Repulsive-Attractive Models for the Impact of Two Predators on Prey Species Varying in Anti-Predator Response

By

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Statement of Declaration

The data used in the compilation of this thesis was taken from both primary and secondary sources. References have been made to all secondary sources utilized.

I, **Hassan Ddumba** with student number **209003577**, in accordance with NMMU general prospectus rule **G4.6.3**, hereby declare that this thesis for my PhD qualification is a result of my own effort and to the best of my knowledge, has not previously been submitted for assessment to any other University or for another qualification.

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Dedication

With affection, I dedicate this thesis to my beloved wife, Zainah Ddumba, and our wonderful children, Mubarak, Abdul-Karim and Hamzah.

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First citation (Qur'an)

In the name of God, the Most Beneficent, the Most Merciful.
"Read in the name of your Lord Who created (everything),
He created man from a clot!
Read And your Lord is the Most Honourable/High!
Who taught the use of the pen,
Taught man what he never knew....."
(Qur'an; al-Alaq 96:1,5)

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Abstract

This study considers the dynamical interaction of two predatory carnivores (Lions (*Panthera leo*) and Spotted Hyaenas (*Crocuta crocuta*)) and three of their common prey (Buffalo (*Syncerus caffer*), Warthog (*Phacochoerus africanus*) and Kudu (*Tragelaphus strepsiceros*)). The dependence on spatial structure of species' interaction stimulated the author to formulate reaction-diffusion models to explain the dynamics of predator-prey relationships in ecology. These models were used to predict and explain the effect of threshold populations, predator additional food and prey refuge on the general species' dynamics. Vital parameters that model additional food to predators, prey refuge and population thresholds were given due attention in the analyses.

The stability of a predator-prey model for an ecosystem faced with a prey out-flux which is analogous to and modelled as an *Allee effect* was investigated. The results highlight the bounds for the conversion efficiency of prey biomass to predator biomass (fertility gain) for which stability of the three species ecosystem model can be attained. Global stability analysis results showed that the prey (warthog) population density should exceed the sum of its carrying capacity and threshold value minus its equilibrium value i.e., $W > (K_w + \varpi) - W^*$. This result shows that the warthog's equilibrium population density is bounded above by population thresholds, i.e., $W^* < (K_w + \varpi)$. Besides showing the occurrence under parameter space of the so-called paradox of enrichment, early indicators of chaos can also be deduced. In addition, numerical results revealed stable oscillatory behaviour and stable spirals of the species as predator fertility rate, mortality rate and prey threshold were varied. The stabilising effect of prey refuge due to variations in predator fertility and proportion of prey in the refuge was studied.

Formulation and analysis of a robust mathematical model for two predators having an overlapping dietary niche were also done. The Beddington-DeAngelis functional and numerical responses which are relevant in addressing the Principle of Competitive Exclusion as species interact were incorporated in the model. The stabilizing effect of additional food in relation to the relative diffusivity D, and wave number k, was investigated. Stability, dissipativity, permanence, persistence and periodicity of the model were studied using the routine and limit cycle perturbation methods. The periodic solutions ($\widehat{\Phi}_1$ and $\widehat{\Phi}_3$), which influence the dispersal rate (φ) of the interacting species, have been shown to be controlled by the wave number. For stability, and in order to overcome predator natural mortality, the nutritional value of predator additional food has been shown to be of high quality that can enhance predator fertility gain. The threshold relationships between various ecosystem parameters and the carrying capacity of the game park for the prey species were also deduced to ensure ecosystem persistence. Besides revealing irregular periodic travelling wave behaviour due to predator interference, numerical results also show oscillatory temporal dynamics resulting from additional food supplements combined with high predation rates.

Key words: *Allee effect*, dilution effect, out-flux, threshold, fitness, conspecifics, *Brusselator*, permanence, persistence, *Burgers* equation, dissipativity, dispersal, wave number.

Chapter 1

Introduction

1.1 Motivation and background to the study

In ecosystems, the fabric of habitats is like a patchwork quilt with a wide variety of local conditions, some favouring one species and some favouring another (Keshet-Edelstein, 2005). Thus, real natural systems behave in a way that reflects an underlying spatial variation, and the effect of such a spatial organisation influences the way individual species interact in an ecosystem (Bazykin, 1998). The fine balance that exists between interdependent species and the spatial diversity of the system can have subtle but important effects (Murray, 1989; Holt, 1984). Conversely, the interactions of different species can result in spatial heterogeneity which leads to changes in stability of steady states and eventually the appearance of wavelike patterns within the ecological predator-prey model (Pearce *et al.*, 2006; Peng & Wang 2005; Murray, 1993). The concepts underlying spatially dependent processes can be described by use of various partial differential equations (Murray, 1993). Owing to its universal existence and importance, the dynamical relationship between predators and their prey has been and will continue to be one of the dominant themes to both empirical and theoretical conservationists (Bazykin, 1998; Starfield & Bleloch 1986; Okubo, 1980).

1.1.1 Interaction of species

It is well known that many species have already become extinct and many others are on the verge of extinction due to several natural and man-made reasons, such as over-exploitation, indiscriminate harvesting, over-predation, environmental pollution, loss of habitat and mismanagement of natural resources (Srinivasu & Gayatri, 2005). For example, the vulnerable roan antelope (*Hippotragus equines*) almost declined to extinction in the Kruger National Park after aerial censuses revealed that the man-made waterholes had opened up the habitat for zebra (*Equus burchelli*) and blue wildebeest (*Connochaetus taurinus*) (Hayward, 2011; Hayward *et al.*, 2007*a*; Harrington *et al.*, 1999).

Despite the lion (*Panthera leo*) having a profound impact on a wide range of prey species, there are various predator species present in various South African game reserves that help in maintaining a natural balance and provision of ecotourism (Hayward *et al.*, 2007*a*; Hayward *et al.*, 2007*b*; Fay & Greef, 2006; Tambling & Du Toit, 2005; Mills & Shenk, 1992; van Orsdol, 1984). The leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*) and cheetah (*Acinonyx jubatus*) have been ranked high among the efficient predators within these various game parks (Hayward *et al.*, 2006). Predators capture and feed on the prey that get exposed, especially during species' dispersal. Through mathematical modelling, we can establish how such species' dispersal can take place or be avoided at minimum risk to the prey (Dao-Duc *et al.*, 2008; Tyutyunov *et al.*, 2007; Fryxell *et al.*, 1988; Okubo, 1980).

In any community, there is always interaction between species, and it is through such interaction that species survive, co-exist, multiply or become extinct. Such dynamics of interacting species have been given considerable attention and have been studied from various perspectives down through the ages (Srinivasu & Gayatri, 2005). For example, during the last three decades of the twentieth century, most studies investigated the effect of prey-density-dependent predator migration on the stability of a predator-prey system (Bhatt *et al.*, 1999; Afolayan & Ajayi, 1980). The variety and complexity of the intricate systems which constitute the fabric of both animal species and the environment in which they live and interact was and still remains a topic that puzzles both empirical and theoretical conservationists (Keshet-Edelstein, 2005; Berryman, 1992; Brown, 1975). Therefore, the characterisation of ecological interactions provides one of the most venerable of venues for mathematical biology, dating back at least as far as Volterra‘s consideration of the fluctuations of the Adriatic fisheries and since then, many mathematical methods of optimal control and adaptive management have been developed to solve problems in ecological management (Ruan & Freedman, 1991; Freedman & Wolkowicz, 1986).

A quantitative and qualitative understanding of the interaction of different species is crucial for the management of wildlife resources (Azar *et al.*, 1993). Therefore, the challenge is to adapt general theoretical models for multiple species in order to postulate and investigate mathematically the effect of introducing terms that represent various phenomena, such as mutualism, seasonal calving, refugia, additional predator food and functional response (Srinivasu *et al.*, 2007; Fay & Greef, 2006; van Baalen *et al.*, 2001; Krivan, 1998; Sih, 1987; McNair, 1986).

1.1.2 Mathematical modelling in ecology

Mathematical models which are broadly of two types; (i) educational (simple and analytically tractable) and (ii) practical (complex and in many cases analytically intractable), have existed and have puzzled researchers in various scientific disciplines throughout many decades (Berryman, 1992; Maynard, 1974). For example, population models are said to have originated from the Malthus model, formulated in the early nineteenth century, and then corrected by Verhulst about 50 years later to compensate for the prediction that either a population grows or dies out exponentially (Murray, 1993; Berryman, 1992; Starfield & Bleloch, 1986). The *logistic* correction by Verhulst allows instead for a horizontal asymptote to which the population tends as time flows, the value of which expresses the carrying capacity of the environment for the population under scrutiny. This notion of mathematical modelling took a new twist when Volterra and Lotka released their independent but similar research findings, and this stimulated more and more research in mathematical modelling that has branded the discipline with yet a new flavour. Predator-prey models that evolved from *logistic* theory or that incorporate *ratio*-dependent functional responses have been found not to have problems such as the paradox of enrichment and biological control and seem to be more biologically plausible (Khan *et al.*, 2004; Berryman, 1992).

With various assumptions, Volterra (1926) first proposed a simple model for the predation of one species by another to explain the oscillatory levels of certain fish catches in the Adriatic sea. Though Volterra's model was proposed in fisheries management, it has been useful to researchers in ecology, epidemiology and other areas. The challenge facing humans today, is the consideration of global change, loss of biodiversity, and achieving a sustainable future. This elevates the complexity to new levels of scientific and technological research.

1.1.3 Migration and switching in ecosystems

In a predator-prey environment, the predator and prey prefer feeding in a habitat for some duration before changing preference to another habitat (Hayward *et al.*, 2006; Khan *et al.*, 2004; Bhatt *et al.*, 1999). This phenomenon of changing habitats is called switching and is due to various reasons which can be explained by using relevant mathematical models (Khan *et al.*, 2004; van Baalen *et al.*, 2001). Despite unclear reasons, Tambling & Du Toit (2005) and Fryxell *et al.* (1988) proposed that migratory populations benefit from (i) escaping year-round predation by migrating out of the territories of large resident predators and (ii) responding to seasonal and spatial heterogeneity in food quality.

Switching may result in routine migration of prey species at regular periods of the year that may lead to the repulsive-attractive effects of predator-prey systems (Tyutyunov *et al.,* 2007). For example, blue wildebeest migrate in large herds across the Serengeti Park in search of resources and predator avoidance (Tambling & Du Toit, 2005; Bhatt *et al.,* 1999). Preventing migratory movements, while in closed reserves, potentially allows predators to benefit from a *"captive"* prey resource. This has led to wildebeest's fragmented distribution together with isolated populations in many game reserves such as Pilanesberg National Park (Tambling & Du Toit, 2005).

1.2 Spatial distribution of species

Underlying all social behaviour of a species is the distribution in space of its members (Liu, 2010; Pearce *et al.*, 2006; Renshaw, 1991; Holt, 1984). This distribution is determined mainly by the behaviour of individuals towards one another. The distribution of animals is important because it places restrictions on the opportunities for social interaction of various types, and it plays an integral role in the population dynamics of the species (Brown 1975).

A population grows slower in some years than in others and in some places better than in others, leading to a temporal and spatial variation that results in variable population growth rates. Furthermore, since real populations occupy physical space and individuals move across it, the ultimate interest is the rate at which the population spreads and disperses in such environments (Petrovskii & Li, 2006; Case, 2000; Okubo, 1980).

1.3 Addo Elephant National Park: Fauna and Flora

Addo Elephant National Park (AENP), which is approximately 1650 km^2, located 70 km north of Port Elizabeth in South Africa's Eastern Cape Province (Addo town), was proclaimed in 1931 to protect and save the remaining 11 Addo elephants (*Loxodonta africana*) from extinction (Hayward & Hayward, 2006; Urquhart *et al.*, 1997). Although originally proclaimed to protect a single species, priorities have now changed to conserve the rich biological diversity found in the area and is currently being expanded to form the Greater Addo Elephant National Park (GAENP) (SANParks, 2006; Kerley & Boshoff, 1997).

AENP encompasses five of South Africa's nine biomes, namely: forest, subtropical thicket (valley bushveld), grassland, fynbos and nama karoo (SANParks, 2006; Urquhart *et al.,* 1997). Today, this finely tuned fenced ecosystem is sanctuary to over 450 elephants, 400 Cape buffaloes (*Syncerus caffer*), black rhinoceros (*Diceros bicornis*), a variety of antelope species (red hartebeest (*Alcephalus buselaphus*), eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*) and bushbuck (*Tragelaphus scriptus*)), abundant warthogs (*Phacochoerus africanus*), various native predators (lions, spotted hyaenas, wild dogs (*Lycaon pictus*), leopards (*Panthera pardus*)), a variety of birds and reptiles all under conservation management (Mgqatsa, 2010; Hayward *et al.,* 2007*a*, *b*; Hayward, 2006; SANParks, 2006; Hayward & Hayward, 2006).

Over the years, most species have suffered extensive range loss within the Eastern Cape Province, with some now extinct in many areas where they formerly occurred, and a wide range of conservation projects within AENP are being implemented (Mgqatsa, 2010; Nyafu, 2009; Hayward & Kerley, 2008; Hayward *et al.,* 2007*b*; Franklin, 2005). This makes AENP one of the best examples of how important these remaining areas are as reserves for species' management, movement and survival.

1.3.1 Predator-prey interaction within AENP

Although warthogs are normally diurnal species, they may switch to a nocturnal lifestyle in areas where they are disturbed by humans (Mgqatsa, 2010; Nyafu, 2009; Somers & Penzhorn, 1992). They sleep and rear young ones in abandoned aardvark (*Orycteropus afer*) burrows and when threatened by predators, run and take refuge in the nearest vacant burrow. Such burrows can act as a refuge and may have numerous effects on species dynamics (Mgqatsa, 2010; Nyafu, 2009). On the other hand, buffaloes like any other mammalian herbivores feed for a high proportion of the time i.e., day and night, and form cohesive groups as a defensive mechanism against predators (especially lions) (Tambling *et al.*, 2011; Prins, 1996).

The lion is the largest African carnivore and a principal predator of various herbivore species (Lehmann *et al.,* 2008; Hayward *et al.,* 2007*a*; Hayward & Kerley, 2005). Adult males are larger (average weight of 230 kg) than adult females (average weight of 160 kg) and are distinguishable by manes of long hair. Lions are distinctly sociable, living in prides of 6 to 12 individuals which are powerful and capable of pulling down prey the size of buffalo and giraffe (*Giraffa cameleopardis*). The size of the lion's territory, whose boundaries are marked regularly with urine and faeces, depends on prey availability (Ravnsborg, 2004; Scheel, 1993; Schaller, 1972). Roaring advertises a lion's presence within territories ranging between $20-400$ km^2 (Schaller, 1972). Lions hunt particularly in the early morning, late afternoon and during the night. Despite sleeping for most of the time, a lion spends its active time on two kinds of activities: searching for prey and prey handling which involves stalking, attacking, capturing and subduing/digesting (Lehmann, 2008). The consumption rate of a lion is limited in such a way that even if prey are so abundant that no time is needed for searching, a lion still needs to spend time on prey handling (Lehmann, 2008). On a full stomach, a lion can go 4 days quite comfortably without having to hunt again (Lehmann, 2008; Mills & Shenk, 1992).

The lions and spotted hyaenas are the largest members of Africa's predator guild that competes for a limited food resource base within most game parks. Their high degree of preferred and dietary overlap has led their competition to be termed as *"the battle of the giants"* (Hayward, 2006; Hayward & Kerley, 2005). However, at very low densities, competition may be minimal as the probability of encountering a competitor also becomes very small. As a common strategy to minimise kleptoparasitic and agonistic interactions from competitively dominant conspecifics, lions opt for differing favourable activity patterns (Hayward & Hayward, 2006).

Six lions and eight unrelated spotted hyaenas from two separate clans were introduced to AENP in late 2003 to fulfill the role of restoring the natural balance (ecological integrity) to the ecosystems in the park by controlling the numbers of herbivores (Wentworth *et al.,* 2011; Hayward & Hayward, 2006) and maximizing ecotourism (Hayward *et al.,* 2007*b*). For quite a long period, this role had been ecologically compromised due to the absence of a large predator other than the leopard. Basing on predation increase, it was hypothesized that the post-lion/hyaena warthog population in AENP main camp would differ from the pre-lion/hyaena introductions (Mgqatsa, 2010).

Prey is hunted by stalking until the lions are close enough to pounce without it being able to get far by running. Female lions hunt more than the males and they are more successful at hunting, partly due to their better camouflage and patience. The full dark manes expose mature male lions and are often seen by their prey from long distances (Schaller, 1972). Despite this limitation, males are very capable of hunting and often join the hunt that involves large prey such as buffalo, rhinoceros and young elephant where extra weight and power is needed to pull down such prey species (Packer *et al.,* 2001; Scheel, 1993; van Orsdol, 1984; Schaller, 1972).

Though lions eat any mammal they come across, the majority of a lion's diet comes from medium- to large-sized herbivorous mammals (Hayward & Kerley, 2005; Ravnsborg, 2004; van Orsdol, 1984). A big male lion will very easily eat 20 kg (10% of its own body mass) of meat. The most common prey include: buffalo, zebra (*Equus burchelli*), blue wildebeest, gemsbok (*Oryx gazelle*), hartebeest, warthog, kob (*Kobus kob*), impala (*Aepyceros melampus*) and Thomsons gazelle (*Gazella thomsoni*) (Hayward *et al.,* 2007*a*; Lehmann *et al.,* 2008; Mills & Shenk, 1992). The choice of preferred prey species depends on their nutritional value besides other ecological constraints, such as prey density (abundance), temporal and spatial distribution, defenses and anti-predator tactics, size, vigilance and habitat cover which differ throughout the predator's geographical distribution (Hayward & Kerley, 2005). As long as a predator can increase its survival chances or reproductive success by hunting more efficiently, natural selection will always favour efficient, optimally foraging predators.

The lion preferentially prey upon species within a weight range of $190 - 550$ kg but the most preferred weight of lion prey being 350 kg (Hayward & Kerley, 2008; Hayward *et al.,* 2007*a*). The mean mass of significantly preferred prey species is 290 kg and of all preferred species is 201 kg (Hayward & Kerley, 2005). Gemsbok, buffalo, blue wildebeest, giraffe and zebra are significantly preferred. Species outside the preferred weight range are generally hunted less than predicted. Species within the preferred weight range that are not significantly preferred (such as eland, roan and sable antelope) generally have features that reduce predation either morphologically (e.g., sable horns), ecologically (e.g., roan antelope and sable occurring at low density), or behaviourally (e.g., the large herd size and increased vigilance of eland) (Hayward, 2011; Hayward & Kerley, 2005). Warthog are below the preferred weight range yet are taken in accordance with their availability and this is probably due to their *sympatry* with the lion, their relatively slow evasion speed and their lower level of vigilance (Hayward & Kerley, 2005).

1.4 Statement of the problem

Historically, many grassland regions and African savanna biome supported a great number of wild animal species. The populations of most of these species have over the past years suffered tremendous declines because of human settlement and activities (Mgqatsa, 2010; Nyafu, 2009; Harrington *et al.*, 1999). As a remedy, species have been confined in closed systems (fenced game reserves) for their management (SANParks, 2006; Urquhart *et al.*, 1997). This prevents migratory movements of herbivore and ungulate species and potentially allows predators to benefit from a *"captive"* prey resource (Fryxell *et al.*, 1988).

Threatened prey species have been placed at risk through inadequate knowledge of predator-prey relationships within game reserves (Lehmann *et al.*, 2008; Hayward *et al.*, 2007*b*; Hayward & Hayward, 2006; Hayward & Kerley, 2005; Harrington *et al.*, 1999). For example, within the closed system of AENP, despite the availability of hypothetical guidelines, species are managed with uncertainty of their threshold populations and the carrying capacity of the park (Hayward *et al.*, 2007*d*; SANParks, 2006; Kerley & Boshoff, 1997).

Understanding the population dynamics of predator-prey interaction involving dispersal of species in game parks is paramount in order to avoid extinction of vulnerable species. In this study, models representing the dynamics of a population and how it reacts to various predation scenarios combined with functional responses have been formulated and analysed. Population thresholds have been considered in order to determine the necessary conditions for maintaining populations at low densities without extinction. Establishment of predation thresholds for survival of endangered prey species in parameter space has been carried out. Such information is essential for the development of management strategies aimed at averting population declines and/or extinction.

1.5 Objectives of the study

1.5.1 General aim

Formulating ecologically plausible mathematical models that establish management strategies of the principal predators and their prey.

1.5.2 Specific objectives

(a) To determine appropriate conditions necessary for maintaining populations of interacting species at low density without extinction.

(b) To determine the impact of prey reserve capacity on the predator-prey dynamics.

(c) To analyse the dynamics of the predator-prey model when additional food is provided to predators.

(d) To establish the effect of predator density-dependent dispersal of prey on stability of a predator-prey system.

1.6 Justification for the study

The problem of declining populations of wild animal species without clearly explained scientific causes is a major concern to managers in most game reserves. There is a need to assess the potential factors that may play a role in the decline of the populations within game parks (Tambling & Du Toit, 2005). In their study, Tambling & Du Toit (2005) acknowledge that by excluding the interacting influences of drought, disease and competition, they might have missed some additional factors contributing to the wildebeest population decline. For sustainable management, species introduction in AENP needs to be carefully studied and evaluated.

1.7 Scope of the study

Models that mimic, predict and explain mathematically the feeding dynamics between two predators (lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*)) and three of their common prey (buffalo (*Syncerus caffer*), warthog (*Phacochoerus africanus*) and kudu (*Tragelaphus strepsiceros*)) are formulated. These species are available in varying densities in most of African savannas and in many grassland regions (Hayward *et al.*, 2007*a*; Hayward *et al.*, 2007*b*; Fay & Greef, 2006; Tambling & Du Toit, 2005; Harrington *et al.*, 1999; Mills & Shenk, 1992).

Data about predation and other dynamics concerning the selected species has been obtained from literature and through direct discussions/interviews with various researchers in AENP. The obtained data have been used to refine the model and to estimate the range of crucial parameters. This has been achieved through computer simulations and qualitative analyses of the formulated mathematical models.

1.7.1 A schematic diagram for the study

The schematic model of Figure 1.1 shows the mental map that is used as a guide through the different model formulations. Additional food to predators, prey refuge, species dispersal (diffusion) and other vital dynamics are motivated in the respective formulated models.

1.8 Methodology

Density-dependent deterministic models with prey refuge and additional food provided to the predators have been formulated and analysed. The formulated models which were calibrated using the obtained data, involve reaction-diffusion partial differential equations (PDEs), and autonomous and non-autonomous systems of ordinary differential equations (ODEs).

Computer simulations using software packages (MatLab, Maple, Scientific Workplace and Mathematica) and qualitative analyses have been used in analysing the models so as to determine equilibrium points, analytic solutions, periodicity and to quantify the stability conditions for the steady states of the ecosystem containing the modelled interacting species. Applying the techniques of nonlinear dynamics in analysing stability and using computer simulations have enabled the author to determine vital parameters that play a major role in the dynamics of the formulated models (sensitivity analysis).

1.9 Structure and format of the presentation

This thesis is presented in six chapters as follows: In Chapter 1, the background to the study, statement of the problem, objectives, justification and scope of the study are presented. A literature review is carried out in Chapter 2 where the importance of wildlife management and modelling in ecosystem management are highlighted. In Chapter 3, derivation of a model that involves a prey out-flux dilution effect and group defense is done, and this model is qualitatively and numerically analyzed to study the dynamics of one predator against two prey. Additional food to predators and prey refuge are incorporated in the model of Chapter 3 and numerically studied further in Chapter 4

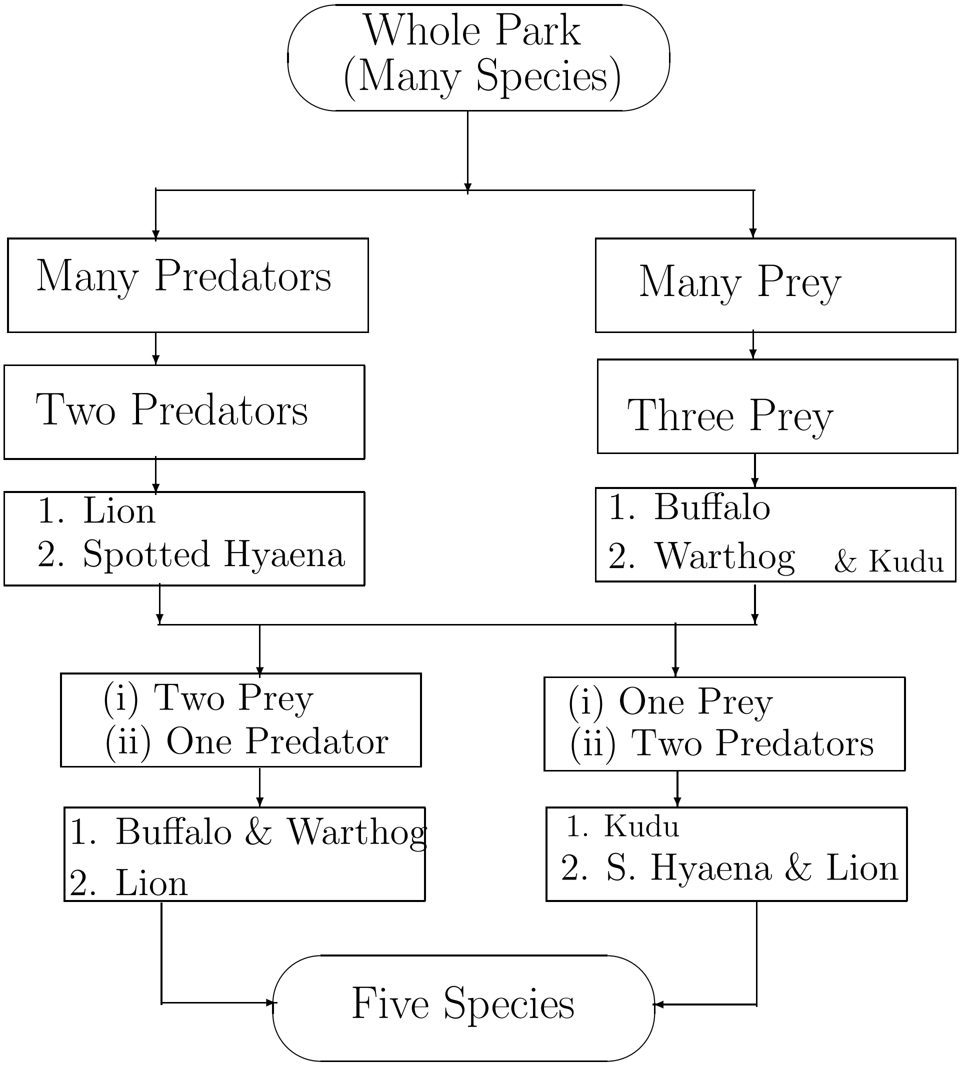

Figure 1.1: *A compartmentalised model for the predator-prey dynamics of this study.*

for more dynamics. In Chapter 5, a one prey-two predators' model that involves predator interference with additional food to both predators is studied. Stability analysis of the reaction-diffusion model is carried out employing the approach used when analysing a generic reaction-diffusion model (the *Brusselator*) for a tri-molecular chemical reaction, morphogenesis and pattern formation. Numerical simulations of the models are generally carried out using the fourth-order Runge-Kutta method supported by Matlab programming language in Chapters 3, 4 and 5. Though each chapter has a section of discussion and conclusion of results, in the final chapter, the author presents the general concluding remarks about the findings of the study.

Chapter 2

Literature Review/Modelling Motivation

2.1 Introduction

Wildlife management, which is achievable through a thorough understanding of species' dynamics, is an important strategy of averting the continued decline and/or extinction of endangered species. Predator-prey interactions among species has direct and indirect effects on prey population size and distribution (Helfman *et al.*, 1997). Direct effects include immediate mortality or delayed mortality due to injury, whereas indirect effects involve habitat shifts caused by a predator's presence, forcing potential prey to use suboptimal habitats, which affects individual growth and reproduction. In suboptimal habitats, population-level responses that arise from functional and numerical responses become part of the dynamics of the species' interaction. Such population-level responses associated with predation are usually density dependent and vary with the population size of the prey, i.e., density-dependent changes occur when the size of the prey population determines the impact of the predator (Haque, 2009; Seo & Kot, 2008; Hsu *et al.*, 2001).

2.1.1 Predator-prey preferences, intelligence and decision-making

Concern over predation, harvesting and competition of species in ecology has stimulated the development of several mathematical models to help in understanding and explaining the population dynamics of the interacting species (Khan *et al.*, 2004; Berryman, 1992). Gaucel *et al.* (2005)

developed mathematical models to explain invading introduced species in insular heterogeneous environments. In their model, they emphasize the importance of accurate estimates of the predation rate on the different age and sex classes, as well as on demographic parameters of prey populations in determining those species that need to be protected.

Gaucel and Pontier (2005) used mathematical models to explain how predator food preference can change the destiny of native prey in predator-prey systems. The predator-prey system behaviour when the predator population has a strong preference for one of the two age stages of the prey population was described in their model in which they showed how the age structure in the prey population can modify the dynamics of the population under study. The prey preference of the alien predator on either juvenile or adult stages of the native prey population was shown to affect the dynamical behaviour of both native and introduced population densities (Gaucel & Pontier 2005). Such ecological interactions of alien and native species are a common phenomena in areas of species reintroduction, necessitating studies in that regard.

2.2 Mathematical modelling in wildlife management

Though given little attention by mathematical modellers partly due to increased complexity of the mathematical analysis and intractable nature of the solutions, multi-species wildlife ecosystems modelling is increasingly becoming a subject of significant interest in ecological research. The formulation and use of reaction-diffusion, deterministic and stochastic models and their qualitative analyses has been a rich area of research in population biology since the famous Lotka-Volterra model (Haque, 2009). The most crucial components in most recent models have been the spatial distribution (spread) of species and the *"functional response"* (the function that describes the number of prey consumed by a single predator per unit time as a function of prey density) (Liu, 2010; Petrovskii & Li, 2006; Ahn, 2003; Abrams *et al.*, 2000; Holt, 1984; Okubo, 1980; Holling, 1965).

Lotka (1925) and Volterra (1926) independently first proposed a simple deterministic model for the predation of one species by another to explain the oscillatory levels of certain fish catches in the Adriatic (Renshaw, 1991). Their model was built around the simple principle of mass action i.e., conversion of energy from one source to another, plus many other elementary assumptions that were later found to be unrealistic (Murray, 1989).

Despite being unrealistic, the Lotka-Volterra model was able to reveal that simple predator-prey interactions can result in oscillatory behaviour of the populations (Murray, 1989). This is not unexpected because as the population of a prey increases, it encourages growth in its predator. The presence of many predators leads to the consumption of many prey causing the population of the latter to decline and with less food around, starvation dominates the predator. The prey population increases when the population of the predator gets low enough, and such a population cycle pattern of the interacting predator-prey species starts over again (Lotka, 1925). Depending on the studied ecosystem, such oscillations can grow or decay or go into a stable limit cycle oscillation or even exhibit chaotic behaviour, although in the latter case there must be at least three interacting species or the model has to have some decay terms (Volterra, 1926).

Since Lotka-Volterra's famous model of 1926, mathematical models have continued to provide basic insights into predator-prey interactions (Khan *et al.*, 2004; Murray, 1993; Berryman, 1992). Fay and Greef (2006), proposed a model to capture the dynamics of the lion-wildebeest-zebra interaction in Kruger National Park (South Africa) in which the lion predated on the wildebeest and zebras. Starting with a simple model, they showed that by carefully incorporating terms to represent plausible biological aspects such as *logistic* growth with mutualism among wildebeest and zebras, Holling Type II functional response for the lions, seasonal calving of zebras and culling of lions, a model which comes close to fitting available empirical data can be formulated. Despite Fay and Greef (2006) leaving out other possible processes and dynamics of the ecosystem in the formulated model, their approach showed how well formulated mathematical concepts should be incorporated in a model.

From the biological perspective, it may not be easy to find any pair of populations that demonstrate the characteristic properties of Lotka-Volterra prey-predator model, minus basic ecological attributes such as predator saturation, limited predator and prey resources and competition even if the prey is so abundant (Berryman, 1992). In addition, lack of essential growth characteristics such as *logistic* growth in the prey in the absence of the predator renders the model simplistic (Bazykin, 1998; Takeuchi, 1996). As a result, a wide range of modifications of the original model have been presented by researchers, including a diversity of additional factors and relationships described by explicitly assigned functions (Seo & Kot, 2008; Petrovskii & Li, 2006; Hsu, 2005; Khan *et al.*, 2004; Holling, 1965). Some of the additional factors that have been given reasonable attention include: trophic predation function, also known as the functional reaction (response) of the predator to the prey population density (Holling Types of response-Holling (1965) and Beddington-DeAngelis), non-linear (quadratic) dependence of the growth rate of the prey population, competition among prey, mortality of the prey, predator saturation, predator competition for prey, predator competition for other resources other than prey, prey refuge, seasonal variation and dispersal of prey or provision of additional food to predator (Srinivasu *et al.*, 2007; Srinivasu & Gayatri, 2005; Cantrel & Cosner, 2001).

2.2.1 Population threshold phenomena in species: *Allee effects*

The growth and decline of populations in ecosystems and the struggle of species to predominate over each other has been a subject of interest through the ages. While there is still much to be studied in the field of over-crowding, there is more to be demonstrated in the area of under-crowding, its mechanisms and its implications (Courchamp *et al.*, 2008; Courchamp *et al.*, 1999*a*). Though its importance in ecology has been under-appreciated (Kent *et al.*, 2003; Courchamp *et al.*, 1999*a*), knowledge of critical population threshold mechanisms is very relevant to many conservation programmes, where scientists and managers are often seen working with populations that have been reduced to low densities or small numbers. The *Allee effect* describes a scenario in which populations at low densities are affected by a positive relationship between population growth and density, which increases their likelihood of extinction (Dennis, 1989).

The *Allee effect* which is widely considered to be an intraspecific phenomenon can be generated by a shortage of interactions (ranging from strict cooperation to unconscious facilitation) among conspecifics at low density. Such effects occur whenever fitness of an individual in a small or sparse population decreases as the population size or density decreases to very low levels (Courchamp *et* *al.*, 1999*a*). Thus, the *Allee effect* results into a critical population threshold below which populations can become extinct. Predation, mating systems, environmental modifications and social interactions of species are some of the mechanisms hypothesised to cause critical thresholds amongst species (Courchamp *et al.*, 2008; Petrovskii *et al.*, 2005; McCarthy, 1997). Various theoretical studies (Stephens *et al.*, 1999; Courchamp *et al.*, 1999*b*; McCarthy, 1997; Dennis, 1989) have been put up for the purpose of motivating the modelling of weak and strong (demographic and component) population threshold phenomena in ecological interactions, and it is imperative to develop and analyse such models further. This is because, an in-depth understanding of ecological interactions, especially in this era of technological advancement, is essential for species management.

Individuals of many prey species use cooperative strategies to evade or fool predators; they forage together, they join forces to survive unfavourable abiotic conditions and they seek sexual reproduction at the same moment and/or place (Courchamp *et al.*, 2008). When the species are too few or many but sparsely distributed, they suffer from a lack of conspecifics which compromises their fitness. Various studies (Courchamp *et al.*, 2008; Courchamp *et al.*, 1999*b*; Stephens *et al.*, 1999) suggest numerous benefits due to presence of conspecifics which include: predator dilution or saturation, anti-predator vigilance or aggression, cooperative predation or resource defense, social thermoregulation, collective modification or amelioration of the environment, increased availability of mates, increased pollination or fertilisation success, conspecific enhancement of reproduction, and reduction of inbreeding, genetic drift or loss of integrity by hybridisation (Courchamp *et al.*, 2008). The advance knowledge of critical threshold threats in a given population permits the redirection of harvesting pressure towards less threatened populations (Courchamp *et al.*, 2008; Dennis, 1989). Similarly, protection efforts for an endangered species, if proven sensitive to *Allee effects*, should be redefined accordingly. As the causes of decline of many populations still remain a puzzle, a more systematic investigation of potential population thresholds in endangered species is crucial to improve our understanding of their dynamics, as well as efficiently protecting them against formally identified threats (Courchamp *et al.*, 1999*b*).

For a population that grows in accordance with the *logistic* law of population growth, the per capita growth rate is negative above and positive below the carrying capacity, κ. However, in the presence of an *Allee effect*, the species' per capita growth rate decreases below a given population size and becomes negative below a critical population threshold, L_0. When a population displaying this type of population dynamics is driven below the critical threshold, sometimes the low negative per capita growth rate leads to extinction (Dennis, 1989). The *Allee effect* usually saturates or disappears as populations get larger. As observed earlier, low population threshold effects arise from a number of sources such as difficulties in finding mates, social dysfunction and inbreeding depression at low population densities (McCarthy, 1997; Kunin, 1993; Landen, 1987). Thus, *Allee effects* are at the heart of the issues which conservationists and managers have to deal with, not only because they are a potential cause of extinction, but also because they are most likely to occur in populations which have suffered a decline from human activity.

Various studies that incorporate an *Allee effect,* depicting a single population that goes extinct when rare, have been conducted. For example, $\frac{dx}{dt} = rx\left(1 - \frac{x}{\kappa}\right)\left(\frac{x}{\kappa} - \frac{A}{\kappa}\right)$, where A i.e., $0 < A < \kappa$, is the threshold population size below which $\frac{dx}{dt} < 0$ due to *Allee effects* (Lewis & Kareiva 1993; Dennis, 1989). Generally, if the growth rate function $f(x)$, in the *logistic* growth model $\frac{dx}{dt} = xf(x)$, is non-negative and increasing for $0 \leq x(t) \leq \kappa$, then it is called a compensation model. On the other hand, if the growth rate function, $f(x)$, is decreasing for small $x(t)$, then the model is depensation. The model is a critical depensation type if the growth rate function, $f(x)$, is negative for small $x(t)$. The occurrence of compensation, depensation and critical depensation growth models in ecological studies necessitates the following condition in determining and distinguishing them: for compensation $f(x) \geq 0,\ f'(x) \leq 0$ for $0 \leq x \leq \kappa$; for depensation $f(x) \geq 0,\ f''(x) \leq 0$ for $0 \leq x \leq \kappa$, $f''(x) > 0$ for $0 \leq x \leq \kappa^*$ and $f'(x) < 0$ for $\kappa^* < x < \kappa$, which shows that $f(x)$ achieves a maximum at κ^*. On the other hand, the growth curve for critical depensation, $g(x) = xf(x)$ is such that $g(x) < 0$ for $0 < x < L_0$, and $g(x) \geq 0$, for $L_0 \leq x \leq \kappa$, and this results in a decrease of reproduction and survival of smaller populations of species. Such effects usually saturate or disappear as populations get larger i.e., through enhancement of conspecifics (Courchamp *et al.*, 2008; Dennis, 1989). Many causes of such population growth effects, ranging from increasing difficulty of reproduction due to lack of mates to reduced anti-predator vigilance, have been studied and modelled for various species as their population density decreases (Courchamp *et al.*, 2008).

2.2.2 Modelling additional food to predators

Scientific findings reveal that there is an apparent contradiction between empirical observations and theoretical results regarding the role of additional food to predators. Several theoretical models (Harmon, 2003; van Rijn *et al.*, 2002; van Baalen *et al.*, 2001; Holt, 1984) conclude that adding a non-pest alternative prey to a predator-prey system lowers the density of the target prey, and this has been found to contradict empirical data (Harwood & Obrycki, 2005; Holt & Lawton, 1994; Murdoch *et al.*, 1985). For example, the effect of consuming non-pest species on rates of pest predation by a generalist predator is twofold: feeding upon the nutritious food items generally enhances fecundity which leads to their population growth, while on the other hand the presence of alternative prey, especially during times when pest regulation is required, results in reduced levels of pest consumption per individual predator (Harwood & Obrycki, 2005).

The above conflict and counter arguments between theory and empirical results necessitates the development of explicit models that can link theoretical studies and empirical results for a better understanding of the predator-prey dynamics that emanates from providing additional food to a predator (Srinivasu *et al.*, 2007; Gaucel & Pontier, 2005). Such models should address the nature i.e., in terms of nutritional quality, quantity/availability, handling time, of additional food that would yield the required equilibrium levels of the predator-prey system for sustainable management. Since providing additional food is not a stand-alone intervention, but a supplement to the strategy of other measures in ecological management, the practice of feeding predators with food supplements presents a very interesting conundrum for conservation and reserve management (Sabelis & van Rijn, 2005; Harwood & Obrycki, 2005; van Baalen *et al.*, 2001).

2.2.3 Optimizing predator energy intake: The optimal foraging theory

Switching prey types as a function of relative prey density is a common phenomenon in ecological studies that has received considerable attention (Khan *et al.*, 2004; van Baalen *et al.*, 2001; Bhatt *et al.*, 1999; Khan *et al.,* 1998). Different prey occupy different micro-habitats, or require different hunting methods (e.g., solitary or group hunting). This necessitates the predator to focus on a single prey/habitat per unit time. Besides, because the predator forages in a micro-habitat that is most profitable, it suggests that for a rare prey species, a predator does better by foraging in another micro-habitat (or with another method), and hence completely ignoring the rare prey, and as prey becomes more common, then it eventually becomes profitable for the predator to switch and hunt them (Bhatt *et al.*, 1999; Khan *et al.*, 1998; Scheel, 1993).

Owing to habitat and predator/prey size constraints, predators eat only a proportion of what is available and such predator behaviour is best explained and motivated by the optimal foraging theory (Toft, 2005; Krivan, 1998). Animal species feed in a manner that is most efficient in terms of their survival and reproductive success, and because many organisms forage in a way so as to maximize their energy intake per unit time (optimal foraging theory), it shows that foraging is in terms of benefits and costs, i.e., natural selection acts to maximize an individual's benefits relative to costs (Hayward, 2011; Hayward & Kerley, 2005). Predatory species, such as lions, behave in a way that enables them to find, capture and consume food items (prey species) containing the most calories while expending the least amount of time possible in doing so (Hayward, 2011; Hayward *et al.*, 2006).

Many studies have been conducted to model prey preferences for different predators (Wentworth *et al.,* 2011; Hayward & Kerley, 2008; 2005; Hayward, 2006; Scheel, 1993). Considering e as the amount of energy (calories) gained from a prey (food) item, h as the handling time which includes capture, killing, eating and digesting i.e., handling time starts once the prey is spotted, and defining s as the search time for the prey (food) item. Then $\psi = \frac{e}{h+s}$ models the profitability of the prey (food) item. Predators typically eat the most profitable prey (food) types more than would be expected by chance since most profitable prey types always appear in the diet more often than it is encountered in the environment (Wentworth *et al.,* 2011; Scheel, 1993). However, because other prey types exist and may be easier to find and besides, e is not the only nutritional requirement, predators do not eat only the most profitable prey types (Maynard, 1974). Toxin levels in a prey and other essential nutrients in the organism's diets are always important components of a plausible ecological model.

2.2.4 Behavioural response of species: Functional and Numerical responses

While carrying out the central goal of understanding the relationship between predators and their prey, it is imperative for both empirical and theoretical ecologists to examine and investigate the predator's functional responses that have been found to be among the significant components of the predator-prey behavioural responses (Seo & Kot, 2008; Abrams *et al.,* 2000; Berryman, 1992). Studies of population growth or decline and the dynamics of these processes are fundamental for the understanding of the survival or extinction of animal species through time (Fay & Greeff, 2006).

In population dynamics, a functional response of the predator to prey density refers to the change in the density of prey attacked per unit time per predator as the prey density changes (Li *et al.,* 2010; Seo & Kot, 2008). The change in the density of prey attacked and captured per unit time per predator depends on the prey density, prey behaviour and the predator's capability and tactics (Haque, 2009; Beddington, 1975; DeAngelis *et al.,* 1975). Various functional responses are widely used when modelling predator-prey dynamics in ecology (i.e., Holling Type I, II, III and IV, ratio dependent, Beddington-DeAngelis, Michaelis-Menten, Monod-Haldane, Hassell-Varley Type I and II, Watts and Crowley-Martin functional responses) whose choice depends on a variety of factors, among which include, feeding behaviour of the predator, aggressive character of the prey and density of species (Chen *et al.,* 2010; 2008; Cantrell & Cosner, 2001; Hsu *et al.,* 2001; Holling, 1965).

According to Courchamp *et al.* (1999b), predators respond behaviourally to the size and density of prey populations in various ways. For example, individual predators move around in search of denser aggregations or larger populations of prey (aggregative response), predators also eat more if more prey are available to be eaten (functional response) up to a limit, and the predator population too respond to changes in the prey population size or density through changes in their own population size and growth rate (numerical response) (Maynard, 1974). As the prey density decreases, there are fewer prey individuals per predator attack, and this suggests that, each prey individual has a higher probability of being eaten (dilution effect), leading to a component *Allee effect* in predation mortality (Courchamp *et al.,* 2008).

For each prey species, as modelled in accordance to the optimal foraging theory, there is always a search time that is independent of predator density (Jeschke *et al.,* 2008). But rather, this predator search time depends on prey density, i.e., at low prey densities, the predator spends most of the time searching and eats every prey it encounters, whereas, at high prey densities, each new prey item is caught almost immediately, necessitating the predator to spend almost all of its time catching, eating or digesting the prey (Jeschke *et al.,* 2008; Scheel, 1993). The predator chooses those prey species with the highest profitability ($\frac{e}{h+s}$, where e is the amount of energy (calories) gained from each prey item, h being the handling time which includes subduing (capturing, killing, eating and digesting), and searching time, $s = 0$ at high prey density) (Scheel, 1993).

A lion, for example, spends its time on two kinds of activities: searching for prey and prey handling which involves chasing, killing, eating and digesting (Jeschke *et al.,* 2008; Hunter, 1998; Schaller, 1972). The consumption rate of a lion is limited in such a way that even if the prey are so abundant that no time is needed for searching, a lion still needs to spend time on prey handling (Lehmann *et al.,* 2008). According to Holling (1965), the total time, T, spent by a lion searching, s, and handling, h, its prey is modelled as: $T = \tau_s + \tau_h$, whereas the number of prey encountered, N_a=(detectability,ϱ)$\times$(area searched)$\times$(prey density,N) i.e., $N_a = \varrho \times$(area searched)$\times N$ where, area searched=(predator speed)$\times$(sensory diameter)$\times$(time spent searching) i.e., area searched $= sd\tau_s$, which implies that $N_a = \varrho \times (sd\tau_s) \times N$. Furthermore, suppose the prey encounter rate per predator, $m = \varrho sd$, then $N_a = m\tau_s N$, and the time spent searching, τ_s, is found by considering the difference of total time and the total handling time, i.e., $\tau_s = T - \tau_h N_a$, τ_h being the handling time per prey. Combining these models and simplifying yields the prototype Holling Type II behavioural response function, $N_a = \frac{mTN}{1+m\tau_h N}$, and the rate at which the prey is consumed by the predator is modelled by $\frac{N_a}{T} = \frac{mN}{1+hN}$; $h = m\tau_h$ (Inchausti & Ballesteros, 2008; Holling, 1965).

The slope of the response curve tends to zero, as $t \to \infty$, because of the *"confusion"* effects that occur at very high prey density and the variable handling time between individual prey (Seo & Kot, 2008; Fenlon & Faddy, 2006). Furthermore, for a Holling Type II functional response, the curve levels off at high prey densities due to satiation effects i.e., when the predator has simply eaten enough (Maynard, 1974). On the other hand, Holling Type III functional response justifies the existence of a *“search image”,* whereby the predator switches to a prey type when it becomes abundant and thus, at high prey densities, each new prey item is caught almost immediately. According to Holling Type III response function, the predator spends most of the time catching, eating or digesting the prey (Jeschke *et al.,* 2008; Inchausti & Ballesteros, 2008; Fenlon & Faddy, 2006).

2.2.5 The role of prey mimicry: Vigilance and predator detection

Group defense mechanisms amongst prey species which have a tendency of feeding and aggregating in herds is a fascinating ecological behaviour that has been given some attention in ecological research (Fryxell *et al.,* 2007; Khan *et al.,* 1998; Prins, 1996). Various studies show that prey defensive mechanisms help in the following way: predators fear attacking big prey groups and/or prey groups devise patterns of running away from the enemy because a predator gets confused as to which prey to concentrate on while chasing (Prins, 1996). Some prey populations tend to aggregate together to benefit from early warning signs i.e., those which are short tend to forage closer to the tall-sized herds to benefit from the height, while others get warnings from birds since birds are always up in trees (Courchamp *et al.,* 2008). Some get associates or feed closer to the tree-climbers like monkeys, to gain from tree height (far sight) and warnings from the climbers (Amakobe *et al.,* 2006). Depending on the availability of empirical data, the above highlighted prey defensive techniques are among the ecological scenarios necessitating mathematical modelling.

Many studies have considered modelling anti-predator behaviour and group defense mechanisms of numerous prey species (Hsu *et al.,* 2001; Khan *et al.,* 1998; Holling, 1965). The response function used depends on the vigilance, mobility and intensity of prey species in relation to its predators. For example, the group defense of a prey (e.g., buffalo) may be modelled using a response function $f(x) = \frac{\alpha x}{a+x^n}$, where n is a positive integer whose value determines the degree of anti-predator behaviour and group defense. In situations of small prey groups (herds) that are non-migratory in nature due to a fenced ecosystem (e.g., AENP), vigilance, mobility and anti-predator behaviour are lowered. This necessitates modelling group defense using a simplified Monod-Haldane response function, $f(x) = \frac{\alpha x}{a+x^2}$, for which $n \leq 2$ (Cantrell & Cosner, 2001; Holling, 1965).

2.3 Diffusion and species' dispersal: Advection-Reaction diffusion models

Species' dispersal is of twofold, namely: self- and cross-dispersal. During self-dispersal, species tend to move from regions of high concentration of their species, e.g., prey (predators) moving away from patches with abundant prey (predators). On the other hand, during cross-dispersal, prey move away from regions with abundant predators (repulsion effect), while predators move towards regions with abundant prey (attraction effect) (Tyutyunov *et al.,* 2007; Amakobe *et al.,* 2006).

The basic Lotka-Volterra model which investigated the temporal variation of groups of individuals of various species, quantifies the interaction within and between species together with their inorganic environment. However, despite time and space being inseparable coordinates, this model does not take into consideration the spatial variations for the interacting animal species (Okubo, 1980). Most of the studies in mathematical ecology that follow consider only time-dependent scalar models partly due to their ever increasing complexity. Mathematical computations become increasingly more difficult when both space and time are incorporated in the modelled scenarios (Ahn, 2003; Renshaw, 1991). Recent developments in mathematical ecology however show a deviation from the time-dependent ordinary differential equation to partial differential equation models which are handy in understanding ecological situations when population dynamics of organisms are considered in both space and time (Liu, 2010; Pearce *et al.,* 2006; Petrovskii & Li, 2006).

2.3.1 Reaction-Diffusion modelling

As motivated before, there are situations where grappling with the detail of dispersal and spatial distribution cannot be avoided. The use of partial differential equations, which describe the changes in population density with respect to both space and time, has found a wide application in such situations (Ahn, 2003; Zauderer, 1989; Okubo, 1980). The classical approach to modelling ecological systems is oversimplified by ignoring space, yet space and time are inseparable *"sister"* coordinates (Okubo, 1980; Renshaw, 1991).

Among the first models to consider both space and time to describe movement of organisms is the Fisher's prototype reaction-diffusion equation (Fisher, 1937), which is a one-dimensional version as a model for the spread of an advantageous gene in a population, $\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + ku(1-\frac{u}{K})$, where $u(t,x)$ is the vector of population densities at spatial position, $x \in \Omega \subset \mathbb{R}$, in time t, and $f(x,t) = ku(1-\frac{u}{K})$ is a function representing logistic growth of population u. The term, $D\frac{\partial^2 u}{\partial x^2}$, defines the random diffusion of the gene within the population u and D, is the diffusion coefficient which in practice is measured in laboratories using some fairly simple experiments (Okubo, 1980). Fisher's equation is an initial-boundary value problem requiring both an initial population density $u(x,0)$, together with boundary conditions.

2.3.2 Initial-boundary value problems in closed regions

Temporal population size variations are basically influenced by two different mechanisms: (i) one associated with local processes such as birth, death, predation etc, and (ii) the other associated with the redistribution of the population in space due to random motion of its individuals. Without loss of generality, various studies describe the rate of change of population size using the following model equation (Petrovskii & Li, 2006):

$$\frac{\partial}{\partial t}\int_{\Omega} u(\bar{\mathbf{x}},t)d\Omega \quad = \quad -\int_{\Gamma} \mathbf{J}\cdot\hat{\mathbf{n}}d\Gamma + \int_{\Omega} F(u(\bar{\mathbf{x}},t))d\Omega \tag{2.1}$$

where $\mathbf{J}$ is the population flux density through the boundary $\Gamma \subset \mathbb{R}^{n-1}$ enclosed by an arbitrary region $\Omega \subset \mathbb{R}^n$, $\hat{\mathbf{n}}$ is the outward-pointed unit vector normal to the boundary and $\mathbf{J}\cdot\hat{\mathbf{n}}$ is the scalar product. The second term on the right-hand side allows for the local processes, $F(u) = f(u)u$, where $f(u)$ is the per capita growth rate of the species' population (Murray, 1993; Okubo, 1980).

Using the Divergence theorem (Petrovskii & Li, 2006; Murray, 1993; Okubo, 1980), the flux term is replaced as follows:

$$\int_{\Gamma} \mathbf{J}\cdot\hat{\mathbf{n}}d\Gamma = \int_{\Omega} \nabla\cdot\mathbf{J}d\Omega$$

then equation (2.1) reduces to

$$\int_{\Omega}\left[\frac{\partial}{\partial t}u(\bar{\mathbf{x}},t) + \nabla\cdot\mathbf{J} - F(u(\bar{\mathbf{x}},t))\right]d\Omega \quad = \quad 0 \tag{2.2}$$

Since the region Ω is arbitrary, and assuming that the integrand is continuous, the integrand vanishes resulting in the inhomogeneous parabolic equation:

$$\frac{\partial}{\partial t} u(\bar{\mathbf{x}}, t) = -\nabla \cdot \mathbf{J} + F(u(\bar{\mathbf{x}}, t)) \tag{2.3}$$

in two or more dimensions that are generally solved numerically or

$$\frac{\partial}{\partial t} u(x, t) = -\frac{\partial J}{\partial x} + F(u(x, t)) \tag{2.4}$$

in one dimension that could be analytically tractable.

The flux $\mathbf{J}$ is modelled as (cf. Kot, 2001):

- Advection/Migration

  $$\mathbf{J} = \mathbf{v}(\bar{\mathbf{x}}, t) u$$

  where $\mathbf{v}(\bar{\mathbf{x}}, t)$ represents a velocity.

- Diffusion/Dispersal

  $$\mathbf{J} = -D \nabla u$$

  is a diffusive flux with D, the diffusion coefficient, also known as Fick's second law.

In the case where $F(u(\bar{\mathbf{x}}, t)) = 0$, the equation represents the heat or diffusion equation, namely;

$$\frac{\partial u}{\partial t} = -\nabla \cdot \mathbf{J} = \nabla \cdot D \nabla u$$

and if the diffusion coefficient is constant, then for a single species model in three dimensions;

$$\frac{\partial u}{\partial t} = D \nabla^2 u$$

Without loss of generality, the corresponding model for any two interacting species is as follows;

$$\begin{aligned} \frac{\partial u}{\partial t} &= D_u \nabla^2 u + F_u(u, v) \\ \frac{\partial v}{\partial t} &= D_v \nabla^2 v + F_v(u, v) \end{aligned}$$

where D_u and D_v are the diffusion coefficients for each species and F_u and F_v, the species interaction terms. If there is both random movement (animal dispersal) and advection (species invasion) then the flux could be modelled as a combination of the above equations resulting in a Burger's type equation. Finally, in order to obtain a *unique* solution, both initial and boundary conditions must be applied to the partial differential equations above.

Despite the profound impact existing studies have had in the discipline of mathematical modelling as eulogised in the literature, there are still more and more challenges in ecosystem ecology. For example, mechanisms for threshold populations, diffusion due to migration and dispersal of species, effectiveness of species' refuges and biological control through provision of additional food are some of the anticipated challenges in predator-prey systems that necessitate extension of existing findings to new levels (Courchamp *et al.*, 2008; Srinivasu *et al.*, 2007; Srinivasu & Gayatri, 2005). This may even be more fascinating due to the current advances in computer software and technology. Therefore, there is a need for one to conceive, formulate and analyse mathematical models that incorporate such pertinent issues.

Chapter 3

Modelling predator fertility, prey threshold and out-flux dilution effect

3.1 Introduction

In this chapter, the interaction of two common prey species (Cape buffalo and warthog) and their common predator (lion), within AENP in the Eastern Cape Province of South Africa, is considered (Hayward *et al.*, 2007*a*; Hayward & Kerley, 2005). Although buffalo and warthog are the potential prey species with different defensive mechanisms, they are equally likely to be preyed upon by the lion within AENP (Hayward *et al.*, 2007*a*). This renders effective comparison of their dynamical behaviour. AENP is a relatively small, approximately 1650 km^2, managed ecosystem containing species at low population densities which makes population threshold, predator fertility rate and carrying capacity vital parameters for this study. Besides other sources, Addo's main camp section, which is approximately 132 km^2 and containing the lions, is the main source of the data for model validation (Wentworth *et al.*, 2011; Hayward *et al.*, 2007*c*).

The desert warthog, also known as the Cape warthog (*Phacochoerus aethiopicus*) once existed and thrived in the Eastern Cape but rapidly disappeared and eventually became extinct during the mid 1800s (Mgqatsa, 2010). Despite unclear and considerable speculated reasons for its extinction, the warthog is an obligate cooperative breeder which is subject to a critical group size below which the group would very likely go extinct. The common warthog species (*Phacochoerus africanus*) was introduced by conservation managers to Eastern Cape game parks (Andries Vosloo Kudu Reserve in 1976 and AENP in 1995) (Nyafu, 2009). Due to a very high fecundity capacity and resistance to African swine fever, warthogs have been able to recover from all population regulation attempts (Mgqatsa, 2010; Nyafu, 2009; Somers & Penzhorn 1992). Besides living a diurnal life: promiscuity, allomothering, possession of functional incisor teeth in the upper jaw and living in self-excavated or disused aardvark burrows, are some of the other factors that have helped the common warthog to expand both its population and range (White & Cameron, 2009; Nyafu, 2009). The salient factors that influence the warthog's population fluctuations have not been adequately elucidated in different environments (Somers & Penzhorn 1992).

The common warthog, which is the most wide-spread extant wild pig species in Africa, occurs practically everywhere in Africa, except in arid regions and in tropical forests (Muwanika *et al.*, 2003). The spread of warthogs in the Eastern Cape exhibits characteristics of an invasive species. They are perceived as a pest by many farmers due to the severe impact they have on grass cover, soil and fences (Nyafu, 2009; Somers & Penzhorn 1992). Warthogs open holes in fences through which they escape along with other game. Landowners and stock farmers within the Eastern Cape Province shoot on sight most warthogs that frequently escape through fences of their confinements (Mgqatsa, 2010) and yet for many warthogs, individual survival is enhanced by a propensity for cooperation, warthogs being facultative cooperative breeders, which outweighs competition and aggression (White & Cameron, 2009; Courchamp *et al.*, 1999*b*). This continued high desire to spread out and expand its range creates an out-flux in the warthog population which can lead to an *Allee effect* (Sherratt *et al.*, 1997). Such population out-fluxes and emigration, if not well studied and reduced, create a sparsely distributed large population which becomes vulnerable and susceptible to critical population threshold threats (Courchamp *et al.*, 2008; Dennis, 1989).

Activities, behaviour and movement of prey species lead to their encounters with numerous predators within the ecosystem. Buffaloes, for example, when encountering lions adopt a variety of anti-predator responses (Tambling *et al.*, 2011; Prins, 1996). Being formidable animals, buffaloes are able to protect themselves against large cats, much better than for example bisons (Prins, 1996).

Lions and buffalo interactions often result in the buffalo chasing lions into deep cover or even up the trees. Sometimes lions are even killed or get severely wounded only to die a few days later (Prins, 1996). Most individual lions refrain from contributing to group hunts except when pursuing buffaloes, which are inaccessible to solitary individual lions (Fryxell *et al.*, 2007; Hayward *et al.*, 2007*a*, *b*; Hayward & Kerley, 2005). Besides a variety of autecological features, the hunting success of lions is also affected by both biotic and abiotic factors (Hayward *et al.*, 2007*a*). Studies have considered a variety of approaches to model anti-predator behaviour and group defense mechanisms of numerous prey species (Seo & Kot, 2008; Khan *et al.*, 2004; Cantrell & Cosner, 2001). The response function used generally depends on the vigilance, mobility and intensity of prey species in relation to the predators.

Despite buffalo herd formation being generally influenced by predation risk (Tambling *et al.*, 2011), habitat, season and food availability also have a significant effect on buffalo herd size formation (Vale, 2007). For example, in dense thicket and forest vegetation, buffaloes split into small family groups of 6-15 individuals, whereas in open savannah woodland, family groups converge into mass herds (Vale, 2007). Furthermore, during the dry season, buffaloes disperse to look for scarce food items and during wet season form massive cohesive herds, suggesting that most lion predation on buffalo takes place during the dry season (Tambling *et al.*, 2011; Prins, 1996). In this study, the buffalo group defense was modelled using a response function $f(B) = \frac{\alpha B}{1+hB^n}$, where n is a positive integer whose value determines the degree of anti-predator behaviour and group defense. The small buffalo herds and the non-migratory nature of the buffalo due to a fenced ecosystem of AENP lead to low vigilance, mobility and anti-predator behaviour i.e., predation is more likely to occur to a *"captive"* prey resource (Fryxell *et al.*, 1988) and as a result, $n \leq 2$ (Holling Type II response function) was considered.

Threatened prey species are always placed at risk through inadequate knowledge of predator-prey relationships within game reserves (Lehmann *et al.*, 2008; Hayward *et al.*, 2007*b*; Hayward & Hayward, 2006; Hayward & Kerley, 2005; Harrington *et al.*, 1999). For example, within the closed system of AENP, despite the availability of hypothetical guidelines, species are still being managed at low population levels with uncertainty of the threshold populations of various species and carrying capacity of the park (Hayward *et al.*, 2007*c*; Hayward *et al.*, 2007*d*). A mathematical model for analysing the prey threshold density within AENP has been formulated.

The rest of this chapter constitutes: an explanation of the meaning of variables, constants and parameters, and the underlying assumptions. Model formulation together with non-dimensionalisation is provided. In addition, existence and stability of the steady states of the model are analysed by exploring local asymptotic stability of all steady states using the method of linearisation. Global stability of the interior equilibrium is investigated via a suitable Lyapunov function. Numerical results are given followed by a brief discussion and conclusion of results.

3.2 Description and formulation of the model

A mathematical model that incorporates *logistic* growth of one prey and *Allee effect* in the other is formulated. The model considers the two common prey species (Cape buffalo (*Syncerus caffer*) and the common warthog (*Phacochoerus africanus*)) and one predator (lion (*Panthera leo*)) within AENP. In the model, the variables $B(t), W(t)$ and $L(t)$ represent the population biomass of the buffalo, the warthog (first and second prey) and the lion (predator), respectively, at time t.

The carrying capacity of the ecosystem for buffalo and warthog are K_b and K_w, respectively, while ϖ is the sparsity constant which models the threshold (critical) population density below which warthog population declines. In the absence of predation, buffalo and warthog populations grow with intrinsic rates r_1 and r_2, respectively. Naturally the predator dies at a rate μ_1 (natural mortality rate), α_i is the rate at which the predator attacks and consumes the prey, β_1 is the efficiency of converting warthog biomass into lion biomass and ϵ_u being the efficiency of converting buffalo biomass into lion biomass (β_1 and ϵ_u are fertility constants). Finally, $\frac{1}{h}$ is the half saturation (satiation) constant of the predator.

Though sparsely distributed because of their expanded range, warthogs are abundant and can easily be captured and eaten by a single lion without too much searching, stalking and with less handling time. In the case of buffaloes, however, besides the handling time per species killed, it requires at least three to four lions to search, stalk and bring down a buffalo (Hayward & Hayward, 2006; Packer *et al.*, 2001; Hunter, 1998). Thus, the predation behaviour of the predator was modelled using a Holling Type I and II response functions for warthog and buffalo, respectively.

The Main Camp section, 132 km^2, of AENP has a substantial number of the species considered for this study (Tambling *et al.*, 2011; Mgqatsa, 2010; Hayward & Hayward, 2006). Most of these species were reintroduced to AENP through game translocation programmes which were aimed at restoring ecological integrity, conserving threatened species and maximising tourism (Wentworth *et al.,* 2011; Hayward *et al.*, 2007*c*). Low population densities of these species render their social group behaviour (buffalo herds, lion prides and warthog sounders are all very small) negligible. The choice of the prey species for this study is due to predator's preferential causes like: herding, easy to capture, abundance, biomass gain per prey killed, taste, hunting risks involved, total handling time and searching effort (Hayward *et al.*, 2007*a*; Hayward & Kerley, 2005; Khan *et al.*, 2004).

According to Hayward *et al.* (2007*a*), it is energetically inefficient for lions to prey upon rare and/or small species compared to abundant and/or larger prey. Based on the *"preference index"* i.e., $\rho = 0.94$ in 1960s and $\rho = 0.91$ in 1980s for Lake Manyara National Park, which is calculated as the proportion of a species being killed divided by the proportion of the same species in the population, lions appear to prey on buffalo in accordance with the relative abundance of the latter in an area (Prins, 1996). The non-exceptional conditions under which buffaloes in AENP live imply that they experience approximately the same risk as those in other populations in Africa. Since the lion population is sufficiently small within AENP (Hayward & Hayward, 2006), predator intraspecific interference does not arise. Despite wildlife managers being sensitive to the sex ratios of the species, studies on solitary predators or groups or sex of animals are still scanty (Hayward, 2006; Hayward & Kerley, 2005).

Using the definitions of the variables and parameters together with the assumptions and management approaches, the temporal dynamics of a predator-prey system is described by the following system of coupled differential equations in which the hard-to-capture prey (buffalo) is *"damped"* by a *logistic* effect while the easy-to-capture prey (warthog) is *"damped"* by an *Allee* effect. In both cases, prototype per capita growth rates of the prey are assumed. The equations of the system are:

$$\frac{dB}{d\tau} = r_1 B\left(1-\frac{B}{K_b}\right)-\alpha_1\frac{BL}{1+hB} \tag{3.1}$$

$$\frac{dW}{d\tau} = r_2 W\left(1-\frac{W}{K_w}\right)\left(\frac{W}{\varpi}-1\right)-\alpha_2 WL \tag{3.2}$$

$$\frac{dL}{d\tau} = \beta_1 WL+\epsilon_u\frac{\alpha_1 BL}{1+hB}-\mu_1 L \tag{3.3}$$

where;

- All parameters are positive constants and the searching efficiency for the predator is embedded in predation rate, α_1.
- In general, for any warthog critical threshold population values, $0<\varpi<K_w$ (i.e., strong and weak critical thresholds). In the presence of Allee effect mechanisms, some of the threshold parameters are off-set to extremely low values that cause the per capita growth rate, $\frac{dW}{d\tau}$, to decrease below a given population size, and can even become negative below a critical population threshold (ϖ). When a population displaying this type of population dynamics is driven below the critical threshold, the low, sometimes negative, per capita growth rate may lead it to extinction (Courchamp *et al.*, 1999*a*; Courchamp *et al.*, 2008).
- $B(0)\geq 0,\ W(0)\geq 0$ and $L(0)\geq 0$.

3.3 Qualitative analysis of the model

3.3.1 Non-dimensionalisation of the model

In order to avoid mathematical complexity and for easy analysis of the model, reduction of the number of parameters is achieved by introducing the following dimensionless variables:

$$x=\frac{B}{K_b},\quad y=\frac{W}{K_w},\quad z=\frac{\alpha_1}{\mu_1}L,\quad t=\mu_1\tau$$

resulting in the following non-dimensionalised model:

$$\frac{dx}{dt} = rx(1-x) - \frac{xz}{1+\phi x} \equiv \hat{f}(x,z) \tag{3.4}$$

$$\frac{dy}{dt} = \lambda y(1-y)(ky-1) - \alpha yz \equiv \hat{g}(y,z) \tag{3.5}$$

$$\frac{dz}{dt} = \beta yz + \gamma\frac{xz}{1+\phi x} - z \equiv \hat{h}(x,y,z) \tag{3.6}$$

whose behaviour is controlled by the following dimensionless parameters:

$$r = \frac{r_1}{\mu_1}, \quad \lambda = \frac{r_2}{\mu_1}, \quad \phi = hK_b, \quad k = \frac{K_w}{\varpi}, \quad \alpha = \frac{\alpha_2}{\alpha_1}, \quad \beta = \frac{\beta_1 K_w}{\mu_1}, \quad \gamma = \frac{\epsilon_u \alpha_1 K_b}{\mu_1}$$

Since the variables x, y and z define population densities, only non-negative solutions make biological sense. It can be verified that the region $\tilde{\Upsilon} = \{(x,y,z) \in \mathbb{R}^3_+ : x \geq 0,\ y \geq 0, \text{ and } z \geq 0\}$ is positively invariant with respect to system (3.4-3.6), where $\mathbb{R}^3_+$ denotes the non-negative cone of $\mathbb{R}^3$ including its lower dimensional faces. Thus, system (3.4-3.6) is bounded.

A qualitative analysis of the model which is crucial in understanding the underlying interaction dynamics of different species for their management is explored. This is carried out by considering the simplified non-dimensionalised system (3.4-3.6), whose steady states are given by; $E_0(0,0,0)$, $E_1(1,0,0)$, $E_2(0,1,0)$, $E_3(1,1,0)$, $E_4\left(0,\frac{1}{k},0\right)$, $E_5\left(1,\frac{1}{k},0\right)$, $E_6\left(0,\frac{1}{\beta},\frac{\lambda(1-\beta)(\beta-k)}{\alpha\beta^2}\right)$, $E_7\left(\frac{1}{\Phi},0,\frac{r\gamma(\Phi-1)}{\Phi^2}\right)$ and $E_8(x^*,y^*,z^*)$ where $\Phi = \gamma - \phi$. It should be noted that when $k=1$ ($K_w = \varpi$); E_2, E_3, E_4 and E_5 reduce to only two steady states. Such a peculiar occurrence of equilibrium points is investigated further and explicitly explained in the analysis.

3.3.2 Conditions for non-negativeness and existence

Since interest is in the growth of biological species, the equilibrium points of the system must satisfy non-negativity conditions. It should also be noted that the predator cannot survive in the absence of its prey. The unconditional existence of equilibrium states $E_0(0,0,0)$, $E_1(1,0,0)$, $E_2(0,1,0)$, $E_3(1,1,0)$, $E_4\left(0,\frac{1}{k},0\right)$ and $E_5\left(1,\frac{1}{k},0\right)$ necessitates the establishment of the existence of the rest.

Non-negativity and existence of $E_6\left(0, \frac{1}{\beta}, \frac{\lambda(1-\beta)(\beta-k)}{\alpha\beta^2}\right)$ and $E_7\left(\frac{1}{\Phi}, 0, \frac{r\gamma(\Phi-1)}{\Phi^2}\right)$

For the existence of $E_6,$ either $\beta < 1$ and $k < \beta$ or $\beta > 1$ and $k > \beta$, where $\beta = \frac{\beta_1 K_w}{\mu_1}$ and $k = \frac{K_w}{\varpi}$ is the ratio of warthog's carrying capacity to its critical threshold density. Different interpretations of the parameter β have been identified (cf. Bazykin, 1998; Takeuchi, 1996): first $\frac{1}{\beta}$ is the stationary population density of the warthog population co-existing with the lion, it is also natural to define $\frac{1}{\beta}$ as a measure of how well the lion adapt to the warthog. The lower the density of warthog that should ensure an equilibrium existence of the lion, the better the lion gets adapted to the warthog. Further, $\frac{1}{\beta}$ should be interpreted as a measure of the lion's mortality, i.e., $\frac{1}{\beta}$ is a quantity that decreases when the lion becomes more adapted. Both k and β are vital parameters for the warthog-lion co-existence equilibrium. Existence of E_6 shows that either $K_w < \frac{\mu_1}{\beta_1} < \varpi$ for which the warthog threshold density is maintained above the carrying capacity, or $\varpi < \frac{\mu_1}{\beta_1} < K_w$ that depicts a riskier situation (when $\varpi \ll K_w$) for the warthog species. The ratio, $\frac{\mu_1}{\beta_1}$, which should be ecologically interpreted as the effective mortality per capita of lions, is critical for the warthog-lion co-existence equilibrium. The effective mortality per capita ratio for the lions is vital for the model equilibrium E_6, because it regulates both the carrying capacity and lower critical population density for the warthog.

The existence of E_7 is governed by the inequality, $\epsilon_u > \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$, since it controls the conversion efficiency of buffalo biomass to lion biomass (fertility factor). It should be noted that the lion fertility biomass gain from buffalo is regulated by the lion's mortality which is also evident from $\Phi = \gamma - \phi$, which shows that for $\Phi > 0$, $\epsilon_u > \frac{h\mu_1}{\alpha_1}$. Furthermore, the inequality $\epsilon_u > \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$ reveals that as the buffalo carrying capacity, $K_b \to \infty$, $\epsilon_u \to \frac{h\mu_1}{\alpha_1}$. This shows that an increase or decrease in the lion's natural mortality μ_1 results in a greater than proportionate increase or decrease in the fertility factor ϵ_u, for the lion-buffalo co-existence to be maintained at equilibrium.

Non-negativity and existence of $E_8(x^*, y^*, z^*)$

The positive equilibrium point $E_8(x^*, y^*, z^*)$ exists if there is a positive solution to the following set of nonlinear equations obtained from system (3.4-3.6):

$$r(1-x) - \frac{z}{1+\phi x} = 0 \tag{3.7}$$

$$\begin{aligned}\lambda\,(1-y)\,(ky-1)-\alpha z &= 0 \qquad (3.8)\\ \beta y+\gamma\frac{x}{1+\phi x}-1 &= 0 \qquad (3.9)\end{aligned}$$

Theorem 3.3.1 *For some y-intercepts y_f and y_g in the xy-plane, the positive equilibrium point $E_8(x^*, y^*, z^*)$ exists in $\tilde{\Upsilon}$ and is unique for system (3.4-3.6) if and only if $\frac{(k+1)^2}{k} > \frac{4(\alpha r+\lambda)}{\lambda}$ is satisfied and in addition, the following conditions hold;*

$$0 < x < Min\left(1, \frac{\phi-1}{2\phi}\right),\ \phi > 1,\ 0 < y < Min\left(\frac{k+1}{2k}, \frac{1}{\beta}\right)\ \textit{and}\ y_f < y_g.$$

Proof: Using the approach of Dubey and Upadhyay (2004), two functions $f(x, y)$ and $g(x, y)$ which intersect at the equilibrium point $E_8(x^*, y^*, z^*)$, need to be identified. Equations (3.7) and (3.8), respectively, lead to:

$$\begin{aligned} z &= r\,(1-x)\,(1+\phi x) \qquad (3.10)\\ z &= \frac{\lambda}{\alpha}\,(1-y)\,(ky-1) \qquad (3.11)\end{aligned}$$

and equations (3.7) and (3.9) give;

$$z = \frac{r\gamma x(1-x)}{1-\beta y} \qquad (3.12)$$

From equations (3.10) and (3.11), we obtain:

$$f(x, y) = r\,(1-x)\,(1+\phi x)-\frac{\lambda}{\alpha}\,(1-y)\,(ky-1) = 0 \qquad (3.13)$$

while equations (3.10) and (3.12) yield the second function:

$$g(x, y) = r\,(1-x)\,(1+\phi x)-\frac{r\gamma x(1-x)}{1-\beta y} = 0 \qquad (3.14)$$

Both equations (3.13) and (3.14) are two functions of x and y. To prove the existence of $E_8(x^*, y^*, z^*)$, requires conditions under which $f(x, y)$ and $g(x, y)$ intersect in the interior of the positive quadrant at a point (x^*, y^*). Knowledge of (x^*, y^*) implies knowing z^* from equations (3.10-3.12). From equation (3.13), as $x \to 0$, $y \to y_f$, which is defined in the quadratic form:

$$\lambda k y_f^2 - \lambda(k+1)y_f + \alpha r + \lambda = 0$$

$$\Rightarrow \qquad y_f = \frac{-Q + \sqrt{Q^2 - 4PR}}{2P} \tag{3.15}$$

where $P = \lambda k$, $Q = -\lambda(k+1)$ and $R = \alpha r + \lambda$. If $\frac{(k+1)^2}{k} > \frac{4(\alpha r + \lambda)}{\lambda}$, then y_f is real and always positive. Similarly, as $x \to 0$, equation (3.14) shows that $y \to y_g$ given by:

$$y_g = \frac{1}{\beta}. \tag{3.16}$$

Clearly y_g is always positive and real. The functions y_f and y_g are the points at which the functions $f(x,y)$ and $g(x,y)$ would cut the y-axis in the (x,y) plane, respectively. From equation (3.13), we also obtain:

$$\frac{dy}{dx} = -\frac{\partial f}{\partial x} / \frac{\partial f}{\partial y} \quad \text{where } \frac{\partial f}{\partial x} = 2\phi r \left(\frac{(\phi - 1)}{2\phi} - x \right) \text{ and } \frac{\partial f}{\partial y} = -\frac{2k\lambda}{\alpha} \left(\frac{k+1}{2k} - y \right)$$

It is noted that $\frac{dy}{dx} > 0$ if either (i) $\frac{\partial f}{\partial x} > 0$ and $\frac{\partial f}{\partial y} < 0$, which requires; $x < \frac{\phi - 1}{2\phi}$, $\phi > 1$ and $y < \frac{k+1}{2k}$, or (ii) $\frac{\partial f}{\partial x} < 0$ and $\frac{\partial f}{\partial y} > 0$, which similarly requires the converse, i.e., $x > \frac{\phi-1}{2\phi}$, $\phi > 1$ and $y > \frac{k+1}{2k}$. Since $\phi = hK_b$, for the co-existence equilibrium, the buffalo carrying capacity should be greater than the half saturation value for lions i.e., $K_b > \frac{1}{h}$. Similarly, equation (3.14) gives:

$$\frac{dy}{dx} = -\frac{\partial g}{\partial x} / \frac{\partial g}{\partial y} \quad \text{where } \frac{\partial g}{\partial x} = \frac{r}{(1 - \beta y)} \left[(\phi + \phi\beta xy + 2\gamma x) - (\phi\beta y + \gamma + \phi x + 1 + (1 - \beta y)(\phi + x)) \right]$$

and $\frac{\partial g}{\partial y} = -\frac{r\gamma\beta x(1-x)}{(1-\beta y)^2}$

It is further, similarly noted that $\frac{dy}{dx} < 0$ if either (i) $\frac{\partial g}{\partial x} < 0$ and $\frac{\partial g}{\partial y} < 0$, which requires; $\phi\beta y + \gamma + \phi x + 1 + (1 - \beta y)(\phi + x) > \phi + \phi\beta xy + 2\gamma x$ provided $y < \frac{1}{\beta}$ and $x < 1$, or (ii) $\frac{\partial g}{\partial x} > 0$ and $\frac{\partial g}{\partial y} > 0$, which similarly requires the converse, i.e., $\phi\beta y + \gamma + \phi x + 1 + (1 - \beta y)(\phi + x) < \phi + \phi\beta xy + 2\gamma x$, $y < \frac{1}{\beta}$ and $x > 1$. Ecologically, since $x = \frac{B}{K_b}$, the buffalo population density should be less than its ecosystem carrying capacity i.e., $B < K_b$, and with a reverse in the theorem conditions, the converse also holds.

Since for $f(x,y)$, we have $\frac{dy}{dx} > 0$ and for $g(x,y)$, we have $\frac{dy}{dx} < 0$, then $f(x,y)$ and $g(x,y)$ will intersect in the positive quadrant if $y_f < y_g$, and this completes the proof. The existence of an interior equilibrium $E_8(x^*, y^*, z^*)$, implies that the Model system (3.4-3.6) is dissipative and uniformly persistent (Takeuchi, 1996; Butler *et al.*, 1986). The ecological implications of Theorem 3.3.1 in terms of the dimensional parameters of Model system (3.1-3.3) leads to the inequality $\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2 + \alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$, which gives a lower bound for the warthog's critical population density if an interior equilibrium for all the three species is to be attained. It is not accidental or surprising, but rather an ecological reality to have both birth rate of buffalo, predation rates of lion on both buffalo and warthog combined with carrying capacity of warthog as control parameters for threshold density, ϖ for the co-existence of the three species. Such a scenario could arise due to encounters and interactions with numerous species and other environmental constraints as a result of the warthog's high desire to expand its range (White & Cameron, 2009; Nyafu, 2009; Somers & Penzhorn, 1992).

3.3.3 Local stability analysis of steady states

Local stability analysis is considered first due to its explicit nature. Linearisation leads to the following variational/community matrix for system (3.4-3.6):

$$J_{E_i} = \begin{bmatrix} \hat{f}_{x^*} & 0 & \hat{f}_{z^*} \\ 0 & \hat{g}_{y^*} & \hat{g}_{z^*} \\ \hat{h}_{x^*} & \hat{h}_{y^*} & \hat{h}_{z^*} \end{bmatrix}$$

where;

$$\hat{f}_{x^*} = r(1-2x^*) - \frac{z^*}{(1+\phi x^*)^2}, \quad \hat{f}_{z^*} = -\frac{x^*}{1+\phi x^*}, \quad \hat{g}_{y^*} = \lambda[(ky^*-1)(1-2y^*) + ky^*(1-y^*)] - \alpha z^*,$$

$$\hat{g}_{z^*} = -\alpha y^*, \qquad \hat{h}_{x^*} = \frac{\gamma z^*}{(1+\phi x^*)^2}, \qquad \hat{h}_{y^*} = \beta z^*, \qquad \hat{h}_{z^*} = \beta y^* + \frac{\gamma x^*}{1+\phi x^*} - 1$$

Substituting the equilibrium $E_0(0,0,0)$, $E_1(1,0,0)$, $E_2(0,1,0)$, $E_3(1,1,0)$, $E_4(0,\frac{1}{k},0)$, $E_5(1,\frac{1}{k},0)$ and $E_7\left(\frac{1}{\Phi}, 0, \frac{r\gamma(\Phi-1)}{\Phi^2}\right)$ into the community matrix, leads to the following characteristic equations:

E_0;

$$|J_{E_0} - \Lambda I| = \begin{vmatrix} r-\Lambda & 0 & 0 \\ 0 & -\lambda-\Lambda & 0 \\ 0 & 0 & -1-\Lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad (r-\Lambda)(\lambda+\Lambda)(1+\Lambda) = 0$$

E_1;

$$|J_{E_1} - \Lambda I| = \begin{vmatrix} -r-\Lambda & 0 & -\frac{1}{1+\phi} \\ 0 & -\lambda-\Lambda & 0 \\ 0 & 0 & \left(\frac{\gamma}{1+\phi}-1\right)-\Lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad (r+\Lambda)(\lambda+\Lambda)\left(\frac{\gamma}{1+\phi}-1-\Lambda\right) = 0$$

E_2;

$$|J_{E_2} - \Lambda I| = \begin{vmatrix} r-\Lambda & 0 & 0 \\ 0 & \lambda(1-k)-\Lambda & -\alpha \\ 0 & 0 & (\beta-1)-\Lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad (r-\Lambda)(\lambda(1-k)-\Lambda)((\beta-1)-\Lambda) = 0$$

E_3;

$$|J_{E_3} - \Lambda I| = \begin{vmatrix} -r-\Lambda & 0 & -\frac{1}{1+\phi} \\ 0 & \lambda(1-k)-\Lambda & -\alpha \\ 0 & 0 & \left(\beta+\frac{\gamma}{1+\phi}-1\right)-\Lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad (r+\Lambda)\left(\lambda(1-k)-\Lambda\right)\left(\left(\beta+\frac{\gamma}{1+\phi}-1\right)-\Lambda\right) = 0$$

E_4;

$$|J_{E_4} - \Lambda I| = \begin{vmatrix} r-\Lambda & 0 & 0 \\ 0 & \frac{\lambda}{k}(k-1)-\Lambda & -\frac{\alpha}{k} \\ 0 & 0 & \left(\frac{\beta}{k}-1\right)-\Lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad (r-\Lambda)\left(\frac{\lambda}{k}(k-1)-\Lambda\right)\left(\left(\frac{\beta}{k}-1\right)-\Lambda\right) = 0$$

E_5;

$$|J_{E_5} - \Lambda I| = \begin{vmatrix} -r-\Lambda & 0 & -\frac{1}{1+\phi} \\ 0 & \frac{\lambda}{k}(k-1)-\Lambda & -\frac{\alpha}{k} \\ 0 & 0 & \left(\frac{\beta}{k}+\frac{\gamma}{1+\phi}-1\right)-\Lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad (r+\Lambda)\left(\frac{\lambda}{k}(k-1)-\Lambda\right)\left(\left(\frac{\beta}{k}+\frac{\gamma}{1+\phi}-1\right)-\Lambda\right) = 0$$

E_7;

$$|J_{E_7} - \Lambda I| = \begin{vmatrix} A_1-\Lambda & 0 & -A_2 \\ 0 & -\lambda-\alpha A_3-\Lambda & 0 \\ \gamma A_4 & \beta A_3 & \gamma A_2-1-\Lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad \Lambda^3 + a_1\Lambda^2 + a_2\Lambda + a_3 = 0$$

for some computed $a_i's$ and $A_j's$ which are defined later. Local stability of equilibrium point E_6 is handled separately due to the complexity of its analysis.

It is well known, through linearisation, that an equilibrium solution is asymptotically stable if all the eigenvalues of the community matrix have negative or zero real parts and are unstable otherwise (Jordan & Smith, 2007; Hsu *et al.*, 2001; Bazykin, 1998; Hsu & Huang, 1995). The stability analysis of the equilibrium solutions, E_0-E_7 excluding E_6, for system (3.4-3.6) whose community matrix is defined above follows. One of the eigenvalues of the following set of characteristic equations $\{(r -$

$\Lambda)(\lambda+\Lambda)(1+\Lambda) = 0$, $(r-\Lambda)(\lambda(1-k)-\Lambda)((\beta-1)-\Lambda) = 0$ and $(r-\Lambda)\left(\frac{\lambda}{k}(k-1)-\Lambda\right)\left((\frac{\beta}{k}-1)-\Lambda\right)\}$ computed for E_0, E_2 and E_4, respectively, is always positive from which it follows that E_0, E_2 and E_4 are locally unstable equilibria. Instability of such equilibria arises due to lack of conspecifics for a species whose population density is below the threshold levels. This causes the population to move away from equilibrium steady states into other states (extinction region) (Tyutyunov *et al.*, 2007; Bazykin, 1998; Takeuchi, 1996). The characteristic equation $(r+\Lambda)(\lambda+\Lambda)\left(\frac{\gamma}{1+\phi}-1-\Lambda\right) = 0$ of equilibrium $E_1(1,0,0)$ shows that E_1 is stable when $\frac{\gamma}{1+\phi} < 1$ and unstable if $\frac{\gamma}{1+\phi} > 1$. This implies that $E_1(1,0,0)$ is stable when $\epsilon_u < \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$ and unstable when $\epsilon_u > \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$.

The local stability of $E_3(1,1,0)$ is attained if $k > 1$ and $\beta + \frac{\gamma}{1+\phi} < 1$, which is equivalent to $K_w > \varpi$ and $\epsilon_u < \left|\frac{(hK_b+1)(\mu_1-\beta_1 K_w)}{\alpha_1 K_b}\right|$. This reveals that for equilibrium to be locally asymptotically stable, the fertility factor ϵ_u for buffalo-alone equilibrium must be greater than the fertility factor ϵ_u for buffalo-warthog equilibrium. This result provides sufficient evidence for the so-called paradox of enrichment. It coincides with numerous hypotheses (Fryxell *et al.*, 2007; Hsu & Huang, 1995; Butler *et al.*, 1986), which assert that population sizes in many interacting communities are stabilized by predation. Many studies (Tyutyunov *et al.*, 2007; Petrovskii *et al.*, 2005; Bazykin, 1998; Sherratt *et al.*, 1997; Takeuchi, 1996) have hypothesised that predation acts to prevent large oscillations or extinction of prey populations. This is evident from and confirmed by the inequalities regarding the lion-buffalo fertility factor ϵ_u. Furthermore, $K_w > \varpi$ shows that local asymptotic stability of E_3 can still be attained and maintained in the presence of low warthog population densities. This can be achieved through advance knowledge of potential causes of population extinction which can help in setting up good protection and other management policies.

The local stability of $E_5(1, \frac{1}{k}, 0)$, which is also a buffalo-warthog equilibrium state, is similar to that of $E_3(1,1,0)$. Here local stability is possible and attained when the warthog threshold population density is above its carrying capacity i.e., $K_w < \varpi$, and the upper bound for the fertility factor $\epsilon_u < \left|\frac{(hK_b+1)(\mu_1-\beta_1\varpi)}{\alpha_1 K_b}\right|$ is *"damped"* by $\beta_1\varpi$. In comparison, for the local asymptotic stability of E_3, the *"damping"* factor, $\beta_1 K_w$, is applicable to $\epsilon_u < \left|\frac{(hK_b+1)(\mu_1-\beta_1 K_w)}{\alpha_1 K_b}\right|$. In both cases i.e., E_3 and E_5, the *"damping"* terms depend on the carrying capacity and the threshold population values of the warthog species.

The variational matrix $J_{E_6} = [a_{ij}]$ for the equilibrium $E_6\left(0, \frac{1}{\beta}, \frac{\lambda(1-\beta)(\beta-k)}{\alpha\beta^2}\right)$ yields a characteristic equation $\Lambda^3 + a_1\Lambda^2 + a_2\Lambda + a_3 = 0$, where $a_1 = -(a_{11} + a_{22})$, $a_2 = a_{11}a_{22} - a_{23}a_{32}$ and $a_3 = a_{11}a_{23}a_{32}$ with $a_{11} = r - \frac{\lambda(1-\beta)(\beta-k)}{\alpha\beta^2}$, $a_{12} = 0$, $a_{13} = 0$, $a_{21} = 0$, $a_{22} = \frac{\lambda}{\beta^2}[\beta(1+k) - 2k], a_{23} = -\frac{\alpha}{\beta}$, $a_{31} = \frac{\gamma\lambda(1-\beta)(\beta-k)}{\alpha\beta^2}$, $a_{32} = \frac{\lambda(1-\beta)(\beta-k)}{\alpha\beta}$ and $a_{33} = 0$. The necessary conditions, using the *Routh-Hurwitz* stability criterion, for local asymptotic stability of equilibrium point E_6 are $a_i > 0;\ \ i = 1, 2, 3$ and $a_1a_2 - a_3 > 0$.

Proposition 3.3.1 *The equilibrium point* E_6 *is locally asymptotically stable whenever* $a_{11} < 0$ *and* $a_{22} < 0$.

Proof: From the signs of the a_{ij}; $i, j = 1, 2, 3$, it can easily be verified that $a_1 > 0, a_2 > 0$ and $a_3 > 0$. Thus, by mathematical computation:

$$a_1a_2 - a_3 = -(a_{11})^2 a_{22} + a_{22}a_{23}a_{32} - a_{11}(a_{22})^2$$

Clearly $a_1a_2 - a_3 > 0$ whenever $a_{11} < 0$ and $a_{22} < 0$.

Lemma 3.3.1 *The warthog's critical threshold stabilizes* E_6 *and local stability is possible provided the following conditions are satisfied.*

(i) *For stabilisation by a weak warthog critical threshold component, either* $\beta_1K_w < \mu_1$ *and* $\mu_1 > \frac{\beta_1K_w(\alpha_1r_2+\alpha_2r_1)}{\alpha_1r_2}$ *or* $\beta_1K_w > \mu_1$ *and* $\mu_1 < \frac{\beta_1K_w(\alpha_1r_2+\alpha_2r_1)}{\alpha_1r_2}$.

(ii) *Stabilisation by a strong warthog critical threshold component is attained when either* $\beta_1K_w < \mu_1$ *and* $\mu_1 < \frac{\beta_1K_w(\alpha_1r_2+\alpha_2r_1)}{\alpha_1r_2}$ *or* $\beta_1K_w > \mu_1$ *and* $\mu_1 > \frac{\beta_1K_w(\alpha_1r_2+\alpha_2r_1)}{\alpha_1r_2}$.

Proof: Using Proposition 3.3.1, it is easy to deduce that $\frac{r\alpha\beta^2}{\lambda(1-\beta)(\beta-k)} < 1$ and $\frac{\beta(1+k)}{2k} < 1$. In terms of dimensional model parameters, these results simplify to $\varpi < \frac{K_w - \frac{\mu_1}{\beta_1}}{\frac{\beta_1K_w(\alpha_1r_2+\alpha_2r_1)}{\alpha_1r_2} - \mu_1}$ provided $\frac{1}{\varpi} < \beta_1 < \frac{\mu_1}{K_w}$ and $\varpi + K_w < \frac{2\mu_1}{\beta_1}$, respectively. The proof of Lemma 3.3.1 is concluded from $\varpi < \frac{K_w - \frac{\mu_1}{\beta_1}}{\frac{\beta_1K_w(\alpha_1r_2+\alpha_2r_1)}{\alpha_1r_2} - \mu_1}$ by using the condition, $0 < \varpi < K_w$, for strong and weak critical thresholds. Further, $\varpi + K_w < \frac{2\mu_1}{\beta_1}$ means that the warthog-lion equilibrium is stabilized by the lion natural mortality to its predation ratio provided the sum of both the lower critical density and carrying capacity for the warthog does not exceed this ratio. The ratio $\frac{2\mu_1}{\beta_1}$, is ecologically defined and interpreted as the lion's (predator's) limiting stabilisation factor for the warthog-lion equilibrium E_6.

The associated eigenvalues for the equilibrium $E_7\left(\frac{1}{\Phi}, 0, \frac{r\gamma(\Phi-1)}{\Phi^2}\right)$ are analysed from the characteristic equation $\Lambda^3 + a_1\Lambda^2 + a_2\Lambda + a_3 = 0$, where:

$$\begin{aligned}
a_1 &= \alpha A_3 + \lambda + 1 - A_1 - \gamma A_2 \\
a_2 &= \gamma A_1 A_2 + \alpha A_3 + \gamma A_3 A_4 + \lambda - \lambda A_1 - \alpha A_1 A_3 - A_1 - \gamma\lambda A_2 - \alpha\gamma A_2 A_3 \\
a_3 &= \lambda\gamma A_1 A_2 + \alpha\gamma A_1 A_2 A_3 - \lambda A_1 - \alpha A_1 A_3 - \lambda\gamma A_3 A_4 - -\alpha\gamma A_3^2 A_4
\end{aligned}$$

for

$$A_1 = r\left(1 - \frac{2}{\Phi}\right) - \frac{r\gamma(\Phi-1)}{(\Phi+\phi)^2}, \quad A_2 = \frac{1}{\Phi+\phi}, \quad A_3 = \frac{r\gamma(\Phi-1)}{\Phi^2}, \quad A_4 = \frac{r\gamma(\Phi-1)}{(\Phi+\phi)^2}$$

Once again employing the *Routh-Hurwitz* conditions, the author notes that $E_7\left(\frac{1}{\Phi}, 0, \frac{r\gamma(\Phi-1)}{\Phi^2}\right)$ is locally asymptotically stable provided $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 > a_3$ are satisfied and for this to occur, $\Phi > 2 \Rightarrow \frac{2+\phi}{\gamma} < 1$. In terms of the dimensional parameters for the Model system (3.1-3.3), local stability condition on E_7 reduces to $\epsilon_u > \frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$ which is compared and related to the non-negativity and existence condition $\epsilon_u > \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$ of E_7. Thus, for the existence and local asymptotic stability of E_7, the lower bounds of the lion fertility factors (biomass gain) from the buffalo population for both situations must differ by a factor $\frac{\mu_1}{\alpha_1 K_b}$. This difference $(\frac{\mu_1}{\alpha_1 K_b})$, is ecologically interpreted as the lion's per capita saturation ratio, as a result of feeding on a single *"average"* buffalo.

3.3.4 Local stability of the co-existence equilibrium solution

The predator-prey system admits a unique positive co-existence equilibrium $E_8(x^*, y^*, z^*)$, with a characteristic polynomial $\Lambda^3 + a_1\Lambda^2 + a_2\Lambda + a_3 = 0$, where; $a_1 = -(\tilde{P} + \tilde{Q} + \tilde{R})$, $a_2 = \tilde{P}\tilde{Q} + \tilde{P}\tilde{R} + \tilde{Q}\tilde{R} + \tilde{S} + \tilde{U}$ and $a_3 = -(\tilde{P}\tilde{Q}\tilde{R} + \tilde{P}\tilde{S} + \tilde{T})$ with:

$$\begin{aligned}
\tilde{P} &= r(1 - 2x^*) - \frac{z^*}{(1+\phi x^*)^2} \\
\tilde{Q} &= \beta y^* + \frac{\gamma x^*}{1+\phi x^*} - 1 \\
\tilde{R} &= \lambda[(ky^* - 1)(1 - 2y^*) + ky^*(1 - y^*)] - \alpha z^* \\
\tilde{S} &= \beta\alpha z^* y^*
\end{aligned}$$

$$
\begin{aligned}
\tilde{T} &= \frac{\gamma x^* z^*}{(1+\phi x^*)^3}\tilde{R} \\
\tilde{U} &= \frac{\gamma x^* z^*}{(1+\phi x^*)^3}
\end{aligned}
$$

Since $\tilde{Q} = 0$ (cf. equation (3.9)), the coefficients of the eigenvalues in the characteristic equation are simplified to the following forms:

$$a_1 = -(\tilde{P} + \tilde{R}), \quad a_2 = \tilde{P}\tilde{R} + \tilde{S} + \tilde{U} \quad \text{and} \quad a_3 = -(\tilde{P}\tilde{S} + \tilde{T})$$

Theorem 3.3.2 *If $x^* > \frac{1}{2}$ and $\frac{2\lambda y^*(k+1)}{\lambda(3ky^{*2}+1)+\alpha z^*} < 1$, then the interior equilibrium $E_8(x^*, y^*, z^*)$ is locally asymptotically stable.*

Proof: If the eigenvalues (characteristic roots) have negative real parts, then the positive equilibrium, $E_8(x^*, y^*, z^*)$, is stable. By carrying out mathematical analysis, it can easily be shown that:

$$a_1 = -(\tilde{P} + \tilde{R}) = \left[2rx^* + \frac{z^*}{(1+\phi x^*)^2} + 3\lambda k y^{*2} + \lambda + \alpha z^*\right] - [r + 2\lambda k y^* + 2\lambda y^*]$$

$$\text{It follows that} \quad a_1 > 0 \quad \text{if} \quad x^* > \frac{1}{2} \quad \text{and} \quad \frac{2\lambda y^*(k+1)}{\lambda(3ky^{*2}+1)+\alpha z^*} < 1$$

Further analysis yields:

$$
\begin{aligned}
a_2 &= \tilde{P}\tilde{R} + \tilde{S} + \tilde{U} \\
&= 2rk\lambda\alpha\beta y^* z^* - 3rk\lambda\alpha\beta y^{*3} z^* - r\lambda\alpha\beta y^* z^* + 2r\lambda\alpha\beta y^{*2} z^* - r\alpha^2\beta y^* z^{*2} - \\
&\quad 4rk\lambda\alpha\beta x^* y^{*2} z^* + 6rk\lambda\alpha\beta x^* y^{*3} z^* + 2r\lambda\alpha\beta x^* y^* z^* - 4r\lambda\alpha\beta x^* y^{*2} z^* + \\
&\quad 2r\alpha^2\beta x^* y^* z^{*2} + \alpha\beta y^* z^* + \frac{\gamma x^* z^*}{(1+\phi x^*)^3} - \\
&\quad \frac{[2k\lambda\alpha\beta y^{*2} z^{*2} + 3k\lambda\alpha\beta y^{*3} z^{*2} + \lambda\alpha\beta y^* z^{*2} - 2\lambda\alpha\beta y^{*2} z^{*2} + \alpha^2\beta y^{*2} z^{*3}]}{(1+\phi x^*)^2} \\
&= \frac{\alpha\beta y^* z^*[2rx^* + 4r\phi x^{*2} - r\phi^2 x^{*2} + z^* + 2r\phi^2 x^{*2} - r - 2r\phi x^*]}{(1+\phi x^*)} \times \\
&\quad \frac{[\alpha z^* + \lambda - 2\lambda k y^* + 3\lambda k y^{*2} - 2\lambda y^*]}{(1+\phi x^*)} + \alpha\beta y^* z^* + \frac{\gamma x^* z^*}{(1+\phi x^*)^3}
\end{aligned}
$$

and

$$\begin{aligned}
a_3 &= -(\tilde{P}\tilde{S}+\tilde{T}) \\
&= 2r\alpha\beta x^*y^*z^* - r\alpha\beta y^*z^* + \frac{\alpha\beta y^*z^{*2}}{(1+\phi x^*)^2} + \\
&\quad \frac{\gamma x^*z^*}{(1+\phi x^*)^3}\left[3\lambda k y^{*2} + \alpha z^* + \lambda - 2\lambda k y^* - 2\lambda y^*\right] \\
&= \alpha\beta y^*z^*\left[r(2x^*-1) + \frac{z^*}{(1+\phi x^*)^2}\right] + \\
&\quad \frac{\gamma x^*z^*}{(1+\phi x^*)^3}\left[\lambda(3ky^{*2}+1) + \alpha z^* - 2\lambda y^*(k+1)\right]
\end{aligned}$$

$$a_3 > 0 \quad \Leftrightarrow \quad x^* > \frac{1}{2} \;\text{ and }\; \frac{2\lambda y^*(k+1)}{\lambda(3ky^{*2}+1)+\alpha z^*} < 1$$

It follows that $a_1a_2 > a_3$ is also satisfied and hence, Theorem 3.3.2 follows.

The condition $x^* > \frac{1}{2}$ implies $B^* > \frac{1}{2}K_b$ and indicates that for a locally asymptotically stable positive steady state, the buffalo population has to be maintained at a population level above half its carrying capacity. Further, the second inequality of Theorem 3.3.2 implies that $\varpi < \frac{r_2W^*(3W^*-2K_w)}{2r_2W^*-K_w(r_2+\alpha_2L^*)}$, provided $K_w < \frac{2r_2W^*}{r_2+\alpha_2L^*}$, and this means that the local stability of the interior equilibrium should always be attained by regulating the upper bounds of ϖ (lower critical density) and K_w (warthog carrying capacity). Moreover, $K_w > \frac{3}{2}W^*$ leads to a weak critical threshold and $K_w < \frac{3}{2}W^*$ yields a strong critical threshold in the warthog species. In terms of ecological reality, $K_w < \frac{2r_2W^*}{r_2+\alpha_2L^*}$ shows that if warthog equilibrium density W^* decreases due to species' out-flux as a result of emigration, then the possible maximum value of warthog carrying capacity reduces further.

3.3.5 Global stability of the interior equilibrium

In this subsection, a condition for the global asymptotic stability of the co-existence (interior) equilibrium point is established. Some definitions and a lemma that are useful for finding a Lyapunov function and proving the global stability of the equilibrium follow:

Definition 3.3.1 (i) *Consider the dynamical system* $\dot{\mathbf{x}} = f(\mathbf{x})$*, then* $V : M \longrightarrow \mathbb{R}$ *is called a Lyapunov function for* $f(\mathbf{x})$ *if* $V \in C^1(M, \mathbb{R}),\ V \geq 0$ *and* $(gradV(\mathbf{x}))f(\mathbf{x}) \leq 0$ *for all* $\mathbf{x} \in M$

(ii) *Suppose* $\mathbf{x}^* \in \mathbb{R}^n$ *is a fixed (equilibrium) point for the dynamical system* $\dot{\mathbf{x}} = f(\mathbf{x}),\ \mathbf{x} \in \mathbb{R}^n,\ f : U \longrightarrow \mathbb{R}^n,\ U \subseteq \mathbb{R}^n$*. If* $\mathbf{x}^*$ *possesses a candidate Lyapunov function* V *in* W*, then* $\mathbf{x}^*$ *is stable. Further, if* V *is a strong Lyapunov function in* W*, then* $\mathbf{x}^*$ *is globally asymptotically stable.*

Lemma 3.3.2 *Lasalle's invariance principle: Suppose* V *is a Lyapunov function for* $f(\mathbf{x})$ *in the sense of Definition 3.3.1(i), and that for every solution of Model system (3.4-3.6) that tends to the maximal invariant set* M*, called a Lasalle's invariant set of the system, containing* $\omega(p)$*, then* $\omega(p) \subseteq \{\mathbf{y} \in M : (gradV(\mathbf{y}))f(\mathbf{y}) = 0\} =: \nu_0$ *for each* $p \in M$*. In addition,* $\omega(p)$ *is contained in the largest invariant subset of* ν_0*.*

To prove global stability of $E_8(x^*, y^*, z^*)$, it is sufficient to show that $M = \{x^*, y^*, z^*\}$. The proof of Lemma 3.3.2 has been carried out in many studies (Hsu, 2005; Takeuchi, 1996; Hsu & Huang, 1995) and is therefore used without proof when deriving the following theorem.

Theorem 3.3.3 *The co-existence interior steady state* $E_8(x^*, y^*, z^*)$ *is globally asymptotically stable if and only if* $y + y^* > \frac{k+1}{k}$, where $y = \frac{W}{K_w}$.

Proof: A widely preferred candidate Lyapunov function (Hsu, 2005; Dubey & Upadhyay, 2004; Cantrell *et al.*, 2004; Cantrell & Cosner, 2001; Takeuchi, 1996; Hsu & Huang, 1995), is chosen as follows:

$$V(x, y, z) = \pi_1 \int_{x^*}^{x} \frac{\xi - x^*}{\xi} d\xi + \pi_2 \int_{y^*}^{y} \frac{\eta - y^*}{\eta} d\eta + \pi_3 \int_{z^*}^{z} \frac{\zeta - z^*}{\zeta} d\zeta$$

where $\pi_1, \pi_2,$ and π_3 are positive constants to be determined. Clearly (true because $lnx \leq x - 1$), $V(x, y, z)$ is a positive definite function for all $\pi_i > 0;\ i = 1, 2, 3$. Therefore, symmetrical functions can now be defined:

$$V_1 = x - x^* - x^* ln\left(\frac{x}{x^*}\right),\ V_2 = y - y^* - y^* ln\left(\frac{y}{y^*}\right)\ \&\ V_3 = z - z^* - z^* ln\left(\frac{z}{z^*}\right)$$

$$\text{so that} \qquad V(x, y, z) = \pi_1 V_1(x) + \pi_2 V_2(y) + \pi_3 V_3(z)$$

Clearly $\frac{\partial V_1}{\partial x} < 0$ when $0 < x < x^*$ and $\frac{\partial V_1}{\partial x} > 0$ when $x > x^*$, and from symmetry, the results are true for $\frac{\partial V_2}{\partial y}$ and $\frac{\partial V_3}{\partial z}$. Now computing $\frac{dV}{dt}$ along the solutions of system (3.4-3.6) gives:

$$\frac{dV}{dt} = \pi_1 \left(1 - \frac{x^*}{x}\right) \frac{dx}{dt} + \pi_2 \left(1 - \frac{y^*}{y}\right) \frac{dy}{dt} + \pi_3 \left(1 - \frac{z^*}{z}\right) \frac{dz}{dt}$$

Using the linearisation theorem and the corresponding linear approximations $x - x^* \cong 1 + \phi x$ and $z - z^* \cong z$, computation of $\frac{dV_1(x(t))}{dt}$, $\frac{dV_2(y(t))}{dt}$ and $\frac{dV_3(z(t))}{dt}$ via system (3.4-3.6) yields:

$$\begin{aligned}
\frac{dV_1(x)}{dt} &= \left(1 - \frac{x^*}{x}\right) \left[r(1-x) - \frac{z}{1+\phi x}\right] x \\
&= (x - x^*) \left[-r(x - x^*) + \frac{z^*}{1+\phi x^*} - \frac{z}{1+\phi x}\right] \\
&= -r(x-x^*)^2 - \left[\frac{(1+\phi x^*)(x-x^*)(z-z^*) - z^*(x-x^*)^2}{(1+\phi x^*)(1+\phi x)}\right]
\end{aligned}$$

Similarly:

$$\begin{aligned}
\frac{dV_2(y)}{dt} &= \left(1 - \frac{y^*}{y}\right) \left[\lambda\,(1-y)\,(ky-1) - \alpha z\right] y \\
&= (y-y^*) \left[\lambda\,(1-y)\,(ky-1) - \alpha z - \lambda\,(1-y^*)\,(ky^*-1) + \alpha z^*\right] \\
&= (y-y^*) \left[\{\lambda + \lambda k[1-(y+y^*)]\}(y-y^*) - \alpha(z-z^*)\right] \\
&= \lambda\left[1 + k[1-(y+y^*)]\right](y-y^*)^2 - \alpha(z-z^*)(y-y^*)
\end{aligned}$$

and:

$$\begin{aligned}
\frac{dV_3(z)}{dt} &= \left(1 - \frac{z^*}{z}\right) \left[\beta y + \frac{\gamma x}{1+\phi x} - 1\right] z \\
&= (z-z^*) \left[\beta y + \frac{\gamma x}{1+\phi x} - \beta y^* - \frac{\gamma x^*}{1+\phi x^*}\right] \\
&= \beta(y-y^*)(z-z^*) + \frac{\gamma(x-x^*)(z-z^*)}{(1+\phi x^*)(1+\phi x)}
\end{aligned}$$

Mathematical computation of $\frac{dV}{dt}$, using $\frac{dV_1(x)}{dt}$, $\frac{dV_2(y)}{dt}$ and $\frac{dV_3(z)}{dt}$ as obtained above yields:

$$\frac{dV}{dt} = -r(x-x^*)^2 + \frac{z^*(x-x^*)^2}{(1+\phi x^*)(1+\phi x)} - \frac{(1+\phi x^*)(x-x^*)(z-z^*)}{(1+\phi x^*)(1+\phi x)} +$$

$$\begin{aligned}&\lambda\left[1+k[1-(y+y^*)]\right](y-y^*)^2-\alpha(z-z^*)(y-y^*)+\beta(z-z^*)(y-y^*)\\&+\frac{\gamma(x-x^*)(z-z^*)}{(1+\phi x^*)(1+\phi x)}\end{aligned}$$

By choosing $\pi_1 = 1,\ \pi_2 = \frac{\beta(1+\phi x^*)}{\alpha\gamma}$ and $\pi_3 = \frac{(1+\phi x^*)}{\gamma}$, where all $\pi_i > 0$ for $i = 1, 2, 3$, a positive definite function $V(x, y, z) = V_1(x) + \frac{\beta(1+\phi x^*)}{\alpha\gamma}V_2(y) + \frac{(1+\phi x^*)}{\gamma}V_3(z)$, is defined as the suitable candidate Lyapunov function. Given the choices for $\pi_1,\ \pi_2$ and π_3, $\frac{dV}{dt}$ simplifies to:

$$\begin{aligned}\frac{dV}{dt} &= -r(x-x^*)^2+\frac{z^*(x-x^*)^2}{(1+\phi x^*)(1+\phi x)}-\frac{(1+\phi x^*)(x-x^*)(z-z^*)}{(1+\phi x^*)(1+\phi x)}+\\&\quad\frac{\lambda\beta(1+\phi x^*)}{\alpha\gamma}\left[1+k[1-(y+y^*)]\right](y-y^*)^2-\frac{\beta(1+\phi x^*)}{\gamma}(z-z^*)(y-y^*)+\\&\quad\frac{\beta(1+\phi x^*)}{\gamma}(z-z^*)(y-y^*)+\frac{(1+\phi x^*)(x-x^*)(z-z^*)}{(1+\phi x^*)(1+\phi x)}\\&= \left[-r+\frac{z^*}{(1+\phi x^*)(1+\phi x)}\right](x-x^*)^2+\frac{\lambda\beta(1+\phi x^*)}{\alpha\gamma}\left[1+k[1-(y+y^*)]\right](y-y^*)^2\end{aligned}$$

Analysing the coefficients of $(x-x^*)^2$ and $(y-y^*)^2$ reveals that:

$$\begin{aligned}\left[-r+\frac{z^*}{(1+\phi x^*)(1+\phi x)}\right] &\leq \left[-r+\frac{z^*}{(1+\phi x^*)}\right]\\&= -rx^*\end{aligned}$$

This shows that the coefficient of $(x-x^*)^2$ is unconditionally negative. It can easily be seen that the coefficient of $(y-y^*)^2$ is negative if and only if $y+y^* > \frac{k+1}{k}$, and this completes the proof of the theorem.

Using Theorem 3.3.3, $\frac{dV}{dt} < 0$ along any trajectory of system (3.4-3.6) and $\frac{dV}{dt} = 0$ if and only if $x = x^*$ and $y = y^*$. In accordance to LaSalle's invariance principle, the largest invariant subset of points where $\frac{dV}{dt} = 0$ is $M = \{(x^*, y^*, z^*)\}$. Thus, $E_8(x^*, y^*, z^*)$ is globally stable as asserted in Theorem 3.3.3. Thus, Theorem 3.3.3 implies that $W > (K_w + \varpi) - W^*$, which is used to detect and explain the future ecosystem trends as a result of warthog out-flux/emigration.

A summary of some of the results from this analysis are now presented in Table 3.1.

3.4 Numerical analysis and model simulation

In this section, numerical simulations of the dynamics and species patterns hidden in the three dimensional Model system (3.1-3.3) are provided. The model equations are numerically integrated using the Runge-Kutta 4th Order algorithm supported by MatLab. Parameters such as mortality rate, predation rate, intrinsic growth rate and carrying capacity are readily available in the research work cited in the introduction and other ecological studies on predator-prey dynamics. Initial population density for each species is chosen to be positive at $B(0) = 4.5$, $W(0) = 15.0$ and $L(0) = 3.0$. Mathematical computations, in accordance with the stability and existence dynamics, of some biological parameters such as predator fertility rate, threshold and satiation, not readily available were carried out.

3.4.1 Parameter estimates

(i) Carrying Capacity

AENP is a managed reserve and the actual number of prey species that will be present when density dependence becomes important is not yet known. Currently, unpublished data from AENP reveals that warthog numbers seem to have stabilised at around 1000 (observations), although the correct value may be in the region of 2500. This stabilisation may however be due to the culling of some 200 and 400 warthogs in the 2008 and 2009 seasons, respectively (Mgqatsa, 2010). Buffalo are considered large stock unit (LSU) and, according to Vale (2007), the agricultural carrying capacity for the area is 20 hectares per LSU. Within AENP, the buffalo have stabilised around 330 (observations), although actual estimate is 350-375 (South African National Parks, SANParks, unpublished data). This is partly due to, according to AENP conservation managers, lion predation and juvenile survival.

Table 3.1: *Existence and stability conditions (parameter bounds) for non-negative equilibrium points of the Model system (3.1-3.3).*

Equilibrium	**Existence**	**Stability**
$E_0(0,0,0)$	always exist	unstable
$E_1(1,0,0)$	always exist	$\epsilon_u < \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$
$E_2(0,1,0)$	always exist	unstable
$E_3(1,1,0)$	always exist	$K_w > \varpi$ and $\epsilon_u < \left\lvert \frac{(hK_b+1)(\mu_1-\beta_1 K_w)}{\alpha_1 K_b} \right\rvert$
$E_4\left(0,\frac{1}{k},0\right)$	always exist	unstable
$E_5\left(1,\frac{1}{k},0\right)$	always exist	$\epsilon_u < \left\lvert \frac{(hK_b+1)(\mu_1-\beta_1\varpi)}{\alpha_1 K_b} \right\rvert$
$E_6\left(0,\frac{1}{\beta},\frac{\lambda(1-\beta)(\beta-k)}{\alpha\beta^2}\right)$	$K_w < \frac{\mu_1}{\beta_1} < \varpi$ no *Allee effect* $\varpi < \frac{\mu_1}{\beta_1} < K_w$ for *Allee effect*	$\beta_1 K_w < \mu_1$ & $\mu_1 > \frac{\beta_1 K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}$ or $\beta_1 K_w > \mu_1$ & $\mu_1 < \frac{\beta_1 K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}$ By weak *Allee effect* component
$E_6\left(0,\frac{1}{\beta},\frac{\lambda(1-\beta)(\beta-k)}{\alpha\beta^2}\right)$	$\varpi + K_w < \frac{2\mu_1}{\beta_1}$ $\frac{1}{\varpi} < \beta_1 < \frac{\mu_1}{K_w}$ $\varpi < \frac{K_w-\frac{\mu_1}{\beta_1}}{\frac{\beta_1 K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}-\mu_1}$	$\beta_1 K_w < \mu_1$ & $\mu_1 < \frac{\beta_1 K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}$ or $\beta_1 K_w > \mu_1$ & $\mu_1 > \frac{\beta_1 K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}$ By strong *Allee effect* component
$E_7\left(\frac{1}{\Phi},0,\frac{r\gamma(\Phi-1)}{\Phi^2}\right)$	$\epsilon_u > \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$ & $\epsilon_u > \frac{h\mu_1}{\alpha_1}$	$\epsilon_u > \frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$
$E_8(x^*,y^*,z^*)$	$\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$	$B^* > \frac{1}{2}K_b$ & $\varpi < \frac{r_2 W^*(3W^*-2K_w)}{2r_2 W^*-K_w(r_2+\alpha_2 L^*)}$ provided $K_w < \frac{2r_2 W^*}{r_2+\alpha_2 L^*}$
$E_8(x^*,y^*,z^*)$		$W > (K_w+\varpi) - W^*$ for global stability

During simulations, the carrying capacities of warthog and buffalo are rescaled [1] to $K_w = 25$ and $K_b = 10$, respectively.

(ii) Fecundity and mortality rates

On average, due to less stress in defending their territories and hunting, female lions in the wild live up to 17 years, while the males live up to 15 years (Packer *et al.,* 1998; Hunter, 1998). Basing on similar reasons, lions living in captivity have longer life spans (25 years) than those in the wild (game parks) (van Orsdol, 1984; Schaller, 1972). Only a small percentage of lions die of natural causes, whereas 75% of lions die by being caught in snares, shot by poachers, or killed in fights with rival lions (Woodroffe & Frank, 2005; Hunter, 1998). Various studies show that females give birth to litters of 1-6 cubs (average 3 cubs) after a gestation period of 110-120 days (approximately 4 months) (Packer *et al.,* 2001; Packer *et al.,* 1998; Hunter, 1998). According to Packer *et al.* (2001) and Hunter (1998), the mortality rate of lion cubs is high (more than half do not survive the first year) and only 20% of cubs reach the age of 2 years. In this study the mortality rate of lions was estimated as the reciprocal of the average life expectancy, thus, $\mu_1 = \frac{1}{16} = 0.0625$.

The data on the calving interval for the buffalo in Lake Manyara National Park resulted in an estimated pregnancy rate of 0.523, and a production of 0.56 calves per female per year (Sinclair, 1977). However, given the average number of calves in the herd ($6 - 12\%$), and considering the early calf mortality of 41.6%, the pregnancy rate estimate of 0.523 seems to be too high. Thus, a more realistic calving interval would be 3 years for most females that live in the large herds (Prins, 1996). Using the formula for calculating compound interest, annual calf mortality was calculated to be 42.9% in 1983 and 55.3% in 1991 (Prins, 1996). The rather high calf mortality combined with the low fecundity, results in a very low population growth. With supplementary feeding to keep the cow and bull in optimum breeding condition, a reproductive rate of 1 calf every year can be attained (Tambling *et al.,* 2009; Packer *et al.,* 1998; Sinclair,

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[1] Scaling of parameters is carried out to overcome the challenge of multiple data sets that explain the variability of model parameters at different scales. Various methods of parameter scaling are readily used.

1977). A conservative reproductive rate of 2 calves in 3 years was considered during model simulations, effectively introducing a mortality factor of 1 calf in three years.

Warthogs on the other hand have a litter size of 1-8 piglets but often only 2-3 babies survive because the female is able to nurse only 4 young ones at a time (Mgqatsa, 2010; Nyafu, 2009). Considering other parameter values, the intrinsic growth rates of both the buffalo (r_1) and the warthog (r_2) are computed basing on $\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$ and $K_w < \frac{2r_2 W^*}{r_2+\alpha_2 L^*}$ which are the existence and stability conditions for the co-existence equilibrium. Thus, intrinsic growth rates, $r_1 = 0.84$ and $r_2 = 2.53$ are considered base values in this study.

(iii) Predation rates and conversion efficiency

In the absence of epidemics (e.g., rinderpest), lion predation accounts for nearly all known buffalo deaths in African game parks, and is the chief cause of death (Prins, 1996). The formation of large groups enables the fight response observed in buffaloes in the AENP and this makes them relatively immune to predation from most large predators (Tambling *et al.*, 2011).

Despite being below the ideal prey weight range (suboptimal prey) for lions, warthogs are amongst the most common prey species for the lions in the AENP (Hayward & Kerley, 2005). This is attributed to their abundance, relatively slow evasion speed and apparent lack of vigilance (Hayward *et al.*, 2007*a*; Scheel, 1993). Warthogs can thus, easily be captured by single subadult or nomadic lions, where cooperative group hunting of larger species is less likely to occur (Scheel, 1993). Literature quantifying the extent of predation on warthogs by lions and spotted hyaenas in the AENP is readily available (Mgqatsa, 2010; Tambling *et al.,* 2009; Franklin, 2005; Ravnsborg, 2004). Warthogs contributed between 5.8% (Mgqatsa, 2010 from Ravnsborg, 2004) and 14% (Mgqatsa, 2010 from Tambling *et al.,* 2009) to the diet of the lions in the AENP main camp, revealing an increase in the predation rate by lions. This could be attributed to an increase in warthog numbers in the AENP main camp (Wentworth *et al.,* 2011).

Between 2003-2004, it was observed that the six AENP lions killed 16 buffaloes and 23 warthogs (Hayward *et al.,* 2007*a*), while the following year, 18 buffaloes and 20 warthogs were killed. Using these observations, on average a lion kills 2.833 buffaloes and 3.583 warthogs per year. Furthermore, unpublished data from AENP (Franklin, 2005; Ravnsborg, 2004) shows that on average a female lion eats 5 kg, whereas a male lion consumes 7.5 kg, of prey biomass per day. This gives 6.25 kg as the average lion's daily prey biomass requirement which closely approximates Prins' lion consumption estimate of 5.8 kg of biomass per day (Prins, 1996). The Cape buffalo has an average adult body mass of 680 kg. Thus, on average a lion eats 3.3547 adult buffaloes per year. Considering predation as the number (biomass) of prey killed/eaten per predator per year and after rescaling, $\alpha_1 = 0.2833yr^{-1}$ and $\alpha_2 = 0.3583yr^{-1}$ are estimated by the author as the base values for lion predation rates. The fertility factor gains (ϵ_u and β_1), and the sparsity constant (ϖ), are estimated in accordance with the stability and existence intervals and bounds i.e., $\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$ for co-existence of all the species and $\epsilon_u > \frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$ for local asymptotic stability of $E_7\left(\frac{1}{\Phi}, 0, \frac{r\gamma(\Phi-1)}{\Phi^2}\right)$. For stability of E_6, either $\beta_1 < \frac{\mu_1}{K_w}$ or $\beta_1 > \frac{\mu_1}{K_w}$ depending on the bounds for lion's natural mortality rate, as defined in Lemma 3.3.1. Basing on unpublished data of AENP which shows that a few offspring are registered per year after consuming a great number and quantity of prey biomass per female lion, a value of $\beta_1 = \frac{\alpha_2}{100}$ is considered for the numerical results of the model. Last, but not least, a computational value of buffalo-lion fertility factor is obtained from the analytical result, $\epsilon_u = \frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$.

The estimated parameter values and their sources are as summarised in Table 3.2.

3.4.2 The effect of prey biomass conversion efficiency to predator offspring (fertility factor)

Numerical results reveal that stable co-existence of the three species is only possible when the predator fertility rate is slightly greater than $\frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$, i.e., $\epsilon_u = 0.7$, as shown in Figure 3.1(a), and that when the fertility rate is low, i.e., $\epsilon_u \ll \frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$, the predator goes to extinction. Increase

Table 3.2: *Parameter descriptions and their base value estimates.*

Symbol	**Description**	**Numerical Value**	**Ref.**
μ_1	natural mortality rate of lion	0.0625	[14][20],AENP*
α_1 & α_2	predation rates for prey	0.2833 & 0.3583	[10],AENP*
r_1 & r_2	intrinsic growth rate for prey species	0.84 & 2.53	[17],[18],[23],AENP*
K_b & K_w	carrying capacity for prey species	10 & 25	[17],[24],AENP*
β_1	prey biomass conversion rate	0.003583	estimate
ϵ_u	prey biomass conversion efficiency	0.7 ($\epsilon_u > 0.5736$)	computed
ϖ	warthog threshold density	8 ($\varpi > 5.15$)	computed
h	$\frac{1}{h}$ the half saturation (satiation)	2.5	estimate

**Unpublished data*

in lion fertility rate (Figure 3.1) helps in the rejuvenation of the predator's population growth at the expense of the warthog population without any significant variation in the buffalo's population. However, stable oscillations are observed between the buffalo and lion as the fertility rate is gradually increased (Figure 3.2). Four parameters namely, predation rate, predator handling time per prey item, predator mortality rate and prey carrying capacity, are found to be very important in controlling the predator fertility as depicted in qualitative analyses. High predation rate and lower values for predator handling time per prey decrease the bounds of predator fertility rate. This in reality, arises as a result of poor quality prey of low nutritional value (low predator fertility gain) to the predator (Srinivasu *et al.*, 2007; van Baalen *et al.*, 2001). However, model analyses show that the prey carrying capacity has a minimum effect on the numerical value of predator fertility rate.

Figures 3.1 and 3.2 reveal that the dynamics of the Model system can change dramatically with slight variations in the lion fertility rate. It is observed that increasing the predator fertility rate leads to extinction of the easy-to-capture prey, the warthogs. This is accompanied by periodic oscillations between the predator (lion) and the hard-to-capture prey (buffalo) (Figures 3.1 and 3.2). Stability analysis of the steady state $E_3(1, 1, 0)$ reveals the so-called paradox of enrichment which, as

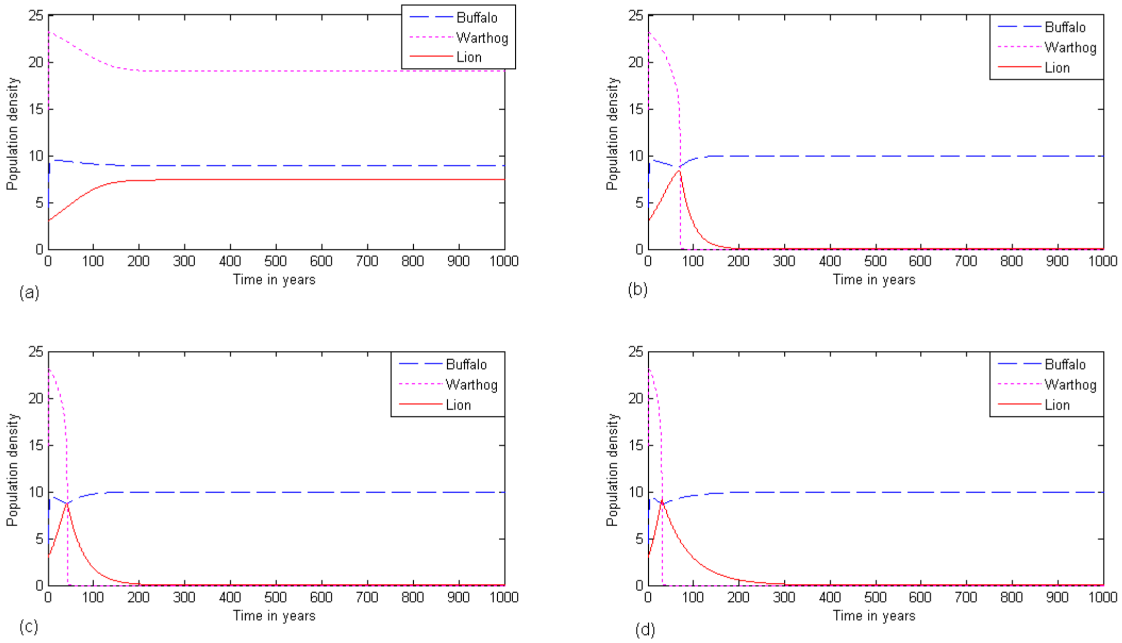

Figure 3.1: *The dynamical effect is shown as the predator fertility rate* $\epsilon_u > \frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$ *is varied from (a)* 0.7, *(b)* 0.8, *(c)* 0.9 *and (d)* 1.0, *while other model parameters are maintained at their base values as depicted in Table 3.2 and the initial population density for each species is chosen to be positive at* $B(0) = 4.5,\ W(0) = 15.0$ *and* $L(0) = 3.0$.

hypothesised by various studies, shows that predation acts to prevent large oscillations or extinction of prey population (Fryxell *et al.*, 2007; Sherratt *et al.*, 1997). Figure 3.3 ($\epsilon_u = 0.8$) and Figure 3.4 ($\epsilon_u = 2.4$) show that large oscillations are indeed reduced in the hard-to-capture prey despite the easy-to-capture prey slipping into extinction. However, existence of a variety of potential prey species amidst other large predators shows that prey switching is likely to occur before any prey species becomes extinct (Khan *et al.*, 2004).

The predator oscillations become more spikelike (depicted in Figures 3.2(g) and (h)) as its fertility rate increases further which is often an early indication of chaos (Gakkhar & Naji, 2003; Hsu *et al.*, 2001; Bazykin, 1998; Sherratt *et al.*, 1997). Anti-predator behaviour (group defense and alertness)

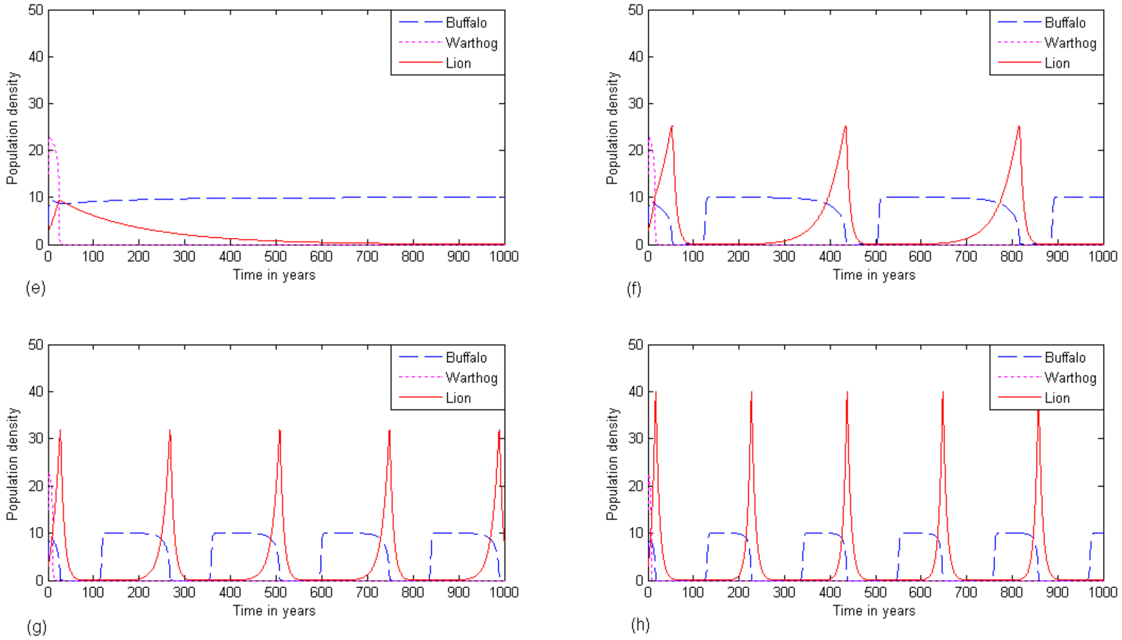

Figure 3.2: *A continuation of Figure 3.1 in which the dynamical effect is shown as the predator fertility rate* $\epsilon_u > \frac{(hK_b+2)\mu_1}{\alpha_1 K_b}$ *is varied from (e)* 1.1, *(f)* 1.4, *(g)* 1.8 *and (h)* 2.4. *Typical chaotic periodic oscillations arise for higher predator fertility rates.*

of prey (buffalo) helps it to co-exist with its predator with periodic oscillations even at high predator fertility rates (Figures 3.1 and 3.2). On the other hand the absence of group defense techniques justifies the decline of warthog population, as predator fertility rate increases.

3.4.3 The effect of threshold (critical) population variability on prey sparsity and general dynamics

Stable spirals and limit cycles arise (Figures 3.5 and 3.6) as the predator handling time per prey (h) is reduced with increasing predator mortality at high predator fertility rates ($\epsilon_u = 2.4$). For lower values of the warthog threshold density, ϖ, asymptotic stability of the system is observed (Figure 3.3). Indeed, as asserted in Theorem 3.3.2, Figures 3.3, 3.4 and 3.7 show that the co-existence

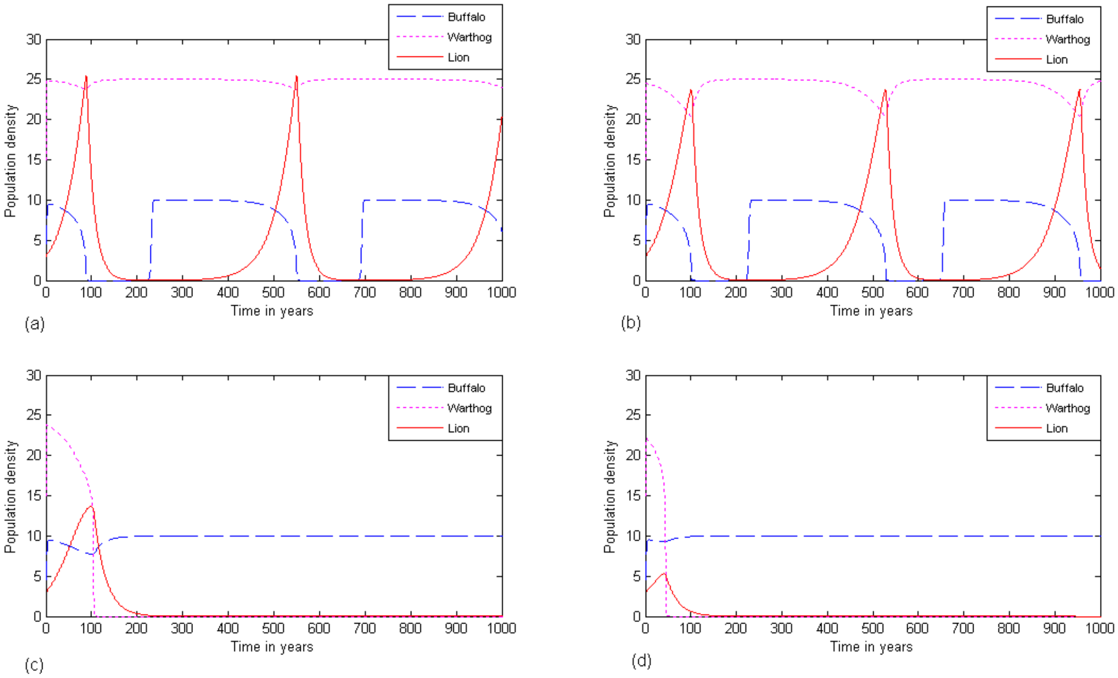

Figure 3.3: *The dynamical effect is shown as the threshold* $\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$ *is varied from (a)* 1.0, *(b)* 3.0, *(c)* 6.0 *and (d)* 10.0, *for a fixed low value of predator fertility rate* ($\epsilon_u = 0.8$).

equilibrium is locally asymptotically stable for lower values of ϖ, i.e., $\varpi < \frac{r_2 W^*(3W^*-2K_w)}{2r_2W^*-K_w(r_2+\alpha_2 L^*)}$. Local asymptotic stability of the co-existence equilibrium is maintained further for lower values of predator handling time (Figure 3.5). Though each threshold value exhibits deterministic chaos (Figure 3.4), predator chaotic smoothing is greater for lower prey threshold.

For a two-prey, one-predator system (3.1-3.3), oscillatory co-existence of the three species is possible only when both the predator fertility gain from the hard-to-capture prey and threshold values of the easy-to-capture prey are as low as possible (Figures 3.3 and 3.7). However, it should be noted that in general predator-mediated co-existence does not imply survival of all species in the system for any positive initial value (*permanence*) (Takeuchi, 1996).

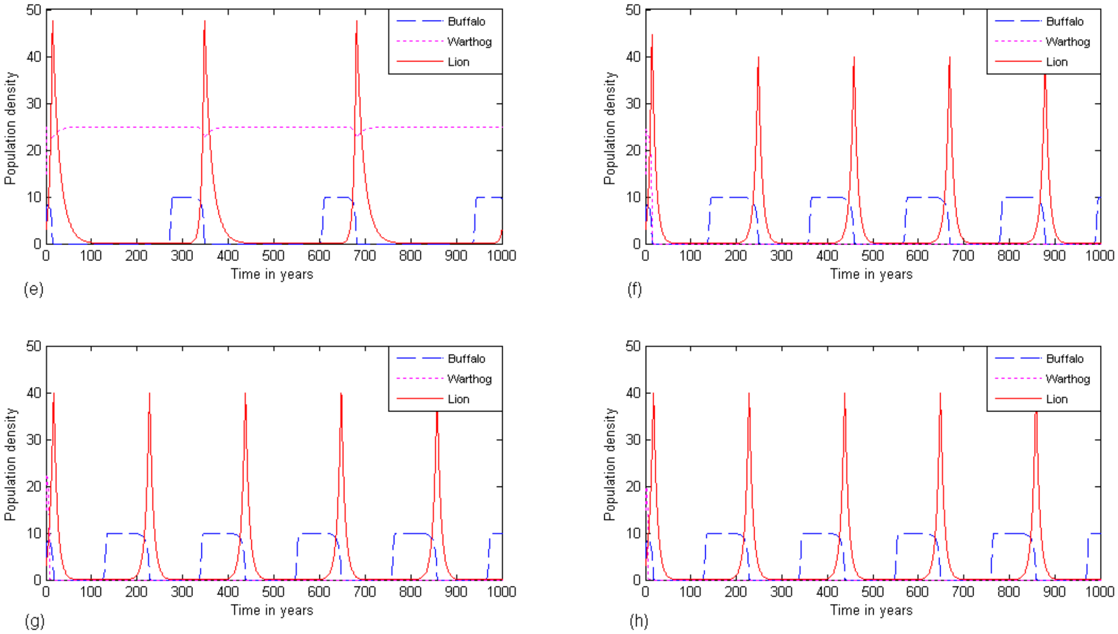

Figure 3.4: *The dynamical effect is shown as the threshold* $\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$ *is varied from (e)* 1.0, *(f)* 3.0, *(g)* 8.0 *and (h)* 10.0, *for a fixed high value of predator fertility rate* ($\epsilon_u = 2.4$).

3.5 Discussion

Analysing qualitatively and quantitatively the dynamical properties of a two-prey one predator system with a prey threshold, it is found that the predator fertility rate and prey population threshold bounds are crucial in determining the ecological trend of the system. As reported by Srinivasu *et al.* (2007) and van Baalen *et al.* (2001), this study also shows that the conversion efficiency (fertility rate, ϵ_u) of the buffalo biomass into lion offspring is vital in controlling the dynamics (existence and stability) of the steady states. The bounds of ϵ_u have been shown to depend on various factors among which include: carrying capacities of the ecosystem for buffalo and warthog (K_b and K_w), the sparsity constant (ϖ), natural mortality rate (μ_1), predation rate (α_1), efficiency of converting warthog biomass into lion biomass (β_1) and half saturation value $\left(\frac{1}{h}\right)$.

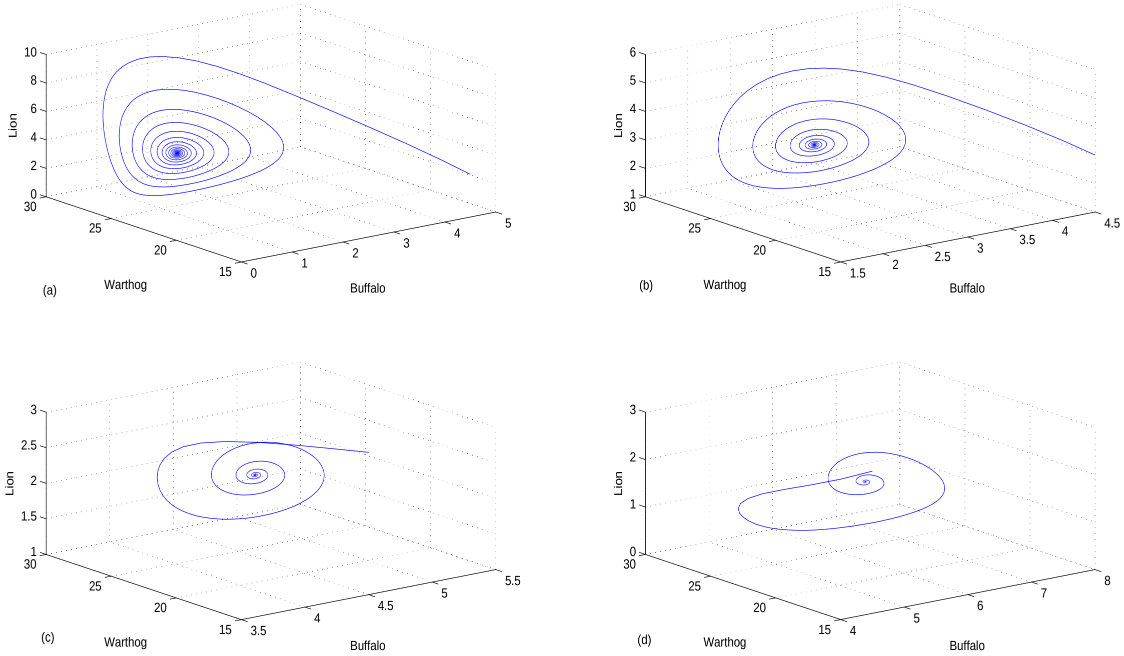

Figure 3.5: *Three dimensional typical closed predator-prey trajectories depicting spirals when* $h = 2.5 \times 10^{-5}$, $\epsilon_u = 2.4$, μ *being varied from (a)* 0.825, *(b)* 1.525, *(c)* 2.525 *and (d)* 3.525. *Any initial population and perturbations about the steady state tends to the steady state asymptotically.*

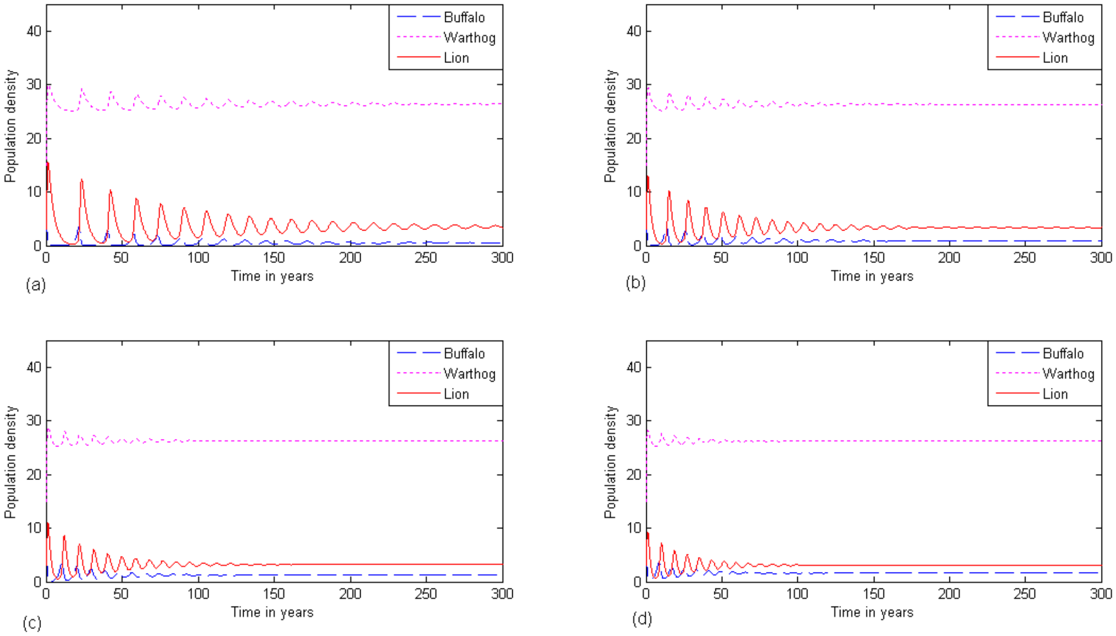

Figure 3.6: *The effect of half saturation value* ($\frac{1}{h}$) *and predator mortality rate for a high predator fertility value* ($\epsilon_u = 2.4$) *i.e., h & μ are varied from (a)* $h = 2.5 \times 10^{-5}, \mu = 0.225$ *(b)* $h = 2.5 \times 10^{-7}, \mu = 0.425$ *(c)* $h = 2.5 \times 10^{-9}, \mu = 0.625$ *and (d)* $h = 2.5 \times 10^{-12}, \mu = 0.825$, *while other model parameters are kept at their base values.*

Within the model framework, the author showed that the warthog-lion co-existence may always be attained by monitoring and varying the lion adaptation to warthog ratio $\left(\frac{1}{\beta} = \frac{\mu_1}{\beta_1 K_w}\right)$. This can be carried out through enhancement of warthog carrying capacity and lion fertility rate while ensuring that lion natural mortality is as low as possible. Furthermore, warthog-lion equilibrium existence reveals that critical threshold threats in warthog can be eliminated by controlling and regulating the effective mortality per capita ratio, $\left(\frac{\mu_1}{\beta_1}\right)$, for the lions, such that $K_w < \frac{\mu_1}{\beta_1} < \varpi$. This can be achieved after the warthog carrying capacity is well established and after focusing most conservation policies in the direction of the reversal of prey population declines (Mgqatsa, 2010; Nyafu, 2009). It is necessary to highlight here that the lion's limiting stabilisation factor, $\frac{2\mu_1}{\beta_1}$, which regulates the stability of warthog-lion equilibrium, and the effective mortality per capita ratio, $\frac{\mu_1}{\beta_1}$, which governs

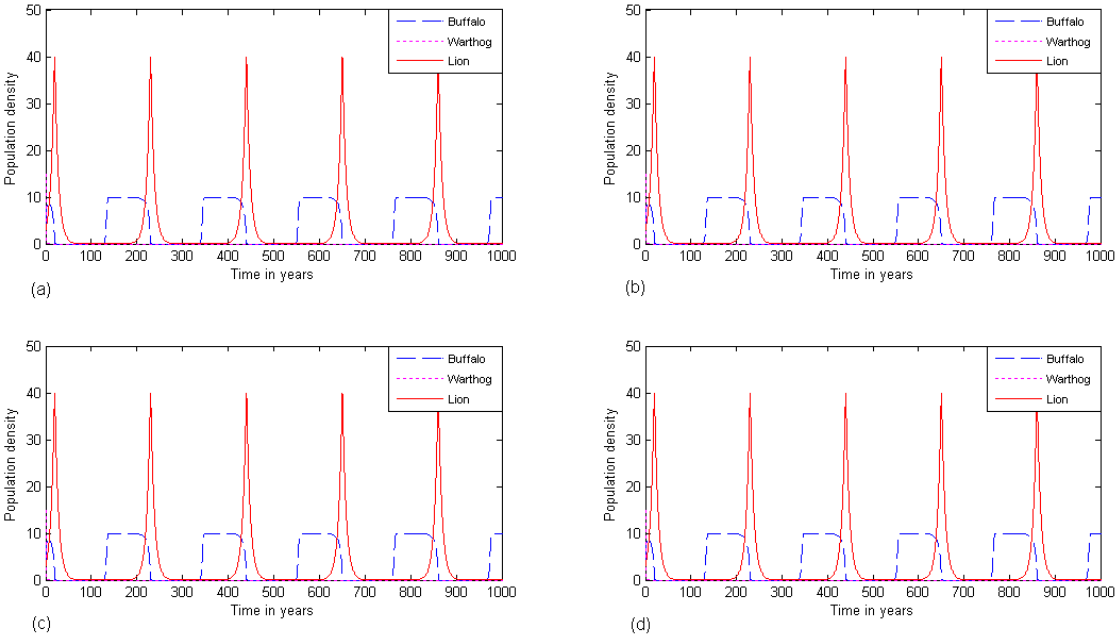

Figure 3.7: *The dynamical effect is shown as the threshold* $\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$ *when* $\epsilon_u = 2.4$, *is varied further to higher values, i.e.,* ϖ *is varied from (a)* 14, *(b)* 18, *(c)* 24 *and (d)* 50.

the warthog-lion equilibrium existence with or without critical population thresholds, are ecologically equivalent.

The buffalo-lion existence equilibrium has been shown to be controlled by the lower bound on the lion fertility rate i.e., $\epsilon_u > \frac{(hK_b+1)\mu_1}{\alpha_1 K_b}$. An increase in lion natural mortality leads to a higher lower bound, whereas an increase in predation rate decreases this lower bound. This result also indicates that the lion fertility lower bound could be increased through conservation policies that should be geared towards decreasing the lion half saturation value $\frac{1}{h}$, increasing predator handling time h, per prey. Using well known methods (Lehmann *et al.*, 2008; Packer *et al.*, 2001; Hunter, 1998), it may not be difficult to regulate and tune these parameters to the required levels for desirable positive outcomes of the ecosystem. For example, the natural mortality of lions may be increased by exposing them to vigilant prey, i.e., prey that form cohesive herds and exhibit group defense techniques, e.g., buffaloes. This could be done through game translocation programmes and/or controlled predator starvation policies such as creation of prey refugia within the game park (Srinivasu & Gayatri, 2005; Krivan, 1998; Sih, 1987; McNair, 1986). Predator handling time per prey may be regulated by controlling the quantity of prey: culling of warthogs in AENP is being carried out (Mgqatsa, 2010). Finally, providing the predator with prey of both high quality (nutritious) and quantity may help to enhance predator fertility rates. The results for the buffalo-lion equilibrium co-existence show that the carrying capacity of the buffalo has a passive effect on the predator lion fertility rate lower bound.

Results about the positive co-existence of the three species show that the lower bound of the warthog threshold value, $\varpi > \left[\sqrt{\frac{4K_w(\alpha_1 r_2+\alpha_2 r_1)}{\alpha_1 r_2}}\right] - K_w$, which depends on the predation rates, prey growth rates and warthog carrying capacity, plays a vital role. It should be observed that the lower bound for ϖ is much sensitive i.e., responds to variations, to lion predation rate (α_2) on the easy-to-capture prey (warthog) and intrinsic growth rate (r_1) of the hard-to-capture prey (buffalo), while an increase in warthog carrying capacity results in an overall relative decrease of the warthog threshold lower bound.

Stability and/or instability of equilibria has been shown to be controlled by bounds of the lion fertility rate and the warthog threshold constant. This has assisted to clearly link this study with the so-called paradox of enrichment which asserts that predation stabilizes predator-prey systems (Freedman & Wolkowicz, 1986; Rosenzweig, 1971). In parameter space, it has been shown that the paradox of enrichment can occur in the system (3.4-3.6) and subsequently in the system (3.1-3.3). Results from the buffalo-lion existence show that if the equilibrium existence is guaranteed, its stability follows by carefully controlling the lion's per capita saturation ratio as a result of feeding on a single *"average"* buffalo $\left(\frac{\mu_1}{\alpha_1 K_b}\right)$. Through conservation policies geared towards regulating buffalo carrying capacity, lion mortality and the reduction in its predation rate, the stability of the buffalo-lion co-existence could be achieved (Tambling *et al.*, 2011; Tambling *et al.*, 2009; Vale, 2007; Prins, 1996; Sinclair, 1977).

Local asymptotic stability of the positive co-existence equilibrium could be attained by maintaining the buffalo population density above half of its carrying capacity i.e., $B^* > \frac{1}{2}K_b$, while taking care of the upper bounds of K_w and ϖ as stated in Theorem 3.3.2. Furthermore, the warthog population density $W^* = \frac{2}{3}K_w$, has been shown to be a critical threshold value that maintains the system with either a weak critical threshold i.e., $W^* < \frac{2}{3}K_w$, or a strong critical threshold i.e., $W^* > \frac{2}{3}K_w$. On the other hand, global stability analysis results show that the warthog population density should exceed the sum of its carrying capacity and threshold value minus its equilibrium value i.e., $W > (K_w + \varpi) - W^*$. This result which was proved in Theorem 3.3.3 about the global stability of the co-existence steady state shows that the warthog's equilibrium population density is bound above, i.e., $W^* < (K_w + \varpi)$. Despite its high fecundity, the warthog's natural desire to expand its range (Nyafu, 2009) may lead to very low values of its threshold density and this leads to the so-called prey out-flux dilution effect (Sherratt *et al.*, 1997). Thus, if such species' range expansion tendencies are not controlled (regulated), their equilibrium population value will always be below the carrying capacity which ultimately implies that further population out-fluxes/emigration may cause the species' population to slip to extinction sooner or later. The strong electric fencing that is closely monitored daily by AENP game rangers does not provide any escape route for warthogs, as is the case for other game reserves (Mgqatsa, 2010; Urquhart *et al.*, 1997). Thus, a random culling policy of warthog is being done within the park (Mgqatsa, 2010). Currently, unpublished AENP data show that between $20\% - 40\%$ of warthogs are being culled per year to keep the population fairly stable. Warthog culling policies in AENP which may lead to the out-flux dilution effect should take into consideration the species' threshold densities (depending on various parameters) if stability is to be realised. Based on the model analysis results, the reproduction and predation rates together with the warthog carrying capacity should be well established before carrying out any culling programme. Numerical results show that Model system (3.1-3.3) is highly sensitive to predator fertility rate, especially when its lower bound is relatively high. Such high predator fertility lower bounds have depicted results (Figures 3.2, 3.4 and 3.7) of chaotic oscillations that lead to eventual extinction of the easy-to-capture prey. Both numerical and analytical results seem to concur about the bounds of the predator fertility rates and sparsity constant. In this study, as reported by Bazykin (1998) and Takeuchi (1996), it has been shown (Theorem 3.3.1) that the formulated model is dissipative and uniformly persistent; early indicators of chaos, as a result of high predator fertility rates, have been deduced from the spikelike predator oscillations (Figures 3.2(g) and (h), 3.4 and 3.7).

The practical management of population numbers, whether aiming to increase or reduce them, is strongly affected by threshold values (Courchamp *et al.*, 2008). Even those species displaying no obvious population depensation can be affected by others that do, which means that most species are probably influenced, either directly or indirectly by the dynamics of other species in an ecosystem. Biodiversity preservation and population management at ecosystem level have much to gain from acknowledging vital processes, mechanisms and factors controlling species interaction (Courchamp *et al.*, 2008; Petrovskii *et al.*, 2005; McCarthy, 1997; Dennis, 1989). Such mechanisms can be mimicked and calls for basic robust population dynamic models that are comparable to the classical Verhulst-Pearl *logistic* model (Berryman, 1992).

Under stochastic events, providing additional food and prey refuge are some of the popular remedies being speculated on to yield an ultimate solution to predator-prey ecosystem challenges by some empirical conservationists. The effects of additional food to a predator, prey refuge, culling of prey, spatial distribution of species and incorporation of another predator in the model remain naturally interesting scenarios to be pursued in future for new and rich ecosystem dynamical trends to be generated. In the absence of the aforementioned dynamics, the theoretical mathematical model in this study/chapter acts as a buffer that may be used to understand the dynamical behaviour of a two-prey one-predator system. In the next chapter, a numerical excursion of the dynamical effects of incorporating a prey refuge and providing additional food to the predator of Model system (3.1-3.3) is carried out.

Chapter 4

Modelling additional food to predator and prey refuge

4.1 Introduction

The aim of this chapter is to numerically bring more dynamics to the fore, and this is done by performing numerical simulations to analyse the effect of prey refuge for the easy-to-capture prey (warthog) and additional food to the predator. The diurnal activities of warthog species exposes them to many predation risks, and as a way of hiding from predators, the warthog live in self-excavated or disused aardvark burrows (Mgqatsa, 2010; Somers & Penzhorn, 1992; cf. Section 3.1). While buffaloes depend on group defense, group vigilance and group alertness as ways of minimizing predation risks, moving to the burrows is among the common anti-predator behaviour exhibited by warthogs (Tambling *et al.*, 2011; Nyafu, 2009; White & Cameron, 2009; Prins, 1996). Thus, warthogs are either in the burrows (refuge patch) or in the open habitat. With the assumption that warthog species use the refugia (burrows) in order to maximize their fitness, measured by instantaneous per capita growth rate, the effect of such warthog burrows as a prey refuge patch is modelled and numerically studied.

According to Krivan (1998), prey move to a patch where their mortality rate to energy intake rate ratio is minimized, the *minimize death per unit energy rule*. Since refugia, the warthog burrows, are safe but do not offer feeding or mating opportunities, prey must balance energy gain against the risk of predation in deciding where and when to feed (White & Cameron, 2009; Dao-Duc *et al.*, 2008). One of the major components of risk is the time spent in the open habitat where the probability of an encounter with a predator is high. Furthermore, if the per capita intrinsic growth rate in the refuge is lower than in the open habitat, then this leads to a classic trade-off dilemma for prey: stay in a safer but less profitable refuge or move to a more profitable but riskier open habitat (Krivan, 1998; Lima & Dill, 1990; Sih, 1987; McNair, 1986).

A refuge is characterised by its *protectiveness* which is inversely related to the product of the attack rate of predators in the refuge and the probability that a predator will access it (Krivan, 1998). Sih (1987) showed that if the proportion of prey in the refuge is decreasing with increasing prey abundance, or increasing with both increasing predator density or increasing predation pressure, then the corresponding ecological equilibrium is locally stable.

Two types of refugia are commonly modelled (Krivan, 1998; Sih, 1987; McNair, 1986): those that protect a constant fraction and those that protect a constant number of prey. In this study, ω_r was considered as a constant fraction of warthog that gets into the burrows (refugia) while $1 - \omega_r$ is the fraction in the open patch that is vulnerable to predation. Though the consequences of refuge type for stability of predator-prey interactions depends on the underlying model (Krivan, 1998; McNair, 1986), the general conclusion from such studies is that refugia which protect a constant number of prey lead to a stable equilibrium and have a stronger stabilizing effect on population dynamics than refugia which protect a constant proportion of prey. This sounds like a hypothesis that should be explored in detail.

In the study of biological control through provision of additional food to predators, Srinivasu *et al.* (2007) addressed the consequences of providing additional food to predators on the predator-prey system dynamics. They showed that varying the quality and quantity of additional food not only controlled and limited the prey, but could also limit or eradicate the predator. Thus, the predator population can be reduced or eliminated by providing it with some additional food of scientifically proven quality and quantity. Such qualitative and quantitative attributes of additional food are modelled with various parameters ranging from the handling time of the predator per unit quantity of added food biomass, to predator fertility. This is because, the ratio of predator handling times for the additional food and prey was observed to play a key role in the controllability of the ecosystem (Srinivasu *et al.*, 2007; van Baalen *et al.*, 2001). Thus, any arbitrary choice of additional food to the predator-prey system may have a negative influence on the now destabilised ecosystem.

The Model system (3.1-3.3) is considered except that ω_r is the proportion of prey species that goes to refugia (burrows burrows for the warthog species) at time τ has been incorporated. Suppose that F_l is the ratio of additional food biomass to normal prey biomass required for predators (lion) survival and that ϵ_{fl} is the efficiency with which the additional food biomass is converted into predators' biomass, energy or fertility gain of predator. Maintaining the remaining parameters and variables' descriptions as defined in Section 3.2, the Model system (3.1-3.3) is extended to obtain the following:

$$\frac{dB}{d\tau} = r_1 B\left(1-\frac{B}{K_b}\right) - \alpha_1\frac{(1-F_l)BL}{1+hB} \tag{4.1}$$

$$\frac{dW}{d\tau} = r_2 W\left(1-\frac{W}{K_w}\right)\left(\frac{W}{\varpi}-1\right) - \alpha_2(1-F_l)(1-\omega_r)WL \tag{4.2}$$

$$\frac{dL}{d\tau} = \beta_1(1-F_l)(1-\omega_r)WL + \epsilon_u\frac{\alpha_1(1-F_l)BL}{1+hB} + \epsilon_{fl}F_lL - \mu_1 L \tag{4.3}$$

where; $0 < \omega_r < 1$ and $0 < F_l < 1$

Qualitative analysis of the Model system (4.1-4.3) can be carried out easily, by once again reducing the number of parameters. By introducing the following dimensionless variables:

$$x = \frac{B}{K_b}, \quad y = \frac{W}{K_w}, \quad z = \frac{\alpha_1}{\mu_1}L, \quad t = \mu_1\tau$$

to equations (4.1-4.3), the following non-dimensional model is obtained:

$$\frac{dx}{dt} = rx(1-x) - \frac{(1-F_l)xz}{1+\phi x} \tag{4.4}$$

$$\frac{dy}{dt} = \lambda y(1-y)(ky-1) - \alpha(1-F_l)(1-\omega_r)yz \tag{4.5}$$

$$\frac{dz}{dt} = \beta(1-F_l)(1-\omega_r)yz + \gamma\frac{(1-F_l)xz}{1+\phi x} + (\theta-1)z \tag{4.6}$$

The model behaviour is now controlled by the following dimensionless parameters:

$$r = \frac{r_1}{\mu_1}, \quad \lambda = \frac{r_2}{\mu_1}, \quad \phi = hK_b, \quad k = \frac{K_w}{\varpi}, \quad \alpha = \frac{\alpha_2}{\alpha_1}, \quad \beta = \frac{\beta_1 K_w}{\mu_1}, \quad \gamma = \frac{\epsilon_u \alpha_1 K_b}{\mu_1}, \quad \theta = \frac{\epsilon_{fl} F_l}{\mu_1}$$

As studied in Chapter 3 (Model (3.4-3.6)), a similar qualitative analysis of the Model system (4.4-4.6) is anticipated to yield similar results. In this chapter however, only numerical simulations of Model (4.1-4.3) are explored. Apart from parameters to cater for predator additional food and prey refuge, the rest of other parameter value sources are as summarised in Table 3.2.

4.1.1 How prey refuge effectiveness responds to predator fertility gain from additional food

In spite of providing additional food to the predator, the three species' system is not sustainable at very low proportion of warthog in burrows (Figure 4.1(a)). This shows that the refuge is beneficial to both predator and prey. Oscillatory behaviour are observed (Figures 4.1(b) and (c)) for all the three species when intermediate proportions of prey (warthog) get into the refuge. As motivated earlier, by and large, the warthog's trade-off dilemma of safety versus energy intake and population growth lead to such oscillatory pulses in the species ecosystem. Due to the *protectiveness* nature of the refuge, these oscillations are higher for the prey that goes to the refuge. When the value of ω_r (proportion of prey that goes to refugia) is reasonably high (Figure 4.1(d)), the predator-prey system stabilizes. Despite considering a constant fraction of prey to refugia as opposed to a constant number, as in Chen *et al.* (2010), Srinivasu and Gayatri (2005) and McNair (1986), the prey refuge causes a stabilizing effect on the predator-prey system.

4.1.2 The effect of additional food: The paradox of biological control and the species' pathological behaviour

The value of predator fertility i.e., offspring production as a result of energy gained and converted into predator reproduction, is used as a measure of the quality of predator additional food and/or prey. The high quality of supplementary food in the model eliminates the observed oscillations (Figure 4.1) for intermediate values of ω_r. Figure 4.2(d), as noted in Srinivasu *et al.* (2007), Sabelis

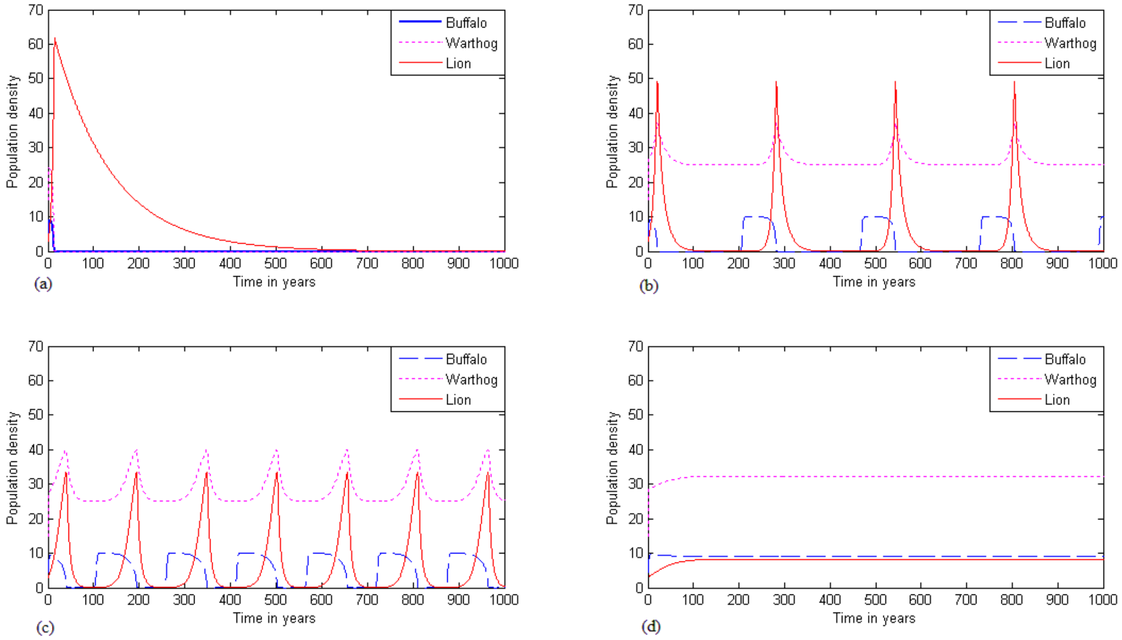

Figure 4.1: *The dynamical effect of a constant proportion prey refuge when additional food ratio* $F_l = 0.195$ *with a predator fertility gain* $\epsilon_{fl} = 0.6$*. The proportion of prey that goes to refugia* (ω_r) *is varied from (a)* 0.06*, (b)* 0.2*, (c)* 0.3 *and (d)* 0.4*, while other model parameters are maintained at their base values as depicted in Table 3.2 and the initial population density for each species is chosen to be positive at:* $B(0) = 4.5,\ W(0) = 15.0$ *and* $L(0) = 3.0$.

and van Rijn (2005) and Murdoch *et al.* (1985), shows that the biological control theory gets evoked at high fertility gain. This figure shows that too much consumption of both added food and prey by a predator causes a decline in the species' population. Despite such population declines, the presence of a prey refuge helps to maintain its population above extinction zones.

4.2 Discussion

The number of prey in a refugia being a constant fraction of the total prey population makes the nature of the equilibrium of the Model system (4.1-4.3) to be preserved. The refugia has a stabilizing

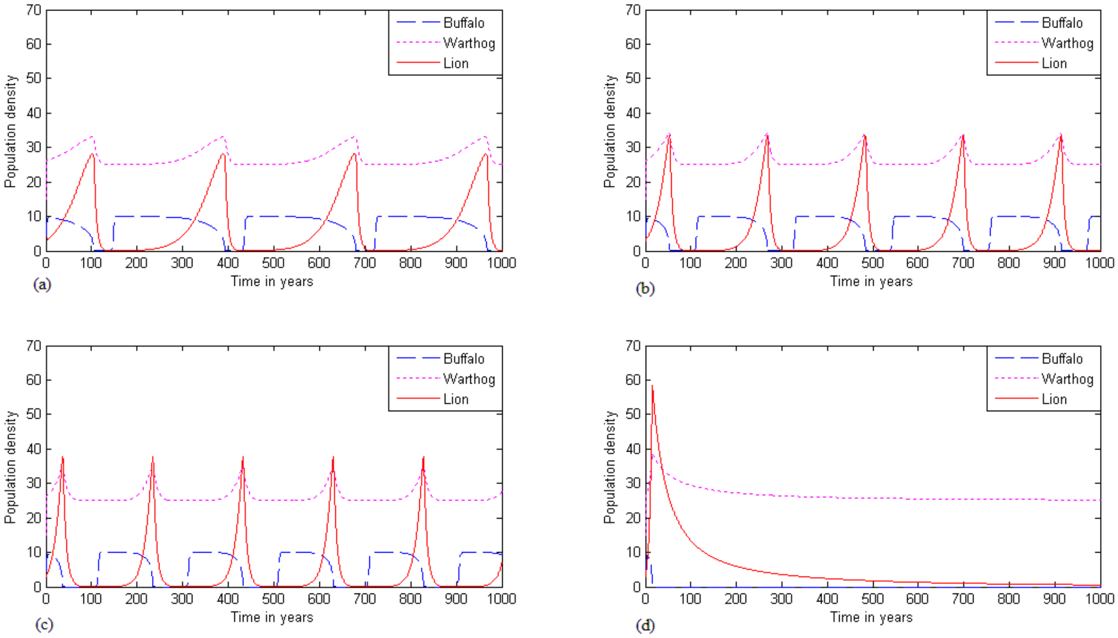

Figure 4.2: *The dynamical effect of a constant proportion prey refuge when additional food ratio* $F_l = 0.195$, *refuge proportion* $\omega_r = 0.2$ *and predator fertility gain* ϵ_{fl}, *being varied from (a)* 0.0006, *(b)* 0.125, *(c)* 0.25 *and (d)* 0.9, *while other model parameters are maintained at their base values as depicted in Table 3.2 and the initial population density for each species is chosen to be positive at:* $B(0) = 4.5$, $W(0) = 15.0$ *and* $L(0) = 3.0$.

effect, since it changes a conservative oscillation into a convergent oscillation. The importance of a refuge in regulating predation rates has been observed (Figures 4.1). This follows from the observed decline, Figure 4.1(a), in populations of the interacting species at low proportion, depending on burrow availability, of warthog in refuge.

Chapter 5

Predator Interference, Additional Food: Lions and Spotted hyaenas

5.1 Introduction

During conservation and management of predator-prey ecosystems, the provision of additional food to predators is one of the options available (Srinivasu *et al.*, 2007; van Baalen *et al.*, 2001). Such additional food is provided for several reasons, among which include the distraction of predators from over-consuming the prey (short term) or increasing the rate of predation (long term), for example, during biological control of pests (Srinivasu *et al.*, 2007). Thus, it turns out that providing additional food to predators must be well formulated for, if unplanned, it may lead to many unexpected and undesired effects on the ecosystem. This calls for careful analysis of the various possible outcomes by both theoretical and empirical conservationists, before providing predators with any form of additional food. The use of ecologically plausible mathematical models has been identified as an efficient way to predict future ecosystem trends (Sabelis & van Rijn, 2005; van Baalen *et al.*, 2001; Murdoch *et al.*, 1985).

Various theoretical studies have shown that it is possible to control the dynamics of an ecosystem by manipulating the quality and supply level (quantity) of additional food to the predators (Srinivasu *et al.*, 2007; Sabelis & van Rijn, 2005; van Baalen *et al.*, 2001). These studies also showed that additional food can drive the prey and predators to desired population levels within specified limits. For example, oscillations can be introduced into the ecosystem or they can be controlled and eliminated by an appropriate choice of additional food (Srinivasu *et al.*, 2007). The paradox of enrichment, permanence and persistence of a system can always be achieved via a suitable choice (depending on numerous parameters of the ecosystem) of additional food (Gaucel & Pontier, 2005; Freedman & Wolkowicz 1986). The type of additional food provided to predators can help eliminate the prey (right food provided to predators), or eliminate the predators by distracting them with a supply of low-quality additional food at high density, which decreases the per capita growth rate of the predator below its starvation rate and this relieves the prey from predation pressure (Srinivasu *et al.*, 2007).

As mentioned in Chapter 1, six lions and eight spotted hyaenas were introduced into Addo Elephant National Park's main camp section in late 2003 to fulfill the role of restoring the natural balance to the ecosystems in the park by controlling the numbers of herbivores (Hayward & Hayward, 2006). Though hyaenas scavenge and steal carrion from other predators (e.g., lions), detailed research reveals that spotted hyaenas are not mere scavengers but are also efficient predators (Wentworth *et al.*, 2011; Hayward, 2006; Hayward & Hayward, 2006; Kruuk, 1972). Within AENP, lion and spotted hyaena activity patterns overlap 75.1% of the time and this is attributed to the low density of each species (0.04 lions km^{-2} and 0.07 spotted hyaenas km^{-2}) (Hayward & Hayward, 2006). As a result of high level of aggression toward each other and having the same activity pattern i.e., killing similar prey at similar times of the day, lions and spotted hyaenas have been identified as the most intense competitors (Hayward & Kerley 2008).

Lions and spotted hyaenas, which are generalist predators that attack multiple prey species with no significant differences between their prey preferences, have been studied assiduously throughout Africa. "The ecology and dietary niche breadth of the spotted hyaena is similar to that of the lion. The two species have a 58.6% actual prey species overlap and a 68.8% preferred prey species overlap" (Hayward, 2006). Despite a large degree of dietary overlap with lions, the spotted hyaena's dietary flexibility and mobility make it one of the most successful predators throughout Africa (Hayward, 2006). Due to their size and team work, the spotted hyaena is capable of taking kills from other carnivores including lions. This incites a competitive relationship between the two species for the available prey (Wentworth *et al.*, 2011). Spotted hyaenas are opportunistic and hunt a wide variety of prey ranging from small mammals to large ungulates; having a preferred body mass range of 56 – 182 kg (Hayward, 2006). On the other hand, the lion, being the largest African carnivore and distinctly social, living in prides of 6 to 12 individuals, is the principal predator of various herbivore species. The lion is capable of pulling down prey the size of a mature buffalo and/or a fully grown giraffe (Lehmann *et al.*, 2008). However, on several occasions lions steal spotted hyaena's kills and carrion, and this results into fierce competition that often results into death (Hayward & Kerley, 2008; Hayward & Hayward, 2006; Hayward, 2006).

The predator's preferences for various prey species has been attributed to various reasons such as herding, easy to capture, abundance, biomass gain per prey killed, taste, hunting risks involved, total handling time and searching effort (Hayward *et al.*, 2007*a*; Hayward & Kerley, 2005; Khan *et al.*, 2004). Within AENP, the buffalo and kudu are highly preferred by both lion and hyaena due to their yield in terms of biomass per killed prey (Hayward, 2006; Hayward & Hayward, 2006; Hayward & Kerley, 2005). However, because of high predation/hunting risks involved as a result of its strength and group vigilance, the buffalo is often avoided by both predators in favour of the kudu which is largely abundant (Hayward, 2011; Prins, 1996; Sinclair, 1977). Thus, lions and spotted hyaenas have a competitive feeding pattern on the kudu that results in interspecific species' interference (Hayward, 2006; Hayward and Hayward, 2006; Franklin, 2005).

On the small private game reserves: Shamwari and Kwandwe, within the vicinity of AENP, predators are provided with supplementary feeding (Hayward *et al.*, 2007*c*). The private farmers buy game for their predators. Due to a limited number of prey species within AENP, providing additional food to predators is one of the conservation principles that would reduce predation pressure. This has been done on various neighbouring private game reserves. Supplementary feeding was among the occasional management interventions that followed species' translocation and reintroduction within the Eastern Cape Province (Hayward *et al.*, 2007*c*). The weak, malnourished and struggling predators would occasionally be provided with additional food. For example, the lionesses at AENP were provided with culled warthog carcasses as they were struggling to keep young cubs alive (Hayward *et al.*, 2007*c*).

This chapter considers the interaction and dynamics of two predatory carnivores, lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) feeding on a common prey resource, kudu (*Tragelaphus strepsiceros*) which is one of the most preyed upon species and highly preferred by both lions and spotted hyaenas in AENP (Hayward *et al.*, 2007*a*; Hayward & Kerley, 2005). Being one of the most abundant prey species in South Africa's Eastern Cape Province, kudus are killed by lions more frequently as shown by the Jacob's index computations (Hayward *et al.*, 2007*a*; Hayward & Kerley, 2005). According to Hayward *et al.* (2007*a*), the relative abundance of kudus within the Eastern Cape Province makes it an optimal strategy to be preferentially hunted by lions.

Encounters between lions and hyaenas and large prey species, in this instance, kudus, involve a lot of dynamics due to adopted anti-predator techniques. As discussed earlier, most individual lions refrain from contributing to group hunts except when pursuing buffaloes, which are inaccessible to solitary individual lions (Hayward *et al.*, 2007*a*, *b*; Fryxell *et al.*, 2007; Hayward & Kerley, 2005). However, the abundant and conspicuous kudus within AENP are vigilant and depend on the group alertness for early warning in case of any sighted predator (Hayward & Kerley, 2005). Despite being ambushed and subdued most often by stalking predators, kudus basically depend on crypsis and their high cruising speed to escape from any predator (Owen-Smith, 1990; Holling, 1965).

The first mathematical studies, after 1970, to reveal the principle of competitive exclusion considered models based upon a combination of the principle of mass action and Holling Type II functional and numerical responses (Muratori & Rinaldi 1989; Armstrong & McGehee 1980; Hsu *et al.*, 1978*a*, *b*). Despite the predominance of strictly prey-dependent functional responses (e.g., Holling family types) in the literature, recent studies (Chen *et al.,* 2008; Inchausti & Ballesteros, 2008; Cantrell *et al.*, 2004; Hsu *et al.*, 2001; Cantrell & Cosner, 2001; Cantrell *et al.*, 1998) have suggested the ratio-dependent, Beddington-DeAngelis functional response (i.e., $\frac{cxy}{1+ax+by}$) and reaction-diffusion to explain the spatial-temporal variations in species. Many studies have considered various approaches when modelling anti-predator behaviour of the numerous prey species (Seo & Kot, 2008; Khan *et al.*, 2004; Cantrell & Cosner, 2001). The response function used depends on the vigilance, mobility and intensity of prey species in relation to its predators. In this chapter, predator-prey dynamics is modelled using the Beddington-DeAngelis functional response that considers: additional food, interspecific interference of predators and group vigilance behaviour of the prey (Cantrell & Cosner, 2001).

This chapter is organised as follows; In Section 5.2 an explanation of the meaning of variables, constants and parameters, and the assumptions they satisfy and model formulation together with non-dimensionalisation were done. In Section 5.3, analysis of the existence and stability of the steady states of the model was carried out. Local stability of all steady states and global stability of the interior equilibrium were investigated in this section. Biological interpretation of the results is presented in Section 5.4. Numerical results are given in Section 5.5 and in the last section, a brief discussion and conclusion of results is provided.

In this chapter, a mathematical model used to understand the predation behaviour of two predators (lion and spotted hyaena) versus one prey (kudu) without a prey refuge but with additional food to predators was formulated and analysed.

5.2 Description and formulation of the model

A mathematical model for two predators (lions, $L(\tau)$ and spotted hyaenas, $H(\tau)$) that experience interspecific interference as they feed on a common prey resource (kudu, $B(\tau)$) at any time τ, is formulated. The underlying cost-benefit that arises as a result of additional food to predators is crucial in this study. Spatial heterogeneity of species is incorporated via a reaction-diffusion model in which a one dimensional situation is assumed that could be extended to the usual two dimensional domain of the game park.

Through this section, the parameter subscripts b, h and l refer to kudu, hyaena and lion dynamics, respectively. Thus, the author defines: predation rates α_h and α_l, interspecific interference coefficients ψ_h and ψ_l, additional food, which we define as the ratio of added food biomass to normal prey biomass required for predator survival and reproduction, F_h and F_l, fertility factors, as a result of newly born predators due to predation, and consumption of additional food, $\epsilon_h,\ \epsilon_l,\ \epsilon_{f_h}$ and ϵ_{f_l}, mortality rates

μ_h and μ_l, and half saturation constants $\frac{1}{a_h}$ and $\frac{1}{a_l}$ of predators are defined accordingly. Further, the kudu population density grows with intrinsic growth rate r_b and has K_b as its ecosystem carrying capacity.

Using definitions of the variables and parameters as described in the paragraph above, together with the assumptions and management approaches, the temporal dynamics of the predator-prey system is explicitly described by the following coupled system of differential equations in which the functional and numerical responses for both consumers and the resource are taken to have Beddington-DeAngelis forms:

$$\frac{dB}{d\tau} = r_b B\left(1-\frac{B}{K_b}\right) - \frac{\alpha_h(1-F_h)BH}{1+a_hB+\psi_lL} - \frac{\alpha_l(1-F_l)BL}{1+a_lB+\psi_hH} \tag{5.1}$$

$$\frac{dH}{d\tau} = \frac{\epsilon_h\alpha_h(1-F_h)BH}{1+a_hB+\psi_lL} - \mu_hH + \epsilon_{f_h}F_hH \tag{5.2}$$

$$\frac{dL}{d\tau} = \frac{\epsilon_l\alpha_l(1-F_l)BL}{1+a_lB+\psi_hH} - \mu_lL + \epsilon_{f_l}F_lL \tag{5.3}$$

where all parameters and constants are positive, $0 \leq F_h \cong F_l \leq 1$ and the underlying initial conditions $B(0) = B_0 \geq 0,\ H(0) = H_0 \geq 0$ and $L(0) = L_0 \geq 0$ are satisfied.

5.3 Analysis of the model

5.3.1 Non-dimensionalisation of the model

To give an insight into the relative magnitudes of the parameters required to yield biologically realistic behaviour and to ease comparison between disparate quantities and analogous parameters and to avoid mathematical complexity, the number of parameters was reduced by introducing the following dimensionless variables (cf. Table 5.1):

$$u = \frac{B}{K_b},\quad v = \frac{\alpha_h}{\mu_h}H,\quad w = \frac{\alpha_l}{\mu_l}L,\quad t = \mu_l\tau$$

Introducing the following chain rule expressions for the temporal variations:

$$\frac{dB}{d\tau} = \frac{dB}{du}\times\frac{du}{dt}\times\frac{dt}{d\tau},\qquad \frac{dH}{d\tau} = \frac{dH}{dv}\times\frac{dv}{dt}\times\frac{dt}{d\tau}\quad \&\quad \frac{dL}{d\tau} = \frac{dL}{dw}\times\frac{dw}{dt}\times\frac{dt}{d\tau}$$

Table 5.1: *Dimensions of variables and parameters; ρ & T defining the dimensions of population density and time respectively.*

Variables	**Dimension**		**Parameters**	**Dimension**
$B,\ H,\ L$	ρ		$r_b,\ \mu_h,\ \mu_l,\ \epsilon_{f_h},\ \epsilon_{f_l}$	T^{-1}
τ	T		K_b	ρ
			$\alpha_h,\ \alpha_l$	$\rho^{-1}T^{-1}$
			$a_h,\ a_l,\ \psi_h,\ \psi_l$	ρ^{-1}
			$F_h, F_l, \epsilon_h, \epsilon_l$	dimensionless

results in

$$\frac{dB}{dt} = K_b\mu_l\frac{du}{dt},\quad \frac{dH}{dt} = \frac{\mu_h\mu_l}{\alpha_h}\frac{dv}{dt} \quad \& \quad \frac{dL}{dt} = \frac{{\mu_l}^2}{\alpha_l}\frac{dw}{dt}$$

Substituting these results into the model equations for the dimensionalised system (5.1-5.3) yields

$$\frac{du}{dt} = ru\,(1-u) - \frac{\mu\eta_h uv}{1+\phi_1 u+\psi_2 w} - \frac{\eta_l uw}{1+\phi_2 u+\psi_1 v} \equiv \hat{f}(u,v,w) \tag{5.4}$$

$$\frac{dv}{dt} = \frac{\gamma_1\eta_h uv}{1+\phi_1 u+\psi_2 w} - \mu v + \beta_1 v \equiv \hat{g}(u,v,w) \tag{5.5}$$

$$\frac{dw}{dt} = \frac{\gamma_2\eta_l uw}{1+\phi_2 u+\psi_1 v} - w + \beta_2 w \equiv \hat{h}(u,v,w) \tag{5.6}$$

whose behaviour is controlled by the dimensionless parameters

$$r = \frac{r_b}{\mu_l},\quad \mu = \frac{\mu_h}{\mu_l},\quad \eta_h = 1-F_h,\quad \eta_l = 1-F_l,\quad \phi_1 = a_h K_b,\quad \phi_2 = a_l K_b,\quad \psi_1 = \frac{\psi_h\mu_h}{\alpha_h},\quad \psi_2 = \frac{\psi_l\mu_l}{\alpha_l}$$

$$\gamma_1 = \frac{\epsilon_l\alpha_l K_b}{\mu_l},\quad \gamma_2 = \frac{\epsilon_h\alpha_h K_b}{\mu_l},\quad \beta_1 = \frac{\epsilon_{f_h}F_h}{\mu_l},\quad \beta_2 = \frac{\epsilon_{f_l}F_l}{\mu_l}$$

A glance at the dimensionless parameters above reveals similar pairs. And therefore, considering this symmetry, some dimensionless parameters and constants are clearly products and/or quotients of approximately analogous dimensional parameters/constants leading to the following approximations:

$$\eta_h \simeq \eta_l = \eta,\quad \phi_1 \simeq \phi_2 = \phi,\quad \psi_1 \simeq \psi_2 = \psi,\quad \gamma_1 \simeq \gamma_2 = \gamma,\quad \beta_1 \simeq \beta_2 = \beta$$

Employing the above approximations reduces the non-dimensionalised model to

$$\frac{du}{dt} = ru\left(1-u\right) - \frac{\mu\eta uv}{1+\phi u+\psi w} - \frac{\eta uw}{1+\phi u+\psi v} \equiv \hat{f}(u,v,w) \tag{5.7}$$

$$\frac{dv}{dt} = \frac{\gamma\eta uv}{1+\phi u+\psi w} - \mu v + \beta v \equiv \hat{g}(u,v,w) \tag{5.8}$$

$$\frac{dw}{dt} = \frac{\gamma\eta uw}{1+\phi u+\psi v} - w + \beta w \equiv \hat{h}(u,v,w) \tag{5.9}$$

Since u, v and w define population densities, only non-negative solutions make biological sense. The functions of system (5.7-5.9) are Lipschitzian and continuous on the positive octant $\mathbb{R}^3_+ = \{(B,H,L) \in \mathbb{R}^3 : B(0) \geq 0,\ W(0) \geq 0 \ \&\ L(0) \geq 0\}$ and therefore, only positive solutions of the model on the invariant interior of $\mathbb{R}^3_+$ are considered.

5.3.2 Steady states of the model

The steady states of the non-dimensionalised Model system (5.7-5.9) are solutions for the following equations:

$$ru^*\left(1-u^*\right) - \frac{\mu\eta u^*v^*}{1+\phi u^*+\psi w^*} - \frac{\eta u^*w^*}{1+\phi u^*+\psi v^*} = 0 \tag{5.10}$$

$$\frac{\gamma\eta u^*v^*}{1+\phi u^*+\psi w^*} - \mu v^* + \beta v^* = 0 \tag{5.11}$$

$$\frac{\gamma\eta u^*w^*}{1+\phi u^*+\psi v^*} - w^* + \beta w^* = 0 \tag{5.12}$$

which allow five equilibrium points of the Model system under this study, $E_0\left(0,0,0\right)$, $E_1\left(1,0,0\right)$, $E_2\left(\frac{\Phi}{\eta\gamma-\phi\Phi}, \frac{r\gamma(\eta\gamma-\Phi(1+\phi))}{\mu[\eta\gamma(\eta\gamma-2\phi\Phi)+\phi^2\Phi^2]}, 0\right)$, $E_3\left(\frac{\Psi}{\eta\gamma-\phi\Psi}, 0, \frac{r\gamma(\eta\gamma-\Psi(1+\phi))}{[\eta\gamma(\eta\gamma-2\phi\Psi)+\phi^2\Psi^2]}\right)$ and $E_4\left(u^*,v^*,w^*\right)$, where $\Phi = \mu-\beta$ and $\Psi = 1-\beta$.

Proposition 5.3.1 *Model system (5.7-5.9) is dissipative, uniformly persistent and hence permanent.*

Before proving the proposition, the following preliminary definitions, which ensure the survival of the interacting biological species, for an ordinary differential equation model $\dot{\mathbf{x}} = \mathbf{x}\mathbf{f}(\mathbf{x})$, where $\mathbf{x}(t)$ is a vector that denotes the density/biomass of n interacting species are stated first (Takeuchi, 1996). Suppose $\mathbf{x}(t) = (x_1(t), x_2(t), ..., x_n(t))$ is a solution of the model with component-wise positive initial values, then the system is said to be:

(i) weakly persistent if $\lim\limits_{t\to\infty} Sup\ x_i(t) > 0$ for all $i = 1, 2, ..., n$

(ii) persistent if $\lim\limits_{t\to\infty} Inf\ x_i(t) > 0$ for all $i = 1, 2, ..., n$

(iii) uniformly persistent if there exists an $\epsilon > 0$ such that $\lim\limits_{t\to\infty} Inf\ x_i(t) \geq 0$ for all $i = 1, 2, ..., n$

(iv) permanent if $0 < \epsilon \leq \lim\limits_{t\to\infty} Inf\ x_i(t) \leq \lim\limits_{t\to\infty} Sup\ x_i(t) \leq U$ for all $i = 1, 2, ..., n$ and some constants ϵ and U.

Definition 5.3.1 *(Permanence): (Takeuchi,* 1996*) The system is said to be permanent if there is a compact set in the interior of the state space,* $\mathbb{R}^n_+$, *such that all orbits initiating at points in the interior end up in the compact set. Equivalently, permanence means that there exists an* $\hbar > 0$ *such that whenever* $x_i(0) > 0$ *for all* i, $\lim\limits_{t\to+\infty} Inf\ x_i(t) > \hbar$ *and* $\lim\limits_{t\to+\infty} Sup\ x_i(t) < \frac{1}{\hbar}$ *i.e., all the orbits are uniformly bounded. In ecological context, permanence implies the survival of all species which exist initially.*

Definition 5.3.2 *(Persistence): (Takeuchi,* 1996*) Whereas* $\lim\limits_{t\to+\infty} Sup\ x_i(t) < 0$ *implies permanence, the system is said to be persistent if for all* i, $\lim\limits_{t\to+\infty} Inf\ x_i(t) > 0$ *i.e., persistence is a weaker concept than permanence. For this case, the system always has a positive globally stable equilibrium point for any* $\epsilon > 0$.

Definition 5.3.3 *(ω-limit set): (Takeuchi,* 1996*) For an autonomous ordinary differential equation model,* $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x});\ \mathbf{x}(0) = \mathbf{x}_0$, *in some region of* $\mathbb{R}^n$, *suppose* $x(t)$ *is a solution defined for all* $t \geq 0$ *initiating* x *at* $t = 0$. *The* ω*-limit set of* x, $\omega(x)$, *is the set of points,* $y \in \mathbb{R}^n$, *such that* $x(t_k) \to y$ *as* $k \to \infty$ *for some sequence* $t_k > 0; t_k \to \infty$.

Remark 5.3.1 *From the definitions above, a permanent system is uniformly persistent and thus, persistent, and hence weakly persistent. Therefore, a permanent system is dissipative and uniformly persistent.*

Remark 5.3.2 *A persistence with initial conditions in the positive cone will persist if there are no ω-limit set of points of the solution on the boundary of the positive cone. This means that if $\Upsilon(X)$ is the orbit through the point $X = (x, y, z)$ with $x > 0,\ y > 0,\ z > 0,$ and if $\Omega(X)$ is the ω-limit set of $\Upsilon(X)$, then $\Omega(X)$ is the interior to the positive cone.*

Proof of Proposition 5.3.1: From equation (5.7); $\frac{du}{dt} \leq ru\,(1-u)$ and the Comparison Principle (cf. Takeuchi, 1996), leads to $\lim_{t\to\infty} Sup\ u(t) \leq 1$. Thus, $u(t) \leq 1+\epsilon$ when t is sufficiently large, for any $\epsilon > 0$ however small. Denoting $\beta_0 = \min\{(\mu-\beta), (1-\beta)\}$, then from Model system (5.7-5.9), it follows that:

$$\begin{aligned}
\frac{du}{dt} + \frac{\mu}{\gamma}\frac{dv}{dt} + \frac{1}{\gamma}\frac{dw}{dt} &= ru\,(1-u) - \frac{\mu(\mu-\beta)}{\gamma}v - \frac{(1-\beta)}{\gamma}w \\
&\leq ru - \beta_0\left(\frac{\mu}{\gamma}v + \frac{1}{\gamma}w\right) \\
\Rightarrow \frac{d}{dt}\left(u + \frac{\mu}{\gamma}v + \frac{1}{\gamma}w\right) &\leq (r+\beta_0)(1+\epsilon) - \beta_0\left(u + \frac{\mu}{\gamma}v + \frac{1}{\gamma}w\right)
\end{aligned}$$

Again, the Comparison Principle leads to $\lim_{t\to\infty} Sup\left(u + \frac{\mu}{\gamma}v + \frac{1}{\gamma}w\right) \leq \frac{(r+\beta_0)(1+\epsilon)}{\beta_0}$. This completes the proof and thus, Model system (5.7-5.9) is dissipative and hence permanent. In biological terms, persistence means that the population biomass of each species remains asymptotically above a positive bound independent of the initial conditions.

Non-negativeness and existence of equilibria

Since we are interested in the growth of biological populations of species, the equilibrium points of the system must satisfy the non-negative conditions. It should be noted that the predator cannot survive in the absence of its prey, i.e., the equilibrium points $\tilde{E}^*(0,0,\xi)$, $\hat{E}^*(0,\zeta,0)$ and $\widehat{E}^*(0,\zeta,\xi)$ with $\zeta, \xi > 0$ do not suffice. The unconditional existence of $E_0(0,0,0)$ and $E_1(1,0,0)$ prioritises the establishment of the existence of the situation where one predator out-competes the other. By defining $\widehat{\tilde{\Theta}} = \{\tilde{\epsilon}_f, \tilde{F}, \tilde{\epsilon}, \tilde{\alpha}, \tilde{\psi}, \tilde{a}\}$ as the set of *"pooled parameters"* and since $\phi > 1$, existence of E_2 implies that $\Phi > 0$ and $\eta\gamma > 2\phi\Psi$. In terms of the *"pooled parameters"* of the dimensional model, this gives the conditions $\mu_h > \tilde{\epsilon}_f \tilde{F}$ and $\mu_h < \frac{(1-\tilde{F})\tilde{\epsilon}\tilde{\alpha}^2}{2\tilde{a}\tilde{\mu}\tilde{\psi}}$, which reveal that without additional food, one of the interfering predators is always out-competed. Similarly, existence of E_3 leads to the conditions $\Psi > 0$ and $\eta\gamma > 2\phi\Psi$; $\mu_l > \tilde{\epsilon}\tilde{F}$ and $\mu_l > \frac{(1-\tilde{F})\tilde{\epsilon}\tilde{\alpha}^2}{2\tilde{a}\tilde{\mu}\tilde{\psi}}$, which shows that additional food, of good quantity and quality, has to be well established to ensure that the lion's mortality is as low as possible.

Classical ordinary differential equation models prove to be useful when populations of species are assumed to be uniformly distributed over the spatial region of interest. Within AENP, there is a heterogeneity in species distribution due to random movements in search of food items and predator avoidance (Hayward & Hayward, 2006; Franklin, 2005). Naturally higher or lower concentrations of species occur at different locations within the ecosystems. This is due to variations in both biotic and abiotic resources (Ahn, 2003). Hence, the ecological niche is always patchy due to species dispersal/movements. Thus, reaction-diffusion predator-prey models are becoming increasingly favoured by both empirical and theoretical ecologists as a more suitable and relevant approach to describe predator-prey spatial-temporal interactions.

In the next subsection, incorporating species heterogeneity to Model system (5.7-5.9) via a reaction-diffusion model is reconsidered.

5.3.3 Species' dispersal

By setting one of the dispersal coefficients to unity, and ignoring the implicit assumption of homogeneity of species with respect to space, and taking the spatial structure (heterogeneity) into account by incorporating the spatial variations of species through addition of dispersal terms to the non-dimensionalised Model (5.7-5.9), directly leads to the following dimensionless form:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + \overbrace{ru(1-u) - \frac{\mu\eta uv}{1+\phi u+\psi w} - \frac{\eta uw}{1+\phi u+\psi v}}^{\hat{f}(u,v,w)} \qquad x \in [a,b] \tag{5.13}$$

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + \overbrace{\frac{\gamma\eta uv}{1+\phi u+\psi w} - \mu v + \beta v}^{\hat{g}(u,v,w)} \qquad x \in [a,b] \tag{5.14}$$

$$\frac{\partial w}{\partial t} = \frac{\partial^2 w}{\partial x^2} + \overbrace{\frac{\gamma\eta u w}{1+\phi u+\psi v} - w + \beta w}^{\hat{h}(u,v,w)} \qquad x \in [a,b] \qquad (5.15)$$

$$\frac{\partial u}{\partial x} = \frac{\partial v}{\partial x} = \frac{\partial w}{\partial x} = 0 \qquad x \in \Gamma = \{a,b\} \qquad (5.16)$$

where $\Omega \subset \mathbb{R}$ is a bounded domain with smooth boundary Γ, and because of a closed species ecosystem, zero-flux Neumann boundaries conditions are assumed. Furthermore, x is the spatial variable and D is the relative dispersal coefficient of prey to predators, i.e., $D = \frac{D_b}{D_p}$ where D_b is the dispersal rate of prey and D_p is the synchronized dispersal rate of the predators.

It is noted that the steady states of the well mixed model are also steady states of the reaction-diffusion model. Thus, at the homogeneous steady state solution $(u,v,w) = (u^*,v^*,w^*)$, both the reaction terms and the spatial derivatives are zero and this leads to zero time derivatives. Using the approach developed by Roussel (2004), a linearisation of the reaction-diffusion system (5.13-5.16) is carried out by defining:

$$u = \delta u + u^*,\ v = \delta v + v^* \quad \text{and} \quad w = \delta w + w^*$$

where $\delta u, \delta v$ and δw are all space and time dependent perturbations about equilibrium points. The important dynamics of the system can always be studied by analysing the limiting situations of these perturbations about the equilibrium points. Due to linearity in perturbations, it should be noted that:

$$\frac{\partial u}{\partial t} = \frac{\partial(\delta u)}{\partial t},\ \frac{\partial^2 u}{\partial x^2} = \frac{\partial^2(\delta u)}{\partial x^2},\ \frac{\partial v}{\partial t} = \frac{\partial(\delta v)}{\partial t},\ \frac{\partial^2 v}{\partial x^2} = \frac{\partial^2(\delta v)}{\partial x^2},\ \frac{\partial w}{\partial t} = \frac{\partial(\delta w)}{\partial t},\ \frac{\partial^2 w}{\partial x^2} = \frac{\partial^2(\delta w)}{\partial x^2}$$

Linearisation of the reaction terms is simply $\mathbf{J}^* \left[\delta u \ \ \delta v \ \ \delta w\right]^T$, where $\mathbf{J}^*$ is the reaction variational/ community matrix evaluated at the steady states and T denotes the usual matrix transpose operation. The following linearized equation is obtained:

$$\frac{\partial}{\partial t}\begin{bmatrix} \delta u \\ \delta v \\ \delta w \end{bmatrix} = \mathbf{D}\frac{\partial^2}{\partial x^2}\begin{bmatrix} \delta u \\ \delta v \\ \delta w \end{bmatrix} + \mathbf{J}^*\begin{bmatrix} \delta u \\ \delta v \\ \delta w \end{bmatrix}$$

where

$$\mathbf{D} = \begin{bmatrix} D & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

is the diagonal dispersal matrix and

$$\mathbf{J}^* = \begin{bmatrix} \hat{f}_{u^*} & \hat{f}_{v^*} & \hat{f}_{w^*} \\ \hat{g}_{u^*} & \hat{g}_{v^*} & \hat{g}_{w^*} \\ \hat{h}_{u^*} & \hat{h}_{v^*} & \hat{h}_{w^*} \end{bmatrix}$$

is the reaction variational matrix whose entries are given as follows:

$$\begin{aligned}
J_{11}^* &= \hat{f}_{u^*} = \left[r(1-u^*) - \frac{\mu\eta v^*}{1+\phi u^* + \psi w^*} - \frac{\eta w^*}{1+\phi u^* + \psi v^*} \right] + \\
& \qquad u^* \left[-r + \frac{\mu\eta\phi v^*}{(1+\phi u^* + \psi w^*)^2} + \frac{\eta\phi w^*}{(1+\phi u^* + \psi v^*)^2} \right], \\
J_{12}^* &= \hat{f}_{v^*} = \eta u^* \left[\frac{\psi w^*}{(1+\phi u^* + \psi v^*)^2} - \frac{\mu}{(1+\phi u^* + \psi w^*)} \right], \\
J_{13}^* &= \hat{f}_{w^*} = \eta u^* \left[\frac{\mu\psi v^*}{(1+\phi u^* + \psi w^*)^2} - \frac{1}{(1+\phi u^* + \psi v^*)} \right], \\
J_{21}^* &= \hat{g}_{u^*} = \frac{\gamma\eta v^*(1+\psi w^*)}{(1+\phi u^* + \psi w^*)^2}, \\
J_{22}^* &= \hat{g}_{v^*} = \frac{\gamma\eta u^*}{(1+\phi u^* + \psi w^*)} + (\beta - \mu), \\
J_{23}^* &= \hat{g}_{w^*} = \frac{-\gamma\eta\psi u^* v^*}{(1+\phi u^* + \psi w^*)^2}, \\
J_{31}^* &= \hat{h}_{u^*} = \frac{\gamma\eta w^*(1+\psi v^*)}{(1+\phi u^* + \psi v^*)^2},
\end{aligned}$$

$$
\begin{aligned}
J_{32}^{*} &= \hat{h}_{v^*} = \frac{-\gamma\eta\psi u^* w^*}{(1+\phi u^* + \psi v^*)^2}, \\
J_{33}^{*} &= \hat{h}_{w^*} = \frac{\gamma\eta u^*}{(1+\phi u^* + \psi v^*)} + (\beta - 1).
\end{aligned}
$$

It should be clearly noted that, at the co-existence equilibrium, the first term of $\hat{f}_{u^*}$ vanishes, $\hat{g}_{v^*} = 0$ and $\hat{h}_{w^*} = 0$. Stability of the steady states under spatial and temporal variations can easily be established by assuming small heterogeneous spatial perturbations. A widely preferred form (Kolokolnikov *et al.*, 2006; Peng & Wang, 2005); $[\delta u \;\; \delta v \;\; \delta w]^T = [\delta u_0 \;\; \delta v_0 \;\; \delta w_0]^T \, e^{\lambda t} e^{ikx}$, that is used in analysing a generic reaction-diffusion model (the *Brusselator*) for a tri-molecular chemical reaction, morphogenesis and pattern formation is used. The complex exponential, $e^{ikx} = \cos kx + i \sin kx$ is a simplified way of representing the spatial wave having a wave number k. For stability of a steady state under any arbitrary small perturbation, $Re(\lambda) < 0$ and instability otherwise. The sine waves are common sources of such arbitrary noise and hence stability of the reaction-diffusion system can be deduced with ease. Substituting the defined perturbation form into the linearized equation and simplifying yields:

$$
\lambda \begin{bmatrix} \delta u_0 \\ \delta v_0 \\ \delta w_0 \end{bmatrix} = -k^2 \mathbf{D} \begin{bmatrix} \delta u_0 \\ \delta v_0 \\ \delta w_0 \end{bmatrix} + \mathbf{J}^* \begin{bmatrix} \delta u_0 \\ \delta v_0 \\ \delta w_0 \end{bmatrix}
$$

which gives the homogeneous equation:

$$
\left(\lambda \mathbf{I} + k^2 \mathbf{D} - \mathbf{J}^*\right) \begin{bmatrix} \delta u_0 \\ \delta v_0 \\ \delta w_0 \end{bmatrix} = 0
$$

where $\mathbf{I}$ is an identity matrix. For a non-trivial solution, $det\,(\lambda\mathbf{I} + k^2\mathbf{D} - \mathbf{J}^*) = 0$, which is a general characteristic equation for reaction-diffusion equations in one spatial dimension (Roussel, 2004).

$$\Rightarrow \qquad \begin{vmatrix} \lambda + P & -\hat{f}_{v^*} & -\hat{f}_{w^*} \\ -\hat{g}_{u^*} & \lambda + Q & -\hat{g}_{w^*} \\ -\hat{h}_{u^*} & -\hat{h}_{v^*} & \lambda + R \end{vmatrix} = 0$$

where $P = k^2D - \hat{f}_{u^*}$, $Q = k^2 - \hat{g}_{v^*}$ and $R = k^2 - \hat{h}_{w^*}$. Further simplification yields:

$$\lambda^3 + a_1\lambda^3 + a_2\lambda + a_3 = 0$$

where:

$$\begin{aligned} a_1 &= P + Q + R \\ a_2 &= PQ + PR + QR - \left(\hat{g}_{w^*}\hat{h}_{v^*} + \hat{f}_{v^*}\hat{g}_{u^*} + \hat{f}_{w^*}\hat{h}_{u^*}\right) \\ a_3 &= PQR - \left(P\hat{g}_{w^*}\hat{h}_{v^*} + Q\hat{f}_{w^*}\hat{h}_{u^*} + R\hat{f}_{v^*}\hat{g}_{u^*} + \hat{f}_{v^*}\hat{g}_{w^*}\hat{h}_{u^*} + \hat{f}_{w^*}\hat{g}_{u^*}\hat{h}_{v^*}\right) \end{aligned}$$

Using the general results obtained about local stability, the stability of the equilibrium points of the reaction-diffusion system (5.13-5.16) then follows. The steady state (u^*, v^*, w^*) is locally asymptotically stable to small perturbations if the parameter values satisfy all conditions, $a_1 > 0$, $a_3 > 0$ and $a_1a_2 - a_3 > 0$, that arise from the *Routh-Hurwitz* stability criterion for a given characteristic polynomial.

At the extinction equilibrium point $E_0\,(0,0,0) : \hat{f}_{u^*} = r,\ \hat{g}_{v^*} = \beta - \mu,\ \hat{h}_{w^*} = \beta - 1$ and the rest of the partial derivatives are annihilated. Thus, $P = k^2D - r$, $Q = k^2 - (\beta - \mu)$ and $R = k^2 - (\beta - 1)$, and the coefficients of the characteristic equation become:

$$\begin{aligned} a_1 &= k^2(2 + D) + (\mu + 1) - (2\beta + r) \\ a_2 &= \tilde{\pi}_1 k^4 + \tilde{\pi}_2 k^2 + \tilde{\pi}_3 \quad \text{where } \tilde{\pi}_1 = 2D + 1,\ \tilde{\pi}_2 = (D + 1)(\mu + 1) - 2(\beta(D + 1) + r) \\ &\quad \text{and } \tilde{\pi}_3 = r(\beta - \mu) + r(\beta - 1) + (\beta - 1)(\beta - \mu) \\ a_3 &= (k^2D - r)(k^2 + \mu - \beta)(k^2 + 1 - \beta) \end{aligned}$$

It is clear that if $a_3 > 0$, then $a_1 > 0$ and $a_1a_2 - a_3 > 0$ follows. Thus the stability condition for extinction steady state is $k^2(2+D) > \frac{(2\epsilon_f F + r_b) - (\mu_h + \mu_l)}{\mu_l}$ for which $a_1 > 0$, $k > \sqrt{\left(\frac{-\tilde{\pi}_2 \pm \sqrt{\tilde{\pi}_2^2 - 4\tilde{\pi}_1\tilde{\pi}_3}}{2\tilde{\pi}_1}\right)}$ for $a_2 > 0$ and when $a_3 > 0$, $k^2 > max\left\{\frac{r}{D}, (\beta - \mu), (\beta - 1)\right\} = max\left\{\frac{r_b D_p}{\mu_l D_b}, \frac{\epsilon_f F - \mu_h}{\mu_l}, \frac{\epsilon_f F - \mu_l}{\mu_l}\right\}$. Since, for stability of E_0 :

$$\begin{aligned} a_1a_2 - a_3 &= \left[2k^2 + \mu + 1 - 2\beta\right]\left[k^2(D+1) + 1 - \beta - r\right]\left[k^2(D+1) + \mu - \beta - r\right], \\ k^2 &> max\left\{\beta - \frac{(\mu+1)}{2}, \frac{(\beta + r - \mu)}{D+1}, \frac{(\beta + r - 1)}{D+1}\right\} \\ &= max\left\{\frac{2\epsilon_f F - (\mu_h + \mu_l)}{2\mu_l}, \frac{D_p(\epsilon_f F + r_b - \mu_h)}{\mu_l(D_b + D_p)}, \frac{D_p(\epsilon_f F + r_b - \mu_l)}{\mu_l(D_b + D_p)}\right\}. \end{aligned}$$

Stability of the extinction steady state depends largely on the wave number k and dispersal of the interacting prey and predator species. At a high relative dispersal rate i.e., prey dispersing faster than the interfering predators, the extinction equilibrium is stable and unstable otherwise. A relative diffusivity $D \neq 1$, i.e., either $D < 1$ or $D > 1$ implies that one of the species disperses faster than the other. This is one of the requirements of Turing bifurcation in the absence of other complex ecosystem dynamics. A high gain from additional food to predators at low predator mortality rates appears to be a realistic trade-off strategy that raises both the wave number and relative dispersal of species. Turing instability arises if the probability of dispersal i.e., $P_r = \frac{D_p}{D_b + D_p}$, of the interfering predators is as low as possible i.e., $P_r \longrightarrow 0$. Such dispersal driven ecosystem instability can be introduced to such a predator-prey system through the provision of additional food to predators. The nutritional value (predator fertility) gained from such additional food should be high enough to overcome predator natural mortality and this result seems to contradict the notion of *“meat is meat”* to a predator. Hence the importance of considering predator preference for prey in a predator-prey ecosystem for sustainable wildlife management (Wentworth *et al.*, 2011; Hayward & Kerley, 2008; Hayward *et al.*, 2007*a*; Franklin, 2005).

The predator-free equilibrium point $E_1\,(1,0,0)$ gives $\hat{f}_{u^*} = -r, \frac{1}{\mu}\hat{f}_{v^*} = \hat{f}_{w^*} = \frac{\eta}{1+\phi}, \hat{g}_{v^*} = \frac{\gamma\eta}{1+\phi} + \beta - \mu, \hat{h}_{w^*} = \frac{\gamma\eta}{1+\phi} + \beta - 1$ and the other partial derivatives vanish. Thus, $P = k^2D + r,\ \ Q = k^2 + \varpi + \mu$ and $R = k^2 + \varpi + 1$, where $\varpi = -(\frac{\gamma\eta}{1+\phi} + \beta)$ for which the coefficients of the characteristic equation reduce to:

$$\begin{aligned}
a_1 &= k^2(2+D)+2\varpi+r+\mu+1\\
a_2 &= \hat{\hat{\pi}}_1k^4+\hat{\hat{\pi}}_2k^2+\hat{\hat{\pi}}_3 \quad \text{where } \hat{\hat{\pi}}_1=2D+1, \;\; \hat{\hat{\pi}}_2=(D+1)(\mu+1)+2(\varpi(D+1)+r)\\
& \quad \& \; \hat{\hat{\pi}}_3=r(\varpi+\mu)+r(\varpi+1)+(\varpi+1)(\varpi+\mu)\\
a_3 &= \left(k^2D+r\right)\left(k^2+\mu+\varpi\right)\left(k^2+1+\varpi\right)
\end{aligned}$$

The *Routh-Hurwitz* criteria are satisfied if $k^2(2+D) > -\varpi-(\mu+r+1)$ under which positive wave numbers and relative diffusivity are guaranteed since $-\varpi > 0$ which further implies that $|-\varpi| > (\mu+r+1)$. This condition about a_1 is equivalent to;

$$k^2(2+D) > \frac{\epsilon\alpha K_b(1-F)+[\epsilon_fF-(r_b+\mu_h+\mu_l)][1+aK_b]}{\mu_l(1+aK_b)},$$

which holds provided $\epsilon_f a > \epsilon\alpha$ and $\epsilon_f F > (r_b+\mu_h+\mu_l)(1+aK_b)$. Since ϵ_f is a measure of quality of additional food as a result of predator fertility gain, this indicates that quality of additional food to predators as compared to prey quality can always relieve predation pressure from prey. Though, as most theories of biological control results reveal (Srinivasu *et al.*, 2007; Sabelis & van Rijn, 2005; van Baalen *et al.*, 2001; Murdoch *et al.*, 1985; Rosenzweig, 1971), this might not be a trade-off strategy since it might result in excessive predation sooner or later. Furthermore,

$$k > \sqrt{\left(\frac{-\hat{\hat{\pi}}_2 \pm \sqrt{\hat{\hat{\pi}}_2^2-4\hat{\hat{\pi}}_1\hat{\hat{\pi}}_3}}{2\hat{\hat{\pi}}_1}\right)}$$

and

$$\begin{aligned}
k^2 &> max\left\{|-\varpi|-\mu, |-\varpi|-1\right\}\\
&= max\left\{\frac{\epsilon\alpha K_b(1-F)+[\epsilon_fF-\mu_h][1+aK_b]}{\mu_l(1+aK_b)}, \frac{\epsilon\alpha K_b(1-F)+[\epsilon_fF-\mu_l][1+aK_b]}{\mu_l(1+aK_b)}\right\}
\end{aligned}$$

show that the diffusive stability and/or instability occurs for an infinite range of wavenumber k. The instability that occurs has been observed to form spatial patterns which arise from a combination of various sine waves within a finite range of wavelengths resulting into a non-trivial wave pattern (Kolokolnikov *et al.*, 2006; Peng & Wang, 2005; Holt, 1984). Further computations leads to;

$$a_1a_2-a_3 = \left[2k^2+\mu+1+2\varpi\right]\left[k^2(D+1)+r+1+\varpi\right]\left[k^2(D+1)+\mu+r+\varpi\right],$$

which is reminiscent of the *Routh-Hurwitz* condition for the extinction equilibrium. Hence, similar stability results are deduced which suggests the feasibility of a wave number $k > 0$ for which the species' dispersal can be controlled. The positive value of the required wave number is assured since $-\varpi > 0$. Permanence (Proposition 5.3.1) of Model system (5.7-5.9) leads to Theorem 5.3.1 (Takeuchi, 1996) that ensures local stability of the co-existence equilibrium under species' interference and competitive exclusion.

Stability of the remaining steady states can be established although mathematically more complex. Though computation of the coefficients, a_i's was possible, reducing the *Routh-Hurwitz* quantity $a_1a_2 - a_3$, to a mathematically tractable form is not possible. It will now be proved that, for the Model system (5.7-5.9), the prey population has a finite upper-limit resulting in the fact that it is impossible for prey populations to become infinite.

Preliminaries

Before extending the limit cycle perturbations method to analyse a three species population advection-reaction-diffusion system (5.19-5.21), the following preliminary motivating definitions are stated first.

Definition 5.3.4 *$\{\chi_A(t) : -\infty < t < \infty$ with $\chi_A(0) = A\}$ defines any orbit Υ of any phase curve through any arbitrary point A. Similarly, $\{\chi_A(t) : t \in \mathbb{R}^-$ with $\chi_A(0) = A\}$ and $\{\chi_A(t) : t \in \mathbb{R}^+$ with $\chi_A(0) = A\}$ define positive and negative (Υ^+ and Υ^-) semi-orbits, respectively.*

Definition 5.3.5 *(Takeuchi,* 1996*) The set of points in $\mathbb{R}^2$ which are approached along an orbit Υ with increasing time i.e., $t \to +\infty$, is the ω-limit set of the orbit. The α-limit set of Υ is similarly defined as the set of points approached with decreasing time i.e., $t \to -\infty$.*

Definition 5.3.6 *(Takeuchi,* 1996*) A periodic orbit Υ_0, that is the ω-limit set or the α-limit set for all other orbits in some neighbourhood of Υ_0 is called a limit cycle.*

Theorem 5.3.1 *For the three dimensional competitive and permanent system (5.7-5.9), let $E_4\,(u^*, v^*, w^*)$ be hyperbolic. Then the stable manifold $\widehat{\Upsilon}$ of E_4, is one dimensional, and for any $\alpha \in \widehat{\Upsilon}$, the ω-limit set $\omega(\alpha)$ is a non-trivial periodic orbit in Ω.*

Theorem 5.3.2 *Any solution of system (5.7-5.9) is bounded.*

Lemma 5.3.1 *Suppose that* $(u(t), v(t), w(t))$ *is a solution to system (5.7-5.9). In addition, assuming that for some* $\epsilon > 0$, $u(t_0) = u,\ v(t_0) = v,\ w(t_0) = w$ *with* $v \geq \frac{-2r}{\beta-\mu} + \frac{\epsilon}{\beta-\mu}$, $w \geq \frac{-2r}{\beta-1} + \frac{\epsilon}{\beta-1}$ *and* $u > u^*$. *Then there exists* $t^* > t_0$ *such that* $u(t^*) = u^*$.

Proof of Lemma 5.3.1: The lemma above is proved and used later to prove Theorem 5.3.2. Since $\hat{f}(u^*, v, w) = 0$ and $\frac{\gamma\eta u}{1+\phi u+\psi w}$, $\frac{\gamma\eta u}{1+\phi u+\psi v}$ are increasing, then $u > u^*$ leads to $\hat{f}(u, v, w) > 0$. Without loss of generality, it follows that:

$$\begin{aligned}
\hat{f}(u,v,w) &< \hat{f}(u,v,w) + \Big[\hat{g}(u,v,w) + \hat{h}(u,v,w)\Big] = ru(1-u) + (\beta-\mu)v + (\beta-1)w \\
&< -2r + (\beta-\mu)v + (\beta-1)w, \quad \Big(\text{since;}\ \ max\{ru(1-u)\} = \frac{1}{4}r \ \sim\ \langle \frac{1}{2}, -2r\rangle\Big) \\
&< -\epsilon \quad \Big(\text{since}\ \ v \geq \frac{-2r}{\beta-\mu} + \frac{\epsilon}{\beta-\mu},\quad w \geq \frac{-2r}{\beta-1} + \frac{\epsilon}{\beta-1}\Big)
\end{aligned}$$

Therefore, $\hat{f}(u, v, w)|_{t \geq t_0} < -\epsilon$ and that the line $B = -\epsilon t + (u + u^*)$ defines the upper bound of the $u(t)$. Furthermore, the line $B = -\epsilon t + (u + u^*)$ contains the points (t_0, u), $(t_1 = \frac{u}{\epsilon}, u^*)$ and has a slope $-\epsilon$. Hence, there exists $t^* > t_0 < t_1$ such that $u(t^*) = u^*$.

Proof of Theorem 5.3.2: Since Theorem 5.3.2 implies Theorem 5.3.1, it suffices to prove the former. The positive octant $\mathbb{R}^3_+ = \{(u, v, w) \in \mathbb{R}^3 : u(0) \geq 0,\ v(0) \geq 0\ \&\ w(0) \geq 0\}$ is invariant under the dynamical system. The solution never leaves $\mathbb{R}^3_+$ since $\frac{du}{dt} = 0$ when $u \equiv 0$, $\frac{dv}{dt} = 0$ when $v \equiv 0$ and $\frac{dw}{dt} = 0$ when $w \equiv 0$. If $0 \leq u \leq 1$, then for every $u \leq 1$, $-\frac{\mu\eta uv}{1+\phi u+\psi w} - \frac{\eta uw}{1+\phi u+\psi v} \leq 0$ and $ru(1-u) \geq 0$ which implies that $\hat{f}(u, v, w) \geq 0$. In addition, if $u \leq u^*$ (equilibrium solution), then $\mu \geq \frac{\gamma\eta u}{1+\phi u+\psi w} + \beta$ and $1 \geq \frac{\gamma\eta u}{1+\phi u+\psi v} + \beta$. Consequently $\frac{\gamma\eta u}{1+\phi u+\psi w} - \mu + \beta \leq 0$ and $\frac{\gamma\eta u}{1+\phi u+\psi v} - 1 + \beta \leq 0$. Therefore, $\hat{g}(u, v, w) = v\left(\frac{\gamma\eta u}{1+\phi u+\psi w} - \mu + \beta\right) \leq 0$ and $\hat{h}(u, v, w) = w\left(\frac{\gamma\eta u}{1+\phi u+\psi v} - 1 + \beta\right) \leq 0$.

Furthermore, for every solution such that $v(0) > \frac{-2r}{\beta-\mu}$, $w(0) > \frac{-2r}{\beta-1}$ and $u(0) > u^*$, there exists some v_2, w_2 such that $v(t) \leq v_2$, $w(t) \leq w_2$ for all $t \geq 0$. Applying Lemma 5.3.1, there is some t^* such that $u(t^*) = u^*$. Let $v_1 = v(t^*)$, $w_1 = w(t^*)$ and then applying Lemma 5.3.1 once more, it is concluded that there is an orbit $\Upsilon(t)$ joining the point $(2, v_1, w_1)$ and the line $u = u^*$, in the point (u^*, v_2, w_2). Since for $u \leq w^*$, $v(t)$ and $w(t)$ are decreasing, and the orbit $[u(t), v(t), w(t)]^T$ cannot cross the orbit $\Upsilon(t)$, then $v(t) \leq v_2$, $w(t) \leq w_2$ for all $t \geq 0$. The proof of the theorem is concluded by noting that $v(0) < \frac{-2r}{\beta-\mu}$, $w(0) < \frac{-2r}{\beta-1}$ or $u(0) < u^*$ lead to the previous scenarios.

Corollary 5.3.1 *Suppose* $\mu_l > \tilde{\epsilon}\tilde{F}$ *and* $\mu_l > \frac{(1-\tilde{F})\tilde{\epsilon}\tilde{\alpha}^2}{2\tilde{a}\tilde{\mu}\tilde{\psi}}$, *then system (5.7-5.9) has periodic solutions.*

Proof: From Theorem 5.3.2, all interior solutions are bounded.

The qualitative analysis in Subsection 5.3.3 shows that under the hypotheses of the corollary, equilibrium point E_3 is a stable steady state. Then by the Poincaré-Bendixson Theorem (Boyce & DiPrima, 2001; Takeuchi, 1996), an interior solution is either a closed periodic orbit or approaches a closed periodic orbit as $t \to \infty$.

5.3.4 On the principle of competitive exclusion

The ecological principle of competitive exclusion asserts that, multiple species cannot indefinitely occupy the same niche. If there are n populations that depend linearly on m resources $(m < n)$, then at least one population will vanish and hence, in the long run, only at most m population can survive (Takeuchi, 1996; Armstrong & McGehee, 1980). The equilibria E_2 $(u^*, v^*, 0)$ and E_3 $(u^*, 0, w^*)$ define scenarios where one predator out-competes the other as a result of interspecific interference. Therefore, global stability for the case when one of the predators is out-competed is investigated in this subsection.

The functions $f(u) = r(1-u)$, $p(u, w) = \frac{\mu\eta u}{1+\phi u+\psi w}$, $q(u, v) = \frac{\eta u}{1+\phi u+\psi v}$, $g(v) = \beta - \mu$ and $h(w) = \beta - 1$, are defined as the specific growth rate of prey, functional responses and predator controlled death rates due to presence of additional food. It is noted that the above functions have been non-dimensionalised and satisfy the usual default conditions for predator-prey systems (Hsu, 2005; Takeuchi, 1996). The following is a preliminary motivating theorem for the global stability of the out-competition result of the two predators.

Theorem 5.3.3 *(Lyapunov's Stability Theorem): (Takeuchi,* 1996*) Consider the dynamical system* $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ *on some region* $\Omega \subseteq \mathbb{R}^n$ *and define the* ω*-limit of* $\mathbf{x}$ *as the set* $\omega(\mathbf{x})$ *of points* $\mathbf{y} \in \mathbb{R}^n$*, such that* $\mathbf{x}(t_k) \longrightarrow \mathbf{y}$ *as* $k \longrightarrow \infty$ *for some sequence* $t_k > 0;\ t_k \longrightarrow \infty$ *and* $V : \Omega \subseteq \mathbb{R}^n \longrightarrow \mathbb{R}$ *be continuously differentiable. If for some solution* $V(t) \longrightarrow \mathbf{x}(t)$*, the derivative* $\dot{V}$ *satisfies* $\dot{V} \geq$ *or* ≤ 0*, then* $\omega(\mathbf{x}) \cap \Omega$ *is contained in the set* $\{\mathbf{x} \in \Omega | \dot{V}(\mathbf{x}) = 0\}$*. Suppose that there exists a Lyapunov function* $V(\mathbf{x})$ *such that* $\dot{V}(\mathbf{x}) < 0$ *for all* $\mathbf{x} \in \mathbb{R}^n$ *except at equilibrium solutions (*$\mathbf{x}^*$*), then the equilibrium point* $\mathbf{x}^*$ *is globally stable.*

Remark 5.3.3 *The maximal invariant set contained in* $\{\mathbf{x} \in \Omega | \dot{V}(\mathbf{x}) = 0\}$ *is a LaSalle's invariant set. In addition, since any solution starting in* $\omega(\mathbf{x})$ *remains there indefinitely, then* $\omega(\mathbf{x})$ *is invariant.*

Remark 5.3.4 *In Theorem 5.3.3 above,* V *is the Lyapunov function and* $\dot{V}(\mathbf{x}) = \sum\limits_{i=1}^{n} \frac{\partial V(\mathbf{x})}{\partial x_i} \dot{x}_i$ *is the time derivative of* V *along the solutions of the dynamical system* $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$.

Theorem 5.3.3 and similar Lyapunov stability theorems have been stated and proved elsewhere (Hsu, 2005; Takeuchi, 1996; Hsu & Huang, 1995), thus, it is justifiable to proceed by using them in establishing the out-competition results. As shown by Cantrell & Cosner (2001), Takeuchi (1996) and Hsu & Huang (1995), a candidate Lyapunov function $V(u, v, w)$ can be defined such that

$$V(u, v, w) = \int_{u^*}^{u} \left[\pi_{11} \left(1 - \frac{p(u^*, w^*)}{p(x)} \right) + \pi_{12} \left(1 - \frac{q(u^*, v^*)}{q(x)} \right) \right] dx + \int_{v^*}^{v} \left(\frac{x - v^*}{x} \right) dx + w$$

For $E_2\,(u^*, v^*, 0) \in \mathbb{R}^3_+$, with suitable choices for the constants $\pi_{11} = \pi_{12} = \gamma$, and because of well known conditions and properties of the functional responses and specific growth rate functions (Seo & Kot, 2008; Hsu, 2005; Takeuchi, 1996), (u, v, w) is positive in the region defined by; $0 < u < u^* < K_b,\ 0 < v^* < v < \xi_1,\ 0 < w < \xi_2$, where ξ_1 and ξ_2 are positive constants. Thus, the Lyapunov function reduces to:

$$\begin{aligned} V(u, v, w) &= \left[\gamma \left(p(u, w) - p(u^*, w^*) \right) + \gamma \left(q(u, v) - q(u^*, v^*) \right) \right] \left[\frac{uf(u)}{q(u, v)} - \frac{vp(u, w)}{q(u, v)} - w \right] + \\ &\quad (v - v^*) \left[-g(v) + \gamma p(u, w) \right] + w \left[-h(w) + \gamma q(u, v) \right] \end{aligned}$$

At $E_2\,(u^*, v^*, 0)$, the system (5.13-5.15) reduces to:

$$u^* f(u^*) - v^* p(u^*) = 0 \tag{5.17}$$

$$v^* p(u^*) + g(v^*) = 0 \tag{5.18}$$

Using the system above and with $\lim_{t\to\infty} Sup\, q(u,v) \sim \lim_{t\to\infty} Sup\, p(u,w) \sim p(u)$, direct algebraic computation yields:

$$\begin{aligned}\frac{dV}{dt} &= \left[\gamma\left(p(u,w)-p(u^*)\right)+\gamma\frac{p(u,w)}{q(u,v)}\left(q(u,v)-q(u^*)\right)\right]\left[\frac{uf(u)}{p(u,w)}-\frac{u^*f(u^*)}{p(u^*)}\right]+\\ &\quad (v-v^*)\left[\left(g(v^*)-g(v)\right)+\gamma\frac{p(u,w)}{q(u,v)}\left(q(u^*,v^*)-q(u,v)\right)\right]+\\ &\quad w\left[\gamma\frac{q(u,v)}{p(u,w)}\left(p(u^*)-p(u,w)\right)+\left(h(0)-h(w)\right)\right]<0\end{aligned}$$

Hence, asymptotic stability of $E_2\left(u^*,v^*,0\right)$ follows if and only if $\frac{dV}{dt}<0$, and this leads to the following lemma.

Lemma 5.3.2 *If in the neighbourhood of* $E_2\left(u^*,v^*,0\right)$ *in the positive cone, the function* $\frac{uf(u)}{p(u,w)}$ *is strictly decreasing, then the equilibrium point* $E_2\left(u^*,v^*,0\right)$ *is globally asymptotically stable.*

Lemma 5.3.3 *Without loss of generality, the global asymptotic stability of* $E_3\left(u^*,0,w^*\right)$ *follows in a similar fashion.*

The proof is similarly done using a candidate Lyapunov function defined as:

$$V(u,v,w) = \int_{u^*}^{u}\left[\pi_{21}\left(1-\frac{p(u^*,w^*)}{p(x)}\right)+\pi_{22}\left(1-\frac{q(u^*,v^*)}{q(x)}\right)\right]dx+v+\int_{w^*}^{w}\left(\frac{x-w^*}{x}\right)dx$$

The permanence and global stability of the Model (5.7-5.9) depends essentially on local stability, i.e., on the eigenvalues of the variational/community matrix evaluated at a steady state, of the coexistence equilibrium $E_4\left(u^*,v^*,w^*\right)$. The variational matrices evaluated at all equilibrium points give eigenvalues with non-zero real parts i.e., hyperbolic solutions.

5.3.5 Periodicity and species' dispersal

Within the game park, prey and predator species diffuse (random movements) and disperse (synchronised motion in defined direction destined to known locations). For example, dispersal rates between female social units of kudus were studied and averaged to 0.5% per individual per year

(Owen-Smith, 2000). Thus, a dimensionless migration coefficient $m = \frac{m_b}{m_p}$, where m_b and m_p are migration coefficients of prey and predators, respectively, is incorporated to the reaction-diffusion system (5.13-5.15), and as defined earlier, $D = \frac{D_b}{D_p}$ remains the relative dispersal coefficient of prey to predators where D_b is the dispersal rate of prey and D_p is the synchronized dispersal rate of the predators. This leads to the advection-reaction-diffusion system:

$$\frac{\partial u}{\partial t} = D\nabla^2 u - m\nabla u + \hat{f}(u, v, w) \tag{5.19}$$

$$\frac{\partial v}{\partial t} = \nabla^2 v - \nabla v + \hat{g}(u, v, w) \tag{5.20}$$

$$\frac{\partial w}{\partial t} = \nabla^2 w - \nabla w + \hat{h}(u, v, w) \tag{5.21}$$

where $\nabla^2 = \frac{\partial^2}{\partial x^2}$ or $\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ is the usual Laplacian operator in one or two-dimensional space and $\nabla = \frac{\partial^2}{\partial x}$.

Using the methods of limit cycle perturbations on *Burgers* equation ($\frac{\partial}{\partial t}u(x,t) + u(x,t)\frac{\partial}{\partial x}u(x,t) = \sigma\frac{\partial^2}{\partial x^2}u(x,t) + F(x,t)$), the dynamical properties of phase waves in reaction-diffusion equations have been assiduously studied (Liu, 2010; Zola *et al.*, 2008; Petrovskii & Li, 2006; Peng & Wang, 2005; Petrovskii, 1999; Burns *et al.*, 1998; Sachdev, 1987). In the sampled literature, the limit cycle perturbation method has been predominantly used in the analysis of one or two interacting quantities (chemicals and/or populations) in which one or two equation mathematical models have been studied. A variety of qualitative dynamics have been deduced from the generic reaction-diffusion *Brusselator* model using such limit cycle perturbation methods (cf. Subsection 5.3.3). Other approaches, for example, the time-dependent wave packet approach used (Luan & Tang, 2005) for analysing qualitatively the quantum dynamics of the *Schrödinger* equation ($i\hbar\frac{\partial}{\partial t}\Psi = \hat{H}\Psi$) may also apply to a variety of ecological predator-prey models.

A limit cycle solution is a closed trajectory in the predator-prey space which is not a member of a continuous family of closed trajectories (Takeuchi, 1996). A stable limit cycle trajectory is such that any small perturbation from the trajectory decays to zero. Both prey and predator populations undergo constant oscillations whose amplitudes bear no relationship to the biology of the species involved but only to the initial sizes of their populations, which is quite arbitrary (Bazykin, 1998; Takeuchi, 1996). Since periodic orbits are compact limit sets, the Poincaré-Bendixson Theorem could be extended to a competitive or cooperative system in three dimensions (Idema, 2005).

Theorem 5.3.4 *(Poincaré-Bendixson Theorem (i)): (Idema, 2005) A compact limit set of a competitive or cooperative system in $\mathbb{R}^3$ that contains no equilibrium points is a periodic orbit.*

Theorem 5.3.5 *(Poincaré-Bendixson Theorem (ii)): Let the reaction (external force) functions $\hat{f}(u,v,w)$, $\hat{g}(u,v,w)$ and $\hat{h}(u,v,w)$ have continuous first partial derivatives in a domain Ω of the $uvw-$space. Further, let $\hat{\Omega}$ be a bounded sub-domain in Ω, and let $\Im$ be the region that consists of $\hat{\Omega}$ together with its boundary, i.e., all points of $\Im$ are in Ω. In addition, suppose that $\Im$ contains no critical point for system (5.19-5.21). If there exists a constant τ_0 such that $u = \varphi(\tau)$, $v = \psi(\tau)$ and $w = \phi(\tau)$ is a solution to system (5.19-5.21) that exists and stays in $\Im$ for all $\tau \geq \tau_0$, then system (5.19-5.21) allows a periodic solution in $\Im$; i.e., either $u = \varphi(\tau)$, $v = \psi(\tau)$ and $w = \phi(\tau)$ is a periodic solution (closed trajectory), or $u = \varphi(\tau)$, $v = \psi(\tau)$ and $w = \phi(\tau)$ spirals toward a closed trajectory as $\tau \longrightarrow \infty$.*

Theorem 5.3.6 *(Poincaré-Bendixson Theorem (iii)): (Takeuchi, 1996) A bounded semi-orbit that does not approach any singular point is either a closed periodic orbit or approaches a closed periodic orbit.*

Theorem 5.3.7 *(Consequence to Green's Theorem): (Boyce & DiPrima, 2001) Let $\hat{f}(u,v)$ and $\hat{g}(u,v)$ be any two reaction (external force) functions for a two equation framework model. Suppose further that $\hat{f}(u,v)$ and $\hat{g}(u,v)$ have continuous first partial derivatives in a simply connected domain Ω of the $uv-$plane. If $\hat{f}_u(u,v) + \hat{g}_v(u,v)$ has the same sign throughout Ω, then there is no closed trajectory lying entirely in Ω for the model system of the interacting variables.*

By assuming that the advection-reaction-diffusion Model (5.19-5.21) admits a limit cycle with frequency φ_0, and employing vector notation, the vector of species' reaction (external force for *Burgers'* equation) $\hat{\mathbf{f}}(\mathbf{u}_0) = \left[\hat{f}, \hat{g}, \hat{h}\right]^T$, vector of interacting species $\mathbf{u_0} = [u_0, v_0, w_0]^T$ such that for an initial periodic solution $\mathbf{u} = \mathbf{u}_0(\tau)$ where $\tau = \varphi_0 t$ for some periods T_b^* and T_p^*. These descriptions yield:

$$\varphi_0 \frac{\partial \mathbf{u}_0}{\partial \tau} = \hat{\mathbf{f}}(\mathbf{u}_0) \text{ for } \mathbf{u}_0(\tau) = \partial \mathbf{u}_0(\tau \pm T_b^*, T_p^*) \tag{5.22}$$

As shown by Liu (2010), Zola *et al.* (2008), Petrovskii (1999) and Burns *et al.* (1998), with $\theta = \theta(G, \O)$ and any small parameter ε, with the introduction of the following multiple scales; $G = \sqrt{\varepsilon}x\text{exp}(\varphi_0\sqrt{\varepsilon}x)$, $\O = \varepsilon t\text{exp}(\varphi_0\varepsilon t)$, $\tau = \nu_0 t\text{exp}(\varphi_0\varepsilon\nu_0 t)$ and the asymptotic expansion:

$$\mathbf{u} = \mathbf{u}_0(\tau + \theta) + \varepsilon\mathbf{u}_i(\tau + \theta)\text{exp}(\varphi_0\varepsilon\tau); \qquad i \in \mathbb{N}; \quad \varepsilon, \varphi_0 > 0$$

into the advection-reaction-diffusion system (5.19-5.21) leads to the following linear equations:

$$\varphi_0\frac{\partial\mathbf{u}_0}{\partial\tau} \;=\; \hat{\mathbf{f}}(\mathbf{u}_0) \tag{5.23}$$

and

$$\begin{bmatrix} a_{ij} \end{bmatrix}\begin{bmatrix} \mathbf{u}_j \end{bmatrix}^T = \begin{bmatrix} P_{i_n} \end{bmatrix}^T; \text{ for } i, j = 1, 2, 3$$

where $a_{11} = \varphi_0\frac{\partial}{\partial\tau} - \frac{\partial\hat{f}}{\partial u}(u_0, v_0, w_0)$, $a_{12} = -\frac{\partial\hat{f}}{\partial v}(u_0, v_0, w_0)$, $a_{13} = -\frac{\partial\hat{f}}{\partial w}(u_0, v_0, w_0)$, $a_{21} = -\frac{\partial\hat{g}}{\partial u}(u_0, v_0, w_0)$, $a_{22} = \varphi_0\frac{\partial}{\partial\tau} - \frac{\partial\hat{g}}{\partial v}(u_0, v_0, w_0)$, $a_{23} = -\frac{\partial\hat{g}}{\partial w}(u_0, v_0, w_0)$, $a_{31} = -\frac{\partial\hat{h}}{\partial u}(u_0, v_0, w_0)$, $a_{32} = -\frac{\partial\hat{h}}{\partial v}(u_0, v_0, w_0)$ and $a_{33} = \varphi_0\frac{\partial}{\partial\tau} - \frac{\partial\hat{h}}{\partial w}(u_0, v_0, w_0)$ are the entries of the non-adiabatic potential matrix, the superscript T denotes the usual transpose operation and P_{i_n}'s are the heterogeneous terms of the n^{th} order equation. By considering a first order situation, i.e., $n = 1$:

$$P_{i_1} = -\mathbf{u}_0'\frac{\partial\theta}{\partial\O} - m_\chi\mathbf{u}_0'\nabla\theta + D_\chi\left(\mathbf{u}_0''|\nabla\theta|^2 + \mathbf{u}_0'\nabla^2\theta\right); \quad i = 1, 2, 3; \ \chi = b \text{ for } u_0', \text{ otherwise } \chi = p$$

Furthermore, as shown by Zola *et al.* (2008) and Burns *et al.* (1998), we define the direct tensor (outer) products; $\zeta_0 \otimes \varsigma_0 = [u_0, v_0, w_0]^T$, $\zeta_1 \otimes \varsigma_1 = [u_1, v_1, w_1]^T$, $\zeta_2 \otimes \varsigma_2 = [u_2, v_2, w_2]^T$, while $\tilde{\zeta} \otimes \hat{\varsigma} = [\tilde{u}, \tilde{v}, \tilde{w}]^T$ is the non-trivial periodic solution to the adjoint differential equation $\tilde{\Gamma}\tilde{\zeta}_0 \otimes \hat{\varsigma}_0 = 0$, where $\tilde{\Gamma} = \begin{bmatrix} \tilde{a}_{ij} \end{bmatrix}$ for which; $\tilde{a}_{11} = -\varphi_0\frac{\partial}{\partial\tau} - \frac{\partial\hat{f}}{\partial u}(u_0, v_0, w_0)$, $\tilde{a}_{12} = -\frac{\partial\hat{f}}{\partial v}(u_0, v_0, w_0)$, $\tilde{a}_{13} = -\frac{\partial\hat{f}}{\partial w}(u_0, v_0, w_0)$, $\tilde{a}_{21} = -\frac{\partial\hat{g}}{\partial u}(u_0, v_0, w_0)$, $\tilde{a}_{22} = -\varphi_0\frac{\partial}{\partial\tau} - \frac{\partial\hat{g}}{\partial v}(u_0, v_0, w_0)$, $\tilde{a}_{23} = -\frac{\partial\hat{g}}{\partial w}(u_0, v_0, w_0)$, $\tilde{a}_{31} = -\frac{\partial\hat{h}}{\partial u}(u_0, v_0, w_0)$, $\tilde{a}_{32} = -\frac{\partial\hat{h}}{\partial v}(u_0, v_0, w_0)$ and $\tilde{a}_{33} = -\varphi_0\frac{\partial}{\partial\tau} - \frac{\partial\hat{h}}{\partial w}(u_0, v_0, w_0)$.

The phase wave periodic solvability condition for ζ_i and ς_i as used by Liu (2010) and Zola *et al.* (2008), gives:

$$\langle\tilde{\zeta}, \hat{\varsigma}, \zeta_0'\rangle\frac{\partial\theta}{\partial\O} = \langle\tilde{\zeta}, \hat{\varsigma}, \xi_1\rangle\nabla\theta + \langle\tilde{\zeta}, \hat{\varsigma}, \xi_2\rangle\nabla^2\theta + \langle\tilde{\zeta}, \hat{\varsigma}, \xi_3\rangle|\nabla\theta|^2$$

$$\Longrightarrow \quad \frac{\partial\theta}{\partial\O} = \widehat{\Phi}_1\frac{\partial\theta}{\partial G} + \widehat{\Phi}_2\frac{\partial^2\theta}{\partial G^2} + \widehat{\Phi}_3\left|\frac{\partial\theta}{\partial G}\right|^2 \tag{5.24}$$

where $\widehat{\Phi}_i = \left|\frac{\langle\tilde{\zeta},\hat{\varsigma},\xi_i\rangle}{\langle\tilde{\zeta},\hat{\varsigma},\zeta_0'\rangle}\right|_{\Im}$, $\widehat{\Phi}_i$ being evaluated in accordance to the Poincaré-Bendixson Theorem (Boyce & DiPrima, 2001; Takeuchi, 1996) over the composite region $\Im$; $\xi_1 = [-m_b u_0', -m_p v_0', -m_p w_0']^T$, $\xi_2 = [D_b u_0', D_p v_0', D_p w_0']^T$ and $\xi_3 = [D_b u_0'', D_p v_0'', D_p w_0'']^T$ and the periodic solvability condition of ζ_i and ς_i as suggested by Petrovskii & Li (2006) and motivated by Liu (2010):

$$\langle\tilde{\zeta},\hat{\varsigma},\xi_i\rangle = \int_0^{T_p^*}\int_0^{T_b^*}(\tilde{\zeta},\hat{\varsigma},\xi_i)d\tau_b d\tau_p \tag{5.25}$$

leads to:

$$\sum_{\chi=b,p}\int_0^{T_p^*}\int_0^{T_b^*}\tilde{\mathbf{u}}\left[-\mathbf{u}_0'\frac{\partial\theta}{\partial\varnothing} - m_\chi\mathbf{u}_0'\nabla\theta + D_\chi\left(\mathbf{u}_0''|\nabla\theta|^2 + \mathbf{u}_0'\nabla^2\theta\right)\right]d\tau_b d\tau_p = 0;\ \chi = b \text{ for } u_0',$$

otherwise $\chi = p$, where:

$$\varphi_0\frac{\partial\tilde{\mathbf{u}}}{\partial\tau} = \left[\ \hat{a}_{ij}\ \right]\tilde{\mathbf{u}};\qquad \tilde{\mathbf{u}} = [\tilde{u},\ \tilde{v},\ \tilde{w}]^T$$

for which; $\hat{a}_{11} = -\frac{\partial\hat{f}}{\partial u}(u_0,v_0,w_0)$, $\hat{a}_{12} = -\frac{\partial\hat{g}}{\partial u}(u_0,v_0,w_0)$, $\hat{a}_{13} = -\frac{\partial\hat{h}}{\partial u}(u_0,v_0,w_0)$, $\hat{a}_{21} = -\frac{\partial\hat{f}}{\partial v}(u_0,v_0,w_0)$, $\hat{a}_{22} = -\frac{\partial\hat{g}}{\partial v}(u_0,v_0,w_0)$, $\hat{a}_{23} = -\frac{\partial\hat{h}}{\partial v}(u_0,v_0,w_0)$, $\hat{a}_{31} = -\frac{\partial\hat{f}}{\partial w}(u_0,v_0,w_0)$, $\hat{a}_{32} = -\frac{\partial\hat{g}}{\partial w}(u_0,v_0,w_0)$, & $\hat{a}_{33} = -\frac{\partial\hat{h}}{\partial w}(u_0,v_0,w_0)$ and T being the matrix/vector transpose. With $\Theta = \varphi_0 t + \theta$, equation (5.24) becomes:

$$\frac{\partial\Theta}{\partial t} = \varphi_0 + \widehat{\Phi}_1\nabla\Theta + \widehat{\Phi}_2\nabla^2\Theta + \widehat{\Phi}_3\left|\nabla\Theta\right|^2 \tag{5.26}$$

The species' dispersal relationships are determined from equations (5.25) and (5.26) by using the standard wave characteristics (Liu, 2010; Petrovskii & Li, 2006; Petrovskii, 1999), $\varphi = \frac{\partial\Theta}{\partial t}$ and $\kappa = \nabla\Theta$:

$$\varphi = \varphi_0 + \widehat{\Phi}_1\kappa + \widehat{\Phi}_3\kappa^2 \tag{5.27}$$

Using equations (5.24) and (5.25), and defining:

$$\widehat{I}_{Migration} = \int_0^{T_p^*}\int_0^{T_b^*}[\tilde{u}(-m_b u_0') + \tilde{v}(-m_p v_0') + \tilde{w}(-m_p w_0')]d\tau_b d\tau_p$$

$$\widehat{I}_{Diffusion} = \int_0^{T_p^*}\int_0^{T_b^*}[\tilde{u}D_b u_0'' + \tilde{v}D_p v_0'' + \tilde{w}D_p w_0'']d\tau_b d\tau_p$$

$$\widehat{I}_{Periodicity} = \int_0^{T_p^*} \int_0^{T_b^*} [\tilde{u}u_0' + \tilde{v}v_0' + \tilde{w}w_0'] d\tau_b d\tau_p$$

and for computational simplicity and mathematical tractability of results, we consider $T_p^* = T_b^* = 2\pi$ for which the smooth and positive periodic solutions are defined by the following relationships:

$$\widehat{\Phi}_1 = \frac{\widehat{I}_{Migration}}{\widehat{I}_{Periodicity}} \qquad \text{and} \qquad \widehat{\Phi}_3 = \frac{\widehat{I}_{Diffusion}}{\widehat{I}_{Periodicity}}$$

5.4 Biological interpretation

Due to an overlap in dietary niche, models for the dynamics of interspecific interference of two predators whose activity feeding patterns are regulated by additional food have been analytically analysed for stability, dissipativity, permanence, periodicity and persistence. Group vigilance of the prey and predator interference have been modelled by the so-called Beddington-DeAngelis functional and numerical responses. The effect of additional food on the dispersal trends of the dynamics of the model has been shown to be of some significance. In particular, the wave number k, and relative diffusion of the species D, whose magnitudes are determined by the nutritional value of additional food, have been shown to provide the necessary stability conditions for analysed equilibrium points. The analytical results show that avoidance of out-competition of one of the interfering predators can be achieved via a given choice of additional predator food. The positivity conditions on the wave number κ, is in agreement with prey preference of most predators and hence a deviation from the notion of *"meat is meat"* to a predator (Hayward & Kerley, 2008; Hayward, *et al.*, 2006; Hayward & Kerley, 2005).

The dispersal properties of the species can be tracked from a clear knowledge of the dispersal rate (φ), which is determined from values of periodic solutions ($\widehat{\Phi}_1$ and $\widehat{\Phi}_3$) for various estimates of the wave numbers (κ). Furthermore, erratic dynamics and more conspicuous heterogeneous patterns arise as a result of an increase in the wave number (amplitude of underlying oscillations) which in turn leads to unstable periodic solutions. Such heterogeneities, as observed by Pearce *et al.* (2006), often result in constant regions of the *"boom-and-bust type"* in predator-prey ecosystems. The results of the phase wave dynamics that have been deduced from equation (5.24) are related to the *Schrödinger* equation results (Luan & Tang, 2005) for a particle moving in any potential gradient, where the velocity (frequency) of such a particle is assumed to be proportional to the potential gradient.

The periodic solutions $\widehat{\Phi}_1$ and $\widehat{\Phi}_3$, which regulate the species dispersal frequency can be controlled when the right choice of additional food to the interfering predators is established. Basing on the formulated model, the underlying governing principle to the right quality and/or quantity of such additional predator food are the $\widehat{I}_{Migration}$ and $\widehat{I}_{Diffusion}$ results. Limited movement of species due to additional food to predators can regulate the populations and prevent population annihilation. Hence, this result helps in resolving the Rosenzweig's paradox of enrichment within species' spatial interactions. Furthermore, as noted by Owen-Smith (1990), perturbations in kudu populations due to predation, disease and extreme weather depress populations below half of the mean density set by food limitations. Such perturbations can be regulated by the dispersal rate φ i.e., limit-cycle frequency φ_0, periodic solutions $\widehat{\Phi}_1$ and $\widehat{\Phi}_3$, and wave numbers κ, which has been shown to depend implicitly on both migration and diffusion rates of the interacting species. Besides other parameters, it has been shown (see Subsection 5.3.3) that diffusion of the interacting species is regulated by quality of additional food to predators and this gives a basis in dictating species' dispersal trends.

Despite initially being proposed as a model of turbulent flow analysis and later becoming well known in nonlinear studies (Zola *et al.,* 2008; Burns *et al.,* 1998; Petrovskii, 1999), we have carried out a study by formulating a mathematically plausible ecological model equivalent to Burger's equation to account for both density-dependent migrations and diffusion. Burger's equation being an advection-reaction-diffusion type, indeed accounts for the species' dispersal (Tyutyunov *et al.,* 2007). Solutions of traveling wave fronts that arise from biological invasion have been deduced from the large-time asymptotic results. Advection-reaction-diffusion equations have been identified as efficient tools for addressing questions relating to species' dispersal, spatial patterning and biological invasions (Liu, 2010; Zola *et al.,* 2008; Tyutyunov *et al.,* 2007; Pearce *et al.*, 2006; Petrovskii, 1999; Burns *et al.,* 1998). This study has addressed the challenges that come along with predator interference and additional food which has led to both unstable and stable equilibria, periodicity and species' dispersal patterns. This suggests that any attempt by man to enrich the ecosystem aimed at increasing food yield should be well formulated, otherwise it may result into the so-called paradox of enrichment.

Such results ecologically suggest that mathematical modelling provides a useful tool to investigate the consequences for a particular ecological system. As observed by Liu (2010), Petrovskii & Li (2006), Peng & Wang (2005), Petrovskii (1999), Burns *et al.* (1998) and Sachdev (1987), since analytical methods seem to be rather tedious in solving the advection-reaction-diffusion partial differential type of models, a great deal of analysis of such models has been carried out (Liu, 2010; Zola *et al.*, 2008; Petrovskii & Li, 2006; Petrovskii, 1999; Burns *et al.*, 1998 and references in them) using numerical methods which are somehow handy *per se*. Indeed as revealed by Liu (2010), the theoretical (qualitative/analytical analyses) results concur with the numerically quantitative results.

A relationship between model parameters and solutions regardless of the actual parameter values (data) has been identified. We hope that this will provide impetus in the research of the usual complex ecosystems involving multi-species interactions under numerous dynamical behaviour. Finally, despite extensive volumes of work that involved modelling of biological population dynamics, spatial modelling and biological invasions, there has been substantial attempts to model multi-species predator-prey dispersal systems in a spatial ecological setting. We anticipate that chaotic behaviour which could be investigated through a thorough bifurcation and numerical analyses of the model may yield further ecosystem dynamical trends.

5.5 Numerical Simulation/Quantitative Results

Reliability and resolution of demographic and environmental data involves quite some challenges making it difficult to numerically integrate and accommodate most of the influencing factors in population models. In this section, we give numerical demonstrations for the dynamics and pattern of the species by numerically integrating Model systems (5.13-5.15) and (5.19-5.21) using the solver, *pdepe,* that uses both finite difference and finite element methods (Skeel & Berzins, 1990). The Matlab solver, *pdepe,* is efficient for solving systems of non-linear partial differential equations and solves initial-boundary value problems for systems of parabolic-elliptic PDEs in the one space variable x and time t (Holzbecher, 2007; Skeel & Berzins, 1990).

While using the Matlab solver, *pdepe,* the ordinary differential equations resulting from discretisation in space are integrated to obtain approximate solutions at times specified in a time vector. The time vector specifies the points at which a solution is requested for every value in distance vector. The *pdepe* function returns values of the solution on a mesh provided in a distance vector. In return, the distance vector specifies the points at which a numerical solution is requested for every value in time vector. It should be pointed out that the discretised system satisfies the positivity property i.e., for any positive initial data, the model system gives positive solutions which are located in the feasible region of the positive octant.

5.5.1 Parameter estimates

Density-dependent changes in both adult kudu survival and juvenile kudu recruitment come into effect when kudu populations exceed about half of the mean density which is dictated by resource (food) limitations (Owen-Smith, 1990). Annual survival rates of particular age classes (social units) of the kudu species depend on resource availability (annual rainfall). The effective carrying capacity K_b is therefore a dynamic variable that depends on rainfall (Owen-Smith, 2000). Using a rainfall-driven model, Owen-Smith (2000) predicted a density of 2.4 kudus per square kilometer which appeared to be higher than the observed density of 1.5 kudus per square kilometer. Basing on the size of AENP's main camp (approximately $134km^2$) and the predicted population density of kudu (i.e., 2.4 kudus per square kilometer), the effective carrying capacity K_b is numerically varied at 320.

On average, female lions in the wild live up to 17 years and the males live up to 15 years (Packer *et al.,* 1998; Hunter, 1998). Due to less stress of defending their territories and hunting, lions living in captivity have longer life spans (25 years) than when in the wild (game parks). Beyond the first few years of life, mortality threats for lions appear due to fighting amongst males, starvation, and poaching/killing by humans (Hunter, 1998; Woodroffe & Frank, 2005). Less than 10% of male lions reach old-age as a result of these factors. Only a small percentage of lions die of natural causes, whereas 75% of lions die by being caught in snares, shot by poachers, or killed in fights with rival lions (Hunter, 1998; Woodroffe & Frank, 2005). Various studies show that females give birth to a litter of 1-6 cubs (average 3 cubs) after a gestation period of 110-120 days (approximately 4 months)

(Packer *et al.,* 1998; Hunter, 1998; Packer *et al.,* 2001). According to Hunter (1998) and Packer *et al.* (2001), the mortality rate of lions is high (more than half do not survive the first year) and only 20% of cubs reach the age of 2 years. Demographic computation of life expectancy of a species being μ^{-1}, we estimate mortality rates $\mu_l = \frac{1}{16} = 0.0625$ for lions and $\mu_h = \frac{1}{12} = 0.0833$ for spotted hyaenas.

Based on regression analysis results, various functional forms of annual survival rates (i.e., $S = f(R/H)$) that are related to the law of diminishing returns and the satiation effects have been proposed and studied (Owen-Smith, 2000). Kudu mortality which involves both pre- and post-natal losses combined with female infertility, is estimated from the calf to cow ratio and normally about half of the annual calf mortality occurs shortly after birth (Owen-Smith, 1990; Owen-Smith, 2000).

Despite evidence of fluctuations in mortality that depend on nutritional well-being as influenced by rainfall relative to kudu density, predation is responsible for a background mortality level of $5 - 10\%$ per annum in most animals (Owen-Smith, 1990). Rarely do 2-year old female kudus give birth to calves that survive for more than a few weeks (Owen-Smith, 1990). Therefore, in kudus, juvenile survival is determined from the ratio of calves to mature females aged three or more years. Besides postnatal mortality, juvenile survival estimates incorporate conception failures and prenatal mortality. Although infertility cases occur, adult female kudus can give birth annually (Owen-Smith, 1990). Newly born kudus lie out and only move with groups after 2-3 months of age. This makes it difficult to determine kudu natality rates (Owen-Smith, 1990). Annual rainfall dictates the survival rates of the various social units of kudus (Owen-Smith, 1990). With a sex ratio of 0.5, an adult female kudu (aged more than 3 years) gives birth to 1 calf per year (Owen-Smith, 2000).

Being alternative prey to lions and spotted hyaenas, kudus are vulnerable to prey switching. In the absence of predation, and at high population density, malnutrition, disease outbreaks, habitat conditions and other weather effects become the major cause of kudu's mortality (Owen-Smith, 2000). Unpublished data of AENP show that on average a female lion eats 5kg whereas a male lion consumes 7.5kg of prey biomass per day. This gives 6.25kg as the average lion's daily prey biomass requirement. A spotted hyaena need $3.8 - 4.0\ kg$ of meat daily to maintain its conditions (Hayward, 2006). Basing on the kudu's average adult body mass of 135kg, it is estimated that on average a lion predates upon 16.90 adult kudus' biomass per year and a spotted hyaena consumes approximately 10.54 adult kudus' biomass per year. Considering predation as the number (biomass) of prey killed/eaten per predator per year (unit time) and after rescaling, we estimate $\alpha_l = 0.1690yr^{-1}$ and $\alpha_h = 0.1054yr^{-1}$ as base values. Basing on the offspring production per year after prey biomass consumption, the fertility factors are estimated as a percentage of the respective predation rates and additional food biomass consumption (i.e., $\epsilon_h = \frac{\alpha_h}{100}$, $\epsilon_l = \frac{\alpha_l}{100}$, $\epsilon_{f_h} = \frac{F_h}{100}$ & $\epsilon_{f_l} = \frac{F_l}{100}$).

As in Shatalov *et al.*, (2008), using the "inverse method," we compute/estimate some of the biological parameters that could not be estimated in accordance with the stability analysis and/or from ecological literature on predator-prey dynamics. Approximations on fine meshes and small time steps are compared for Model system (5.13-5.15) i.e., $\Delta t = 0.02,\ \Delta h = 0.01,\ x = 2$ and $t = 3$ whereas for Model system (5.19-5.21); $\Delta t = 0.5,\ \Delta h = 0.005,\ x = 1$ and $t = 4$ are considered. With the initial set of data and parameter values as summarised in Table 5.2, numerical simulations are carried out to examine the behaviour of the model systems due to variations in predator additional food, interspecific interference coefficients, predator fertility rate as a result of predation and feeding on additional food.

5.6 Discussion

The primary interest, from an ecological point of view, is the situation that involves oscillatory densities of predators and prey. In the numerical experiments, we chose parameter sets that guarantee stable oscillatory dynamics of the system i.e., stable limit cycles, spirals and nodes in the reaction kinetics surrounding an unstable steady state (u^*, v^*, w^*) . The numerical solutions reflect the intrinsic properties of the system. Such properties are important in revealing how the system responds to parameter variations. In Figures 5.1-5.3, surface numerical results of Model system (5.13-5.15) alongside their analogous contour snapshots (Figures 5.4-5.6) are presented. In Figures 5.7-5.9, we present the surface plots for Model system (5.19-5.21) that correspond to the parameter values of Figures 5.1-5.3, respectively.

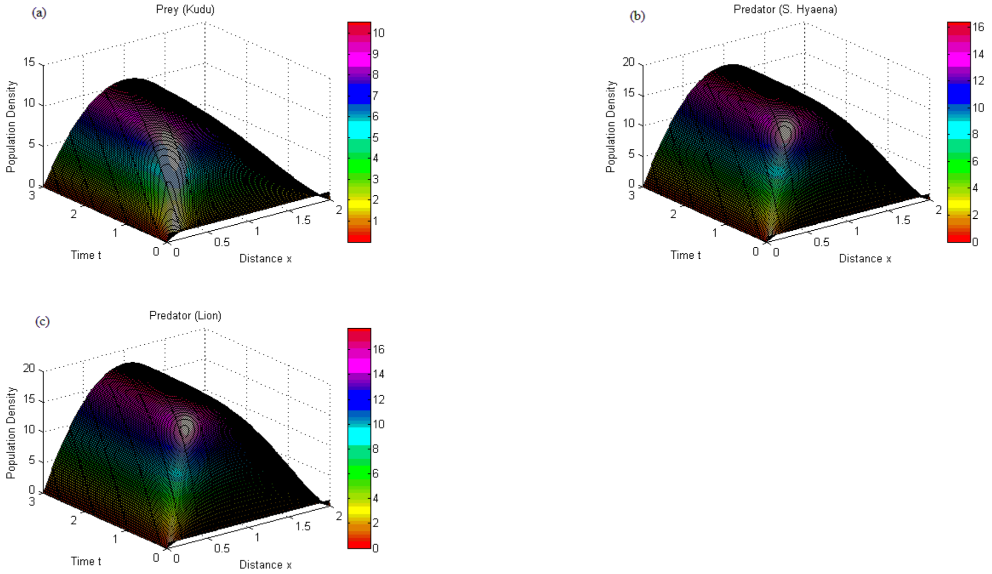

Figure 5.1: *Approximate species densities with temporal and spatial discretization of parameters of Model (5.13-5.15). Parameter values are as described in Table 5.2. Dispersal rates:* $D_b = 4 \times\ 10^{-1}$, $D_p = 9 \times\ 10^{-1}$. *The initial population density chosen as:* $B(0) = 19.0$, $H(0) = 6.0$ *and* $L(0) = 3.0$.

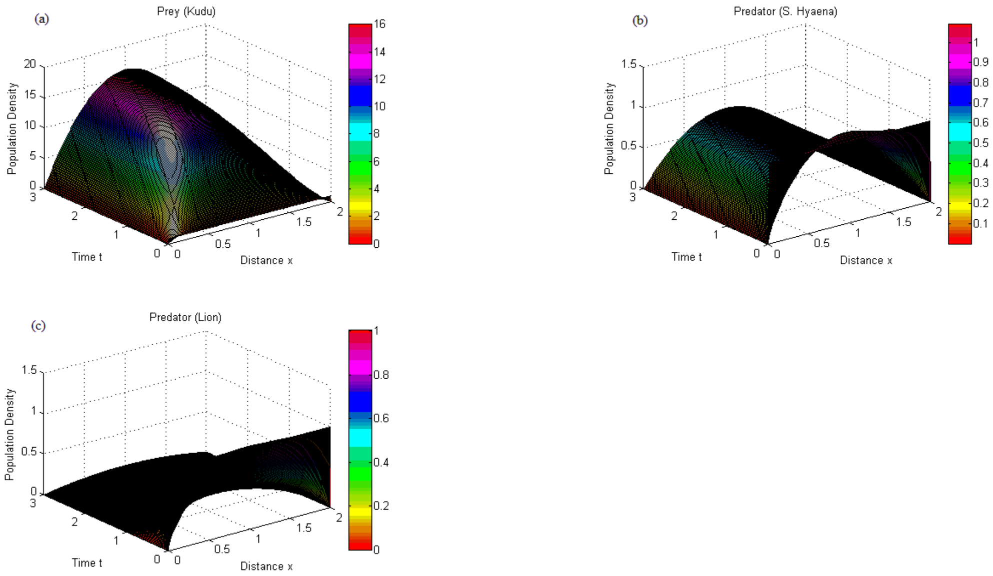

Figure 5.2: *Space-time evolution of species density for Model system (5.13-5.15) when predators face a high interspecific interference as a result of overlap of activity patterns (i.e.,* $\psi_h = 0.02365 \times 10^3$ *and* $\psi_l = 0.0153 \times 10^3$*).*

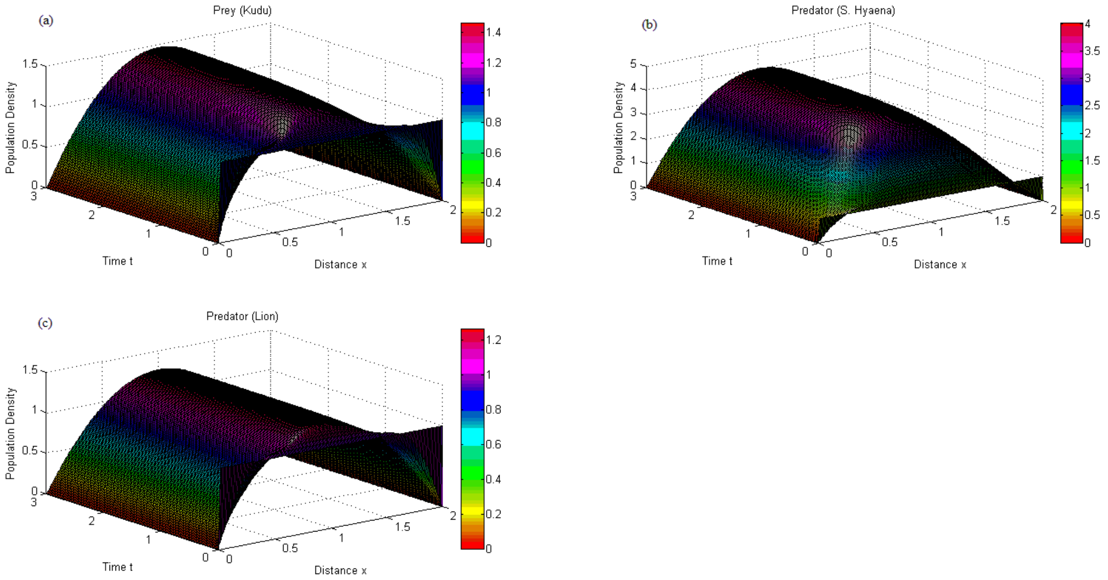

Figure 5.3: *The effect of high predation rates (i.e.,* $\alpha_h = 0.1054 \times 10^3$ *and* $\alpha_l = 0.1690 \times 10^3$*) at high fertility gain (i.e.,* $\epsilon_h = 0.001054 \times 10^3$ *and* $\epsilon_l = 0.001690 \times 10^3$*) when a steady additional food input is maintained. Perturbations have both positive and negative small values around the equilibrium state.*

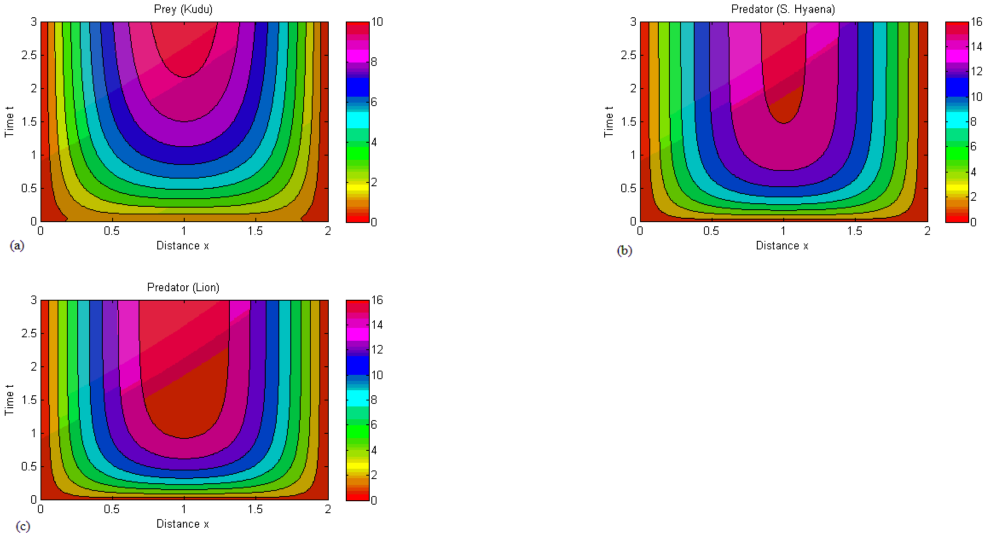

Figure 5.4: *Contour snapshots of approximate species densities corresponding to parameter values for the respective surface plots in Figure 5.1 for Model system (5.13-5.15) where in all plots;* $\Delta t = 0.02,\ \Delta h = 0.01,\ x = 2$ *and* $t = 3$. *Any initial population and perturbations about the steady state tends to the steady state asymptotically.*

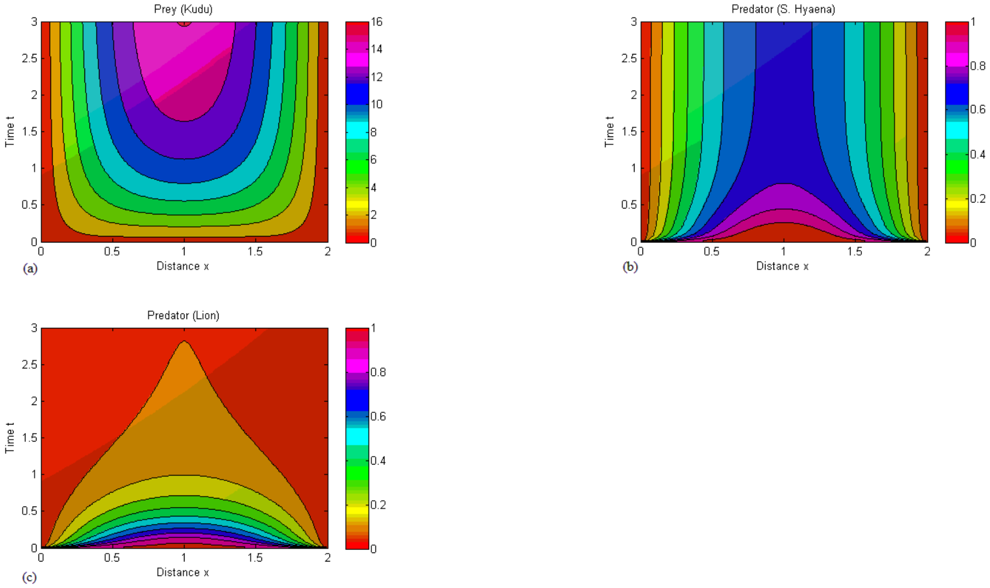

Figure 5.5: *Snapshots of approximate species densities corresponding to parameter values for the respective surface plots in Figure 5.2 i.e., when predators face a high interspecific interference. Any initial population and perturbations about the steady state tends to the steady state asymptotically.*

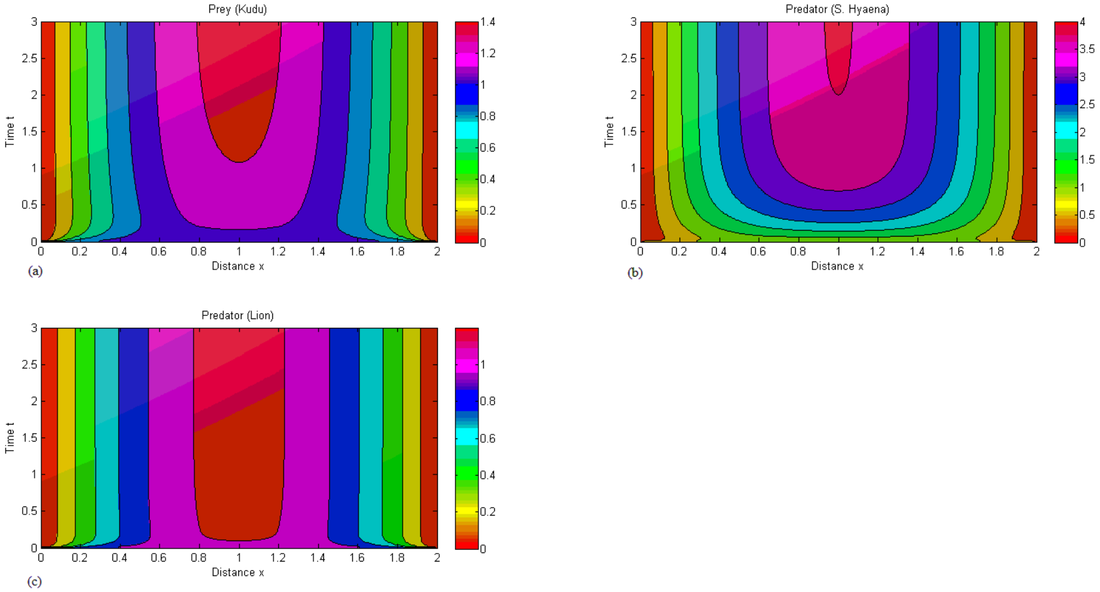

Figure 5.6: *Snapshots of approximate species densities corresponding to parameter values for the respective surface plots in Figure 5.3 i.e., high predation rates that results in high fertility gain. Any initial population and perturbations about the steady state tends to the steady state asymptotically.*

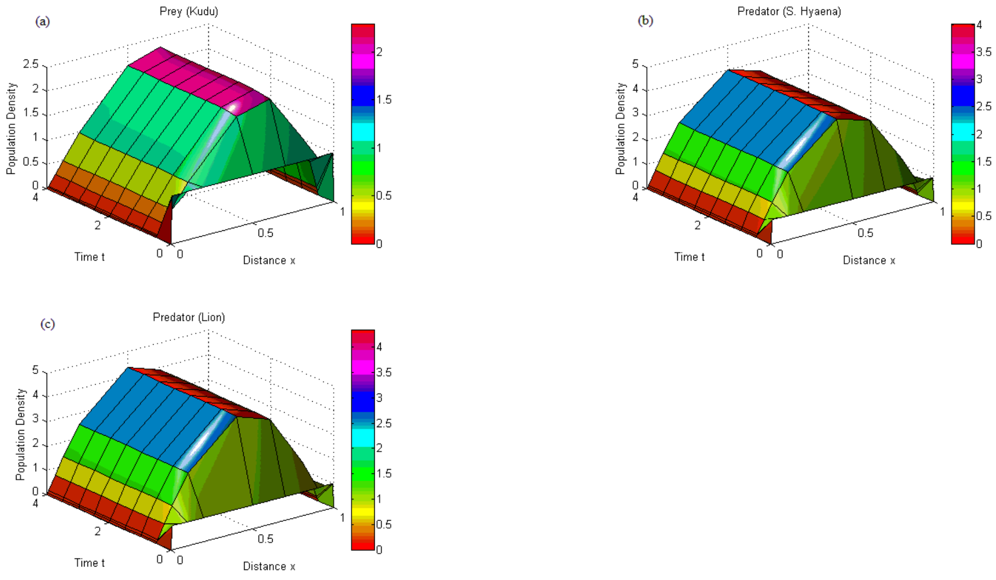

Figure 5.7: *Approximate species densities with temporal and spatial discretization of parameters for Model system (5.19-5.21). Parameter values are as described in Table 5.2 (same as Figure 5.1). Dispersal rates:* $D_b = 4 \times\ 10^{-1}$, $D_p = 9 \times\ 10^{-1}$, $m_b = 6.5 \times\ 10^{-1}$ *and* $m_p = 3.5 \times\ 10^{-1}$. *Like for Model system (5.13-5.15), the initial population density for each species is chosen to be positive at* $B(0) = 19.0, H(0) = 6.0$ *and* $L(0) = 3.0$.

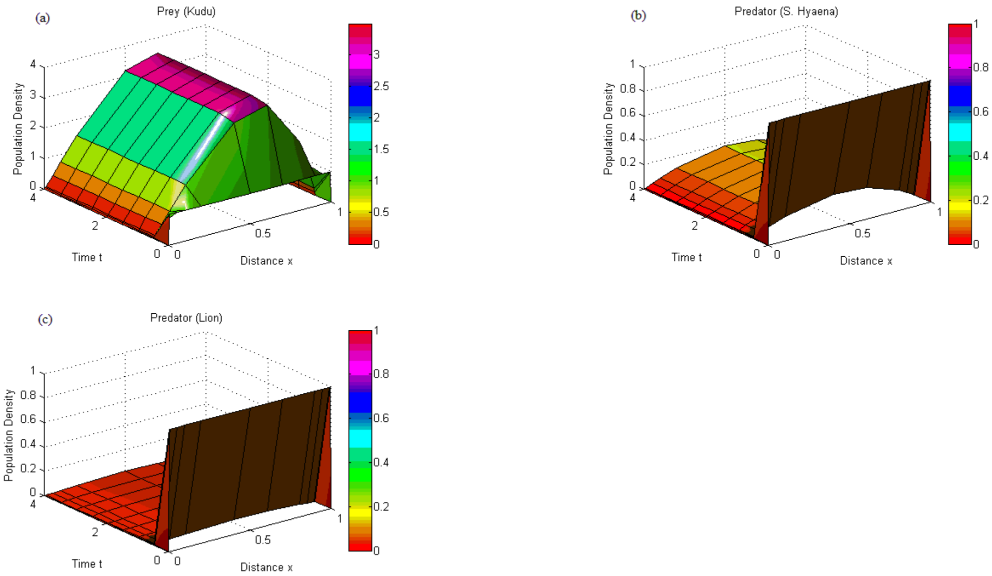

Figure 5.8: *Space-time evolution of species density for Model system (5.19-5.21) when predators face a high interspecific interference as a result of overlap of activity patterns, same as Figure 5.2 (i.e.,* $\psi_h = 0.02365 \times 10^3$ *and* $\psi_l = 0.0153 \times 10^3$*).*

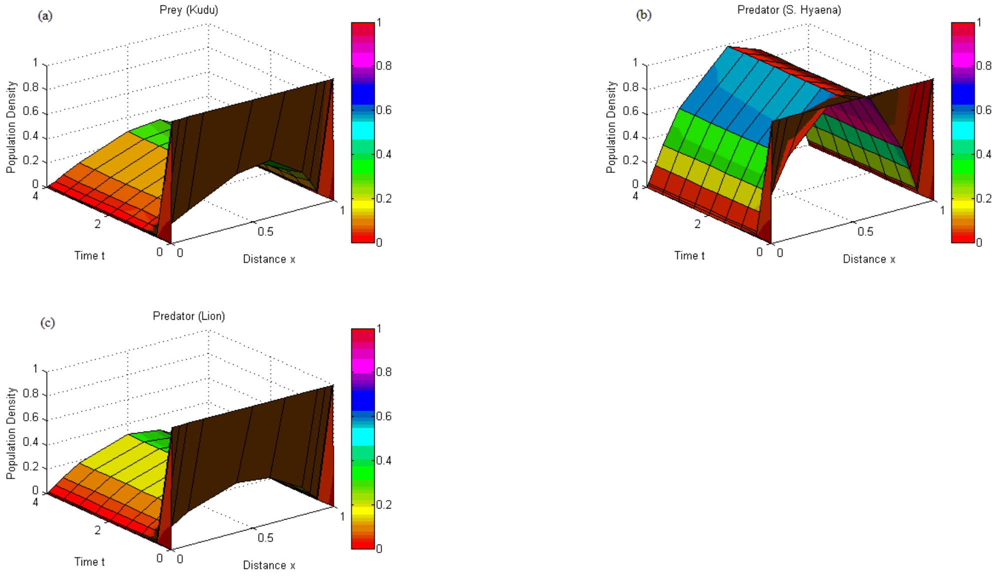

Figure 5.9: *The effect of high predation rates (i.e.,* $\alpha_h = 0.1054 \times 10^3$ *and* $\alpha_l = 0.1690 \times 10^3$*) at high fertility gain, same as Figure 5.3 (i.e.,* $\epsilon_h = 0.001054 \times 10^3$ *and* $\epsilon_l = 0.001690 \times 10^3$*) when a steady additional food input is maintained. Perturbations have both positive and negative small values around the equilibrium state.*

Table 5.2: *Parameter descriptions and their base value estimates*

Symbol	**Description**	**Numerical Value**	**Ref.**
μ_h & μ_l	natural mortality rate	0.0833 & 0.0625	[32,45,46,64]
α_h & α_l	predation rates	0.1054 & 0.1690	[16],AENP*
ψ_h & ψ_l	interspecific interference coefficients	0.02365 & 0.0153	[16,17,22]
F_h & F_l	additional food biomass	0.2500 & 0.5000	estimate
r_b	intrinsic growth rate	0.84	[43,44],AENP*
K_b	carrying capacity for prey species	320	[43,44]
ϵ_h & ϵ_l	fertility factors due to predation	0.001054 & 0.001690	estimate
ϵ_{f_h} & ϵ_{f_l}	fertility factors due to added food	0.002500 & 0.005000	estimate
$\frac{1}{a_h}$ & $\frac{1}{a_l}$	half saturation constants	10.54 & 16.90	[16]

**Unpublished data*

A typical response resulting from a steady food input is observed in Figures 5.3,5.6 and 5.9. In the absence of additional food supply, starvation gives rise to an unstable stationary state. Thus, a stationary and uniform source of food input leads to a stationary steady state of the system. However, as shown in Figures 5.2,5.5 and 5.8, at high interspecific interference as a result of overlap of activity patterns, predators nearly obtain a saturation value under minimal starvation conditions. Availability of food leads to the ordered component of food intake to give a saturation shift towards a saturation level (Figures 5.3 and 5.6). This can arise from neglecting the saturation decline force that emanates from high predator fertility factors. The saturation spread is smaller for high food concentrations and high predation rates than for low cases. This spread as shown in Figures 5.4-5.6 eventually reduce as species dispersal rates are increased further. When the food supply is constant in both space and time, the high predator fertility factor arising from the food intake at high predation rates evokes both the "linear conjecture" and the ecological principle of competitive exclusion among the interfering predators (Figures 5.2,5.8 and 5.9).

Comparing Figures 5.4 and 5.6, a longer period of damped oscillations behind the invasion front are observed in Figure 5.6. High predation rates that results in high fertility gain coupled with high interspecific interference among predators lead to longer temporal dynamical convergence to the stable equilibrium state resulting into longer period of damped oscillations (Figures 5.5 and 5.6). Spatio-temporal heterogeneity is temporarily observed within the interfering predators, however, this does not persist at later times. The stability of the positive steady state has a fundamental impact on the spatio-temporal dynamics of the interacting species (Figures 5.4-5.6). Stable travelling waves of the interfering predators exhibit increasingly irregular periodic travelling wave behaviour when key parameter values are increased beyond their baseline values. Such irregular periodic travelling waves, as observed by Pearce *et al.* (2006), often result in heterogeneous spatio-temporal patterns of prey (host) and predator (parasitoid) abundance. The generation of such heterogeneous patterns has various ecological implications (Pearce *et al.,* 2006).

From the numerical experimental results, it is noted that spatial dispersal of the predators does not damp out population fluctuations in predator-prey systems involving additional food supply. The heterogeneous patterns continue to evolve over time and a fixed spatial distribution does not arise. This suggests that temporally and spatially fixed niches will not arise in dispersive predator-prey systems that are provided with additional food. Thus, dispersal amplifies the impact of temporal oscillations on the population dynamics leading to the quasi-chaotic heterogeneous spatio-temporal patterns as observed by Pearce *et al.* (2006). The results of this study highlight the value of further investigation of predator-prey interactions that are; provided with additional food, involving predator interference and modelled by reaction-diffusion equations. Furthermore, the results reveal the behaviour of such interactions, while also suggesting ways of improving the models under this study. The many open questions regarding multi-species predator-prey interactions in a spatial setting which have remained unanswered call for more similar/related studies.

Chapter 6

Discussion, Conclusions and Recommendations

6.1 Scope and methods used

Even though by no means can this project be considered exhaustive, a brief excursion into mathematical techniques used in the modelling of biological species' interaction has been undertaken. It has greatly depended on explanations of the complexity of ecosystem dynamics together with recent developments in applied mathematics and computer science, the tools of which are used in contemporary mathematical ecology. In an attempt to provide some clarity to the basic ideas of migration and dispersal (diffusion), prey refuge, species' interference, biological control via additional food, species' mimicry and group defense in complex ecosystem, mathematical models mimicking these concepts have been formulated and analysed. It should be mentioned that, although a large number of available mathematical tools is certainly a positive factor enhancing theoretical studies, a question about consistency of the different approaches often arises.

6.1.1 Supporting theorems and basic principles

To comply with the notion of scientific studies being conducted alongside sounding laws and theorems, as in Hsu (2005), Bazykin (1998) and Takeuchi (1996), the linearisation theorem, Lyapunov stability theory, Fick's law, Fisher's hypothetical formulations, the competitive exclusion principle, limit cycle perturbation theory and the Poincaré-Bendixson theorem are among the fundamental applied mathematical theories that have been used in the formulations and analyses of the models studied. The common challenge of spatial modelling that often elevates the discrepancy/inconsistency of different modelling approaches has been resolved and addressed, as in Pearce *et al.* (2006) and Holt (1984), by incorporating spatial heterogeneity into the reaction-diffusion models via explicit space-dependence of corresponding parameters. The modified models then exhibit properties qualitatively similar to those described by the space discrete approach, in particular; travelling waves, periodicity and limit cycle solutions (Kolokolnikov *et al.,* 2006; Petrovskii & Li, 2006; Petrovskii *et al.,* 2005; Murray, 1993). Similar arguments apply to the relationship between the advection-reaction-diffusion models and integral-difference models (Tyutyunov *et al.,* 2007). In particular, as used by Liu (2010), Petrovskii & Li (2006) and Roussel (2004), accelerating population waves of invasive species has been described by the reaction-diffusion models by taking into account the scale-dependence of the diffusion coefficient, relative diffusivity, as well as the wave number. Irrespective of the species' habitat, such scale-dependence was shown to be a common property of the models of biological invasion in turbulence-driven dispersal (Okubo, 1980).

6.2 Results of the study

6.2.1 On the qualitative and quantitative analyses

In exploring how the model parameters affect the behaviour of the various systems, reasonable attention has been focused on specifically identified sensitive parameters in the formulated models of Chapters 3, 4 and 5. In Chapter 3, the predator fertility rate, ϵ_u, and the threshold/critical prey population, ϖ, were given special attention and their results were presented in Sections 3.3-3.4 and discussed in Section 3.5. Various stability and existence conditions were derived. Global stability analysis results showed that the warthog population density should exceed the sum of its carrying capacity and threshold value minus its equilibrium value i.e., $W > (K_w + \varpi) - W^*$. This result which was proved in Theorem 3.3.3, about the global stability of the co-existence steady state, shows that the warthog's equilibrium population density is bound above, i.e., $W^* < (K_w + \varpi)$. Prey refuge, ω_r, and predator additional food, F_l, are numerically varied in Chapter 4, while in Chapter 5, the effect of predator interference has been studied. Stability of the systems steady states have been studied for the various models using linearisation techniques, the *Routh-Hurwitz* stability criterion and the Lyapunov stability theorem. The obtained results are mathematically intriguing and their ecological implications were discussed/presented in Sections 3.5, 4.2 and 5.4.

The conditions that guarantee purely imaginary roots for the nonlinear predator-prey Model systems (3.1-3.3) and (5.1-5.3), do not necessarily guarantee the existence of simple periodic solutions as is the case for the linearised predator-prey systems (cf. Petrovskii & Li, 2006; Petrovskii *et al.,* 2005; Takeuchi, 1996). The structurally unstable nature of the nonlinear systems studied has been deduced based on the fact that some perturbations near a centre can sometimes lead to unstable behaviour. Such unnatural structural instability in the neighbourhood of the steady states leads to limitations in the applications of the Lotka-Volterra predator-prey model. Furthermore, as mentioned in Bazykin (1998), the nonlinear systems are conservative so that any additional factors put into the models qualitatively change their behaviour.

Despite the deviation from the *paradox of enrichment* as observed by numerous field studies (Khan *et al.,* 2004; Sherratt *et al.,* 1997; Berryman, 1992), it was shown that system (3.4-3.6) exhibits this paradox. The *paradox of enrichment* asserts that enriching a predator-prey system causes an increase in the steady state density of the predator but not that of the prey. As observed by Freedman & Wolkowicz (1986), this destabilizes the positive steady state leading to a higher probability of predator extinction. Neutrally stable periodic solutions in system (5.1-5.3) have been deduced, with oscillatory amplitudes that depend on many factors such as, wave number, dispersal behaviour, relative diffusivity and migration coefficients. It was shown (see Subsection 5.3.5) that the periodic solutions ($\widehat{\Phi}_1$ and $\widehat{\Phi}_3$), which influence the dispersal frequency (φ) of the interacting species, are controlled by the wave number. In addition, the wave number was shown to depend on various parameters among which include additional food and species' diffusion (see Subsection 5.3.3). For stability, and in order to overcome predator natural mortality, the nutritional value of such additional food has to be high enough i.e., high predator fertility gain.

Although the origin of the *Allee effect* is rather poorly understood, spatio-temporal dynamics of populations with such threshold mechanisms have attracted reasonable attention recently (Courchamp *et al.,* 2008; Stephens *et al.,* 1999; McCarthy, 1997). Despite the many biological and environmental factors which have been identified as its possible cause (cf. Courchamp *et al.,* 2008; Dennis, 1989), mechanistic theories are often lacking resulting in many open questions. The choice of growth rate parameterisation, and hence the general properties of the formulated model are affected due to the uncertain profound impact exhibited by threshold population among interacting species. For example, *Allee effect* exhibits itself in intermediate and large values of the population density where the effect of intraspecific competition is essential. For instance, the cubic polynomial of the chosen growth rate function for Model system (3.1-3.3), which is one of the usual parameterisation assumes implicitly that the impact of the *Allee effect* and that of intraspecific competition interfere for intermediate values of the population density.

6.2.2 Principle of Competitive Exclusion

If two competitors co-exist, there must be a reason for them to do so, and the principle of competitive exclusion focuses attention on this situation (Armstrong & McGehee, 1980; Hsu *et al.,* 1978a, b). For any two species occupying the same ecological niche at the same time, interacting in the same way, and requiring the same nutrients i.e., same food type, the principle of competitive exclusion prevails (Takeuchi, 1996; Muratori & Rinaldi, 1989). Considerable effort has been invested in mitigating the competitive exclusion dilemma through evoking the competitive exclusion principle on the predator (lion-spotted hyaena) interference Model system (5.1-5.3) in order to establish the out-competition conditions. Species interaction at different trophic levels can sometimes lead to a stable co-existence, which renders the competitive exclusion principle not to be satisfied at all times.

6.3 Recommendations and Further development of the study

The situation that involves/relates the duality of ecosystem dynamics emanating from the interplay between deterministic and stochastic factors poses seemingly challenging and more complicated open questions. As revealed by Berryman (1992), the simple misunderstanding of the origin of deterministic models seems to be one of the major causes of this mathematical modelling dilemma. Due to the intrinsic stochasticity of ecosystem dynamics as a result of irregular fluctuations in ecological data, stochastic processes are often described by deterministic equations which are either integral in nature or of partial differential type involving varying assumptions (Bazykin, 1998; Takeuchi, 1996; Murray, 1993).

In spite of the predictive power provided by deterministic models, a lot of limitations of predictability in ecosystem dynamics for particular stochastic fluctuations often arise and this renders the question of reproducing exact simulations somehow challenging. For example, predicting the exact time and magnitude of a particular stochastic fluctuation in an ecological process may be as challenging as predicting the exact position of a quantum particle using the *Schrödinger* theory (Luan & Tang, 2005). It should also be mentioned that the advection-reaction-diffusion equations do not necessarily exhaust the deterministic models, hence a need to integrate other modelling theories and approaches. For example, ignoring the species' random walk within an ecosystem paves way for the development of other explicit reaction-diffusion partial differential equation type of models (Petrovskii & Li, 2006; Okubo, 1980).

Besides the model's capacity to describe a given ecological phenomenon, another important feature is its solvability. Taking into consideration that population dynamical models are usually nonlinear and can usually only be solved by means of computer simulations because existing analytical methods are often inadequate. Since numerical studies require particular parameter values, the lack of analytical methods and relevant analytical solutions decrease the generality of results and so reduce their reliability. Ideal theoretical studies combine both analytical and numerical methods, a more in-depth qualitative analyses of the Model system (4.4-4.6) need to be undertaken in future studies.

For co-existence and stability of equilibria of the species interaction in Model system (3.1-3.3), the prey carrying capacities were shown to play a pivotal role (see Theorems 3.3.1 and 3.3.3). Thus, establishment of the carrying capacity of the game park and its threshold relationships with other ecosystem parameters (see Chapters 3 and 5) for each prey species should be one of the management considerations.

The stabilising effect of prey refuge due to variations in predator fertility and proportion of prey that access the refuge (see Chapter 4) suggest that expansion/provision of warthog burrows should be considered a management programme rather than leaving the warthog to depend on the abandoned/disused aardvark (*Orycteropus afer*) burrows.

Finally, despite the supplementary feeding rendered to predators, as motivated earlier, empirical data and methods used in carrying out this activity are still scanty. Thus, matching the importance of additional food to predator-prey systems with empirical data of game parks within the Eastern Cape province e.g., Shamwari and Kwandwe, remains an open challenge. This could be tested by carrying out numerical simulations on Model systems (5.1-5.3), (5.13-5.16) and (5.19-5.21). The results could then be used as a basis for recommendation of supplementary feeding in other game parks.

Chapter 7

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Appendix A

Research outputs of the author

1. Ddumba, H., Mugisha, J.Y.T., Gonsalves, J.W. and Kerley, G.I.H. Periodicity and limit cycle perturbation analysis of a predator-prey model with interspecific species' interference, predator additional food and dispersal. *Submitted for publication.*
2. Ddumba, H., Mugisha, J.Y.T., Gonsalves, J.W. and Kerley, G.I.H. (2012). The role of predator fertility and prey threshold bounds on the global and local dynamics of a predator-prey model with a prey out-flux dilution effect. *Applied Mathematics and Computation,* **218**(18): 9169 – 9186.
3. Ddumba, H., Mugisha, J.Y.T., Gonsalves, J.W. and Kerley, G.I.H. *"The role of predator fertility factor and prey threshold bounds on the global and local dynamics of a predator-prey model with a prey out-flux dilution effect: The paradox of enrichment."* The Southern Africa Mathematical Sciences Association (SAMSA) Symposium In Collaboration with Africa Society for Biomathematics (ASB), Botswana 29th November to 4th December 2010.
4. Ddumba, H. *On predator-prey modelling: predator fertility, prey threshold, out-flux dilution effect, additional food and prey refuge.* **Keynote Lecture:** Annual Postgraduate Seminar in Mathematics, Department of Mathematics and Applied Mathematics, Summerstrand South Campus, NMMU 24th – 25th September 2010.

5. Ddumba, H. *Reaction-diffusion predator-prey modelling with partial differential equations.* Annual Postgraduate Seminar in Mathematics, Department of Mathematics and Applied Mathematics, Summerstrand South Campus, NMMU $25^{th} - 26^{th}$ September 2009.

Appendix B

MatLab computer programs used for numerical simulation of the models

```
! ******************************************************************
!   The MatLab Codes for Numerically Integrating the Ordinary Differential   *
!          Equations Model For Prey out-flux dilution effect   *
!********************************************************************
clear
clc
disp(’Predator -Prey simulation using Runge-Kutta 4th order’);
disp(’’);
disp(’Enter the following constants of the dynamical system consisting of 2 prey
and 1 predator (Lion)’);
r1 = input(’Enter (r1) buffalo intr birth rate : ’);
Kb = input(’Enter (Kb) : ’);
Fl = input(’Enter (Fl) : ’);
h = input(’Enter (h) : ’);
alpha_1 = input(’Enter (alpha_1) : ’);
r2 = input(’Enter (r2) : ’);
Kw = input(’Enter (Kw) : ’);
```

```
Lo = input('Enter (Lo) : ');
alpha_3 = input('Enter (alpha_3) : ');
Wr = input('Enter (Wr) : ');
beta_1 = input('Enter (beta_1) : ');
epsi_u = input('Enter epsiplon_u : ');
epsi_fl = input('Enter epsiplon_fl : ');
mu = input('Enter (mu) : ');
disp('Time data');
dt = input('Enter steplength in time (delta t) : ');
Tf = input('Enter final time (Tf) : ');
T = (0:dt:Tf);
it = length(T);
B = zeros(1,it); % Buffalo
W = zeros(1,it); % Warthog
L = zeros(1,it); % Lion
disp('Initial populations');
B(1) = input('Enter initial population of prey 1 [N1(0)] : ');
W(1) = input('Enter initial population of prey 2 [N2(0)] : ');
L(1) = input('Enter initial population of predator 1 [P1(0)] : ');
Bdot = inline('r1*n1*(1-n1/Kb)-alpha_1*(1-Fl)*n1*p/(1+h*n1)','r1','Kb','alpha_1',
'Fl','h','n1','p');
Wdot = inline('r2*n2*(1-n2/Kw)*((n2/Lo)-1)-alpha_3*(1-Fl)*(1-Wr)*n2*p','r2','Kw',
'Lo','alpha_3','Fl','Wr','n2','p');
Ldot = inline('beta_1*(1-Fl)*(1-Wr)*n2*p+(epsi_u*alpha_1*(1-Fl)*n1*p/(1+h*n1))+
(epsi_fl*Fl-mu)*p','beta_1','Fl','Wr','epsi_u','alpha_1','h','mu','epsi_fl','p',
'n1','n2');
for j = 2:it
    %disp(j);
        k1 = dt*Bdot(r1,Kb,alpha_1,Fl,h,B(j-1),L(j-1));
        k2 = dt*Bdot(r1,Kb,alpha_1,Fl,h,(B(j-1)+0.5*k1),L(j-1));
```

```
        k3 = dt*Bdot(r1,Kb,alpha_1,Fl,h,(B(j-1)+0.5*k2),L(j-1));
        k4 = dt*Bdot(r1,Kb,alpha_1,Fl,h,(B(j-1)+k3),L(j-1));
        B(j) = B(j-1)+((k1+2*k2+2*k3+k4)/6);
        k1 = dt*Wdot(r2,Kw,Lo,alpha_3,Fl,Wr,W(j-1),L(j-1));
        k2 = dt*Wdot(r2,Kw,Lo,alpha_3,Fl,Wr,(W(j-1)+0.5*k1),L(j-1));
        k3 = dt*Wdot(r2,Kw,Lo,alpha_3,Fl,Wr,(W(j-1)+0.5*k2),L(j-1));
        k4 = dt*Wdot(r2,Kw,Lo,alpha_3,Fl,Wr,(W(j-1)+k3),L(j-1));
        W(j) = W(j-1)+((k1+2*k2+2*k3+k4)/6);
        k1 = dt*Ldot(beta_1,Fl,Wr,epsi_u,alpha_1,h,mu,epsi_fl,L(j-1),B(j-1),
             W(j-1));
        k2 = dt*Ldot(beta_1,Fl,Wr,epsi_u,alpha_1,h,mu,epsi_fl,(L(j-1)+0.5*k1),
             B(j-1),W(j-1));
        k3 = dt*Ldot(beta_1,Fl,Wr,epsi_u,alpha_1,h,mu,epsi_fl,(L(j-1)+0.5*k2),
             B(j-1),W(j-1));
        k4 = dt*Ldot(beta_1,Fl,Wr,epsi_u,alpha_1,h,mu,epsi_fl,(L(j-1)+k3),
             B(j-1),W(j-1));
        L(j) = L(j-1)+((k1+2*k2+2*k3+k4)/6);
end
ipop = sprintf('Initial values for Buffalo: %2.3f, Warthog: %2.3f and Lion:
%2.3f',B(1),W(1),L(1));
plot(T,B,'r-.',T,W,'b:',T,L,'c-');
%title({'One Predator Two Prey Population Dynamics',ipop});
xlabel('Time in years');
ylabel('Population density');
legend('Buffalo','Warthog','Lion','Location','Best');
! ------------------------------------------------------------
!  THESE CODES PRODUCE 4 PLOTS PER PAGE OF THE MODEL SYSTEM (3.1-3.3) FOR VARIOUS
                              PARAMETER VALUES
%program plots
clear;clc;
```

```
fig_count=0;
for M=1:4
    disp(M);
    Time=[0.01,1000];
    Initlpop=[4.5,15,3];
    if M==1
        PMU=[0.84,10,0,2.5,0.2833,2.53,25,14.0,0.11283,0,0.002583,2.4,0,0.125];
    elseif M==2
        PMU=[0.84,10,0,2.5,0.2833,2.53,25,18.0,0.11283,0,0.002583,2.4,0,0.125];
    elseif M==3
        PMU=[0.84,10,0,2.5,0.2833,2.53,25,24.0,0.11283,0,0.002583,2.4,0,0.125];
    else
        PMU=[0.84,10,0,2.5,0.2833,2.53,25,50.0,0.11283,0,0.002583,2.4,0,0.125];
    end
    fig_count=fig_count+1;
    subplot(2,2,fig_count);
    [t,x,y,z]=fourplotsdata(PMU,Time,Initlpop);
    plot(t,x,t,y,t,z,'k-','LineWidth',2);
    axis([0 1000 0 50]);
    ipop = sprintf('Initial values for Buffalo: %2.3f, Warthog: %2.3f and Lion:
    %2.3f',Initlpop(1),Initlpop(2),Initlpop(3));
    title({'One Predator Two Prey Population Dynamics',ipop});
    xlabel('Time in years');
    ylabel('Population density');
    legend('Buffalo','Warthog','Lion','Location','Best');
end
!*******************************************************************
! ****************************************************************
!   The MatLab Codes for Numerically Integrating the Reaction-Diffusion   *
!                          Model System 5.13-5.15   *
```

```
!********************************************************************
function pdex4
m = 0;
%x = [0 0.005 0.01 0.05 0.1 0.2 0.5 0.7 0.9 0.95 0.99 0.995 1];
%t = [0 0.005 0.01 0.05 0.1 0.5 1 1.5 2];
x = [0:0.01:2];
t = [0:0.02:3];
sol = pdepe(m,@pdex4pde,@pdex4ic,@pdex4bc,x,t);
u1 = sol(:,:,1);
subplot(2,2,1);
surf(x,t,u1)
camlight left;
lighting phong
title('Du/Dt')
xlabel('Distance x')
ylabel('Time t')
colormap hsv;
colorbar
sol = pdepe(m,@pdex4pdev,@pdex4ic,@pdex4bc,x,t);
u2 = sol(:,:,1);
subplot(2,2,2);
surf(x,t,u2)
camlight left;
lighting phong
title('Dv/Dt')
xlabel('Distance x')
ylabel('Time t')
colormap hsv;
colorbar
sol = pdepe(m,@pdex4pdew,@pdex4ic,@pdex4bc,x,t);
```

```
u3 = sol(:,:,1);
subplot(2,2,3);
surf(x,t,u3)
camlight left;
lighting phong
title(’Dw/Dt’)
xlabel(’Distance x’)
ylabel(’Time t’)
colormap hsv;
colorbar
% --------------------------------------------------------------
function [c,f,s] = pdex4pde(x,t,u,DuDx)
edata = [1 2 3 4 5  6 7 8 9 10 11 12 13 14 1 16 17 18 19 20 21 22 23];
rb = edata(1);
kb = edata(2);
Db = edata(3);
Dp = edata(4);
mb = edata(5);
mp = edata(6);
Fl = edata(7);
Fh = edata(8);
ah = edata(9);
al = edata(10);
psi_h = edata(11);
psi_l = edata(12);
alpha_h = edata(13);
alpha_l = edata(14);
epsi_h = edata(15);
epsi_l = edata(16);
epsi_fh = edata(17);
```

```
epsi_fl = edata(18);
muh = edata(19);
mul = edata(20);
B = edata(21);
H = edata(22)
L = edata(23)
udot = (rb/mul)*(B/kb)*(1-(B/kb))  - (muh/mul)*(1 - Fl)*(B/kb)*((alpha_h/muh)*H) -
       ((1 - Fl)*(B/kb)*((alpha_l*L)/mul))/(1 + (ah/kb)*(B/kb) +
       ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H));
vdot =  ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/(1 + (ah/kb)*(B/kb) +
        ((psi_h*muh)/alpha_h)*((alpha_l*L)/mul)) - ((muh/mul)*((alpha_h/muh)*H) +
        ((alpha_h/muh)*H) * (epsi_fh*Fh/mul));
wdot = ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/((1 + (ah/kb)*(B/kb) +
        ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H))) - ((alpha_l*L)/mul) +
        (epsi_fh*Fh/mul)*((alpha_l*L)/mul);
c = 1;
f = DuDx*(Db/Dp);
s = udot;
% --------------------------------------------------------------
function u0 = pdex4ic(x);
u0 = 1;
% --------------------------------------------------------------
function [pl,ql,pr,qr] = pdex4bc(xl,ul,xr,ur,t)
pl = ul;
ql = 0;
pr = ur;
qr = 0;
function [c,f,s] = pdex4pdev(x,t,u,DvDx)     %Dv/dx
edata = [1 2 3 4 5  6 7 8 9 10 11 12 13 14 1 16 17 18 19 20 21 22 23];
rb = edata(1);
```

```
kb = edata(2);
Db = edata(3);
Dp = edata(4);
mb = edata(5);
mp = edata(6);
Fl = edata(7);
Fh = edata(8);
ah = edata(9);
al = edata(10);
psi_h = edata(11);
psi_l = edata(12);
alpha_h = edata(13);
alpha_l = edata(14);
epsi_h = edata(15);
epsi_l = edata(16);
epsi_fh = edata(17);
epsi_fl = edata(18);
muh = edata(19);
mul = edata(20);
B = edata(21);
H = edata(22)
L = edata(23)
udot = (rb/mul)*(B/kb)*(1-(B/kb))  - (muh/mul)*(1 - Fl)*(B/kb)*((alpha_h/muh)*H) -
       ((1 - Fl)*(B/kb)*((alpha_l*L)/mul))/(1 + (ah/kb)*(B/kb) +
       ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H));
vdot =  ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/(1 + (ah/kb)*(B/kb) +
       ((psi_h*muh)/alpha_h)*((alpha_l*L)/mul)) - ((muh/mul)*((alpha_h/muh)*H) +
       ((alpha_h/muh)*H) * (epsi_fh*Fh/mul));
wdot = ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/((1 + (ah/kb)*(B/kb) +
       ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H))) - ((alpha_l*L)/mul) +
```

```
       (epsi_fh*Fh/mul)*((alpha_l*L)/mul);
c = 1;
f = DvDx;
s = vdot;
%---------------------------------------------------------------------------
%-----------
function [c,f,s] = pdex4pdew(x,t,u,DwDx)     %Dv/dx
edata = [.1 .002 .0053 4 5  6 7 8 9 10 11 12 13 14 1 16 17 18 19 20 21 22 23];
rb = edata(1);
kb = edata(2);
Db = edata(3);
Dp = edata(4);
mb = edata(5);
mp = edata(6);
Fl = edata(7);
Fh = edata(8);
ah = edata(9);
al = edata(10);
psi_h = edata(11);
psi_l = edata(12);
alpha_h = edata(13);
alpha_l = edata(14);
epsi_h = edata(15);
epsi_l = edata(16);
epsi_fh = edata(17);
epsi_fl = edata(18);
muh = edata(19);
mul = edata(20);
B = edata(21);
H = edata(22)
```

```
L = edata(23)
udot = (rb/mul)*(B/kb)*(1-(B/kb))  - (muh/mul)*(1 - Fl)*(B/kb)*((alpha_h/muh)*H) -
       ((1 - Fl)*(B/kb)*((alpha_l*L)/mul))/(1 + (ah/kb)*(B/kb) +
       ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H));
vdot =  ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/(1 + (ah/kb)*(B/kb) +
        ((psi_h*muh)/alpha_h)*((alpha_l*L)/mul)) - ((muh/mul)*((alpha_h/muh)*H) +
        ((alpha_h/muh)*H) * (epsi_fh*Fh/mul));
wdot = ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/((1 + (ah/kb)*(B/kb) +
       ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H))) - ((alpha_l*L)/mul) +
       (epsi_fh*Fh/mul)*((alpha_l*L)/mul);
c = 1;
f = DwDx;
s = wdot;
! *****************************************************************
!   The MatLab Codes for Numerically Integrating the Advection-Reaction-Diffusion   *
!                          Model System 5.19-5.21   *
!******************************************************************
function pdex4
m = 0;
x = [0 0.005 0.01 0.05 0.1 0.2 0.5 0.7 0.9 0.95 0.99 0.995 1];
t = 0:0.5:4;
sol = pdepe(m,@pdex4pde,@pdex4ic,@pdex4bc,x,t);
u1 = sol(:,:,1);
subplot(2,2,1);
contourf(x,t,u1)
camlight left;
lighting phong
title('Du/Dt')
xlabel('Distance x')
ylabel('Time t')
```

```
colormap hsv;
colorbar
sol = pdepe(m,@pdex4pdev,@pdex4ic,@pdex4bc,x,t);
u2 = sol(:,:,1);
subplot(2,2,2);
contourf(x,t,u2)
camlight left;
lighting phong
title('Dv/Dt')
xlabel('Distance x')
ylabel('Time t')
colormap hsv;
colorbar
sol = pdepe(m,@pdex4pdew,@pdex4ic,@pdex4bc,x,t);
u3 = sol(:,:,1);
subplot(2,2,3);
contourf(x,t,u3)
camlight left;
lighting phong
title('Dw/Dt')
xlabel('Distance x')
ylabel('Time t')
colormap hsv;
colorbar
% --------------------------------------------------------------
function [udot,vdot,wdot,Db,Dp,mp,mb] = returndot()
%line = input('Enter me');
edata = [.2 2 3 4 5  6 7 8 9 10 11 12 13 14 1 16 17 18 19 20 21 22 23];
rb = edata(1);
kb = edata(2);
```

```
Db = edata(3);
Dp = edata(4);
mb = edata(5);
mp = edata(6);
Fl = edata(7);
Fh = edata(8);
ah = edata(9);
al = edata(10);
psi_h = edata(11);
psi_l = edata(12);
alpha_h = edata(13);
alpha_l = edata(14);
epsi_h = edata(15);
epsi_l = edata(16);
epsi_fh = edata(17);
epsi_fl = edata(18);
muh = edata(19);
mul = edata(20);
B = edata(21);
H = edata(22)
L = edata(23)
udot = (rb/mul)*(B/kb)*(1-(B/kb))  - (muh/mul)*(1 - Fl)*(B/kb)*((alpha_h/muh)*H) -
       ((1 - Fl)*(B/kb)*((alpha_l*L)/mul))/(1 + (ah/kb)*(B/kb) +
       ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H));
vdot =  ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/(1 + (ah/kb)*(B/kb) +
        ((psi_h*muh)/alpha_h)*((alpha_l*L)/mul)) - ((muh/mul)*((alpha_h/muh)*H) +
        ((alpha_h/muh)*H) * (epsi_fh*Fh/mul));
wdot = ((epsi_l*alpha_l*kb/mul)* (muh/mul)*(B/kb)*((alpha_h/muh)*H))/((1 + (ah/kb)*(B/kb) +
        ((psi_h*muh)/alpha_h)*((alpha_h/muh)*H))) - ((alpha_l*L)/mul) +
        (epsi_fh*Fh/mul)*((alpha_l*L)/mul);
```

```
function [c,f,s] = pdex4pde(x,t,u,DuDx)%DuDt

[udot,vdot,wdot,Db,Dp,mp,mb] = returndot();

c = 1;

f = DuDx*(Db/Dp);

s = -(mb/mp)*DuDx + udot;

% --------------------------------------------------------------

function u0 = pdex4ic(x);

u0 = 1;

% --------------------------------------------------------------

function [pl,ql,pr,qr] = pdex4bc(xl,ul,xr,ur,t)

pl = ul;

ql = 0;

pr = ur;

qr = 0;

function [c,f,s] = pdex4pdev(x,t,u,DvDx)     %Dv/dt

[udot,vdot,wdot,Db,Dp,mp,mb] = returndot();

c = 1;

f = DvDx;

s = -(DvDx) + vdot;

%-------------------------------------------------------------------------

%-----------

function [c,f,s] = pdex4pdew(x,t,u,DwDx)     %Dv/dt

[udot,vdot,wdot,Db,Dp,mp,mb] = returndot();

c = 1;

f = DwDx;

s = -(DwDx) + wdot;
```

“Riding The Tiger”

Last citation (Psalms)

In the name of God, the Most Beneficent, the Most Merciful.

"Lord, you have assigned me my portion and my cup,
You have made my lot secure.
The boundary lines have fallen for me
in pleasant places;
surely I have a delightful inheritance."
(Psalm 16:5,6)