Modelling Seasonal Migration Patterns of Wildebeest under Climate-Driven Changes: A Predator-Prey Model with De Angelis Functional Response

ABSTRACT

This study models the dynamics of a predator-prey system influenced by seasonal resource availability and prey migration. A two-dimensional spatial model simulates prey and predator populations, where prey growth is driven by seasonal resource fluctuations, and migration is guided by the spatial distribution of resources. The results show that higher resources during the wet season leads to increased prey density and migration, while lower resources in the dry season reduce prey growth and movement. Predator populations follow prey density changes, with a delayed increase in response to prey population peaks. Overall, the model highlights the critical role of seasonal resource variability in shaping predator-prey interactions and migration patterns.

Keywords: Spatial heterogeneity, resource distribution, migration patterns, seasonal variations.

1. INTRODUCTION

The Serengeti ecosystem, spanning northern Tanzania and extending into southwestern Kenya, is renowned for its rich biodiversity and the iconic Great Migration of wildebeest, zebras, and other herbivores (Torney, 2018). This ecosystem hosts more than 1.3 million wildebeest (TAWIRI, 2023), is of global importance, significantly shaped by the migration habits of these animals. As the primary species in the area, wildebeests drive a natural cycle that affects food availability and influences the movement of predators and scavengers. Their large numbers are essential for maintaining the region's biodiversity, functioning as both prey and regulators of the ecosystem (TAWIRI, 2023); (Kisoma L. N., 2020). Their selective grazing patterns help shape the composition and structure of vegetation but also provide food for the predators like lions, hyenas, and crocodiles (Kisoma L. N., 2020), (Sinclair, 2003), (Anderson, 2008). As they move, wildebeests interact with other herbivores like zebras and gazelles, sharing grazing areas and water sources (Hopcraft, 2010), (Kisoma L. N., 2020). These interactions affect competition for resources and influence coexistence strategies within the ecosystem's wildlife community.

Over the past few decades, human-caused emissions, mainly of carbon dioxide (CO_2), have significantly increased global temperatures and disrupted climate patterns (Blaise, 2023). This has led to widespread and rapid changes in the atmosphere, oceans, ice-covered regions, and ecosystems, affecting both average conditions and yearly variations, especially the frequency of extreme events patterns (Blaise, 2023), (Ritchie, 2008). Climate change has already caused considerable harm and is leading to increasingly irreversible losses among many species in terrestrial, freshwater, and marine environments

Climate change is increasingly jeopardizing the survival of different species. Shifting weather patterns, including changes in rainfall (Ritchie, 2008), impact grass growth, which is vital for wildebeests during their calving and migration periods. An aerial survey conducted in the Serengeti during the 2023 wet season (TAWIRI, 2023) revealed persistent challenges in stabilizing the wildebeest population. The movement patterns of wildebeest have remained consistent for centuries, but their population within the Serengeti ecosystem has shown significant variability. The population increased from 263,000 in 1961 to approximately 1.3 million today (Kisoma L. N., 2020), (TAWIRI, 2023) Apart from moving in search of food, wildebeest, like many other ungulates, also choose their habitats based on predator presence (Hopcraft, 2010). Wildebeest migration is a dynamic ecological process significantly influenced by predator-prey interactions. Primary predators of wildebeests include lions (*Panthera leo*) and hyenas (*Crocuta crocuta*), which have been well-documented (Kisoma, 2023), (Mduma S. A., 1999). These predators often rely on opportunistic hunting strategies that exploit the abundance and movement patterns of wildebeests during migration.

In addition to terrestrial predators, crocodiles (*Crocodylusniloticus.*) play a crucial role in shaping the migratory dynamics, particularly at river crossings such as the Mara and Grumeti rivers (Kisoma, 2023), (Mduma S. A., 1996). These aquatic predators are strategically stationed along these bottleneck points, creating a unique interface where predation pressure is heightened due to the wildebeests' limited mobility in water.

The interaction between these predator types creates a complex web of ecological relationships (Kisoma L. N., 2020). For instance, terrestrial predators might indirectly benefit from crocodile-induced mortality by scavenging carcasses, while crocodiles might benefit from weakened or injured prey escaping from lions or hyenas.

Understanding these interactions is critical for comprehensive modeling of wildebeest migration, as they influence movement patterns, population dynamics, and survival rates throughout the migratory cycle.

Wildebeests' heavy reliance on grasslands, particularly in the southern and eastern Serengeti, makes them highly susceptible to environmental changes such as extreme weather events, prolonged droughts, and habitat degradation. These factors disrupt forage availability, forcing wildebeests to adapt their migratory behavior to locate better forage refuges across different regions.

In this study, the focus is on understanding the dynamics of wildebeest movement as influenced by seasonal climatic variations, which alter resource availability and habitat conditions. These climatic factors not only motivate their movement but also interact with predation risks, as predators exploit seasonal vulnerabilities during migration.

To capture the complexity of wildebeest seasonal movements, the study incorporates predator dynamics, including the roles of lions, hyenas, and crocodiles. This approach enables a holistic exploration of how both biotic (predators) and abiotic (climatic factors) pressures shape the spatiotemporal patterns of migration, contributing to a deeper understanding of these interconnected ecological processes.

2. MATERIAL AND METHODS

2.1. The mathematical model

Let $u(t)$ and $v(t)$ represent the prey and predator populations (lions, hyena, crocodiles etc.), respectively, at time t. The prey predator modeled with De Angelis functional response can be written as

$$\left.\begin{aligned} \frac{du}{dt} &= ru\left(1-\frac{u}{K}\right)-\frac{auv}{1+bu+cv}-\gamma u \\ \frac{dv}{dt} &= \frac{euv}{1+bu+cv}-dv \end{aligned}\right\} \qquad (1)$$

Where:

- r is the prey intrinsic growth rate of wildebeest (prey)
- K is the environmental carrying capacity for prey
- γ is the prey's natural mortality rate
- a predators attack rate on prey
- b Prey handling parameter for functional response
- c Predators' saturation parameter
- e is the conversion rate of the prey to predator
- d is the predators' natural death

The effects of climate change were included in the mathematical model. The climate dependent factors are introduced in the model as follows:

$$\left.\begin{aligned} \frac{du}{dt} &= r(t)u\left(1-\frac{u}{K(t)}\right)-\frac{auv}{1+bu+cv}-\gamma u \\ \frac{dv}{dt} &= \frac{euv}{1+bu+cv}-dv \end{aligned}\right\} \qquad (2)$$

Where:

- $r(t)$ is the time-dependent wildebeest intrinsic growth rate influenced by climate change.
- $K(t)$ is the time-dependent environmental carrying capacity influenced by climate change

2.2. Climate conditions in the mathematical model

In the context of the predator-prey model, the terms amplitude, phase shift, and frequency refer to the seasonal variation in climate conditions and how they influence the population dynamics of the prey and predator species. These parameters are part of the mathematical representation of seasonal environmental fluctuations.

The amplitude (A) represents the maximum deviation (positive or negative) of the climate factor from its baseline level over time. The wet season is characterized by high amplitude due to abundant fresh grass and dry season has low amplitude as resources dwindles.

The phase shift **(ϕ)** determines the timing of the seasonal variation. It shifts the sine wave (which represents seasonal variation) along the time axis. In this study, the phase shift describes how the timing of environmental changes (especially rainfall) influences biological cycles, such as the timing of prey (wildebeest) birth could differ depending on local weather patterns or geographic location. A phase shift of $\phi = 0$ represent seasonal changes starting from the beginning of the year, whereas a phase shift of $\phi = \pi/2$ indicate a seasonal peak in the middle of the year. This shift affects when predators and prey are most active or abundant, influencing their interactions.

The frequency **(ω)** determines how often the seasonal fluctuations occur, which in the equations corresponds to the periodicity of the climate variations (e.g., yearly, monthly). In this study, a frequency of $\omega = 2\pi$ corresponds to a 1-year cycle, which is common for seasonal events like rainfall or prey birth. Therefore, $\omega = \frac{2\pi}{T}$, where $T = 12$ months.

In the equations provided, these three parameters: amplitude, phase shift, and frequency are embedded in the climate factor $C(t)$. Therefore, the equation,

$$C(t) = C_0 + A\sin(\omega t + \phi) \quad (3)$$

represents how the environment changes over time. The effect of this climate variability is added to the growth rate and carrying capacity of the prey population. In this equation the parameter

2.3. Growth Rate

The prey growth rate (r) is modified by the climate factor where the reproduction and survival of the prey are influenced by climate fluctuations as follows:

- Amplitude changes could make the prey more sensitive to environmental changes, either increasing or decreasing their growth rate based on extreme weather conditions.
- Phase shift, this shifts the timing of when these climate effects happen, influencing when prey populations might experience favorable or harsh conditions.
- Frequency affects how often these changes occur and could create seasonal oscillations in the prey and populations.

The growth equation is $r(t) = r_0(1 + \alpha C(t))$ and $C(t) = C_0 + A\sin(\omega t + \phi)$

Therefore,

$$r(t) = r_0(1 + \alpha(C_0 + A\sin(\omega t + \phi))) \quad (4)$$

2.4 Carrying Capacity

The prey's environment (resources like food or shelter) is also affected by climate variations, and the carrying capacity K can increase or decrease depending on the environmental conditions:

- Amplitude can make the carrying capacity vary greatly between seasons, which can cause prey populations to fluctuate more drastically.
- Phase shift determines when the prey's environment is most favorable for growth, again affecting when the population might experience growth or decline.
- Frequency dictates how often such variations happen, creating periodic oscillations in prey and predator populations.

The carrying capacity equation $K(t) = K_0(1 + \beta C(t))$ and $C(t) = C_0 + A\sin(\omega t + \phi)$

Therefore,

$$K(t) = K_0(1 + \beta(C_0 + A\sin(\omega t + \phi))) \quad (5)$$

Where:

- r_0 and K_0 are the baseline growth rate and carrying capacity without climate change
- $C(t)$ is the function representing the impact of climate change (for instance temperature, rainfall, anomalies, extreme weather events)
- α and β are coefficients that quantify the sensitivity of the growth rate and carrying capacity induced by climate change.
- C_0 is the baseline climate condition
- A is the amplitude of climate variation.
- ω is the frequency of seasonal variations
- ϕ is the phase shift

Combining the subsections, the full mode is

$$\left.\begin{aligned} \frac{du}{dt} &= r_0\left(1+\alpha(C_0 + A\sin(\omega t+\phi))\right)u\left(1-\frac{u}{K_0\left(1+\beta\left(C_0 + A\sin(\omega t+\phi)\right)\right)}\right)-\frac{auv}{1+bu+cv}-\gamma u \\ \frac{dv}{dt} &= \frac{euv}{1+bu+cv}-dv \end{aligned}\right\} \tag{6}$$

2.5 Diffusion and migration

To accurately represent the spatial dynamics of the wildebeest and their predators, diffusion and migration parameters were integrated into the model. Diffusion accounts for random movements by both prey and predators, reflecting their exploratory behavior within the ecosystem (Fagan, 2019), (Okubo A, 2001). This process models the dispersal of individuals in response to local population densities and environmental factors.

Migration, on the other hand, is specific to the prey (wildebeests) and is driven by their dependence on rainfall gradients. Rainfall influences forage availability, and wildebeests respond by undertaking directional, large-scale movements to track favorable conditions across the landscape (Okubo, 1986). This assumption aligns with observed migratory patterns where wildebeests move seasonally between the Serengeti and Maasai Mara ecosystems in response to the shifting wet and dry seasons.

By combining diffusion and migration, the model captures both local interactions and large-scale spatiotemporal dynamics, providing a comprehensive framework to study the interplay between environmental drivers and predator-prey interactions. This dual approach is critical for understanding the mechanisms underlying seasonal migration and predator responses within the ecosystem.

Let

$$f(u,v) = r_0\left(1+\alpha(C_0 + A\sin(\omega t+\phi))\right)u\left(1-\frac{u}{K_0\left(1+\beta\left(C_0 + A\sin(\omega t+\phi)\right)\right)}\right)-\frac{auv}{1+bu+cv}-\gamma u$$

and $g(u,v) = \dfrac{euv}{1+bu+cv} - dv$,

Then

$$\left.\begin{aligned}\frac{\partial u}{\partial t} &= f(u,v) + D_u\nabla^2 u - \nabla(\mu u\nabla M)\\ \frac{\partial v}{\partial t} &= g(u,v) + D_v\nabla^2 v\end{aligned}\right\} \quad (7)$$

Equation (7) shows that prey populations are influenced by climate, diffusion, and directed migration while predator populations follow prey movement via diffusion.

The terms $D_u\nabla^2 u$ and $D_v\nabla^2 v$ represent the diffusion of the prey and predator respectively where D_u and D_v are diffusion coefficients for prey and predator respectively. The term $-\nabla(\mu u\nabla M)$ represents directed migration of prey. The parameters μ is the migration sensitivity coefficient and $M(x,y,t)$ is the environmental factor (e.g., resource availability or climate gradient) influencing prey migration. This parameter can be written as $M(x,y,t) = f(x,y,t)$ which represents forage resource and water modulated by season that motivates movement patterns of wildebeest. The gradient vector ∇M is the gradient of the environmental factor.

The mathematical model (7) was used to investigate the effects of climate change on the prey species.

2.6. Simulation

2.6.1. Spatial and Temporal Discretization

A 2D rectangular spatial grid $x, y \in [0, L]$ with a uniform grid spacing Δx and Δy .

Initial condition $u(x,y,0)$ and $v(x,y,0)$.

The Boundary Conditions is a zero-flux boundary conditions. No population flux across domain boundaries, that is $\dfrac{\partial u}{\partial n} = 0$ and $\dfrac{\partial v}{\partial n} = 0$, where n is the outward normal at the boundary.

The simulation of the system of equations over a time period $[0,T]$ iteratively updating $u(x,y,t)$ and $v(x,y,t)$.

3. RESULTS AND DISCUSSION

The wildebeest growth rate $r(t)$ was plotted showing how the climate change $C(t)$ and resource availability $R(t)$ contributes to wildebeest growth rate.

- Frequency $\omega = \frac{2\pi}{T} = \frac{2\pi}{12} = 0.52$ rad/month
- The phase shift aligns the oscillation to match real-world seasonal events. The wet season begins in November ($t = 11$). The phase shift was set such that the peak resource availability aligns with January (mid-wet season), when the sine function is 1.

  Therefore, $\phi = -\omega \cdot \Delta t = -0.52 \cdot (11-1) = -5.2$.
- The amplitude of resource fluctuation $A = 50$.

The following plot shows the relationship between the seasonal variation in resource availability and the prey (wildebeest) growth rate

$r_0 = 1, \alpha = 0.7, \beta = 0.2, \gamma = 0.2, a = 0.7, b = 0.5, c = 0.5, d = 0.38, e = 0.4,$
$C_0 = 0.5, A = 0.5, \phi = -5.2, K_0 = 2000, u_0 = 1300, v_0 = 30$

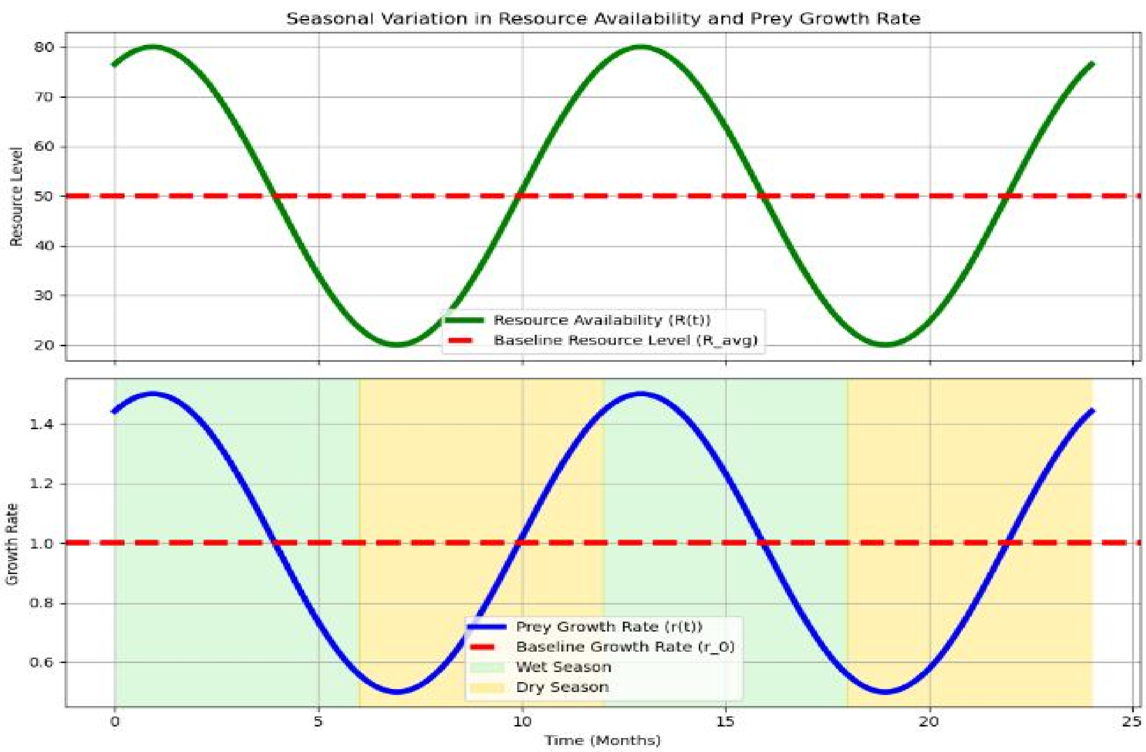

Figure 1: seasonal variations in resource availability and prey growth

Figure 1 shows the seasonal oscillations in resource levels, with higher values during the wet season (November to May) and lower values during the dry season (June to October). Also, there is a seasonal fluctuation in prey growth rate, showing higher growth during the wet season when resources are abundant and lower growth during the dry season.

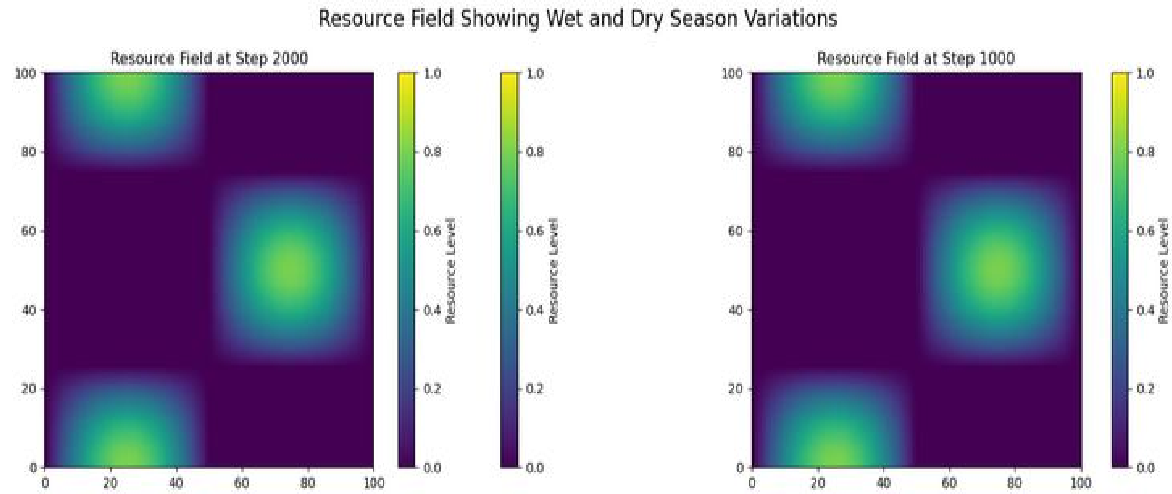

Figure 2: The resource field plot will show seasonal variations (wet vs dry seasons) and highlight how the resource levels change across the landscape**.**

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Late January to early February marks the calving season, with thousands of wildebeest giving birth within a short timeframe. This synchronized calving provides safety in numbers and ensures the survival of a significant portion of the offspring.

The predator-prey relationship was further plotted to illustrate how the populations of prey and predators interact over time (figure 3). The trajectory of the plot reveals that the total populations of both prey and predators do not remain constant; instead, they fluctuate periodically throughout the simulation period. These fluctuations reflect the dynamic nature of the predator-prey system, where changes in one population influence the other. For example, an increase in prey population can lead to a subsequent rise in predator numbers, while a decrease in prey availability may result in a decline in predator population, creating a cyclical pattern.

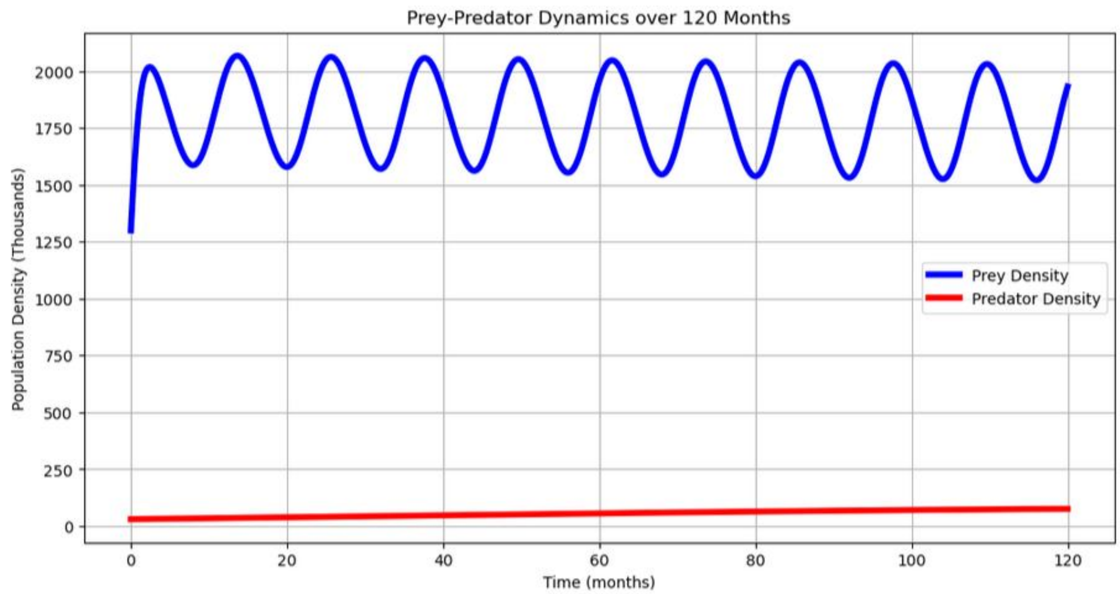

Figure 3: The trajectory shows total prey and predator populations fluctuate across the simulation period

3.1. Diffusion in the Serengeti Ecosystem

Wildebeest are grazers that move in search of fresh grass and water.Their movement can be thought of as a natural diffusion process, where they spread out to avoid overgrazing and to exploit new resources.Environmental cues, like grass density or water availability, create gradients that influence their movement, leading to a directed-diffusion phenomenon (biased diffusion).

Most predators like Lions are territorial predators that often patrol and defend specific areas but may also spread out if prey becomes scarce or competition with other predators intensifies. predators' diffusion is slower and less extensive than wildebeest diffusion because of their territoriality and lower population density. The emergency of diffusion leads to Turing instabilities. The prey and predator density plots (Figure 4) shows how the prey and predator populations evolve over time in response to the seasonal resource variations.

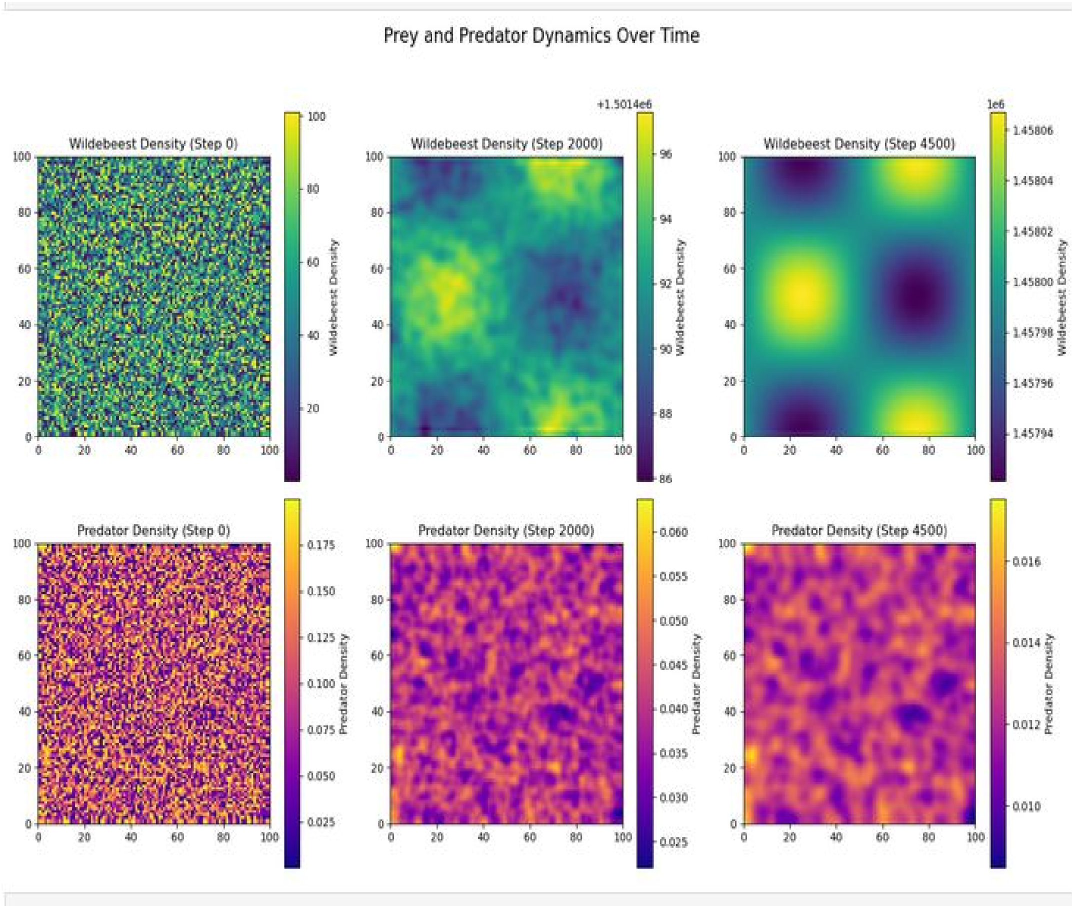

Figure 4: prey and predator dynamics over time

3.2. Extinction Scenarios

If the climate variability (through changes in amplitude, frequency, or phase) exceeds the tolerance of a species, the model may show population crashes or even extinction. For example, if the prey experiences frequent extreme conditions, it may fail to reproduce effectively, leading to a population decline, which in turn affects predators. Figures 5 and 6 show this phenomena.

$r_0 = 0.4, \alpha = 0.5, \beta = 0.1, \gamma = 0.35, a = 0.7, b = 0.5, c = 0.5,$

$d = 0.4, e = 0.2, C_0 = 0.5, A = 0.5, \phi = -5.2, K_0 = 2000, u_0 = 1300, v_0 = 30$

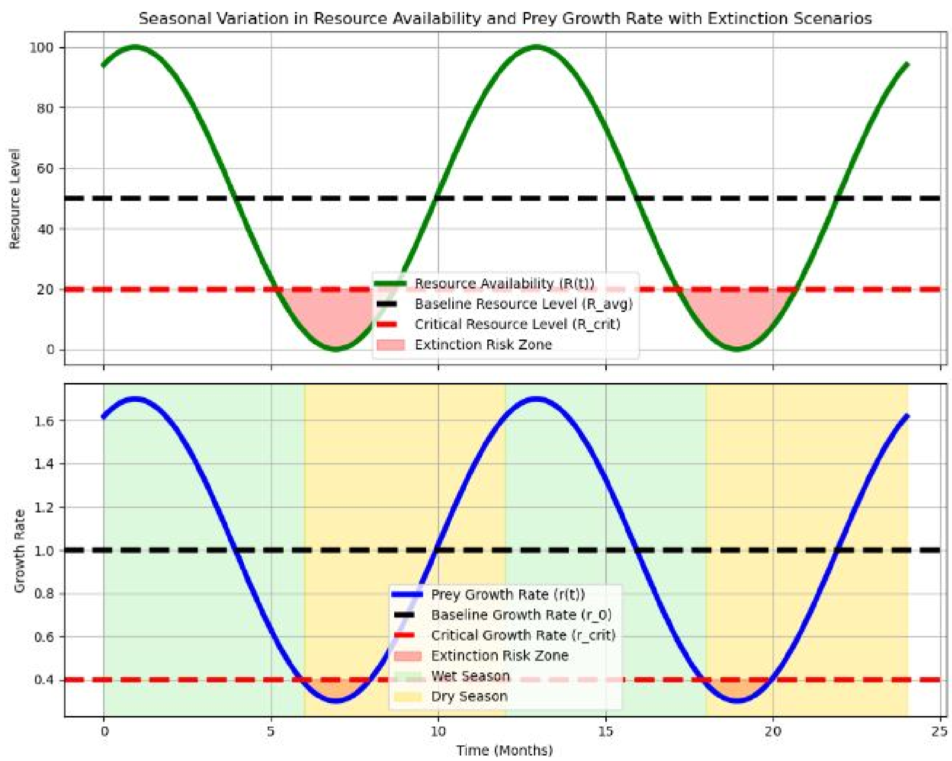

Figure 5: Extinction scenarios for both the resource availability and prey growth rate with critical thresholds.

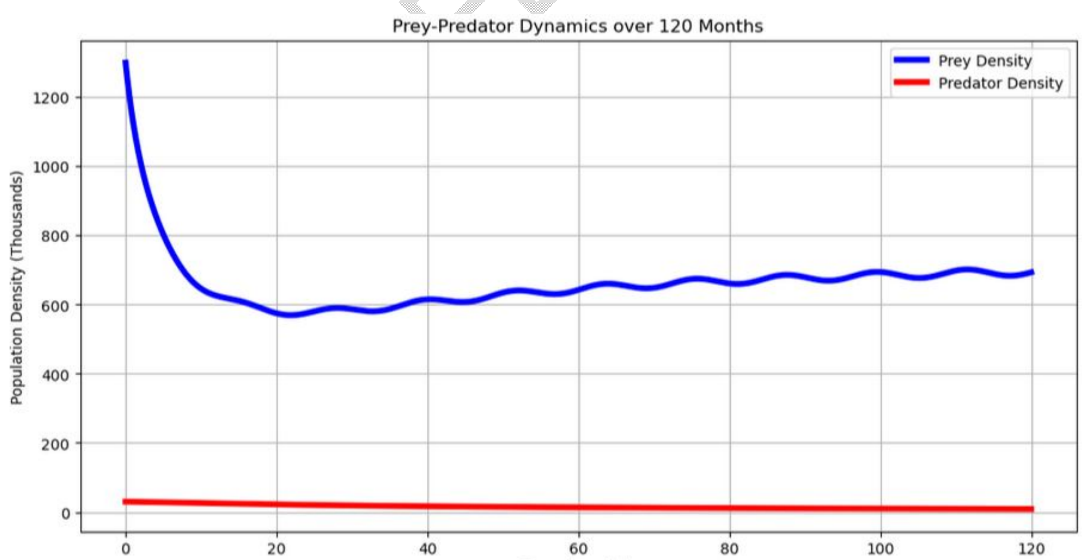

Figure 6: The trajectory shows total prey and predator populations for extensive dry seasons

The mathematical mode (7) with sinusoidal function was used to model seasonal rainfall patterns, with the carrying capacity varying both spatially and temporally in response to these fluctuations. Wildebeest movement (Figure 2) is driven by the gradient of rainfall, simulating their migration toward regions with higher vegetation or water availability.

Meanwhile, the prey and predator populations are dynamically updated at each time step, accounting for factors such as growth, mortality, predation, diffusion, and migration.

The wildebeest population demonstrates clear fluctuations driven by wet and dry seasons. During the wet season, increased resources (e.g., vegetation) enhance prey growth rates, leading to a temporary rise in wildebeest density. Conversely, in the dry season, resource scarcity reduces prey growth and carrying capacity, causing a decline in wildebeest density.

Also, predation plays a critical role in regulating wildebeest density. As prey density increases, predator populations also grow due to an abundance of food. However, when prey density declines, predator mortality rates result in a subsequent decrease in predator populations.

4. CONCLUSION

The dynamics of wildebeest and predator populations exhibit significant spatial heterogeneity driven by resource distribution and migration patterns. Wildebeest tend to aggregate in resource-rich areas, while predators follow their movement to remain near food sources. Migration is strongly influenced by seasonal resource gradients: during the wet season, wildebeest disperse across the landscape as resources become abundant, while in the dry season, they concentrate in areas with residual resources, demonstrating a clear reliance on spatial resource variability. This directed migration creates additional spatial heterogeneity in prey density, particularly along resource-rich corridors, and plays a crucial role in maintaining population stability under seasonal resource constraints.

The coupled predator-prey system exhibits dynamic stability, with oscillations in population densities. These oscillations reflect a typical ecological pattern, where predator populations lag behind prey populations due to their reliance on prey for sustenance. The diffusion (random movement) of both species further supports system stability by preventing overpopulation in specific regions, thus reducing the risk of local extinction from overgrazing or excessive predation pressure.

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