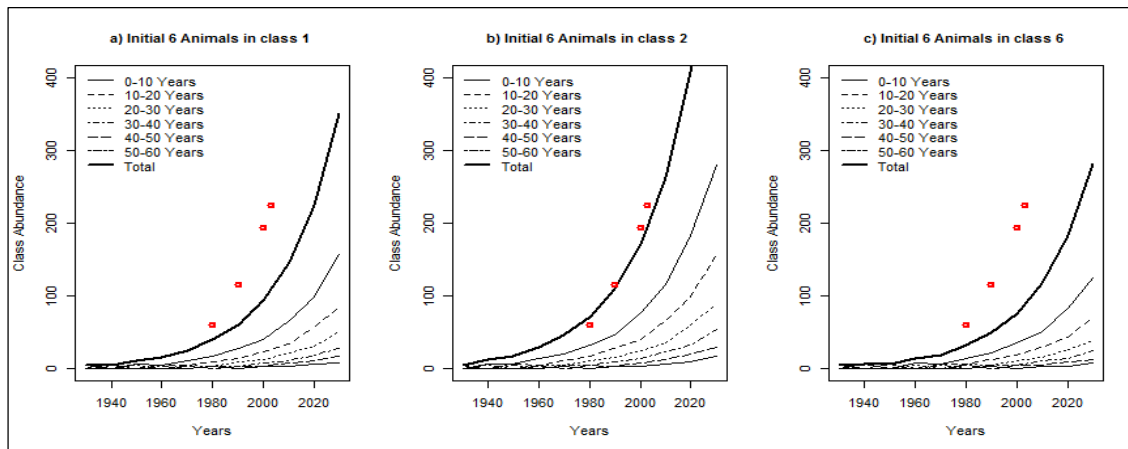


Figure 5.7 Studying effects of initial conditions. A hypothetical population of six animals is introduced in a similar ecosystem but assuming the animals are either, all juveniles in the first class 1 (as in figure 5.5a), or aged between 10-19 years and thus in class 2 (as in figure 5.5a), or aged between 50-59 years and thus in class 6 (as in figure 5.5c).

To show the effect of perturbations or what happens when the entries in transition matrix are changed, we vary for case (b) above the survival of class 1, 3 and 6 by allowing them to vary by at most 25 percent separately and latter the reproductively of class 2, 4 and 6 by allowing them to vary

also by at most 25 percent separately. Perturbations of survival on the survival of juvenile showed that the most drastic effect on the observed population behavior compared to the other two cases. Perturbations on survival of the older adult showed the least effect on the population behavior (Figure 5.8a, b and c). As shown by sensitivity analysis change in fecundity of the middle aged animals causes the highest change in population projections.

The one year transition scheme for the 10-year class model with 4.5 years calving interval, age at first calving of 14 years and annual survival parameters selected to fit ANP is;

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} 0.88 & 0.07 & 0.11 & 0.11 & 0.132 & 0.07 \\ 0.1 & 0.88 & 0 & 0 & 0 & 0 \\ 0 & 0.1 & 0.89 & 0 & 0 & 0 \\ 0 & 0 & 0.1 & 0.87 & 0 & 0 \\ 0 & 0 & 0 & 0.1 & 0.86 & 0 \\ 0 & 0 & 0 & 0 & 0.1 & 0.85 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}. \quad (5.24)$$

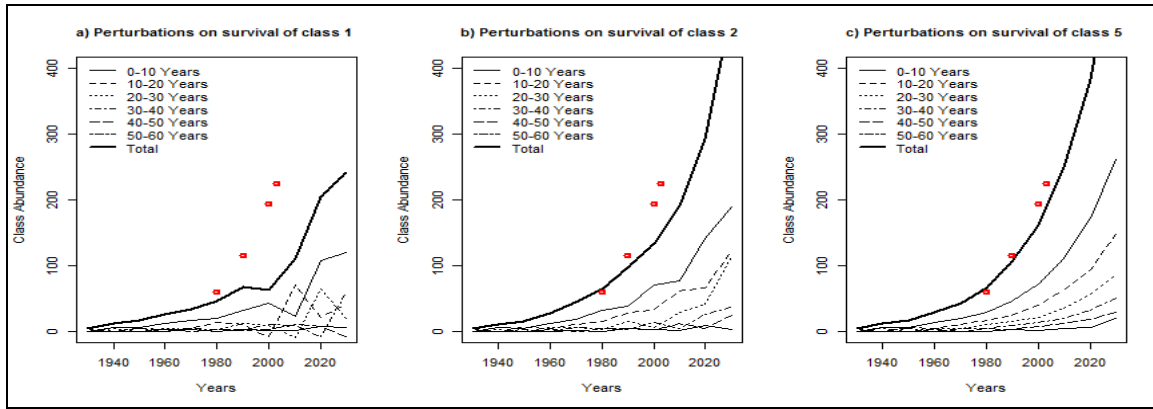


Figure 5.8 Studying effects of perturbations. Perturbations on survival of the survival of juvenile shows the most drastic effect on the observed population behavior compared to the other two cases

By analysis of model (5.24) showed that;

- The population grows annually ($\lambda = 1.031$), with the reproductive rates of the ages 10-19 and 20-29 being the most significant in the population growth.
- The survival rate of the first three classes, i.e. 0-9, 10-19 and 20-29 are the most vital in determining the population trend. This is evident from the elasticity matrix below

$$\begin{pmatrix} 0.26 & 0.01 & 0.02 & 0.001 & 0.01 & 0.00 \\ 0.04 & 0.26 & 0 & 0 & 0 & 0 \\ 0 & 0.03 & 0.20 & 0 & 0 & 0 \\ 0 & 0 & 0.017 & 0.09 & 0 & 0 \\ 0 & 0 & 0 & 0.01 & 0.04 & 0 \\ 0 & 0 & 0 & 0 & 0.00 & 0.01 \end{pmatrix}.$$

iii. The stable age distribution is given by

$$\lambda_1^L = 1.031, \quad \hat{x}_L = (0.38, 0.25, 0.17, 0.11, 0.06, 0.03)'. \quad (5.25)$$

iv. The corresponding reproductive values are,

$$RV_1^L = (1.0, 1.52, 1.64, 1.22, 0.86, 0.37)'. \quad (5.26)$$

v. The induced annual mortality required to stabilize the population are given in Table (5.8),

Table 5.8; Increase in class specific mortality for 6-CEPMM (at one year frequency).

Class or category	3.8 years calving I.	4.5 years calving I
0-9	29.8%	15.2%
10-19	27.3%	15.2%
20-29	54.5%	22.7%
30-39	---	----

vi. Increase mortality of classes above 30 years does not reduce population growth to zero if average calving interval is less 4.5 years. For average calving intervals of 5.5 years the annual population growth tends to zero percent.

5.5.2 Fifteen Classes (15-CEPMM) Structured Population Model

Result 5.2: The African elephant population can be modeled using a deterministic or a stochastic matrix model with fifteen classes each of 4-year class interval.

Using a matrix approach to the model definition, we considered an African Elephant population with 15 age classes, updated using a simple Leslie matrix model. Each age group was selected to be of length 4 years. Four was selected, since we can assume approximate age at first calving is twelve years and hence the first three classes that do not reproduce. These three classes include infants (0-3 years), weaned calves (4-7 years) and sub-adults (8-11years). We also assumed that African Elephant do not live beyond the age of 60 years. The one year transition model as derived above is of the form,

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ \vdots \\ n_{14,t} \\ n_{15,t} \end{pmatrix} = \begin{pmatrix} 1-\mu_1-p_{12} & 0 & 0 & F_4 & \cdots & F_{15} \\ p_{1,2} & 1-\mu_2-p_{23} & 0 & 0 & \cdots & 0 \\ 0 & p_{2,3} & 1-\mu_3-p_{34} & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & p_{14,15} & 1-\mu_{14}-p_{15,16} & 0 \\ 0 & 0 & 0 & 0 & p_{15,16} & 1-\mu_{15} \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ \vdots \\ n_{15,t-1} \\ n_{16,t-1} \end{pmatrix}. \quad (5.27)$$

We can also derive the four year survival rates from the annual survival rate as per Table 5.2 above to acquire the four year transition model as.

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ \vdots \\ n_{14,t} \\ n_{15,t} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & f_4 & \cdots & f_{13} & f_{14} & f_{15} \\ \phi_1 & 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_4 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & \phi_{13} & 0 & 0 \\ 0 & 0 & 0 & 0 & \cdots & 0 & \phi_{14} & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ \vdots \\ n_{14,t-1} \\ n_{15,t-1} \end{pmatrix}, \quad (5.28)$$

where $n_{i,t}$ is the number of animals of age i in year t , $i = 1, 2, \dots$, f_i is the mean number of young produced per four-year time unit per animal, and ϕ_i is the per period probability of survival of an animal of age-class i . The following is a life table for elephant population using 4-year class intervals (Table 5.8).

Table 5.8 Life table for Amboseli (ANP) with 4-year class intervals

Age	P_x	l_x	b_x
0	0.94	0.94	0
1	0.99	0.931	
$\vdots$	$\vdots$	$\vdots$	
4	0.99	0.902	
5	0.99	0.894	0
$\vdots$	$\vdots$	$\vdots$	
8	0.99	0.867	
9	0.98	0.859	0
$\vdots$	$\vdots$	$\vdots$	
12	0.98	0.808	
13	0.98	0.792	0.33
$\vdots$	$\vdots$	$\vdots$	
16	0.98	0.645	
17	0.98	0.731	0.43
$\vdots$	$\vdots$	$\vdots$	
20	0.99	0.695	
21	0.99	0.688	0.44
$\vdots$	$\vdots$	$\vdots$	
24	0.99	0.667	
$\vdots$	$\vdots$	$\vdots$	$\vdots$
53	0.95	0.253	0.43
$\vdots$	$\vdots$	$\vdots$	
56	0.95	0.217	
57	0.95	0.206	0.43
$\vdots$	$\vdots$	$\vdots$	
60	0.95	0.177	
61	0	0	0

The following assumptions and parameter estimates were used.

- i. Elephant population attain a maximum age limit of 60 years,
- ii. Average calving interval of 4.6 years (Moss 2001),
- iii. Average age at sexual maturity of 14 years
- iv. The number b_x is the number of female off-spring produced by an individual in age class x while in that age class. The ratio of male to female was taken to be 1:1.
- v. Survival rates adapted are as in Table (5.2) above.

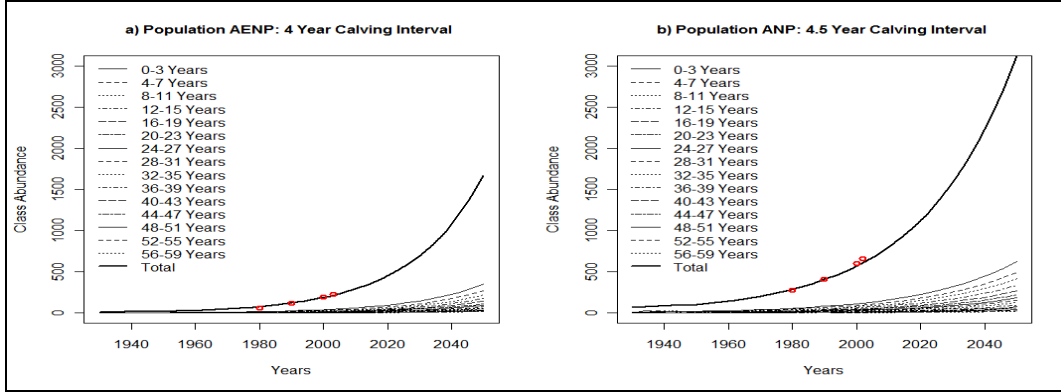


Figure 5.9 15-Classes Structured Elephants Population model. Figure a and b gives the population projection for AENP and ANP with 4 years and 4.5 calving interval respectively for a 15 classes deterministic population model.

Using parameters in Table (5.4), we selected two scenarios using AENP and ANP data. Figure (5.9a) and b shows population dynamics for the AENP and ANP respectively. All the four year class models considered assumed age at reproductive maturity of 12 years. Natural survival parameters were selected to fit population estimates from, AENP, ANP and Tsavo national parks. Calving interval were selected to be 3.8, 4.6 and 5.5 for AENP, ANP and Tsavo national parks respectively. The population increase in every four years for AENP, ANP and Tsavo are given by $\lambda_A = 1.20$, $\lambda_L = 1.15$ and $\lambda_T = 1.00$ respectively. The stable age distribution given by,

$$\bar{x}_A = (.22, .16, .13, .11, .08, .07, .05, .04, .03, .03, .02, .02, .01, .01, .01)',$$

$$\bar{x}_L = (.20, .16, .14, .11, .09, .07, .06, .05, .04, .03, .02, .02, .01, .01, .01)',$$

$$\bar{x}_T = (.19, .16, .13, .10, .09, .07, .06, .05, .04, .03, .03, .02, .02, .01, .01)'$$

The reproductive values give by,

$$RV_A = (1.0, 1.32, 1.65, 2.06, 2.02, 1.97, 1.91, 1.84, 1.74, 1.63, 1.48, 1.30, 1.08, .79, .44)',$$

$$RV_L = (1.0, 1.26, 1.50, 1.86, 1.83, 1.79, 1.66, 1.51, 1.40, 1.30, 1.17, 1.01, .87, .67, .39)',$$

$$RV_T = (1.0, 1.23, 1.53, 1.84, 1.80, 1.75, 1.69, 1.61, 1.52, 1.41, 1.28, 1.11, .91, .67, .37)'$$

After attaining the stable age distribution the population structure remains constant as in Figure 5.9 (a), (b) and (c). Population dynamics of model *A* and *L* showed that the population will grow at rates $\lambda_A = 1.20$ and $\lambda_L = 1.15$ in every four years. The population represented by model *T*, where the calving interval is 5.5 years and natural survival rate for all class were 0.95, remains stable with 0% population change.

Sensitivity and elasticity analysis of the two models gave similar results with equivalent interpretations. The sensitivity of transitions from 0-3, 4-7, 8-11 and 12-15 gives the highest values in decreasing order of importance. The elasticity of survival, of classes 0-3, 4-7, 8-11 and 12-15 gave the highest values while the fecundity of classes 12-15, 16-19 and 20-23 had the most significant values.

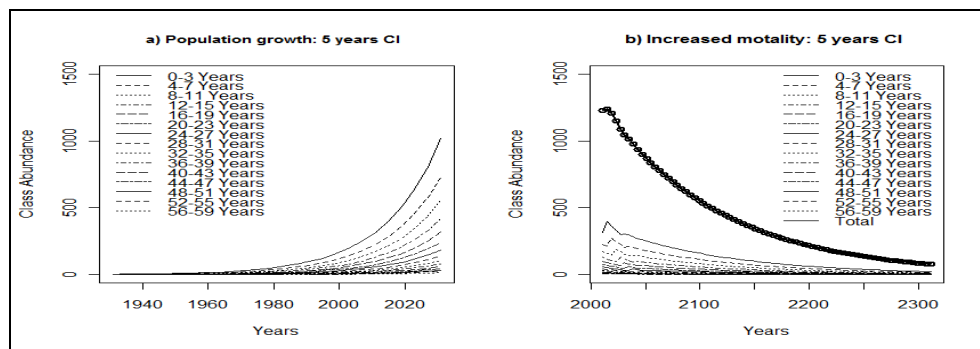


Figure 5.10: Effect of increased mortality. Indiscriminate application of management strategy that causes population to stabilize in one ecosystem may lead to population extinction in another.

Figure 5.10 demonstrate the effect of exposing a population with 5 year calving interval (Figure 5.10, a) to the same level of mortality that courses a population with four years calving interval to be stationary. This would lead to the population having growth rate less than one, leading to extinction of the population in due time (Figure 5.10, b).

Table 5.9, Increase in age specific mortality schemes, (4-years frequency).

4-year Age class	3.8 calving interval	4.5 calving interval
0 to 4	69.6	58.6
4 to 8	70.5	59.4
9 to 12	73.5	62.5
13 to 16	73.7	61.3
17 to 20	82.2	68.9
21 to 24	92.3	79.6
25 to 28	---	---

The Table (5.9) gives the mortality level required every four years in order to stabilize the population. The percentage is specific to each class assuming that the survival rates of the other classes are normal. Percentages of induced mortality required to stabilize the population is dependent on the population calving interval and the selected age interval. Figure (5.11) below demonstrate the stable population for two scenarios selected from Table (5.9). Figure (5.11a). shows the induced mortality specific to the 2nd class for 3.8 years calving interval, whereas figure b. shows induced mortality specific to the 4th class for 4.5 years calving interval.

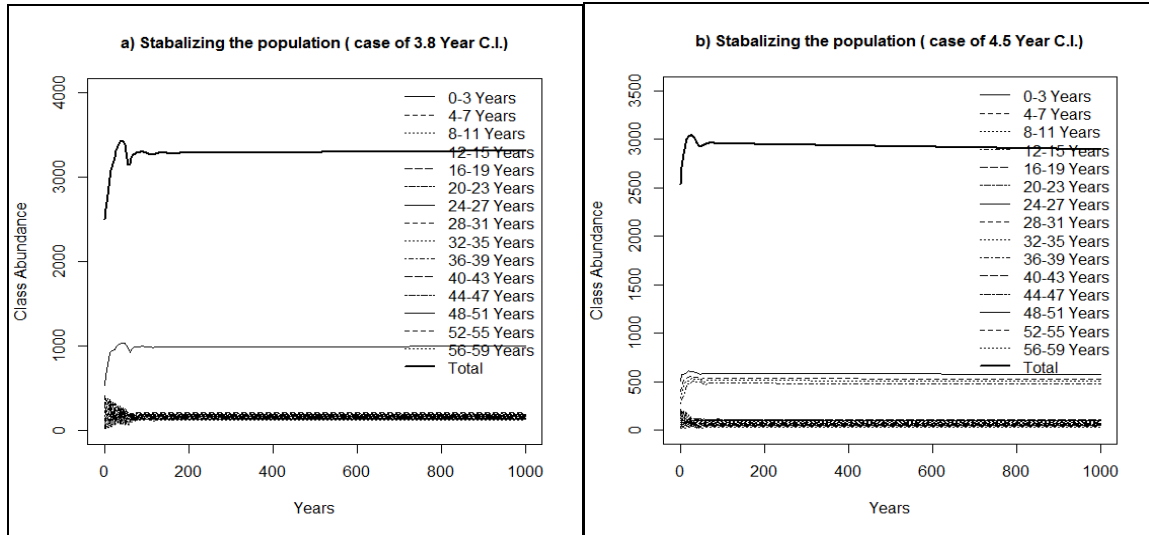


Figure 5.11: Stabilizing population by increased mortality. Induced mortality percentage depends on the population parameters and class interval selected.

We considered the deterministic behavior of the 4-year class model with a one year projection scheme. We used the transition matrix of the form in equation (5.17) to evaluate three scenarios. The three scenarios were for average calving intervals of 3.8, 4.5 and 5 years. Assuming that,

- i. Age at sexual maturity is 12 years and fecundity of animals above 52 years decreases by a half that of other fertile animals.
- ii. Animals between ages 12 and 52 are assumed to be equally likely to conceive.
- iii. Juveniles aged between ages 0 to 10 do not reproduce.
- iv. Annual natural mortality is selected using estimates of mortality from ANP. The age dependent annual mortality required for zero percent population growth rate in the long run are.

As in Table (5.10) below, results from this model showed that;

- i. Populations in all the three scenarios would grow exponentially for normal natural mortality with, $\lambda_{3.8} = 1.05$, $\lambda_{4.5} = 1.043$ and $\lambda_5 = 1.039$. Additional annual mortality rates of 5%, 4.3% and 3.9% is required for zero population growth rate in the case of 3.8, 4.5 and 5 years average calving interval respectively.
- ii. Annual mortality of 15.2%, 13% and 11.6% of juveniles (0-12 years) causes zero percent population growth rate, for the scenarios of 3.8, 4.5 and 5 years average calving interval respectively.
- iii. Annual mortality of 10.0 %, 8.1% and 7.1% of adults (13-60 years) causes zero percent population growth rate, for the scenarios of 3.8, 4.5 and 5 years average calving interval respectively.
- iv. No age specific mortality scheme for classes with age greater than 24 years produces zero percent population growth rate.

Table 5.10, Annual age class specific mortality rates, (1-year frequency).

4-year Age classes	3.8 calving interval	4.5 calving interval	5 calving interval
0 to 4	64.5%	52.8%	43.9
4 to 8	64.5%	50.5%	41.9
9 to 12	64.5%	50.5%	41.9
13 to 16	64.6%	50.5%	41.9
17 to 20	74.1%	69.0%	45%
21 to 24	87%	80.7%	76.1%
25 to 28	----	----	----

5.6 Stochastic population dynamics models

5.6.1 Deterministic modular matrix models

We started by assuming that there three processes governing the dynamics of elephant population dynamics are survival, birth and aging. Later we considered migration (M) and removal (R) due to a given management policy.

The survival process, for example, is represented as a matrix of the form S below, where ϕ_i is the interval's or annual probability of survival for an animal belonging to age class i . The other

process may also be represented using matrices using a modular approach. The modular matrices model for the six age-classes (6-CEPMM) is;

$$S = \begin{pmatrix} \phi_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_6 \end{pmatrix}, B = \begin{pmatrix} 0 & \pi_2 & \pi_3 & \pi_4 & \pi_5 & \pi_6 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}, A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix}. \quad (5.29)$$

Assuming that migration and removal are treated as affecting survival in an additive manner we have,

$$R = \begin{pmatrix} \varphi_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \varphi_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \varphi_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \varphi_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & \varphi_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & \varphi_6 \end{pmatrix}, M = \begin{pmatrix} m_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & m_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & m_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & m_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & m_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & m_6 \end{pmatrix},$$

where π_i , $i = 2, 3, \dots$ are age specific reproduction rates. Management policies may affect one or multiple age classes. The population dynamics model can then be expressed as a product of the three matrices representing the individual sub-processes. The dynamics model for this population can then be written as:

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \\ n_{5,t} \\ n_{6,t} \end{pmatrix} = \begin{pmatrix} \phi_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_4 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_5 \end{pmatrix} \begin{pmatrix} 0 & \pi_2 & \pi_3 & \pi_4 & \pi_5 & \pi_6 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}, \quad (5.30)$$

$$n_t = SBAn_{t-1},$$

$$n_t = Ln_{t-1}.$$

Explicitly modeling each sub-process in this way increases the flexibility of the modeling approach. This particular formulation of the model is deterministic as stochastic variation has not been incorporated in any of the sub-processes. The order of the sub-process may also be altered to fit actual processes or stages when they occur. For example to model survival, aging and then birth sequentially we have,

$$\begin{aligned}
& n_t \rightarrow u_{s,t} \quad u_{s,t} \rightarrow u_{a,t} \\
& \begin{pmatrix} u_{s1,t} \\ u_{s2,t} \\ u_{s3,t} \\ u_{s4,t} \\ u_{s5,t} \\ u_{s6,t} \end{pmatrix} = \begin{pmatrix} \phi_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_4 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_5 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \\ n_{5,t-1} \\ n_{6,t-1} \end{pmatrix}, \quad \begin{pmatrix} n_{a1,t} \\ n_{a2,t} \\ n_{a3,t} \\ n_{a4,t} \\ n_{a5,t} \\ n_{a6,t} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} u_{s1,t} \\ u_{s2,t} \\ u_{s3,t} \\ u_{s4,t} \\ u_{s5,t} \\ u_{s6,t} \end{pmatrix}, \quad (5.31) \\
& u_{a,t} \rightarrow u_{b,t} \equiv n_{t+1} \\
& \begin{pmatrix} u_{b1,t} \\ u_{b2,t} \\ u_{b3,t} \\ u_{b4,t} \\ u_{b5,t} \\ u_{b6,t} \end{pmatrix} = \begin{pmatrix} 0 & \pi_2 & \pi_3 & \pi_4 & \pi_5 & \pi_6 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} u_{a1,t} \\ u_{a2,t} \\ u_{a3,t} \\ u_{a4,t} \\ u_{a5,t} \\ u_{a6,t} \end{pmatrix}.
\end{aligned}$$

For example, we could consider $u_{sj,t} \approx \text{binomial}(n_{jt}, \phi_j)$ and $n_{j,t+1} \approx \text{multinomial}(u_{a,j,t}, p_{1,j}, p_{2,j}, \dots)$ we then study more on ϕ_j and $p_{i,j}$, where $\lambda_i = \sum_i p_{i,j}$.

A realization of the state process at time t , here defined as $n_t : t=1, 2, \dots, T$, is a vector of states, some of which may be unobservable. The other time series is the observation process, a realization of which at time t is here defined as $y_t : t=1, 2, \dots, T$. The observation process provides a correspondence between the unobserved true states and the recorded measurement on the population and is completely observable. An important process that requires further studies is the observation process probability distribution;

$$f_t(y_t | n_t). \quad (5.32)$$

This would determine the probability density function of the observation process (census). Assume the two sub-processes S and B are stochastic with aging A being deterministic. If the survival of each individual is independent of others, the total individuals surviving in each category are binomially distributed. Assuming mature elephant have a chance of giving birth in every interval of five years, then the number born is distributed as $\text{Binomial}(n_{i,t}, \pi_i)$.

5.6.2 Stochastic matrix simulations

The different approach to capturing random variability include; making the individual matrix elements element to be random or considering the modular approach to the processes where each individual process is governed by a probability distribution. Stochastic and modular approach to population sub process is discussed in the next section.

We start with the Leslie matrix model similar to equation Leslie (1945) where the elements are random variable. We simulate stochastic models for parameters estimates corresponding to AENP and ANP population scenarios, as in equation (5.19) and (5.20). The transition and fecundity element are selected to be normally distributed random variable with mean equivalent to values in equation (5.19) and (5.20) and variance selected individually for each element. The following is observed;

- i. If the variability in vital rates has low variance and can increase or decrease the vital rates randomly, the mean population trajectory are almost equivalent to the deterministic model,
- ii. If the variations affect the population negatively by decreasing fecundity, i.e. increasing calving interval, population trajectories have much less means. The population with calving intervals of 5.5 years or more declines to extinction for high variability.

Increasing the variability of survival and fecundity by increasing their variance reduces the chance of acquiring population close to the observed levels. It is important to note that the model does not attain a constant stable age distribution for large variability of survival and fecundity parameters. For low variability the population stable age distribution converges to the equivalent deterministic models equation (5.19) and (5.20).

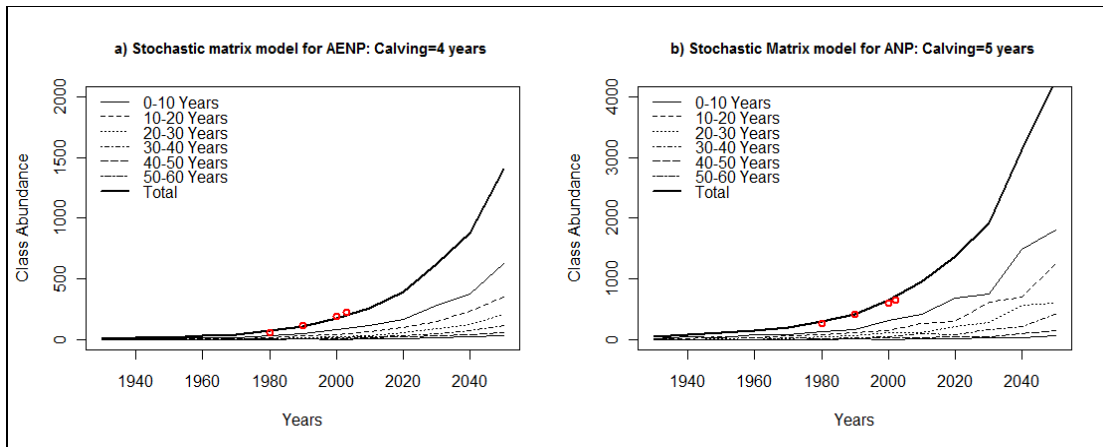


Figure 5.12. 10-year classes stochastic matrix model. Simulation of stochastic matrix model with fecundity determined by calving interval and survival parameters selected from a normal distributions.

In Figure 5.12, fecundity is selected to be a normal random variable with its mean and variability determined by the calving interval. Survival parameters are also normal random variable with mean values selected or calculated from Table 5.2 and variance allowed to vary from 0.05 to 0.2. Figure gives one such scenario showing the population dynamics for both AENP and ANP. Model projections are plotted together with the observed female population for verification purposes.

5.6.3 Stochastic modular matrix approach

If elephants are aggregated into juveniles from 0 to 9 years, middle-aged from 10 to 39 years and old-aged from 40 to 60 years. Then the juveniles have not yet reached sexual maturity. Middle-aged and many of the old-aged elephants can reproduce. Juveniles (0-9) make one class, middle-aged elephant can be partitioned into three classes of 10-19, 20-29 and 30-39, while old-aged adults are in classes 40-49 and 50-59. The simple deterministic models is of the form

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix} = \begin{pmatrix} 1 - \mu_1 - p_{12} & F_2 & F_3 \\ p_{12} & (1 - \mu_2 - p_{23}) & 0 \\ 0 & p_{23} & (1 - \mu_3) \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \end{pmatrix}. \quad (5.33)$$

When this model is fitted for a population with average calving interval of 4.5 years and annual survival parameters derived from the ANP data we have,

$$\begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix} = \begin{pmatrix} 0.89 & 0.11 & 0.11 \\ 0.1 & 0.95 & 0 \\ 0 & 0.033 & 0.93 \end{pmatrix} \begin{pmatrix} n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \end{pmatrix}. \quad (5.34)$$

This model has $\lambda_1 = 1.044$, a stable age distribution given by $\hat{n} = (0.42 \ 0.45 \ 0.13)$, and a reproductive value of $RV = (1.0 \ 1.54 \ 0.98)$. Investigating the model further showed that the annual mortality required to produce zero percent growth rate are (see figure 5.13),

- i. 4.4% for the entire population,
- ii. 21.8% and 9.9% for juveniles (0-10 years) and middle-aged adults (11-39 years) respectively.

No percentage mortality causes zero percent growth rate for old-aged adults (40-60).

We note that for a population with no animals aged 40 years and above, 3% induced mortality for the remaining population cause population to stabilize. If total annual mortality is more than natural mortality plus the given percentages required to cause a zero population growth rate, the population decline to extinctions in the long run.

Result 5.3: Assuming there is a population of n_i animals in class i , and each has a chance ϕ_i of surviving to the next time interval independent of other animals, the structured elephant population dynamics can be modeled using a three class modular stochastic matrix model (SMM) such that;

$$\begin{aligned}
& n_{t-1} \rightarrow u_{s,t} \rightarrow u_{a,t} \rightarrow u_{b,t} \equiv n_t \\
& u_{s,t} \sim H_{s,t}(n_{t-1}): \begin{bmatrix} u_{1,s,t} \sim \text{Bin}(n_{1,t-1}, \phi_1) \\ u_{2,s,t} \sim \text{Bin}(n_{2,t-1}, \phi_2) \\ u_{3,s,t} \sim \text{Bin}(n_{3,t-1}, \phi_3) \end{bmatrix}, \text{ where } \phi_i = 1 - \mu_i - p_{i,i+1} \\
& u_{a,t} \sim H_{a,t}(n_{t-1}): \begin{bmatrix} u_{1,a,t} = u_{1,s,t} \\ u_{2,a,t} = p_{12}u_{1,s,t} + u_{2,s,t} \\ u_{3,a,t} = p_{23}u_{2,s,t} + u_{3,s,t} \end{bmatrix}, \\
& u_{b,t} \sim H_{b,t}(n_{t-1}): \begin{bmatrix} n_{1,b,t} \sim \text{Bin}(u_{2,a,t}, \pi_2) + \text{Bin}(u_{3,a,t}, \pi_3) \\ n_{2,b,t} = u_{2,a,t} \\ n_{3,b,t} = u_{3,a,t} \end{bmatrix}.
\end{aligned} \tag{5.35}$$

Aging was assumed to be deterministic, that is, the $p_{i,i+1}$ are constant which can be determined for a population with stable age distribution. By intuition, if the probability of an individual in class i surviving in a time interval is ϕ_i independent of other individuals, the total number of individuals who will survive to the next time interval is given by a binomial distribution $\text{bin}(n_i, \phi_i)$. If only demographic stochasticity is operating, the probability distribution of those who survive will be binomial. The initial state vector is n_0 , the number of adults ($u_{3,a,0}$) at time $t = 0$.

The distribution for the state process was found by integrating the joint distribution for the survival and birth sub-processes over the survival process with the constraint that the number of adults at time t equals the sum of the number of surviving juveniles and the number of surviving adults from time $t-1$,

$$g(n_t, \Theta | n_{t-1}) = \int \int_{u_{a,t} u_{s,t}} g_{b,t}(n_t, \Theta | u_{a,t}) g_{a,t}(u_{a,t}, \Theta | u_{s,t}) g_{s,t}(u_{s,t}, \Theta | n_{t-1}) du_{s,t} du_{a,t}. \tag{5.36}$$

If in the observation process the number in each class is modeled by $N(n_{i,t}, \sigma_i^2)$ and the initial distribution n_0 is an unknown vector;

$$f(y, \Theta | n_t) \propto N_{y_{1,t}}(n_{1,t}, \sigma_{1,t}^2) \times N_{y_{2,t}}(n_{2,t}, \sigma_{2,t}^2) \times N_{y_{3,t}}(n_{3,t}, \sigma_{3,t}^2), \tag{5.37}$$

where $\Theta = (\phi_1, \phi_2, \phi_3, \pi_2, \pi_3, \sigma_1^2, \sigma_2^2, \sigma_3^2)$, is a vector of the unknown parameters.

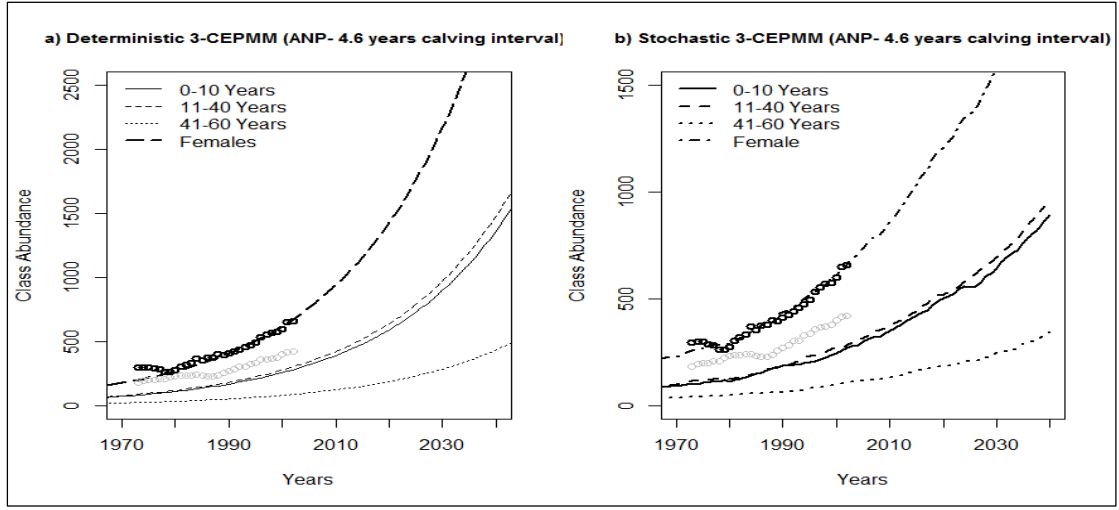


Figure 5.13 A comparison of deterministic and stochastic (3-CEPMM) for ANP. Simulations of deterministic and stochastic matrix model with fecundity determined by the calving interval. In figure a) survival is deterministic while in figure b) it is stochastic with the binomial probability distribution.

Figure 5.13 illustrates the stochastic population growth of model in equation 5.44. The second class dominates the population structure due to the fact that stage interval is large catering for all the middle-age adults between the age of 10 to 39 years. This is a hypothetical scenario with initial population of 80 mature elephants, $\phi_1 = 0.89$, $\phi_2 = 0.95$, $\phi_3 = 0.93$, $\pi_2 = 0.11$ and $\pi_3 = 0.11$. The model illustrates a density independent population growth with stochastic survival only. The theorem above enables us to study each of the sub-processes in details.

Assuming there were n_i animals and the probability of an animal being removed from a population, independent of each other is ϕ_i , the removal sub-process R can be modeled using the binomial distribution. The sub-process R can be modeled as effecting survival in an additive manner and hence, model 5.44 becomes,

$$\begin{aligned}
 u_{s,t} &\sim H_{s,t}(n_{t-1}): \begin{bmatrix} u_{1,s,t} \sim \text{Bin}(n_{1,t-1}, \phi_1) - \text{Bin}(n_{1,t-1}, \phi_1) \\ u_{2,s,t} \sim \text{Bin}(n_{2,t-1}, \phi_2) - \text{Bin}(n_{2,t-1}, \phi_2) \\ u_{3,s,t} \sim \text{Bin}(n_{3,t-1}, \phi_3) - \text{Bin}(n_{3,t-1}, \phi_3) \end{bmatrix}, \text{ where } \phi_i = 1 - \mu_i - p_{i,i+1}, \\
 u_{a,t} &\sim H_{a,t}(n_{t-1}): \begin{bmatrix} u_{1,a,t} = u_{1,s,t} \\ u_{2,a,t} = p_{12}u_{1,s,t} + u_{2,s,t} \\ u_{3,a,t} = p_{23}u_{2,s,t} + u_{3,s,t} \end{bmatrix}, \\
 u_{b,t} &\sim H_{b,t}(n_{t-1}): \begin{bmatrix} n_{1,b,t} \sim \text{Bin}(u_{2,a,t}, \pi_2) + \text{Bin}(u_{3,a,t}, \pi_3) \\ n_{2,b,t} = u_{2,a,t} \\ n_{3,b,t} = u_{3,a,t} \end{bmatrix}.
 \end{aligned} \tag{5.38}$$

If the number animals removed from the population is a random variable with a binomial distribution ($\text{binomial}(n_{i,t-1}, \varphi_i)$), we investigated the removal rate that causes a population with stochastic survival to stagnate. We noted that in a stochastic environment different realizations are attained for similar parameters. The following results are in comparison to the results of the deterministic model (5.43) above. Investigating the model further showed that the annual mortalities (φ_i) required for the populations' trend to stagnate are,

- i. 3.0% for the entire population,
- ii. 9% and 6.1% causes the population trend to stagnate for juveniles (0-10 years) and middle-aged adults (11-39 years) (figure 5.14). No percentage mortality causes population trend to stagnate growth rate for old-aged adults (40-60) .
- iii. Summary statistics of multiple simulation realizations should be used to make inferences for stochastic models and not a single realization. Another source of variation, is the stochastic nature of the calving interval, due to individual variations and environmental variability. Populations in a stochastic model do not actually become fully stationary, although a form of stability may be obtained (Figure 5.14). Distribution of multiple realization may be analyzed and empirical distributions derived.

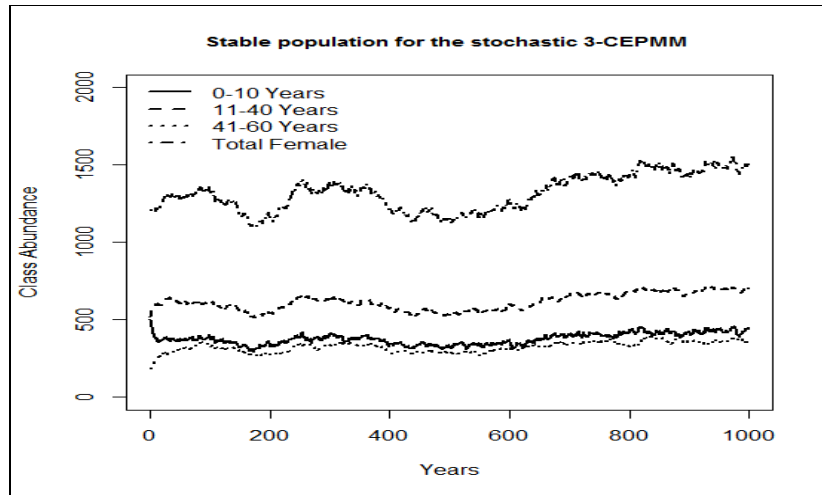


Figure 5.14 Stochastic population removals. Figure a represent population trend by assuming survival and removal (e.g. by emigration) have a binomial distribution.

Since population estimates are not without errors, lower population percentages ought to be removed in the effort to stabilize the population. Accurate population survey or estimate is required in order to remove a constant proportion of total abundance. Thus, percentage removed ought to be lower than those acquired for the deterministic population models.

If the entire elephant population is divided into fifteen classes each having 4-years interval, then, the resulting model framework in analogy to model 5.37, is a stochastic 15-CEPMM (fifteen-class model) below. The parameters in this case were for one year population projection.

$$\begin{aligned}
 u_{s,t} \sim H_{s,t}(n_{t-1}): & \begin{bmatrix} u_{1,s,t} \sim \text{Bin}(n_{1,t-1}, \phi_1) \\ u_{2,s,t} \sim \text{Bin}(n_{2,t-1}, \phi_2) \\ u_{3,s,t} \sim \text{Bin}(n_{3,t-1}, \phi_3) \\ \vdots \\ u_{14,s,t} \sim \text{Bin}(n_{14,t-1}, \phi_{14}) \\ u_{15,s,t} \sim \text{Bin}(n_{15,t-1}, \phi_{15}) \end{bmatrix}, \quad u_{a,t} \sim H_{a,t}(n_{t-1}): \begin{bmatrix} u_{1,a,t} = u_{1,a,t} \\ u_{2,a,t} = p_{1,2}u_{1,s,t} + u_{2,s,t} \\ u_{3,a,t} = p_{2,3}u_{2,s,t} + u_{3,s,t} \\ \vdots \\ u_{14,a,t} = p_{13,14}u_{13,s,t} + u_{14,s,t} \\ u_{15,a,t} = p_{14,15}u_{14,s,t} + u_{15,s,t} \end{bmatrix}, \\
 u_{b,t} \sim H_{b,t}(n_{t-1}): & \begin{bmatrix} n_{1,b,t} \sim \sum_{i=4}^{15} \text{Binomial}_i(u_{i,a,t}, \pi_i) \\ n_{2,b,t} = u_{2,a,t} \\ n_{3,b,t} = u_{3,a,t} \\ \vdots \\ n_{14,b,t} = u_{14,a,t} \\ n_{15,b,t} = u_{15,a,t} \end{bmatrix}.
 \end{aligned} \tag{5.39}$$

For a four years population projection all the individuals in a class age and proceed to the next class. The resulting simpler model framework is,

$$\begin{aligned}
 u_{s,t} \sim H_{s,t}(n_{t-1}): & \begin{bmatrix} u_{1,s,t} \sim \text{Bin}(n_{1,t-1}, \phi_1) \\ u_{2,s,t} \sim \text{Bin}(n_{2,t-1}, \phi_2) \\ u_{3,s,t} \sim \text{Bin}(n_{3,t-1}, \phi_3) \\ \vdots \\ u_{14,s,t} \sim \text{Bin}(n_{14,t-1}, \phi_{14}) \\ u_{15,s,t} \sim \text{Bin}(n_{15,t-1}, \phi_{15}) \end{bmatrix}, \quad u_{a,t} \sim H_{a,t}(n_{t-1}): \begin{bmatrix} u_{1,a,t} = 0 \\ u_{2,a,t} = u_{1,s,t} \\ u_{3,a,t} = u_{2,s,t} \\ \vdots \\ u_{14,a,t} = u_{13,s,t} \\ u_{15,a,t} = u_{14,s,t} \end{bmatrix}, \\
 u_{b,t} \sim H_{b,t}(n_{t-1}): & \begin{bmatrix} n_{1,b,t} \sim \sum_{i=4}^{15} \text{Bin}_i(u_{i,a,t}, \pi_i) \\ n_{2,b,t} = u_{2,a,t} \\ n_{3,b,t} = u_{3,a,t} \\ \vdots \\ n_{14,b,t} = u_{14,a,t} \\ n_{15,b,t} = u_{15,a,t} \end{bmatrix}.
 \end{aligned} \tag{5.40}$$

Such a model requires greater monitoring of a population to be able to classify individual's age up to 60 years. Predicted distribution can be used for population management strategy decisions such as examining the future effect on the population management policy.

In this chapter, we started by looking at the relation between different approaches to structured population models. We considered the Leslie (1945) and Usher (1969) matrix models with 10 years and 4 years class interval. In general, the models gave similar results and the class structure

and projection time didn't influence the results significantly. In general, the following results were obtained:

- i. Elephant population growth is highly influenced by average calving interval compared to age at sexual maturity, age at reproductive menopause. Assuming low natural mortality, a population tends to stabilize for average calving interval of about 5 years. If average calving interval is more than 5.5 years, a population is most likely to decline.
- ii. Sensitivity and elasticity analysis showed that survival of age classes below 24 years is most crucial for population viability and the reproduction of classes between the ages 10 and 30 were the vital in the population dynamics.
- iii. Age specific mortality levels required for zero population growth rate, were lower for juvenile classes, aged between 0-12 years, than for adult classes, aged between 12-60 years. For four years and 10 years induced mortality frequencies, no percentage mortality levels, of classes above 30 years, produces zero percent population growth rate.

A framework for studying structured population dynamics incorporating process and observation error was also discussed. In this framework individual process were incorporated in a modular approach, enhancing our ability to study individual processes. A Bayesian approach is necessary in evaluating the resulting distributions and expectations that involve multidimensional integrals.

Prediction of future populations, given a management strategy is pivotal to population management. It is also necessary to know the important threshold of the population vital parameters that are affected by a management strategy, if we wish to conserve a population successfully. Application of management strategies must be based on the specific population that we desire to conserve, otherwise the population may become extinct due to indiscriminate application of management policies. Scientifically verifiable methods of population conservation are thus encouraged.

Due to the mathematical simplifications in most models, managing real populations requires models to be customized to the specific conditions of areas in question. Models show sensitivity to initial conditions and on whether environmental and demographic stochasticity is incorporated. In using the binomial distribution to model survival, destruction, dispersal, and the number of recruits (Akçakaya, 1991), the occurrence of each event is assumed to independent distributed. We also note that the Poisson distribution can be used as an estimator of the binomial distribution for the case of recruits or offspring's. Stochastic structured population models do not attain a stable age

distribution, but level of stochasticity on the demographic parameters determined whether the model exhibit a small fluctuations or becomes chaotic.

Population predictions or projections based on time series models, linear models, deterministic or stochastic structured models and simulations play an important role in population management. A selected combination of the models to rely on should be informed by the data available. Data on age specific fecundity, age specific mortality, age at first reproduction, inter-calving intervals, the number of individuals by age class, and age at senescence are important in modelling and predicting elephant populations.

It should be noted that the age structure of elephant population may be nonstationary and may contain variation due to demographic parameters that are correlated to environmental factors. Rainfall, for example, may affect survival and fecundity of selected age groups due to increase or decrease of available resources. Thus, elephant population models should include time varying process, individual variations, demographic variations, and, process and observation error among other form of variation. One approach to capture such variation is the use of structured population models incorporating process and observation error as discussed in this chapter. Another method would be the use of systems of stochastic differential equations in a varying environment.

There is also spatial variation in elephant population that both the single cohort and age/stage structured models considered here do not capture. First the spatial range of elephant population is usually larger than officially recognized areas, where the population counts are usually conducted. Second there is spatial autocorrelation in population spread due to reproduction, dispersal and resource availability. The effect of population size or population density of the environment will also depend on spatial spread of the elephant population in a selected ecosystem. Thus, models and management strategies that incorporate spatial variations together with consider population size would be more appropriate.

CHAPTER SIX: DISCUSSIONS AND CONCLUSIONS

6.1 Population Models

Population modelling and other ecological modelling has rapidly increased recently, partially due to development of computer technology and our increased knowledge in population and ecological problems. We have endeavoured to illustrate that a model is able to encompass our understanding about a system. Using such models, better study of the population processes and population regulation strategies can be developed.

The different classes of models, we have discussed and developed including, the log-linear model, autoregressive models, and deterministic and stochastic matrix models, are useful for different purposes and users. Their abstraction levels of the population dynamics are different and have different parameter and data requirements. Simple difference and differential equation models of the total population can be used to access the overall population trend. Where few observations of the population abundance or growth rates are recorded, bootstrapping of the parameters can be used to increase the pool of values available. We have discussed, constructed and applied the age structured population model to:

- i. Determine the growth rate of a population for selected or real population parameters. Sensitivity analysis enables us to determine the sensitivity of the dominant eigenvalue to change in transition rate.
- ii. Determine the age distribution that the population attains over time.
- iii. Project future population size and determine population viability over time.
- iv. Evaluate population regulation methods, by varying the vital parameters or transition rates.

By the use of population models for elephant population we were able to evaluate, expose important properties and conduct analysis that can be used to test hypothesis related to these populations. Simulations were used due to the absence of sufficient historical data to evaluate every hypothetical scenario. Simple model with few parameters can be used to set up more research studies on the population and to develop data collection schemes. Improvement can be done on the simple models in order to capture more complex relation that exist in the population processes, hence leading to better models.

6.2 Total population abundance models

Important mathematical principles of both linear and nonlinear in population models were discussed in the literature review and methods. These phenomena include equilibria, cycles, bifurcations, multiple attractors, transient phenomena and chaos. Studies of the short term and long term dynamics of population models which make use of transient, asymptotic, ergodic and perturbation analyses are necessary especially for models which capture practical population processes and ecological assumptions. Analysis of stochastic models benefits from our understanding of the dynamics of the deterministic skeleton.

Starting with discrete time and continuous time population models in chapter two, we discussed issues and concepts that relate to density independence and density dependence. The important role that the per-capita growth rate plays in population dynamics and model fitting for population data was discussed. The relationship between per capita growth rate $\left(\frac{1}{N} \frac{dN}{dt}\right)$, and population size or density is important in determining the form of population dynamics.

In the case of logistic growth the population growth rate declines linearly with increasing populations. For the theta logistic model, the growth rate is given by $r = r_m [1 - (\frac{N_t}{K})^\theta]$, where r_m is the maximum growth rate, when there is no resource scarcity and no predators. The value of theta determine the type of curvature with values of θ greater or less than 1 corresponding to convex and concave relationships, respectively.

The type of relationship between rate of growth and population abundance is also important in population forecasting and evaluating population management strategies. Determinant of the growth rate r , such as resource availability, intra-specific competition and predator prey relationship can be varied so as to increase, stabilize or reduce the growth rate. The goals of varying the per capita growth rate may be to conserve, maintain a stationary population or reduce population.

Relating population models statistically to data is central to answering many important questions in ecology and population management. Although real ecological data of population abundance are stochastic, they contain patterns that can be explained using deterministic models.

To effectively manage an elephant's population, the managers will require knowledge about the population trend and the rates at which their populations is growing. Three approaches were used to model single-population dynamics of the elephant population in chapter four. All the three, the log-linear models, ARIMA models and bootstrapping showed close similarity in the projected values.

The log-linear fit has slope, $r = 0.055$ for the AENP elephants' population and $r = 0.0362$, for the ANP population. Using the conversion $(e^r - 1)100\%$ to acquire an approximate 6% and 4% annual population increase in AENP and ANP respectively. It is important to note that due to the log transformation of the data and the subsequent inverse transformation, the log-linear model has a bias (Eberhardt 1992). Yet, these models are crucial in populations that show an exponential growth rate where there is no evidence of density dependence.

Integrated autoregressive moving average (ARIMA) methods for modeling autoregressive data and forecasting techniques are well established. An advantage of these models is that we can consider the total population figures observed, as capturing both biological processes and environmental variability in the data. ARIMA models fitted were used to forecast and compare elephant population of AENP in South Africa and ANP in Kenya. An *ARIMA*(0,2,2) was fitted for both populations although *ARIMA*(1,2,1) was also sufficiently adequate for ANP and an *ARIMA*(2,2,2) for AENP. Time series models for the growth rate of each of these populations were also fitted and used in forecasting.

The ARIMA models showed longer population doubling time in AENP of 14 to 16 years compared to forecasts of structured population models (Woodd (1999)) of 13.5 years. ARIMA models forecasts are accurate only for a short forecast time horizon. The main challenge of fitting ARIMA models is that the number of observations available was few and some counts were not done on uniform time intervals.

Bootstrapping using crude growth rate, R , for the selected populations, gives forecast that agree with the ARIMA and log-linear fits. Bootstrapping methods also offer extra statistics from the empirical distribution which the log-linear and ARIMA methods don't. The linear model gives a population doubling time of about 18 years and 12 years for ANP and AENP respectively. These doubling time are similar for the bootstrapping method. The forecasts for ARIMA models are only useful in the near future and become very unreliable as the forecast time horizon increases.

We have gone a step further to derive the Bayesian distribution of the instantaneous growth rate (continuous exponential growth rate r). This method can be used to compare populations that differ terms of dynamics, size, location and structure. The method has been used to compare two elephant population in South Africa, one that has had population control policy applied and one that is recovering. The result agrees with the general study by Hones (1999) on rate of increase r and has

implication on population management. Population culling shifts the distribution of the net growth rate to lower values.

Given sample data we were able to calculate the growth rate of elephant population and use simulations to determine the chances that an endangered population will persist for given time period and what will be the general population trend. We can also predict what will be the population size in future years and attach a measure of uncertainty on the prediction.

Models where the population is considered as homogeneous are useful in determining the general trend of a population but cannot be used to study the effect of the age dependent parameters. Both the AENP and ANP projections showed that the populations will continue to increase exponentially, if the conditions remain relatively similar.

6.3 Age structured population models

Structured population models for biological species are applicable to populations that can be classified to groups that are more homogeneous. Elephants have characteristics and life histories that enable us to classify them into age classes that are more homogeneous. The population dynamics of the African elephant, which is a long lived species has been shown to be affected by the age structure of the population, since birth and death are age dependent. Birth and death or other transition probabilities are also affected by other sources of variation including time varying environmental processes.

The construction, properties, theorems and application of matrix models similar to the Leslie (1945) and Usher (1969) matrix were explained. The models which are deterministic and linear were used to incorporate age structure in the population of female elephants. The three models developed including the three, six and fifteen age classes models, are simple and easy to analyze. These models may not fully describe the elephant population dynamics but offer an important tool for evaluating population trends for selected hypothetical scenarios. The simulation of the linear structured population growths for the African elephant population has emphasized on explanatory models for evaluating the impact of change in vital rates due to a hypothetical change, natural change or management actions. The models can be improved to cater for effects of density dependence and stochasticity on population vital parameters.

A structured model, where the age groups for elephant's population were aggregated into juveniles from 0 to 9 years, middle aged from 10 to 39 years and old aged from 40 to 60 years was the simplest structured model considered. This approach would be supported by the fact that determining the exact age of free roaming wild population is hard and can only be estimated with low

accuracy. A model that classifies elephant using the three classes is important since determining the exact age of wild population is not viable and the populations are large (Akçakaya H R. 2000). A stochastic framework for studying the three classes' model and other age structured models were given. Migration and immigration data is not easily available and management decision ought to be reached using the scant details available.

The Leslie (1945) and Usher (1969) transition matrix were used to evaluate induced age specific mortality regimes, average calving interval and age at reproductive maturity. Sensitivity and elasticity analysis was used to determining the role that each class plays in the population dynamics. We applied sensitivity analysis of the deterministic matrix models to make decisions about which vital rates to focus on in management and conservation efforts. Thus, sensitivity analyses of the models provide some insight into how best to manage a population.

Sensitivity and elasticity analysis showed that the survival of animals less than 30 years and fecundity of animals aged between 10 to 30 years have the greatest effect on population trend. In the ten-year model, projections were found to be more sensitive to survival parameters of the first class and fecundity of the second class. For the ten-year structured population models, the most sensitive transitions were from juvenile (0-10) to 11-20 years and 11-21 to 21-30 years. Elasticity of the survival of class 0-10 years, survival of 11-20 years and fecundity of class 10-20 years and 20-30 showed the highest value. This indicates that management policies that target survival would be most effective if attention is focused on the survival of juveniles and young adults. Management policies that alter fecundity will be most effective if targeted at ages between 10 to 30 years animals. A management strategy may affect many of the vital strategies concurrently and thus compound the effect on population dynamics.

Similar observations were made for the fifteen classes' model. Survival of animals less than 24 years, and fecundity of animals between the ages of 10 and 32 years showed highest sensitivity and elasticity. The results are in agreement with Whitehouse & Hall-Martin (2005) that, in all elephant's populations, elephants that are between 15 and 25 years old, contribute most to future growth of populations. The fifteen classes' model and the six classes' matrix models give comparable population projection for similar assumption about the population vital parameters. In the fifteen classes' model, projections were more sensitive to survival parameters of the first three classes and fecundity of the next three classes.

Population projections are most sensitive to changes in calving interval and probability of survival than the age at sexual maturity. These results support the fact that removal of proportions of

animals in the older classes (40 – 60 years) has the least effect on population viability. In general, population projections were highly sensitive to survival of the juveniles and fecundity of the middle aged elephants.

Assuming the vital rates are not correlated we can use elasticity analysis to provide insights into the effectiveness of selective management pressures on age-specific vital rates (Rose *et al.* 2002). Recovery of a population highly depends on the survival of the animals, especially of juveniles, and the fecundity of middle aged elephants. Removal of animals of age greater than 40 years showed least effect on the viability and regulation of a well established population.

Management policies that put in to consideration population demographic structure are bound to be more efficient. Management strategies that aimed at conserving elephant population should be guided by the conservation goal. Strategies intended to increase population growth should focus on increasing survival rate of the juvenile or reducing the calving interval for the reproducing females between the ages of 10 to 30 years. To stabilize an elephant population growth or reduce population growth, focus should be on reducing the survival of the juvenile and adults below 30 years and reducing the fecundity of female between the ages of 10 to 30 years. The stable age distribution show that the population proportion of animals below 24 year is higher than those above and hence the emphasis on the classes below 24 years.

The analysis of age specific mortality required to cause zero percent growth, showed that natural limitation of elephant populations, through natural mortality is unlikely to stabilize a population with average calving intervals less than 5 years. The percentage reduction in survival rates required in order to attain a stationary population was found to be affected more by the calving interval. There is need for management intervention to stabilize a population with calving interval less than 5 years, especially if natural mortality is low and the population is within a protected area.

Our analysis also showed that elephant population dynamics are sensitive to number of individuals and age structure of the initial population. All simulated populations attained a stable age distribution but after different time intervals. When the proportion of individuals in a given age class does not change from one time interval to the next, the structured population has attained the stable age distribution.

In the stochastic matrix model of population dynamics, the transition matrix elements were allowed to vary from one time unit to the next. The individual chance of survival or reproduction was considered to be probabilistic and determined by a probability distribution. Such stochastic models do not attain a stable age distribution especially if the variability is high. If the stochastic variations are low then the model's stable age distribution tend to the equivalent deterministic model. The main

challenge in a stochastic model was quantifying the variability to be attached to an individual, the environment, and other sources of variability.

We sought to establish the maximum number or proportion of animals that should be removed in order to cause the population to stagnate for a stochastic model. For selected population vital parameters, it was realised that the level of population mortality required to cause population to stabilise was much lower than the corresponding deterministic scenarios. Results showed that a management policy that causes population to stagnate in one ecosystem may lead to extinction, if applied indiscriminately in another ecosystem. The vital elephant population parameters and the management goals, determines the best management policy for a given ecosystem.

Related age structure population models include Woolley et al (2008) and Wood A.M (1999), which show comparable results for population projections and intrinsic growth rate. The study by Woolley et al (2008) is a concurrent study which focused on episodic and annual mortality required to produce zero percent population growth.

The challenges that arise, while using Leslie like models for the case of elephant population include, overlapping calving intervals, environmental seasonality correlated with vital parameters and individual animals' variability. Due to social and family ties within the elephant population, the removal of animals may affect population vital parameters directly or indirectly. The effect of such social dynamics was not considered.

6.5 Conclusions and recommendations

We start this section by noting that continued longitudinal studies should be done on African elephant population in the eastern and southern Africa to ensure continued information on population trend and identify changes, if any, in numbers and demographic characteristics. The population studied and simulations can be used to inform management of newly introduced populations with close or equivalent ecological conditions.

Considering the population as a single homogeneous group improved deterministic models for the total population abundance $y(t)$, may include emigration and immigration data. Such models can be explored in a varying environment. The per capita birth, death rates and migration, $b(t)$, $d(t)$, and $m(t)$ respectively would be functions of time and additional environmental variables. They would for example, have the forms $b(t, v_1, v_2, \dots, v_n)$, $d(t, v_1, v_2, \dots, v_n)$ and $m(t, v_1, v_2, \dots, v_n)$, respectively, where $v_1, v_2, \dots, v_n$ represent the different environmental variables. This way of extending the model

would incorporate stochastic and temporal variation in an open ecosystem. Modeling of long term climatic data and other environmental data and their relation to population dynamics parameters can be pursued to enhance population management in light of climatic and environmental changes expected.

Spatially explicit statistical models can be used to model the spatial distribution, environmental variations and effect of human disturbances on elephant's population. The effectiveness of such spatially explicit models would be evaluated in characterising the environmental response of elephant's population distribution, predicting their probability of occurrence, assessing variability and landscape transformation. There is spatial autocorrelation in population spread due to reproduction, dispersal and resource availability that both age structured and unstructured models do not capture.

ARIMA models were basically used to model total population abundance and population growth rate. Models on population growth rate combines birth, death and migration into a single series. Multivariate autoregressive models offer better tool for analyzing the series but require more data on the series. Another way to improve the ARIMA models is to use the additive approach of the state space models in modeling population time series with trend, seasonal component, and process and measurement error. The Bayesian state space approach makes it possible to quantify multiple sources of uncertainty including, uncertainty in data, parameters and model choice.

Matrix population models considered were linear and did not incorporate density dependence and variability. Although we have made effort to incorporate stochastic variation, more realistic models that incorporate nonlinear relations are required. The modular approach to population process gives a more flexible way of studying individual processes of an elephant's population. More studies on individual process such as survival, birth or fecundity functions can then be done and their distributions established, as more data becomes available.

Processes that are not Markovian can be used to model non-linear processes in the population dynamics. The application of HPM models in the study of individual process involved in elephant population can be studied further. The single step dependence structure assumed in Markov chains can be relaxed and analysis of non-linear non-Gaussian state space model fitted. Such models would also be vital in modelling African elephant population dynamics, where the dimension of the state vector differs from the dimension of the observation vector.

More data on population trends is still necessary to be able to make clear conclusion on elephant's population behavior and it's relation to environmental variability. The accuracy of the data

also determines the reliability of the prediction results and the management decisions arrived at. Data observed and recorded ought to capture more variables relating to population age structure. These variables may be used to establish whether a give population has attained a stable age distribution, and if not, establish the age classes deviating from expected scenario.

In conclusion, we have endeavored to demonstrate the important role played by mathematical and statistical models in modeling population dynamics of elephants. Both simple models with few parameters requirements and more detailed models have important role to play in understanding the dynamics of elephant's population and their management. In the absence of sufficient historical data population analysts may perform simulations using the available information. Using models we increase our understanding of the underlying population processes, forecast future population trend, and study the effect of selected population parameters.

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APPENDICES

Appendix A: Definitions

Hadamard product: The Hadamard product of two matrices is denoted by $A \circ B$ is given by

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \circ \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} = \begin{pmatrix} a_{11}b_{11} & a_{12}b_{12} \\ a_{21}b_{21} & a_{22}b_{22} \end{pmatrix}$$

Appendix B: Data

Table B1: Elephant population estimates. African Elephants population estimates in some sub-Saharan African countries.

COUNTRY	POPULATION	COUNTRY	POPULATION
South Africa	17270	Swaziland	30
Nambia	10820	Botswana	156020
Zimbabwe	99080	Zambia	25270
Angola	1580	Malawi	2380
Mozambique	12870	Tanzania	143650
Kenya	42100	Uganda	10500
DRC	15150	Rwanda	40
Ethiopia	260	Sudan	16840
Central A R	3400	Congo	17800
Gabon	76700	Cameroon	17920
Nigeria	430	Benin	2580
Togo	10	Guinea	210
Liberia	310	Mali	320
Niger	90	Chad	350

Table B2: Mortality rates for Tsavo National Park. Mortality rates for the Tsavo National Park (Kenya), expressed as a percentage per year per annual age group ((Laws, 1969) and (Corfield, 1973))

Age	Mortality before 1970-71		Mortality during 1970-71	
	Female	Male	Female	Male
0-1	36	36	18.2	18.2
2-5	10.2	10.2	37.6	37.6
6-10	2.4	2.4	17.1	17.1
11-15	2.4	2.4	7.8	7.7
16-20	2.1	2.1	6.5	1.9
21-25	2	1.6	12.1	3.3
26-30	2.5	7	29.3	3.7
31-35	2.5	7.5	28.4	6.5
36-40	2.6	6.9	61.3	12.1
41-45	3	8.8	33.4	6.1
46-50	8.1	27.4	66.3	26.7
51-55	18.4	19	83.7	31.3
56-60	29.8	100	63.2	100

Table B3: Demography rates AENP, Woodd A.M. (1999).

Demographic parameters for the Addo elephant population based on data for the period 1976--1998			
Age of first conception	11.2		
Inter calf interval	3.8		
Age of reproductive senescence	49.2		
Age and Sex specific mortalities	Age class	Male	Female
	0	0.062	0.062
	1--9	0.009	0.001
	10--19	0.02	0.004
	20--29	0.031	0.003
	30--44	0.051	0.012
	45--59	1	0.016
	60+		1

Table B4: Demography rates. Gough K.F. and Kerley I.H.G. (2006)

	Mortality rate (%)				
Age class	Male	Female	Total	z	P
0	3.5	4.6	4	0.23	0.82
1	0	0.6	0.3	0.05	0.96
2	1.8	0	1	1.05	0.29
3	2	0.4	1.7	4.98	0.001
4	0.7	0	0.4	2.89	0.004
5–9	0.4	0.2	0.3	0.04	0.97
10–14	0.8	0	0.4	6.05	0.001
15–19	1.9	0.6	1.1	1.11	0.27
20–24	3.4	0	1.4	2.51	0.01
25–29	4.7	0.5	2.1	2.18	0.03
30–34	5.4	0	1.9	1.64	0.03
35–39	10.6	2.3	5.3	1.65	0.1
40–44	7.7	2.4	4.3	0.04	0.67
45–49	0	3.2	2.6		
50–54	n/a	0	0		
55–59	n/a	0	0		
60–64	n/a	41.7	41.7		

Table B4: Age of sexual maturity. Age of sexual maturity in seven different elephant populations

Sample	Mean Age of sexual maturity	Confidence limits
Mkomazi	12.24	11.33-13.15
Mkomazi East	12.18	10.92-13.44
Tsavo National Park	11.73	10.8-12.66
Murchison Falls National Park N.	16.28	15.48-17.08
Murchison Falls National Park S.	17.82	16.96-18.68
Budongo Forest Reserve	22.38	19.86-24.90
Luangwa Valley National Park	14	-

Table B6: Calving intervals for African Elephant: Lengths of calving intervals for elephant populations across Africa. Source: Van Aarde R., Sam Ferreira, Tim Jackson, and Bruce Page. (2008).

Locality	Method	Calving interval (years)		
		Mean	95% CI	Range
Addo	Individual histories	3.8	–	–
	Individual histories	3.8	3.6–4.0	–
	Individual histories	3.3	–	–
	Cow-calf associations	4	3.3–4.6	–
Kruger	Placental scars	4.5	4.0–5.0	–
	Culled samples	3.7	–	–
Mabula	Cow-calf associations	2.4	2.3–2.5	–
Phinda	Cow-calf associations	3.9	3.5–4.3	–
Pilanesberg	Cow-calf associations	3.3	3.1–3.5	–
Pongola	Cow-calf associations	3.1	2.7–3.5	–
Amboseli	Individual histories	4.5	–	1.8–11.7
	Cow-calf associations	4.6	4.1–5.1	–
Bugongo	Culled samples	7.7	5.4–13.5	–
Etosha	Culled samples	3.8	–	–
	Placental scars	2.1	–	–
	Placental scars	2.5	–	–
Kasungu	Cow-calf associations	3.9	2.2–5.3	–
	Cow-calf associations	3.3	–	–
Kidepo	Culled samples	2.2	–	–
	Culled samples	3.2	–	–
Luangwa	Culled samples	3	–	–
	Placental scars	4	–	–
Maputo	Cow-calf associations	3.1	3.0–4.2	–
Mkomazi	Culled samples	2.9	2.6–3.4	–
Mkomazi East	Culled samples	4.2	3.1–5.0	–
Murchison North	Culled samples	–	–	2.6–5.8
	Culled samples	9.1	7.5–11.5	–
Murchison South	Culled samples	5.6	4.8–6.8	–
Tsavo	Cow-calf associations	4.6	–	–
	Cow-calf associations	5	3.2–6.8	–
	Culled samples	6.8	5.1–10.3	–
Zambezi	Culled samples	2.8	–	–
	Culled samples	3.4	–	–
	Placental scars	3.8	3.0–4.6	–

Table B5: Addo National Park elephant population. Gough K.F. and Kerley I.H.G. (2006).

Year	Population	Births	Deaths	Sex ratio M/(M+F)	Exponential rate	Population Growth %	Mortality
1976	94	11	0	0.45	0.12	13.3	0
1977	96	4	2	0.5	0.02	2.1	2.1
1978	96	2	2	1	0	0	2.1
1979	98	9	7	0.38	0.02	2.1	3.1
1980	103	5	0	0.4	0.05	5.1	0
1981	111	12	4	0.25	0.07	7.8	3.6
1982	113	4	2	0.75	0.02	1.8	1.8
1983	120	8	1	0.75	0.06	6.2	0.8
1984	128	9	1	0.67	0.06	6.7	0.8
1985	138	10	0	0.3	0.08	7.8	0
1986	142	11	7	0.5	0.03	2.9	4.9
1987	151	10	1	0.5	0.06	6.3	0.7
1988	160	11	2	0.36	0.06	6	1.3
1989	170	10	0	0.4	0.06	6.3	0
1990	181	11	0	0.36	0.06	6.5	0
1991	189	8	0	0.5	0.04	4.4	0
1992	199	12	2	0.83	0.05	5.3	1
1993	205	13	7	0.69	0.03	3	3.4
1994	220	15	0	0.67	0.07	7.3	0
1995	232	18	6	0.69	0.05	5.5	2.6
1996	249	19	2	0.32	0.07	7.3	0.8
1997	261	17	5	0.56	0.05	4.8	1.9
1998	284	29	6	0.36	0.08	8.8	2.1
1999	315	32	1	0.66	0.1	10.9	0.3
2000	324	15	6	0.4	0.03	2.9	1.9
2001	336	16	4	0.81	0.04	3.7	1.2
2002	377	42	1	0.62	0.12	12.2	0.3
2003	388	18	7	0.42	0.03	2.9	1.8

Appendix C. Sample R-codes

Sample R-codes from chapter two

```
#-----  
#Theta-logistic dynamics with and without error  
#-----  
>Time<-seq(0.1,40,0.2); set.seed(0); paramaters <- c(r <- 0.65, alpha <- 0.0001, theta = 1)  
>Abundance <- sapply(theta, function(th) {paramaters["theta"] <- th  
      +ode(y = 1, Time, thetalogistic, paramaters)[, 2]})  
>matplot(Time, Abundance, type = "l",lwd=2)  
>legend("bottomright", legend = paste("theta =", c(1,0.9,0.7,0.5,0.3)),lty = 5:1,lwd=2, bty = "n")  
>title("(A)Theta logistic growths without Error ",cex.main = 0.85,)  
#-----  
#Theta-logistic dynamics  
#-----  
>Time<-seq(0.1,80,0.2); set.seed(0); paramaters <- c(r <- 0.25, alpha <- 0.0001, theta = 1)  
>Abundance <- sapply(theta, function(th) {paramaters["theta"] <- th  
      +ode(y = 20, Time, thetalogistic, paramaters)[, 2]+rnorm(1,mean=0,sd=1.25)})  
>matplot(Time, Abundance, type = "l",lwd=2)  
>legend("topleft", legend = paste("theta =", c(1,0.9,0.7,0.5,0.3)),lty = 5:1,lwd=2, bty = "n")  
>title("(B)Theta logistic growths with Error ",cex.main = 0.85)  
#-----  
#Deterministic Riker dynamical model  
#-----  
>ricker <- function(alpha = 0.001, rd = 0.5, N0 = 2, t = 400) { N <- c(N0, numeric(t))  
      +for (i in 1:t) N[i + 1] <- {N[i] *exp (rd * (1 - alpha * N[i])) }  
      +return(N)}  
#-----  
#Deterministic Riker dynamical model with declining K  
#-----  
>ricker2 <- function(alpha = 0.001, beta=0.002,rd = 0.5, N0 = 2, t = 400)  
      +{ N <- c(N0, numeric(t))  
      +for (i in 1:t) N[i + 1] <- {N[i] *exp (rd * (1 - alpha * N[i]/(1-beta)^i)) }  
      + return(N)}  
>Abundance1 <- sapply(R, function(th) {ricker(rd=th)})  
>Abundance2 <- sapply(R, function(th) {ricker2(rd=th)})  
>par(mfrow=c(1,2)) # Two plots.  
>matplot(1:401,Abundance1,type="l",lty=1:5,ylab="Abundance",xlab="Time",lwd=2)  
>title("[a]Population Simulations with Constant K ",cex.main = 0.85,)  
>matplot(1:401,Abundance2,type="l",lty=1:5,ylab="Abundance",xlab="Time",lwd=2)  
>title("[b]Population Simulations with Declining K ",cex.main = 0.85,)  
#-----
```

```

#-----
#Ricker population model with process error
#-----
dricker <- function(alpha = 0.001, rd = 0.5, N0 = 2, t = 400) {N <- c(N0, numeric(t))
  +for (i in 1:t) N[i + 1] <- {N[i] *exp (rd * (1 - alpha * N[i])+rnorm(1,0,0.125))}
  +return(N)}

#-----
#Ricker population Model with process error and declining K
#-----
>dricker2 <- function(alpha = 0.001, beta=0.002,rd = 0.5, N0 = 2, t = 400) {
  +N <- c(N0, numeric(t))
  +for (i in 1:t) N[i + 1] <- {
  +N[i] *exp (rd * (1 - alpha * N[i]/(1-beta)^i)+rnorm(1,0,0.125))}
  +return(N)}

#-----
# Riker dynamical model with process and measurement error plot
#-----
>par(mfrow=c(1,2)); Time<-1:401
>Abundance_1 <- sapply(R, function(th) {dricker(rd=th)})
>matplot(Time,Abundance_1,type="l",lty=1:5,lwd=1)
>abline(v=50,lty=2,lwd=2); abline(v=54,lty=2,lwd=2); abline(h=500,lty=2,lwd=2)
>title("(a)Population Simulations with Process Error ",cex.main = 0.85,)

#-----
# Riker dynamical model with process and measurement error; declining K plot
#-----
>Time<-1:401
>Abundance_2 <- sapply(R, function(th) {dricker2(rd=th)})
>matplot(Time,Abundance_2,type="l",lty=1:5,lwd=1)
>abline(v=50,lty=2,lwd=2); abline(v=54,lty=2,lwd=2); abline(h=400,lty=2,lwd=2)
>title("(b)Population Simulations with Declining K ",cex.main = 0.85,)

#-----
Sample R-code from chapter four
#-----
>library(lattice); library(MASS); library(tseries);
>library(timeSeries);library(timeDate); library(dlm);
#-----
>par(mfrow=c(1,2))
>anp.fit1<-arima(Total,order=c(0,2,2))      #Total is the population abundance data
>anp.pr=predict(anp.fit1,n.ahead=40)        #Predict using fit above
>cbind(c(2009:2048),c(round(anp.pr$pred)),c(round(anp.pr$se)))
      U = anp.pr$pred + 1.64*anp.pr$se    #confidence limits
      L = anp.pr$pred - 1.64*anp.pr$se

```

```

    U1 = anp.pr$pred + 2*anp.pr$se
    L1 = anp.pr$pred - 2*anp.pr$se
    U2 = anp.pr$pred + 2.6*anp.pr$se
    L2 = anp.pr$pred - 2.6*anp.pr$se
> YEAR=1973:2008
>plot(YEAR, Total, type="o", xlim=c(1973,2050),          #Plot the data
>ylim=c(300,3500), xlab="Year",ylab="Population Forecast",main="a)
    ARIMA(0,2,2) forecasts for ANP")
>lines(2009:2048,anp.pr$pred, col="red", type="o")        #Plot the predicted values
>lines(2009:2048,U1, col="blue", lty="dashed",lwd=2)     #Plot confidence limits
>lines(2009:2048,L1, col="blue", lty="dashed",lwd=2)
>lines(2009:2048,U2, col="black", lty="dashed",lwd=2)
>lines(2009:2048,L2, col="black", lty="dashed",lwd=2)
>lines(2009:2048,U, col="red", lty="dashed",lwd=2)
>lines(2009:2048,L, col="red", lty="dashed",lwd=2)       #Plot confidence limits
>abline(v=2008,lty="dotted")
>AIC(anp.fit1)/length(Total)                             #model diagnosis
>hist(resid(anp.fit1),col="grey")                         #model diagnosis
>tsdiag(anp.fit1)                                         #model diagnosis
>title(main=("(a) Model ARIMA(0,2,2) for ANP diagnosis")
#-----
# Bootstrapping: 1967:1999 KNP
#-----
>PopSimulate <- function(R, N0, years = 21, sims = 50) {
  +R_Mat = matrix(sample(R, size=no.sims * years, replace = TRUE),
  +nrow = years, ncol = sims)
  +population <- numeric(years + 1)
  +population[1] <- N0
  +POPULATIONS <- sapply(1:no.sims, function(i) {
  +for (t in 1:years) population[t + 1] <- round(population[t] *
  +R_Mat[t, i], 0)
  +population})
  +return(POPULATIONS)}
>set.seed(100)
>POPULATION2 <- PopSimulate(R = Observe_R2, N0 = 9152, sims = 50)
>matplot( 1999:(1999+years),POPULATION2, type = "l", log = "y",lwd=2)
>title("Kruger NP Prediction R 1967:1999 ",cex.main = 0.95,)
>N2.2050 <- POPULATION2[52, ]
>summary(N2.2050, digits = 6)
>quantile(N2.2050, prob = c(0.0275, 0.975))
>par(mfrow=c(1,2)) # Plotting the graphs
>hist(N2.2050, main = "N",col="darkgrey")
>hist(log10(N2.2050 + 1), main = "log(N+1)",col="darkgrey")

```

```
>abline(v = log10(quantile(N2.2050, prob = c(0.0275, 0.975)) +1), lty = 3)
```

```
#-----
```

Sample R-codes from chapter five

```
#-----
```

Data, box plot and summary statistics of calving interval. Figure 5.2

```
#-----
```

Eigenanalysis

```
E<-eigen(A)           # eigenanalysis
lambda<-Re(E$values[1]) # dominant eigenvalue
## right eigenvector
w<-Re(E$vectors[,1])   # stable age distribution
w<-v/sum(v)            # standardize to total density
## left eigenvector
ET<- eigen(t(A))
v<- Re(ET$vectors[,1])
v<-w/w[1]              # reproductive value
```

```
#-----
```

```
E<-eigen(A)           # eigenanalysis
lambda<-Re(E$values[1]) # dominant eigenvalue
w<-Re(E$vectors[,1])   # stable age distribution
w<-v/sum(v)            # standardize to total density
ET<- eigen(t(A))
v<- Re(ET$vectors[,1])
v<-w/w[1]              # reproductive value
```

```
#-----
```

```
P <- as.vector(v%*%w)
W <- t(w)
M <- v %*%W           # Sensitivities of lambda to matrix elements
SE <- M/P             # Elasticities of lambda to matrix elements
elas <- A/lambda*SE
```

```
#-----
```

Deterministic matrix population projection, example.

```
#-----
```

ANP model

```
>L15=diag(x=0,nrow=15,ncol=15)
>L15[1,]<-c(0,0,0,0.45,0.45,0.45,0.45,0.45,0.45,0.45,0.45,0.45,0.45,0.45,0.45);
>L15[2,1]=0.94*0.99^3; L15[3,2]=0.99^4; L15[4,3]=(0.98^2)*0.98^2
>L15[5,4]=0.98^4; L15[6,5]=0.98^4;L15[7,6]=0.99^4;L15[8,7]=0.99^4
>L15[9,8]=0.99^2*(0.97^2);L15[10,9]=0.97^4;L15[11,10]=0.97^4;L15[12,11]=0.97^4
>L15[13,12]=0.95^4;L15[14,13]=0.95^4; L15[15,14]=0.95^4; L15;      eigen(L15)
```

```
#-----
```

```

#Simulations and projection graph)
>N1<-matrix(c(1, 2, 2,2,2,2, 2, 3,5,7,9,9,7,6,5), ncol = 1); years <- 30
>projections <- matrix(0, nrow = nrow(L15), ncol = years +1)
>totals <- matrix(0, nrow = years, ncol = 1); projections[, 1] <- N1; totals[1]=sum(N1)
>for (i in 1:years) {projections[, i + 1] <- L15 %*% projections[,i];
  totals[i+1]=sum(projections[,i+1])}
>Time<-ts(seq(1930,2050,4))
>matplot(seq(1930,2050,4,start=1930,frequency=4), t(projections), type = "l",
  lty = 1:15,lwd=1,col = 1, ylab = "Class Abundance", xlab = "Years",ylim=c(0,3000))
>legend("topleft", legend = c("0-3 Years", "4-7 Years", "8-11 Years","12-15 Years",
  "16-19 Years","20-23 Years", "24-27 Years", "28-31 Years","32-35 Years", "36-39 Years",
  "40-43 Years", "44-47 Years", "48-51 Years", "52-55 Years", "56-59 Years", "Total"),
  lty = c(1:6,1:6,1,2,3,1),lwd=c(rep(1,15),2), col = 1, bty = "n")
>lines(seq(1930,2050,4),totals,lwd=2)
>title("b) Population ANP: 4.5 Year Calving Interval ",cex.main = 1)
>points(1980,276,lwd=2,col="red"); points(1990,412,lwd=2,col="red")
>points(2000,599,lwd=2,col="red"); points(2002,659,lwd=2,col="red")
#-----
# Stochastic Sub-process model matrix model (Figure 5.13)
#-----
#data
>t<-c(1973,1974,1975,1976,1977,1978,1979,1980,1981,1982,1983,1984,1985,1986,1987,
  1988,1989,1990,1991,1992,1993,1994,1995,1996,1997,1998,1999,2000,2001,2002)
>p<-c(184,195,202,201,210,210,226,232,239,238,240,241,234,231,228,
  238,257, 270,282,305,305,330,337,360,365,371,379,401,418,422)
>f<-c(296,300,302,289,282,263,262,276,305,319,333,372,353,375,379,
  401,397,412,425,440,460,474,496,535,556,572,575,599,650,659)
#-----
># Simulating stochastic sub-process models
># Stage structured growth - multiple steps
>s1<-matrix(c(52, 57,27), ncol = 1); years <- 90;
>sproject1 <- matrix(0, nrow = length(s1), ncol = years +1)
>sproject2 <- matrix(0, nrow = length(s1), ncol = years +1)
>sproject3 <- matrix(0, nrow = length(s1), ncol = years +1)
>Total <- matrix(0, nrow = 1, ncol = years +1)
>sproject1[, 1] <- s1; sproject2[, 1] <- s1; sproject3[, 1] <- s1; Total[1]=sum(s1);
>for (i in 1:years) {
  sproject1[1, i + 1] <- rbinom(1,round(sproject3[1,i],0),0.91)
  sproject1[2, i + 1] <- rbinom(1,round(sproject3[2,i],0),0.95)
  sproject1[3, i + 1] <- rbinom(1,round(sproject3[3,i],0),0.94)
  sproject2[1, i + 1]=sproject1[1, i + 1]
  sproject2[2, i + 1]=((1/10)*sproject1[1, i + 1])+sproject1[2, i + 1]
  sproject2[3, i + 1]=((1/30)*sproject1[2, i + 1])+sproject1[3, i + 1]
}

```

```

sproject3[1, i + 1] <- sproject2[1, i+1]+((sproject2[2, i+1])*0.11)+ ((sproject2[3, i+1 ])*0.11)
sproject3[2, i + 1] <- sproject2[2, i+1 ]
sproject3[3, i + 1] <- sproject2[3, i+1 ]
Total[i+1]=sproject3[1, i+1 ]+sproject3[2, i+1 ]+sproject3[3, i+1 ]
>}
>Time<-ts(seq(1950,2040,1))
>Data<-cbind(t(sproject3),t(Total))
>matplot(seq(1950,2040,1,start=1950,frequency=1), Data, type = "l", lty = c(1,2,3,4),col=1,
          lwd=2, ylab = "Class Abundance", xlab = "Years",xlim=c(1970,2040),
          ylim=c(0,1500))
          legend("topleft", legend = c("0-10 Years", "11-40 Years", "41-60 Years","Female"),
          lty = 1:4,lwd=2, col = 1, bty = "n")
>title("b) Stochastic 3-CEPMM (ANP- 4.6 years calving interval)",cex.main = 0.95)
>points(t,p,lwd=1,col="grey")
>points(t,f,lwd=2,col="black")
#-----

```