Modeling and analysis of a two prey-one predator system with harvesting, Holling Type II and ratio-dependent responses

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Declaration

This dissertation is a result of my efforts and to the best of my knowledge, no part of it has been submitted for any award in any college or university.

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Signature..... Date.....

Approval

This dissertation has been under my supervision and is submitted with my approval.

.....

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Dedication

I dedicate this work to my parents, Mr and Mrs KITUGWANIDDE for the care and support they gave and still give me.

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Abstract

A Mathematical model is proposed and analysed to study the dynamics of a system of two prey and one predator in which the predator shows a Holling Type II response to one prey that is also harvested, and a ratio-dependent response to the other prey. The model is used to study the ecological dynamics of the lion-buffalo-Uganda Kob prey-predator system of Queen Elizabeth National Park, Western Uganda.

Results of analysis of the model showed that the 3 species would co-exist if the Uganda Kobs were not harvested beyond their intrinsic growth rate. Another important result of analysis was that the lion should convert the biomass of the Uganda Kobs into fertility at a rate greater than its natural mortality rate and the time it took to handle the Uganda Kobs. Also, the rate at which the lion captures the buffalo should be greater than the product of the buffalo's intrinsic growth rate and its anti-predator behaviour.

One of the major observations from results of numerical simulation is that the predator population density increased significantly when the intrinsic growth rate of both prey increased. This can imply that a high intrinsic growth rate of the prey initially increases their population density which increases the predator's chance of capturing the prey and so the predator's population density increases.

Numerical simulation of the model also revealed that the dynamical behaviour of the system changes mostly from a limit cycle to a stable spiral and vice - versa when values of some parameters such as the harvesting rate, natural death rate of the predator and food conversion rate of predator are varied. This implied that these parameters can be controlled so that the dynamical behaviour of the steady state is a stable spiral which implies that the steady state is globally asymptotically stable. However, varying some parameters such as the inter-specific competition among prey does not change the dynamical behaviour of the system.

Chapter 1

Introduction

1.1 Background to the study

Mathematical population models have been used to study the dynamics of prey predator systems since Lotka (1925) and Volterra (1927) proposed the simple model of preypredator interactions now called the Lotka-Volterra model. Since then, many mathematical models, some reviewed in this study, have been constructed based on more realistic explicit and implicit biological assumptions.

Modeling is a frequently evolving process, to gain a deep understanding of the mathematical aspects of the problem and to yield non trivial biological insights, one must carefully construct biologically meaningful and mathematically tractable population models (Kuang, 2002).

Some of the aspects that need to be critically considered in a realistic and plausible mathematical model include; carrying capacity which is the maximum number of prey that the ecosystem can sustain in absence of predator, competition among prey and predators which can be intraspecific or interspecific, harvesting of prey or predators and functional responses of predators. In this research, a mathematical model to study the ecological dynamics of the lionbuffalo-Uganda Kob prey-predator system of Queen Elizabeth National Park, Western Uganda is proposed and analysed. Although most of the information necessary for this study from the park is not easily available, the current trends on the dynamics of the three species have been obtained from face-to-face interview with Mr. Abitegeka Gerald, a game ranger with Queen Elizabeth National Park (see interview guide in Appendix B).

Queen Elizabeth National Park occupies an area of 2000 square miles (5120 square kilometers) of the low grasslands of Kasese district, Western Uganda. The main predator species in the park are the lions, leopards and hyaenas while the main prey species are the Uganda Kobs (Kobus kob thomasi), warthogs, bushbucks, buffaloes and waterbucks. Due to the complexity of constructing a mathematical model that incorporates all predator species and prey species in the park, the study considers only the lion as the predator species, and its two main prey species which, in order of preference, are the Uganda Kobs and buffaloes. According to Abitegeka Gerald (see interview guide in Appendix B), the choice of prey specie the lion goes for depends on many factors among which include: abundance of prey, ease of capture, taste and quantity of biomass per prey killed. A high abundance (high population density), the ease of capture and their taste make the Uganda Kobs the most favoured prey species for the lions. The bigger and hard-to-capture buffaloes are the lions other main prev species rather than the smaller and easier-to-capture warthogs or waterbucks. Two reasons dictate this: first the buffalo's meat tastes better than that of the waterbuck which is salty and secondly the lions get a good yield in terms of biomass per buffalo killed and this enables them to share with their cubs.

According to the population census of the animals carried out in 2002 by the authorities of Queen Elizabeth National Park (see interview guide in Appendix B), there were 90 lions, 30,000 Uganda Kobs and 12,000 buffaloes. The numbers for the 3 species have been increasing gradually and, according to game rangers of the park, are now estimated to be 120 lions, over 40,000 Uganda Kobs and over 20,000 buffaloes.

The lions live in a pride of 1-10 animals. On average, 20 Uganda Kobs are born daily, 6

cubs are born in a year while 4 buffaloes are born daily. The lions predate on both the Uganda Kobs and buffaloes. It is easier for the lion to predate on the Uganda Kobs since the kobs are many and are easily sited because both the lion and Uganda Kobs are brown in colour and so the lion disguises itself. It takes one lion to kill a Uganda Kob and this involves first stalking, targeting and then ambushing the Uganda Kob. On the other hand it requires a minimum of 3 lions to attack a mature buffalo. The lions attack the buffalo from its rear to avoid being injured, some times fatally, by the buffalo's horn. The lions tend to go for the buffaloes if they are at least 3, hungry and if the buffalo is isolated or weak. Female lions hunt more than the males, while the male opens the carcass. Other than being predated on, the Uganda Kobs are poached by human beings and many die due to accidents on the highway road.

In the interview (Appendix B), Abitegeka Gerald stated that poaching has greatly been minimised by sensitizing and carrying out social responsibilities to the neighbouring communities. However people still poison lions that stray to their gardens. Most lions, buffaloes and Uganda Kobs die due to natural causes and this, on average, occurs at the age of 25 years for the female lion, 18 years for the male lion, 12 years for the Uganda Kob and 16 years for the buffalo.

Due to the different ways in which the lion predates on the Uganda Kob and the buffalo, different functional responses of the predator are used for each prey specie, in this study. The Uganda Kob is the easy-to-capture prey while the buffalo has adopted anti-predator behaviour and is hard-to-capture. Constant effort harvesting of the prey is incorporated in the model to cater for the effects of human poaching on the Uganda Kobs.

1.1.1 Functional Responses

A functional response is described as a predator's instantaneous per capita feeding rate as a function of prey abundance (Holling, 1959a). This means that the consumption rate of an individual predator depends on the prey density. Understanding and clearly quantifying functional responses is at the heart of ecological modeling.

According to Abrams and Ginzburg (2000), functional responses are generally categorized as; prey density-dependent, f(N), ratio-dependent, f(N/P) and prey-predator densitydependent, f(N, P).

For prey density-dependent responses, the consumption rate of the predator varies with the prey density alone. Holling (1959b) categorized the prey-dependent responses into three types;



Figure 1.1: Graphs of Holling Type functional responses; Ha is the number of prey species captured per unit area. H is the prey density per unit area, d is mortality rate of the prey species

(Source; http://home.comcast.net/ sharov/PopEcol/lec10/funcresp.html)

(a) Holling Type I functional response which is the standard mass action or linear response

$$f(N) = aN \tag{1.1}$$

Here a > 0 is the attack rate of the predator. This type of response is found in passive predators like spiders. The number of flies caught in the net is proportional to fly density. Prey mortality due to predation is constant.

(b) Holling Type II, also called the cyrtoid functional response, is represented by the equation below

$$f(N) = \frac{bN}{1+cN} \tag{1.2}$$

where b (units; 1/time) and c (units; 1/prey) are positive constants that describe the effects of capture rate and handling time on the feeding rate of the predator (Skalski and Gillian, 2001). The Holling Type II response is the most common type of functional response and is well documented. According to Sharov (1996), at low prey densities, the predator spends more time in searching the prey while at high prey densities, the predator spends more time handling the prey. Relating this to equation (1.2), we see that at low prey densities, b is greater than c. However, at high prey densities, c is greater than b. Either way, the number of prey that a predator can consume is limited and consequently the predator reaches a saturation level. This is clearly showed in the graphs of Figure 1.1. Predators of this type cause maximum mortality at low prey density. For example, small mammals destroy most of gypsy moth pupae in sparse populations of gypsy moth. However in high-density defoliating populations, small mammals kill a negligible proportion of pupae (Sharov, 1996).

(c) Holling Type III functional response is represented by the equation below

$$f(N) = \frac{dN^x}{F + N^x} \tag{1.3}$$

where x > 1 is the encounter rate between predator and prey before the predator reaches maximum efficiency. According to Sharov (1996), Holling Type III functional response occurs in predators which increase their search activity with increasing prey density. For example, many predators respond to kairomones (chemicals emitted by prey) and increase their activity. Polyphagous vertebrate predators (e.g., birds) can switch to the most abundant prey species by learning to recognize it visually. Mortality first increases with prey increasing density, and then declines. If predator density is constant (e.g., birds, small mammals) then they can regulate prey density only if they have a Holling Type III functional response because this is the only type of functional response for which prey mortality can increase with increasing prey density. However, regulating effect of predators is limited to the interval of prey density where mortality increases. If prey density exceeds the threshold value of this interval, then mortality due to predation starts declining, and predation will cause a positive feed-back. As a result, the number of prey will get out of control. They will grow in numbers until some other factors (diseases or food shortage) will stop their reproduction.

Ratio-dependency is obtained by substituting the prey-predator ratio (N/P) for prey density (N) in the Holling Type II equation;

$$f(N/P) = \frac{dN/P}{m+N/P} = \frac{dN}{mP+N}$$
(1.4)

Here d and m are positive constants that stand for capturing rate and half saturation constant for predator P respectively (Xiao and Ruan, 2001). Beddington (1975) derived and DeAngeles *et al*. (1975) proposed independently a more general form of ratiodependent functional response

$$f(N/P) = \frac{aN}{1 + bN + c(P - 1)}$$
(1.5)

where c > 0 describes the magnitude of interference among predators. Thus, this functional response takes into account the delay in time incurred by the predators as a result of interspecific competition for the same prey species.

For prey-predator-dependency, the consumption rate of the predator depends on both the prey and predator density. Examples of prey-predator-dependency functional response are the Crowley-Martin model and the Hassel-Varley model, both documented in (Skalski and Gillian, 2001). The Crowley-Martin model is as below;

$$f(N,P) = \frac{aN}{1 + bN + c(P-1) + bcN(P-1)}.$$
(1.6)

An important distinction between the Beddington-DeAngelis model and the Crowley-Martin model is that the former predicts that the effects of predator interference (competition/ infighting among predators) on the feeding rate becomes negligible under conditions of high prey density while the latter assumes that the interference remains important even at high prey density (Skalski and Gillian, 2001). This can be seen by letting $N(t) \to \infty$ in both models. It is noticed that the Beddington-DeAngelis model gives an expression

$$\lim_{N \to \infty} f(N/P) = \frac{a}{b},\tag{1.7}$$

independent of predator interference parameter c, while the Crowley-Martin model gives an expression

$$\lim_{N \to \infty} f(N, P) = \frac{a}{b + bc(P-1)},\tag{1.8}$$

dependent on predator interference and density.

1.1.2 Ratio-dependent versus prey-dependent functional responses

There has been considerable debate concerning the merits and demerits of ratio-dependent versus prey-dependent functional responses with Abrams (1994), Gleeson (1994) and Sarnelle (1994) supporting prey-dependency while Arditi and Berryman (1991), Akcakaya *et al.* (1995) and Berryman *et al.* (1995) supporting ratio-dependency.

The ratio-dependent functional response has been criticized especially for what has been termed as its pathological behaviour at the origin or trivial equilibrium point. One such pathological behaviour is that for ratio-dependent functional response, even if there is a positive steady state, both prey and predator can go extinct (Kuang, 2002). However, as explained by Kuang (2002), this is not a pathological behaviour. The extinction can occur in two distinct ways. In one way, both species become extinct regardless of the initial densities. In the other case, both species will die out only if the initial prey/predator ratio is too low. In the first case, extinction often occurs as a result of high predator efficiency in catching and/or converting prey biomass. The second scenario shows that altering the ratio of prey to predators through over-harvesting of prey species or over-stocking of predators may lead to the collapse of the whole system and extinction of both species.

More recent research has provided evidence that ratio-dependent responses provide rich dynamics and are more appropriate for predator-prey interactions where predation involves serious searching process. Schenk *et al.* (2005) carried out research on a paper wasp-shield beetle system in a natural setting. In the research, they discovered that neither a pure prey nor a pure ratio-dependent model fitted perfectly well their observations. However, the functional response of the paper wasps was closer to ratio-dependency. Jost *et al.* (2005) in their research on the wolf-moose interaction on Isle Royale National park (Michigan, USA) discovered that the wolves displayed a scale invariant satiation and ratiodependent predation on the moose. Jost and Ellner (2000) found out that the data of a protozoan predator- prey interaction was predator-dependent and could be represented by the Hassel-Varley predator interference model. DeAngelis and Holland (2006) discovered that pollinators interaction with plants or flowers was a ratio-dependent functional response.

According to Abrams and Matsuda (1996), generally, ratio-dependent type of functional response is more appropriate in predator-prey interactions in which; the predator takes too much time in handling the prey, aggression and/or competition among predators is time consuming which prolongs searching time, the prey adopt an anti-predator behaviour and try to evade the predator.

With advent of knew knowledge and understanding of how prey and predators interact, more realistic and plausible mathematical models have to be constructed and analysed. A Mathematical model is proposed and analysed to study the dynamics of the lion-Uganda Kob-buffalo prey-predator system in which the lion predates on both the Uganda Kob and the buffalo.

In this research, the Uganda Kobs are the easy to capture prey and the predator's response to the easy-to-capture prey is Holling Type II. On the other hand, the buffaloes are assumed to have developed anti-predator behaviour and as a result, the lion's functional response to this behaviour is ratio-dependent. The basis for this assumption is due to the way the lions predate on the buffaloes, which requires that the lions must be at least 3 to attack one mature buffalo; they have to first isolate it, then attack it from the rear to avoid possibilities of being fatally wounded by the buffalo, thus the lion spends much time searching and handling the buffalo.

1.2 Statement of the problem

Whereas game park authorities can estimate the number of animals in Queen Elizabeth National Park in the short term basing on prevailing circumstances, the effects of a drastic change in circumstances such as a considerable reduction in the number of the Uganda Kobs due to human poaching or controlled harvesting by game park authorities, or an increase in the number of buffaloes or lions, may not be easily estimated in the long term. This would require a good mathematical model that incorporates a wide range of prey-predator factors to be able to come up with a reasonable analysis of the dynamics of lion-Uganda Kob-buffalo prey-predator interactions of Queen Elizabeth National Park.

1.3 Objectives

The main aim of this study is to investigate how parameters such as birth rate, death rate, predator handling time of the prey, competition among prey, harvesting rate of the prey affect the dynamics of the population densities of the lion-Uganda Kob-buffalo preypredator system. The specific objectives for this study are to:

(i) Analyse the effects of drastic increase or decrease on the number of a particular specie to the ecosystem.

(ii) Find out how harvesting or hunting of the Uganda Kobs impacts on the long term stability of the ecosystem so as to establish conditions for optimal harvest of the Uganda Kobs.

(iii) Analyse the various topological structures, limit cycles, bifurcations and chaotic behaviour of the Queen Elizabeth National Park ecosystem.

1.4 Scope of the study

The research was based on formulating a mathematical model to study the dynamics of the population densities of the lion-Uganda Kob-buffalo prey-predator system of Queen Elizabeth National Park, Kasese district, Western Uganda. Field data was obtained by interviewing Mr. Abitegeka Gerald, a game ranger of the park.

1.5 Significance of the study

It is hoped that if the effect of parameters such as intrinsic growth rate, carrying capacity of the park, harvesting rate of the Uganda Kobs etc, on the long term stable co-existence of the 3 species is known, this will enable the park authorities to manage the population of the lions, Uganda Kobs and buffaloes in the park, especially taking well established measures to avoid extinction of any of the species.

1.6 Structure and presentation

This dissertation is presented in five chapters. Chapter 1 gives the background to the study, statement of the problem, scope of the study, objectives of the study and significance of the study. Chapter 2 presents the literature review, focussing on two prey-one predator or one prey-two predator systems and mathematical models with ratio-dependent response. Chapter 3 deals with formulating and qualitative analysis of the model while Chapter 4 deals with numerical simulation of the model. Chapter 5 includes discussion of results, conclusion and recommendations.

Chapter 2

Literature review

2.1 Historical background

Mathematical modeling and analysis of multiple species ecological problems was first done by Volterra (1927). Volterra had been introduced to an ecological problem that in the years after the first World War, the proportion of the predatory fishes caught in the Upper Adriatic Sea was found to be considerably higher than in the years before the war, whereas the proportion of prey fishes was down. In order to come out with an explanation to this ecological problem, Volterra formulated and analysed a system of ordinary differential equations which is represented as below:

$$\dot{x} = x(a - by)$$

$$\dot{y} = y(-c + dx)$$

where x and y were the densities of the prey fish and predator fish respectively. This system of differential equations was also studied independently by Lotka (1925) in the context of chemical kinetics and is now known as the Lotka-Volterra model. Volterra's study showed that the steady state for the co-existence of the prey fish and predatory fish was periodic and that a pause of fishery would indeed lead to an increase of the predators and a decrease in the prey. Since then, many ecological models have been formulated and analysed to study various phenomena. Freedman (1980) came up with a generalised prey-predator model represented by the system of differential equations below:

$$\dot{x} = xg(x) - yf(x)$$

$$\dot{y} = y[-e + p(x)],$$

where x and y are the densities of the prey and predator respectively, g(x) is the growth rate of the prey in absence of the predators, f(x) is the functional response of the predators with respect to prey x, and p(x) is the numerical response of the predator. In most cases, p(x) is a product of a constant and f(x). The functions g(x), f(x) and p(x) are continuous and differentiable and have the following specific properties:

(i) $g(x) = \alpha > 0$, $\dot{g}(x) < 0$ for all $x \ge 0$ and there exists a real number k called the carrying capacity such that g(k) = 0.

(ii)
$$f(0) = 0$$
, $f(x) > 0$ for all $x \ge 0$

(iii) p(x) = 0, $\dot{p}(x) > 0$ for all $x \ge 0$ and $\lim_{x \to \infty} p(x) = p_{\infty} \le \infty$.

In recent prey-predator models (Abrahams and Ginzburg, 2000), the functional response term can be: prey density-dependent, f(x), ratio-dependent, f(x/y) and prey-predator density-dependent, f(x, y).

Arditi and Michalski (1996) pointed out that internal consistence of a theory of trophic interactions requires that model equations of prey-predator models or food webs should obey some basic logical conditions below:

(i) The equations must be invariant under identification of identical species.

(ii) The system of equations for a food web must separate into independent subsystems if the community splits into disconnected sub webs.

Recently, many mathematical models incorporating diverse areas of interest such as Holling Type functional responses, ratio-dependent functional responses, bio-economic exploitation or harvesting, delayed harvesting and age-structured models have been formulated and analysed.

In this literature review, focus is on mathematical models of two prey-one predator systems

or one prey-two predator systems and models incorporating ratio-dependent responses.

2.2 Models for two prey-one predator system with harvesting

Chaudhuri and Kar (2004) proposed and analysed a fishery model of a two prey-one predator system in which the prey were being harvested and the feeding rate of the predator increases linearly with prey density. They derived conditions for global stability of the system using a Lyapunov function. Using Pontryagin's maximal principal, they established the conditions for optimal harvest. However, the prey dependent-linear functional response used in their model does not represent the feeding patterns of most species as compared to Holling Type II or ratio-dependent responses which are used in our model.

Vlastmil and Eisner (2006) studied a one consumer-two resource population dynamics system in which the resource was spatially distributed between two patches. The study showed that when resources grow exponentially, handling times are zero and apparent competition always leads to extinction of the weaker resource. However, with logistic growth and Holling Type II functional response included in the model, species permanence was guaranteed. This showed the importance of incorporating logistic growth in prey-predator models.

Kar (2003) studied a prey-predator system with delay, Holling Type II functional response and harvesting of the prey. The study showed that as harvesting effort increased, the predator's population decreased as expected. More importantly, if the harvesting effort was above a critical value which was determined in the study, the dynamics of the system changed from limit cycle to global asymptotic stability. This showed that harvesting of the prey alone indirectly affected the population density of the predators and also played a crutial role in stabilising the dynamics of the prey-predator systems. The delay term was included to ensure that only mature prey were harvested. Green (2004) studied a model on two prey-one predator system in which the prey were non competing and predation followed the density gradient of the prey. It was discovered that when the predator divides its time between the two prey depending on their comparative density, the predator stabilized the system. Limit cycles and chaotic behaviour in the system were also investigated. The model did not consider competition among prey and prey harvesting.

Fay and Greeff (2006) proposed a model to study the dynamics of the lion-wildebeestzebra interaction in Kruger National Park (South Africa) in which the lion predated on the wildebeests and zebras. Starting with a simple model, they showed that by carefully incorporating in the simple model, terms to represent plausible biological aspects such as logistic growth with mutualism among wildebeests and zebras, Type II functional response for the lions, seasonal calving of zebras, cropping of lions, you get a model which comes close to fitting experimental data available. Their approach showed how well thought mathematical concepts should be incorporated in a model.

Kabuye (1995) worked on a model on the interactions within a four species ecosystem. The model was based on his research on the interactions among the four main species in Queen Elizabeth National Park (Uganda) namely; lions, hyaenas, Uganda Kobs and waterbucks. The lions and hyaenas were the predators while the Uganda Kobs and the waterbucks were the prey. Using the Routh-Hurwitz criteria, he established conditions for stable existence of all four species. He also investigated how mutual cooperation, intraspecific and/or interspecific competition among species affected the equilibrium of the ecosystem. However, the system was based on the general linear prey-predator competition model and excluded terms such as logistic growth with carrying capacity and functional responses.

2.3 Models incorporating ratio-dependent response

Xiao and Ruan (2001) studied a model on the global dynamics of a ratio-dependent predator-prey system. Knowing that their model was not well-defined at the origin, they transformed it into a polynomial system by using a time variable transformation. It was discovered that the origin in the interior of the first quadrant is indeed a critical point of higher order and there can exist numerous kinds of topological structures in a neighborhood of the origin including the parabolic orbits, the elliptic orbits, the hyperbolic orbits and any combination of them. These structures have important behaviour for the global dynamics of the model. They showed that the origin though not well defined, still provided rich dynamics for a ratio-dependent functional response. However, the model proposed here has a DeAngelis ratio-dependent functional response and the origin is well defined thus making it different from the one studied by (Xiao and Ruan, 2001).

Dubey and Upadhay (2004) studied a model on two predator-one prey system with ratiodependent predators growth. Their results showed that the role of food conversion coefficients of predators in ratio-dependent models were crucial in determining the stability behaviour of planer-equilibria. They derived sufficient conditions for the system to be uniformly persistent. Conditions were derived for the co-existence equilibrium to be globally asymptotically stable. Some methods they used in analysing their model are applied in this research work especially on establishing the co-existence equilibrium point and analysing it for stability and uniform persistence. The role of food conversion coefficients of predators in stabilising the model is also compared to that of the effect of harvesting.

The model proposed for this research incorporates both the Holling Type II and ratiodependent responses, something none of the models above have done. The justification for our model is that it seeks to capture the dynamics of one predator feeding on two prey. One prey is easy-to-capture and the predator takes less time in searching and handling it, this behaviour is modeled by the Holling Type II response. The second prey is hardto-capture and the predator takes much more time in searching and handling the prey, this behaviour is modeled by the ratio-dependent response. The easy-to-capture prey is harvested and this has an impact on the stability of the ecosystem.

It is noted, that in the Beddington-DeAngelis ratio-dependent response in equation (1.5), parameter c > 0 describes the magnitude of interference among predators. However, the model proposed here has only one predator species and as such interference among predators is not considered. Therefore parameter c > 0 is replaced with $d_2 > 0$ to represent the magnitude of anti-predator behaviour by the hard-to-capture prey. Also, as in Skalski and Gillian (2001), we replace P - 1 with a continuous variable P (P = P(t)) since in our model, predator abundance is modeled as a continuous variable.

In conclusion, the literature review focussed on various types of functional responses and mathematical models with emphasis on two prey-one predator mathematical models. In this research, a mathematical model is formulated and analysed to study the dynamics of a one predator-two prey eco-system in which one prey is being harvested and is easy-tocapture by the predator, while the alternative prey has adopted anti-predator behaviour and so it requires a lot of searching and handling time for the predator to capture. The model is intended to explain the dynamics of the lion-Uganda Kob-buffalo interactions in Queen Elizabeth National Park, Western Uganda.

Chapter 3

Model formulation and analysis

In this chapter, we present model description, formulation and analysis. Consider a prey predator model in which the lion is the predator specie while the Uganda Kob and buffalo are the prey species. Let $N_1(t)$, $N_2(t)$ and P(t) represent the population of the Uganda Kobs, buffaloes and lions at any time t. The main feature of the model is that two different functional responses of the predator are incorporated in the model to represent the difference in the way the predator feeds on each of the prey species. The Uganda Kob is the easy-to-capture prey and the predator's response to the easy-to-capture prey is Holling Type II. The buffalo has adopted anti-predator behaviour and is hard-to-capture prey and this behaviour is represented by the ratio-dependent response of the predator. Constant effort harvesting of the prey is incorporated in the model to cater for the effects of human poaching on the Uganda Kobs. Terms representing logistic growth of the prey species in absence of the predator are included in the prey equations. Interspecific competition among the prey species is also included in the model. The model has 3 non linear autonomous ordinary differential equations describing how the population densities of the 3 species would vary with time.

3.1 Assumptions, variables and parameters of the model

3.1.1 The assumptions

The following assumptions are made in order to construct the model:

(i) The species live in an ecosystem where external factors such as droughts, fires, epidemics are stable or have a similar effect on the interacting species.

(ii) One prey is easy-to-capture by the predator, while the other prey has adopted antipredator behaviour and so it requires a lot of searching and handling time for the predator to capture it.

(iii) The rate of human poaching of the Uganda Kobs is on average constant per unit time and so it is represented as constant effort harvesting of the prey.

(iv) There is logistic growth of the prey in absence of the predator or human poaching of the prey. That is the population of the prey would increase (or decrease) exponentially until it reaches the maximum density of the National Park, which is its carrying capacity.

(v) The rate of increase of the predator population depends on the amount of prey biomass it converts as food.

3.1.2 The Variables

The following variables are used in the model:

- (i) $N_1(t)$ the population of the Uganda Kobs at time t.
- (ii) $N_2(t)$ the population of the buffaloes at time t.
- (iii) P(t) the population of the lions at time t.

For simplicity let $N_1(t)$, $N_2(t)$ and P(t) be represented as N_1 , N_2 and P.

3.1.3 The parameters

The following are the parameters used in the model:

(i) r_1 and r_2 are per capita intrinsic growth rates for prey N_1 and N_2 respectively.

(ii) K_1 and K_2 are carrying capacities for prey N_1 and N_2 respectively.

(iii) α_1 and α_2 are coefficients for interspecific competition between prey N_1 and N_2 respectively.

(iv) a_1 and c are capturing rates of predator P on N_1 and N_2 respectively.

(v) b_1/a_1 and d_1/c are the predator's handling time on prey N_1 and N_2 respectively.

(vi) E is constant effort harvesting rate of prey N_1 .

(vii) e is natural mortality rate of predator P.

(viii) d_2 measures the effect of anti-predator behaviour of prey N_2 .

(ix) λ_1 and λ_2 are coefficients which measure the predator's efficiency to convert prey biomass of N_1 and N_2 respectively into fertility (reproductivity).

3.2 The model equations

From the model description, assumptions and definition of variables and parameters in Section 3.1, the equations to represent the dynamics of the lion-buffalo-Uganda Kob ecosystem are formulated as below,

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} \right) - \alpha_1 N_1 N_2 - \left(\frac{a_1 N_1}{1 + b_1 N_1} \right) P - E N_1$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} \right) - \alpha_2 N_1 N_2 - \left(\frac{c N_2}{1 + d_1 N_2 + d_2 P} \right) P \qquad (3.1)$$

$$\frac{dP}{dt} = -eP + \lambda_1 \left(\frac{a_1 N_1}{1 + b_1 N_1} \right) P + \lambda_2 \left(\frac{c N_2}{1 + d_1 N_2 + d_2 P} \right) P,$$

where all parameters in the model are positive.

For ease of computations, non dimensionalization of the model represented by equations (3.1) is done so as to reduce the number of parameters as follows: Let $X_1 = b_1 N_1$, $X_2 = d_1 N_2$, $Y = d_2 P$, Then equations (3.1) become:

$$\frac{dX_1}{dt} = r_1 X_1 \left[\left(1 - \frac{X_1}{b_1 K_1} \right) - \frac{\alpha_1 X_2}{r_1 d_1} - \frac{a_1 Y}{r_1 d_2 (1 + X_1)} - E/r_1 \right]$$

$$\frac{dX_2}{dt} = r_2 X_2 \left[\left(1 - \frac{X_2}{d_1 K_2} \right) - \frac{\alpha_2 X_1}{r_2 b_1} - \frac{cY}{r_2 d_2 (1 + X_2 + Y)} \right]$$

$$\frac{dY}{dt} = eY \left[-1 + \frac{\lambda_1 a_1 X_1}{eb_1 (1 + X_1)} + \frac{\lambda_2 cX_2}{ed_1 (1 + X_2 + Y)} \right].$$
(3.2)

Also letting, $\beta_1 = 1/K_1b_1$, $\delta_1 = \alpha_1/r_1d_1$, $g_1 = a_1/r_1d_2$, $M = E/r_1$, $\beta_2 = 1/K_2d_1$, $\delta_2 = \alpha_2/r_2b_1$, $g_2 = c/r_2d_2$, $h_1 = \lambda_1a_1/eb_1$, $h_2 = \lambda_2c/ed_1$ gives":

$$\frac{dX_1}{dt} = r_1 X_1 \left[\left(1 - \beta_1 X_1 \right) - \delta_1 X_2 - \frac{g_1 Y}{1 + X_1} - M \right]$$

$$\frac{dX_2}{dt} = r_2 X_2 \left[\left(1 - \beta_2 X_2 \right) - \delta_2 X_1 - \frac{g_2 Y}{1 + X_2 + Y} \right]$$

$$\frac{dY}{dt} = eY \left[-1 + \frac{h_1 X_1}{1 + X_1} + \frac{h_2 X_2}{1 + X_2 + Y} \right].$$
(3.3)

System (3.3) has 12 parameters compared to 15 of system (3.1).

3.3 Existence of equilibrium points of the system

In this section, we establish conditions for the existence of the equilibrium points of the system. By equating (3.3) to zero, we find that the system has 7 possible nonnegative equilibria, namely $E_0(0,0,0)$, $E_1(X_1^*,0,0)$, $E_2(0,X_2^*,0)$, $E_3(X_1^*,X_2^*,0)$, $E_4(X_1^*,0,Y^*)$, $E_5(0,X_2^*,Y^*)$ and the co-existence equilibrium $E_6(X_1^*,X_2^*,Y^*)$. The existence of $E_0(0,0,0)$ is trivial. We show the existence of other equilibria as follows:

(i) Existence of $E_1(X_1^*, 0, 0)$ with $X_1^* > 0$

Let $X_2 = 0$ and Y = 0. Then equations (3.3) give: $r_1X_1(1 - \beta_1X_1 - M) = 0$, from which we have $X_1^* = \frac{1-M}{\beta_1}$. Thus, $E_1(X_1^*, 0, 0) = E_1(\frac{1-M}{\beta_1}, 0, 0)$. Therefore the equilibrium E_1 exists if,

$$M < 1 \tag{3.4}$$

Condition (3.4) implies $E < r_1$. Thus, in absence of prey N_2 and predator P, the harvesting rate of prey N_1 must be less than its intrinsic growth rate for equilibrium $E_1(X_1^*, 0, 0)$ to exist.

(ii) Existence of $E_2(0, X_2^*, 0)$ with $X_2^* > 0$

Let $X_1 = 0$ and Y = 0. Then equations (3.3) give $r_2X_2(1 - \beta_2X_2) = 0$. This gives $X_2^* = \frac{1}{\beta_2}$. Therefore, $E_2(0, X_2^*, 0) = E_2(0, \frac{1}{\beta_2}, 0)$. $X_2^* = \frac{1}{\beta_2}$ implies $N_2 = K_2$. Thus, in the absence of prey N_1 and predator P, the density of prey N_2 will increase or decrease until it reaches the carrying capacity K_2 of the National Park.

(iii) Existence of $E_3(X_1^*, X_2^*, 0)$ with $X_1^* > 0$ and $X_2^* > 0$

Let Y = 0. Then equations (3.3) give $r_1 X_1 (1 - \beta_1 X_1 - \delta_1 X_2 - M) = 0$ and $r_2 X_2 (1 - \beta_2 X_2 - \delta_2 X_1) = 0$. From these we have $X_1^* = \frac{\delta_1 - \beta_2 (1 - M)}{\delta_1 \delta_2 - \beta_1 \beta_2}$ and $X_2^* = \frac{\delta_2 (1 - M) - \beta_1}{\delta_1 \delta_2 - \beta_1 \beta_2}$. Thus, $E_3(X_1^*, X_2^*, 0) = E_3(\frac{\delta_1 - \beta_2 (1 - M)}{\delta_1 \delta_2 - \beta_1 \beta_2}, \frac{\delta_2 (1 - M) - \beta_1}{\delta_1 \delta_2 - \beta_1 \beta_2}, 0)$. This exists if, for M < 1, $\beta_1 > \delta_2(1 - M)$ and $\beta_2 > \frac{\delta_1}{1 - M}$

$$\beta_1 \beta_2 > \delta_1 \delta_2. \tag{3.5}$$

We note also that $E_3(X_1^*, X_2^*, 0) = E_3(\frac{\delta_1 - \beta_2(1-M)}{\delta_1\delta_2 - \beta_1\beta_2}, \frac{\delta_2(1-M) - \beta_1}{\delta_1\delta_2 - \beta_1\beta_2}, 0)$ can exist if, for $M < 1, \beta_1 < \delta_2(1-M)$ and $\beta_2 < \frac{\delta_1}{1-M}$

$$\beta_1 \beta_2 < \delta_1 \delta_2. \tag{3.6}$$

Condition (3.5) implies $\alpha_1 \alpha_2 < \frac{r_1}{K_1} \frac{r_2}{K_2}$. This condition in addition to $E < r_1$ implies that, in absence of the predator, the vital parameters for existence of the two prey species are; per capita intrinsic growth rates of the prey, constant effort harvesting rate of prey N_1 , carrying capacities of the prey and interspecific competition among the prey. In the case of the Uganda Kobs and buffaloes where interspecific competition among the prey species is negligible, then these two prey species will co-exist provided the constant effort harvesting rate of the Uganda Kobs is less than its per capita intrinsic growth rate.

We also comment that because of the non existence of interspecific competition among the Uganda kobs and buffaloes, condition (3.6) is not as realistic as condition (3.5).

(iv) Existence of $E_4(X_1^*, 0, Y^*)$ with $X_1^* > 0$ and $Y^* > 0$

Let $X_2 = 0$. Then, equations (3.3) give:

$$X_1 r_1 [1 - \beta_1 X_1 - \frac{g_1 Y}{1 + X_1} - M] = 0$$
(3.7)

$$eY[-1 + \frac{h_1 X_1}{1 + X_1}] = 0. ag{3.8}$$

From (3.8) and (3.7), for $Y \neq 0$ and $X_1 \neq 0$, we have,

$$X_1^* = \frac{1}{h_1 - 1}, \text{ provided } h_1 > 1$$
 (3.9)

$$Y^* = \frac{h_1}{(h_1 - 1)^2 g_1} [(h_1 - 1)(1 - M) - \beta_1]$$
(3.10)

Therefore, $E_4(X_1^*, 0, Y^*) = E_4\left(\frac{1}{h_1 - 1}, 0, \frac{h_1}{(h_1 - 1)^2 g_1}[(h_1 - 1)(1 - M) - \beta_1]\right)$ exists if, for M < 1,

$$h_1 > 1$$
 (3.11)

$$(1 - M)(h_1 - 1) > \beta_1. \tag{3.12}$$

Condition (3.11) implies that $\lambda_1 > e \frac{b_1}{a_1}$ i.e. λ_1 , the proportion of biomass of prey N_1 converted into food by the predator P must be greater than the product of the predator's natural mortality rate, e and the time it takes to handle the prey, $\frac{b_1}{a_1}$.

(v) Existence of $E_5(0, X_2^*, Y^*)$ with $X_2^* > 0$ and $Y^* > 0$

Let $X_1 = 0$, then equations (3.3) give

$$X_2 r_2 [1 - \beta_2 X_2 - \frac{g_2 Y}{1 + X_2 + Y}] = 0, \qquad (3.13)$$

$$eY[-1 + \frac{h_2 X_2}{1 + X_2 + Y}] = 0. ag{3.14}$$

Equation (3.14) gives, for $X_2 \neq 0$ and $Y \neq 0$,

$$Y = h_2 X_2 - X_2 - 1 \tag{3.15}$$

Substituting (3.15) in (3.13) gives,

$$h_2\beta_2 X_2^2 + (g_2h_2 - h_2 - g_2)X_2 - g_2 = 0$$
(3.16)

which is of the form, $AX_2^2 + BX_2 + C = 0$, with $A = h_2\beta_2$, $B = (g_2h_2 - h_2 - g_2)$ and $C = -g_2$. This gives,

$$X_2^* = \frac{-B + \sqrt{(B^2 - 4AC)}}{2A}.$$
(3.17)

Since C < 0, A > 0 and B > 0, X_2^* is positive and therefore exists. Thus, from (3.15), $Y^* = X_2^*(h_2 - 1) - 1$ will be positive if,

$$X_2^* > \frac{1}{h_2 - 1}$$
, provided $h_2 > 1$. (3.18)

The condition $h_2 > 1$ implies $\lambda_2 > e \frac{d_1}{c}$. That is, λ_2 the proportion of biomass of prey N_2 converted into fertility (ability to reproduce) by the predator P must be greater than the product of the predator's natural mortality rate, e and the time it takes to handle the prey, $\frac{d_1}{c}$.

(vi) Co-existence equilibrium point $E_6(X_1^*, X_2^*, Y^*)$

As in Dubey and Upadhay (2000), we equate equations (3.3) to zero and from this we find two functions $f(X_1, X_2)$ and $g(X_1, X_2)$ which intersect at the equilibrium point $E_6(X_1^*, X_2^*, Y^*)$. Equating equations (3.3) to zero gives,

$$1 - \beta_1 X_1 - \delta_1 X_2 - \frac{g_1 Y}{1 + X_1} - M = 0, \qquad (3.19)$$

$$1 - \beta_2 X_2 - \delta_2 X_1 - \frac{g_2 Y}{1 + X_2 + Y} = 0, \qquad (3.20)$$

$$-1 + \frac{h_1 X_1}{1 + X_1} + \frac{h_2 X_2}{1 + X_2 + Y} = 0.$$
(3.21)

From (3.19)

$$Y = \frac{(1+X_1)}{g_1} (1 - \beta_1 X_1 - \delta_1 X_2 - M).$$
(3.22)

From (3.20)

$$Y = \frac{(1+X_2)(1-\beta_2 X_2 - \delta_2 X_1)}{g_2 - (1-\beta_2 X_2 - \delta_2 X_1)}.$$
(3.23)

Equations (3.20) and (3.21) give,

$$Y = \frac{h_2 X_2 (1 + X_1) (1 - \beta_2 X_2 - \delta_2 X_1)}{g_2 (1 + X_1 - X_1 h_1)}$$
(3.24)

Equations (3.23) and (3.24) give,

$$f(X_1, X_2) = \frac{h_2 X_2 (1 + X_1)}{g_2 (1 + X_1 - X_1 h_1)} - \frac{(1 + X_2)}{g_2 - (1 - \beta_2 X_2 - \delta_2 X_1)} = 0$$
(3.25)
and from equations (3.22) and (3.24), we get,

$$g(X_1, X_2) = \frac{(1 - \beta_1 X_1 - \delta_1 X_2 - M)}{g_1} - \frac{h_2 X_2 (1 - \beta_2 X_2 - \delta_2 X_1)}{g_2 (1 + X_1 - X_1 h_1)} = 0.$$
(3.26)

Equations (3.25) and (3.26) are two functions of X_1 and X_2 . To prove the existence of $E_6(X_1^*, X_2^*, Y^*)$, conditions under which $f(X_1, X_2)$ and $g(X_1, X_2)$ meet in the interior of the positive (X_1, X_2) plane, at a point (X_1^*, X_2^*) , are found. Knowing (X_1^*, X_2^*) , Y^* can be obtained from (3.23). From (3.25), as $X_1 \to 0$, X_2 tends to X_{2f} given by,

$$X_{2f} = \frac{-D_2 + \sqrt{D_2^2 - 4D_1 D_3}}{2D_1} \tag{3.27}$$

where $D_1 = h_2\beta_2$, $D_2 = h_2g_2 - h_2 - g_2$ and $D_3 = -g_2$. X_{2f} is positive and real since $D_3 < 0$. We notice that, X_{2f} is the same as X_2^* of $E_5(0, X_2^*, Y^*)$. From (3.26), as $X_1 \to 0$, X_2 tends to X_{2g} given by,

$$X_{2g} = \frac{-E_2 + \sqrt{E_2^2 - 4E_1E_3}}{2E_1} \tag{3.28}$$

where $E_1 = g_1 h_2 \beta_2$, $E_2 = -(\delta_1 + h_2)$ and $E_3 = g_2(1 - M)$. It is seen that X_{2b} is positive and real if M > 1.

$$\begin{split} &X_{2f} \text{ and } X_{2g} \text{ are the points at which the functions } f(X_1, X_2) \text{ and } g(X_1, X_2) \text{ would} \\ &\text{cut the } X_2 \text{ axis in the } (X_1, X_2) \text{ plane respectively. Also from } (3.25), \quad \frac{dX_2}{dX_1} = -\frac{\partial f}{\partial X_1} / \frac{\partial f}{\partial X_2} \\ &\text{where } \frac{\partial f}{\partial X_1} = \frac{h_1 h_2 X_2}{g_2 (1+X_1-X_1h_1)^2} + \frac{\delta_2 (1+X_1)}{[g_2 - (1-\beta_2 X_2 - \delta_2 X_1)]^2} \text{ and } \frac{\partial f}{\partial X_2} = \frac{h_2 (1+X_1)}{g_2 (1+X_1-X_1h_1)} - \frac{(g_2 - \beta_2) + (\delta_2 X_1 - 1)}{[g_2 - (1-\beta_2 X_2 - \delta_2 X_1)]^2}. \\ &\text{We note that } \frac{dX_2}{dX_1} > 0 \text{ if } \frac{\partial f}{\partial X_1} > 0 \text{ and } \frac{\partial f}{\partial X_2} < 0 \text{ and this requires } h_1 > 1, \\ &g_2 > \beta_2 \text{ and } X_1 > Max \left(\frac{1}{\delta_2}, \frac{1}{h_{1-1}}\right). \text{ Similarly, } \frac{dX_2}{g(1+X_1-h_1)} - \frac{\partial g}{\partial X_1} / \frac{\partial g}{\partial X_2} \text{ where } \\ &\frac{\partial g}{\partial X_1} = -[\frac{\beta_1}{g_1} + (\frac{h_2 X_2}{g_2}) \frac{[(1-\beta_2 X_2)(h_1 - 1) - \delta_2]}{(1+X_1 - X_1h_1)^2}] \text{ and } \frac{\partial g}{\partial X_2} = -[\frac{\delta_1}{g_1} + \frac{h_2 (1-\delta_2 X_1 - 2\beta_2 X_2)}{g(1+X_1 - h_1 X_1)}]. \\ &\text{ we also note that } \frac{dX_2}{dX_1} < 0 \text{ if } \frac{\partial g}{\partial X_1} < 0 \text{ and } \frac{\partial g}{\partial X_2} < 0 \text{ and this requires: } h_1 > 1, \\ &Max \left(\frac{1}{\delta_2}, \frac{1}{h_1 - 1}\right) \text{ and } 0 < X_2 < \frac{1}{\beta_2} \left(1 - \frac{\delta_2}{h_1 - 1}\right). \\ &\text{ Since for } f(X_1, X_2), \text{ we have } \frac{dX_2}{dX_1} > 0 \text{ and } \\ &\text{ for } g(X_1, X_2), \text{ we have } \frac{dX_2}{dX_1} < 0, \text{ then, } f(X_1, X_2) \text{ and } g(X_1, X_2) \text{ will meet if } X_{2f} < X_{2g}. \end{aligned}$$

We therefore, state the existence of the positive equilibrium point $E_6(X_1^*, X_2^*, Y^*)$ in the following theorem:

Theorem 3.3.1 : The positive equilibrium point $E_6(X_1^*, X_2^*, Y^*)$ will exist if, for $h_1 > 1$, the conditions below are satisfied:

$$g_2 > \beta_2, \ X_1 > Max\left(\frac{1}{\delta_2}, \ \frac{1}{h_1 - 1}\right), \ 0 < X_2 < \frac{1}{\beta_2}\left(1 - \frac{\delta_2}{h_1 - 1}\right), \ X_{2f} < X_{2g}$$
(3.29)

where X_{2f} and X_{2g} are as defined in (3.27) and (3.28) respectively.

In terms of original parameters, $h_1 > 1$ implies that $\lambda_1 > e_{a_1}^{\underline{b_1}}$ i.e. λ_1 , the proportion of biomass of prey N_1 converted into food by the predator P must be greater than the product of the predator's natural mortality rate, e and the time it takes to handle the prey, $\frac{b_1}{a_1}$. Condition $g_2 > \beta_2$ gives $c > \frac{r_2}{K_2} \frac{d_2}{d_1}$. That is, the rate at which the predator captures prey N_2 should be greater than the product of the intrinsic growth rate of N_2 and the effect of the anti-predator behaviour of prey N_2 .

3.4 Local stability of the equilibrium points

The local asymptotic stability of each equilibrium point is studied by computing the Jacobian matrix and finding the eigenvalues evaluated at each equilibrium point. For stability of the equilibrium points, the real parts of the eigenvalues of the Jacobian matrix must be negative. From equations (3.3), the Jacobian matrix of the system is given by

$$J(E_i) = \begin{pmatrix} \frac{\partial f_1}{\partial X_1} & \frac{\partial f_1}{\partial X_2} & \frac{\partial f_1}{\partial X_3} \\ \frac{\partial f_2}{\partial X_1} & \frac{\partial f_2}{\partial X_2} & \frac{\partial f_2}{\partial X_3} \\ \frac{\partial f_3}{\partial X_1} & \frac{\partial f_3}{\partial X_2} & \frac{\partial f_3}{\partial X_3} \end{pmatrix}$$

which gives

$$J(E_i) = \begin{pmatrix} A^{**} & -\delta_1 r_1 X_1 & \frac{-g_1 r_1 X_1}{1 + X_1} \\ -\delta_2 r_2 X_2 & B^{**} & g_2 r_2 X_2 \frac{(1 + X_2)}{(1 + X_2 + Y)^2} \\ \frac{h_1 eY}{(1 + X_1)^2} & h_2 eY \frac{(1 + Y)}{(1 + X_2 + Y)^2} & C^{**} \end{pmatrix},$$
(3.30)

where $A^{**} = r_1 - 2\beta_1 r_1 X_1 - \delta_1 r_1 X_2 - \frac{g_1 r_1 Y}{(1+X_1)^2} - Mr_1$, $B^{**} = r_2 - 2\beta_2 r_2 X_2 - \delta_2 r_2 X_1 - g_2 r_2 Y \frac{(1+Y)}{(1+X_2+Y)^2}$ and $C^{**} = -e + \frac{h_1 e X_1}{(1+X_1)} + h_2 e X_2 \frac{(1+X_2)}{(1+X_2+Y)^2}$.

The local asymptotic stability for each equilibrium point is analysed as below:

(i) $E_0(0,0,0)$. The Jacobian matrix evaluated at E_0 gives,

$$J(E_0) = \begin{pmatrix} r_1 - Mr_1 & 0 & 0\\ 0 & r_2 & 0\\ 0 & 0 & -e \end{pmatrix}.$$
 (3.31)

The eigenvalues of $J(E_0)$ are $r_1 - Mr_1$, r_2 and -e. We see that $r_2 > 0$ is always positive and so $E_0(0, 0, 0)$ is unstable.

(ii) $E_1(X_1^*, 0, 0) = (\frac{1-M}{\beta_1}, 0, 0)$. The Jacobian matrix evaluated at E_1 gives

$$J(E_1) = \begin{pmatrix} r_1(M-1) & -\delta_1 r_1 \frac{1-M}{\beta_1} & \frac{g_1 r_1(M-1)}{\beta_1 - (M-1)} \\ 0 & r_2 [1 + \frac{\delta_2(M-1)}{\beta_1}] & 0 \\ 0 & 0 & e[\frac{(M-1)(1-h_1) - \beta_1}{\beta_1 - (M-1)}] \end{pmatrix}$$
(3.32)

The eigenvalues of matrix $J(E_1)$ are $r_1(M-1)$, $r_2[1 + \frac{\delta_2(M-1)}{\beta_1}]$ and $e[\frac{(M-1)(1-h_1)-\beta_1}{\beta_1-(M-1)}]$. The eigenvalues above are negative if, for M < 1 and $\beta_1 < \delta_2(1-M)$,

$$0 < h_1 < 1. (3.33)$$

Hence, the equilibrium point $E_1(X_1^*, 0, 0)$ is locally asymptotically stable if conditions M < 1, $\beta_1 < \delta_2(1 - M)$ and $0 < h_1 < 1$ hold.

The condition M < 1 implies $E < r_1$ and condition $h_1 < 1$ implies $\lambda_1 < e \frac{b_1}{a_1}$. Therefore, for local asymptotic stability of $E_1(X_1^*, 0, 0)$, E, the harvesting rate of prey N_1 must be less than r_1 , which is the intrinsic growth rate of prey N_1 . Also, λ_1 , which measures the efficiency of the predator to convert the biomass of prey N_1 into fertility or reproductivity must be less than the predator's natural mortality rate, e, and the time it takes to handle prey N_1 , $\frac{b_1}{a_1}$.

(iii) $E_2(0, X_2^*, 0) = (0, \frac{1}{\beta_1}, 0)$. The Jacobian matrix evaluated at E_2 gives

$$J(E_2) = \begin{pmatrix} r_1(1-M) - \delta_1 r_1 \frac{1}{\beta_2} & 0 & 0 \\ -\delta_2 r_2 \frac{1}{\beta_2} & -r_2 & g_2 r_2 \frac{1}{\beta_2 + 1} \\ 0 & 0 & -e + h_2 e \frac{1}{\beta_2 + 1} \end{pmatrix}.$$
 (3.34)

The eigenvalues of the matrix $J(E_2)$ are, $r_1(1-M) - \delta_1 r_1 \frac{1}{\beta_2}$, $-r_2$ and $-e + h_2 e \frac{1}{\beta_2+1}$. The eigenvalues are negative if,

$$M > 1 \text{ or } 1 - \frac{\delta_1}{\beta_1} < M \le 1$$
 (3.35)

$$h_2 < \beta_2 + 1.$$
 (3.36)

Thus, $E_2(0, X_2^*, 0)$ is locally asymptotically stable if conditions (3.35) and (3.36) hold. Condition M > 1 implies $E > r_1$ i.e. the constant effort harvesting rate of prey N_1 must be greater than its per capita intrinsic growth rate. Condition (3.36) implies $\frac{\lambda_1 e}{c} < \frac{1}{K_2} + d_1$. This inequality, shows parameters that are vital for the local asymptotic stability of $E_2(0, X_2^*, 0)$.

(iv)
$$E_3(X_1^*, X_2^*, 0) = \left(\frac{\delta_1 - \beta_2(1-m)}{\delta_1 \delta_2 - \beta_1 \beta_2}, \frac{\delta_2(1-m) - \beta_1}{\delta_1 \delta_2 - \beta_1 \beta_2}, 0\right)$$
. The Jacobian matrix evaluated at E_3

gives,

$$J(E_3) = \begin{pmatrix} A^* & B^* & C^* \\ D^* & E^* & F^* \\ 0 & 0 & G^* \end{pmatrix},$$
(3.37)

where, $A^* = r_1 - 2\beta_1 r_1 X_1^* - \delta_1 r_1 X_2^* - M r_1$, $B^* = -\delta_1 r_1 X_1^*$, $C^* = \frac{-g_1 r_1 X_1^*}{1 + X_1^*}$, $D^* = -\delta_2 r_2 X_2^*$, $E^* = r_2 - 2\beta_2 r_2 X_2^* - \delta_2 r_2 X_1^*$, $F^* = \frac{g_2 r_2 X_2^*}{(1 + X_2^*)}$ and $G^* = -e + \frac{h_1 e X_1^*}{(1 + X_1^*)} + \frac{h_2 e X_2^*}{(1 + X_2^*)}$. The eigenvalues of $J(E_3)$ are obtained by solving

$$det \begin{pmatrix} A^* - \lambda & B^* & C^* \\ D^* & E^* - \lambda & F^* \\ 0 & 0 & G^* - \lambda \end{pmatrix} = 0.$$
 This gives $(G^* - \lambda)[(A^* - \lambda)(E^* - \lambda) - D^*B^*] = 0,$

which simplifies to a characteristic equation,

 $\lambda^3 - (A^* + E^* + G^*)\lambda^2 + (A^*G^* + E^*G^* + A^*E^* - D^*B^*)\lambda + G^*D^*B^* - G^*A^*E^* = 0$ which is of the form, $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$. By Routh-Hurwitz criteria (Murray, 1989), the $\lambda's$ are negative if, $a_1 > 0$, $a_3 > 0$, $a_1a_2 - a_3 > 0$. Each of these conditions are considered next as follows:

(a) $a_1 > 0 \Rightarrow -(A^* + E^* + G^*) > 0$ or

$$A^* + E^* + G^* < 0. (3.38)$$

This can be satisfied if, $G^* < 0$, $A^* < 0$ and $B^* < 0$.

(i) $G^* < 0$ implies $-e + \frac{h_1 e X_1^*}{(1+X_1^*)} + \frac{h_2 e X_2^*}{(1+X_2^*)} < 0$ where $X_1^* = \frac{\delta_1 - \beta_2(1-m)}{\delta_1 \delta_2 - \beta_1 \beta_2}$ and $X_2^* = \frac{\delta_2(1-m) - \beta_1}{\delta_1 \delta_2 - \beta_1 \beta_2}$. This inequality, after simplifying gives $G^* = X_1^* X_2^* (h_1 + h_2 - 1) + X_1^* (h_1 - 1) + X_2^* (h_2 - 1) - 1 < 0$. This will hold if, for M < 1, $\beta_1 > \delta_2(1-M)$, $\beta_2 > \frac{\delta_1}{1-M}$,

 $\beta_1\beta_2 > \delta_1\delta_2, \quad h_1 < 1 \quad \text{and} \ h_2 < 1,$

$$h_1 + h_2 < 1. (3.39)$$

In terms of original parameters, $h_1 + h_2 < 1$ gives, $\frac{\lambda_1 a_1}{eb_1} + \frac{\lambda_2 c}{ed_1} < 1$. This implies that, the predator's efficiency in converting the biomass of both prey into fertility or reproductivity must be less than the predator's natural mortality rate and the time it takes to handle both prey.

(ii) $A^* < 0$ implies $r_1 - 2\beta_1 r_1 X_1^* - \delta_1 r_1 X_2^* - Mr_1 < 0$. Substituting for X_1^* and X_2^* in this inequality gives,

$$\begin{split} A^* &= r_1 - 2\beta_1 r_1 [\frac{\delta_1 - \beta_2 (1-M)}{\delta_1 \delta_2 - \beta_1 \beta_2}] - \delta_1 r_1 [\frac{\delta_2 (1-M) - \beta_1}{\delta_1 \delta_2 - \beta_1 \beta_2}] - Mr_1 < 0 \quad \text{which gives,} \\ A^* &= r_1 [\frac{\delta_1 \delta_2 - \beta_1 \beta_2 - 2\beta_1 \delta_1 + 2\beta_1 \beta_2 - 2\beta_1 \beta_2 M - \delta_1 \delta_2 + \delta_1 \beta_1 - M \delta_1 \delta_2 + M \beta_1 \beta_2}{\delta_1 \delta_2 - \beta_1 \beta_2}] < 0. \quad \text{This simplifies to} \\ A^* &= \beta_1 r_1 [\frac{\beta_2 (1-M) - \delta_1}{\delta_1 \delta_2 - \beta_1 \beta_2}] < 0. \quad \text{Therefore, } A^* < 0 \text{ if } M < 1, \quad \beta_2 > \frac{\delta_1}{1 - M} \text{ and } \beta_1 \beta_2 > \delta_1 \delta_2. \end{split}$$

(iii) $E^* < 0$ implies $r_2 - 2\beta_2 r_2 X_2^* - \delta_2 r_2 X_1^* < 0$. Substituting for X_1^* and X_2^* in this inequality gives, $E^* = r_2 - 2\beta_2 r_2 [\frac{\delta_2(1-M)-\beta_1}{\delta_1\delta_2-\beta_1\beta_2}] - \delta_2 r_2 [\frac{\delta_1-\beta_2(1-M)}{\delta_1\delta_2-\beta_1\beta_2}] < 0$, which gives $E^* = r_2 [\frac{\delta_1\delta_2-\beta_1\beta_2-2\beta_2\delta_2+2\beta_2\delta_2M+2\beta_1\beta_2-\delta_1\delta_2+\beta_2\delta_2-\beta_2\delta_2M}{\delta_1\delta_2-\beta_1\beta_2}] < 0$. This simplifies to $E^* = \beta_2 r_2 [\frac{\beta_1-\delta_2(1-M)}{\delta_1\delta_2-\beta_1\beta_2}] < 0$. Therefore $E^* < 0$ if, M < 1, $\beta_1 > \delta_2(1-M)$, $\beta_1\beta_2 > \delta_1\delta_2$.

(b) $a_3 > 0$ implies $G^*(D^*B^* - A^*E^*) > 0$. This is satisfied if, for $G^* < 0$,

$$D^*B^* - A^*E^* < 0, (3.40)$$

which gives $B^*D^* - A^*E^* = r_1r_2[X_2^*(\Lambda_1) + X_1^*(\Lambda_2) + (M-1) - 4\beta_1\beta_2X_1^*X_2^*]$, where, $\Lambda_1 = 2\beta_2 + \delta_1 - 2M\beta_2 - 2\delta_1\beta_2X_2^*$, $\Lambda_2 = \delta_2 + 2\beta_1 - M\delta_2 - 2\beta_1\delta_2X_1^*$. Therefore, $B^*D^* - A^*E^* < 0$ if $\Lambda_1 < 0$, $\Lambda_2 < 0$ and M < 1. Substituting for $X_2^* = \frac{\delta_2(1-M)-\beta_1}{\delta_1\delta_2-\beta_1\beta_2}$ in Λ_1 gives, $\Lambda_1 = 2\beta_2 + \delta_1 - 2M\beta_2 - 2\delta_1\beta_2[\frac{\delta_2(1-M)-\beta_1}{\delta_1\delta_2-\beta_1\beta_2}]$. This on simplifying gives $\Lambda_1 = \frac{2\beta_1\beta_2^2(M-1)+\delta_1(\delta_1\delta_2+\beta_1\beta_2)}{\delta_1\delta_2-\beta_1\beta_2}$. Thus, $\Lambda_1 < 0$ if for M < 1 and $\beta_1\beta_2 > \delta_1\delta_2$:

$$\frac{2\beta_1\beta_2^2}{\delta_1\delta_2 + \beta_1\beta_2} > \frac{\delta_1}{1-M}.$$
(3.41)

Similarly, substituting for X_1^* in Λ_2 gives, $\Lambda_2 = \delta_2 + 2\beta_1 - M\delta_2 - 2\beta_1\delta_2[\frac{\delta_1 - \beta_2(1-M)}{\delta_1\delta_2 - \beta_1\beta_2}]$. This on simplifying gives $\Lambda_2 = \frac{\delta_2(\delta_1\delta_2 + \beta_1\beta_2)(1-M) - 2\beta_1\beta_2^2}{\delta_1\delta_2 - \beta_1\beta_2}$. Thus, $\Lambda_2 < 0$ if for M < 1, and $\beta_1\beta_2 > \delta_1\delta_2$:

$$\frac{2\beta_1\beta_2^2}{\delta_1\delta_2 + \beta_1\beta_2} > \delta_2(1-M)$$
(3.42)

Therefore, $B^*D^* - A^*E^* < 0$ if for M < 1, $\beta_1 > \delta_2(1 - M)$, $\beta_2 > \frac{\delta_1}{1 - M}$ and $\beta_1\beta_2 > \delta_1\delta_2$:

$$\frac{2\beta_1\beta_2^2}{\delta_1\delta_2 + \beta_1\beta_2} > max\left(\frac{\delta_1}{1-M}, \delta_2(1-M)\right)$$
(3.43)

(c) $a_1a_2 - a_3 > 0$ implies $-(A^* + E^* + G^*)(A^*G^* + E^*G^* + A^*E^* - D^*B^*) - (G^*D^*B^* - G^*A^*E^*) > 0$. This simplifies to $(A^* + E^*)[(B^*D^* - A^*E^*) - G^*(A^* + E^* + G^*))] > 0$. This is satisfied if $A^* < 0$, $B^* < 0$, $G^* < 0$, and $B^*D^* - A^*E^* < 0$ which have been prior established.

Therefore, $E_3^*(X_1^*, X_2^*, 0)$ is locally asymptotically stable if conditions (3.4), (3.5), (3.39) and (3.43) hold.

(v) $E_4(X_1^*, 0, Y^*) = E_4\left(\frac{1}{h_1-1}, 0, \frac{h_1}{(h_1-1)^2g_1}[(h_1-1)(1-M)-\beta_1]\right)$. The Jacobian matrix evaluated at E_4 gives

$$J(E_4) = \begin{pmatrix} A_2^* & -\delta_1 r_1 X_1^* & \frac{-g_1 r_1 X_1^*}{1 + X_1^*} \\ 0 & B_2^* & 0 \\ \frac{h_1 e Y^*}{(1 + X_1^*)^2} & \frac{h_2 e Y^*}{(1 + Y^*)} & 0 \end{pmatrix},$$
(3.44)

where $A_2^* = r_1 - 2\beta_1 r_1 X_1^* - \frac{g_1 r_1 Y^*}{(1+X_1^*)^2} - Mr_1$, $B_2^* = r_2 - \delta_2 r_2 X_1^* - \frac{g_2 r_2 Y^*}{(1+Y^*)}$. The eigenvalues of matrix $J(E_4)$ have negative real parts if $A_2^* < 0$ and $B_2^* < 0$. Further $A_2^* < 0$ implies $r_1 - 2\beta_1 r_1 X_1^* - \frac{g_1 r_1 Y^*}{(1+X_1^*)^2} - Mr_1 < 0$ which gives, $\frac{r_1}{(1+X_1^*)^2} [(1+X_1^*)^2(1-2\beta_1 X_1^* - M) - g_1 X_1^*] < 0$. Thus, $A_2^* < 0$ if $1 - 2\beta_1 X_1^* - M < 0$. Substituting for $X_1^* = \frac{1}{h_1 - 1}$ in this expression and simplifying gives, (1-M)(h-1) < 0. $2\beta_1$. Also, $B_2^* < 0$ if $\frac{1}{X_1^*} < \delta_2$ which gives $h_1 < \delta_2 + 1$. Therefore, E_4 is locally asymptotically stable if, for M < 1 and $h_1 > 1$:

$$\beta_1 < (1 - M)(h_1 - 1) < 2\beta_1 \tag{3.45}$$

$$0 < h_1 < \delta_2 + 1. \tag{3.46}$$

(vi) $E_5(0, X_2^*, Y^*)$. The Jacobian matrix evaluated at E_5 gives

$$J(E_5) = \begin{pmatrix} A_3^* & 0 & 0\\ -\delta_2 r_2 X_2^* & B_3^* & -\frac{g_2 r_2 X_2^* (1+X_2^*)}{(h_2 X_2^*)^2} \\ h_1 e Y^* & \frac{h_2 e Y^* (1+Y^*)}{(h X_2^*)^2} & C_3^* \end{pmatrix},$$
 (3.47)

where $A_3^* = r_1 - g_1 r_1 Y^* - M r_1$, $B_3^* = r_2 - 2\beta_2 r_2 X_2^* - \frac{g_2 r_2 Y^* (1+Y^*)}{(h_2 X_2^*)^2}$ and $C_3^* = -e + \frac{e(1+X_2^*)}{(h_2 X_2^*)^2}$. The matrix $J(E_5)$ will have eigenvalues with negative real parts if, $A_3^* < 0, B_3^* < 0$ and $C_3^* < 0$. These conditions will hold if for M > 1 and $h_2 > 1$,

$$X_2^* < \min\{\frac{1}{\beta_2} , \frac{1}{h_2 - 1}\}.$$
(3.48)

3.5 Global stability of the steady states

3.5.1 Global stability of E_1 , E_2 and E_3

The global stability of E_1 , E_2 and E_3 will be analysed by transforming the system of equations (3.3) into a linear system and then choosing a suitable Lyapunov function to analyse each equilibrium point. By letting $X_1 = X_1^* + x_1$, $X_2 = X_2^* + x_2$, $Y = Y^* + y$, where x_1, x_2 and y are small perturbations about X_1^* , X_2^* and Y^* respectively, the system of equations (3.3) is turned into a linear system which is of the form $\dot{x}_i = J(E_i)x_i$, where $J(E_i)$ is the Jacobian matrix of equations (3.3). Thus, the linear system of equations (3.3) is,

$$\frac{dx_1}{dt} = \left[-\beta_1 r_1 X_1^* + \frac{g r_1 X_1^* Y^*}{(1+X_1^*)^2} \right] x_1 - \left[\delta_1 r_1 X_1^* \right] x_2 - \left[\frac{g_1 r_1 X_1^*}{(1+X_1^*)} \right] y$$

$$\frac{dx_2}{dt} = -\left[\delta_2 r_2 X_2^* \right] x_1 + \left[-\beta_2 r_2 X_2^* + \frac{g_2 r_2 X_2^* Y^*}{(1+X_2^*+Y^*)^2} \right] x_2 - \left[\frac{g_2 r_2 X_2^* (1+X_2^*)}{(1+X_2^*+Y^*)^2} \right] y$$

$$\frac{dy}{dt} = \left[\frac{h_1 e Y^*}{(1+X_1)^*} \right] x_1 + \left[\frac{e h_2 Y^* (1+Y^*)}{(1+X_2^*+Y^*)^2} \right] x_2 - \left[\frac{e h_2 X_2^* Y^*}{(1+X_2^*+Y^*)^2} \right] y.$$
(3.49)

(i) Global stability of $E_1(X_1^*, 0, 0) = (\frac{1-M}{\beta_1}, 0, 0)$. We define a Lyapunov function as $V(x_1, x_2, y) = \frac{x_1^2}{2X_1^*} + \frac{x_2^2}{2} + \frac{y^2}{2}$, where X_1^* is a component of the equilibrium point $E_1(X_1^*, 0, 0) = (\frac{1-M}{\beta_1}, 0, 0)$. Clearly $V(x_1, x_2, y)$ is a positive definite function. Differentiating V with respect to time t we get, $\dot{V}(x_1, x_2, y) = \frac{x_1}{X_1^*}\dot{x_1} + x_2\dot{x_2} + y\dot{y}$. Substituting for $\dot{x_1}, \dot{x_2}$ and \dot{y} using (3.49) gives,

$$\dot{V}(x_1, x_2, y) = x_1 \left[x_1 \left(-\beta_1 r_1 + \frac{g r_1 Y^*}{(1 + X_1^*)^2} \right) - \delta_1 r_1 x_2 - y \left(\frac{g_1 r_1}{1 + X_1^*} \right) \right]$$

$$+x_2X_2^*\left[-\delta_2r_2x_1+x_2(-\beta_2r_2+\frac{g_2r_2Y^*}{(1+X_2^*+Y^*)^2})-y(\frac{g_2r_2(1+X_2^*)}{(1+X_2^*+Y^*)^2})\right]$$

$$+yY^*\left[x_1(\frac{h_1e}{1+X_1^*})+x_2(\frac{eh_2(1+Y^*)}{(1+X_2^*+Y^*)^2})-y(\frac{eh_2X_2^*}{(1+X_2^*+Y^*)^2})\right].$$

For $E_1(X_1^*, 0, 0)$, $X_2^* = 0$ and $Y^* = 0$. Thus, $\dot{V}(x_1, x_2, y) = -\beta_1 r_1 x_1^2 - \delta_1 r_1 x_1 x_2 - \frac{g_1 r_1}{(1+X_1^*)} x_1 y$, which is negative semi-definite if existence condition (3.4) holds. So $E_1(X_1^*, 0, 0)$ is Lyapunov stable. However, the set $S_1 = \{(x_1, x_2, y) / \dot{V}(x_1, x_2, y) = 0\}$, which is the set $S_1 = \{(x_1, x_2, y) / x_1 = 0\}$, does not contain any trajectory of the system except the trivial trajectory $(x_1, x_2, y) = (0, 0, 0)$. Therefore, by LaSalle's invariance principle (/http://en.wikipedia.org/wiki/Krasovskii-LaSalle-principle.endnote-nd1). $E_1(X_1^*, 0, 0)$ is globally asymptotically stable if M < 1 holds. In terms of original parameters, this implies that, in absence of the bufallo and lion species, the population of

rameters, this implies that, in absence of the bufallo and lion species, the population of Uganda Kobs is globally stable provided their intrinsic per capita growth rate is more than the rate at which they are harvested.

(ii) Global stability of $E_2(0, X_2^*, 0) = (0, \frac{1}{\beta_2}, 0)$. We define a Lyapunov function $V(x_1, x_2, y) = \frac{x_2^2}{2} + \frac{x_2^2}{2X_2^*} + \frac{y^2}{2}$. From which we get, after simplifying, $\dot{V}(x_1, x_2, y) = -\delta_2 r_2 x_1 x_2 - \beta_2 r_2 x_2^2 - (\frac{g_2 r_2}{1+X_2^*})yx_2$, which is negative semi definite. Thus, $E_2(0, X_2^*, 0)$ is Lyapunov stable. However, the set $S_2 = \{(x_1, x_2, y) / \dot{V}(x_1, x_2, y) = 0\}$, which is the set $S_2 = \{(x_1, x_2, y) / x_2 = 0\}$, does not contain any trajectory of the system except the trivial trajectory $(x_1, x_2, y) = (0, 0, 0)$. Therefore, by LaSalle's invariance principle, $E_2(0, X_2^*, 0)$ is globally asymptotically stable . Thus, $E_2(0, X_2^*, 0)$ is globally asymptotically stable . Thus, the Uganda Kobs and lions, the buffaloes will exist for any starting population density. However, the population would eventually level off to that of the carrying capacity of the game park.

(iii) Global stability of $E_3(X_1^*, X_2^*, 0) = (\frac{\delta_1 - \beta_2(1-M)}{\delta_1 \delta_2 - \beta_1 \beta_2}, \frac{\delta_2(1-M) - \beta_1}{\delta_1 \delta_2 - \beta_1 \beta_2}, 0)$. We define a Lyapunov function $V(x_1, x_2, y) = \frac{x_1^2}{2X_1^*} + \frac{x_2^2}{2X_2^*} + \frac{y^2}{2}$ which gives, after simplifying, $\dot{V}(x_1, x_2, y) = -\beta_1 r_1 x_1^2 - (\delta_1 r_1 + \delta_2 r_2) x_1 x_2 - \frac{g_1 r_1}{(1+X_1^*)} x_1 y - \beta_2 r_2 x_2^2 - (\frac{g_2 r_2}{1+X_2^*}) y x_2$.

This is negative definite if existence conditions (3.4) and (3.5) hold i.e. M < 1 and $\beta_1\beta_2 > \delta_1\delta_2$. Therefore, with these conditions, $E_3(X_1^*, X_2^*, 0)$ is globally asymptotically stable.

In terms of original parameters, M < 1 implies $E < r_1$ while $\beta_1\beta_2 > \delta_1\delta_2$ implies $\alpha_1\alpha_2 < \frac{r_1}{K_1}\frac{r_2}{K_2}$. Therefore, for global stability of the two prey species, in absence of the predator species, the Uganda Kobs must not be harvested at a rate higher than that of their intrinsic per capita growth rate. Also, the ratio of the per capita growth rate of one specie to its carrying capacity should be greater than the effect of interspecific competition caused by the other prey. This implies that, in the case of Uganda Kobs and buffaloes where interspecific competition among the prey species is negligible, these species can co-exist even when the Uganda Kobs are poached or harvested provided such harvesting does not exceed their per capita intrinsic growth rate.

3.5.2 Global stability of E_4 and E_5

As in Dubey and Upadhay (2004), and Castillo-Chave'z and Brauer (1999), we prove the global stability of E_4 and E_5 by using Bendixson-Dulac's criteria to find conditions for non existence of periodic orbits within the positive plane containing each equilibrium point.

(i) For E_4 , we define a continuously differentiable function in $X_1 > 0, Y > 0$ plane as, $H_1(X_1, Y) = \frac{1}{X_1 Y^2}$. From the system of equations (3.3), we have, $P_1(X_1, Y) = r_1 X_1[(1 - \beta_1 X_1) - \frac{g_1 Y}{1 + X_1} - M]$ and $P_2(X_1, Y) = eY[-1 + \frac{h_1 X_1}{1 + X_1}]$. This gives $H_1 P_1 = \frac{r_1}{Y^2}[(1 - \beta_1 X_1) - \frac{g_1 Y}{1 + X_1} - M]$ and $H_1 P_2 = \frac{e}{X_1 Y}[-1 + \frac{h_1 X_1}{1 + X_1}]$. We then compute $\frac{\partial(H_1 P_1)}{\partial X_1}$ and $\frac{\partial(H_1 P_2)}{\partial Y}$ which gives $\frac{\partial H_1 P_1}{\partial X_1} = \frac{r_1}{Y^2}[-\beta_1 + \frac{gY}{(1 + X_1)^2}]$ and $\frac{\partial H_1 P_2}{\partial Y} = -\frac{e}{X_1 Y^2}[-1 + \frac{h_1 X_1}{1 + X_1}]$. From the above we get $\frac{\partial H_1 P_1}{\partial X_1} + \frac{\partial H_1 P_2}{\partial Y} = \frac{1}{Y^2}[\frac{e - r_1 \beta_1 X_1}{X_1} + \frac{r_1 g_1 Y - eh_1 - eh_1 X_1}{(1 + X_1)^2}]$ which is negative in the plane $(X_1 > 0, Y > 0)$ in the region $\Omega_1 = \{0 < \frac{e}{r_1 \beta_1} < X_1, 0 < Y < \frac{eh_1}{r_1 g_1}\}$. Therefore, by Bendixson-Dulac criteria $E_4(X_1, Y)$ is globally asymptotically stable in Ω_1 . Using original parameters, this region is, $\Omega_1 = \{0 < \frac{K_1}{r_1} e < N_1, 0 < P < \frac{\lambda_1}{b_1}\}$.

(ii) For E_5 , we define a continuously differentiable function in $X_2 > 0, Y > 0$ plane as, $H_2(X_2, Y) = \frac{1}{X_2Y}$. From the system of equations (3.3), we have, $Q_1(X_2, Y) = X_2r_2[(1 - \beta_2 X - 2) - \frac{g_2Y}{1 + X_2 + Y}]$ and $Q_2(X_2, Y) = eY[-1 + \frac{h_2X_2}{1 + X_2 + Y}]$. From this, we get $\frac{\partial(H_2Q_1)}{\partial X_2} + \frac{\partial(H_2Q_2)}{\partial Y} = \frac{-r_2\beta_2}{Y} - \frac{(h_2e-g_2)}{(1+X_2+Y)^2}$, which is negative in the $X_2 > 0, Y > 0$ plane if $h_2e > g_2$ and so by Bendixson-Dulac criterion, there are no periodic solutions in the interior of the $(X_2 > 0, Y > 0)$ plane. Thus, $E_5(0, X_2^*, Y^*)$ is globally asymptotically stable. Condition $h_2e > g_2$ gives $r_2\lambda_2 > \frac{d_1}{d_2}$. This implies that, the product of the buffalo's per capita intrinsic growth rate and the lion's efficiency to convert prey biomass into fertility must be greater than the ratio of the prey biomass handled per unit time to the effect of anti-predator's behaviour.

3.5.3 Global stability of the co-existence equilibrium point $E_6(X_1^*, X_2^*, Y^*)$

In this section, a suitable Lyapunov function is chosen, from which conditions for the global asymptotic stability of the co-existence point $E_6(X_1^*, X_2^*, Y^*)$ are derived. First, we provide a lemma, to establish a region of attraction for the system represented by equations (3.3). The approach is based on work by Takeuchi (1996), Chaudhuri and Kar (2002) and Dubey and Upadhay (2004).

Lemma 3.5.1 The set

$$\Omega = \{ 0 \le X_1 \le \frac{1}{\beta_1}, \ 0 \le X_2 \le \frac{1}{\beta_2}, \ 0 \le \varepsilon_1 X_1 + \varepsilon_2 X_2 + Y \le \frac{\rho}{\eta} \}$$
(3.50)

where $\varepsilon_1 = \frac{e_1h_1}{r_1g_1}$, $\varepsilon_2 = \frac{e_2h_2}{r_2g_2}$, $\rho = \frac{\varepsilon_1}{\beta_1}(r_1 + \eta) + \frac{\varepsilon_2}{\beta_2}(r_2 + \eta)$ and $\eta \leq e$ is a region of attraction for all solutions initiating in the interior of the positive region (X_1, X_2, Y) .

Proof: From the first equation of (3.3), we note that $\frac{dX_1}{dt} \leq r_1 X_1 (1 - \beta_1 X_1)$. This gives, $X_1(t) \leq \frac{\Gamma}{e^{-rt} + \Gamma\beta_1}$, where $\Gamma = \frac{X_1(0)}{1 - X_1(0)\beta_1}$. As $t \to \infty$, we get

$$X_1(t) \le \frac{1}{\beta_1}.\tag{3.51}$$

Similarly from the second equation of (3.3), we get

$$X_2(t) \le \frac{1}{\beta_2}.$$
 (3.52)

We define a function $W(t) = \varepsilon_1 X_1(t) + \varepsilon_2 X_2(t) + Y(t)$, where $\varepsilon_1 = \frac{e_1 h_1}{r_1 g_1}$, $\varepsilon_2 = \frac{e_2 h_2}{r_2 g_2}$. For a real positive number η ,

$$\dot{W}(t) + \eta W(t) = \varepsilon_1 \dot{X}_1(t) + \varepsilon_2 \dot{X}_2(t) + \dot{Y}(t) + \eta (\varepsilon_1 X_1(t) + \varepsilon_2 X_2(t) + Y(t))$$
(3.53)

Substituting for $\dot{X}_1(t)$, $\dot{X}_2(t)$ and $\dot{Y}(t)$ using (3.3) into equation (3.53) and simplifying gives, $\dot{W}(t) + \eta W(t) = \varepsilon_1 X_1(r_1 + \eta) + \varepsilon_2 X_2(r_2 + \eta) - \varepsilon_1 r_1 \beta_1 X_1^2 - \varepsilon_2 r_2 \beta_2 X_2^2 - \varepsilon_1 r_1 \delta_1 X_1 X_2 - \varepsilon_2 r_2 \delta_2 X_1 X_2 - \varepsilon_1 r_1 M X_1 + (\eta - e) Y$. If we choose $\eta \leq e$, we shall have, $\frac{dW(t)}{dt} + \eta W(t) \leq \frac{\varepsilon_1}{\beta_1}(r_1 + \eta) + \frac{\varepsilon_2}{\beta_2}(r_2 + \eta) = \rho$. This gives $W(t) \leq \frac{\rho}{\eta}(1 - e^{-\eta t}) + W(0)e^{-\eta t}$. As $t \to \infty$, $0 \leq W(t) \leq \frac{\rho}{\eta}$. This completes the proof.

Theorem 3.5.1 Let the following inequalities hold in the region Ω defined in (3.50). Then the co-existence equilibrium point $E_6(X_1^*, X_2^*, Y^*)$ is globally asymptotically stable with respect to all solutions initiating in the interior of Ω

$$Y^* < \min\{\frac{\beta_2 R_2}{g_2}, \frac{\beta_1 R_1}{g_1}\}, \ \delta_1 + \delta_2 > 2\sqrt{\beta_1 \beta_2}, \ X_1^* = \frac{h_1 - g_1}{g_1}, \ X_2^* < \frac{h_2(g_1 + \beta_1 R_1) - g_1 g_2}{g_1 g_2},$$
$$(\beta_1 - \frac{g_1 Y^*}{R_1})(\beta_2 - \frac{g_2 Y^*}{R_2}) > (\frac{\delta_1 + \delta_2}{2})^2, \ h_1 > g_1, \ h_2 > g_2.$$

Proof: Consider the following Lyapunov function,

$$V(X_1, X_2, Y) = \frac{1}{r_1} (X_1 - X_1^* - X_1^* \ln(\frac{X_1}{X_1^*})) + \frac{1}{r_2} (X_2 - X_2^* - X_2^* \ln(\frac{X_2}{X_2^*})) + \frac{1}{e} (Y - Y^* - Y^* \ln(\frac{Y}{Y^*})).$$

Differentiating V with respect to time t we get,

$$\dot{V}(X_1, X_2, Y) = \frac{(X_1 - X_1^*)}{r_1 X_1} \dot{X}_1(t) + \frac{(X_2 - X_2^*)}{r_2 X_2} \dot{X}_2(t) + \frac{(Y - Y^*)}{eY} \dot{Y}(t)$$

Substituting in the expressions for $\dot{X}_1(t)$, $\dot{X}_2(t)$, $\dot{Y}(t)$ from equations (3.3), we get $\dot{V}(X_1, X_2, Y) = (X_1 - X_1^*) \left(1 - \beta_1 X_1 - \delta_1 X_2 - \frac{g_1 Y}{1 + X_1} - M \right)$

$$+(X_2-X_2^*)\left(1-\beta_2X_2-\delta_2X_1-\frac{g_2Y}{1+X_1+Y}\right)+(Y-Y^*)\left(-1+\frac{h_1X_1}{1+X_1}+\frac{h_2X_2}{1+X_2+Y}\right).$$
 From this, we get,

$$\dot{V}(X_1, X_2, Y) = (X_1 - X_1^*) \left((\beta_1 X_1^* + \delta_1 X_2^* + \frac{g_1 Y^*}{1 + X_1^*}) - (\beta_1 X_1 + \delta_1 X_2 + \frac{g_1 Y}{1 + X_1}) \right)$$

$$+(X_2-X_2^*)\left((\beta_2X_2^*-\delta_2X_1^*-\frac{g_2Y^*}{1+X_1^*+Y^*})-(\beta_2X_2+\delta_2X_1+\frac{g_2Y}{1+X_1+Y})\right)$$

$$+(Y-Y^*)\bigg(\big(\tfrac{h_1X_1}{1+X_1}+\tfrac{h_2X_2}{1+X_2+Y}\big)-\big(\tfrac{h_1X_1^*}{1+X_1^*}+\tfrac{h_2X_2^*}{1+X_2^*+Y^*}\big)\bigg)$$

which simplifies to,

$$\dot{V}(X_1, X_2, Y) = -(X_1 - X_1^*)^2 (\beta_1 - \frac{g_1 Y^*}{N_1}) - (X_1 - X_1^*) (X_2 - X_2^*) (\delta_1 + \delta_2) - (X_1 - X_1^*) (Y - Y^*) (\frac{g_1(1 + X_1^*) - h_1}{N_1}) - (X_2 - X_2^*)^2 (\beta_2 - \frac{g_2 Y^*}{N_2}) - (X_2 - X_2^*) (Y - Y^*) (\frac{g_2(1 + X_2^*) - h_2(1 + Y^*)}{N_2}) - (Y - Y^*)^2 (\frac{h_2 X_2^*}{N_2})$$

where $N_1 = (1+X_1)(1+X_1^*)$, $N_2 = (1+X_2+Y)(1+X_2^*+Y^*)$. Thus, $\dot{V}(X_1, X_2, Y)$ is a quadratic form which can be expressed as $\dot{V} = -X^T A X$, where $X^T = (X_1 - X_1^*, X_2 - X_2^*, Y - Y^*)$ and A is a symmetric matrix given by,

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{12} & a_{22} & a_{23} \\ a_{13} & a_{23} & a_{33} \end{pmatrix}$$
(3.54)

with $a_{11} = \beta_1 - \frac{g_1 Y^*}{N_1}$, $a_{12} = \frac{\delta_1 + \delta_2}{2}$, $a_{13} = \frac{g_1(1 + X_1^*) - h_1}{2N_1}$, $a_{22} = \beta_2 - \frac{g_2 Y^*}{N_2}$, $a_{23} = \frac{g_2(1 + X_2^*) - h_2(1 + Y^*)}{2N_2}$ and $a_{33} = \frac{h_2 X_2^*}{N_2}$.

We note that $\dot{V} < 0$ if the matrix A is positive definite (Chaudhuri and Kar, 2004). The matrix A is positive definite if:

 $a_{11} > 0, \ a_{13} = 0, \ a_{22} > 0, \ a_{23} = 0, \ a_{33} > 0, \ a_{11}a_{22} - a_{12}^2 > 0.$ We observe that, $a_{11} > 0$ and $a_{22} > 0$, give $Y^* < \frac{\beta_1 N_1}{g_1}$. $a_{13} = 0$ gives $X_1^* = \frac{h_1 - g_1}{g_1}$, provided $h_1 > g_1$. $a_{23} = 0$ gives, $X_2^* < \frac{h_2(g_1 + \beta_1 N_1) - g_{1g_2}}{g_{1g_2}}$ and $a_{11}a_{22} - a_{12}^2 > 0$, gives $(\beta_1 - \frac{g_1 Y^*}{N_1})(\beta_2 - \frac{g_2 Y^*}{2N_2}) - (\frac{\delta_1 + \delta_2}{2})^2 > 0$, provided $\delta_1 + \delta_2 > 2\sqrt{\beta_1\beta_2}$. This completes the proof.

3.6 Conclusion

In this chapter, conditions for existence of all the seven possible equilibrium points (steady states) were established. It was found out that the Uganda Kobs can exist on their own or in presense of the buffaloes and/ or the lions only if the intrinsic rate of the Uganda Kobs was greater than the rate at which they are harvested. The Uganda Kobs and buffaloes would co-exist in the absence of the lions so long as the intrinsic rate of the Uganda Kobs was greater than the rate at which they are harvested and the interspecific competition among the Uganda Kobs and buffaloes was negligible. The existence of the lions with either the Uganda Kobs alone or the buffaloes alone required that the proportion of biomass of each prey specie converted into fertility (reproductivity rate) by the predator must be greater than the product of the predator's natural mortality rate, and the time it takes to handle the prey. The co-existence of all three species required among others, $c > \frac{r_2}{K_2} \frac{d_2}{d_1}$. This inequality shows the parameters that must be controlled for the co-existence of the three species.

Also, conditions for the local and global asymptotic stability of the steady states were established. The conditions for local asymptotic stability of the steady states were in most cases found to be similar to those for the existence of the steady states. Conditions for the global asymptotic stability of the steady states E_1, E_2 and E_3 were established by choosing a suitable Lyapunov function and applying LaSalle's invariance principle. These steady states would be globally asymptotically stable if the existence conditions prevailed. By using Bendixson-Dulac criteria, global asymptotic stability of the steady states E_4 and E_5 were established. The state E_5 , which is the existence of the lion with the buffalo alone, would be globally asymptotically stable if $r_2\lambda_2 > \frac{d_1}{d_2}$ which implied that the product of the buffalo's per capita intrinsic growth rate and the lion's efficiency to convert prey biomass into fertility must be greater than the ratio of the prey biomass handled per unit time to the effect of anti-predator's behaviour. The global stability of the co-existence steady state E_6 was stated in form of Theorem (3.5.1).

Chapter 4

Numerical Simulation

In this section numerical simulation of the model represented by equations (3.1) is done using MATLAB computer program. Data obtained by interviewing Mr. Abitegeka Gerald (see interview guide in Appendix B) of Queen Elizabeth National Park, Western Uganda, on the 3 species namely lions, buffaloes and Uganda Kobs is used to estimate some parameters. Estimation of parameters is done basing on work by Fay and Greeff (1999). Other parameters that are not easily estimated from the field data have been allowed to vary within corresponding possible intervals.

4.1 Parameter values

(i) The intrinsic growth rate, r_1 , r_2 and e (Units: per year)

Borelli and Coleman (2004) defined the intrinsic growth rate as the measure of the difference in birth rate and death rate per unit time if there is no overcrowding and harvesting. Fay and Greeff (1999) calculated the intrinsic growth rate of a given specie as the number of young ones produced per year per adult female. It is positive for the prey species but is taken to be negative for the predator as the cubs die in absence of the prey. Since the ratio of the females of the Uganda Kobs, buffaloes and lions was not established, we estimate the intrinsic growth rate for each specie as the ratio of the number of young ones produced per year, to the total population, of each specie. Thus, $r_1 = \frac{20 \times 365}{40,000} = 0.185$, $r_2 = \frac{4 \times 365}{20,000} = 0.073$, $e = \frac{6}{120} = 0.05$. We shall rescale this to be $r_1 = 1.825$ $r_2 = 0.73$, e = 0.5. Rescaling is done so as to have better numerical analysis graphs.

(ii) Carrying capacity, K_1 and K_2 (Units: per unit area)

According to Borelli and Coleman (2004), the carrying capacity is the maximum number of prey that the ecosystem can sustain in absence of the predator. Game park authorities of Queen Elizabeth National Park estimate it to be 100,000 for the Uganda Kobs and 60,000 for the buffaloes (see interview guide in Appendix). This shall be rescaled to $K_1 =$ 50 and $K_2 = 30$ respectively. Rescaling is done so as to have better numerical analysis graphs.

(iii) The predator's efficiency to convert prey biomass of N_1 and N_2 respectively into fertility, λ_1 and λ_2 respectively (Units: per prey)

Fay and Greeff (1999) calculated the predator's efficiency to convert food into fertility as the ratio of the number of cubs to the number of kills per adult lion multiplied by the ratio of adult females to the pride, which turned out to be 0.125. We shall take $\lambda_1 = 0.125$ and allow λ_2 to vary within feasible ranges.

The other parameters that are not easily estimated from the field data have been allowed to vary within corresponding possible intervals. Therefore, the base parameter values used in the model are given in the following table.

Table 4.1: The table that shows base paramete	r values
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Parameter description	Symbol	Base value	Ref
Per capita intrinsic growth rate for prey	r_1 and r_2	1.82 and 0.73	$[16], QEP^*$
Carrying capacities for prey N_1 and N_2	K_1 and K_2	50 and 30	$[9], QEP^*$
Interspecific competition between prey	α_1 and α_2	0.01 and 0.001	[15]
Capturing rates of predator P	a_1 and c	1 and 0.001	[15]
Prey biomass handled per unit time	b_1 and d_1	0.04 and 0.001	[15]
Constant effort harvesting rate of prey N_1	E	0.5	$[12], QEP^*$
Natural mortality rate of predator P	e	0.5	$[16], QEP^*$
Effect of anti-predator behaviour of prey N_2	d_2	1	[32]
Efficiency to convert prey biomass			
of N_1 and N_2 respectively into fertility.	$\lambda_1 \text{ and } \lambda_2$	0.125 and 0.5	[16]

 QEP^\ast Data obtained from interviews with game park rangers of Queen Elizabeth national park.

4.2 Numerical simulation results

By keeping all other parameters constant, we shall vary only the parameter under investigation and interpret the resulting graphs.

4.2.1 The effect of harvesting prey N_1

Harvesting of one or more animal species of an ecosystem can stabilise or destabilise the dynamics of the ecosystem. In a linear Lotka- Volterra model with constant effort harvesting of both prey and predator, it is known that constant effort harvesting raises the average number of prey per cycle and lowers the average number of predators (Borelli



Figure 4.1: Graph of prey N_1 , N_2 and P against time when $r_1 = E = 3$ and $r_2 = 2$. The graph shows that prey N_1 and predator P become extinct if the harvesting rate E is greater or equal to its intrinsic growth rate r_1

and Coleman, 2004). In our model, only the prev N_1 is harvested. Figure 4.1 shows that when prev N_1 is harvested at a rate slightly lower or equal to that of its intrinsic growth rate, the predator P dies off, and the population density of prev N_1 is small, though that of N_2 is high. When $E > r_1$ the system is not ecologically feasible as it gives negatives. This implies that the harvesting rate of the Uganda Kobs should never be allowed to exceed its intrinsic growth rate. However, controlled harvesting of the Uganda Kobs can be done so long as it is much less than the intrinsic growth rate.



Figure 4.2: Graph of prey N_1 , N_2 and P against time (in years) when $r_1 = 10$ and $r_2 = 2$.

Simulation result show that for r_1 , the system is only ecologically feasible if $r_1 > E$. However the system is ecologically feasible for any positive r_2 value, though N_2 becomes extinct if $r_2 < 0.3$. Setting high values of r_1 and r_2 results in an increase in the population density of the predator. Figure 4.2 shows that when $r_1 = 10$, and $r_2 = 2$, N_2 increases upto 30 (its carrying capacity), P increases upto 25 while N_1 decreases down to 5. This clearly illustrates that as the intrinsic growth rate of the prey increases, the population density of the predator species will increase as well.

4.2.3 The effect of varying death rate of the predator

Simulation results show that for 0.069 < e < 0.9, the system is ecologically feasible. The implication of these results is that for e < 0.069, the natural mortality rate of the predator species is too low, this may lead to a high predation rate of the prey and so the system is not ecologically feasible. On the other hand, for e > 0.9, the natural mortality rate of the predator species is too high, and so the predator species are faced with extinction. Figure 4.3 (a) and (b) show a limit cycle when e = 0.5 and Figure 4.4(a) and (b) show a stable spiral at e = 0.7. Thus, e = 0.7 is a bifurcation point. This implies that for values of 0.7 < e < 0.9 the co-existence steady state is a stable spiral which means it is globally asymptotically stable.



Figure 4.3: Graphs of prey N_1 , N_2 and predator P when e = 0.5. a) shows a limit cycle. b) shows N_1 , N_2 and P against time.





Figure 4.4: Graphs of prey N_1 , N_2 and predator P when e = 0.7. a) shows a stable spiral. b) shows N_1 , N_2 and P against time

4.2.4 The effect of varying the predator's efficiency to convert prey biomass into fertility, λ_1 and λ_2

Ecological models are based on the assumption that the fertility rate or reproductivity rate of the predator depends on the amount of prey biomass converted into food by the predator. While we were unable to scientifically establish this parameter from the field data, we carried out numerical simulations by varying values so as to establish ranges within which the model gives feasible results and also to study the effect of the parameter on the dynamics of the model. The system is ecologically feasible for $0.06 < \lambda_1 < 0.5$. Figure 4.5 (a) and (b) show a stable spiral at $\lambda_1 = 0.09$ and Figure 4.6(a) and (b) show a limit cycle at $\lambda_1 = 0.15$. Thus, $\lambda_1 = 0.15$ is a bifurcation point. As λ_1 increases, N_1 decreases as expected while N_2 increases. Also the amplitude of oscillations for P increases. This implies that as the coefficient of the predator's efficiency to convert prey biomass of N_1 , into fertility increases, the population density of prey N_1 decreases while that of prey N_2 and predator P increases.

For λ_2 , the system is ecologically feasible even when $\lambda_2 = 0$ but would become infeasible at higher values, e.g. $\lambda_2 > 2$. We deduce from these simulation results that the predator P depends mainly on prey biomass of N_1 than N_2 for its survival. This implies that lions depend mainly on the prey biomass of Uganda Kobs than buffaloes for survival. Also, the predator's efficiency to convert prey biomass into fertility should not be too low or too high.





Figure 4.5: Graphs of prey N_1 , N_2 and predator P when $\lambda_1 = 0.09$. a) shows a stable spiral. b) shows N_1 , N_2 and P against time. 50





Figure 4.6: Graphs of prey N_1 , N_2 and predator P when $\lambda_1 = 0.15$. a) shows N_1 , N_2 and P against time. b) shows a limit cycle. 51

4.2.5 The effect of varying the coefficient for inter-specific competition α_1 and α_2

Inter-specific competition among prey is usually a result of scarce resources shared by both prey species. By the law of mass action, this tends to reduce the population densities of the prey species.

While inter-specific competitions among prey has been included in our model, it is well known that the Uganda Kobs and buffaloes of Queen Elizabeth National Park actually show mutual cooperation while feeding on the grass. In absence of inter-specific competition we take $\alpha_1 = 0$ and $\alpha_2 = 0$. Figure 4.7 shows the graph when $\alpha_1 = 0$ and $\alpha_2 = 0$. This implies that in absence of inter-specific competition among prey, as is the case with Uganda Kobs and buffaloes, the system is still ecologically feasible and the dynamical behaviour of the system does not change. Numerical simulation results indeed show that the system is ecologically feasible for a small range of low values of coefficients for inter-specific competition, that is, $0 \leq \alpha_1 < 0.9$ and $0 \leq \alpha_2 < 0.6$. But for high values of α_1 and α_2 , that is , when inter-specific competition among the prey species is high, the ecosystem is infeasible.



Figure 4.7: Graph of prey N_1 , N_2 and predator P when $\alpha_1 = 0$ and $\alpha_2 = 0$. The graph shows a limit cycle.

4.2.6 The effect of varying the capturing rates of predator, a_1 and c

The predator's rate of capturing the prey is the number of prey killed by one predator per unit time (Units: per time). Owing to the different ways in which the lion predates on the Uganda Kobs and buffaloes, the predator's capturing rate is different for each prey specie. While actual values for these parameters were not established from the field data, numerical simulations were done using values varied within possible ranges for ecological feasibility of the model. Figure 4.8 shows that the system is ecologically stable even when c = 0. Simulation results show that a_1 is more important than c for survival of predator P since when $a_1 = 0$ but $c \neq 0$ the population density of P remains zero. As the value of a_1 increases, the predator population density increases. However for values of $a_1 > 1$ and c > 1, the system is ecologically infeasible



Figure 4.8: Graph of prey N_1 and N_2 when $a_1 = 0$ and $c \neq 0$. The graph shows a limit cycle.



Figure 4.9: Graph of prey N_1 , N_2 and predator P when $d_2 = 4$. The graph shows a limit cycle.

4.2.7 The effect of varying the anti-predator behaviour d_2

The anti-predator behaviour means the tendency for the prey to resist being predated (Units: per prey). In our model, the buffaloes were assumed to have developed anti-predator behaviour since they put up a fierce resistance against the lions. Numerical simulation results show that $d_2 = 4$ is a bifurcation point since the behaviour of the dynamical system changes from a limit cycle to a spiral. An increase in d_2 does not significantly affect the population density of predator P.

4.3 Summary

In this chapter, we have seen that whenever $E > r_1$, the system is not ecologically feasible as it gives negatives. This implies that the harvesting rate of the Uganda Kobs should never be allowed to exceed its intrinsic grown rate. In Section (4.2.2), we noted that when r_1 , and r_2 increased, the population density of N_2 and P increased while that of N_1 decreased. This clearly illustrates that as the intrinsic growth rate of the prey increases, the population density of the predator species will increase as well. It was noted also that varying parameters such as $e, \lambda_1, \lambda_2, d_2$ changed the dynamics of the equilibrium point from limit cycle to stable spiral and vice-verser. This implied that these parameters can be controlled so that the dynamical behaviour of the steady state is a stable spiral which implies that the steady state is globally asymptotically stable.

Chapter 5

Discussion, Conclusion and Recommendations

5.1 Discussion

A mathematical model was proposed and analysed to study the dynamics of a two preyone predator system in which the predator showed a Holling Type II response to one prey which was also harvested and a ratio-dependent response to the other prey. All the seven possible equilibrium points were analysed for local and global stability. The model was used to study the ecological dynamics of the lion-buffalo-Uganda Kob preypredator system of Queen Elizabeth National Park, Western Uganda. In the model the population of the Uganda Kobs, buffaloes and lions at any time were represented simply by N_1 , N_2 and P.

The harvesting rate was found to play a crucial role in stabilizing the system. Results of Section 3.3 (i) and Figure 4.1 showed that, prev N_1 becomes extinct whenever the harvesting rate E exceeds the intrinsic growth rate r_1 . This implies that harvesting of the Uganda Kobs should never exceed their intrinsic growth rate. However, harvesting of the Uganda Kobs at a rate much lower than their intrinsic growth rate would not lead to collapse of the system. This result is similar to one obtained by Chaudhuri and Kar (2004) on the existence conditions for the system they studied.

In Section 3.3 (iii) and 3.5 (iii), we showed that in absence of the predator, the two species can co-exist and are globally asymptotically stable if the inter specific competition among the prey was minimal or negligible and prey N_1 was not harvested beyond its intrinsic growth rate. Numerical analysis results indeed confirmed this.

In section 3.5.2 (ii) we showed that the existence of the lion with the buffalo alone, would be globally asymptotically stable if the product of the buffalo's per capita intrinsic growth rate and the lion's efficiency to convert prey biomass into fertility must be greater than the ratio of the prey biomass handled per unit time to the effect of anti-predator's behaviour.

Theorem 3.3.1 showed that the 3 species would co-exist if prev N_1 was not harvested beyond its intrinsic growth rate, the predator P converted the biomass of prev N_1 into fertility at a rate greater than the predator's natural mortality rate and the time it took to handle prev N_1 . Also, the rate at which the predator captures prev N_2 should be greater than the product of the intrinsic growth rate of N_2 and the effect of the anti-predator behaviour of prev N_2 . Dubey and Upadhyay (2004) also discovered that the predator's mortality rate and food conversion coefficients played a crucial role in determining the stability behaviour of planar equilibria in ratio-dependent models.

One major observation from results of numerical simulation (as showed by Figure 4.2) is that the predator population density increased significantly when the intrinsic growth rate of both prey increased. This implies that a gradual increase in the number of Uganda Kobs would result in significant increase in the number of lions, which would in the long term lead to the population density of the Uganda Kobs to fall to a level lower than the original one.

Numerical simulation of the model also revealed that the dynamical behaviour of the system changes mostly from a limit cycle to a stable spiral and vice - versa when values of some parameters such as the natural death rate of the predator (Figures 4.3 and 4.4) and food conversion rate of predator (Figures 4.5 and 4.6) are varied. This implied that these parameters can be controlled so that the dynamical behaviour of the steady state is a stable spiral which implies that the steady state is globally asymptotically stable. In Akcakaya *et al.* (1995), it was discovered that ratio-dependent models can have stable equilibria, limit cycles and extinction of both prey. It should be noted however, that in this model, varying some parameters such as the inter-specific competition among prey does not change the dynamical behaviour of the system.

5.2 Conclusion

The model is rich in dynamical behaviour and establishes various conditions under which the prey can exist with or without predation. Both qualitative and numerical analysis results indicated that if the harvesting rate of the Uganda Kobs exceeds their intrinsic growth rate, the population of the Uganda Kobs and lions would become extinct with time. The model also indicated that based on the current estimates of the population density and the parameter values, limit cycle behaviour will occur which means that the population density of the 3 species will increase or decrease slightly but not deviate much from the current figures.

5.3 Recommendations

Basing on the results of qualitative analysis and numerical analysis of the model, we recommend that;

(i) The Uganda Kobs should not be harvested at a rate higher than their intrinsic growth rate. However optimal harvesting of the Uganda Kobs at a rate much lower than their intrinsic growth rate is permissible, since this would not lead to collapse of the system in the long term. (ii) The population density of the lions can be increased drastically by increasing the intrinsic growth rate of the prey species e.g regular recruiting more Uganda Kobs into the park. Since regular recruiting of Uganda kobs may not be realistic, the best alternative is to minimize or stop poaching of the Uganda kobs so as to greatly increase their population, which will in turn result in an increase in the population of the lions.

(iii) The population density of the lions depends mainly on the biomass of the Uganda Kobs than of buffaloes, hence any attempt to control the population density of the lions should be based on controlling the population density of the Uganda Kobs.

5.4 Further development of the model

Further research can be carried out on this study especially regarding how to estimate parameter values used in the model from field data. The model can be improved by incorporating the effects of animals leaving in area patches since Queen Elizabeth National Park has two main area patches where the animals stay. Also since Queen Elizabeth National Park has more prey and predator species besides Uganda Kobs, buffaloes and lions, more equations can be incorporated in the model to cater for this. Qualitative analysis on how to find the co-existence equilibrium point and conditions for local and global stability can be done following a different approach. Hopf bifurcation can be carried out on the model.

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Appendix A

Simulation Program

! ______ ļ THE MATLAB PROGRAM TO SOLVE THE SYSTEM OF DIFFERENTIAL ! ! EQUATIONS FOR SYSTEM (3.1) ! _____ ! function dy = EDWIN1(t,y) r1 = 0.5;r2 = 0.4;k1 = 50;k2 = 30;alp1 = 0.001; alp2 = 0.002; a1 = 0.002;b1 = 0.04;

E = 0.3; d1 = 0.01; d2 = 1; c = 0.01; lamb1 = 0.1; lamb2 = 0.8; e = 0.01;

```
dy = [0 0 0]';
dy(1) = r1*y(1)*(1 - y(1)./k1) - alp1*y(1)*y(2) - (a1*y(1)./(1 + b1*y(1)))*y(3)
- E*y(1);
dy(2) = r2*y(2)*(1 - y(2)./k2) - alp2*y(1)*y(2) - (c*y(2)./(1 + d1*y(2)
+ d2*y(3)))*y(3);
dy(3) = -e*y(3) + lamb1*(a1*y(1)./(1 + b1*y(1)))*y(3)
+ lamb2*(c*y(2)./(1 + d1*y(2) + d2*y(3)))*y(3);
```

```
clear all
format long
options = odeset('RelTol',1e-4,'AbsTol',[1e-4 1e-4 1e-5]);
[T,Y] = ode45(@EDWIN1,[0 50],[50 20 30],options)
plot(T,Y(:,1),'-',T,Y(:,2),'-.',T,Y(:,3),'.');
%plot(T,Y(:,1),'-',T,Y(:,2),'-.');
%plot(Y(:,1),Y(:,2))
%plot3(Y(:,1),Y(:,2),Y(:,3))
```

```
clear all
options = odeset('RelTol',1e-4,'AbsTol',[1e-3 1e-4 1e-5]);
```

```
[T1,Y1] = ode45(@EDWIN1,[0:1:50],[.01 .2 0.02 ],options);
[T2,Y2] = ode45(@EDWIN2,[0:1:50],[.01 .2 0.02 ],options);
[T3,Y3] = ode45(@EDWIN3,[0:1:50],[.01 .2 0.02],options);
plot(T1,Y1(:,1),'-',T2,Y2(:,2),'-.',T3,Y3(:,3),'.');
%plot(T1,Y1(:,1),'-',T2,Y2(:,2),'-.');
%title('Graph of prey N1, N2')
%xlabel('Time')
%ylabel('prey N1, N2')
```

Appendix B

Field interview with Abitegeka Gerald of Queen Elizabeth National Park

Date of interview: 27/12/2008 Name of park official: ABITEGEKA GERALD Job description: Game ranger Queen Elizabeth National Park Contact: Mobile phone number 0772341214 Interviewer: AKUGIZIBWE EDWIN Interviewee: ABITEGEKA GERALD

B.1 INTERVIEW

(i) QUESTION(Q) What is the size of this park?

ANSWER (A) The park covers an area of approximately 2000 square miles. It has two

main patches where you find the animals; the eastern patch and the western patch.

(ii) (Q) What are the main prey and predator species in the park?

(A) The main predator species are the lions, leopards and hyaenas. The main prey species are the Uganda Kobs, warthogs, buffaloes and waterbucks.

(iii) (Q) Describe the nature of lions as predators

(A) The lions live in a pride of 1 to 10 animals with the females more than the males in a pride. The lions hunt during night and day since they have a clear vision at night. The males mark their territory using their urine or the hair on their mane. The females hunt more than males, the males mainly open the carcass. The lions mainly predate on Uganda Kobs and buffaloes.

(iv) (Q) How do the lions predate on the Uganda Kobs and buffaloes?

(A) The lions usually hunt for the Uganda Kobs more than buffaloes since they are many and are easily sited because both the lions and Uganda Kobs are brown and so the lions disguise themselves. It takes one lion to kill a Uganda Kob and this involves first stalking, targeting and then ambushing the Uganda Kob. On the other hand it requires a minimum of 3 lions to attack a mature buffalo. The lions attack the buffalo from its rear to avoid being injured, some times fatally, by the buffalo's horn. The lions tend to go for the buffaloes if they are at least 3, hungry and if the buffalo is isolated or weak.

(v) (Q) What is the animal population of the Uganda Kobs and buffaloes?

(A) During the times of political instability in the country, the number of animals in the park was very small, but not well estimated or known. However, an animal population

census carried out in 2002 established that there were 90 lions, 30, 000 Uganda Kobs and 12, 000 buffaloes. The numbers for the three species have been increasing gradually and, according to game rangers, are now estimated to be 120 lions, over 40, 000 Uganda Kobs and 20, 000 buffaloes. The numbers are expected to continue increasing gradually.

(vi) (Q) What is the average birth rate of the 3 species?

(A) On average, 20 Uganda knobs are born daily, 6 cubs are born in a year while 4 buffaloes are born daily.

(vii) (Q) On average, how many animals are poached by the neighbouring communities?

(A) Poaching has greatly been minimised by sensitizing and carrying out social responsibilities to the neighbouring communities. However people still poison lions that stray to their gardens.

(viii) (Q) Why does the lion go for the hard-to-capture buffalo instead of the smaller animals e.g. the warthogs?

(A) The choice of prey specie the lion goes for depends on many factors among which include: abundance of prey, ease of capture, taste and quantity of biomass per prey killed. The lions mainly go for the Uganda Kobs because they are many, it requires only one lion to kill a Uganda Kob, the Uganda Kobs are easy to ambush and as a matter of fact, they have a better taste than the other animals in the park. The bigger and hard-to-capture buffaloes are the lions other main prey species rather than the smaller and easier-tocapture warthogs or waterbucks. Two reasons dictate this: first the buffalo's meat tastes better than that of the waterbuck which is salty and secondly the lions get a good yield in terms of biomass per buffalo killed and this enables them to share with their cubs.