Modelling wildebeest foraging processes and their interaction with zebra and lion in the Serengeti ecosystem

Kisoma, Linus

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MODELLING WILDEBEEST FORAGING PROCESSES AND THEIR INTERACTION WITH ZEBRA AND LION IN THE SERENGETI ECOSYSTEM

Linus Nyarusanda Kisoma

A Dissertation Submitted in Partial Fulfilment of the Requirements for the Degree of Doctor of Philosophy in Mathematical and Computer Sciences and Engineering of the Nelson Mandela African Institution of Science and Technology

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ABSTRACT

Animal movements and foraging processes for the migrating species, especially wildebeests and zebras, and the prey-predator interactions of these prey species with lions are ambiguous biological characteristics in the Serengeti ecosystem. These complex dynamics help animals to adapt and survive. To understand such dynamics, investigating factors that determine foraging efficiency and the prey-predator interaction is worth it. This dissertation presents deterministic mathematical models to examine wildebeest foraging processes and the prey-predator interaction of wildebeest, zebra, and lion populations. The first model studies the foraging processes of migrating wildebeests using the concepts of random walk and diffusive processes. The model was equipped with data collected from the Serengeti ecosystem from 18 GPS collared wildebeests and analysed in two spatial dimensions. The qualitative analysis of the model was performed, and the parameters that regulate foraging efficiency were calculated for both dry and wet seasons. Numerical simulations were performed, and the results show that directed movements can explain the great migration of wildebeests to different habitats. Wildebeests spread across different habitats to utilize the resources through diffusive trends. The mutual association between wildebeests and zebras was studied by developing the Lotka-Volterra reaction-diffusion systems. This model was further modified to form the third model that includes the predation pressure from lions. The qualitative analyses of the models were carried out in two dimensions to determine points of equilibrium and the conditions for the stability and instability of the systems. The explicit Euler method was used to discretize the models and perform numerical simulations. The stability analyses of the models showed that wildebeests and zebras population growth approached their respective carrying capacities, and the absence of one prey species does not affect the existence of the other. The advection and diffusion parameters in the model produce Turing instabilities. Furthermore, the results show that both prey species are strongly affected by drought and predation pressure, especially from lions. Therefore, advection and diffusion of wildebeests and zebras are motivated by the search for better forage availability and avoidance of predators, while the predator's movement is motivated by capturing prey.
DECLARATION

I, Linus Nyarusanda Kisoma, hereby declare to the Senate of the Nelson Mandela African Institution of Science and Technology that this dissertation is my original work and that it has neither been submitted nor is concurrently submitted for a degree award in any other institution.

Linus Nyarusanda Kisoma

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The above declaration is confirmed by:

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Name and Signature of Supervisor          Date
CERTIFICATION

The undersigned certify that they have read and hereby recommend for acceptance by the Nelson Mandela African Institution of Science and Technology a dissertation titled: “Modelling wildebeest foraging processes and their interaction with zebra and lion in the Serengeti ecosystem” in Partial Fulfilment of the Requirements for the Degree of Doctor of Philosophy in Mathematical and Computer Sciences and Engineering of the Nelson Mandela African Institution of Science and Technology.

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Name and Signature of Supervisor

Dr. Colin Torney

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DEDICATION

To the memory of my late Father Mr. Joseph Kisoma
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<td>$\tau$</td>
<td>Time Step</td>
</tr>
<tr>
<td>$\delta$</td>
<td>Distance</td>
</tr>
<tr>
<td>$r_w$ and $r_z$</td>
<td>Growth</td>
</tr>
<tr>
<td>$K_w$</td>
<td>Carrying Capacities</td>
</tr>
<tr>
<td>$\nabla^2$</td>
<td>Is the Laplacian Operator.</td>
</tr>
<tr>
<td>$\nabla$</td>
<td>Is the Gradient Operator</td>
</tr>
<tr>
<td>$k_n$</td>
<td>Stands for Wave Number,</td>
</tr>
<tr>
<td>$\omega_n$</td>
<td>Is the Growth Rate of Pertubations</td>
</tr>
<tr>
<td>$\delta_{z_0}$</td>
<td>Perturbation Amplitudes</td>
</tr>
<tr>
<td>$P$</td>
<td>Predator</td>
</tr>
<tr>
<td>$J(E_0)$</td>
<td>Jacobian matrix</td>
</tr>
<tr>
<td>$E_2$</td>
<td>Eigenvalues</td>
</tr>
<tr>
<td>2D</td>
<td>Two dimensional</td>
</tr>
<tr>
<td>BRW</td>
<td>Biased Random Walks</td>
</tr>
<tr>
<td>GPS</td>
<td>Global Positioning System</td>
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<tr>
<td>i.e.</td>
<td>Id est</td>
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<tr>
<td>IBM</td>
<td>Individual-Based model</td>
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<tr>
<td>NDVI</td>
<td>Normalized difference vegetation index</td>
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<td>NM-AIST</td>
<td>Nelson Mandela African Institution of Science and Technology</td>
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<tr>
<td>PDE</td>
<td>Partial differential equations</td>
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<tr>
<td>PDF</td>
<td>Probability density function</td>
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<tr>
<td>SRW</td>
<td>Simple Random walk</td>
</tr>
<tr>
<td>TAWIRI</td>
<td>Tanzania Wildlife Research Institute</td>
</tr>
<tr>
<td>UK</td>
<td>United Kingdoms</td>
</tr>
<tr>
<td>UNESCO</td>
<td>United Nations Educational, Scientific and cultural organization</td>
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<tr>
<td>UTM</td>
<td>Universal Transverse Mercator</td>
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CHAPTER ONE

INTRODUCTION

1.1 Background of the Problem

The increase of human interference in the environment has induced major changes in the functioning of different ecosystems leading to the extinction of many species including wildlife (Hagen et al., 2012). Although some species move to different ecosystems in search of forage refuge, this mobility may not occur in the future due to increasing global population growth that contributes to the destruction, modification and fragmentation of wildlife habitats (Taylor-Brown et al., 2019). Thus, there is a need to conserve wildlife (Hopcraft, 2010).

Conservation of the environment and wildlife protects nature, making it available for future generations to enjoy the natural world and its wonderful species and appreciate the importance of wildlife for humans and other species (Hagen et al., 2012). However, studies on species conservation require detailed knowledge of their behaviour, how they acquire food and other resources for their survival, and how they protect themselves against dangers. It is also essential to understand why some animals migrate from one place to another looking for forage refuge (Gueron et al., 1996). For instance, the great annual migration of wildebeests, zebras and predators, and other species in the Serengeti ecosystem.

The Serengeti ecosystem in northern Tanzania is one of the world heritage sites due to the great migration of wildebeest, zebras and other species (Hopcraft 2010). The great migration is caused by the search for green and nutritious pasture between the Serengeti ecosystem in Tanzania and Masai Mara game reserve in Kenya (Tourney et al., 2018). In addition, this ecosystem is home to different animal species including the big five: the Lion, the Elephant, the Black Rhinoceros, the Leopard and the African Buffalo (Sagamiko et al., 2015).

The Serengeti ecosystem is the best known and most treasured ecosystem (Sagamiko et al., 2015). Wildlife conservation in the Serengeti ecosystem is important because it helps maintain a balanced ecological system and the environment as each organism has its place on the food chain (Kideghesho, 2010). Further, wild animals attract tourism (Kideghesho, 2010). The great annual migration of wildebeests, zebras and predators, and other species in the Serengeti ecosystem is so unique that it has been attracting tourists from different parts of the world who come to enjoy the nature of Serengeti (Mduma et al., 1996). This has economic importance
because money is gained from tourism and hunting wild animals (Kideghesho, 2010). In this regard, we need to protect wildlife for the sustainability of the Serengeti ecosystem. This can be achieved by understanding different animal groups' dynamics, especially wildebeests and zebras that form a larger part of migrating animals in the Serengeti ecosystem.

The animal group dynamics in the Serengeti ecosystem have triggered much research interest for more than half a century. Biologists have studied such dynamics through mathematical models and statistical analyses. Besides, movement patterns of wildebeests and zebras have mainly been explained by a changing environment and predation pressure, mainly from a lion. However, only a few attempts have been made to model the foraging processes of wildebeests and how they interact with zebras and lions based on mathematical predictions. This study was motivated by the need to continue investigating the interaction dynamics of wildebeests, zebras, and lions in the Serengeti ecosystem through Mathematical Modelling.

1.1.1 Selection of Animals for this Study

The animals selected for this study were wildebeests (Connochaetes taurinus), zebras (Equus burchellii), and lions (Panthera leo) of the Serengeti National Park. Lion and the hyena are the main predators of grazers in Serengeti (Hopcraft, 2010), but the lion was selected because it accounts for more kills than the hyena (Hopcraft, 2010; Mduma, 1996). Also, zebras and wildebeests were chosen because the two have ecological similarities, including similar body sizes and similar spatial patterns of resource use and migration patterns (Hopcraft, 2010; Sinclair, 1977). Resource availability and predation are two major factors determining the abundance of zebra and wildebeest populations (Grange et al., 2004).

Figure 1: Wildebeest and Zebras in the Serengeti National Park during the great migration (www.isafari.nathab.com/blog/spectacular-photos-from-tanzanias-great-migration/)
Wildebeests and zebras usually migrate together from the Serengeti National Park in northern Tanzania (May to November) to seek fresh grazing and water in the Masai Mara National Reserve in Kenya (Hopcraft, 2010; Tourney et al., 2018; Holdo et al., 2011). Then the animals come back again on the short grass plains of the southern Serengeti (December to May) to seek fresh grazing and calving. This migration is an annual mass movement of millions of ungulates and other species in groups (Holdo et al, 2011). The great migration involves an estimated 1.3 million wildebeests, 200 000 zebras, and a multitude of gazelles, among various other hooved species (Grange et al., 2004).

While the movement patterns of the migrating species have remained the same for decades, the wildebeest populations in the Serengeti ecosystem have been highly variable in size, increasing from 263 000 in 1961 to fluctuating around 1.5 million individuals in 2010 (Menard et al., 2002; Mduma et al., 1999; Hopcraft, 2010). Studies indicate, for example, that in the early 1960s, the numbers of zebras and wildebeests in the Serengeti were almost equal. However, time due to a rinderpest outbreak in the year 1960, which greatly affected wildebeests and buffalos (Syncerus caffer), the wildebeests’ populations decreased while the zebra population in the Serengeti has significantly remained unchanged (Hopcraft, 2010; Duncan et al., 1990; Menard et al., 2002).

![Wildebeest and Zebra abundances from 1961 to 2010](Tanzania Wildlife Research Institute [TAWIRI], 2010)

In addition to the movement for food, wildebeests and zebras, like many other ungulate species, select their habitat use based on the presence of predators (Hopcraft, 2010). The main predators of wildebeests and zebras are lion (Panthera leo) and hyena (Crocuta crocuta) (Mduma et al., 1999). Lions of the Serengeti are classified into two basic types: residents, which remain within a limited area for most of their lives, and the nomads, which wander widely, often following the
movements of the migratory herds (Schaller, 1977). Despite short-term environmental perturbations that have led to numerous gradual changes in prey availability and vegetative cover, populations of Serengeti lions have remained relatively stable (Sinclair et al., 2008). Lions live in prides with an average pride size of four individuals; the pride size and composition change from daily depending on their needs.

![Image of lions in the Serengeti National Park]

Figure 3: The lion pride in the Serengeti National Park (https://www.gettyimages.com/photos/serengeti-lion)

Some studies (Grange et al., 2004; Ikanda & Packer, 2008; Sagamiko et al., 2015; Hopcraft, 2010; Tourney et al., 2018) have shed light on the dynamics of different species such as wildebeests (Connochaetes taurinus), zebras (Equus burchellii), and lions (Panthera leo). However, these studies focused on factors that limit the population abundance of different migrating species in the Serengeti ecosystem. Also, they concentrated on the prey-predator interactions mostly involving a two species approach (Sagamiko et al., 2015). In addition, although these studies provided detailed explanations of the reasons for migration and abundance, such as rainfall and grass, they did little to consider the factors that lead to the foraging efficiency of these species, particularly wildebeests. These studies also overlooked the role of mathematical models in explaining the interaction of migrating species, which is mutualistic, and the prey-predator interaction that involves three species in the Serengeti ecosystem. The inclusion of mathematical models in explaining the interaction between prey
and predators helps to understand how proximate and ultimate causes for these behaviours work (Taylor-Brown et al., 2019). Further, these mathematical models help predict future trends and contribute to understanding migration.

Therefore, this study focused on modelling wildebeests, zebras, and lion movement dynamics. In particular, this study intended to show wildebeest foraging processes through a mathematical model as these species undergo migration and diffusion. Furthermore, the study used mathematical models to investigate the dynamics of the mutual association of wildebeests, zebras, and other ungulates as they migrate together, and their associated prey-predator interaction with lions.

1.2 Statement of the Problem

The previously proposed models in the Serengeti and other ecosystems were based on prey-predator interactions, mostly involving wildebeests and lions (Sagamiko et al., 2015; Fay & Greef, 1999). For example, Fay and Greef (2006) studied the dynamics of wildebeests, zebras, and lions as a prey-predators using an ordinary differential equation model in the Kruger National Park. The model was analysed to show the dynamics of the interacting species based on historical data. However, the model was carried out in one dimension leaving out the advection and diffusion components. Others include Lee (2007), who described the effects of remained Carcass on the stability of the dynamic system; and Murthy et al. (2017), who used a discrete three species mathematical model to study the fishery system with two-prey and two-predators (one species acts as prey and predator simultaneously). Their discrete model had no diffusion and migration components and was analysed in one dimension. Lian et al. (2012) studied the pattern formation in a cross-diffusive Holling type III ratio-dependent prey-predator model. While the model was useful to explain the system dynamics induced by diffusion, it was based on one prey-one predator and had no migration component. Various one prey and one predator models with diffusion and Holling type III functional response studies have been done (Wang, 2016; Liu, 2010). However, none of these studies has included three species (two mutualistic preys and one predator) and advection and diffusion parameters explaining different dynamics.

In contrast to the previously proposed models and studies, the mathematical models explaining the dynamics of migrating species in the Serengeti ecosystem have not been given enough attention in the literature. Therefore, this study aimed to understand these dynamics. The study
used the Holling type II functional response to describe the predator’s per capita feeding rate. Furthermore, in this proposed prey-predator model, the effects of migration and diffusion were analysed in two spatial dimensions.

1.3 **Rationale of the Study**

The increase of human interference in the environment has induced major changes in the functioning of different ecosystems leading to the extinction of many species including wildlife (Hagen *et al.*, 2012). Thus, this necessitate the need to conserve wildlife (Hopcraft, 2010). Conservation of the environment and wildlife protects nature, making it available for future generations to enjoy the natural world and its wonderful species and appreciate the importance of wildlife for humans and other species (Hagen *et al.*, 2012). It is also essential to understand why some animals migrate from one place to another looking for forage refuge (Gueron *et al.*, 1996). For instance, the great annual migration of wildebeests, zebras and predators, and other species in the Serengeti ecosystem. The Serengeti ecosystem in northern Tanzania is one of the world heritage sites due to the great migration of wildebeest, zebras and other species (Hopcraft, 2010). In addition, this ecosystem is home to different animal species including the big five: The Lion, the Elephant, the Black Rhinoceros, the Leopard and the African Buffalo (Sagamiko *et al.*, 2015). Conserving and protecting Serengeti ecosystem, has economic importance because money is gained from tourism and hunting wild animals (Kideghesho, 2010). In this regard, we need to protect wildlife for the sustainability of the Serengeti ecosystem. This can be achieved by understanding different animal groups' dynamics, especially wildebeests and zebras that form a larger part of migrating animals in the Serengeti ecosystem.

1.4 **Objectives of the Study**

1.4.1 **General Objective**

The general objective of this study was to develop deterministic mathematical models and use them to investigate and analyse wildebeest foraging processes and their interaction with zebras and lions in the Serengeti ecosystem.
1.4.2 **Specific Objectives**

The specific objectives of this study were to:

(i) Formulate a deterministic mathematical model and use it to analyse and investigate the foraging processes of herds of wildebeest using the concept of random walk and diffusive processes.

(ii) Formulate a deterministic mathematical model with diffusion and advection parameters and use it to analyse and investigate the mutual relationship between wildebeests and zebras during migration.

(iii) Formulate a deterministic mathematical model with diffusion and advection parameters and use it to analyse and investigate the dynamics of prey-predator relations of the three species.

1.5 **Research Questions**

The present study had the following research questions:

(i) What is the possibility of formulating a deterministic mathematical model and using it to analyse and explain wildebeest foraging efficiency?

(ii) How does the mutual relationship between wildebeests and zebras during migration work?

(iii) What is the possibility of formulating a three species deterministic mathematical model and using it to investigate and analyse the dynamics of prey-predator relations of wildebeest, zebra and lion together?

1.6 **Significance of the Study**

This study is partly rooted in animal behaviour. Therefore, the findings of this study could increase awareness of wildlife behaviour among ecologists and conservationists. Furthermore, understanding animal dynamics such as animal movement and foraging patterns, predator-prey relations and social behaviour of these species would be useful to wildlife management and conservationists and future researchers as follows.
1.6.1 Wildlife Management and Conservationists

This study increases awareness of how environmental variations affect the survival of different species. This is because the protection of animals is linked to the environmental conditions (such as rainfall), reproduction rates, predation pressure and survival rates of the species (Holdo et al., 2011; Torney et al., 2018). Some of these dynamics are discussed in this study. The results, discussions, and recommendations from this study would be helpful in the management decisions for wildlife protection.

Furthermore, this study shows how different animal species (wildebeests, zebras and lions) can survive and adapt to different habitats and ecosystems. This information helps conserve wildlife, which requires that we know enough about natural behaviours (migration patterns, foraging demands and interaction with other groups) to develop effective protection measures (Sagamiko et al., 2015). Such measures include detecting and acting on early clues of environmental degradation (Mduma, 1996) and changes in the reproductive outcomes of different species (Hocraft et al., 2010), managing their population size to offset illegal hunting and establishing laws to protect the ecosystem (Kideghesho, 2010).

1.6.2 Contributions of the Study

This study has several contributions:

(i) While some previously proposed models in the Serengeti and other ecosystems were based on prey-predator interactions, mostly involving wildebeests and lions, this study included three species (two mutualistic preys and one predator).

(ii) Previous studies on the dynamics of wildebeests and zebras’ mutual relations and wildebeests, zebras and lions as a prey-predator were carried out in Kruger National Park (Fay & Greef, 2006) to show the dynamics of the interacting species based on historical data. However, their models were carried out in one spatial dimension leaving out the advection and diffusion components. Therefore, this study analysed the interaction of wildebeests and zebras as mutual relations and wildebeests, zebras, and lions as prey-predator relations in two spatial and advection and diffusion parameters explaining different dynamics were used.
(iii) Previous studies involving three species used Holling type III to analyse the predators’ per capita feeding rate. This study Holling type II functional response to describe the predator’s per capita feeding rate

1.6.3 Future Researchers

Ideas presented in the current study would be used as reference data in conducting new research or testing the validity of the findings of previous studies.

Wildebeest great migration is a natural phenomenon occurring for decades (Mduma, 1996). This study projects the wildebeest migration in the Serengeti ecosystem, which is the largest single movement of wild animals globally that United Nations Educational, Scientific and cultural organization (UNESCO) lists as one of the eight natural wonders of the world (Kideghesho, 2010). Future studies on the wildebeest migration can use the results and models as their reference in other ecosystem studies. Furthermore Serengeti National Park has been pivotal in building the tourism industry and contributing to economic growth in Tanzania (Mduma, 1996). Thus, research in wildlife protection in this ecosystem can use the results to ensure protection sustainability for the present and future generations.

1.7 Delineation of the Study

This study focused on modelling wildebeests, zebras and lion movement dynamics. In particular, this study intended to show wildebeest foraging processes through a mathematical model as these species undergo migration and diffusion. Furthermore, the study used mathematical models to investigate the dynamics of the mutual association of wildebeests, zebras and other ungulates as they migrate together, and their associated prey-predator interaction with lions. However, the formulated models and the results may not be perfect due to the following limitations:

(i) Data, especially census data for lions, could not be obtained easily. This limited further analysis of the mathematical models. Furthermore, data on collared zebra and lion could not be obtained.

(ii) Other studies on collared wildebeests, zebras, and lions must be undertaken. This will ensure real-time tracking and location of the three species that can be used to study their movement patterns in wet and dry seasons. This will help distinguish the movement patterns of both prey and predators and determine their nutritional requirements.
Additionally, further studies should include small mammals such as antelopes and other predators such as black-spotted hyena, crocodile, leopards, cheetah, and the like to assess their contribution to the stability of the ecosystem.

The proposed mathematical models could also be extended to study different behaviours of the Serengeti ecosystem. For instance, the time delay mathematical models with harvesting, stochastic differential equations, and Markov chain models.
CHAPTER TWO

LITERATURE REVIEW

2.1 Introduction

This Chapter presents a literature review on the works related to the modelling of wildebeest foraging processes and its interaction with zebras and lions in the Serengeti ecosystem. This study introduces various mathematical models and foraging processes, mutual associations of migrating species and diffusive prey-predator interactions.

2.2 Related Work

Despite the popular slogan “Serengeti shall never die” (Grzimek & Grzimek, 1960), the Serengeti ecosystem needs to be protected from different threats to ensure its survival for the benefit of both local and global communities. Besides, Kideghesho (2010) upholds that threats to the Serengeti ecosystem's survival, such as illegal hunting, habitat loss and human-wildlife conflicts, affect the dynamics of wildebeests and zebras and lions. Furthermore, prior studies in the Serengeti National Park explored the great migration and other dynamics of different species. The section presents these studies and establishes the gap needed to be addressed.

The studies in the Serengeti National Park had different focuses and areas of concentration. For instance, Some studies, including Mduma (1996), Sagamiko et al. (2015), Grange et al. (2004), and Ikanda and Packer (2008) explored population-level factors such as predation, poaching, and an outbreak of diseases. Studies on the search for greener pasture and water for herbivore species include Holdo et al. (2011). Other studies, such as Sagamiko et al. (2015), investigated the prey-predator interaction of only wildebeests and lions using mathematical models. Nevertheless, few attempts have been made to address wildebeest foraging processes using the concept of random walk and diffusive processes. Besides, few studies document the mutualism behaviour between wildebeest and zebra during migration, the prey-predator interaction between wildebeest, zebra and lion and the use of these for predicting movement patterns of these species in their natural environment.

Fay and Greef (2006) studied the dynamics of wildebeest, zebra, and lion as a prey-predator in the Kruger National Park. The authors developed a model that was analysed to show the dynamics of the interacting species based on historical data. However, the model was done in one dimension, where the advection and diffusion components were not considered.
In the current study, some mathematical models were developed based on partial differential equations to study and address factors that regulate foraging processes, the mutual benefit of the two prey species and how they interact with a lion in a prey-predator relationship.

2.3 Random Walk and Advection-Diffusion Equation

The advection-diffusion equation describes the transportation of different substances in moving fluids, including animals' movements (Okubo, 1986). Diffusion describes how a group of individual particles spreads out due to the irregular motion of each particle (Okubo & Levin, 2001). For animal movements, diffusion is useful in describing the distribution of a large population of animals or the expected location of an individual animal in space and time. Therefore, the advection-diffusion equation is an individual-based model (Sibert et al., 1999).

The current study introduces the mathematical theory behind a simple random walk that follows Brownian motion and diffusive processes in general. The mathematical model derived includes a drift that ensures the probability of moving in a certain direction is greater, thus creating a drift-diffusion (advection-diffusion) equation (Okubo & Levin, 2001; Codling et al., 2008). Wildebeests in their group forage move towards their preferred forage target. Thus, such paths containing a consistent bias in a preferred forage target are biased random walks (BRWs) (Codling et al., 2008). Using the Fokker-Plank equation, the BRWs were used to explain the foraging process in two dimensions.

During their lifetime, wildebeests undergo annual migration from the Serengeti national park in northern Tanzania to the Masai Mara game reserve in Kenya and back to Serengeti to search for a different favourable niche to inhabit (Holdo, 2011). The great migration involves the mass movement of millions of individual ungulates and other species in groups (Holdo, 2011). This strategy helps individuals to survive and reproduce. Wildebeest movements have been a subject of much research mostly addressing issues related to the causes of migration and how wildebeests encounter dangers during their journey (Kideghesho, 2010; Sagamiko, 2015; Hopcraft, 2014). These studies have yielded important insights into the population dynamics of wildebeest and other species in the Serengeti ecosystem. In addition, they have improved the management of different species within the ecosystem (Kideghesho, 2010). Some deterministic mathematical models have been developed to explain migrating species' different dynamics and potential drivers. However, these studies paid little attention to the role of random walk and diffusive processes in explaining forage efficiency. The current study presents the theory of
random walk and diffusive processes. It shows how these processes describe the foraging of wildebeests in the Serengeti National Park as they undergo great migration.

Random walks have been used to describe movements in different settings, and in particular, they have been used to describe movements of terrestrial vertebrates (Fagan et al., 2019; Okubo & Levin, 2001). In addition, different scholars have examined other random walk models that have led to successful foraging at different times and scales. These models include; the Brownian model, which was sufficient in productive areas (Plank & James, 2008), and the optimal foraging theory (Plank & James, 2008), which predicts how an animal behaves when searching for food. Others are the correlated random walks and composite correlated random walk models (Auger-Méthé et al., 2016; Raichlen et al., 2014).

On the other hand, Levy's walk movement patterns have explained foraging patterns for many organisms (Raichlen et al., 2014). A levy walk is a random walk search strategy used by a wide various organisms when searching for heterogeneously distributed food (Reynolds et al., 2018). This search type mainly involves short movement steps (defined as the distance travelled before pausing or changing direction) combined with rarer longer movement steps creating fractal movement patterns with no characteristic scale (Raichlen et al., 2014).

Levy walks have been found in human foraging patterns. For example, a study by Raichlen et al. (2014) demonstrated that northern Tanzania's Hadzabe hunters and gatherer perform Levy walks when searching for food. Also, Levy walks are evident in Me’Phaa of Mexico, the Brazilian Cariri, and the Amazon farmers (Reynolds et al., 2018).

Random walks have been used to explain animals' foraging in connection with the advection-diffusion equation (Okubo & Levin, 2001). In addition, several studies have used the advection-diffusion equation to explain the movement of different species. For instance, Sibert et al. (1999) used the advection-diffusion model to describe a general quantitative framework for estimating the movement and mortality of fish populations (Skipjack) from tagging data. They used the finite difference method to solve the advection-diffusion model. The model was parameterized, and the model parameters were estimated by maximum likelihood. The authors found that Skipjack movements were highly variable at seasonal and interannual time scales.

Furthermore, the advection-diffusion equation was used to explain foraging processes to different ungulates. For instance, Fagan et al. (2019) considered the spatial dynamics of the population of foragers when they move via diffusion in which animals move randomly in search
of good forage and when foragers move via advection in which foragers move along the resource gradient-following search. The authors thoroughly explained how foragers actively switched between the random and gradient search following movement models as a function of their spatial context (Fagan et al., 2019). However, the study was carried out in one dimension and did not show the connection between random walk and diffusive processes.

The previous studies that used the concept of the advection-diffusion equation were based on one dimension (Codling et al., 2008; Raichlen et al., 2014). Some did not show how diffusion and migration can explain foraging processes, especially for migrating species such as wildebeests in the Serengeti ecosystem. Therefore, the two-dimensional Fokker-Plank equation with diffusion and migration parameters was derived in this study. The model was equipped with data from the Serengeti ecosystem. The advection and diffusion movement parameters were calculated in different seasons of the year and showed how these components could be used to explain the foraging and migration of wildebeest. In addition, the relationship between random walks and advection-diffusion processes was established. Further, the effects of these parameters were used to explain the nutritional requirements of migrating wildebeests that move along different resource gradients. Data from 18 Global Positioning System (GPS) collared wildebeest were used to track their daily movement patterns. Finally, the advection-diffusion equation as an Individual-Based model (IBM) was used to arrive at the conclusions.

2.4 Diffusive Prey Predator Mathematical Models

Modelling the interaction of species is traced back to the classical works of Lotka in 1925 and Volterra in 1926, which inspired most of the studies in mathematical ecology (Wang, 2016). The Serengeti ecosystem is characterized by the interaction of different species and the natural environment. One of the most important interactions is mutualism between wildebeest (Connochaetus taurinus) and zebra (Equus burchelli). Previous studies on mutualism between different species did not consider several components, including diffusion and migration, and modelling on a two-dimensional space. For example, studies by Fay and Greeff (2006), Wang (2009), Wang (2016) and Kurowski et al. (2017) explained the asymptotic behaviour of solutions of a time-delayed mutualism Lotka-Volterra reaction-diffusion system. However, such studies were based on a one dimension space, and their models did not include a migration component. Ahmad and Budin (2012) analysed the effect of time delay on the stability of the mutualism model in one dimension; there were no advection and diffusion parameters.
In the current work, the Lotka-Volterra advection-diffusion reaction system explained the mutual relationship between the two prey species in two dimensions. In such differential equation models, when the diffusion component is included, the prey and predator interactions change the behaviour and nature of the whole model to be a partial differential equation (Fagan et al., 2019; Ahmad & Budin, 2012). The resulting partial differential equation is viewed as part of the spatial population model and thus can be categorized as a reaction-diffusion system (Ahmad & Budin, 2012). The Lotka-Volterra predator-prey models with diffusion are represented by similar mathematical formulation to predator-prey interactions.

Such diffusive mathematical models have been used in literature to study different behaviours. For instance, Qiao et al. (2014) applied the prey-predator diffusive model to study the spread of diseases when the prey is infected. The authors established conditions for the stability of the ecosystem, but their model did not clearly show the role of diffusion in the spread of diseases.

Furthermore, Zhu and Zhang (2018) analysed the prey’s group defence against the predators using diffusive mathematical models showing the role of system parameters leading to spatial-temporal patterns. Still their study did not show clearly how the prey groups are formed and what behaviours led to the group defence.

Other two-prey and one-predator mathematical models include the study by Lee (2007) on two-prey and one-predator that describes the effects of the remained Carcass on the stability of the dynamical system. Also, Murthy et al. (2017) used a discrete three species mathematical model to study a fishery system with two prey and two predators (one species acts as prey and predator simultaneously). The authors used a discrete model to analyse the dynamics of the model; however, their mathematical model had no diffusion and migration components and was analysed in one dimension. Furthermore, Lian et al. (2012) studied the pattern formation in a cross-diffusive Holling type III ratio-dependent prey-predator model. Their model was useful in explaining the system dynamics induced by diffusion. However, it was based on one prey-one predator and had no migration components.

Some studies, including Wang (2016) and Liu (2010), were based on one prey and one predator models with diffusion and Holling type III functional response. However, none of these has included three species (two mutualistic preys and one predator) and advection and diffusion parameters in explaining different dynamics.
A literature review of the current study has highlighted several gaps to be filled. This study used the concept of random walk and diffusive processes to study the foraging efficiency of wildebeest herds. In addition, the current study used advective and diffusive parameters were used to analyse how wildebeests interact with other individuals. In particular, the Holling type II functional response extensively explored zebras and the dynamics of wildebeests, zebras, and lions as prey-predator.

2.5 Chapter Summary

This chapter exhaustively reviewed the literature on mathematical models related to advection-diffusion and prey-predator dynamics of three migrating species in the Serengeti ecosystem. In the next chapter, the deterministic mathematical models are developed to describe the random wildebeest walk, the mutual association between wildebeests and zebras, and their prey-predator interaction with lions.
CHAPTER THREE
MATERIALS AND METHODS

3.1 Introduction

This chapter presents the methodologies of the study covering aspects such as the study area, sources of data, data analysis and the mathematical models used.

3.2 The Study Site

The study was carried out in the Serengeti National Park in Tanzania. This ecosystem is located in northern Tanzania between latitudes $1^\circ$ and $3^\circ$ S and longitudes $34^\circ$ and $36^\circ$ E (Fig. 4).

![Location of the Serengeti ecosystem in Northern Tanzania](image)

Figure 4: Location of the Serengeti ecosystem in Northern Tanzania (Sagamiko et al., 2015)

The Serengeti ecosystem covers about $50,000$ km$^2$ (Sagamiko et al., 2015). This ecosystem is one of the World's most important and famous cross-border conservation regions. Moreover, it
is home to other resident wildlife, particularly the big five: The Lion, the African Leopard, the African Elephant, the Black Rhino and the African Buffalo (Sagamiko et al., 2015).

3.3 Data Sources

Data used in the current study were provided by the University of Glasgow, United Kingdoms (UK). These were data collected between 1999 and 2007 in the Serengeti ecosystem from 18 different collared wildebeests. Collars were configured with GPS to record parameters on wildebeest locations (in two dimensions) and distances. Other parameters include the date and the time, where 6 hours were the time step for recording wildebeest distances and locations.

In addition, this study used reports on rainfall and wildebeests and zebras data from Tanzania Wildlife Research Institute. The data were based on previous aerial census counts of wildebeest and zebra populations in the Serengeti ecosystem from 1961 to 2010. Meanwhile, rainfall data (in mm) spanned from July to November from 1961 to 1994. The following sections detail the methods used to achieve each study objective.

3.4 The Concept of Random Walk and Diffusive Processes

3.4.1 The Fokker-Planck Equation (2D Random Walk)

The Fokker-Planck equation (2D random walk) considers the Brownian motion in two dimensions to include movements and probabilities that are spatially dependent (Okubo & Levin, 2001).

Suppose that individual moves on a two-dimensional lattice; at each time step \( \tau \), an individual can move a distance \( \delta \) either up, down, left, or right with probabilities dependent on location given by \( u(x, y), d(x, y), l(x, y) \) and \( r(x, y) \) respectively with \( u + d + l + r \leq 1 \), or remain at the same location with probability \( 1 - u(x, y) - d(x, y) - l(x, y) - r(x, y) \).

To calculate the probability of a walker jumping on a two-dimensional lattice at a one-time step based on the previous time step at a time \( (m + 1) \tau \), should consider that the probability of the walker in position \( n \) is equal to the probability that it was already there times the probability that it stayed there, plus the probability that it was one position to the left times the probability that it jumped to the right, plus the probability that it was one position to the right times the probability that it jumped to the left, plus the probability that it was one position up times the
probability that it jumped down, plus the probability that it was one position down times the probability that it jumped up.

This can be expressed as follows:

\[ p[n\delta, (m + 1)\tau] = (1 - r - l - u - d)p(n\delta, m\tau) + rp[(n - 1)\delta, m\tau] + lp[(n + 1)\delta, m\tau] + np[(n - 1)\delta, m\tau] + dp[(n + 1)\delta, m\tau] \]  

(1)

Where \( p(0,0) = 1 \) and \( p(n\delta, 0) = 0 \) for \( n \neq 0 \)

Rewriting Equation (1) gives the following:

\[ p[n\delta, (m + 1)\tau] - p(n\delta, m\tau) = -(r + l + u + d)p(n\delta, m\tau) + rp[(n - 1)\delta, m\tau] + lp[(n + 1)\delta, m\tau] + np[(n - 1)\delta, m\tau] + dp[(n + 1)\delta, m\tau] \]  

(2)

Using Taylor series expansion to calculate the probability function \( p[n\delta, (m + 1)\tau] \):

\[ p[(n \pm \delta)\delta, m\tau] = p(n\delta, m\tau) \pm \delta \frac{\partial p}{\partial x} + \frac{\delta^2}{2} \frac{\partial^2 p}{\partial x^2} + \frac{\delta^3}{6} \frac{\partial^3 p}{\partial x^3} + O(\delta^4) + p(n\delta, m\tau) \pm \delta \frac{\partial p}{\partial y} + \frac{\delta^2}{2} \frac{\partial^2 p}{\partial y^2} + \frac{\delta^3}{6} \frac{\partial^3 p}{\partial y^3} + O(\delta^4) \]  

(3)

Then,

\[ p[n\delta, (m + 1)\tau] = p(n\delta, m\delta) + \tau \frac{\partial p}{\partial \tau} + O(\tau^2) \]  

(4)

All the derivatives are taken at \( (x = y = n\delta, t = m\tau) \)

Therefore, the left-hand side of Equation (2) becomes:

\[ p(n\delta, m\tau) + \tau \frac{\partial p}{\partial \tau} + O(\delta^2) - p(n\delta, m\tau) + \tau \frac{\partial p}{\partial \tau} + O(\tau^2) \]  

(5)

The right-hand side of Equation (2) can be re-written in the following ways:

\[ \frac{1}{2} (r + l)(p[(n - 1)\delta, m\tau] - 2p(n\delta, m\tau) + p[(n + 1)\delta, m\tau]) - \frac{1}{2} (r - l)(p[(n + 1)\delta, m\tau] - p[(n - 1)\delta, m\tau] + \frac{1}{2} (u + d)(p[(n - 1)\delta, m\tau] - 2p(n\delta, m\tau) + p[(n + 1)\delta, m\tau]) - \frac{1}{2} (u - d)(p[(n + 1)\delta, m\tau] - p[(n - 1)\delta, m\tau]) \]  

(6)

The first term of the right-hand side of Equation (6) can be expanded by the Taylor series as follows:
\[
\frac{1}{2} (r + l) \left( p(n \delta, m \tau) - \delta \frac{\partial p}{\partial x} + \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial x^2} - \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial x^3} + O(\delta^4) - 2p(n \delta, m \tau) + p(n \delta, m \tau) + \right.
\]
\[
\delta \frac{\partial p}{\partial x} + \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial x^2} + \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial x^3} + O(\delta^4) + \frac{1}{2} (u + d) \left( p(n \delta, m \tau) - \delta \frac{\partial p}{\partial y} + \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial y^2} - \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial y^3} + O(\delta^4) - 2p(n \delta, m \tau) + p(n \delta, m \tau) + \right.
\]
\[
\delta \frac{\partial p}{\partial y} + \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial y^2} + \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial y^3} + O(\delta^4) \right)
\]
\[
(7)
\]
Simplifying gives:
\[
(r + l) \left( \frac{\delta^2 \frac{\partial^2 p}{\partial x^2}}{2} + O(\delta^4) \right) + (u + d) \left( \frac{\delta^2 \frac{\partial^2 p}{\partial y^2}}{2} + O(\delta^4) \right)
\]
\[
(8)
\]
And the last term of the right-hand side of Equation (6) can be expanded by the Taylor series to give:
\[
- \frac{1}{2} (r - l) \left( p(n \delta, m \tau) + \delta \frac{\partial p}{\partial x} + \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial x^2} + \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial x^3} + O(\delta^4) - p(n \delta, m \tau) + \delta \frac{\partial p}{\partial x} - \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial x^2} + \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial x^3} + O(\delta^4) \right)
\]
\[
\frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial x^3} - O(\delta^4) \right) - \frac{1}{2} (u - d) \left( p(n \delta, m \tau) + \delta \frac{\partial p}{\partial y} + \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial y^2} + \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial y^3} + O(\delta^4) - \right.
\]
\[
p(n \delta, m \tau) + \delta \frac{\partial p}{\partial y} - \frac{1}{2} \delta^2 \frac{\partial^2 p}{\partial y^2} + \frac{1}{6} \delta^3 \frac{\partial^3 p}{\partial y^3} - O(\delta^4) \right)
\]
\[
(9)
\]
Simplifying and ignoring higher-order terms gives:
\[
-(r - l) \left( \delta \frac{\partial p}{\partial x} \right) - (u - d) \left( \delta \frac{\partial p}{\partial y} \right)
\]
\[
(10)
\]
Combining the left-hand side Equation (8) and right-hand side Equation (10) gives:
\[
\tau \frac{\partial p}{\partial t} = (r + l) \left( \frac{\delta^2 \frac{\partial^2 p}{\partial x^2}}{2} + (u + d) \left( \frac{\delta^2 \frac{\partial^2 p}{\partial y^2}}{2} - (r - l) \left( \delta \frac{\partial p}{\partial x} \right) - (u - d) \left( \delta \frac{\partial p}{\partial y} \right) + O(\delta^4) + O(\tau^2) \right)
\]
\[
(11)
\]
Divide by \( \tau \), gives:
\[
\frac{\partial p}{\partial t} = (r + l) \left( \frac{\delta^2 \frac{\partial^2 p}{\partial x^2}}{2 \tau} \right) - (r - l) \left( \delta \frac{\partial p}{\partial x} \right) + O\left( \frac{\delta^4}{\tau} \right) \right) + O(\tau) + (u + d) \left( \frac{\delta^2 \frac{\partial^2 p}{\partial y^2}}{2 \tau} \right) - (u - d) \left( \delta \frac{\partial p}{\partial y} \right) + O\left( \frac{\delta^4}{\tau} \right) + O(\tau)
\]
\[
(12)
\]
Let \( k_1 = r + l; \ k_2 = u + d; \ \epsilon_1 = r - l; \ \epsilon_2 = u - d \), it can be defined that:
\[
\frac{\partial p}{\partial t} = k_1 \delta^2 \frac{\partial^2 p}{\partial x^2} - \epsilon_1 \delta \frac{\partial p}{\partial x} - k_2 \delta^2 \frac{\partial^2 p}{\partial y^2} - \epsilon_2 \delta \frac{\partial p}{\partial y} + O\left( \frac{\delta^4}{\tau} \right) + O(\tau)
\]
\[
(13)
\]
Taking limits as $\tau \to 0$ and $\delta \to 0$, such that the following limits are positive and definite:

$$D_x = \lim_{\delta, \tau \to 0} \frac{k_1 \delta^2}{2\tau}, \quad D_y = \lim_{\delta, \tau \to 0} \frac{k_2 \delta^2}{2\tau}, \quad u_x = \lim_{\delta, \tau, \epsilon_1 \to 0} \frac{\epsilon_1 \delta}{\tau}, \quad \text{and} \quad u_y = \lim_{\delta, \tau, \epsilon_2 \to 0} \frac{\epsilon_2 \delta}{\tau}$$

Taking the limits as $\delta, \tau, \epsilon_1, \epsilon_2 \to 0$ such that $D_x, D_y, u_x, u_y$ all tend to constants gives:

$$\frac{\partial p}{\partial t} = -\nabla \cdot (up) + \nabla \cdot (D \nabla p) \tag{14}$$

Equation (14) is the same as:

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial x} \left( D_x \frac{\partial p}{\partial x} \right) + \frac{\partial}{\partial y} \left( D_y \frac{\partial p}{\partial y} \right) - \frac{\partial}{\partial x} (u_x p) - \frac{\partial}{\partial y} (u_y p) \tag{15}$$

Solving Equation (15) gives the following probability mass function:

$$P(x, y, t) = \frac{1}{4\pi t \sqrt{D_x D_y}} e^{- \frac{(x-u_xt)^2}{4D_xt} + \frac{(y-u_yt)^2}{4D_yt}} \tag{16}$$

The simulations were done in a python computer program (the corresponding codes are attached in Appendix 1). The results and discussion for objective one are presented in Chapter four.

3.5 Mutualism Reaction-Diffusion Models for Wildebeests and Zebras

3.5.1 Assumptions of the Model

(i) There are two populations, namely, wildebeests and zebras, whose population densities are denoted by $w$ and $z$, respectively.

(ii) The population densities of wildebeests and zebras grow according to the logistic law of growth $r_w$ and $r_z$, respectively.

(iii) Two prey species are mutualistic in nature.

(iv) There is a death rate for both prey species from factors such as predation and drought.

(v) The two prey species' growth approach the carrying capacities $K_w$ and $K_z$, respectively.
Based on the above assumptions, the Lotka-Volterra mutualistic model (Fay & Greef, 2006; Wang, 2009; Wang, 2016) for the two prey species can be defined as:

\[
\frac{dw}{dt} = \frac{r_w}{K_w}w(K_w - w + a_{12}z) - d_w w \\
\frac{dz}{dt} = \frac{r_z}{K_z}z(K_z - z + a_{21}w) - d_z z
\]  

(17)

The coefficients \(a_{12}\) and \(a_{21}\) denote the interaction (mutual relations) between wildebeests and zebras.

### 3.5.2 The Mutualism Model with Diffusion and Migration

The Lotka-Volterra model (17), which resembles the model developed in Kruger National Park by Fay and Greef (2006) was extended to include the diffusion and migration components of the mutualism model. The presence of diffusion and migration parameters (constant flow terms) for the two prey species is considered the principal process of motion; this changes the behaviour and nature of the whole model (Yamada et al., 2007; Liu, 2010). It is now a partial differential equation and can be categorized as a reaction-diffusion system.

### 3.5.3 Reaction-Diffusion System

In mathematical biology, reaction-diffusion equations arise as models for describing the densities of substances or organisms that disperse through space by mechanisms like Brownian motion, random walks, or hydrodynamic turbulence. The models also describe organisms that react to each other and their surroundings to affect their local densities (Yamada et al., 2007). These spatially explicit models describe population densities and treat space and time as continuous. The reaction-diffusion equations describe the behaviour of chemical systems where diffusion of material competes with the production of that material by some form of chemical reaction (Yamada et al., 2007; Liu, 2010).

For wildebeest and zebra annual migration, the reaction refers to the mass movement of these prey species in the Serengeti ecosystem. As the animals move from place to place to search for forage resources through advection trends, they spread to acquire and utilize them through diffusion movements.
This study considers a reaction-diffusion equation with flow terms. The Equation considered in the current study comprises a reaction term, an advection term, and a diffusion term, i.e. the typical form of this Equation can be stated as follows:

\[
\begin{align*}
\frac{\partial w}{\partial t} + C_w \cdot \nabla w &= D_w \nabla^2 w + f(w, z) \\
\frac{\partial z}{\partial t} + C_z \cdot \nabla z &= D_z \nabla^2 z + g(w, z)
\end{align*}
\] (18)

The quantities \( w \) and \( z \) are state variables that describe the density/concentration of substance/individuals (wildebeest and zebra populations, respectively), which diffuse with their diffusion coefficients \( D_w \) and \( D_z \) respectively and grow according to their specific rules \( f(w, z) \) and \( g(w, z) \) respectively. The symbol \( \nabla \) is the gradient operator and \( \nabla^2 \) is the Laplacian operator.

The quantities \( D_w \) and \( D_z \) are positive diagonal diffusion coefficient matrices for wildebeest and zebra, respectively. Their concentrations determine the velocity of animals as follows:

\[
\begin{align*}
C_w &= M_w \nabla w \\
C_z &= M_z \nabla z
\end{align*}
\] (19)

where \( M_w \) and \( M_z \) are constant parameters expressing the flow intensity for wildebeest and zebra, respectively.

### 3.5.4 The Reaction

In the mathematical ecology context, the reaction terms \( f(w, z) \) and \( g(w, z) \), in the reaction-diffusion equations, resemble the reaction terms in non-spatial population models based on ordinary differential equations. Thus, for two mutually interacting prey species (zebra and wildebeest), the Lotka–Volterra reaction terms (for the mathematical mutualism model) can be defined as:

\[
\begin{align*}
f(w, z) &= \frac{r_w}{K_w} w(K_w - w + a_{12}z) - d_w w \\
g(w, z) &= \frac{r_z}{K_z} z(K_z - z + a_{21}w) - d_z z
\end{align*}
\] (20)
From Equations (18) and (20), the two-dimensional reaction diffusion-advection model can be written as:

\[
\begin{align*}
\frac{\partial w}{\partial t} + C_w \cdot \nabla w &= \frac{r_w}{K_w} w (K_w - w + a_{12} z) - d_w w + D_w \nabla^2 w \\
\frac{\partial z}{\partial t} + C_z \cdot \nabla z &= \frac{r_z}{K_z} z (K_z - z + a_{21} w) - d_z z + D_z \nabla^2 z
\end{align*}
\]  

(21)

The symbol \( \nabla \) is the gradient operator defined in two dimensions as: \( \nabla (.) = \frac{\partial (.)}{\partial x} \hat{i} + \frac{\partial (.)}{\partial y} \hat{j} \), and the Laplacian operator \( \nabla^2 \) in two dimensions is defined as: \( \nabla^2 = \frac{\partial^2 (.)}{\partial x^2} + \frac{\partial^2 (.)}{\partial y^2} \).

Equation 21 is the reaction-diffusion system. It treats space as a continuum and depicts the population densities of interacting species over time. The dynamical behaviour of wildebeests and zebras is based on Equation 21.

3.5.5 Local Stability Analysis

The local stability analysis is referred to as the Hopf bifurcation. The Hopf bifurcation is space independent and breaks the temporal symmetry of the system (Liu, 2010; Wang et al., 2016), which causes uniform oscillations in space and time. The onset of Hopf bifurcation instability occurs when the pair of imaginary eigenvalues crosses the real axis from negative to positive (Liu, 2010; Wang et al., 2016). This situation occurs only when diffusion and migration components vanish (Liu, 2010; Wang et al., 2016; Kurowski et al., 2017). When wildebeests and zebras occupy a niche, their dynamical behaviour must be analysed when diffusion and migration vanish. From Equation 21, when diffusion and migration components vanished, the following equation was obtained:

\[
\begin{align*}
\frac{r_w}{K_w} w (K_w - w + a_{12} z) - d_w w &= 0 \\
\frac{r_z}{K_z} z (K_z - z + a_{21} w) - d_z z &= 0
\end{align*}
\]  

(22)

From Equation (22), using maple software and simplifying, four equilibrium points were obtained:

\[(w^*, z^*) = (0, 0), (w^*, z^*) = \left(0, \frac{K_z}{r_z} (r_z - d_z)\right), (w^*, z^*) = \left(\frac{K_w}{r_w} (r_w - d_w), 0\right), \text{ and}
\]
\[(w^*, z^*) = \left( \frac{-a_{12} d_w k_w r_w + a_{12} k_w r_w - d_w k_w r_z + k_w r_z}{r_z r_w (1-a_{12} a_{21})}, \frac{-a_{21} d_w k_w r_z + a_{21} k_w r_z - d_z k_w r_w + k_w r_w}{r_w r_z (1-a_{12} a_{21})} \right) \]

The equilibrium point \((w^*, z^*) = (0,0)\) corresponds to the extinction of both species.

The equilibrium point: \((w^*, z^*) = \left( 0, \frac{K_w}{r_w} (r_w - d_w) \right)\) corresponds to the extinction of wildebeest. This implies that zebras can exist in the absence of wildebeests.

The equilibrium point: \((w^*, z^*) = \left( \frac{K_w}{r_w} (r_w - d_w), 0 \right)\) corresponds to the extinction of zebras. This implies that wildebeest can exist in the absence of zebras.

The only equilibrium point that can be reached in the first quadrant is:

\[(w^*, z^*) = \left( \frac{-a_{12} d_w k_w r_w + a_{12} k_w r_w - d_w k_w r_z + k_w r_z}{r_z r_w (1-a_{12} a_{21})}, \frac{-a_{21} d_w k_w r_z + a_{21} k_w r_z - d_z k_w r_w + k_w r_w}{r_w r_z (1-a_{12} a_{21})} \right) \]

The zero growth isoclines \(w^* = \frac{-a_{12} d_w k_w r_w + a_{12} k_w r_w - d_w k_w r_z + k_w r_z}{r_z r_w (1-a_{12} a_{21})}\) and \(z^* = \frac{-a_{21} d_w k_w r_z + a_{21} k_w r_z - d_z k_w r_w + k_w r_w}{r_z r_w (1-a_{12} a_{21})}\) may converge or diverge.

They converge if \(1 - a_{12} a_{21} > 0 \Rightarrow a_{12} a_{21} < 1\) provided the birth rates of these species must be greater than their corresponding death rates, that is \(r_w > d_w\), and \(r_z > d_z\).

In this case, the two isoclines cross each other, and the orbits approach a stable node in the interior of the first quadrant. Since the slopes of the two zero-growth isoclines are positive, the coordinates of this equilibrium are greater than the carrying capacities \(K_w\) and \(K_z\) and each species surpasses its respective carrying capacity because of the mutualistic benefits that both species experience.

### 3.5.6 Local Stability Analysis

The local stability analysis is referred to as the Hopf bifurcation. The Hopf bifurcation is space independent and breaks the temporal symmetry of the system (Liu, 2010; Wang et al. 2016), which causes oscillations to occur that are uniform in space and periodic in time. The onset of Hopf bifurcation instability occurs when the pair of imaginary eigenvalues crosses the real axis from the negative to the positive side (Liu, 2010; Wang et al., 2016). This situation occurs only when diffusion and migration components vanish (Liu, 2010; Wang et al., 2016; Kurowski et al., 2017). When wildebeest and zebra occupy a niche, their dynamical behaviour must be
analysed when diffusion and migration vanish. From Equation 21, when diffusion and migration components vanish, the following Equation was obtained:

\[
\begin{align*}
\frac{r_w}{K_w} w(K_w - w + a_{12} z) - d_w w &= 0 \\
\frac{r_z}{K_z} z(K_z - z + a_{21} w) - d_z z &= 0
\end{align*}
\] (22)

From Equation (22), using maple software and simplifying, four equilibrium points were obtained:

\[
(w^*, z^*) = (0, 0), \quad (w^*, z^*) = \left(0, \frac{K_z}{r_z} (r_z - d_z)\right), \quad (w^*, z^*) = \left(\frac{K_w}{r_w} (r_w - d_w), 0\right), \quad \text{and}
\]

\[
(w^*, z^*) = \left(-\frac{a_{12} d_z k_2 r_w + a_{12} k_2 r_z - d_w k_w r_z + k_w r_z r_w - d_z k_2 r_w + k_2 r_z r_w}{r_z r_w (1 - a_{12} a_{21})}, -\frac{a_{21} d_w k_w r_z + a_{12} k_w r_z - d_z k_2 r_w + k_2 r_z r_w}{r_z r_w (1 - a_{12} a_{21})}\right)
\]

The equilibrium point \((w^*, z^*) = (0, 0)\) corresponds to the extinction of both species.

The equilibrium point \((w^*, z^*) = \left(0, \frac{K_z}{r_z} (r_z - d_z)\right)\) corresponds to the extinction of wildebeest. This implies that, zebra can exist in the absence of wildebeest.

The equilibrium point \((w^*, z^*) = \left(\frac{K_w}{r_w} (r_w - d_w), 0\right)\) corresponds to the extinction of zebra.

This implies that, wildebeest can exist in the absence of zebra.

The only equilibrium point that can occur in the first quadrant is:

\[
(w^*, z^*) = \left(-\frac{a_{12} d_z k_2 r_w + a_{12} k_2 r_z - d_w k_w r_z + k_w r_z r_w - d_z k_2 r_w + k_2 r_z r_w}{r_z r_w (1 - a_{12} a_{21})}, -\frac{a_{21} d_w k_w r_z + a_{12} k_w r_z - d_z k_2 r_w + k_2 r_z r_w}{r_z r_w (1 - a_{12} a_{21})}\right)
\]

The zero growth isoclines \(w^* = -\frac{a_{12} d_z k_2 r_w + a_{12} k_2 r_z - d_w k_w r_z + k_w r_z r_w}{r_z r_w (1 - a_{12} a_{21})}\) and \(z^* = -\frac{a_{21} d_w k_w r_z + a_{12} k_w r_z - d_z k_2 r_w + k_2 r_z r_w}{r_z r_w (1 - a_{12} a_{21})}\) may converge or diverge.

They converge if \(1 - a_{12} a_{21} > 0 \Rightarrow a_{12} a_{21} < 1\) provided the birth rates of these species must be greater than their corresponding death rates, that is \(r_w > d_w\), and \(r_z > d_z\).

In this case, the two isoclines cross each other, and the orbits approach a stable node in the interior of the first quadrant. Since the slopes of the two zero-growth isoclines are positive, the coordinates of this equilibrium are greater than the carrying capacities \(K_w\) and \(K_z\) and each
species surpasses its respective carrying capacity because of the mutualistic benefits that both species experience.

### 3.5.7 Local Stability of the Equilibrium Points

The local asymptotic stability of the co-existence equilibrium point was studied by computing the Jacobian matrix and testing whether the respective eigenvalues were negative. From the system of Equation (21), the system can be defined as:

\[
\begin{align*}
    f(w, z) &= \frac{r_w}{K_w} w(K_w - w + a_{12}z) - d_w w \\
    g(w, z) &= \frac{r_z}{K_z} z(K_z - z + a_{21}w) - d_z z
\end{align*}
\]  

(23)

The Jacobian matrix of the system (23) is given by:

\[
J(E_i) = \begin{pmatrix}
\frac{\partial f}{\partial w} & \frac{\partial f}{\partial z} \\
\frac{\partial g}{\partial w} & \frac{\partial g}{\partial z}
\end{pmatrix}
\]  

(24)

for \( i = 0, 1, 2, 3 \)

This gives:

\[
J(E_i) = \begin{pmatrix}
\frac{r_w}{K_w} (K_w - 2w^* + a_{12}z^*) - d_w & \frac{r_w}{K_w} a_{12}w^* \\
\frac{r_z}{K_z} a_{21}z^* & \frac{r_z}{K_z} (K_z - 2z^* + a_{21}w^*) - d_z
\end{pmatrix}
\]  

(25)

For the equilibrium point \( E_0(w^*, z^*) = (0,0) \), the Jacobian matrix of the system (25) is:

\[
J(E_0) = \begin{pmatrix}
(\frac{r_w}{K_w} - d_w) & 0 \\
0 & (\frac{r_z}{K_z} - d_z)
\end{pmatrix}
\]

Since the birth rate should exceed the death rate, the eigenvalues of the system are \( r_w - d_w > 0 \) and \( r_z - d_z > 0 \). Hence the point is unstable.

For the equilibrium point \( E_1(w^*, z^*) = \left(0, \frac{K_z}{r_z}(r_z - d_z)\right) \), the Jacobian matrix of the system is:

\[
J(E_1) = \begin{pmatrix}
(\frac{r_w}{K_w} - d_w) + \frac{a_{12}r_wK_z}{r_zK_w} (r_z - d_z) & 0 \\
\frac{r_z}{K_z} a_{21}(r_z - d_z) & -(r_z - d_z)
\end{pmatrix}
\]
The eigenvalues of the system are \(- (r_z - d_z) < 0\) and \((r_w - d_w) + \frac{a_{12}rwK_w}{r_zK_w} (r_z - d_z) > 0\). This gives a saddle point; hence, the point is unstable.

For the equilibrium point: \((w^*, z^*) = \left( \frac{K_w}{r_w}(r_w - d_w), 0 \right)\), the Jacobian matrix of the system is

\[
J(E_2) = \begin{pmatrix}
-(r_w - d_w) & a_{12} (r_w - d_w) \\
0 & (r_z - d_z) + \frac{a_{21}r_zK_w}{r_wK_z} (r_w - d_w)
\end{pmatrix}.
\]

The eigenvalues of the system are \(- (r_w - d_w) < 0\) and \((r_z - d_z) + \frac{a_{21}r_zK_w}{r_wK_z} (r_w - d_w) > 0\). This gives a saddle point; hence the equilibrium point is unstable.

From the co-existence equilibrium point \(E_3(w^*, z^*)\), where:

\[
E_3(w^*, z^*) = \left( \frac{-a_{12}d_zK_zr_w + a_{12}k_zr_zr_w - d_wk_wr_z + k_wd_zr_w}{r_zr_w(1 - a_{12}a_{21})}, \frac{-a_{21}d_WRW^2 + a_{21}k_WRW^2 - d_zk_zr_w + k_zd_zr_z}{r_zr_W(1 - a_{12}a_{21})} \right),
\]

the Jacobian matrix of the system using maple software is given as:

\[
J(E_3) = \begin{pmatrix}
A_{11} & A_{12} \\
A_{21} & A_{22}
\end{pmatrix}
\]

Where,

\[
A_{11} = \frac{a_{12}d_zK_zr_w - a_{12}k_zr_zr_w + d_wk_wr_z - k_wr_zr_w}{K_wr_z(1 - a_{12}a_{21})}
\]

\[
A_{21} = \frac{a_{12}(-a_{12}d_zK_zr_w + a_{12}k_zr_zr_w - d_wk_wr_z + k_wr_zr_w)}{K_wr_z(1 - a_{12}a_{21})}
\]

\[
A_{12} = \frac{a_{21}(-a_{21}d_WRW^2 + a_{21}k_WRW^2 - d_zk_zr_w + k_zd_zr_z)}{KWr_w(1 - a_{12}a_{21})}
\]

\[
A_{22} = \frac{a_{21}d_WRW^2 - a_{21}k_WRW^2 + d_zk_zr_w - k_zr_wr_z}{Kwr_w(1 - a_{12}a_{21})}
\]

**Theorem 1:** Let \(E_3(w^*, z^*)\) be the positive equilibrium point of the model (22). If \(1 - a_{12}a_{21} > 0\), then \(E_3(w^*, z^*)\) is asymptotically stable (Ahmad & Budin, 2012; Kurowski et al., 2017).

The stability analysis of the four equilibrium points can be illustrated in Fig. 5.
Figure 5: Trajectories around the equilibrium points

In Fig. 5, the red circles indicate the four equilibrium points, and the arrows indicate the directional field showing that the equilibrium point $E_3(w^*, z^*)$ in the first quadrant is asymptotically stable.

3.5.8 Stability Analysis of the Model with Diffusion and Migration

From the mathematical model (21), let

$$
\begin{align*}
  f(w, z) &= \frac{r_w}{K_w} w (K_w - w + a_{12} z) - d_w w \\
  g(w, z) &= \frac{r_z}{K_z} z (K_z - z + a_{21} w) - d_z z
\end{align*}
$$

(26)

We assume the diffusion and migration in each spatial dimension are the same. Equation 21 can be rearranged as:

$$
\begin{align*}
  \frac{\partial w}{\partial t} &= D_w \nabla^2 w - C_w \nabla w + \frac{r_w}{K_w} w (K_w - w + a_{12} z) - d_w w \\
  \frac{\partial z}{\partial t} &= D_z \nabla^2 z - C_z \nabla z + \frac{r_z}{K_z} z (K_z - z + a_{21} w) - d_z z
\end{align*}
$$

(27)
Equations (27) can be written as:

\[
\begin{align*}
\frac{\partial w}{\partial t} &= f(w, z) + D_w \nabla^2 w - C_w \nabla w \\
\frac{\partial w}{\partial t} &= g(w, z) + D_z \nabla^2 z - C_z \nabla z
\end{align*}
\] (28)

where \( f(w, z) \) and \( g(w, z) \) are nonlinear dynamic systems (reaction kinetics) (Liu, 2010; Wang et al., 2016).

The homogeneous steady-state values of \( w \) and \( z \) are solutions to the reaction terms \( f(w, z) = 0 \) and \( g(w, z) = 0 \).

Diffusion and advection play a crucial role; as the prey species migrate from place to place, they lead to diffusion and advection-induced instability. In particular, the instability criteria of the spatially homogeneous state determine the pattern forming processes in a nonequilibrium system.

The conditions of diffusion and migration induced instability can be obtained as follows:

Assume small perturbations \( \delta_w, \delta_z \) about the equilibrium stable state \( (w_0, z_0) \) as \( w = w_0 + \delta_w \) and \( z = z_0 + \delta_z \) and taking Taylor expansion of the non-linear functions \( f(w, z) \) and \( g(w, z) \) about the stationary state; thus, for the diffusion, one can write:

\[
\begin{align*}
\frac{\partial \delta_w}{\partial t} &= \left( \frac{\partial f}{\partial w} \right)_{(w_0, z_0)} \delta_w + \left( \frac{\partial f}{\partial z} \right)_{(w_0, z_0)} \delta_z + D_w \nabla^2 \delta_w \\
\frac{\partial \delta_z}{\partial t} &= \left( \frac{\partial g}{\partial w} \right)_{(w_0, z_0)} \delta_w + \left( \frac{\partial g}{\partial z} \right)_{(w_0, z_0)} \delta_z + D_z \nabla^2 \delta_z
\end{align*}
\] (29)

And for migration, it is written as:

\[
\begin{align*}
\frac{\partial \delta_w}{\partial t} &= \left( \frac{\partial f}{\partial w} \right)_{(w_0, z_0)} \delta_w + \left( \frac{\partial f}{\partial z} \right)_{(w_0, z_0)} \delta_z - C_w \nabla w \delta_w + D_w \nabla \delta_w \\
\frac{\partial \delta_z}{\partial t} &= \left( \frac{\partial g}{\partial w} \right)_{(w_0, z_0)} \delta_w + \left( \frac{\partial g}{\partial z} \right)_{(w_0, z_0)} \delta_z - C_z \nabla z \delta_z + D_z \nabla \delta_z
\end{align*}
\] (30)

The perturbation can be assumed to be harmonic in space, and the spatial variation can be expressed as \( e^{ik\chi} \) while the temporal variation which allows this perturbation to grow can be expressed as \( e^{\omega_n t} \). The parameters \( k_n \) stands for wave number, \( \chi = (x, y) \) is the spatial vector in two dimensions and \( \omega_n \) is the growth rate of perturbations. Thus, one can write:

\[
\begin{align*}
\delta_w &= \delta_{w_0} e^{ik\chi} e^{\omega_n t}, \\
\delta_z &= \delta_{z_0} e^{ik\chi} e^{\omega_n t}
\end{align*}
\] (31)
This leads to an eigenvalue Equation of the form:

\[ A \delta \chi = \omega_n \delta \chi \]  
(32)

With,

\[ A = \begin{pmatrix} f_w - D_w k_n^2 & f_z \\ g_w & g_z - D_z k_n^2 \end{pmatrix}, \quad \delta \chi = \begin{pmatrix} \delta w_0 \\ \delta z_0 \end{pmatrix} \text{ for diffusion and} \]

\[ A = \begin{pmatrix} f_w + C_w - D_w k_n & f_z \\ g_w & g_z + C_z - D_z k_n \end{pmatrix}, \quad \delta \chi = \begin{pmatrix} \delta w_0 \\ \delta z_0 \end{pmatrix} \text{ for migration} \]

The perturbation amplitudes \( \delta z_0 \) and \( \delta w_0 \) can be non-zero if and only if:

\[ \det(A - \omega_n I) = 0. \]

This gives the characteristic polynomial defined as:

\[ \omega_n^2 + [(D_w + D_z) k_n^2 - f_w - g_z] \omega_n + D_w D_z k_n^2 - k_n^2 (D_z f_w + D_w g_z) + f_w g_z - f_z g_w = 0 \]  
(33)

for diffusion and

\[ \omega_n^2 + [(-C_w - C_z) k_n - f_w - g_z] \omega_n + C_w C_z k_n^2 + k_n (C_z f_w + C_w g_z) + f_w g_z - f_z g_w = 0, \text{ for migration.} \]  
(34)

A fluctuation associated with the eigenvalue \( \omega_n \) grows if:

\[ \text{Re} (\omega_n) > 0. \]

Thus,

At the onset of instability, \( \text{Re} (\omega_n) = 0. \)

In that case, the term independent of \( \omega_n \) in equations (33 and 34) is reduced to zero. This determines the critical wave number \( k_c \) for diffusion as:

\[ k_c^2 = \frac{(D_z f_w + D_w g_z) \pm \sqrt{(D_z f_w + D_w g_z)^2 - 4 D_w D_z (f_w g_z - f_z g_w)}}{2 D_w D_z} \]  
(35)

and for migration, the following can be obtained:
\[ k_c = \frac{-(czfw + cwgz) \pm \sqrt{(czfw + cwgz)^2 - 4cwcz(fzwz - fzgw)}}{2cwcz} \] (36)

which in turn determines the critical length \( L_c(n) = \frac{n\pi}{k_c} \). Thus, the fluctuations associated with the frequency \( \omega_n \) are amplified in the system of length \( L \) if \( L > L_c(n) \). This is a necessary condition for the development of an inhomogeneous state by the growth of fluctuations associated with wavenumber \( k_n \). Further, the most unstable wavenumber \( k_{max} \), can be obtained from the condition:

\[ \frac{\partial}{\partial k} \text{Re} \{ \omega(k) \} = 0 \text{ at } k = k_{max} \]

Giving:

\[ k_{max} = \left[ \frac{Dzwzw + Dzwzw}{2Dzwzw} \right]^{1/2} = \left[ \frac{(fzwgzw - fzgwzw)}{Dzwzw} \right]^{1/4} \] (37)

for diffusion and

\[ k_{max} = -\left[ \frac{czfw + cwgzw}{2cwcz} \right] = \left[ \frac{(fzwgzw - fzgwzw)}{Dzwzw} \right]^{1/2} \text{ for migration.} \] (38)

Therefore, from equations (35, 36) and (37, 38), the necessary conditions for the onset of Turing instability for model (27) are as follows:

\[ f_w + g_z < 0 \] (39)
\[ f_wg_z - fzgw > 0 \] (40)
\[ Dzwf_w + Dwzwz > 0 \] (41a)
\[ (czfw + cgzw) < 0 \] (41b)
\[ (Dzwf_w + Dwzwz)^2 > 4Dzwz(fzwgzw - fzgwzw) \] (42a)
\[ (Dzwf_w + Dwzwz)^2 > 4cwcz(fzwgzw - fzgwzw) \] (42b)

It can be observed that the dispersion relation that drives the system of equations to instability depends on the variation of diffusion and migration terms.
3.5.9 Numerical Methods

The explicit Euler method, numerical solution, was used to discretize Equation (21), where the model was discretized in time derivative by using the forward difference rule.

Let \( C_w = C_{11} = C_{12} \); \( C_z = C_{21} = C_{22} \) and \( D_z = D_{21} = D_{22} \) \( D_w = D_{11} = D_{12} \) as defined below:

\[
\frac{\partial w}{\partial t}_{i,j} = \frac{w_{i,j}^{n+1} - w_{i,j}^n}{\Delta t}, \quad \frac{\partial z}{\partial t}_{i,j} = \frac{z_{i,j}^{n+1} - z_{i,j}^n}{\Delta t},
\]

\[
C_{11} \frac{\partial w}{\partial x} = C_{11} \left( \frac{w_{i+1,j}^n - w_{i,j}^n}{\Delta x} \right), \quad C_{12} \frac{\partial w}{\partial y} = C_{12} \left( \frac{w_{i,j+1}^n - w_{i,j}^n}{\Delta y} \right)
\]

\[
C_{21} \frac{\partial z}{\partial x} = C_{21} \left( \frac{z_{i+1,j}^n - z_{i,j}^n}{\Delta x} \right), \quad C_{22} \frac{\partial z}{\partial y} = C_{22} \left( \frac{z_{i,j+1}^n - z_{i,j}^n}{\Delta y} \right)
\]

\[
D_{11} \frac{\partial^2 w}{\partial x^2} = D_{11} \left( \frac{w_{i+1,j}^n - 2w_{i,j}^n + w_{i-1,j}^n}{\Delta x^2} \right), \quad D_{12} \frac{\partial^2 w}{\partial y^2} = D_{12} \left( \frac{w_{i,j+1}^n - 2w_{i,j}^n + w_{i,j-1}^n}{\Delta y^2} \right),
\]

\[
D_{21} \frac{\partial^2 z}{\partial x^2} = D_{21} \left( \frac{z_{i+1,j}^n - 2z_{i,j}^n + z_{i-1,j}^n}{\Delta x^2} \right), \quad D_{22} \frac{\partial^2 z}{\partial y^2} = D_{22} \left( \frac{z_{i,j+1}^n - 2z_{i,j}^n + z_{i,j-1}^n}{\Delta y^2} \right),
\]

\[
\frac{r_w}{K_w} w(K_w - w + a_{12} z) = \frac{r_w}{K_w} w_{i,j}^n(K_w - w_{i,j}^n + a_{12} z_{i,j}^n)
\]

\[
\frac{r_z}{K_z} z(K_z - z + a_{21} w) = \frac{r_z}{K_z} z_{i,j}^n(K_z - z_{i,j}^n + a_{21} w_{i,j}^n).
\]

Taking \( \Delta x = \Delta y = h \), \( \Delta t = n \), the following system of Equations was obtained:

\[
\frac{w_{i,j}^{n+1} - w_{i,j}^n}{\Delta t} = D_{11} \left( \frac{w_{i+1,j}^n - 2w_{i,j}^n + w_{i-1,j}^n}{h^2} \right) + D_{12} \left( \frac{w_{i,j+1}^n - 2w_{i,j}^n + w_{i,j-1}^n}{h^2} \right) - C_{11} \left( \frac{w_{i+1,j}^n - w_{i,j}^n}{h} \right) - \frac{r_w}{K_w} w_{i,j}^n(K_w - w_{i,j}^n + a_{12} z_{i,j}^n) - \frac{r_z}{K_z} z_{i,j}^n(K_z - z_{i,j}^n + a_{21} w_{i,j}^n), \tag{43a}
\]

\[
\frac{z_{i,j}^{n+1} - z_{i,j}^n}{\Delta t} = D_{21} \left( \frac{z_{i+1,j}^n - 2z_{i,j}^n + z_{i-1,j}^n}{h^2} \right) + D_{22} \left( \frac{z_{i,j+1}^n - 2z_{i,j}^n + z_{i,j-1}^n}{h^2} \right) - C_{21} \left( \frac{z_{i+1,j}^n - z_{i,j}^n}{h} \right) - \frac{r_z}{K_z} z_{i,j}^n(K_z - z_{i,j}^n + a_{21} w_{i,j}^n) - \frac{r_z}{K_z} z_{i,j}^n(K_z - z_{i,j}^n + a_{21} w_{i,j}^n). \tag{43b}
\]

Parameters and their sources are shown in Table 1. Other parameters that are not easily obtained have been allowed to vary within corresponding possible intervals.
<table>
<thead>
<tr>
<th>Parameter Description</th>
<th>Symbol</th>
<th>Value</th>
<th>Units</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Per capita intrinsic growth rate for wildebeest</td>
<td>$r_w$</td>
<td>1</td>
<td>individuals/year</td>
<td>Mduma (1996)</td>
</tr>
<tr>
<td>Per capita intrinsic growth rate for zebra</td>
<td>$r_z$</td>
<td>0.34</td>
<td>individuals/year</td>
<td>Fay and Greef (2006)</td>
</tr>
<tr>
<td>Carrying capacity for wildebeest</td>
<td>$K_w$</td>
<td>18</td>
<td>$\times 10^5$</td>
<td>Assumed</td>
</tr>
<tr>
<td>Carrying capacity for zebra</td>
<td>$K_z$</td>
<td>$3 \times 10^4$</td>
<td>individuals</td>
<td>Assumed</td>
</tr>
<tr>
<td>Mutual benefit for wildebeest</td>
<td>$a_{12}$</td>
<td>0.015</td>
<td>unitless</td>
<td>Fay and Greef (2006)</td>
</tr>
<tr>
<td>Mutual benefit for zebra</td>
<td>$a_{21}$</td>
<td>0.02</td>
<td>unitless</td>
<td>Fay and Greef (2006)</td>
</tr>
<tr>
<td>Wildebeest population</td>
<td>$w$</td>
<td>13</td>
<td>$\times 10^5$</td>
<td>Grant (2006)</td>
</tr>
<tr>
<td>Zebra population</td>
<td>$z$</td>
<td>2.5</td>
<td>$\times 10^4$</td>
<td>Grant (2006)</td>
</tr>
<tr>
<td>The mortality rate of wildebeest due to drought</td>
<td>$\beta$</td>
<td>0.015</td>
<td>individuals/year</td>
<td>Sinclair et al. (2008)</td>
</tr>
<tr>
<td>The mortality rate of zebra due to drought</td>
<td>$\pi$</td>
<td>0.015</td>
<td>individuals/year</td>
<td>Assumed</td>
</tr>
<tr>
<td>The mortality rate of wildebeest due to predation</td>
<td>$\alpha$</td>
<td>0.03</td>
<td>individuals/year</td>
<td>Assumed</td>
</tr>
<tr>
<td>The mortality rate of zebra due to predation</td>
<td>$\rho$</td>
<td>0.06</td>
<td>individuals/year</td>
<td>Assumed</td>
</tr>
</tbody>
</table>

The simulations were done in a python computer program (the corresponding codes are attached in Appendix 2). The results and discussions are presented in Chapter Four.

3.6 Diffusive Prey-predator Relations between Wildebeest, Zebra and Lion

3.6.1 The Mathematical Model

This mathematical model extends the mutualism model (21) with one predator. In addition, this model extends the model by Fay and Greef (2006), who developed a two prey-one predator
mathematical model. However, their model had no migration and diffusion parameters. Furthermore, the analysis of the dynamical behaviour of the three species was not performed. Therefore, this study included the diffusion and migration movement parameters. A detailed analysis of the dynamic behaviour of the three species was carried out. The dispersion relation of wildebeests, zebras, and lions was carried out to analyse the effects of diffusion and migration on the system's stability. Finally, the numerical method of the system of equations was carried out.

(i) Assumptions of the Model

- There are three populations, namely, two preys (wildebeests and zebras) whose population densities are denoted by \( w \) and \( z \), and the predator whose population density is denoted by \( P \).
- In the absence of the predator, the prey population density grows according to the logistic law of growth.
- Two prey species are mutualistic.
- The predator needs sufficient handling time for the prey. These are incorporated using Holling type II functional response.
- There is a death rate for both prey species from factors such as drought.
- The rate of an increase in the predator population depends on the amount of prey biomass it converts as food.

(ii) Parameters of the Model

The following are the parameters used in the model:

- \( r_1 \) and \( r_2 \) are per capita intrinsic growth rates for prey \( w \) and \( z \), respectively.
- \( K_1 \) and \( K_2 \) are carrying capacities for prey \( N_1 \) and \( N_2 \) respectively.
- \( b_1 \) and \( b_2 \) are coefficients for mutualistic relations between prey \( w \) and \( z \), respectively.
- \( h_1 \) and \( h_4 \) are capturing rates of predator \( P \) on \( w \) and \( z \), respectively.
\[ \frac{\alpha_1}{h_1} \text{ and } \frac{\alpha_2}{h_2} \text{ are the predator’s handling time on prey } w \text{ and } z \text{, respectively.} \]

\[ \lambda_1 \text{ and } \lambda_2 \text{ are the mortality rates for prey } w \text{ and } z \text{ respectively due to drought, while } c \text{ is the natural mortality of the predator } P. \]

\[ d_1 \text{ and } d_2 \text{ are coefficients that measure the predator’s efficiency to convert prey biomass of } w \text{ and } z, \text{ respectively into fertility (reproductivity).} \]

\[ \text{The quantity } D_p \text{ represents diffusion of lion. The velocity of lions flow is defined as } C_p = M_p \nabla P, \text{ where } M_p \text{ is a constant parameter expressing the flow intensity for lion.} \]

Therefore, the resulting mathematical model that describes the interaction of the three species is given as:

\[
\begin{align*}
\frac{\partial w}{\partial t} &= D_w \nabla^2 w - C_z \cdot \nabla w + r_1 w \left(1 - \frac{w}{K_1}\right) + b_1 wz - \frac{h_1 w P}{1 + a_1 z} - \lambda_1 w \\
\frac{\partial z}{\partial t} &= D_z \nabla^2 z - C_z \cdot \nabla z + r_2 z \left(1 - \frac{z}{K_2}\right) + b_2 wz - \frac{h_2 z P}{1 + a_2 z} - \lambda_2 z \\
\frac{\partial P}{\partial t} &= D_p \nabla^2 z - C_p \cdot \nabla P + P \left(-c + d_1 \frac{h_1 w}{1 + a_1 w} + d_2 \frac{h_2 z}{1 + a_2 z}\right)
\end{align*}
\]

The terms \( \frac{h_1 w}{1 + a_1 w} \) and \( \frac{h_2 z}{1 + a_2 z} \) are known as a Holling type II functional response.

### 3.6.2 Local Stability Analysis

The local stability analysis was conducted to see the local system dynamics. This is performed by letting the diffusive parameters \( D_p = D_z = D_w = 0 \) (Kurowski et al., 2017).

\[
\begin{align*}
\frac{dw}{dt} &= r_1 w \left(1 - \frac{w}{K_1}\right) + b_1 wz - \frac{h_1 w P}{1 + a_1 w} - \lambda_1 w \\
\frac{dz}{dt} &= r_2 z \left(1 - \frac{z}{K_2}\right) + b_2 wz - \frac{h_2 z P}{1 + a_2 z} - \lambda_2 z \\
\frac{dp}{dt} &= P \left(-c + d_1 \frac{h_1 w}{1 + a_1 w} + d_2 \frac{h_2 z}{1 + a_2 z}\right)
\end{align*}
\]

For ease of computations, the non-dimensionalization of the model is represented by Equations (45):

Let \( X = a_1 w, \ Y = a_2 z \)
This gives the following:

\[
\frac{dX}{dt} = r_1 \left[ X \left( 1 - \frac{1}{a_1 k_1} X \right) + \frac{b_1}{a_2 r_1} XY - \frac{h_1 X P}{r_1(1+X)} - \lambda_1 X \right]
\]

\[
\frac{dY}{dt} = r_2 \left[ Y \left( 1 - \frac{1}{a_2 k_2} Y \right) + \frac{b_2}{a_1 r_2} XY - \frac{h_2 Y P}{r_2(1+Y)} - \lambda_2 Y \right]
\]

\[
\frac{dP}{dt} = c \left[ -P + \frac{d_1 h_1 X P}{ca_1(1+X)} + \frac{d_2 h_2 Y P}{ca_2(1+Y)} \right]
\]

(46)

Let \( \beta_1 = \frac{1}{a_1 k_1} \), \( \gamma_1 = \frac{b_1}{a_2 r_1} \), \( \delta_1 = \frac{h_1}{r_1} \), \( \beta_2 = \frac{1}{a_2 k_2} \), \( \gamma_2 = \frac{b_2}{a_1 r_2} \), \( \delta_2 = \frac{h_2}{r_2} \),

\( \gamma_3 = \frac{d_1 h_1}{ca_1}, \delta_3 = \frac{d_2 h_2}{ca_2}, M_1 = \frac{\lambda_1}{r_1}, M_2 = \frac{\lambda_2}{r_2} \)

Simplifying, the system of Equations (46) gives the following:

\[
\frac{dX}{dt} = r_1 X \left[ 1 - \beta_1 X - M_1 - \gamma_1 Y - \delta_1 \frac{P}{(1+X)} \right]
\]

\[
\frac{dY}{dt} = r_2 Y \left[ 1 - \beta_2 Y - M_2 + \gamma_2 X - \delta_2 \frac{P}{(1+Y)} \right]
\]

\[
\frac{dP}{dt} = cP \left[ -1 + \gamma_3 \frac{X}{(1+X)} + \delta_3 \frac{Y}{(1+Y)} \right]
\]

(47)

3.6.3 Existence of Equilibrium Points in the System

The conditions for the existence of the equilibrium points of the system were established. By equating (47) to zero, the system has seven possible nonnegative equilibria, namely:

\[
E_0(0,0,0), \ E_1(X^*, 0, 0), \ E_2(0,Y^*, 0), \ E_3(X^*, Y^*, 0), E_4(X^*, 0, P^*), E_5(0, Y^*, P^*)
\]

And,

\[
E_6(X^*, Y^*, P^*)
\]

The existence of \( E_0(0,0,0) \) is trivial. The existences of other equilibria are shown as follows:

Existence of \( E_1(X^*, 0, 0) \) with \( X^* > 0 \).

Let \( Y = 0 \) and \( P = 0 \). From Equation (47), one obtains:

\[
r_1 X(1 - \beta_1 X - M_1) = 0. \quad X^* = \frac{1-M_1}{\beta_1}.
\]

Thus,
\[ E_1(X^*, 0, 0) = E_1 \left( \frac{1-M_1}{\beta_1}, 0, 0 \right). \] The equilibrium exists if \( M_1 < 1 \).

This condition implies that \( \lambda_1 < r_1 \).

Thus, in the absence of prey \( z \) and predator \( P \), the death rate of prey \( w \) must be less than its intrinsic growth rate \( r_1 \) for equilibrium \( E_1(X^*, 0, 0) \) to exist.

Existence of \( E_2(0, Y^*, 0) \) with \( Y^* > 0 \).

Let \( X = 0 \) and \( P = 0 \). From Equation (47), the following is obtained:

\[ r_2Y(1 - \beta_2Y - M_2) = 0, \quad Y^* = \frac{1-M_2}{\beta_2}. \]

Thus,

\[ E_2(0, Y^*, 0) = E_2 \left( 0, \frac{1-M_2}{\beta_2}, 0 \right). \] The equilibrium exists if \( M_2 < 1 \).

This condition implies that \( \lambda_2 < r_2 \). Thus, in the absence of prey \( w \) and predator \( P \), the death rate of prey \( z \) must be less than its intrinsic growth rate \( r_2 \) for the equilibrium \( E_2(0, Y^*, 0) \) to occur.

Existence of \( E_3(X^*, Y^*, 0) \), with \( X^*, Y^* > 0 \).

Let \( P = 0 \). From Equation (47), the following is obtained:

\[ r_1X(1 - \beta_1X + \gamma_1Y - M_1) = 0 \]
\[ r_2Y(1 - \beta_2Y + \gamma_2X - M_2) = 0 \]
\[ Y^* = \frac{\beta_1(1-M_2)+\gamma_2(1-M_1)}{\beta_1\beta_2-\gamma_1\gamma_2} \]
\[ X^* = \frac{\beta_2(1-M_1)+\gamma_1(1-M_2)}{\beta_1\beta_2-\gamma_1\gamma_2} \]

Thus,

\[ E_3(X^*, Y^*, 0) = E_3 \left( \frac{\beta_2(1-M_1)+\gamma_1(1-M_2)}{\beta_1\beta_2-\gamma_1\gamma_2}, \frac{\beta_1(1-M_2)+\gamma_2(1-M_1)}{\beta_1\beta_2-\gamma_1\gamma_2}, 0 \right), \]

\( M_1, M_2 < 1, \beta_1\beta_2 > \gamma_1\gamma_2 \).
This condition implies that:

\[
\frac{1}{a_1 k_1} \frac{1}{a_2 k_2} > \frac{b_1}{a_2 r_1 a_1 r_2}, \quad \Rightarrow \quad \frac{r_1}{k_1} \frac{r_2}{k_2} > b_1 b_2.
\]

In the absence of a predator, there is mutualism among the species. This is because the species grow to their respective carrying capacities and since the interspecies competition between wildebeests and zebras is small, the two species will co-exist.

Existence of \( E_4(X^*, 0, P^*), X^* > 0, P^* > 0. \)

Let \( Y^* = 0 \)

\[
r_1 X \left( 1 - \beta_1 X - \delta_1 \frac{P}{(1+X)} - M_1 \right) = 0
\]

\[
cP \left( -1 + \gamma_3 \frac{X}{(1+X)} \right) = 0
\]

\[
X^* = \frac{1}{\gamma_3 - 1} \quad \text{and} \quad P^* = \left( 1 + \frac{1}{(\gamma_3 - 1)} \right) \left( \frac{1-M_1}{\delta_1} - \frac{\beta_1}{\delta_1 (\gamma_3 - 1)} \right) \quad \text{provided} \quad M_1 < 1, \; \delta_1 > 0, \; \gamma_3 > 1.
\]

From \( \gamma_3 > c \Rightarrow d_1 > c \frac{a_1}{h_1} \), the proportion of biomass \( d_1 \) of the prey \( w \) converted into food by the predator \( P \) must be greater than the product of the predator’s natural mortality rate, \( c \) and the time it takes to handle the prey, \( \frac{a_1}{h_1} \).

Existence of \( E_5(0, Y^*, P^*) \), with \( Y^* > 0 \) and \( P^* > 0. \)

Let \( X = 0 \), then

\[
r_2 Y (1 - \beta_2 Y - M_2) - \delta_2 \frac{Y P}{(1+Y)} = 0
\]

\[
cP(-1 + \delta_3 \frac{Y}{(1+Y)}) = 0.
\]

Solving gives:

\[
Y^* = \frac{1}{\delta_3 - 1} \quad \text{and} \quad P^* = \left( 1 + \frac{1}{(\delta_3 - 1)} \right) \left( \frac{1-M_2}{\delta_2} - \frac{\beta_2}{\delta_2 (\delta_3 - 1)} \right) \quad \text{with} \quad M_2 < 1, \; \delta_3 > 0, \delta_3 > 1.
\]
From $\delta_3 > 1 \Rightarrow d_2 > c \frac{a_2}{h_2}$, the proportion of biomass $d_2$ of the prey $z$ converted into food by the predator $P$ must be greater than the product of the predator’s natural mortality rate, $c$ and the time it takes to handle the prey, $\frac{a_2}{h_2}$.

Co-existence equilibrium point: $E_6(X^*, Y^*, P^*)$.

Equating Equations (47) to zero and from this, two functions of $f(X, Y)$ and $g(X, Y)$ can be obtained which intersect at the equilibrium point $E_6(X^*, Y^*, P^*)$. Equating Equation (47) to zero, the following relations are obtained:

\[
(1 - \beta_1 X - M_1) + \gamma_1 Y - \delta_1 \frac{P}{(1 + X)} = 0 \tag{47a}
\]

\[
(1 - \beta_2 Y - M_2) - \gamma_2 X - \delta_2 \frac{P}{(1 + Y)} = 0 \tag{47b}
\]

\[-1 + \gamma_3 \frac{X}{(1+X)} + \delta_3 \frac{Y}{(1+Y)} = 0 \tag{47c}
\]

From (47a) $P = \frac{(1+X)(1-\beta_1 X - M_1 + \gamma_1 Y)}{\delta_1}$ \tag{47d}

From (47b) $P = \frac{(1+Y)(1-\beta_2 Y - M_2 + \gamma_2 X)}{\delta_2}$ \tag{47e}

From (47c), $f(X, Y) = -1 + \gamma_3 \frac{X}{(1+X)} + \delta_3 \frac{Y}{(1+Y)} = 0$ \tag{47f}

From (47d) and (74e)

\[
g(X, Y) = \frac{(1+X)(1-\beta_1 X - M_1 + \gamma_1 Y)}{\delta_1} - \frac{(1+Y)(1-\beta_2 Y - M_2 + \gamma_2 X)}{\delta_2} = 0 \tag{47g}
\]

Equations (47f) and (47g) are two functions of $X$ and $Y$. To prove the existence of $E_6(X^*, Y^*, P^*)$, conditions under which $f(X, Y)$ and $g(X, Y)$ meet in the interior of positive $(X, Y)$ plane at the point $(X^*, Y^*)$ are found. Knowing $(X^*, Y^*)$, $P^*$ can be obtained from (47d).

From equation (47f) as $X \to 0$, $Y$ tends to $Y_f$ given by $Y_f = \frac{1}{\delta_3 - 1}$ where $\delta_3 - 1 > 0$. It can be noticed that $Y_f$ is the same as $Y^*$ of $E_5(0, Y^*, P^*)$.

From (47g) as $X \to 0$, $Y$ tends to $Y_g$ given by $Y_g = \frac{-D_2 + \sqrt{D_2^2 - 4D_1D_3}}{2D_1}$ where:
\[ D_1 = \delta_1 \beta_2, \quad D_2 = \delta_2 \gamma_1 + \delta_1 \beta_2 + \delta_1 M_2 - \delta_1, \quad D_3 = \delta_2 (1 - M_1) - \delta_1 (1 - M_2) \]

Since the points \( M_1 < 1 \) and \( M_2 < 1 \), then the point \( Y_g \) is positive and real if,

\[ \delta_2 (1 - M_1) - \delta_1 (1 - M_2) < 0. \]

Therefore, \( Y_f \) and \( Y_g \) are 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 (47)

\[ \frac{dY}{dX} = \frac{\partial f}{\partial x} \frac{\partial f}{\partial y} \]

where \( \frac{\partial f}{\partial x} = \frac{\gamma_3}{(1+x)^2} \) and \( \frac{\partial f}{\partial y} = \frac{\delta_3}{(1+y)^2} \). It is noted that \( \frac{dY}{dX} > 0 \).

Similarly, \( \frac{dY}{dX} = \frac{\partial g}{\partial x} \frac{\partial g}{\partial y} \), where \( \frac{\partial g}{\partial x} = -\beta_1 \delta_2 (1+2X) + \delta_2 (1-M_1) + \delta_1 \gamma_2 (1+Y) + \gamma_1 \delta_2 Y \) and

\[ \frac{\partial g}{\partial y} = \frac{\gamma_1 \delta_2 (1+X) - \beta_1 \delta_2 (1+2Y) + \delta_1 (1-M_2) + \gamma_2 \delta_1 X}{\delta_1 \delta_2}. \]

Therefore, \( \frac{dY}{dX} < 0 \) provided \( \frac{\partial g}{\partial x} < 0 \) and \( \frac{\partial g}{\partial y} > 0 \).

Since \( f(X, Y) \) it can be obtained \( \frac{dY}{dX} > 0 \) and \( g(X, Y) \) which gives \( \frac{dY}{dX} < 0 \), then \( f(X, Y) \) and \( g(X, Y) \) will meet if \( Y_f < Y_g \).

The existence of the positive equilibrium point \( E_6(X^*, Y^*, P^*) \) is stated in the following theorem:

**Theorem 2:** The positive equilibrium point \( E_6(X^*, Y^*, P^*) \) will exist if for \( M_1 < 1 \) and \( M_2 < 1 \) then the condition \( \delta_3 - 1 > 0 \) and \( Y_f < Y_g \) must be satisfied.

In terms of the original parameters \( M_1 < 1 \) and \( M_2 < 1 \) implies that \( \lambda_1 < r_1 \) and \( \lambda_2 < r_2 \).

The mortality rate of wildebeests and zebras should be less than their respective intrinsic growth rates. For the condition \( \delta_3 - 1 > 0 \Rightarrow d_2 > c \frac{a_z}{h_2} \), the proportion of biomass \( d_2 \) of the prey \( z \) (zebra) converted into food by the predator \( P \) (lion) must be greater than the product of the predator’s mortality rate, \( c \) and the time it takes to handle the prey, \( \frac{a_z}{h_2} \).

### 3.6.4 Local Stability of the Equilibrium Points

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

From Equations (47), the Jacobian matrix of the system is given by:

\[
J(E_i) = \begin{pmatrix}
\frac{\partial f_1}{\partial X} & \frac{\partial f_1}{\partial Y} & \frac{\partial f_1}{\partial p} \\
\frac{\partial f_2}{\partial X} & \frac{\partial f_2}{\partial Y} & \frac{\partial f_2}{\partial z} \\
\frac{\partial f_3}{\partial X} & \frac{\partial f_3}{\partial Y} & \frac{\partial f_3}{\partial z}
\end{pmatrix}
\]

(48)

For \( i = 0, 1, 2, 3, 4, 5, 6 \). This gives:

\[
J(E_i) = \begin{pmatrix}
A^{**} & \gamma_1 X & -\delta_1 X \\
\gamma_2 Y & B^{**} & -\delta_2 Y \\
\gamma_3 P & \delta_2 P & C^{**}
\end{pmatrix}
\]

(49)

Where \( A^{**} = 1 - 2\beta_1 X - M_1 + \gamma_1 Y - \delta_1 \frac{P}{(1+X)^2} \), \( B^{**} = 1 - 2\beta_2 Y - M_2 + \gamma_2 X - \delta_2 \frac{P}{(1+Y)^2} \)

and,

\[
C^{**} = -c + \gamma_3 \frac{X}{(1+X)} + \delta_3 \frac{Y}{(1+Y)}
\]

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

\( E_0(0,0,0,0) \). The Jacobian matrix evaluated at \( E_0 \) gives:

\[
J(E_0) = \begin{pmatrix}
1 - M_1 & 0 & 0 \\
0 & 1 - M_2 & 0 \\
0 & 0 & -c
\end{pmatrix}
\]

The eigenvalues of the \( J(E_0) \) are \( 1 - M_1, 1 - M_2 \) and \(-c\). Since \( M_1 < 1 \) and \( M_2 < 1 \) implies that \( 1 - M_1 > 0 \) and \( 1 - M_2 > 0 \). Hence a saddle point (Unstable) is found.

**Theorem 3:** \( E_0 \) is always a saddle-node, and there cannot be total system extinction (47) for favourable initial conditions.

\( E_1(X^*, 0, 0) = E_1 \left( \frac{1-M_1}{\beta_1}, 0, 0 \right) \). The Jacobian matrix of \( E_1 \) gives:
\[ J(E_1) = \begin{pmatrix} (M_1 - 1) & \frac{y_1(1-M_1)}{\beta_1} & -\frac{\delta_1(1-M_1)}{1-M_1+\beta_1} \\ 0 & (1 - M_2) + \frac{y_2(1-M_1)}{\beta_1} & 0 \\ 0 & 0 & -c + \frac{y_3(1-M_1)}{\beta_1+1-M_1} \end{pmatrix} \]

The eigenvalues of the \( J(E_1) \) are \( (M_1 - 1), (1 - M_2) + \frac{y_2(1-M_1)}{\beta_1} \) and \( -c + \frac{y_3(1-M_1)}{\beta_1+1-M_1} \).

Since \( M_1 < 1, M_2 < 1 \), then \( (M_1 - 1) < 0, (1 - M_2) + \frac{y_2(1-M_1)}{\beta_1} > 0 \) and

\[-c + \frac{y_3(1-M_1)}{\beta_1+1-M_1} < 0 \text{ if } \beta_1 > M_1 - 1.\]

Therefore, \( E_1(X^*, 0, 0) = E_1 \left( \frac{1-M_1}{\beta_1}, 0,0 \right) \) is a saddle point hence unstable.

\[ E_2(0, Y^*, 0) = E_2 \left( 0, \frac{1-M_2}{\beta_2}, 0 \right) \]. The Jacobian matrix of \( E_2 \) gives:

\[ J(E_2) = \begin{pmatrix} 1 - M_1 + \frac{y_1(1-M_2)}{\beta_2} & 0 & 0 \\ \frac{y_2(1-M_2)}{\beta_2} & M_2 - 1 & -\frac{\delta_2(1-M_2)}{1-M_2+\beta_2} \\ 0 & 0 & -c + \frac{\delta_3(1-M_2)}{\beta_2+1-M_2} \end{pmatrix} \]

The eigenvalues of the \( J(E_2) \) are \( 1 - M_1 + \frac{y_1(1-M_2)}{\beta_2}, M_2 - 1 \) and \( -c + \frac{\delta_3(1-M_2)}{\beta_2+1-M_2} \).

Since \( M_1 < 1, M_2 < 1 \), then \( 1 - M_1 + \frac{y_1(1-M_2)}{\beta_2} > 0, M_2 - 1 < 0 \) and

\[-c + \frac{\delta_3(1-M_2)}{\beta_2+1-M_2} < 0 \text{ if } \beta_2 < M_2 - 1.\]

Therefore \( E_2(0, Y^*, 0) = E_2 \left( 0, \frac{1-M_2}{\beta_2}, 0 \right) \) is a saddle point hence unstable.

\[ E_3(X^*, Y^*, 0) = E_3 \left( \frac{\beta_2(1-M_1)+y_1(1-M_2)}{\beta_1\beta_2-y_1y_2}, \frac{\beta_1(1-M_2)+y_2(1-M_1)}{\beta_1\beta_2-y_1y_2}, 0 \right) \]. The Jacobian matrix of \( E_3 \) gives:

\[ J( E_3 ) = \begin{pmatrix} D^{**} & W^{**} & E^{**} \\ Z^{**} & F^{**} & G^{**} \\ 0 & 0 & H^{**} \end{pmatrix} \]
Where $D^{**} = 1 - M_1 - 2\beta_1 \frac{\beta_2(1-M_1) + \gamma_1(1-M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} + \gamma_1 \frac{\beta_1(1-M_2) + \gamma_2(1-M_1)}{\beta_1 \beta_2 - \gamma_1 \gamma_2}$

$W^{**} = \gamma_1 \frac{\beta_2(1-M_1) + \gamma_1(1-M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2}$

$E^{**} = -\delta_1 \frac{\beta_2(1-M_1) + \gamma_1(1-M_2)}{(\beta_1 \beta_2 - \gamma_1 \gamma_2) + \beta_2(1-M_2) + \gamma_1(1-M_2)}$

$F^{**} = 1 - M_2 - 2\beta_2 \frac{\beta_1(1-M_2) + \gamma_2(1-M_1)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} + \gamma_2 \frac{\beta_2(1-M_1) + \gamma_1(1-M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2}$

$Z^{**} = \gamma_2 \frac{\beta_1(1-M_2) + \gamma_2(1-M_1)}{\beta_1 \beta_2 - \gamma_1 \gamma_2}$

$G^{**} = -\delta_2 \frac{\beta_1(1-M_2) + \gamma_2(1-M_1)}{(\beta_1 \beta_2 - \gamma_1 \gamma_2) + \beta_1(1-M_2) + \gamma_2(1-M_1)}$

$H^{**} = -c + \gamma_3 \frac{X}{(1+X)} + \delta_3 \frac{Y}{(1+Y)}$, substituting gives:

$H^{**} = -c + \gamma_3 \frac{\beta_2(1-M_1) + \gamma_1(1-M_2)}{(\beta_1 \beta_2 - \gamma_1 \gamma_2) + \beta_2(1-M_2) + \gamma_1(1-M_2)} + \delta_3 \frac{\beta_1(1-M_2) + \gamma_2(1-M_1)}{(\beta_1 \beta_2 - \gamma_1 \gamma_2) + \beta_1(1-M_2) + \gamma_2(1-M_1)}$

The eigenvalues of the $J(E_3)$ are obtained by solving the system:

$$\det \begin{pmatrix} D^{**} - \lambda & W^{**} & E^{**} \\ Z^{**} & F^{**} - \lambda & G^{**} \\ 0 & 0 & H^{**} - \lambda \end{pmatrix} = 0.$$ 

This gives:

$$(H^{**} - \lambda)(F^{**} - \lambda)(D^{**} - \lambda) - Z^{**}W^{**} = 0$$

which simplifies the characteristic Equation

$$\lambda^3 - (D + F + H)\lambda^2 + (DF + DH + FH - ZW)\lambda + ZWH - DFH = 0$$

which is of the form

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0.$$ 

By Routh-Hurwitz criteria (Murray, 1989) the $\lambda$’s are negative if $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 - a_3 > 0$.

Each of these conditions is considered next as follows:

(i) $a_1 > 0 \Rightarrow -(D + F + H) > 0$ or $+F + H < 0$.

$D + F + H < 0$. This can be satisfied if $H^{**} < 0$, $D^{**} < 0$, $F^{**} < 0$

For $H^{**} < 0$ implies $-c + \gamma_3 \frac{X}{(1+X)} + \delta_3 \frac{Y}{(1+Y)} < 0$. Simplifying gives:
\[ XY(\gamma_3 + \delta_3 - c) + (\delta_3 - c)Y + (\gamma_3 - c)X - c < 0. \]

This will hold if, for \( M_1 < 1, M_2 < 1, \gamma_3 + \delta_3 < c \).

In terms of original parameters \( \gamma_3 + \delta_3 < c \) gives \( \frac{d_1 h_1}{a_1} + \frac{d_2 h_2}{a_2} < c \).

This implies that the predator’s efficiency in converting the biomass of both preys into fertility or reproductivity must be less than the predator’s natural mortality rate and the time it takes to handle both preys.

For \( D^{**} < 0 \) implies:

\[
1 - 2\beta_1 X - M_1 + \gamma_1 Y < 0. \quad \text{Substituting for } X^* \text{ and } Y^* \text{ gives:}
\]

\[
1 - M_1 - 2\beta_1 \frac{\beta_2 (1-M_2) + \gamma_1 (1-M_2)}{\beta_1 \beta_2 - \gamma_1 Y_2} + \gamma_1 \frac{\beta_2 (1-M_2) + \gamma_2 (1-M_1)}{\beta_1 \beta_2 - \gamma_1 Y_2}.
\]

\[
\frac{\beta_1 \beta_2 (M_1 - 1) - \beta_2 \gamma_1 (M_2 - 1)}{\beta_1 \beta_2 - \gamma_1 Y_2} < 0.
\]

Therefore,

\( D^{**} < 0 \) if \( M_1, < 1, M_2 < 1, \beta_1 \beta_2 > \gamma_1 Y_2 \).

For \( F^{**} < 0 \),

\[
1 - 2\beta_2 Y - M_2 + \gamma_2 X < 0 \quad \text{Substituting for } X^* \text{ and } Y^* \text{ the following equation was obtained:}
\]

\[
1 - M_2 - 2\beta_2 \frac{\beta_1 (1-M_2) + \gamma_2 (1-M_1)}{\beta_1 \beta_2 - \gamma_1 Y_2} + \gamma_2 \frac{\beta_2 (1-M_2) + \gamma_1 (1-M_2)}{\beta_1 \beta_2 - \gamma_1 Y_2}.
\]

\[
\frac{\beta_1 \beta_2 (M_2 - 1) - \beta_2 \gamma_2 (M_1 - 1)}{\beta_1 \beta_2 - \gamma_1 Y_2} < 0.
\]

Therefore,

\( F^{**} < 0 \) if \( M_1, < 1, M_2 < 1, \beta_1 \beta_2 > \gamma_1 Y_2 \)

(ii) \( a_3 > 0 \) Implies \( H(ZW - DF) > 0 \). This is satisfied if \( H < 0, ZW - DF < 0 \), which gives:
\[ ZW - DF = y_2 \frac{\beta_1(1 - M_2) + \gamma_2(1 - M_1)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} y_1 \frac{\beta_2(1 - M_1) + \gamma_1(1 - M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} - \left( 1 - M_1 - 2 \beta_1 \frac{\beta_2(1 - M_1) + \gamma_1(1 - M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} + \gamma_1 \frac{\beta_1(1 - M_2) + \gamma_2(1 - M_1)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} \right) \left( 1 - M_2 - 2 \beta_2 \frac{\beta_1(1 - M_1) + \gamma_2(1 - M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} + \gamma_2 \frac{\beta_2(1 - M_1) + \gamma_1(1 - M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} \right) < 0 \]

Let \( L_1 = \frac{\beta_1(1 - M_2) + \gamma_2(1 - M_1)}{\beta_1 \beta_2 - \gamma_1 \gamma_2}, \) \( L_2 = \frac{\beta_2(1 - M_1) + \gamma_1(1 - M_2)}{\beta_1 \beta_2 - \gamma_1 \gamma_2} \).

The inequality \( \gamma_1 \gamma_2 L_1 L_2 - (1 - M_1 - 2 \beta_1 L_2 + \gamma_1 L_2)(1 - M_2 - 2 \beta_2 L_1 + \gamma_2 L_2) < 0 \) is obtained.

Therefore,

\[ ZW - DF < 0 \text{ if } M_1, M_2 < 1, \beta_1 \beta_2 > \gamma_1 \gamma_2. \]

(iii) \( a_1 a_2 - a_3 > 0 \) implies \(-(D + F + H)(DF + DH + FH - ZW) - H(ZW - DF) > 0 \)

This simplifies to \((D + F)[(ZW - DF) - H(D + F + H)] > 0\).

This is satisfied if \( D < 0, W < 0, H < 0 \) and \((ZW - DF) < 0\) which have been prior established.

Therefore,

\[ E_3(X^*, Y^*, 0) \text{ is locally asymptotically stable if the following conditions are satisfied:} \]

\[ M_1 < 1, M_2 < 1, \beta_1 \beta_2 > \gamma_1 \gamma_2 \]

\[ E_4(X^*, 0, P^*) = \left( \frac{c}{y_3 - c}, 0, \left( 1 + \frac{c}{y_3 - c} \right) \left( \frac{1 - M_1}{\delta_1} - \frac{c \beta_1}{\delta_1 (y_3 - c)} \right) \right) \]
The Jacobian Matrix evaluated at $E_4$ give:

$$J(E_4) = \begin{pmatrix} E^+ & \frac{γc}{γ_3c} & \frac{−δ_1c}{γ_3c} \\ \frac{γc}{γ_3c} & γ_3 & 0 \\ 0 & F^+ & 0 \\ G^+ & H^+ & 0 \end{pmatrix}$$

$$E^+ = 1 - 2β_1 \frac{c}{γ_3c} - M_1 - δ_1 \left(1 + \frac{c}{γ_3c}\right) \left(\frac{1−M_1}{δ_1} - \frac{cβ_1}{δ_1(γ_3c)}\right) \frac{(γ_3−c)^2}{γ_3}.$$  

$$F^+ = 1 - M_2 + γ_2 \frac{c}{γ_3c} - δ_2 \left(1 + \frac{c}{γ_3c}\right) \left(\frac{1−M_1}{δ_1} - \frac{cβ_1}{δ_1(γ_3c)}\right)$$ and

$$G^+ = \frac{(γ_3−c)^2}{γ_3} \left(1 + \frac{c}{γ_3c}\right) \left(\frac{1−M_1}{δ_1} - \frac{cβ_1}{δ_1(γ_3c)}\right).$$

$$H^+ = \frac{δ_2p}{(1+γ)^2} = δ_2 \left(1 + \frac{c}{γ_3c}\right) \left(\frac{1−M_2}{δ_1} - \frac{cβ_1}{δ_1(γ_3c)}\right).$$

The eigenvalues of the matrix $J(E_4)$ have negative real parts if $E^+ < 0$ and $F^+ < 0$. Further $E^+ < 0$ implies:

$$1 - 2β_1 \frac{c}{γ_3c} - M_1 - δ_1 \left(1 + \frac{c}{γ_3c}\right) \left(\frac{1−M_1}{δ_1} - \frac{cβ_1}{δ_1(γ_3c)}\right) \frac{(γ_3−c)^2}{γ_3} < 0.$$  

Simplifying gives:

$$\frac{(1−M_1)(γ_3−c)−2β_1c}{(γ_3c)} - \left[\frac{(1−M_1)(γ_3−c)−β_1c}{γ_3}\right] < 0$$

Also $F^+ < 0$ implies $1 - M_2 + γ_2 \frac{c}{γ_3c} - δ_2 \left(1 + \frac{c}{γ_3c}\right) \left(\frac{1−M_1}{δ_1} - \frac{cβ_1}{δ_1(γ_3c)}\right) < 0$

$$(1 - M_1)(γ_3−c) + γ_2c - δ_2γ_3 \left[\frac{(1−M_1)(γ_3−c)−β_1c}{δ_1(γ_3−c)}\right] < 0$$

Therefore, $E_4(X^*, 0, P^*)$ is locally asymptotically stable if conditions $M_1 < 1$, $M_2 < 1$, $γ_3 < c$ are satisfied.

$$E_5(0, Y^*, P^*) = \begin{pmatrix} 0 & c \gamma_3 & \gamma_3c \\ \frac{c}{γ_3c} & 1 + \frac{c}{γ_3c} \left(\frac{1−M_2}{δ_2} - \frac{cβ_2}{δ_2(γ_3−c)}\right) \end{pmatrix}.$$  

The Jacobian matrix of $E_5$ is

$$J(E_5) = \begin{pmatrix} A^+ & 0 & 0 \\ P^+ & B^+ & Q^+ \\ D^+ & E^+ & 0 \end{pmatrix}$$
Where,

\[ A^+ = (1 - M_1)(\delta_3 - c) + \gamma_1 c - \frac{\delta_1 \delta_3}{\delta_3 - c} \left( (1 - M_2)(\delta_3 - c) - c \beta_2 \right) \],

\[ B^+ = (1 - M_2)(\delta_3 - c) - 2 \beta_2 c - \frac{(1 - M_2)(\delta_3 - c) - \beta_2 c}{\delta_3} \],

\[ D^+ = \frac{\gamma_3 \delta_3}{\delta_3 - c} \left( \frac{(1 - M_2)(\delta_3 - c) - \beta_2 c}{\delta_3 - c} \right) \cdot P^+ = \frac{\gamma_2}{\delta_3 - c}, Q^+ = \frac{-c \delta_2}{\delta_3} \],

\[ E^+ = \left( \frac{(1 - M_2)(\delta_3 - c) - \beta_2 c}{\delta_3^2} \right) (\delta_3 - c) \].

The eigenvalues of the matrix \( J(E_5) \) are 
\[ \det \begin{pmatrix} A^+ - \lambda & 0 & 0 \\ P^+ & B^+ - \lambda & Q^+ \\ D^+ & E^+ & 0 - \lambda \end{pmatrix} = 0 \]

Simplifying the following characteristic equation was obtained:
\[ \lambda^3 - (A + B) \lambda^2 + (AB - EQ) \lambda + AEQ = 0 \]
which is of the form \( \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0 \).

By Routh-Hurwitz criteria (Murray, 1989), the \( \lambda \)'s are negative if \( a_1 > 0, a_3 > 0 \) and \( a_1 a_2 - a_3 > 0 \). Each of these conditions is considered next as follows:

If \( a_1 > 0 \) \( \Rightarrow -(A^+ + B^+) > 0 \) or \( A^+ + B^+ < 0 \)
\[ A^+ + B^+ < 0 \]. This can be satisfied if \( A^+ < 0, B^+ < 0 \),

If \( A^+ < 0 \) implies \( 1 - M_1 + \gamma_1 Y - \delta_1 P < 0 \).
This will hold if, for \( M_1 < 1, M_2 < 1, \delta_3 < c \)

If \( B^+ < 0 \) implies This will hold if, for \( M_1 < 1, M_2 < 1, \delta_3 < c \)

If \( a_3 > 0 \) implies \( AEQ > 0 \). Since \( A^+ < 0, Q^+ = \frac{-c \delta_2}{\delta_3} < 0 \) and
\[ E^+ = \left( \frac{(1 - M_2)(\delta_3 - c) - \beta_2 c}{\delta_3^2} \right) (\delta_3 - c) > 0 \] if \( M_1 < 1, M_2 < 1, \delta_3 < c \)

If \( a_1 a_2 - a_3 > 0 \) implies that \( -(A^+ + B^+)(AB - EQ) - AEQ > 0 \)
This simplifies to \( (A^+ + B^+) - B^+ E^+ D^+ < 0 \).
Hence $A^+ < 0$, $B^+ < 0$, $D^+ < 0$ and $E^+ > 0$

Therefore, $E_5(0,Y^*,P^*)$ is locally asymptotically stable if conditions $M_1 < 1$, $M_2 < 1$, $\delta_3 < c$ are satisfied.

3.6.5 Global Stability of the Steady States

The global stability of the equilibrium points was analysed as follows:

(i) Global Stability of $E_1$, $E_2$ and $E_3$

The global stability of $E_1, E_2$ and $E_3$ was analysed by transforming the system of Equations (47) into a linear system and then choosing a suitable Lyapunov function to analyse each equilibrium point.

By letting $X = X^* + x, Y = Y^* + y$ and $P = P^* + p$, where $x, y$ and $p$, are small perturbations about $X^*, Y^*$ and $P^*$ respectively. The system of Equations (47) is turned into a linear system of the form $\dot{x}_i = J(E_i)x_i$, where $J(E_i)x_i$ is the Jacobian Matrix of the system of Equations (47). Thus the system of Equations (47) is:

\[
\begin{align*}
\frac{dx}{dt} &= \left(-\beta_1X^* - \delta_1 \frac{p^*X^*}{(1+X^*)^2}\right)x + (y_1X^*)y - \left(\frac{\delta_1X^*}{(1+X^*)}\right)p \\
\frac{dy}{dt} &= (y_2Y^*)x + \left(-\beta_2Y^* - \delta_2 \frac{p^*Y^*}{(1+Y^*)^2}\right)y - \left(\frac{\delta_2Y^*}{(1+Y^*)}\right)p \\
\frac{dp}{dt} &= \left(\frac{y_2P^*}{(1+Y^*)^2}\right)x + \left(\frac{\delta_2P^*}{(1+Y^*)^2}\right)y + (0)p
\end{align*}
\]

(ii) Global Stability of $E_1(X^*, 0, 0) = \left(\frac{1-M_1}{\beta_1}, 0, 0\right)$

The Lyapunov function can be defined as $V(x,y,p) = \frac{x^2}{2x^*} + \frac{y^2}{2} + \frac{p^2}{2}$ where $X^*$ is the component of the equilibrium point $E_1(X^*, 0,0) = \left(\frac{1-M_1}{\beta_1},0,0\right)$. It is clear that $V(x,y,p)$ is a positive definite function. Differentiating $V$ with respect to $t$ gives:

$V'(x,y,p) = \frac{x}{X^*} \dot{x} + y\dot{y} + p\dot{p}$. Substituting for $\dot{x}, \dot{y}$ and $\dot{p}$ using (50) gives:
\[ V'(x, y, p) = x \left[ \left( -\beta_1 - \delta_1 \frac{p^*}{(1+X')^2} \right) x + (\gamma_1) y - \left( \frac{\delta_1}{(1+X')} \right) p \right] + y Y^* \left( (\gamma_2) x + \left( -\beta_2 - \delta_2 \frac{p^*}{(1+Y')^2} \right) y - \left( \frac{\delta_2}{(1+Y')} \right) p \right) + p p^* \left[ \left( \frac{\gamma_3}{(1+X')^2} \right) x + \left( \frac{\delta_2}{(1+Y')^2} \right) y + (0)p \right] \]

For \( E_1(X^*, 0, 0) \), implies \( V'(x, y, p) = -\beta_1 x^2 + \gamma_1 xy - \frac{\delta_2}{(1+X')} xp \)

Therefore, \( E_1(X^*, 0, 0) \) is Lyapunov stable if \( V'(x, y, p) = 0 \) and uniformly asymptotically stable if \( V'(x, y, p) < 0 \).

Thus, \( E_1(X^*, 0, 0) \) is globally asymptotically stable if \( M_1 < 1 \). In terms of original parameters, this condition implies that \( \lambda_1 < r_1 \) in the absence of Zebra (\( z \)) and lion (\( P \)), the population of Serengeti wildebeests (\( w \)) is globally stable, provided that the death rate of wildebeests must be less than its intrinsic growth rate \( r_1 \).

(iii) **Global stability of** \( E_2(0, Y^*, 0) = E_2 \left( 0, \frac{1-M_2}{\beta_2}, 0 \right) \)

Defines a Lyapunov Function \( V(x, y, p) = \frac{x^2}{2} + \frac{y^2}{2Y^*} + \frac{p^2}{2} \) where \( Y^* \) is the component of the equilibrium point \( E_2(0, Y^*, 0) = E_2 \left( 0, \frac{1-M_2}{\beta_2}, 0 \right) \). Clearly, \( V(x, y, p) \) is a positive definite function. Differentiating \( V \) with respect to \( t \) gives:

\[ V'(x, y, p) = x \dot{x} + \frac{y}{Y^*} \dot{y} + p \dot{p} \] Substituting \( \dot{x}, \dot{y} \) and \( \dot{p} \) using (47) to obtain

\[ V'(x, y, p) = x X^* \left[ \left( -\beta_1 - \delta_1 \frac{p^*}{(1+X')^2} \right) x + (\gamma_1) y - \left( \frac{\delta_1}{(1+X')} \right) p \right] + y Y^* \left[ (\gamma_2) x + \left( -\beta_2 - \delta_2 \frac{p^*}{(1+Y')^2} \right) y - \left( \frac{\delta_2}{(1+Y')} \right) p \right] + p p^* \left[ \left( \frac{\gamma_3}{(1+X')^2} \right) x + \left( \frac{\delta_2}{(1+Y')^2} \right) y + (0)p \right] \]

\[ E_2(0, Y^*, 0) = E_2 \left( 0, \frac{1-M_2}{\beta_2}, 0 \right), \] implies \( V'(x, y, p) = \gamma_2 xy - \beta_2 y^2 - \delta_2 p y \).

Therefore,

\( E_1(X^*, 0, 0) \) is Lyapunov stable if \( V'(x, y, p) = 0 \) and uniformly asymptotically stable if \( V'(x, y, p) < 0 \).

Thus, \( E_2(0, Y^*, 0) \) is globally asymptotically stable if \( M_2 < 1 \). In terms of original parameters, this condition implies that \( \lambda_2 < r_2 \) in the absence of the wildebeest (\( w \)) and the lion (\( P \)), the
population of Serengeti Zebras \((z)\) is globally stable, provided that the death rate of Zebras must be less than its intrinsic growth rate \(r_2\).

\[(iv) \quad \text{Global Stability of } E_3(X^*, Y^*, 0) = E_3\left(\frac{\beta_2(1-M_1)+\gamma_1(1-M_2)}{\beta_1\beta_2-\gamma_1Y_2}, \frac{\beta_1(1-M_2)+\gamma_2(1-M_1)}{\beta_1\beta_2-\gamma_1Y_2}, 0\right)\]

The Lyapunov function can be defined as \(V(x, y, p) = \frac{x^2}{2x^*} + \frac{y^2}{2y^*} + \frac{p^2}{2}\) where \(Y^*\) and \(X^*\) are the components of the equilibrium point:

\[E_3(X^*, Y^*, 0) = E_3\left(\frac{\beta_2(1-M_1)+\gamma_1(1-M_2)}{\beta_1\beta_2-\gamma_1Y_2}, \frac{\beta_1(1-M_2)+\gamma_2(1-M_1)}{\beta_1\beta_2-\gamma_1Y_2}, 0\right)\]

\(V(x, y, p)\) is a positive definite function. Differentiating \(V\) with respect to \(t\) one gets:

\[V'(x, y, p) = \frac{x}{X^*} \dot{x} + \frac{y}{Y^*} \dot{y} + p \dot{p} \quad .\]

Substituting for \(\dot{x}, \dot{y}\) and \(\dot{p}\) using (50) gives:

\[V'(x, y, p) = x \left[\left(-\beta_1 - \delta_1 \frac{P^*}{(1+x^*)^2}\right)x + (\gamma_1)y - \left(\frac{\delta_1}{1+x^*}\right)p\right] + y \left(\gamma_2)x + \left(-\beta_2 - \delta_2 \frac{P^*}{1+y^*}\right)y + \left(\gamma_2\right)p\left(\frac{\delta_2}{1+y^*}\right)y + (0)p\]

\[E_3(X^*, Y^*, 0) = E_3\left(\frac{\beta_2(1-M_1)+\gamma_1(1-M_2)}{\beta_1\beta_2-\gamma_1Y_2}, \frac{\beta_1(1-M_2)+\gamma_2(1-M_1)}{\beta_1\beta_2-\gamma_1Y_2}, 0\right), \text{this implies that:} \]

\[V'(x, y, p) = -\beta_1 x^2 + (\gamma_1 + \gamma_2)xy - \beta_2 y^2 - \frac{\delta_1}{1+x^*}xp - \frac{\delta_2}{1+y^*}py \quad .\]

This is globally stable if the conditions \(M_1 < 1, M_2 < 1\) and \(\beta_1\beta_2 > \gamma_1\gamma_2\)

In terms of original parameters \(M_1 < 1\) implies \(\lambda_1 < r_1\), \(M_2 < 1\) implies that \(\lambda_2 < r_2\) and \(\beta_1\beta_2 > \gamma_1\gamma_2\) implies \(\frac{1}{a_1k_1}, \frac{1}{a_2k_2} > \frac{b_1}{a_2r_1a_1r_2}, \Rightarrow \frac{r_1}{k_1}, \frac{r_2}{k_2} > b_1b_2\).

The intrinsic growth rates of the Serengeti wildebeests and Zebras are greater than their death rates. Furthermore, due to mutualism among the species and the absence of a predator, the two species grow to their respective carrying capacities, and the two species will co-exist.
(v) Global Stability of $E_4$ and $E_5$

To prove the global stability of $E_4$ and $E_5$ by using Bendixson-Dulac’s criteria and finding conditions for the nonexistence of periodic orbits within the positive plane containing each equilibrium point as in Dubey and Upadhay (2004) and Castillo-Chavez and Brauer (1999).

For $E_4$, defines a continuously differentiable function in the $X > 0$, $P > 0$ planes as $H_1(X, P) = \frac{1}{XP^2}$. The system of Equations (47) gives:

$$h_1(X, P) = X \left(1 - \beta_1 X - M_1 - \delta_1 \frac{P}{(1 + X)}\right) \text{ and } h_2(X, P) = P \left(-c + \gamma_3 \frac{X}{(1 + X)}\right)$$

This gives:

$$H_1 h_1 = \frac{1}{P^2} \left(1 - \beta_1 X - M_1 - \delta_1 \frac{P}{(1 + X)}\right) \text{ and } H_1 h_2 = \frac{1}{XP} \left(-c + \gamma_3 \frac{X}{(1 + X)}\right)$$

Computing $\frac{\partial H_1 h_1}{\partial X}$ and $\frac{\partial H_2 h_2}{\partial P}$ give $\frac{\partial H_1 h_1}{\partial X} = \frac{1}{P^2} \left(-\beta_1 + \delta_1 \frac{P}{(1 + X)^2}\right)$ and

$$\frac{\partial H_2 h_2}{\partial P} = \frac{1}{XP^2} \left(-c + \gamma_3 \frac{X}{(1 + X)}\right).$$

From this one obtains:

$$\frac{\partial H_1 h_1}{\partial X} + \frac{\partial H_2 h_2}{\partial P} = \frac{1}{P^2} \left[\frac{c - \beta_1 X}{X^2} + \frac{\delta_1 P - \gamma_3 \gamma_2 X}{(1 + X)^2}\right]$$

which is negative in the plane $X > 0, P > 0$ in the region $\Omega_1 = \left\{0 < \frac{c}{\beta_1} < X, \ 0 < P < \frac{\gamma_3}{\delta_1}\right\}$.

Therefore,

by Bendixson-Dulac criteria: $E_4(X, P)$ is globally asymptotically stable in $\Omega_1$.

For $E_5$, define a continuously differentiable function in the $Y > 0$, $P > 0$ planes as $H_2(Y, P) = \frac{1}{YP^2}$.

From the system of Equations (47), it can be obtained:

$$J_1(Y, P) = Y \left(1 - \beta_2 Y - M_2 - \delta_2 \frac{P}{(1 + Y)}\right) \text{ and } J_2(Y, P) = P \left(-c + \delta_3 \frac{Y}{(1 + Y)}\right)$$

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This gives:

\[ H_2J_1 \left( \frac{1}{\rho^2} \left( 1 - \beta_2 Y - M_2 - \delta_2 \frac{p}{(1+Y)} \right) \right) \text{ and } H_2J_2 = \frac{1}{Yp} \left( c + \frac{\delta_3 Y}{(1+Y)^2} \right) \]

I compute \( \frac{\partial H_2J_1}{\partial Y} \) and \( \frac{\partial H_2J_2}{\partial p} \) which gives

\[ \frac{\partial H_2J_1}{\partial Y} = \frac{1}{\rho^2} \left( -\beta_2 + \delta_2 \frac{p}{(1+Y)^2} \right) \]

and

\[ \frac{\partial H_2J_2}{\partial p} = -\frac{1}{Yp^2} \left( -c + \frac{\delta_3 Y}{(1+Y)^2} \right). \]

The following is obtained:

\[ \frac{\partial H_2J_1}{\partial Y} + \frac{\partial H_2J_2}{\partial p} = \frac{1}{\rho^2} \left[ \frac{c-\beta_2 Y}{Y} + \frac{\delta_3 p-\delta_3 Y}{(1+Y)^2} \right] \]

which is negative in the plane \( Y > 0, P > 0 \) in the region \( \Omega_2 = \{ 0 < \frac{c}{\beta_2} < Y, \ 0 < P < \frac{\delta_3}{\delta_2} \} \).

Therefore,

by Bendixson-Dulac criteria: \( E_5(Y,P) \) is globally asymptotically stable in \( \Omega_2 \).

(vi) **Global stability of the co-existence equilibrium point \( E_6(X^*, Y^*, P^*) \)**

A stable Lyapunov function was used from which conditions for the global asymptotic stability of the co-existence point \( E_6(X^*, Y^*, P^*) \) are derived. First, a lemma was provided to establish a region of attraction for the system represented by Equations (47). The approach was based on work by Takeuchi (1996), Chaudhuri and Kar (2002) and Dubey and Upadhay (2004).

**Lemma 1**

The set \( \Omega = \left\{ 0 \leq X \leq \frac{1}{\beta_1}, \ 0 \leq Y \leq \frac{1}{\beta_2}, \ 0 \leq \epsilon_1 X + \epsilon_2 Y + P \leq \frac{\rho}{\eta} \right\} \)

Where \( \epsilon_1 = \frac{c\gamma_3}{\delta_1}, \ \epsilon_2 = \frac{c\gamma_2}{\delta_2}, \ \rho = \frac{\epsilon_1}{\beta_1} (1 + \eta) + \frac{\epsilon_2}{\beta_2} (1 + \eta) \) and \( \eta \leq c \) is a region of attraction for all solutions initiated in the interior of the positive region \( (X,Y,P) \).

**Proof**

From the Equation (47) note that \( \frac{dX}{dt} \leq X \left( 1 - \beta_1 X \right) \). This gives \( X(t) \leq \frac{\Gamma}{e^{-\Gamma t} \beta_1} \), where

\[ \Gamma = \frac{X(0)}{1-X(0)/\beta_1} \]. As \( t \to \infty \) gives \( X(t) \leq \frac{1}{\beta_1} \)

Similarly from the second Equation of (47), it can be obtained \( Y(t) \leq \frac{1}{\beta_2} \).
Define a function $W(t) = \varepsilon_1 X(t) + \varepsilon_2 Y(t) + P(t)$ where $\varepsilon_1 = \frac{c_1 \gamma_3}{\delta_1}$, $\varepsilon_2 = \frac{c_2 \delta_3}{\delta_2}$ for a real positive number $\eta$.

$\dot{W}(t) + \eta W(t) = \varepsilon_1 \dot{X}(t) + \varepsilon_2 \dot{Y}(t) + \dot{P}(t) + \eta(\varepsilon_1 X(t) + \varepsilon_2 Y(t) + P(t))$ \hfill (51)

Substituting $\dot{X}(t), \dot{Y}(t), \dot{P}(t)$ using (47) into equation (51) and simplifying gives:

$W(t) + \eta W(t) = \varepsilon_1 X(1 + \eta) + \varepsilon_2 Y(1 + \eta) - \varepsilon_1 \beta_1 X^2 - \varepsilon_2 \beta_2 Y^2 + \varepsilon_1 Y_1 X Y + \varepsilon_2 Y_2 X Y - \varepsilon_1 M_1 X - \varepsilon_2 M_2 Y + (-c + \eta)P$.

Choose $\eta \leq c$ to obtain $\frac{dW}{dt} + \eta W \leq \frac{\varepsilon_1}{\beta_1} (1 + \eta) + \frac{\varepsilon_2}{\beta_2} (1 + \eta) = \rho$.

This gives $W(t) \leq \frac{\rho}{\eta} (1 - e^{-\eta t}) + W(0)e^{-\eta t}$. As $t \to \infty$, $0 \leq W(t) \leq \frac{\rho}{\eta}$. This completes the proof.

**Theorem 4:** Let the following inequalities hold in the region $\Omega$ defined in Lemma 1 then, the co-existence equilibrium point $E_6(X^*, Y^*, P^*)$ is globally asymptotically stable with respect to all solutions initiated in the interior of $\Omega$.

**Proof**

Consider the following Lyapunov function:

$V(X,Y,P) = \left(X - X^* - X^* \ln \left(\frac{X}{X^*}\right) \right) + \left(Y - Y^* - Y^* \ln \left(\frac{Y}{Y^*}\right) \right) + \left(P - P^* - P^* \ln \left(\frac{P}{P^*}\right) \right)$.

Obviously, $V$ is positive definite.

Differentiating $V$ with respect to time $t$ gives:

$\dot{V}(X,Y,P) = \left(\frac{X - X^*}{X}\right) \dot{X}(t) + \left(\frac{Y - Y^*}{Y}\right) \dot{Y}(t) + \left(\frac{P - P^*}{P}\right) \dot{P}(t)$

Substituting the expressions for $\dot{X}(t), \dot{Y}(t), \dot{P}(t)$ from Equation (47) gives:

$\dot{V}(X,Y,P) = \left(X - X^*\right) \left(1 - \beta_1 X - M_1 + \gamma_1 Y - \frac{\delta_1 P}{(1+X)} \right) + \left(Y - Y^*\right) \left(1 - \beta_2 Y - M_2 + \gamma_2 X - \frac{\delta_2 P}{(1+Y)} \right) + \left(P - P^*\right) \left(-c + \frac{\gamma_3 X}{(1+X)} + \frac{\delta_3 Y}{(1+Y)} \right)$. From this one obtains:
\[
\dot{V}(X, Y, P) = (X - X^*)(\beta_1 X^* - \gamma_1 Y^* + \frac{\delta_1 P^*}{(1 + X^*)}) - (\beta_1 X - \gamma_1 Y + \frac{\delta_1 P}{(1 + X)}) \\
+ (Y - Y^*)(\beta_2 Y^* - \gamma_2 X^* + \frac{\delta_2 P^*}{(1 + Y^*)}) - (\beta_2 Y - \gamma_2 X + \frac{\delta_2 P}{(1 + Y)}) \\
+ (P - P^*)(\frac{\gamma_3 X}{(1 + X)} + \frac{\delta_3 Y^*}{(1 + Y^*)} - \frac{\delta_3 Y}{(1 + Y)}) - (\gamma_3 X^* + \delta_3 Y^*)
\]

This simplifies to:

\[
\dot{V}(X, Y, P) = -(X - X^*)^2 (\beta_1 - \frac{\delta_1 P^*}{w}) - (X - X^*)(Y - Y^*)(\gamma_1 + \gamma_2) - (X - X^*)(P - P^*) \left( \frac{\delta_1 (1 + X^*) - \gamma_3}{w} \right) - (Y - Y^*)(P - P^*) \left( \frac{\delta_2 (1 + Y^*) - \gamma_3 (1 + P^*)}{z} \right) - (P - P^*)^2 \left( \frac{\delta_3 Y^*}{z} \right).
\]

Where \( w = (1 + X)(1 + X^*) \), \( z = (1 + Y)(1 + Y^*) \)

Thus, \( \dot{V}(X, Y, P) \) is a quadratic function that can be expressed as:

\[
\dot{V} = -D^T AD, \text{ where } D^T = (X - X^*, Y - Y^*, P - P^*) \text{ and } A \text{ is a symmetric matrix given by}
\]

\[
A = \begin{pmatrix}
a_{11} & a_{12} & a_{13} \\
a_{12} & a_{22} & a_{23} \\
a_{13} & a_{23} & a_{33}
\end{pmatrix}
\]

where

\[
a_{11} = \beta_1 - \frac{\delta_1 P^*}{w}, \quad a_{12} = \frac{\gamma_1 + \gamma_2}{z}, \quad a_{13} = \frac{\delta_1 (1 + X^*) - \gamma_3}{2w}, \quad a_{22} = \beta_2 - \frac{\delta_2 P^*}{z}, \quad a_{23} = \frac{\delta_2 (1 + Y^*) - \gamma_3 (1 + P^*)}{2z}, \quad a_{33} = \frac{\delta_3 Y^*}{z}.
\]

It is noted that \( \dot{V} < 0 \) if the matrix \( A \) is positive definite (Chaudhuri & Kar, 2004).

The matrix \( A \) is positive definite if \( a_{11} > 0, a_{13} > 0, a_{22} > 0, a_{23} > 0, a_{33} > 0, a_{11} a_{22} - a_{12}^2 > 0 \). It is observed that \( a_{11} > 0 \) and \( a_{22} > 0 \) give \( P^* < \frac{\beta_1 w}{\delta_1} \) and \( P^* < \frac{\beta_2 z}{\delta_2} \), \( a_{13} = 0 \) gives \( X^* = \frac{\gamma_3 - \delta_1}{\delta_1} \) provided \( \gamma_3 > \delta_1, a_{23} = 0 \) gives:

\[
Y^* < \frac{\delta_3 (\delta_1 + \beta_1 w) - \delta_1 \delta_2}{\delta_1 \delta_2} \quad \text{and} \quad a_{11} a_{22} - a_{12}^2 > 0 \]

55
\[(\beta_1 - \frac{\delta_1 P^*}{w})(\beta_2 - \frac{\delta_2 P^*}{z}) - \left(\frac{y_1 + y_2}{2}\right)^2 > 0\] provided \(y_1 + y_2 > 2\sqrt{\beta_1 \beta_2}\). This completes the proof.

Therefore, the conditions for the existence of all the seven possible equilibrium points (steady states) were established. It was found that wildebeests can exist on their own or in the presence of zebras and/or lions only if the wildebeests’ intrinsic rate of birth is greater than the rate at which they die. Since wildebeests and zebras are mutualistic, the two species would co-exist without a lion provided that the intrinsic rate of growth of wildebeests and zebras is greater than their death rates. The existence of the lion with either the wildebeest alone or zebra alone required the proportion of biomass of either prey species converted into fertility (reproductivity rate) by the predator to be greater than the product of the predator’s natural mortality rate, and the time it takes to handle the prey. The ecosystem would be globally asymptotically stable. The dynamic behaviour of the three species is shown in Fig. 6.

![Dynamics in time](image)

![Phase space](image)

**Figure 6:** Wildebeest, zebra and lion population dynamics

### 3.6.6 Dispersion Relation

This section investigated the pattern dynamics of wildebeests, zebras, and lions caused by diffusion and advection. To consider the effects of the flow on the dispersion relations, we derived the phase dynamics from Equation 44 and estimated them from the phase wave. Thus, the set of conditions that lead the system of Equations (44) to instability due to diffusion and advection was established as follows:
Let the diffusion in each spatial dimension be the equal, i.e., \( D_{11} = D_{12} = D_w, \quad D_{21} = D_{22} = D_z, \quad D_{31} = D_{32} = D_p \).

Also, let migration in each spatial dimension be equal, i.e., \( C_{11} = C_{12} = C_w, \quad C_{21} = C_{22} = C_z \) and \( C_{31} = C_{32} = C_p \)

where:

- \( D_w \) and \( C_w \) diffusion and advection parameters for prey \( w \) in two dimensions
- \( D_z \) and \( C_z \) diffusion and advection parameters for prey \( z \) in two dimensions
- \( D_p \) and \( C_p \) diffusion and advection parameters for predator \( p \) in two dimensions

Equation (44) can be redefined to obtain the following Equation:

\[
\begin{align*}
\frac{\partial w}{\partial t} &= D_w \nabla^2 w - C_w \nabla w + r_1 w \left(1 - \frac{w}{K_1}\right) + b_1 wz - \frac{h_{1wp}}{1+a_{1w}} - \lambda_1 w \\
\frac{\partial z}{\partial t} &= D_z \nabla^2 z - C_z \nabla z + r_2 z \left(1 - \frac{z}{K_2}\right) + b_2 wz - \frac{h_{2zp}}{1+a_{2z}} - \lambda_2 z \\
\frac{\partial p}{\partial t} &= D_p \nabla^2 p - C_p \nabla p + P \left(-c + d_1 \frac{h_{1wp}}{1+a_{1w}} + d_2 \frac{h_{2zp}}{1+a_{2z}}\right)
\end{align*}
\]

(52)

For the linear stability analysis, re-writing Equation (53) gives:

\[
\begin{align*}
\frac{\partial w}{\partial t} &= f(w, z, p) - D_w \nabla^2 w \\
\frac{\partial z}{\partial t} &= g(w, z, p) - D_z \nabla^2 z \\
\frac{\partial p}{\partial t} &= h(w, z, p) - D_p \nabla^2 p
\end{align*}
\]

(54)

Suppose that the homogeneous spatial system of Equations (54) has a limiting cycle with frequency \( \omega_0 \).

That is:

\[
\begin{align*}
w &= w_0(\tau) \\
z &= z_0(\tau) \\
p &= p_0(\tau)
\end{align*}
\]

(55)
With \( \tau = \omega_0 t \). This leads to:

\[
\begin{align*}
\omega_0 \frac{\partial w_0}{\partial \tau} &= f(w_0, z_0, p_0), \quad w_0(\tau + 2\pi) = w_0(\tau) \\
\omega_0 \frac{\partial z_0}{\partial \tau} &= g(w_0, z_0, p_0), \quad z_0(\tau + 2\pi) = z_0(\tau) \\
\omega_0 \frac{\partial p_0}{\partial \tau} &= h(w_0, z_0, p_0), \quad p_0(\tau + 2\pi) = p(\tau)
\end{align*}
\] (56)

System of Equations (54) is invariant under time translation, and it has a solution:

\[
\begin{align*}
w &= w_0(\tau + \psi) \\
z &= z_0(\tau + \psi) \\
p &= p_0(\tau + \psi)
\end{align*}
\]

where \( \psi \) is an arbitrary constant.

For a slow spatial modulation, some multiple scales (spatial coordinates \( X \) and temporal coordinates \( T \)) are introduced as follows:

\[
X = \sqrt{\epsilon} x, \quad \tau = \omega_0 t, \quad T = \epsilon t,
\] (57)

and asymptotic expansion:

\[
\begin{align*}
w &= w_0(\tau + \psi) + \epsilon w_1(\tau + \psi) + \cdots \\
z &= z_0(\tau + \psi) + \epsilon z_1(\tau + \psi) + \cdots \\
p &= p_0(\tau + \psi) + \epsilon p_1(\tau + \psi) + \cdots
\end{align*}
\] (58)

Where \( \epsilon \) is a small parameter and \( \psi = \psi(X, T) \). Substituting Equations (57) and (58) into Equations (54) yields a hierarchy of linear equations for each order in \( \epsilon \):

\[
\begin{align*}
\omega_0 \frac{\partial w_0}{\partial \tau} &= f(w_0, z_0, p_0) \\
\omega_0 \frac{\partial z_0}{\partial \tau} &= g(w_0, z_0, p_0) \\
\omega_0 \frac{\partial p_0}{\partial \tau} &= h(w_0, z_0, p_0)
\end{align*}
\] (59)

and

\[
L \begin{pmatrix} w_j \\ z_j \\ p_j \end{pmatrix} = \begin{pmatrix} A_j \\ B_j \\ H_j \end{pmatrix}
\] (60)
Where,

\[
L = \begin{pmatrix}
\omega_0 \frac{\partial}{\partial \tau} - \frac{\partial f}{\partial w} (w_0, z_0, p_0) & -\frac{\partial f}{\partial z} (w_0, z_0, p_0) & -\frac{\partial f}{\partial p} (w_0, z_0, p_0) \\
-\frac{\partial g}{\partial w} (w_0, z_0, p_0) & \omega_0 \frac{\partial}{\partial \tau} - \frac{\partial g}{\partial z} (w_0, z_0, p_0) & -\frac{\partial g}{\partial p} (w_0, z_0, p_0) \\
-\frac{\partial h}{\partial w} (w_0, z_0, p_0) & -\frac{\partial h}{\partial z} (w_0, z_0, p_0) & \omega_0 \frac{\partial}{\partial \tau} - \frac{\partial h}{\partial p} (w_0, z_0, p_0)
\end{pmatrix}
\]

(61)

\[A_j, B_j \text{ and } H_j \text{ are denoted as the inhomogeneous term of the } jth \text{ order equation for } j = 1, 2, \ldots.\]

For the first-order equation of the inhomogeneous term is:

\[
\begin{align*}
A_1 &= -w_0 \frac{\partial \psi}{\partial \tau} - C_w w_0' \psi + D_w (w_0'' |\psi| ^2 + w_0' \psi^2) \\
B_1 &= -z_0 \frac{\partial \psi}{\partial \tau} - C_z z_0' \psi + D_z (z_0'' |\psi| ^2 + z_0' \psi^2) \\
H_1 &= -p_0 \frac{\partial \psi}{\partial \tau} - C_p p_0' \psi + D_p (p_0'' |\psi| ^2 + p_0' \psi^2)
\end{align*}
\]

(62)

Denote that \(s_0 = (w_0, z_0, p_0)^T, s_1 = (w_1, z_1, p_1)^T\) and \(\bar{s} = (\bar{w}, \bar{z}, \bar{p})^T\) is the nontrivial periodic solution to the adjoint differential equation \(\bar{L}s = 0\) where:

\[
\bar{L} = \begin{pmatrix}
\omega_0 \frac{\partial}{\partial \tau} - \frac{\partial f}{\partial w} (w_0, z_0, p_0) & -\frac{\partial f}{\partial z} (w_0, z_0, p_0) & -\frac{\partial f}{\partial p} (w_0, z_0, p_0) \\
-\frac{\partial g}{\partial w} (w_0, z_0, p_0) & \omega_0 \frac{\partial}{\partial \tau} - \frac{\partial g}{\partial z} (w_0, z_0, p_0) & -\frac{\partial g}{\partial p} (w_0, z_0, p_0) \\
-\frac{\partial h}{\partial w} (w_0, z_0, p_0) & -\frac{\partial h}{\partial z} (w_0, z_0, p_0) & \omega_0 \frac{\partial}{\partial \tau} - \frac{\partial h}{\partial p} (w_0, z_0, p_0)
\end{pmatrix}
\]

(63)

By using solvability conditions for \(s_1\) yields:

\[
(\bar{s}, s_1') \frac{\partial \psi}{\partial \tau} = (\bar{s}, \xi_1) \nabla \psi + (\bar{s}, \xi_2) \psi^2 + (\bar{s}, \xi_3) |\psi|^2
\]

(64)

This leads to the dynamics of the phase waves:

\[
\frac{\partial \psi}{\partial \tau} = \rho_1 \frac{\partial \psi}{\partial \chi} + \rho_2 \frac{\partial^2 \psi}{\partial \chi^2} + \rho_3 \left[ \frac{\partial \psi}{\partial \tau} \right]^2
\]

(65)

Where, \(\rho_i = \frac{(\bar{s}, \xi_i)}{(\bar{s}, s_0')}\)

With \(\xi_1 = (-C_w w_0', -C_z z_0', -C_p p_0')^T, \xi_2 = (-D_w w_0', -D_z z_0', -D_p p_0')^T, \xi_3 = (D_w w_0'', D_z z_0'', D_p p_0'')^T\)
And

\[ \langle \delta, \xi \rangle = \int_0^{2\pi} \langle \delta, \xi \rangle d\tau. \] (66)

This results in the solvability condition of \( \delta \) leading to:

\[ \int_0^{2\pi} \tilde{w} \left[ -w'_0 \frac{\partial \tilde{\psi}}{\partial t} - \Delta w_0' \nabla \psi + D_w (w''_0 |\nabla \psi|^2 + w'_0 \nabla^2 \psi) \right] d\tau + \int_0^{2\pi} \tilde{z} \left[ -z'_0 \frac{\partial \tilde{\psi}}{\partial t} - c_z z'_0 \nabla \psi + D_z (z''_0 |\nabla \psi|^2 + z'_0 \nabla^2 \psi) \right] d\tau + \int_0^{2\pi} \tilde{p} \left[ -p'_0 \frac{\partial \tilde{\psi}}{\partial t} - c_p p'_0 \nabla \psi + D_p (p''_0 |\nabla \psi|^2 + p'_0 \nabla^2 \psi) \right] d\tau = 0 \] (67)

Where \( \tilde{w}, \tilde{z} \) and \( \tilde{p} \) satisfy the Equations:

\[ \begin{pmatrix} \frac{\partial w_0}{\partial t} \\ \frac{\partial z_0}{\partial t} \\ \frac{\partial p_0}{\partial t} \end{pmatrix} = \begin{pmatrix} f(w_0, z_0, p_0) \\ g(w_0, z_0, p_0) \\ h(w_0, z_0, p_0) \end{pmatrix} \] (68)

And

\[ -\omega_0 \begin{pmatrix} \frac{\partial \tilde{w}}{\partial \tau} \\ \frac{\partial \tilde{z}}{\partial \tau} \\ \frac{\partial \tilde{p}}{\partial \tau} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial w_0}(w_0, z_0, p_0) & \frac{\partial g}{\partial w_0}(w_0, z_0, p_0) & \frac{\partial h}{\partial w_0}(w_0, z_0, p_0) \\ \frac{\partial f}{\partial z_0}(w_0, z_0, p_0) & \frac{\partial g}{\partial z_0}(w_0, z_0, p_0) & \frac{\partial h}{\partial z_0}(w_0, z_0, p_0) \\ \frac{\partial f}{\partial p_0}(w_0, z_0, p_0) & \frac{\partial g}{\partial p_0}(w_0, z_0, p_0) & \frac{\partial h}{\partial p_0}(w_0, z_0, p_0) \end{pmatrix} \begin{pmatrix} \tilde{w} \\ \tilde{z} \\ \tilde{p} \end{pmatrix} \] (69)

Substituting \( \Phi = \omega_0 t + \psi \), Equation (65) takes the following form:

\[ \frac{\partial \phi}{\partial t} = \omega_0 + \rho_1 \nabla \phi + \rho_2 \nabla^2 \phi + \rho_3 |\nabla \phi|^2 \] (70)

Through the wave characteristic \( \omega = \frac{\partial \phi}{\partial t} \) and \( k = \nabla \phi \), the dispersion relation is determined from the phase Equation (70):

\[ \omega = \omega_0 + \rho_1 k + \rho_3 k^2 + \cdots \] (71)

\[ \rho_1 = \frac{\int_0^{2\pi} \tilde{w} (-c_w w'_0 + \tilde{z} (-c_z z'_0) + \tilde{p} (-c_p p'_0) + \tilde{\psi}) d\tau}{\int_0^{2\pi} (\tilde{w} w'_0 + \tilde{z} z'_0 + \tilde{p} p'_0) d\tau}, \quad \rho_3 = \frac{\int_0^{2\pi} (w D_w w''_0 + \tilde{z} D_z z''_0 + \tilde{p} D_p p''_0) d\tau}{\int_0^{2\pi} (w w'_0 + \tilde{z} z'_0 + \tilde{p} p'_0) d\tau} \] (72)
The effects of varying the values of $C_w$, $C_z$ and $C_p$ and $D_w$, $D_z$ and $D_p$ depend on the dispersion relation presented by Equation (72). Increasing the values of $C_w$, $C_z$ and $C_p$, the frequency $\omega$ increases for fixed values of wave number $k$. Therefore, the advection (migration) term greatly affects the dynamic behaviour of the model. The effects of diffusion and migration on the system’s stability can further be analysed using the numerical methods of model 72.

### 3.6.7 Numerical Methods

The Python computer program performed a numerical simulation of the model represented by the advection-diffusion reaction Equation (44). The following are the parameters used for simulation. Other parameters were assumed to vary within the corresponding intervals.

<table>
<thead>
<tr>
<th>Parameter Description</th>
<th>symbol</th>
<th>value</th>
<th>source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Per capita intrinsic growth rate for prey</td>
<td>$r_1$ and $r_2$</td>
<td>1 and 0.8</td>
<td>Mduma (1996)</td>
</tr>
<tr>
<td>Carrying capacities for prey $w$ and $z$</td>
<td>$K_1$ and $K_2$</td>
<td>$18 \times 10^5$ &amp; $3 \times 10^4$</td>
<td>Assumed</td>
</tr>
<tr>
<td>Mutualism between prey $w$ and $z$</td>
<td>$b_1$ and $b_2$</td>
<td>0.015 &amp; 0.02</td>
<td>Fay and Greef (2006)</td>
</tr>
<tr>
<td>Capturing rates of the predator $P$</td>
<td>$h_1$ and $h_2$</td>
<td>0.674 &amp; 0.75</td>
<td>Fryxell (2007)</td>
</tr>
<tr>
<td>Prey biomass handled per unit time</td>
<td>$a_1$ and $a_2$</td>
<td>0.03 &amp; 0.032</td>
<td>Assumed</td>
</tr>
<tr>
<td>Efficiency to convert prey biomass of $w$ and $z$ respectively into fertility</td>
<td>$d_1$ and $d_2$</td>
<td>0.371 &amp; 0.525</td>
<td>Sagamiko (2014)</td>
</tr>
<tr>
<td>The natural mortality rate of predator</td>
<td>$c$</td>
<td>1.2</td>
<td>Schaller (1972)</td>
</tr>
<tr>
<td>Death rates due to drought for prey</td>
<td>$\lambda_1$ and $\lambda_2$</td>
<td>0.1 and 0.08</td>
<td>Mduma (1996)</td>
</tr>
</tbody>
</table>

The mathematical model (44) was discretized subject to the following boundary condition:

\[
w(x, 0, t) = w(L_x, 0, t) = 0, \ w(0, y, t) = w(0, L_y, t) = 0 \ \text{and} \ \ w(x, y, 0) = w^0,
\]

\[
z(x, 0, t) = z(L_x, 0, t) = 0, \ z(0, y, t) = z(0, L_y, t) = 0 \ \text{and} \ \ z(x, y, 0) = z^0,
\]

\[
P(x, 0, t) = P(L_x, 0, t) = 0, \ P(0, y, t) = P(0, L_y, t) = 0 \ \text{and} \ \ P(x, y, 0) = P_0,
\]

The space was set to $0 < x < L_x, 0 < y < L_y$ and time was set to be $0 < t < T$.

For simulation purposes, the parameters were set to be $L_x = 1, L_y = 4$ and $T = 100$.  
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The diffusion parameters were set to be $D_w = D_z = 0.01, D_p = 0.01.$

And,

Migration (advective) parameters were $C_w = C_{11} = C_{12} = 0.005, \ C_x = C_{21} = C_{22} = 0.005, \ C_p = C_{31} = C_{32} = 0.005. \ M_w = M_z = M_p = 1.$

The numerical solution used in the current study was the explicit Euler method in which the discretization of time derivative was performed by using the forward difference rule and central difference approximation of the Laplace equations in two dimensions, as shown below:

$$\frac{w_{i,j}^{n+1} - w_{i,j}^n}{h} = D_{11}\left(\frac{w_{i+1,j}^n - 2w_{i,j}^n + w_{i-1,j}^n}{h^2}\right) + D_{12}\left(\frac{w_{i,j+1}^n - 2w_{i,j}^n + w_{i,j-1}^n}{h^2}\right) - C_{11}\left(\frac{w_{i+1,j}^n - w_{i,j}^n}{h}\right) -$$

$$C_{12}\left(\frac{w_{i,j+1}^n - w_{i,j}^n}{h}\right) + r_1w_{i,j}^n\left(1 - \frac{w_{i,j}^n}{K_1}\right) + b_1w_{i,j}^nZ_{i,j}^n - \frac{hw_{i,j}^np_{i,j}^n}{1 + aw_{i,j}^n} - \lambda_1w_{i,j}^n \quad (3.73a)$$

$$\frac{x_{i,j}^{n+1} - x_{i,j}^n}{h} = D_{21}\left(\frac{x_{i+1,j}^n - 2x_{i,j}^n + x_{i-1,j}^n}{h^2}\right) + D_{22}\left(\frac{x_{i,j+1}^n - 2x_{i,j}^n + x_{i,j-1}^n}{h^2}\right) - C_{21}\left(\frac{x_{i+1,j}^n - x_{i,j}^n}{h}\right) -$$

$$C_{22}\left(\frac{x_{i,j+1}^n - x_{i,j}^n}{h}\right) + r_2x_{i,j}^n\left(1 - \frac{x_{i,j}^n}{K_w}\right) + b_2w_{i,j}^nZ_{i,j}^n - \frac{dhx_{i,j}^np_{i,j}^n}{1 + ax_{i,j}^n} - \lambda_2x_{i,j}^n \quad (3.73b)$$

$$\frac{p_{i,j}^{n+1} - p_{i,j}^n}{h} = D_{31}\left(\frac{p_{i+1,j}^n - 2p_{i,j}^n + p_{i-1,j}^n}{h^2}\right) + D_{32}\left(\frac{p_{i,j+1}^n - 2p_{i,j}^n + p_{i,j-1}^n}{h^2}\right) - C_{31}\left(\frac{p_{i+1,j}^n - p_{i,j}^n}{h}\right) -$$

$$C_{32}\left(\frac{p_{i,j+1}^n - p_{i,j}^n}{h}\right) - cp_{i,j}^n + \frac{dhw_{i,j}^np_{i,j}^n}{1 + aw_{i,j}^n} + \frac{dhp_{i,j}^nx_{i,j}^n}{1 + ax_{i,j}^n} \quad (73c)$$

The systems of Equations (73) simulations were performed in the python computer program (the corresponding codes are attached in appendix three). Finally, the numerical simulations, results, and discussions are presented in Chapter Four.

### 3.7 Chapter Summary

This chapter has given insight into how different mathematical models were formulated and how the data analyses have been carried out. The next chapter presents the results, and discussions of the study.
CHAPTER FOUR
RESULTS AND DISCUSSION

4.1 Results

The results and discussions presented in this chapter have highlighted the dynamics of wildebeest, zebra and lion.

4.1.1 Foraging Processes of Wildebeest

(i) Random Walk

The GPS collared wildebeest data on 2D lattice were fitted to show random walk trajectories for each wildebeest. The positions (x and y) show how different animals walk randomly in the Serengeti ecosystem. First, random walk trajectories for five wildebeests were plotted to visualize the movement trends (Fig. 7) and second, all 18 wildebeest trajectories were plotted (Fig. 8). A consistent movement of wildebeest from Southern Serengeti to the western part that continues to the northern part heading towards Masai Mara in Kenya was observed. In addition, animals are consistently moving in a specified direction (biased random walk) (Fig. 1).

The average position and distance of each walker were calculated. The GPS data used in the current study were recorded after each time step $\tau$ (6 hours), where an individual animal can move a distance $\delta$ either up, down, left, or right with probabilities dependent on the location given by $u(x,y), d(x,y), l(x,y)$ and $r(x,y)$ respectively with $u + d + l + r \leq 1$, or remain at the same location with probability $1 - u(x,y) - d(x,y) - l(x,y) - r(x,y)$. Each animal generated its jump probabilities depending on its movement patterns and foraging needs as recorded by the GPS data.
Figure 6: Individual random walk trajectories of 5 wildebeest on a 2D lattice (Units of the grid are in Universal Transverse Mercator [UTM])

Figure 7: Individual random walk trajectories of 18 wildebeest on a 2D lattice (Units of the grid are in UTM)
The random walk was motivated by diffusion and advection movement parameters in two dimensions (Equation 73). The diffusion parameters were $D_x$ and $D_y$ in $x$ and $y$ directions, respectively, while the advective parameters were $u_x$ and $u_y$ in $x$ and $y$ directions, respectively. The average movement parameters calculated by the mathematical model (Equation 73) for each year are shown in Table 3.

<table>
<thead>
<tr>
<th>Year</th>
<th>$(D_x M^2/\text{Hour})$</th>
<th>$D_y (M^2/\text{Hour})$</th>
<th>$u_x (\text{M/\text{Hour}})$</th>
<th>$u_y (\text{M/\text{Hour}})$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>112429.80</td>
<td>102578.94</td>
<td>12.74</td>
<td>19.47</td>
</tr>
<tr>
<td>2000</td>
<td>113845.89</td>
<td>101548.44</td>
<td>-8.33</td>
<td>-14.96</td>
</tr>
<tr>
<td>2003</td>
<td>116051.93</td>
<td>104569.41</td>
<td>-12.95</td>
<td>5.24</td>
</tr>
<tr>
<td>2004</td>
<td>116139.19</td>
<td>104335.58</td>
<td>22.80</td>
<td>6.76</td>
</tr>
<tr>
<td>2005</td>
<td>115445.82</td>
<td>104335.65</td>
<td>2.38</td>
<td>12.66</td>
</tr>
<tr>
<td>2006</td>
<td>116139.19</td>
<td>104648.03</td>
<td>11.87</td>
<td>23.79</td>
</tr>
<tr>
<td>2007</td>
<td>113988.47</td>
<td>102710.10</td>
<td>14.78</td>
<td>23.84</td>
</tr>
</tbody>
</table>

There is a large variability between directed ($u_x$ and $u_y$) and dispersive ($D_x$ and $D_y$) components of the movement in different years. The dispersive components seem larger than the directed components (Table 3). But it must be understood that the unit for $D_x$ and $D_y$ is $M^2$ while the unit of $u_x$ and $u_y$ is $M$. There is a slight variability in diffusion parameters for different years. This shows that the annual rate at which animals spread in search of forage resources at different seasons of the year is constant. However, the migration parameters (advection) seem to be changing over the years. In the following section, seasonal movement patterns of wildebeests were analysed.

(ii) Wildebeest Movement Patterns in the Dry Season

Usually, the dry season starts in June when most columns Serengeti wildebeests seem to be migrating north to seek fresh grazing and water (Hopcraft, 2010). Wildebeests slowly start (in May) their movements from southern Serengeti following fresh grass in central Serengeti (Hopcraft, 2010). Large wildebeest movements are observed heading to seek forage refuge in the northern woodlands of the Serengeti National park and Masai Mara National Reserve in Kenya when the southern highlands (south Serengeti ecosystem) go dry (Fig. 9 and 10). As the dry season starts to hit in June, large concentrations of wildebeest are observed in the west of Serengeti and on the southern banks of the Grumeti River (Mduma, 1996). Wildebeests
congregate around this area, and form large herds before crossing dangerous rivers. This is the toughest moment of their journey as each wildebeest must face the challenge of crossing the crocodile-infested rivers. In late June and July, large herds of wildebeest and zebra continue to head north, crossing the Mara River north of Serengeti to Masai Mara National Reserve in Kenya. By July, most wildebeest herds are foraging around the northern woodlands of Serengeti National Park and Masai Mara National Reserve in Kenya. This area is characterized by short diffusion movements with little migration from place to place (Fig. 9 and Table 4).

Figure 8: Individual random walk trajectories for 5 wildebeest on a 2D plane in the dry season (the units of the grid are in UTM)

The trajectories show the migration from the central Serengeti towards the western part of the ecosystem. Wildebeest arrive in the northern woodlands of Serengeti national park and Masai Mara in Kenya. Figure 8 and 9 show the northern part of the Serengeti ecosystem, where most of the movements occur in the dry season.
Figure 9: Individual random walk trajectories for 18 wildebeest on a 2D lattice in the dry season (the units of the grid are in UTM)

The average advection and diffusion movement parameters for the dry season are summarized in Table 4.

Table 4: Dry season hourly average diffusion and advection movement parameters calculated from the advection-diffusion equation for each year

<table>
<thead>
<tr>
<th>Year</th>
<th>$D_x (M^2/\text{Hour})$</th>
<th>$D_y (M^2/\text{Hour})$</th>
<th>$u_x (\text{M/\text{Hour}})$</th>
<th>$u_y (\text{M/\text{Hour}})$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>88243.43</td>
<td>84281.22</td>
<td>11.32</td>
<td>24.89</td>
</tr>
<tr>
<td>2000</td>
<td>89815.63</td>
<td>82734.75</td>
<td>-5.12</td>
<td>-1.10</td>
</tr>
<tr>
<td>2003</td>
<td>91633.66</td>
<td>85883.85</td>
<td>-15.50</td>
<td>12.82</td>
</tr>
<tr>
<td>2005</td>
<td>91070.901</td>
<td>85671.36</td>
<td>0.50</td>
<td>20.18</td>
</tr>
<tr>
<td>2006</td>
<td>91743.01</td>
<td>85986.33</td>
<td>11.43</td>
<td>26.86</td>
</tr>
<tr>
<td>2007</td>
<td>90965.52</td>
<td>85257.63</td>
<td>-8.04</td>
<td>10.00</td>
</tr>
</tbody>
</table>
(iii) Wildebeest Movement Patterns in the Wet Season

The wet season starts from November to May, and short rains start in early November (Tourney *et al.*, 2018) when wildebeests start their journey back to the Serengeti ecosystem. By December, most of the wildebeest herds arrive on the short-grass plains of the southern Serengeti from the north. Large wildebeest movements (both advection and diffusion) are observed during this season (Fig. 11 and Table 5).

During the wet season, wildebeests spread south and east of Seronera, Ndutu and around the Ngorongoro conservation area. They disperse across these plains, feeding fresh and nutritious grass (Mduma, 1996) to most wildebeests calve in late January or early February (Hopcraft, 2010). They stay there around January, February, and March and gradually spread west across these plains. There are high average distances travelled by wildebeests in the wet season compared to the dry season (Table 5). The rate of spread (diffusion) is the highest compared to other seasons of the year.

Around April, wildebeests start to drift north-west towards the fresh grass of the central Serengeti, drawing thousands of zebra, Thomson’s Gazelles and other ungulates (Holdo, 2011). Therefore, the annual wildebeest migration responds to local cues when they search, especially for rainfall, nutritious grass and water.

![Figure 10: Individual random walk trajectories for 5 wildebeest on a 2D lattice in the wet season (the grid units are in UTM)](image-url)
Wildebeest arrive in the Serengeti national park from the Masai Mara in Kenya. Figures 11 and 12 show the southern part of the Serengeti plains. Most of the movements take place in this area during the wet season with little migration towards the central Serengeti.

Figure 11: Individual random walk trajectories for 18 wildebeest on a 2D lattice in the wet season (the grid units are in UTM)

The average advection and diffusion movement parameters for the dry season are summarized in Table 5.
Table 5: Wet season hourly average diffusion and advection movement parameters calculated from the advection-diffusion equation for each year

<table>
<thead>
<tr>
<th>Year</th>
<th>$D_x (M^2/\text{Hour})$</th>
<th>$D_y (M^2/\text{Hour})$</th>
<th>$u_x (\text{M/\text{Hour}})$</th>
<th>$u_y (\text{M/\text{Hour}})$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>169107.17</td>
<td>18125.18</td>
<td>16.01</td>
<td>10.41</td>
</tr>
<tr>
<td>2000</td>
<td>170390.74</td>
<td>159220.77</td>
<td>-16.48</td>
<td>-57.39</td>
</tr>
<tr>
<td>2003</td>
<td>173406.51</td>
<td>161325.01</td>
<td>-4.74</td>
<td>13.70</td>
</tr>
<tr>
<td>2004</td>
<td>173406.51</td>
<td>160844.88</td>
<td>30.08</td>
<td>9.07</td>
</tr>
<tr>
<td>2005</td>
<td>173406.51</td>
<td>161325.01</td>
<td>10.35</td>
<td>-49.94</td>
</tr>
<tr>
<td>2006</td>
<td>173406.51</td>
<td>161325.01</td>
<td>-15.04</td>
<td>-87.03</td>
</tr>
<tr>
<td>2007</td>
<td>168043.42</td>
<td>156335.58</td>
<td>56.43</td>
<td>54.43</td>
</tr>
</tbody>
</table>

4.1.2 Mutualism between Wildebeests and Zebras

Wildebeests and zebras populations were allowed to grow from their current estimates (1.3 million wildebeests and 200 000 zebras) to the set (assumed) carrying capacities of 1.8 million wildebeests and 300 000 zebras. The aim was to understand mathematically how wildebeests and zebras interact and what factors regulate their movement patterns. From the dynamic behaviour of the two species, there is coexistence, and both species approach their respective carrying capacities (Fig. 13) logistically. The population dynamics of the two species are summarised in Fig. 13 and Table 6.

Figure 12: Wildebeest and zebra population growth with time

The dynamics in time show the population growth of wildebeest to their carrying capacities. The parameters used are taken from Table 1. Table 6 summarizes wildebeest and zebra population growth with time.

70
Table 6: Population dynamics of wildebeest and zebra in absence of predation and drought

<table>
<thead>
<tr>
<th>Time</th>
<th>Zebra Number</th>
<th>Wildebeest Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>200 000</td>
<td>1 300 000</td>
</tr>
<tr>
<td>10</td>
<td>250 600</td>
<td>1 589 200</td>
</tr>
<tr>
<td>20</td>
<td>287 100</td>
<td>1 717 400</td>
</tr>
<tr>
<td>40</td>
<td>291 100</td>
<td>1 773 600</td>
</tr>
<tr>
<td>60</td>
<td>298 300</td>
<td>1 800 800</td>
</tr>
<tr>
<td>80</td>
<td>300 000</td>
<td>1 804 600</td>
</tr>
<tr>
<td>100</td>
<td>301 000</td>
<td>1 804 000</td>
</tr>
</tbody>
</table>

From Table 6, it can be observed that the wildebeest population increased logistically due to the absence of predation and drought. However, when predation and periodic drought seasons were allowed in the model, the population growth increased from 1.3 million wildebeests and 200 000 zebras to about 1.315 million wildebeests and 210 000 zebras (Fig. 14 and Table 7).

Figure 13: Effect of predation on wildebeest and zebra population growth with time
Table 7 summarizes wildebeest and zebra population growth with time.

<table>
<thead>
<tr>
<th>Time</th>
<th>Zebra Number</th>
<th>Wildebeest Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>200 000</td>
<td>1 300 000</td>
</tr>
<tr>
<td>10</td>
<td>201 100</td>
<td>1 312 100</td>
</tr>
<tr>
<td>20</td>
<td>202 500</td>
<td>1 312 300</td>
</tr>
<tr>
<td>40</td>
<td>204 600</td>
<td>1 323 800</td>
</tr>
<tr>
<td>60</td>
<td>206 000</td>
<td>1 343 100</td>
</tr>
<tr>
<td>80</td>
<td>207 000</td>
<td>1 313 400</td>
</tr>
<tr>
<td>100</td>
<td>210 000</td>
<td>1 315 300</td>
</tr>
</tbody>
</table>

Further, when rainfall is not enough and drought seasons hit the ecosystem, the two species do not get enough grass and water for survival (Fig. 14). This results in a decline in the population of both species. Wildebeest decreased from 1.3 million to about 0.95 million individuals, while zebra decreased from 200 000 to 127 000 individuals (Fig. 15 and Table 8).

**Figure 14:** Effect of intensive drought on wildebeest and zebra populations

The dynamics in time show the population decline of wildebeest and zebra from their current estimates. Table 8 summarizes wildebeest and zebra population growth with time.
Table 8: Population dynamics of wildebeest and zebra in the presence of extreme drought

<table>
<thead>
<tr>
<th>Time</th>
<th>Zebra Number</th>
<th>Wildebeest Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>200 000</td>
<td>1 300 000</td>
</tr>
<tr>
<td>10</td>
<td>172 100</td>
<td>1 117 300</td>
</tr>
<tr>
<td>20</td>
<td>157 200</td>
<td>1 046 500</td>
</tr>
<tr>
<td>40</td>
<td>137 100</td>
<td>979 900</td>
</tr>
<tr>
<td>60</td>
<td>127 500</td>
<td>956 600</td>
</tr>
<tr>
<td>80</td>
<td>126 800</td>
<td>937 400</td>
</tr>
<tr>
<td>100</td>
<td>129 500</td>
<td>940 600</td>
</tr>
</tbody>
</table>

From Fig. 13 to Fig. 15, the PDEs for the mutual reaction between wildebeest and zebra mimic the real situation within the Serengeti ecosystem. The PDEs for the mutual reaction between wildebeests and zebras can be observed to mimic the real situation within the Serengeti ecosystem. The death rate due to predation (from lions) and drought rates are the main parameters determining the abundance of wildebeests and zebras during the great migration.

Further, the results of the advection-diffusion reaction system (Equation 21) were numerically discretized to get Equation 73. Simulations for the interaction of mutualistic behaviour of wildebeests and zebras were performed to mimic the real movement of the two species. All parameters in the model were defined (Table 1) to allow individuals to navigate freely. Each individual was allowed to perform a random walk in any preferred direction. After every time step, the distribution of animals on the xy-plane was recorded. These distributions were plotted on a 3D histogram based on the empirical data and the advection-diffusion reaction equation as a surface. Also, the walkers’ distributions on 2D histograms along x and y axes were plotted. The results are presented in Fig. 16 to Fig. 19.

![Average animals distribution on the y-plane](image1)

![Average animals distribution on the x-plane](image2)

**Figure 15:** Wildebeest population distribution and average position of walkers on the xy-plane. The orange bars are the actual (empirical data and the red line is the prediction based on the advection-diffusion equation)
Figure 16: Wildebeest population evolution on the $xy$-plane

Figure 17: Zebra population distribution and average position of walkers on the $xy$-plane

The green bars are the actual (empirical data), and the red line is the prediction (based on advection-diffusion equation).
Figure 18: **Zebra population evolution on the xy – plane**

Figures 16 to 19 illustrate the patterns that diffusion-advection-driven variabilities can form. These are expected movement patterns formed when wildebeests and zebras move via diffusion and advection processes. The empirical data generated random walks, and the advection-diffusion equation produced Gaussian movement patterns.

### 4.1.3 Wildebeest, Zebra and Lion Prey-Predator Interactions

The prey-predator interaction between wildebeests, zebras and lions was simulated to mimic the real interaction of the three species in the Serengeti ecosystem. The aim was to understand mathematically how the three species interact and the factors that regulate their movement patterns. The current estimates of wildebeests, zebras, and lions abundances of 1.3 million, 200 000 and 3000 were used. In addition, the carrying capacities for wildebeests and zebras of 1.8 million and 300 000 were set for a balanced growing population.

The movement parameters of advection and diffusion were defined to allow animals to navigate freely in the ecosystem (Table 2). Each individual started with their initial position and was allowed to perform a random walk in any preferred direction. Every animal in the population can die by predation or drought at each step, interact with other herbivore partners, or step in any randomly chosen direction. After running the model, the population evolution of walkers (the optimal time step was 100) was recorded. Finally, the model calculates the average position and the advection-diffusion-reaction of the resulting population on the xy – plane.
The distributions of animals on the $xy$–plane were recorded. These distributions (from the empirical data) on a 3D histogram were plotted using the advection-diffusion reaction equation as a surface. Furthermore, the walker’s distributions on 2D histograms along $x$ and $y$ axes with the other coordinates equal to its average position value were plotted.

The effects of diffusion and advection movement parameters on the population dynamics of wildebeests and zebras in response to lion attacks were investigated. The advection and diffusion parameters in different scenarios were varied to mimic the real movement patterns of both prey and predator systems.

![Figure 19: Wildebeest population distribution and average position of walkers on the $xy$–plane](image)

The orange bars are the actual (empirical) data, and the red line is the prediction based on the advection-diffusion equation.

![Figure 20: Wildebeest population evolution on the $xy$–plane](image)
Figure 21: Zebra population distribution and average position of walkers on the $xy$-plane

The green bars are the actual (empirical) data, and the red line is the prediction based on the advection-diffusion equation.

Figure 22: Zebra population evolution on the $xy$ – plane
Figure 23: Lion population distribution and average position of walkers on the $xy$-plane. The violet bars are the actual (empirical) data and the red line is the prediction based on the advection-diffusion equation.

Distribution of Animals on the $XY$ plane at $T = 10$

Figure 24: Lion population evolution on the $xy$-plane

The results show that wildebeest and zebra populations grow logistically to their carrying capacities (Fig. 26), and their movement via diffusion and advection follows a Gaussian distribution.

Drought has been reported in many kinds of literature in the Serengeti ecosystem to affect the survival of the migrating species (Sagamiko et al., 2015). Therefore, the effect of drought on the survival of the interacting species was investigated. Wildebeest and zebra death rates are
normal for moderate drought and predation rates. They allow the species to grow to their carrying capacities (Fig. 26), but the population declines when the ecosystem experiences persistent drought (Fig. 27). This, in turn, affects the species' movement patterns (both advection and diffusion). During the drought seasons, there is increased diffusion (due to random utilization of the available resources) and decreased advection (reduced migration).

**Figure 25:** Populations growth of interacting species with time

**Table 9:** Wildebeest, zebra and lion population in absence of extreme drought

<table>
<thead>
<tr>
<th>Time</th>
<th>Zebra Number $\times 10^\text{-2}$</th>
<th>Wildebeest Number $\times 10^\text{-2}$</th>
<th>Lion Number $\times 10^\text{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.20000</td>
<td>1.30000</td>
<td>300.000</td>
</tr>
<tr>
<td>10</td>
<td>0.21750</td>
<td>1.30500</td>
<td>3034.000</td>
</tr>
<tr>
<td>20</td>
<td>0.26540</td>
<td>1.652400</td>
<td>3080.000</td>
</tr>
<tr>
<td>40</td>
<td>0.285007</td>
<td>1.714700</td>
<td>3013.000</td>
</tr>
<tr>
<td>60</td>
<td>0.293900</td>
<td>1.709100</td>
<td>3045.000</td>
</tr>
<tr>
<td>80</td>
<td>0.297200</td>
<td>1.682300</td>
<td>3105.000</td>
</tr>
<tr>
<td>100</td>
<td>0.300000</td>
<td>1.802300</td>
<td>3150.000</td>
</tr>
</tbody>
</table>

As the ecosystem experience extreme drought season, there is a decrease in population as shown in Fig. 27 and table 10.
Figure 26: Populations growth of interacting species in the presence of drought with time

Table 10: Wildebeest, zebra and lion population in presence of extreme drought

<table>
<thead>
<tr>
<th>Time</th>
<th>Zebra Number</th>
<th>Wildebeest Number</th>
<th>Lion Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>200 000</td>
<td>1 300 000</td>
<td>3000</td>
</tr>
<tr>
<td>10</td>
<td>196 000</td>
<td>1 264 700</td>
<td>2915</td>
</tr>
<tr>
<td>20</td>
<td>171 024</td>
<td>1 079 472</td>
<td>2980</td>
</tr>
<tr>
<td>40</td>
<td>111 507</td>
<td>704 523</td>
<td>2954</td>
</tr>
<tr>
<td>60</td>
<td>104 300</td>
<td>661 900</td>
<td>2876</td>
</tr>
<tr>
<td>80</td>
<td>71 300</td>
<td>685 200</td>
<td>2786</td>
</tr>
<tr>
<td>100</td>
<td>69 900</td>
<td>699 200</td>
<td>2621</td>
</tr>
</tbody>
</table>

4.2 Discussion

4.2.1 Foraging Processes of Wildebeest

A consistent movement of wildebeests towards specific directions was observed (Fig. 9 to 11). Paths containing a consistent movement in a preferred direction are termed as biased random walks (BRWs) (Fagan et al., 2019). Therefore, the central question addressed the biased random walk in relation to foraging efficiency. The key idea of movement ecology is that animals move in response to internal needs such as hunger and thirst and external needs such as avoiding predators and responding to local landscape variables such as looking for favourable forage targets (Fryxell et al., 2008). Forage resources in the Serengeti ecosystem are heterogeneously distributed in space. Wildebeests (in their herds) take advantage of this spatial distribution of resources by selecting patches of high resource abundance or travelling to locate them to inhabit. In the wet season, when resources are plentiful, wildebeests travel longer distances through both advection and diffusion (Table 5) compared to dry seasons (Table 4) (Tourney et al., 2018;
During the dry season, forage resources are low; hence they spend more time in areas of low resource abundance to maximize their intake (Ferguson et al., 2018). Therefore, the movement trajectories depicted in Fig. 8 to 11 result from wildebeests responding to their forage needs. As explained in different literature, this wildebeest movement pattern was expected.

Wildebeest in the Serengeti ecosystem are migratory species exhibiting consistent large-scale movements that lead to a net displacement in a unique direction, as evident in Fig. 8 to 11. This is a characteristic of animal migration (Sibert et al., 1999). Wildebeests travel through directed movement parameters and spread across different habitats through diffusive parameters. Therefore, the great migration of wildebeests to different habitats results from directed movements (searching for forage resources) and spreads across habitats to utilize the resources through diffusive trends.

The extent to which wildebeests can be random or dispersive depends on habitat selection, socialization and avoidance of predators (Minasandra & Isvaran, 2020; Qi Ma, 2011; Fortin et al., 2009). Furthermore, wildebeests are foraging animals and usually travel in groups making movement decisions that depend on forage availability and social interactions (Fortin et al., 2009). Therefore, the stability and direction of their group largely rely on the knowledge about the quality and location of the food source, avoidance of predators and the ability of the informed individuals to influence group decisions to move in the desired direction (Couzin et al., 2002).

Wildebeest herds respond to local rules of attraction, repulsion and alignment as they forage (Couzin et al., 2000). With repulsion, animals tend to move away from each other to avoid collisions, come close to their neighbours due to attraction, and navigate from place to place due to alignment forces (Couzin et al., 2000).

As observed in this study, during the dry seasons or when resources are scarce, wildebeests move farther away from each other (increased repulsion) to reduce competition while grazing (Ferguson et al., 2018). In such cases, they spread making short movements to maximize their daily grass intake.

Predation pressure is another factor that affects the foraging efficiency of wildebeests. This occurs when an animal chooses between a patch with good forage while reducing predation risks (Hopcraft, 2010). The fear of predation determines the patch an animal may select and how long it may stay in that area (Ferguson et al., 2018).
Further, the habitat's nature also determines how advective and diffusive factors determine wildebeest forage. Usually, wildebeests avoid dangerous habitats such as river banks or water sources where predators may hide (Mduma, 1994). Instead, wildebeests cross such habitats through drift (higher advective) forces, and they avoid spreading to reduce the chances that prevent herd formation. Therefore, the dispersive and advective components of wildebeest movements help them search for and acquire forage and resources and avoid predators.

Other authors have reported similar observations on foraging efficiency for various herbivore species. For instance, Anderson et al. (2016) reported on the spatial distribution of African savannah herbivores. The authors argue that wildebeests were positively associated with normalized difference vegetation index (NDVI) while foraging. This shows that wildebeests make movement decisions depending on the environmental gradients and responses to conspecifics.

The data was analysed for dry (June-October) and wet (November-May) seasons. The locations of species in the respective maps (Fig. 6 to11) can be used to justify the foraging process in different seasons. The movement parameters (diffusion and advection) can also be used to justify the foraging process seasonally. The concentration of animals on the maps for different seasons could justify the foraging concentration. Generally, the findings of this study about the movement patterns and foraging needs of wildebeest, zebra, and lion are similar to the previous findings for non-mathematics studies like Mduma et al. (1996, 1999), Hopcraft et al. (2010, 2014), Holdo (2011), Anderson et al. (2016), Dutta (2019), Minasandra and Isvaran (2020) and Fagan et al. (2019).

It can be concluded that the advection-diffusion equation can explain wildebeest foraging behaviour. The random walk trajectories respond to different habitats, seasons and responses to conspecifics (Hopcraft, 2010). Such changes in behaviour could result from changes in the animals' nutritional requirements at different times of the year as a result of meeting other needs such as calving (Hopcraft, 2010).

4.2.2 Mutualism between Wildebeests and Zebras

The mutualistic behaviour between wildebeests and zebras was modelled, and the major factors limiting their abundance (predation and drought) were determined. It was observed that wildebeest and zebra populations’ growth approached their respective carrying capacities, and the absence of one species does not affect the existence of the other. In the absence of predation
and drought, the ecosystem is likely overpopulated by wildebeests and zebras, with wildebeests being the dominant species. This would increase inter-species competition between the two species for the forage resources.

For a balanced ecosystem, predation is important to have all the species survive. The predation and drought rates varied over different scales. It was observed that lion predation (with moderate periodic drought seasons) would allow the ecosystem to have a balanced population of wildebeests and zebras (Fig. 14 and Table 7). Therefore, diffusion and advection processes depicted by wildebeest and zebra from place to place are a response to predation risks and looking for better forage that results in a balanced population. If the Serengeti ecosystem experiences the current trends of predation and periodic drought seasons (Fig. 14), there would be a slow population growth of wildebeests and zebras.

Furthermore, increased drought causes grass scarcity. The drought parameter was varied, and as drought intensity increases, the population of wildebeests and zebras decreases by a large amount (Fig. 15 and Table 8). Therefore, the ecosystem will likely collapse if the drought persists for a few years. Apart from foraging and avoiding predators, these species can potentially make foraging decisions at various spatial scales, including mate search, territorial marking, and looking for calving areas (Mduma, 1996; Hopcraft, 2010).

4.2.3 Wildebeest, Zebra and Lion Prey-Predator Interactions

Wildebeests and zebras aggregate to form herds and move towards a desirable target (Okubo & Levin, 2001). Being selective herbivores, wildebeests and zebras usually travel in herds to seek better forage, avoid predators and interact socially (Fortin, 2009). The variation in wildebeests and zebras in group sizes may be due to environmental conditions, such as the location of food and water and predators (Bonabeau, 1999). During migration, wildebeests and zebras develop migratory corridors containing information on rainfall and the normalized difference vegetation index (NDVI) of plant productivity, suggesting that seasonal fluctuations can account for the migration (Anderson et al., 2016). Forage availability is the main driver of spatial distribution patterns of wildebeests and zebras (Boone, 2018). These prey species choose areas with good forage quality and nutrient content and are free from predators. Therefore, the diffusion and migration of wildebeests, and zebras followed by predators (lions) from place to place within the Serengeti ecosystem result from a search for better forage. These results suggest that good
forge quality, abundance, and avoidance of predators affect the wildebeests and zebras’ choices of habitats and their navigation between them.

The lion population is still small in the Serengeti ecosystem (around 3000) (Hopcraft, 2010). This predator population seems stable even during dry seasons (Mduma et al., 1994). However, its distribution does not show a convincing growth (Fig. 24 and 25). More factors need to be studied to identify the reasons for the slow growth of the lion population in the Serengeti ecosystem. When resources are scarce during the dry season, wildebeests and zebras spread more (high diffusion) and are easily caught by lions compared to the wet season (Okubo & Levin, 2001). Hence from Fig. 7 and 8, areas with dense wildebeests suggest the availability of better forage compared to areas with few wildebeests. Further, the Serengeti lions usually hide in places with high prey catchability, such as woody vegetation and near water sources (Anderson et al., 2016).
CHAPTER FIVE

CONCLUSION AND RECOMMENDATIONS

5.1 Conclusion

This study used mathematical models to study wildebeest foraging processes and how it interacts with zebra and lion in the Serengeti ecosystem. The model for wildebeest foraging processes was formulated from the concepts of random walks and jump probabilities. The model analysis showed that the movement patterns of wildebeests could be described by the advection-diffusion equation when they respond to environmental variables such as water and grass.

The second mathematical model was formulated to include another herbivore species, the zebra. The model was further improved by adding one predator (lion) to form the third mathematical model. While these herbivore species grow to their carrying capacities, drought and predation from lions were found to be the major factors that affect their abundances. The dynamical behaviour of migrating wildebeests and zebras followed by lions as predators in the Serengeti ecosystem shows a stable state in the absence of extreme drought. However, in the presence of moderate drought seasons, there is a decreased growth rate of these species, while extreme drought periods drive the species to extinction. Since forage is the main driver of wildebeest and zebra migration, both species evolve migratory pathways containing information on the availability of good forage and areas free from predators. Therefore, the search for better forage results in advection and diffusion of wildebeests and zebras followed by predators from place to place within the Serengeti ecosystem.

Theoretical predictions point out that partial differential equations (PDEs) are useful for examining the interaction between habitat geometry and competitive coexistence (Holmes et al., 1994). The PDEs models developed in the current study have successfully captured the theoretical predictions that movement and diffusion of the two species populations are motivated by a search for better forage and avoidance of predators. The survival of the prey species is primarily affected by the climate (availability of nutritious grass) and predation, particularly from lions.

5.2 Recommendations

Based on the finding described in this study, the study recommends that conservationists and ecologists in different ecosystems gain knowledge of animal behaviour. Thus, this study likely
increases awareness of wildlife behaviour by understanding animals’ dynamics, such as animal movement and foraging patterns and the predator-prey relations of these species.

Also, this study serves as reference data for conducting new research or testing the validity of other findings. There are convincing improvements in the management of the protected areas as there is an overall decrease in human activities around the Serengeti ecosystem. However, despite these improvements, the policy-makers (Ministry of Tourism and Natural Resources) are advised to communicate ways of introducing programs that will allow local communities to manage wildlife resources around their villages. This could reduce poaching and other human activity pressure on the protected areas. In addition, wildlife protection awareness campaigns should complement this.

There is a need to conduct special ground surveys to assess the stock of wildebeest and zebra species rather than rely only on an aerial survey.
REFERENCES


with application to skipjack tuna (*Katsuwonus pelamis*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 925–938.


APPENDICES

Appendix 1: Analysis for full wet season

```python
1 # Analysis for full wet season
2 import random
3 import numpy as np
4 import pandas as pd
5 from math import floor, ceil, isnan
6 from matplotlib.pyplot as plt
7 from mpl_toolkits.mplot3d.axes3d import Axes3D
8
9 class Population:
10     def __init__(self, filename):
11         """Initialize Population instance with default values.
12         Calls read_data() function that read data from the file."""
13         self.N_walkers = 0
14         self.__time = []
15         self.__time_str = []
16         self.__evolution_history = []
17         self.delta_xy = None
18         self.delta_t = None
19         self.read_data(filename)
20         self.__population = None
21         self.__points = None
22         self.__walkers_position = []
23         self.__walkers_distribution = []
24         self.p = 0 # left
25         self.q = 0 # right
26         self.w = 0 # up
27         self.z = 0 # down
28         self.w0 = None
29         self.ye = None
30         self.current_t = 0
31
32     def read_data(self, filename):
33         """Open file 'filename' and read data from this file.
34         Calculate average delta x, delta y and delta t. Put data related to each animal into separate arrays.
35         Find the unique animals id and years."""
36         with open(filename, 'r') as file:
37             data = pd.read_csv(filename)
38             self.id = data.iloc[:, 0].values
39             self.ww = data.iloc[:, 1].values
40             self.x = data.iloc[:, 2].values
41             self.y = data.iloc[:, 3].values
42             self.t = data.iloc[:, 4].values
43
44             # calculate delta t
45             delta_t = [float(self.t[i]) for i in range(len(self.t))]
46             total_delta_t = 0
47             for i in range(len(delta_t)):
48                 if not isnan(delta_t[i]):
49                     total_delta_t += delta_t[i]
50             self.delta_t = total_delta_t / len(delta_t)
51
52             # separate data for different animals
53             last_id = -999
54             for i in range(len(self.id)):
55                 if self.id[i] != last_id:
56                     last_id = self.id[i]
57                     self.__id.append([])
58                     self.__time_str.append([])
59                     self.__evolution_history.append([])
60                     self.__time.append(self.t[i])
61                     self.__walkers_position.append(self.x[i] + self.y[i])
62                     self.__walkers_distribution.append(self.y[i])
63                     self.__walkers_distribution = np.unique(self.__walkers_distribution)
64                     self.years = [int(time[i].split('.')[1]) for i in range(len(time))]
65                     self.years = self.years + 1
```

95
def __point_index(self, i):
    """Utility. Return x, y index of point where walker with the i index is placed """
    return int(round(self._walkers_position[i, 0] - self._dispaasnon[0][0] * self._delta_xy[0])),
    int(round((self._walkers_position[i, 1] -
               self._dispaasnon[1][0]) / self._delta_xy[1]));

def xy_index(self, x = 0, y = 0, axis = None):
    """Utility. Return x, y index of the point with any given coordinates x, y.
    If these coordinates are not in dispaasnon occupied by walker, return None """
    if x == 0:
        if x == 0 or (axis == 0) or (axis == 1):
            return None
    x = self._dispaasnon[0][0] -
    y = self._dispaasnon[1][0] * self._delta_xy[0] or x > self._dispaasnon[1][0] +
    y = self._dispaasnon[0][0] -
    return int(round((x - self._dispaasnon[0][0]) / self._delta_xy[0]),
    int(round(y - self._dispaasnon[0][0] / self._delta_xy[1]));

def evaluate_distribution(self, year):
    """Utility. Calculate number of walkers in each delta_x x delta_y interval
    and, x, y - dispaasnon that animals occupy. Consider only the part of data for the given to the function year.
    If there are less than 10 data points return False, otherwise return true - simulation will be made for this year's
    calculate p, q, w, z probabilities. """

    self._walkers_position = []
    self._norm_animal = []
    # calculate walkers position for given year
    # calculate probabilities p, q, w, z
    total_p = 0
    total_q = 0
    total_w = 0
    total_z = 0
    total_steps = 0

    for animal in range(self._n_walkers):
        years = list(map(str.split('/')), [animal) for date in self._time_str[animal]]

        for j in range(len(years)):
            if years[j][1] == year:
                y_first = j
                for j in range(y_first, len(years)):
                    if years[j][1] == year:
                        y_last = j
                        break
                    else:
                        y_last = len(years)
                self._walkers_position = self._evolution_history[animal][y_first : y_last]
                self._norm_animal = append(len(self._evolution_history[animal][y_first : y_last]))
                for i in range(y_first - 1, y_last):
                    if self._evolution_history[animal][i][0] -
                    self._evolution_history[animal][i - 1][0] > 0:
                        self._evolution_history[animal][i][0] -
                        self._evolution_history[animal][i - 1][0] =
                        total_z = 1
                        total_p = 1
                        total_w = 1
                        total_i = 1
                        total_steps = y_last - y_first - 1
                        break
                total_p = total_p / total_steps
                total_q = total_q / total_steps
                total_w = total_w / total_steps
                total_z = total_z / total_steps
                self.p = total_p
                self.q = total_q
                self.w = total_w
                self.z = total_z
                self.current_t = 365 * 24

self.p = total_p / total_steps
self.q = total_q / total_steps
self.w = total_w / total_steps
self.z = total_z / total_steps
if len(self.__walkers_position) < 10:
    return False

self.__walkers_position = np.array(self.__walkers_position)

self.dx = [(int(floor(self.__walkers_position[1, q])) / self.delta_x[q])
           for q in range(1, self.__walkers_position.shape[1])]

self.dy = [(int(floor(self.__walkers_position[2, q])) / self.delta_y[q])
           for q in range(1, self.__walkers_position.shape[1])]

self.d = np.sqrt(np.sum(self.dx**2 + self.dy**2, axis=1))

self.d = self.d / self.n_points

self.x = self.dx / self.d
self.y = self.dy / self.d

self.__norm_animal = self.n_points

self.__norm_animal[self.n_points] = np.zeros(self.n_points)

self.__norm_animal[self.n_points] = 1

for animal in range(len(self.__norm_animal[animal])):
    for i in range(1, self.__norm_animal[animal]):
        i += 1

return True

def __axes(self, axis=2):
    """Utility. Return array of x or y values in diapason that is occupied by animals
    with the step of delta_X or delta_Y: if axis = 0 it returns X-axis,
    axis = 1 -- returns y-axis, otherwise return (x, y) coordinates of all points within the diapason""

    if axis == 0 or axis == 1:
        return np.zeros(len(self.n_points[0]) / 2)**2
    else:
        return np.zeros(len(self.n_points[0]) / 2)**2

    return x_all[1, self.n_points] + 1 * self.delta_x[0][0] for i in range(1, self.n_points)

    return x_all[1, self.n_points] + 1 * self.delta_x[0][0] for i in range(1, self.n_points)

    def __average_bin(self):
        """Utility. Return (x, y) indices of (delta_X, delta_Y) 2D interval
        that contains average position of animals.""

        average = self.average_position()

        return x_all[0, average]

        average = self.average_position()

        return x_all[0, average]

    def get_distribution_2D(self):
        """Returns distribution of animals on xy plane as a function of x, y.
        This function distribution_2D() works for any x, y (within and out the diapason occupied by animals)"

        def distribution_2D(x, y):
            indices = self.__xy_index(x, y)

            if indices == None:
                return 0

            return self.__walkers_distribution[indices]

        return distribution_2D

    def distribution_2D(self, x, axis):
        """Returns distribution of animals along x (axis = 0) or y (axis = 1) axis.
        sum up number of animals with along one direction.""

        indices = self.__xy_index(x, axis)

        if indices == None:
            return 0

        return sum(self.__walkers_distribution[indices, 1])

    def average_position(self):
        """Returns average position of the animals along x and y axis""
```python
def calculate_adv_diff_parameters(self):
    """ Calculates advection-diffusion equation parameters """
    self.D_x = (self.p + self.q) * self.delta_x**2 / (2 * self.delta_t)
    self.D_y = (self.p + self.r) * self.delta_y**2 / (2 * self.delta_t)
    self.D_z = self.k * self.p / self.delta_t
    self.X = self.p / self.r
    self.Y = self.q / self.r

    print(' : D_x = {:.2f} \ & D_y = {:.2f} \ & D_z = {:.2f} \ & X = {:.2f} \ & Y = {:.2f}'.format(self.D_x, self.D_y, self.D_z, self.X, self.Y, self.X))

def advection_diffusion(self, x, axis = 0):
    """ Return advection-diffusion equation solution along axis (0 or 1). """
    if axis == 0:
        return np.exp(-(x - self.u_x * self.current_t - self.x0))**2 / (4 * self.D_x * self.current_t) / (4 * np.pi * self.D_x)
    else:
        return np.exp(-(x - self.u_y * self.current_t - self.y0))**2 / (4 * self.D_y * self.current_t) / (4 * np.pi * self.D_y)

def plot_distribution(self, save_figure = False, fname = "distribution.png"):
    """ Plot distribution of all the animals on XY plane as 3D histogram """
    fig = plt.figure()
    fig.suptitle('Distribution of the turtles on the XY plane', fontsize = 16)
    ax = fig.add_subplot(1, 1, 1, projection = '3d')
    ax.set_title('Distribution of turtles')
    distribution = self.get_distribution_2D()
    X, Y, Z = distribution[:len(x)], y[1] for i in range(len(x))
    while True:
        for i in range(len(zs()):
            if i > len(zs):
                break
            if i == 0:
                del z[i], x[i], y[i]
            else:
                break
        cmap = cm.get_cmap('viridis')
        norm = colors.Normalize(vmin = min(zs, vmax = max(zs))
        colormap = [cmap(k / max_height) for k in z]
        z = zeros(2)
        ax.bar3d(x, y, z, self.delta_x[0], self.delta_y[1], 1, color = colormap, antialiased = True, shade = False)
        ax.set_xlabel("x")
        ax.set_ylabel("y")
        ax.set_zlabel("z")
        plt.locator_params(nbins = 5)
        if save_figure:
            fig.suptitle('distribution.png')
        plt.close()

    def plot_distribution_3D(self, save_figure = False, fname = 'distribution.png'):
        """ Plot the animals' distribution 3D histograms along x and y axis with the sum of animals number along other axis. """
        x = self.x_axis
        z = self.get_distribution_3D(nz, axis = 0) for i in range(len(x))
        y = self.y_axis
        z = self.get_distribution_3D(nz, axis = 1) for i in range(len(y))
```

for i in range(animals_plot):
    evolution = np.array(self._evolution_history[i])
    ax.plot(evolution[:, 0], evolution[:, 1], linewidth=2)

    ax.set_xlabel('X', fontsize=12)
    ax.set_ylabel('Y', fontsize=12)

    ax.set_title('Animals' movement Paths', fontsize=14)
    ax.grid()

    if save_figure:
        fig.savefig(filename + '.png')

plt.show()

def main():
    """ Example of working with Population class """

    population = Population('full_set_season.csv') # create population instance, the data is readed from file 'animals.csv'

    population.plot_evolution(save_figure=True, filename="Animals_migration") # plot migration path of all animals separately

    population.plot_evolution(X=(animals_plot = 5, save_figure=True, filename="Animals_S")) # plot migration paths on XY plane

    population.plot_evolution_XY(save_figure=True, filename="Animals_18")

    population.plot_evolution()

    for year in population.years:
        if population.evaluate_distribution(year):
            print(year, end=' ')
            population.calculate_adv_diff_parameters() # find advection-diffusion parameters

            population.plot_distributions2D(save_figure=True, filename='DistributionID{}.png'.format(year))

            population.plot_distribution2D(save_figure=True, filename='Distribution2D{}.png'.format(year))

if __name__ == "__main__":
    main()
Appendix 2: Mutual Relationship between Wildebeests and Zebras during Migration

```python
import numpy as np
import pandas as pd
import matplotlib.pyplot as plt
from mpl_toolkits.mplot3d.axis3d import Axes3D

class Animals:
    """ Class contains all options that are general for all interacting species: Zebra and Wildebeest""
    def __init__(self, N_start, Dxy, Dy, Cx, Cy, D, r, K, b = 0, delta_x = 1, delta_y = 1, delta_t = 1, initial_x = 0, initial_y = 0):
        """ Initialize instance with given initial number of animals N_start;
        diffusion parameters Dxy, Dy;
        advection parameters Cx, Cy;
        calculates corresponding probabilities to make step in different direction p,q,r,z. ""
        self.N_walkers = N_start
        self.Dxy = Dxy
        self.Dy = Dy
        self.Cx = Cx
        self.Cy = Cy
        self.D = D
        self.r = r
        self.K = K
        self.b = b
        self.N_t = delta_t
        self.initial_x = initial_x
        self.initial_y = initial_y
        self.N_points = (int(initial_x/delta_x), int(initial_y/delta_y), [int(initial_x/delta_x) int(initial_y/delta_y)])

        self.q = self.delta_t ** (2 * self.Dxy / self.Dyx + self.Cy / self.delta_y / 2)
        self.r = self.delta_t ** (2 * self.Dxy / self.Dyx + self.D / self.delta_t / 2)
        self.z = self.delta_t ** (2 * self.Dxy / self.Dyx + self.D / self.delta_t / 2)

        if self.p <= 0 or self.q <= 0 or self.r <= 0 or self.z <= 0 or self.p + self.q + self.r + self.z > 1:
            raise Exception("Invalid probabilities p, q, r, z were calculated according to the given advection-diffusion")

        # private attributes:
        self.N_walker_position = [(int(initial_x/delta_x), int(initial_y/delta_y), [int(initial_x/delta_x) int(initial_y/delta_y)]) for _ in range(self.N_walkers[0])]
        self.N_walker_distribution = [(self.N_walkers[0])]

    def set_interactions(self, other, main_class = False):
        """ Set partner instance, define if this instance will be main_class,
        main_class will run evolution for all interacting species. ""
        if main_class:
            self.main_class = main_class

    def __onestep(self):
        """ Perform one delta_t period for animal population.
        On each time step every animal in population can die, add new animal in their current space position,
        interact with partner species or make a step in randomly chosen direction."
        for i in range(self.N_walkers[0]):
            if i % 10000 == 0:
                print("Step: ")
            # mortality
            if random.choices([true, False], [self.D + self.delta_t, 1 - self.D + self.delta_t])[0]:
                del self.N_walker_position[i]
                self.N_walker_distribution[i] -= 1

                self.N_walker_distribution[i] += 1

            else:
                # birth
                    self.N_walker_distribution[i] += 1

        while True:
            while walkers_next_step:
                # mortality
                if random.choices([true, False], [self.D + self.delta_t, 1 - self.D + self.delta_t])[0]:
                    del self.N_walker_position[i]
                    self.N_walker_distribution[i] -= 1
                # birth
                    self.N_walker_distribution[i] += 1
                # move
                    self.N_walker_distribution[i] += 1
                walkers_next_step -= 1
            break
```
```
# Introduction

```python
def evolve(self, T):
    """Model full animals population evolutions, run one_step() utility T/delta_t times.
    After that run __evaluate_distribution() utility to calculate the number of walkers in each x, y interval.""
    self.time += T
    self.n_steps = int(T/self.delta_t)
    if self.main_class:
        self.partner.time += T
        self.partner.n_steps = int(T/self.delta_t)
    for n in range(self.n_steps):
        self.__one_step()
    if self.main_class:
        self.partner.__one_step()
    self.__evaluate_distribution()
    self.partner.__evaluate_distribution()

def __evaluate_distribution(self):
    """Utility, calculate special distribution of animals, number of animals in each delta_x x delta_y interval.""
    self.dispersion = [[min(np.array(self.__walkers_position)[:,0], 0)],
                       [max(np.array(self.__walkers_position)[:,0], 0)],
                       [min(np.array(self.__walkers_position)[:,1], 0)],
                       [max(np.array(self.__walkers_position)[:,1], 0)]]
    self.n_points = (self.dispersion[1][0] - self.dispersion[0][0] + 1, self.dispersion[1][1] - self.dispersion[0][1] + 1)
    self.__walkers_distribution = np.zeros((np.prod(self.n_points) + 1, self.n_walkers) + 1)
    for i in range(self.n_walkers):
        self.__walkers_distribution[self.__point_index(self, i)] = 1 / self.n_walkers

def __point_index(self, i):
    """Utility, return x, y index of point where animal with the i index is placed,""
    return self.__walkers_position[i][0] - self.dispersion[0][0],
    self.__walkers_position[i][1] - self.dispersion[0][1]

def xy_index(self, x, y):
    """Utility, Return x, y index of the point with any given coordinates x, y.
    If these coordinates are out of dispersion occupied by animals, return None.""
    if x < self.dispersion[0][0] or self.delta_xy[0] * x > self.dispersion[1][0] or y < self.dispersion[0][1] or y > self.dispersion[1][1]:
        return None
    return int(round(x / self.delta_xy[0]) - self.dispersion[0][0]),
    int(round(y / self.delta_xy[1]) - self.dispersion[0][1])

def __axes(self, axis = 2):
    """Utility, return array of x or y values in dispersion that is occupied by animals
    with the step of delta_x or delta_y, if axis = 0 it returns x-axis,
    axis = 1 returns y-axis, otherwise return (x,y) coordinates or all points within the dispersion.""
    if axis == 0 or axis == 1:
        return [self.dispersion[0][axis] + i * self.delta_xy[axis] for i in range(self.n_points[axis])]
    else:
        x_all = [self.dispersion[0][0] + i * self.delta_xy[0] for i in range(self.n_points[0])]
        y_all = [self.dispersion[0][1] + j * self.delta_xy[1] for j in range(self.n_points[1])]
        return x_all, y_all
```
```
```python
def __average_bin(self):
    """utility. return (x, y) indices of (delta_x, delta_y) 2D interval that contains average animal's position"""
    average = self.average_position()
    bins = self.__bins(0), self.__bins(1)
    average_bin = [0, 0]
    for i in range(len(self.u_pos[0])):
        if average[i] == bins[0][1]:
            break
        if bins[1][i] - average[i] <= average[i] - bins[1][i-1]:
            average_bin[1] = i - 1
        else:
            average_bin[1] = i + 1
    return average_bin

def get_distribution_2D(self):
    """Returns distribution of animals on XY plane as a function of x, y.
    This function distribution_2D() work for any x, y (within and out the animal's dispacon)"""
    def distribution_2D(x, y):
        indices = self.__w_index(x, y)
        if indices == None:
            return 0
        return self.__walkers_distribution[indices[0]][indices[1]]
    return distribution_2D

def get_walker_position(self):
    """Return physical (i.e., taking into account delta_x, delta_y values) x, y positions of each animal 2D array."
    def walkers_physical_position(arr):
        return [arr[0], arr[1], arr[2], arr[3]]
    return walkers_physical_position

def average_position(self):
    """return average position of the animals on x and y axis"""

    def __calculation_diffusion(self, x, y, u_x = None, u_y = None, D_x = None, D_y = None):
        """Calculates advection-diffusion function for given x and y"""
        if not((D_x and not D_y) or (u_x and not u_y)):
            D_x = self.Dx
            D_y = self.Dy
            u_x = self.u_x
            u_y = self.u_y
        if self.time <= 0 or np.min(D_x) <= 0 or np.min(D_y) <= 0:
            raise ValueError
        return np.exp(-((x - u_x * self.time - self.__zero[0]) ** 2 / (4 * D_x * self.time)) - (y - u_y * self.time - self.__zero[1]) ** 2 / (4 * D_y * self.time))

    def plot_distribution_2D(self, show_average = True, save_figure = True, filename = "distribution2D.png", set_parameters = False):
        """Plot distribution of the animals on XY plane as 2D histogram
        and the solution of advection-diffusion equation as a surface."
        if self.time == 0:
            print("WARNING: no step is made to print evolution of distribution. Please evolve Population first.")
        def add_average(ax):
            x_exis = np.linspace(min(x), max(x), 201)
            y_exis = np.linspace(min(y), max(y), 201)
            x_avg = [self.__average_position(x, y) for x in x_exis]
            y_avg = [self.__average_position(x, y) for y in y_exis]
            ax.plot(x_exis, y_avg, color = 'crimson', linewidth = 3)
            ax.plot(y_exis, x_avg, color = 'crimson', linewidth = 3)

def fig_normalise(ax):
```
```python
def fig_normalizer(ax):
    ax.set_xlabel('x')
    ax.set_ylabel('y')
    ax.view_init(elev=12.5)
    plt.locator_params(nbins=5)

    fig = plt.figure(fignsize=(11, 5))
    plt.title('Distribution of animals on the xy plane at t = {}'.format(self.time), fontsize=14)
    ax = fig.add_subplot(1, 2.5, 1, projection='3d')
    ax.set_title('Empirical data')
    distribution = self.get_distribution_2D()
    x, y = self.axes(x)
    i = [distribution[x[i], y[i]] for i in range(len(z[i]))]

    while True:
        for i in range(len(c[i])):
            if i == len(c[i]):
                break
            if :i == e:
                del z[i], x[i], y[i]
        else:
            break

    # choose different color theme for main class and its partners
    if self.main_class:
        cmap = cm.get_cmap('viridis')
        color = cm.viridis
    else:
        cmap = cm.get_cmap('plasma')
        color = cm.plasma
    max_height = max(z)
    colormap = [cmap(k / max_height) for k in z]
    x, y, z = np.meshgrid(x, y, z)
    ax.bar3d(x, y, z, self.delta_xy[0], self.delta_xy[1], z, color=colormap, antialiased=True, shade=False)

    if show_average:
        add_average(ax)

    fig_normalizer(ax)
    ax = fig.add_subplot(1, 2.5, 2, projection='3d')
    ax.set_title('Advection diffusion equation')

    x_std = np.linspace(min(x), max(x), 1000)
    y_std = np.linspace(min(y), max(y), 1000)
    x_std, y_std = np.meshgrid(x_std, y_std)
    norm = self.delta_xy[0] * self.delta_xy[1]

    try:
        if not set_parameters:
            z_std = norm * self.advection_diffusion(x_std, y_std)
        else:
            z_std = norm * self.advection_diffusion(x_std, y_std, mu_x, mu_y, sigma_x, sigma_y)
        print('WARNINGS: invalid values encountered in advection_diffusion(x_std, y_std, mu_x, mu_y, sigma_x, sigma_y)')
        z_std = np.zeros_like(x_std)
    except:
        print('ERRORS: no step is made to print evolution of distribution. Please evolve Population first.')

    if show_average:
        add_average(ax)

    fig_normalizer(ax)
    fig.savefig(filename + '.png')
    plt.show()

def plot_distributions2D(self, show_average=True, save_figure=True, True, colormap='distribution', set_parameters=False):
    """ Plot the walker's distribution 2D histograms along x and y axes with the other coordinates equal to its average value. """

    if self.time == 0:
        print('WARNINGS: no step is made to print evolution of distribution. Please evolve Population first.')
        return 0

    # choose different colors for main animals class and its partners
    if self.main_class:
        color_dict = 'turquoise'
    else:
        color_dict = 'coral'

    print('

```
x = self._axes(0)
y = self._axes(1)
x_0 = self.averages[0]
y_0 = self.averages[1]

z_0 = [self.get_distribution(x, y, (i, j)) for i in range(len(x))]

z = [self.get_distribution(x, y, (i, j)) for i in range(len(y))]

norm = self.delta_wy[0] * self.delta_wy[1]

x_std = np.linspace(min(x) - 2 * self.delta_wy[0], max(x) + 2 * self.delta_wy[0], 100)
y_std = np.linspace(min(y) - 2 * self.delta_wy[1], max(y) + 2 * self.delta_wy[1], 100)

try:
    if not set_parameters:
        cl_std = [norm * self.advection_diffusion(x, y, z, w) for x in x_std]
    else:
        cl_std = [norm * self.advection_diffusion(x, y, z, w, m, L, M, D, y) for x in x_std]
    y_std = [norm * self.advection_diffusion(x, y, z, w, m, L, M, D, y) for x in y_std]
except:
    print("Invalid values encountered in {}".format(advection_diffusion))

x_std = [y for y in x_std]
y_std = [y for y in y_std]

fig, ax = plt.subplots(1, 2, figsize=(12, 5))

ax1.bar(x, z, width = self.delta_wy[0], color = color_dist)
ax1.bar(y, z, width = self.delta_wy[1], color = color_dist)

ax1.plot(x_std, cl_std, linewidth = 2, label = 'Advection-diffusion equation', color = 'crimson')

ax1.plot(y_std, cl_std, linewidth = 2, label = 'Advection-diffusion equation', color = 'crimson')

if show_average:
    ax1.plot([self._averages[0]], [self._average_bin[0]], 'o', mfc = 'None', mec = color_dist)
    ax1.plot([self._averages[1]], [self._average_bin[1]], 'o', mfc = 'None', mec = color_dist)

ax1.legend()

plt.legend()

if save_figure:
    fig.savefig(filename + '.png')
plt.show()
```python
if save_figure:
    fig.savefig(filename + '.png')
plt.show()

def main():
    # create instances of animal class zebra and wildebeest
    zebra = Animal(start = 2000, Dx = 0.01, Dy = 0.01, Cy = 0.005, Cx = 0.005, d = 0, r = 0.01, k = 4000, b = 2 / 10**3)
    wildebeest = Animal(start = 12000, Dx = 0.01, Dy = 0.01, Cy = 0.005, Cx = 0.005, d = 0, r = 0.01, k = 24000, D = 15 /
    # d = 0, d = 0.03, d = 0.1
    # set interaction between zebra and wildebeest
    zebra.set_interaction(wildebeest, main_class = True) # zebra will be main interacting class
    wildebeest.set_interaction(zebra)
    # run evolution for interacting species (zebra is main interacting class so it runs evolution for wildebeest on each time step)
    zebra.evolve(T = 100)
    zebra.plot_distribution(filename = 'zebra_distribution.png')
    zebra.plot_distribution(filename = 'zebra_distribution.png')
    wildebeest.plot_distribution(filename = 'wildebeest_distribution.png')
    wildebeest.plot_distribution(filename = 'wildebeest_distribution.png')
    # plot how the number of zebra and wildebeest changes with time
    zebra.plot_num_animals(filename = 'zebra_wildebeest_number.png')
    zebra.save_num_animals()

if __name__ == '__main__':
    main()
```
Appendix 3: Analysis of Prey-Predator Relations of the three Species

```python
# Objective three
import random
import numpy as np
import matplotlib.pyplot as plt
from matplotlib import colorbar
from mpl_toolkits.mplot3d.axes3d import Axes3D
import Axes3D

class Animals:
    """Class contains all options that are general for all interacting species: zebra and wildebeest """
    def __init__(self, N_start, dx, dy, cx, cy, d = 0.0, r = 0.0, K = 1.0, b = 0.0, delta_x = 1.0, delta_y = 1.0, delta_t = 1.0, initial_x = 0.0, initial_y = 0.0):
        self.N_walkers = N_start
        self.dx = dx
        self.dy = dy
        self.cx = cx
        self.cy = cy
        self.d = d
        self.r = r
        self.K = K
        self.b = b
        self.delta_x = delta_x
        self.delta_y = delta_y
        self.delta_t = delta_t
        self.initial_x = initial_x
        self.initial_y = initial_y

    def f(self):
        """Calculate probabilities to make step in different directions. """
        self.f1 = 0
        self.f2 = 0
        self.f3 = 0
        self.f4 = 0
        self.f5 = 0
        self.f6 = 0
        self.f7 = 0
        self.f8 = 0

    def p(self, x, y):
        """Calculate rate of birth and death. """
        self.p1 = 0
        self.p2 = 0
        self.p3 = 0
        self.p4 = 0
        self.p5 = 0
        self.p6 = 0
        self.p7 = 0
        self.p8 = 0

    def eval(self):
        """Calculate size of population. """
        self.eval1 = 0
        self.eval2 = 0
        self.eval3 = 0
        self.eval4 = 0
        self.eval5 = 0
        self.eval6 = 0
        self.eval7 = 0
        self.eval8 = 0

    def simulate(self):
        """Simulate population. """
        self.simulate1 = 0
        self.simulate2 = 0
        self.simulate3 = 0
        self.simulate4 = 0
        self.simulate5 = 0
        self.simulate6 = 0
        self.simulate7 = 0
        self.simulate8 = 0

    def run_simulation(self):
        """Run simulation. """
        self.run_simulation1 = 0
        self.run_simulation2 = 0
        self.run_simulation3 = 0
        self.run_simulation4 = 0
        self.run_simulation5 = 0
        self.run_simulation6 = 0
        self.run_simulation7 = 0
        self.run_simulation8 = 0

    def plot_simulation(self):
        """Plot simulation. """
        self.plot_simulation1 = 0
        self.plot_simulation2 = 0
        self.plot_simulation3 = 0
        self.plot_simulation4 = 0
        self.plot_simulation5 = 0
        self.plot_simulation6 = 0
        self.plot_simulation7 = 0
        self.plot_simulation8 = 0
```

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def average_bin(self):
    """ utility. Return (x, y) indices of (delta_x, delta_y) 2D interval that contains average animal's position"""
    average = self.averages(self.x, self.y)
    for i in range(self.x.shape[0]):
        if average[i] == 0:
            continue
        if self.delta_xy[i] < 0:
            self.delta_xy[i] = -self.delta_xy[i]
        x = self.x[i] + self.delta_xy[i]
        y = self.y[i] + self.delta_y[i]
        return (x, y)

def get_distribution_2d(self):
    """ Returns distribution of animals on XY plane as a function of X, Y. This function distribution_2d() works for any X, Y (within and out the animals diapason)""
    distribution = np.zeros((self.x.shape[0], self.y.shape[0]))
    for i in range(self.x.shape[0]):
        for j in range(self.y.shape[0]):
            if self.x[i] > 0 and self.y[j] > 0:
                distribution[i, j] += 1
            elif self.x[i] < 0 and self.y[j] < 0:
                distribution[i, j] -= 1
            else:
                distribution[i, j] = 0
    return distribution

def get_walkers_position(self):
    """ Return physical (i.e. taking into account delta_x, delta_y values) X, Y positions of each animal 2D array.""
    for i in range(self.n_walkers):
        for j in range(self.n_points):
            if self.x[i] > 0 and self.y[j] > 0:
                self.x[i] += self.delta_x[i] + self.delta_y[j]
            elif self.x[i] < 0 and self.y[j] < 0:
                self.x[i] -= self.delta_x[i] + self.delta_y[j]
            else:
                self.x[i] = self.x[i]
                self.y[j] = self.y[j]

def advection_diffusion(self, x, y, u_x = None, u_y = None, D_x = None, D_y = None):
    """ Calculates advection-diffusion function value for given x and y.""
    if not (D_x and D_y and u_x and u_y):
        return np.exp(-((x - u_x) * self.time - self.zero[0]) ** 2 / (2 * D_x) + ((y - u_y) * self.time - self.zero[1]) ** 2 / (2 * D_y))
else:
    cmap = cm.get_cmap('plasma')
    color = cm.cmap
    max_height = max(z)
    colormap = [z / max_height for z in z]
    z_bottom = np.zeros_like(z)
    ax.bar3d(x, y, z_bottom, self.delta_xz[0], self.delta_xz[1], z, color = colormap, antialiased = True, shade = False)
    if show_average:
        add_average(ax)

fig_normsize(ax)
ax = fig.add_subplot(1, 2, 1, projection='3d')
ax.set_title('Advection diffusion equation')
X_std = np.linspace(min(x), max(x), 1e+02)
Y_std = np.linspace(min(y), max(y), 1e+02)
X_std, Y_std = np.meshgrid(x_std, y_std)

norm = self.delta_xz[0] * self.delta_xz[1]

if not set_parameters:
    X_std = norm * self.advection_diffusion(x_std, y_std)
else:
    X_std = norm * self.advection_diffusion(x_std, y_std, mu_x, mu_y, D_x, D_y)
ax.plot_surface(x_std, y_std, z_std, rstride=1, cstride=1, linewidth=3, color='0.2')

if show_average:
    add_average(ax)

fig_normsize(ax)

if save_figure:
    fig.savefig(filename = '.png')

plt.show()

def plot_distributions3D(self, show_average = True, save_figure = True, filename = "distribution", set_parameters = False):
    *** Plot the walker's distribution 3D histograms along x and y axis with the other coordinate
equal to its average value. ***

    *** Plot distribution of the ashes on xy plane as a histogram
    and the solution of advection-diffusion equation as a surface ***

    if self.time == 0:
        print("Warning: no step is made to print the evolution of distribution. Please evolve population first.")
        return 0

    def add_average(ax):
        x_axis = np.linspace(min(x), max(x), 1e+02)
        y_axis = np.linspace(min(y), max(y), 1e+02)
        z_axis = [self.average_position[i][0] for i in y_axis]
        x_axis = [self.average_position[i][1] for i in x_axis]
        ax.plot(x_axis, z_axis, zdir='x', cstridex=1, linewidth = 3, color = 'c')
        ax.plot(y_axis, z_axis, zdir='y', cstridey=1, linewidth = 3, color = 'c')

    def fig_normsize(ax):
        ax.spines['top'].set_visible(False)
        ax.spines['right'].set_visible(False)
        ax.set_xlabel("x")
        ax.set_ylabel("y")
        ax.set_zlabel("z")

    fig = plt.figure(figsize = (11, 5))
    fig.suptitle('Distribution of Ashes on the XY plane at T = {}'.format(self.time), fontsize = 16)
    ax = fig.add_subplot(1, 1, 1, projection='3d')
    ax.set_title('Advection and Diffusion is a Distribution
    self.get_distribution_3d()
    x, y, z = self.ash[0]
    x, y = distribution(x[i], y[i])

    while True:
        for i in range(len(z)):
            if i == len(z):
                break
            if z[i] == 0:
                break
            self.ash[0] = u[i, x[i], y[i]]
            else:
                break

    # Choose different color for main_class, predator and herbivore partner
    if self.main_class:
        cmap = cm.get_cmap('viridis')
        color = cm.viridis
    elif self.main_class == "Prey":
        cmap = cm.get_cmap('gnome')
        color = cm.magma
    else:
        break
if self.time == 0:
    print("Warning: no step is made to print evolution of distribution. Please evolve population first.")
    return

# choose different colors for main class and its herbivore partner and predator
if self.main_class:
    color_dist = 'turquoise'
    color_av = 'greyblue'
else:
    color_dist = 'violet'
    color_av = 'deepink'

x = self.aves(0)
y_av = self.aves(1)
z = [self.get_distribution_3D(x[1], y_av) for 1 in range(len(x))]
y = self.aves(0)
z_av = self.aves(0)
z = [self.get_distribution_3D(x[1], y_av) for 1 in range(len(x))]

try:
    if not self.parameters:
        cl_std = [norm * self.advection_diffusion(x, y_av) for x in x_std]
    else:
        cl_std = [norm * self.advection_diffusion(x, y_av, mu, sigma, CL, CL_2, CL_3) for x in x_std]
    except:
        print("Warning: invalid values encountered in (x,y)")

fig, (ax1, ax2) = plt.subplots(1, 2, figsize = (12, 6))

ax1.bar(x, z1, width = self.delta_w[0], color = color_dist)
ax2.bar(y, z2, width = self.delta_w[1], color = color_av)

ax1.plot(x_std, cl_std, linewidth = 2, label = 'Theoretical distribution', color = 'crimson')
ax2.plot(y_std, cl_std, linewidth = 2, label = 'Theoretical distribution', color = 'crimson')

if show_average:
    av_wbin = [len(self.averages_w[0][i])
    av_ybin = [len(self.averages_y[1][i])]
    av = [norm * self.advection_diffusion(x, y_av, mu, sigma, CL, CL_2, CL_3) for x in x_std]

ax1.bar(av_wbin, z1, width = self.delta_w[0], label = 'Average x = [z[1]]', color = color_dist)
ax2.bar(av_ybin, z2, width = self.delta_w[1], label = 'Average y = [z[1]]', color = color_av)

ax1.legend()
ax2.legend()

if save_figure:
    fig.savefig(filenname = '.png')

plt.show()
class Herbivore(Animals):
    ''' Class contains all functionality for Zebra and Wildebeest species interacting one with another 
    and with one predator instance -- Lions '''

    def set_interaction(self, partner, predator, a, h, main_class = False):
        ''' Set partner and predator instances and parameters of interaction with predator a, h. '''
        self.partner = partner
        self.main_class = main_class
        self.p = predator
        self.a = a
        self.h = h

    def evolve(self, T):
        ''' Model full animals population evolutions, run one_step() utility T/delta_t times. 
        After that run _evaluate_distribution() utility 
        to calculate the number of walkers in each a, h interval. 
        If is main_class also run evolution for partner herbivore and predator. '''
        self.time = T
        self.T = int(T/self.delta_t)
        self.p.time = T
        self.p.T = int(T/self.delta_t)
        self.a.time = T
        self.a.T = int(T/self.delta_t)
        self.h.time = T
        self.h.T = int(T/self.delta_t)
        for n in range(self.N_steps):
            self.one_step()
            if self.main_class:
                self.partner.one_step()
                self.p.one_step()
                self.a.one_step()
                self.h.one_step()

    def one_step(self):
        ''' Model one delta_t period for herbivore population. 
        On each time step every animal in population can die, add new animal in their current space position, 
        interact with herbivore partner, be eaten by predator or make a step in randomly chosen direction. '''
        for i in range(N_walkers):
            self.p.next_step = self.p.walkers[i] + 1
            while i < self.next_step:
                # mortality
                if random.choices((True, False), [self.d + self.delta_t, 1 - self.d + self.delta_t])[0]:
                    del self.walkers[i]
                    self.next_step += 1
                elif random.choices((True, False), [self.r + self.delta_t, 1 - self.r + self.delta_t])[0]:
                    self.walkers[i].append(self.next_step)
                    self.next_step += 1
                # interaction with predator
                if random.choices((True, False), [self.h + self.delta_t, 1 - self.h])[0]:
                    self.walkers[i].append(self.next_step)
                    self.next_step += 1
                else:
                    # birth
                    if random.choices((True, False), [self.r + self.delta_t, 1 - self.r + self.delta_t])[0]:
                        self.walkers[i].append(self.next_step)
                        self.next_step += 1
                    # interaction
                    elif self.i:
                        self.i -= 1
                        if random.choices((True, False), [self.s + self.delta_t, 1 - self.s + self.delta_t])[0]:
                            self.walkers[i].append(self.next_step)
                            self.next_step += 1
                    else:
                        while direction:
                            direction = random.choices([1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0], [self.p, self.q, self.w, self.s, 1 - self.p - self.q - self.w])
                            self.walkers[i].append(direction)
if direction == 'l':
    self.walkers_position[i][0] += 1
elif direction == 'r':
    self.walkers_position[i][0] -= 1
elif direction == 'u':
    self.walkers_position[i][1] += 1
elif direction == 'd':
    self.walkers_position[i][1] -= 1
i += 1

self.N_walkers.append(walkers_next_step)

def plot_run_animals(self, save_figure = True, filename = "animals_number", show_legends = True):
    """Plot evolution of number each species animals together on the same plot."""
    fig, nx = plt.subplots()
    t = [i for i in range(self.time + 1)]
    ax.plot(t, self.N_w, label = 'Zebra', color = 'turquoise')
    ax.plot(t, self.N_w_h, label = 'Wildebeest', color = 'mediumvioletred')
    ax.plot(t, self.N_p_w, label = 'Lion', color = 'firebrick')
    ax.set_xlabel('TIME', fontsize = 22)
    ax.set_ylabel('NUMBER OF ANIMALS (X10^2)')
    ax.set_title('Populations of Interesting Species')
    ax.legend()

    if save_figure:
        fig.savefig(filename + '.png')
    plt.show()

    def save_run_animals(self):
        """Save evolution of number of population in txt file"""
        t = [[i] for i in range(self.time + 1)]
        n1 = []
        n2 = []
        for i in range(len(self.N_w)):
            n1.append([self.N_w[i]])
            n2.append([self.N_p_w[i]])
        table = np.concatenate([t, n1, n2], axis = 1)
        df = pd.DataFrame(table)
        df.columns = ['TIME', 'N Zebras', 'N Wildebeest', 'N Lions']
        df.to_csv('Three_species_interaction.txt', index = False)

class Predator(Animals):
    """Class models predator animal, its interaction with two herbivore partners,
    mortality and random walk."""
    def set_interaction(self, partners, partner, gi, g2):
        """Set two herbivore partners and parameters of interaction gi, g2."""
        self.partners = (partner, partners)
        self.g = (gi, g2)

    def one_step(self):
        """Model one delta_t period for predator population.
        on the each time step every predator animal in population can dis,
        add new animal through interaction with herbivore
        or make a step in randomly chosen direction.""
        j = 0
        walkers_next_step = self.N_walkers[-1]
        while j < walkers_next_step:
            x = random.choices([True, False], [self.d * self.delta_t, 1 - self.d * self.delta_t] )[0]:
                del self.walkers_position[i]
                walkers_next_step -= 1
            else:
                # interaction with herbivore
                for i in range(len(self.partners[1])):
                    partner = self.partners[1][i]
                    probability = self.g[1] * self.delta_t * partner.h * partner.N_walkers[-1] / (1 + partner.a * partner.N_a)
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if random.choices([True, False], [probability, 1 - probability]) == [0):
    self.walkers_position.append(self.walkers_position[0][1])
    j += 1
else:
    # random walk (diffusion + convection)
    direction = random.choices(['J', 'R', 'U', 'D', 'O'])[0]
    [self.p, self.q, self.w, self.z, 1 - self.p - self.q - self.w - self.z]
    if direction == 'J':
        self.walkers_position[j][1] += 1
    elif direction == 'R':
        self.walkers_position[j][1] -= 1
    elif direction == 'U':
        self.walkers_position[j][1] += 1
    elif direction == 'D':
        self.walkers_position[j][1] -= 1
    j += 1

self.H_walkers.append(self.walkers_next_step)

def main():
    # creates zebra and wildebeest instances of Herbivore class and lion instance of Predator class
    zebra = Herbivore(N_start = 3000, DX = 0.01, DY = 0.01, CX = 0.009, CY = 0.009, D = 0.02, R = 0.04, K = 2000, B = 2 / 10)
    wildebeest = Herbivore(N_start = 30000, DX = 0.01, DY = 0.01, CX = 0.009, CY = 0.009, D = 0.02, R = 0.04, K = 100000, B = 2)
    lion = Predator(N_start = 30, DX = 0.01, DY = 0.01, CX = 0.006, CY = 0.009, D = 0.02)

    # set interaction between zebra and wildebeest, and between zebra(wildebeest) and lion
    wildebeest.set_interaction(partner = zebra, predator = lion, a = 1, h = 0.9)
    zebra.set_interaction(partner = wildebeest, predator = lion, a = 1, h = 0.9, main_class = True)
    lion.set_interaction(zebra, wildebeest, 0.9, 0.9)
    # zebra will be main class
    zebra.evolve(100) # run evolution for zebra and its partners wildebeests and lion

    # plot special distributions of zebras, wildebeests and lions after all evolution steps.
    zebra.plot_distribution2D(filename = 'zebra_model2_2D')
    wildebeest.plot_distribution2D(filename = 'wildebeest_model2_2D')
    lion.plot_distribution2D(filename = 'lion_model2_2D')
    wildebeest.plot_distribution3D(filename = 'wildebeest_model3_3D')
    zebra.plot_distribution3D(filename = 'zebra_model3_3D')
    lion.plot_distribution3D(filename = 'lion_model3_3D')
    # number of animals
    zebra.plot_num_animals(filename = 'zebra_wildebeest_lions_num')
    # zebra save_num_animals()

if __name__ == '__main__':
    main()
```
RESEARCH OUTPUTS

(i) Publications


(ii) Poster Presentation