Periodicity and limit cycle perturbation analysis of a predator–prey model with interspecific species' interference, predator additional food and dispersal

H. Ddumba a,b,⇑, J.Y.T. Mugisha a,b,⇑, J.W. Gonsalves a, G.I.H. Kerley c

a Department of Mathematics and Applied Mathematics, Nelson Mandela Metropolitan University, P.O. Box 77000, Port Elizabeth 6031, South Africa
b Department of Mathematics, Makerere University, P.O. Box 7062 Kampala, Uganda
c Department of Zoology, Nelson Mandela Metropolitan University, South Africa

ARTICLE INFO
Keywords:
Brusselator
Dispersal
Permanence
Persistence
Burgers equation
Dissipativity
Wave number

ABSTRACT
We formulate a robust mathematical model for two predators having an overlapping dietary niche breadth. We use the Beddington–DeAngelis functional and numerical responses which are relevant in addressing the principle of competitive exclusion as species interact. The stabilizing effect of additional food in relation to the relative diffusivity $D$, and wave number $k$, has been investigated. Stability, dissipativity, permanence, persistence and periodicity of the model have been studied using the routine and limit cycle perturbation methods. Besides revealing irregular periodic travelling wave behaviour due to predator interference, numerical results also show oscillatory temporal dynamics resulting from additional food supplements combined with high predation rates.

1. Introduction

During conservation and management of predator–prey ecosystems, the provision of additional food to predators is one of the options available [60,63]. Such additional food is provided for several reasons, among which include the distraction of predators from over-consuming the prey (short term) or increasing the rate of predation (long term). For example during biological control of pests [60]. Thus, it turns out that providing additional food to predators must be well formulated because, if unplanned, it may lead to many unexpected and undesired effects on the ecosystem. This calls for careful analysis of the various possible outcomes, by both theoretical and empirical conservationists, before providing predators with any form of additional food. Use of ecologically plausible mathematical models has been identified as an efficient way to predict future ecosystem trends [54,63,41].

Various theoretical studies have shown that it is possible to control the dynamics of an ecosystem by manipulating the quality and supply level (quantity) of additional food to the predators [60,54,63]. These studies also show that additional food can drive the prey and predators to desired population levels within specified limits. For example, oscillations can be introduced into the ecosystem or they can be controlled and eliminated by an appropriate choice of additional food [60]. The so-called paradox of enrichment, permanence and persistence of systems can always be achieved via a suitable choice (depending on numerous parameters of the ecosystem) of additional food [14,12]. The type of additional food provided to predators can help eliminate the prey (right food provided to predators), or eliminate the predators by distracting...
them with a supply of low-quality additional food at high density, which decreases the per capita growth rate of the predator below its starvation rate and this relieves the prey from predation pressure [60].

Six lions and eight spotted hyaenas were introduced into Addo Elephant National Park’s (AENP) main camp section (approximately 132 km$^2$) in late 2003 to fulfill the role of restoring the natural balance to the ecosystems in the park by controlling the numbers of herbivores [17]. Though hyaenas scavenge and steal carrion from other predators (e.g., lions), detailed research reveals that spotted hyaenas are not mere scavengers but are also efficient predators [64,16,17,36]. Within AENP, lion and spotted hyaena activity patterns overlap 75.1% of the time and this is attributed to the low density of each species (0.04 lions km$^{-2}$ and 0.07 spotted hyaenas km$^{-2}$) [17]. As a result of high level of aggression toward each other and having the same activity pattern i.e., killing similar prey at similar times of the day, lions and spotted hyaenas have been identified as the most intense competitors [22].

Lions and spotted hyaenas which are generalist predators, attacking multiple prey species with no significant differences between their prey preferences, have been studied assiduously throughout Africa. “The ecology and dietary niche breadth of the spotted hyaena is similar to that of the lion and the two species have a 58.6% actual prey species overlap and a 68.8% preferred prey species overlap” [16]. Despite a large degree of dietary overlap with lions, the spotted hyaena’s dietary flexibility and mobility make it one of the most successful predators throughout Africa [16]. Because of their size and team work, the spotted hyaena is capable of taking kills from other carnivores including lions and this sets up a competitive relationship between the species for the available prey [64]. Spotted hyaenas are opportunistic and hunt a wide variety of prey ranging from small mammals to large ungulates having a preferred body mass range of 56–182 kg [16]. On the other hand, the lion, being the largest African carnivore and distinctly social, living in prides of 6 to 12 individuals, is the principal predator of various herbivores species. Capable of pulling down prey the size of buffalo and giraffe [37]. However, on several occasions lions steal spotted hyaena’s kills and carrion, and this results into fierce competition that often results into death [22,17,16].

The predator’s preferences for various prey species has been attributed to various reasons such as herding, easy to capture, abundance, biomass gain per prey killed, taste, hunting risks involved, total handling time and searching effort [21,23,34]. Within AENP, the buffalo and kudu are highly preferred by both lion and hyaena due to their yield in terms of biomass per killed prey [16,17,23]. However, because of high predation/hunting risks involved as a result of its strength and group vigilance, the buffalo is often avoided by both predators in favour of the kudu which is highly abundant hence frequently encountered [15,51,58]. Thus, lions and spotted hyaenas have a competitive feeding pattern on the kudu that results in interspecific species’ interference [16,17,11].

Within the vicinity of AENP, on small private game reserves, Shamwari and Kwandwe, predators are provided with supplementary feeding [19]. The private farmers buy game for their predators. Due to a limited number of prey species within AENP, providing additional food to predators is one of the conservation principles that would reduce predation pressure as it has been done within neighbouring private game reserves. Supplementary feeding is among the occasional management interventions that followed species’ translocation and reintroduction within the Eastern Cape Province [19]. The weak, malnourished and struggling predators would occasionally be provided by additional food. For example, the lionesses at AENP were provided with culled warthog carcasses while they were struggling to keep young cubs alive [19].

In this study, we consider the interaction and dynamics of two predatory carnivores, lions (Panthera leo) and spotted hyaenas (Crocuta crocuta) feeding on a common prey resource, kudu (Tragelaphus strepsiceros) which is one of the most preyed upon species and highly preferred by both lions and spotted hyaenas in AENP [21,23]. Being one of the most abundant prey species in South Africa’s Eastern Cape Province, kudus are killed by lions more frequently as shown by the Jacob’s index computations [21,23]. According to [21], the relative abundance of kudus within the Eastern Cape Province makes it an optimal strategy to be preferentially hunted by lions.

Encounters between lions and hyaenas and large prey species, in this instance, kudus, involves a lot of dynamics due to adopted anti-predator techniques. As discussed earlier, most individual lions refrain from contributing to group hunts except when pursuing buffaloes, which are inaccessible to solitary individual lions [20,21,13,23]. However, the abundant and conspicuous kudus within AENP are vigilant and depend on the group alertness for early warning in case of any sighted predator [23]. Despite being ambushed and subdued most often by stalking predators, kudus basically depend on cryptis and their high cruising speed to escape from any predator [44,24]. The first mathematical studies, after 1970, to reveal the principle of competitive exclusion considered models based upon a combination of the principle of mass action and Holling Type II functional and numerical responses [40,2,30,31]. Despite the predominance of strictly prey-dependent functional responses (e.g., Holling family types) in the literature, recent studies [9,33,6,29,7,8] have suggested the ratio-dependent, Beddington–DeAngelis functional response that considers: additional food, interspecific interference of predators and group defense mechanisms of the prey [7].

2. Model description and analysis

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

In general, the respective parameter subscripts \( h, b, l \) refer to kudu, hyaena and lion dynamics, respectively. Thus, we accordingly define: predation rates \( z_h \) and \( z_l \), interspecific interference coefficients \( \psi_h \) and \( \psi_l \), additional food, which we define as the ratio of added food biomass to normal prey biomass required for predator survival and reproduction, \( F_h \) and \( F_l \), mortality rates \( \mu_h \) and \( \mu_l \), and half saturation constants \( \frac{1}{h} \) and \( \frac{1}{l} \) of predators. Further, the kudu population density grows with intrinsic growth rate \( r_s \) and has \( K_h \) as its ecosystem carrying capacity.

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

\[
\begin{align*}
\frac{dB}{dt} &= r_s B \left( 1 - \frac{B}{K_h} \right) - \frac{z_h (1 - F_h) BH}{1 + a_h B + \psi_l L} - \frac{z_l (1 - F_l) BL}{1 + a_l B + \psi_h H}, \\
\frac{dH}{dt} &= \frac{\epsilon_h z_h (1 - F_h) BH}{1 + a_h B + \psi_l L} - \frac{\epsilon_h F_h H}{1 + a_h B + \psi_h H}, \\
\frac{dL}{dt} &= \frac{\epsilon_l z_l (1 - F_l) BL}{1 + a_l B + \psi_h H} - \frac{\epsilon_l F_l L}{1 + a_l B + \psi_l L},
\end{align*}
\]

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

### 2.1. Non-dimensionalization of the model

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

\[
u = \frac{B}{K_h}, \quad \psi = \frac{\mu_h}{\mu_l}, \quad \omega = \frac{\mu_l}{\mu_l}, \quad \tau = \mu_l \tau
\]

Substituting these results into the model equations for the dimensionalised system (1)–(3) yields:

\[
\begin{align*}
\frac{du}{dt} &= ru(1 - u) - \frac{\mu_h u v}{1 + \phi_1 u + \psi_2 w} - \frac{\eta_3 u w}{1 + \phi_2 u + \psi_1 v}, \\
\frac{dv}{dt} &= \frac{\gamma_1 \eta_3 u v}{1 + \phi_1 u + \psi_2 w} - \mu v + \beta_1 v, \\
\frac{dw}{dt} &= \frac{\gamma_2 \eta_3 u w}{1 + \phi_2 u + \psi_1 v} - w + \beta_2 w,
\end{align*}
\]

whose behaviour is controlled by the dimensionless groups

\[
\begin{align*}
r &= \frac{r_s}{\mu_l}, \quad \mu = \frac{H_h}{\mu_l}, \quad \eta_h = 1 - F_h, \quad \eta_l = 1 - F_l, \quad \phi_1 = \frac{a_h K_h}{\mu_l}, \quad \phi_2 = \frac{a_l K_h}{\mu_l}, \quad \psi_1 = \frac{\psi_h H_h}{K_h}, \quad \psi_2 = \frac{\psi_l L_l}{K_l}, \\
\gamma_1 &= \frac{\epsilon_h z_h K_h}{\mu_l}, \quad \gamma_2 = \frac{\epsilon_l z_l K_l}{\mu_l}, \quad \beta_1 = \frac{\epsilon_h F_h}{\mu_l}, \quad \beta_2 = \frac{\epsilon_l F_l}{\mu_l}.
\end{align*}
\]

A glance at the dimensionless groups above reveals symmetrical identities and thus, considering the symmetry of the dimensionless groups above, some dimensionless parameters and constants are clearly products and/or quotients of approximately analogous dimensional parameters/ constants which leads to the following approximations:

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

Employing the above approximations reduces the non-dimensionalised model to

\[
\frac{du}{dt} = ru(1 - u) - \frac{\mu u v}{1 + \phi u + \psi w} - \frac{\eta u w}{1 + \phi u + \psi v} \equiv f(u, v, w),
\]
\[
\begin{align*}
\frac{du}{dt} &= \frac{\gamma u v}{1 + \phi u + \psi w} - \mu u + \beta v \equiv g(u,v,w), \\
\frac{dw}{dt} &= \frac{\gamma u w}{1 + \phi u + \psi v} - w + \beta v \equiv h(u,v,w).
\end{align*}
\]

Since \(u, v\) and \(w\) define population densities, only non-negative solutions make biological sense. The functions of system (7)-(9) are Lipschitzian and continuous on the positive octant \(\mathbb{R}_+^3 = \{ (B, H, I) \in \mathbb{R}^3 : B(0) \geq 0, W(0) \geq 0, L(0) \geq 0 \}\) and therefore, only positive solutions of the model on the invariant interior of \(\mathbb{R}_+^3\) are considered.

### 2.2. Steady states

The steady states of the non-dimensionalised model system (7)-(9) are solutions for the following equations:

\[
\begin{align*}
ru'(1 - u') - \frac{\mu u v}{1 + \phi u + \psi w} - \frac{\gamma u w}{1 + \phi u + \psi v} &= 0, \\
\frac{\gamma u v}{1 + \phi u + \psi w} - \mu v' + \beta v' &= 0, \\
\frac{\gamma u w}{1 + \phi u + \psi v} - w' + \beta w' &= 0,
\end{align*}
\]

which allow five equilibrium points of the model system under this study, \(E_0(0,0,0), E_1(1,0,0), E_2(u',v',w'), E_3(u',v',w'), E_4(u',v',w')\), where \(u = \mu - \beta\) and \(\Psi = 1 - \beta\).

**Proposition 2.1.** Model system (7)-(9) is dissipative, uniformly persistent and hence permanent.

Before proving the proposition, the following preliminary definitions for an ordinary differential equation model \(x = xf(x)\), where \(x(t)\) is a vector that denotes the density/biomass of \(n\) interacting species are stated first [61]. Suppose \(x(t) = (x_1(t), x_2(t), \ldots, x_n(t))\) is a solution of the model with component-wise positive initial values, then the system is said to be:

(i) weakly persistent if \(\lim_{t \to \infty} \sup x_i(t) > 0\) for all \(i = 1, 2, \ldots, n\)

(ii) persistent if \(\lim_{t \to \infty} \inf x_i(t) > 0\) for all \(i = 1, 2, \ldots, n\)

(iii) uniformly persistent if there exists an \(\epsilon > 0\) such that \(\lim_{t \to \infty} \inf x_i(t) \geq \epsilon\) for all \(i = 1, 2, \ldots, n\)

(iv) permanent if \(0 < \epsilon < \lim_{t \to \infty} \inf x_i(t) \leq \lim_{t \to \infty} \sup x_i(t) \leq U\) for all \(i = 1, 2, \ldots, n\) and some constants \(\epsilon\) and \(U\).

**Definition 2.1 (Permanence: Takeuchi, 1996).** The system is said to be permanent if there is a compact set in the interior of the state space, \(\mathbb{R}_+^n\), such that all orbits initiating at points in the interior end up in the compact set. Equivalently, permanence means that there exist an \(h > 0\) such that whenever \(x_i(0) > 0\) for all \(i\), \(\lim_{t \to \infty} \inf x_i(t) > h\) and \(\lim_{t \to \infty} \sup x_i(t) < \frac{1}{h}\) i.e., all the orbits are uniformly bounded. In ecological context, permanence implies the survival of all species which exist initially.

**Definition 2.2 (Persistence: Takeuchi, 1996).** Whereas \(\lim_{t \to \infty} \sup x_i(t) < 0\) implies permanence, the system is said to be persistent if for all \(i\), \(\lim_{t \to \infty} \inf x_i(t) > 0\) i.e., persistence is a weaker concept than permanence. For this case, the system always has a positive globally stable equilibrium point for any \(\epsilon > 0\).

**Definition 2.3 (\(\omega\)-limit set: Takeuchi, 1996).** For an autonomous ordinary differential equation model, \(x = f(x)\); if \(x(0) = x_0\) in some region of \(\mathbb{R}^n\), suppose \(x(t)\) is a solution defined for all \(t > 0\) initiating \(x\) at \(t = 0\). The \(\omega\)-limit set of \(x\), \(\omega(x)\), is the set of points, \(y \in \mathbb{R}^n\), such that \(x(t_k) \to y \) as \(k \to \infty\) for some sequence \(t_k > 0; t_k \to \infty\).

**Remark 2.1.** From the definitions above, a permanent system is uniformly persistent and thus persistent, and hence weakly persistent. Therefore, a permanent system is dissipative and uniformly persistent.

**Remark 2.2.** A persistence with initial conditions in the positive cone will persist if there are no \(\omega\)-limit set of points of the solution on the boundary of the positive cone. This means that if \(\Gamma(X)\) is the orbit through the point \(X = (x,y,z)\) with \(x > 0, y > 0, z > 0\), and if \(\Omega(X)\) is the \(\omega\)-limit set of \(\Gamma(X)\), then \(\Omega(X)\) is the interior to the positive cone.

**Proof of Proposition 2.1.** From Eq. (7): \(\frac{dw}{dt} \leq ru(1-u)\) and the comparison principle (cf. [61]), leads to \(\lim_{t \to \infty} \sup u(t) \leq 1\). Thus, \(u(t) \leq 1 + \epsilon\) when \(t\) is sufficiently large, for any \(\epsilon > 0\) however small. Denoting \(\beta_0 = \min\{(\mu - \beta), (1 - \beta)\}\), then from model system (7)-(9), it follows that:
\[
\frac{du}{dt} + \frac{\mu}{\gamma} \frac{dv}{dt} + \frac{1}{\gamma} \frac{dw}{dt} = ru(1-u) - \frac{\mu(\mu - \beta)}{\gamma} v - \frac{(1 - \beta)}{\gamma} w \leq ru - \beta_0 \left( \frac{\mu}{\gamma} v + \frac{1}{\gamma} w \right) = \frac{d}{dt} \left( u + \frac{\mu}{\gamma} v + \frac{1}{\gamma} w \right)
\]

\[
\leq (r + \beta_0) \left( 1 - \epsilon \right) - \beta_0 \left( u + \frac{\mu}{\gamma} v + \frac{1}{\gamma} w \right)
\]

Again, the comparison principle leads to \( \lim_{t \to 0} \text{Sup} \left( u + \frac{\mu}{\gamma} v + \frac{1}{\gamma} w \right) \leq \frac{(r + \beta_0)(1 - \epsilon)}{\beta_0} \). This completes the proof and thus, model system (7)–(9) is dissipative and hence permanent. In biological terms, persistence means that the population biomass of each species remains asymptotically above a positive bound independent of the initial conditions.

2.3. Conditions for non-negativeness and existence of equilibria

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

The classical ordinary differential equation models prove to be useful when populations of species are assumed to be uniformly distributed over the spatial region of interest. Within AENP, there is a heterogeneity in species distribution due to random movements in search of food items and predator avoidance [17,11]. Naturally higher or lower concentrations of species occur at different locations within the ecosystems. This is due to variations in both biotic and abiotic resources [1]. Hence, the ecological niche is always patchy due to species dispersal/movements. Thus, reaction–diffusion predator–prey models are becoming increasingly favoured by both empirical and theoretical ecologists as a more suitable and relevant approach to describe predator–prey spatial–temporal interactions.

In the next subsection, incorporating species heterogeneity to model system (7)–(9) via a reaction–diffusion model is reconsidered.

2.4. Random movements of species

Despite space and time being inseparable coordinates [42], several models in mathematical ecology treat only temporal variation due to the difficulty of mathematical computation involved with both space and time incorporated in the model. However, the ecological situation is well understood when population dynamics of organisms are considered in both space and time. Diffusion of species may be of two fold; self and cross-diffusion. During self-diffusion, species tend to move from regions of high concentrations of their species e.g prey (predators) moving away from patches with abundant prey (predators). On the other hand, during cross-diffusion, prey move away from regions with abundant predators (repulsion effect) and predators move towards regions with abundant prey (attraction effect).

Among the first models to consider both space and time to describe movement of organisms is the Fisher’s prototype reaction–diffusion equation [10], which is a one-dimensional version as a model for the spread of an advantageous gene in a population, \( \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + ku(1 - \frac{u}{\phi}) \), where \( u(x, t) \) is the vector of population densities at spatial position, \( x \in \Omega \subset \mathbb{R} \), in time \( t \), and \( f(x, t) = ku(1 - \frac{u}{\phi}) \) is a function representing logistic growth of population \( u \). The term, \( D \frac{\partial^2 u}{\partial x^2} \), defines the random diffusion of the gene within the population \( u \) and \( D \) is the diffusion coefficient which in practice is measured in laboratories using some fairly simple experiments [42]. Fisher’s equation is an initial-boundary value problem requiring both an initial population density \( u(x, 0) \), together with boundary conditions.

By setting one of the dispersal coefficients to unity, and ignoring the implicit assumption of homogeneity of species with respect to space, and taking the spatial structure (heterogeneity) into account by incorporating the spatial variations of species through addition of dispersal terms to the non-dimensionalised model (7)–(9), directly leads to the following dimensionless form:

\[
\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + ru(1-u) - \frac{\mu u v}{1 + \phi u + \psi w} - \frac{\eta w}{1 + \phi u + \psi w} \quad x \in [a, b],
\]

(13)
The complex exponential, $e^{ikx} = \cos kx + i \sin kx$ is a simplified way of representing the spatial wave having a wave number $k$. It should be clearly noted that, at the co-existence equilibrium, the first term of $\dot{u} + \dot{v} + \dot{w} = 0$ and $\dot{w} + \dot{v} + \dot{u} = 0$ leads to zero time derivatives. Using the approach developed by [53], a linearisation of the reaction–diffusion system (13)–(16) is carried out by defining:

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

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

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

Linearization of the reaction terms is simply $J^\top (\delta u \delta v \delta w)^T$, where $J$ is the reaction variational matrix (Jacobian) evaluated at the steady states and $T$ denotes the usual matrix transpose operation. The following linearized equation is obtained:

$$\frac{\partial}{\partial t} \left[ \begin{array}{c} \delta u \\ \delta v \\ \delta w \end{array} \right] = D \frac{\partial^2}{\partial x^2} \left[ \begin{array}{c} \delta u \\ \delta v \\ \delta w \end{array} \right] + J \left[ \begin{array}{c} \delta u \\ \delta v \\ \delta w \end{array} \right],$$

where $D = \begin{bmatrix} D & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$ and $J = \begin{bmatrix} f_w & f_v & f_w \\ \dot{g}_w & \dot{g}_v & \dot{g}_w \\ \dot{h}_w & \dot{h}_v & \dot{h}_w \end{bmatrix}$

i.e., $D$ is the diagonal dispersal matrix and the entries of the reaction variational matrix are:

$$\dot{f}_w = \left[ r(1 - u^*) - \frac{\mu \eta w^*}{(1 + \phi u^* + \psi w^*)^2} - \frac{\eta \mu w^*}{(1 + \phi u^* + \psi w^*)} \right], \quad \dot{f}_v = \eta \mu w^* \left[ \frac{\psi w^*}{(1 + \phi u^* + \psi w^*)^2} - \frac{\mu}{(1 + \phi u^* + \psi w^*)} \right],$$

$$\dot{f}_w = \eta \mu w^* \left[ \frac{\psi w^*}{(1 + \phi u^* + \psi w^*)^2} - \frac{1}{(1 + \phi u^* + \psi w^*)} \right], \quad \dot{g}_w = \frac{\gamma \eta w^*}{(1 + \phi u^* + \psi w^*)^2}, \quad \dot{g}_v = \frac{\gamma \eta w^*}{(1 + \phi u^* + \psi w^*)^2} + (\beta - \mu), \quad \dot{g}_w = \frac{-\gamma \eta w^*}{(1 + \phi u^* + \psi w^*)^2},$$

$$\dot{h}_w = \frac{\gamma \eta w^*}{(1 + \phi u^* + \psi w^*)^2}, \quad \dot{h}_v = \frac{-\gamma \eta w^*}{(1 + \phi u^* + \psi w^*)^2} \quad \text{and} \quad \dot{h}_w = \frac{\gamma \eta w^*}{(1 + \phi u^* + \psi w^*)^2} + (\beta - 1).$$

It should be clearly noted that, at the co-existence equilibrium, the first term of $\dot{f}_w$ vanishes, $\dot{g}_v = 0$ and $\dot{h}_w = 0$. Stability of the steady states under spatial and temporal variations can easily be established by assuming small heterogeneous spatial perturbations. A widely preferred form [35,48]: $[\delta u \delta v \delta w]^T = [\delta u_0 \delta v_0 \delta w_0]^T e^{it} e^{ikx}$, that is used in analysing a generic reaction–diffusion model (the Brusselator) for a tri-molecular chemical reaction, morphogenesis and pattern formation is used.
For stability of a steady state under any arbitrary small perturbation, Re(λ) < 0 and instability otherwise. The sine waves are common sources of such arbitrary noise and hence stability of the reaction–diffusion system can be deduced with ease. Substituting the defined perturbation form into the linearized equation and simplifying yields:

\[
\lambda \left[ \begin{array}{c} \frac{\partial u_0}{\partial t} \\ \frac{\partial v_0}{\partial t} \\ \frac{\partial w_0}{\partial t} 
\end{array} \right] = -k^2 \mathbf{D} \left[ \begin{array}{c} \frac{\partial u_0}{\partial t} \\ \frac{\partial v_0}{\partial t} \\ \frac{\partial w_0}{\partial t} 
\end{array} \right] + \mathbf{J} \left[ \begin{array}{c} \frac{\partial u_0}{\partial t} \\ \frac{\partial v_0}{\partial t} \\ \frac{\partial w_0}{\partial t} 
\end{array} \right],
\]

which gives the homogeneous equation:

\[
\left( \mathbf{I} + k^2 \mathbf{D} - \mathbf{J} \right) \left[ \begin{array}{c} \frac{\partial u_0}{\partial t} \\ \frac{\partial v_0}{\partial t} \\ \frac{\partial w_0}{\partial t} 
\end{array} \right] = 0.
\]

where \( \mathbf{I} \) is an identity matrix. For a non-trivial solution, \( \det \left( \mathbf{I} + k^2 \mathbf{D} - \mathbf{J} \right) = 0 \), which is a general characteristic equation for reaction–diffusion equations in one spatial dimension [53].

\[
\Rightarrow \left| \begin{array}{ccc} \lambda + P & -\hat{f}_v & -\hat{f}_w \\ -\hat{g}_w & \lambda + Q & -\hat{g}_v \\ -\hat{h}_w & -\hat{h}_v & \lambda + R 
\end{array} \right| = 0.
\]

where \( P = k^2 D - \hat{f}_v, \ Q = k^2 - \hat{g}_v \) and \( R = k^2 - \hat{h}_v \). Further simplification yields:

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

where:

\[
\begin{align*}
a_1 &= P + Q + R, \\
a_2 &= PQ + PR + QR - \left( \hat{g}_w \hat{h}_v + \hat{f}_v \hat{g}_w + \hat{f}_w \hat{h}_v \right), \\
a_3 &= PQR - \left( P \hat{g}_w \hat{h}_v + Q \hat{f}_w \hat{h}_v + R \hat{f}_v \hat{g}_w + \hat{f}_v \hat{g}_w \hat{h}_v + \hat{f}_w \hat{g}_w \hat{h}_v \right).
\end{align*}
\]

Using the general results obtained about local stability, the stability of the equilibrium points of the reaction–diffusion system (13)-(16) then follows. The steady state \((u', v', w')\) is locally asymptotically stable to small perturbations if the parameter values satisfy all conditions, \( a_1 > 0, a_3 > 0 \) and \( a_1 a_2 - a_3 > 0 \), that arise from the Routh–Hurwitz stability criterion for a given characteristic polynomial.

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

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

It is clear that if \( a_3 > 0 \), then \( a_1 > 0 \) and \( a_1 a_2 - a_3 > 0 \) follows. Thus, the stability condition for extinction steady state is \( k^2 (2 + D) > \frac{(2\beta F - r)(\beta - \mu)}{\mu} \) for which \( a_1 > 0, k > \sqrt{\frac{2\beta F - r}{\mu}} \frac{\sqrt{\pi_1 - \pi_2 - \pi_3}}{\pi_1} \) for \( a_2 > 0 \) and when \( a_1 > 0, k^2 > \max\{\tilde{\pi}_1, (\beta - \mu), \beta - 1\} \) for \( a_2 > 0 \). Stability of the extinction steady state depends largely on the wave number \( k \) and dispersal of the interacting prey and predator species. At a high relative dispersal rate i.e., prey dispersing faster than the interfering predators, the extinction equilibrium is stable and unstable otherwise. A relative diffusivity \( D \neq 1 \), i.e., either \( D < 1 \) or \( D > 1 \) implies that one of the species disperses faster than the other. This is one of the requirements of Turing bifurcation in the absence of other complex ecosystem dynamics. A high gain from additional food to predators at low predator mortality rates appears to be a realistic trade-off strategy that raises both the wave number and relative dispersal of species. Turing instability arises if the probability of dispersal i.e. \( P_r = \frac{D_r}{D_t + D_r} \), of the interfering predators is as low as possible i.e. \( P_r \to 0 \). Such dispersal driven ecosystem instability can be introduced to such a predator–prey system through provision of additional food to predators. The nutritional value (predator fertility) gained from such additional food should be high enough to overcome predator natural mortality and this result seems to contradict the notion of “meat is meat” to a predator. Hence the importance of considering predator preference for prey in a predator–prey ecosystem for sustainable wildlife management [64,22,21,11].
The predator-free equilibrium point $E_1(1,0,0)$ gives $f_{v_1} = -r_1 f_{v_2} = f_{w_1} = \frac{q}{1+r_1}$, $g_{v_2} = \frac{q}{1+r_1} \beta - \mu$, $h_{w_1} = \frac{q}{1+r_1} \beta - 1$ and the other partial derivatives vanish. Thus, $P = k^2 D + r$, $Q = k^2 + \sigma + \mu$ and $R = k^2 + \sigma + 1$, where $\sigma = -(\frac{q}{1+r_1} + \beta)$ for which the coefficients of the characteristic equation reduce to:

$$a_1 = k^2(2 + D) + 2\sigma + r + \mu + 1,$$

$$a_2 = \hat{\pi}_1 k^2 + \hat{\pi}_2 \hat{\pi}_3 \quad \text{where} \quad \hat{\pi}_1 = 2D + 1, \quad \hat{\pi}_2 = (D+1)(\mu + 1) + 2(\sigma(D+1) + r)k\hat{\pi}_3$$

$$a_3 = (k^2 D + r)(k^2 + \mu + \sigma)(k^2 + 1 + \sigma).$$

The Routh–Hurwitz criteria are satisfied if $k^2(2 + D) > -\sigma - (\mu + r + 1)$ under which positive wave numbers and relative diffusivity are guaranteed since $-\sigma > 0$ which further implies that $| - \sigma | > (\mu + r + 1)$. This condition about $a_1$ is equivalent to $k^2(2 + D) > \frac{\epsilon \sigma K_b(1 - F) - \mu_0 \sigma}{\mu_i(1 + aK_0)}$, which holds provided $\epsilon F > (r_0 + \mu_0 + \mu_i)(1 + aK_0)$. Since $\epsilon F$ is a measure of quality of additional food as a result of predator fertility gain, this indicates that quality of additional food to predators as compared to prey quality can always relieve predation pressure from prey. Though, as most theories of biological control results reveal [60,54,63,41,52], this might not be a trade-off strategy since it might result in excessive predation sooner or later. Furthermore,

$$k > \sqrt{\frac{-\hat{\pi}_2 \pm \sqrt{\hat{\pi}_2^2 - 4\hat{\pi}_1 \hat{\pi}_3}}{2\hat{\pi}_1}} \quad \text{and} \quad k^2 > \max\{|-\sigma| - \mu, |-\sigma| - 1\}$$

$$= \max\left\{\frac{\epsilon \sigma K_b(1 - F) - |\epsilon F - \mu_0|}{\mu_i(1 + aK_0)}, \frac{\epsilon \sigma K_b(1 - F) + |\epsilon F - \mu_i|}{\mu_i(1 + aK_0)}\right\}$$

show that the diffusive stability and/or instability occurs for an infinite range of wavenumber $k$. The instability that occurs has been observed to form spatial patterns which arise from a combination of various sine waves within a finite range of wavelengths resulting into a non-trivial wave pattern [35,48,25]. Further computations leads to $a_1 a_2 - a_3 = [2k^2 + \mu + 1 + 2\sigma][k^2(D + 1) + r + \sigma + 1 + \sigma][k^2(D + 1) + \mu + r + \sigma]$, which is reminiscent of the Hurwitz condition for the extinction equilibrium. Hence, similar stability results are deduced which suggests the feasibility of a wave number $k > 0$ for which the species’ dispersal can be controlled. The positive value of the required wave number is assured since $-\sigma > 0$. Permanence (Proposition 2.1) of model system (7)–(9) leads to the following theorem [61] that ensures local stability of the co-existence equilibrium under species’ interference and competitive exclusion.

Stability of the remaining steady states can be established although mathematically more complex. Though computation of the coefficients, $a_i$’s was possible, reducing the Routh–Hurwitz quantity $a_1 a_2 - a_3$, to a mathematically tractable form is not possible. It will now be proved that, for the model system (7)–(9), the prey population has a finite upper-limit resulting in the fact that it is impossible for prey populations to become infinite.

### 2.4.1. Preliminaries

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

**Definition 2.4.** \( \{ x_A(t) : -\infty < t < \infty \} \) with $x_A(0) = A$ defines any orbit $Y$ of any phase curve through any arbitrary point $A$. Similarly, \( \{ x_A(t) : t \in \mathbb{R}^- \} \) with $x_A(0) = A$ and \( \{ x_A(t) : t \in \mathbb{R}^+ \} \) with $x_A(0) = A$ define positive and negative ($Y^+$ and $Y^-$) semi-orbits, respectively.

**Definition 2.5** [61]. The set of points in $\mathbb{R}^2$ which are approached along an orbit $Y$ with increasing time i.e., $t \rightarrow +\infty$, is the $\omega$-limit set of the orbit. The $\alpha$-limit set of $Y$ is similarly defined as the set of points approached with decreasing time i.e., $t \rightarrow -\infty$.

**Definition 2.6** [61]. A periodic orbit $Y_0$, that is the $\omega$-limit set or the $\alpha$-limit set for all other orbits in some neighbourhood of $Y_0$ is called a limit cycle.

**Theorem 2.1.** For the three dimensional competitive and permanent system (7)–(9), let $E_4(w', v', w')$ be hyperbolic. Then the stable manifold $\tilde{Y}$ of $E_4$, is one dimensional, and for any $x Y$, the $\omega$-limit set $\omega(x)$ is a non-trivial periodic orbit in $\Omega$. 


Theorem 2.2. Any solution of system (7)–(9) is bounded.

Lemma 2.1. Suppose that \((u(t), v(t), w(t))\) is a solution to system (7)–(9). In addition, assuming that for some \(\epsilon > 0\), \(u(t_0) = u, v(t_0) = v, w(t_0) = w\) with \(v > \frac{\beta}{\mu - \beta} + \frac{\epsilon}{\mu} W > \frac{\beta}{\mu} + \frac{\epsilon}{\mu} W\) and \(u > v\). Then there exists \(t^* > t_0\) such that \(u(t^*) = u^*\).

Proof of Lemma 2.1. The lemma above is proved and used later to prove Theorem 2.2. Since \(\dot{f}(u, v, w) = 0\) and \(\frac{\partial f}{\partial u}, \frac{\partial f}{\partial v}, \frac{\partial f}{\partial w}\) are increasing, then \(u > v\) leads to \(\dot{f}(u, v, w) > 0\). Without loss of generality, it follows that:

\[
\dot{f}(u, v, w) = \dot{f}(u, v, w) + \left[\dot{g}(u, v, w) + \dot{h}(u, v, w)\right] = ru(1-u) + (\beta - \mu)\nu + (\beta - 1)w
\]

\[
< -2r + (\beta - \mu)\nu + (\beta - 1)w, \quad \text{since; max}\{ru(1-u)\} = \frac{1}{2}r < 2r
\]

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

Proof of Theorem 2.1. Since Theorem 2.2 implies Theorem 2.1, it suffices to prove the former. The positive octant \(R^3_+ = \{(u, v, w) \in R^3 : u(0) > 0, v(0) > 0, w(0) > 0\}\) is invariant under the dynamical system. The solution never leaves \(R^3_+\) since \(\frac{\partial f}{\partial u} = 0\) when \(u \equiv 0, \frac{\partial f}{\partial v} = 0\) when \(v \equiv 0\) and \(\frac{\partial f}{\partial w} = 0\) when \(w \equiv 0\). If \(0 < u < 1\), then for every \(u < 1\), \(-\frac{\partial f}{\partial u} = -\frac{\partial f}{\partial v} \leq 0\) and \(ru(1-u) \leq 0\) which implies that \(\dot{f}(u, v, w) \leq 0\). In addition, if \(u < u^*\) (equilibrium solution), then \(\mu > 0\) and \(1 > \beta - \mu\). Consequently, \(\frac{\partial f}{\partial u} > 0\) and \(\dot{f}(u, v, w) = 0\) and \(h(u, v, w) = 0\).

Furthermore, for every solution such that \(v(0) < \frac{\beta}{\mu - \mu}, w(0) > \frac{\beta}{\mu - \mu}\) and \(u(0) > u^*\), there exists some \(v_2, w_2\) such that \(v(t) < v_2, w(t) < w_2\) for all \(t \geq 0\). Applying Lemma 2.1, there is some \(t^*\) such that \(u(t^*) = u^*\). Let \(v_1 = v(t^*), v_1 = w(t^*)\) and then applying Lemma 2.1 once more, it is concluded that there is an orbit \(\gamma(t)\) joining the point \((2, v_1, w_1)\) and the line \(u = u^*\), in the point \((2, v_2, w_2)\). Since for \(u < u^*\), \(v(t)\) and \(w(t)\) are decreasing, and the orbit \((u(t), v(t), w(t))\) cannot cross the orbit \(\gamma(t)\), then \(v(t) < v_2, w(t) < w_2\) for all \(t \geq 0\). The proof of the theorem is concluded by noting that if \(v(0) < \frac{\beta}{\mu - \mu}\) and \(v(0) < \frac{\beta}{\mu - \mu}\) or \(u(0) < u^*\), lead to the previous scenarios.

Corollary 2.1. Suppose \(\mu_i > \epsilon \dot{F}\) and \(\mu_i > (1 - F) \frac{\beta^2}{2 \mu^2}\), then system (7)–(9) has periodic solutions.

Proof. From Theorem 2.2, all interior solutions are bounded.

The qualitative analysis in Section (2.4) shows that under the hypotheses of the corollary, equilibrium point \(E_3\) is a stable steady state. Then by the Poincaré–Bendixson Theorem [4,61], an interior solution is either a closed periodic orbit or approaches a closed periodic orbit as \(t \to \infty\).

2.5. On the principle of competitive exclusion

The ecological principle of competitive exclusion asserts that, multiple species cannot indefinitely occupy the same niche. If there are \(n\) populations that depend linearly on \(m\) resources \((m < n)\), then at least one population will vanish and hence, in the long run, only at most \(m\) population can survive \([61,2]\). The equilibria \(E_2(u^*, v^*, 0)\) and \(E_3(u^*, 0, w^*)\) define scenarios where one predator out-competes the other as a result of interspecific interference. Therefore, global stability for the case when one of the predators is out-competed is investigated in this subsection.

The functions \(f(u) = r(1-u), p(u, w) = \frac{ru}{1+uw}, q(u, v) = \frac{ru}{1+uv}, g(v) = \frac{\mu}{\beta - \mu}, \beta = \beta - 1, h(w) = \beta - 1\), are defined as the specific growth rate of prey, functional responses and predator controlled death rates due to presence of additional food. It is noted that the above functions have been non-dimensionalised and satisfy the usual default conditions for predator–prey systems \([27,61]\). The following is a preliminary motivating theorem for the global stability of the out-competition result of the two predators.

Theorem 2.3 (Lyapunov’s stability theorem; \([61]\)). Consider the dynamical system \(x = f(x)\) on some region \(\Omega \subseteq \mathbb{R}^n\) and define the \(O\)-limit of \(x\) as the set \(o(x)\) of \(y \in \mathbb{R}^n\), such that \(x(t_k) \to y\) as \(k \to \infty\) for some sequence \(t_k \to 0\), \(t_k \to \infty\) and \(V: \Omega \subseteq \mathbb{R}^n \to \mathbb{R}\) be continuously differentiable. If for some solution \(t \to x(t)\), the derivative \(V\) satisfies \(V > 0\) or \(\leq 0\), then \(o(x) \cap \Omega\) is contained in the set \(\{x \in \Omega \mid V(x) = 0\}\). Suppose that there exists a Lyapunov function \(V(x)\) such that \(V(x) < 0\) for all \(x \in \mathbb{R}^n\) except at equilibrium solutions \((x^*)\), then the equilibrium point \(x^*\) is globally stable.
Remark 2.3. The maximal invariant set contained in \( \{ x \in \Omega : V(x) = 0 \} \) is a LaSalle’s invariant set. In addition, since any solution starting in \( \omega(x) \) remains there indefinitely, then \( \omega(x) \) is invariant.

Remark 2.4. In Theorem 2.3 above, \( V \) is the Lyapunov function and \( \dot{V}(x) = \sum_{i=1}^{n} \frac{\partial V}{\partial x_i} \dot{x}_i \) is the time derivative of \( V \) along the solutions of the dynamical system \( \dot{x} = f(x) \).

Theorem 2.3 and similar Lyapunov stability theorems have been stated and proved elsewhere [27,61,28], thus, it is justifiable to proceed by using them in establishing the out-competition results. As shown by [7,61,28], a candidate Lyapunov function \( V(u, v, w) \) can be defined such that

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

For \( E_{2}(u', v', 0) \in \mathbb{R}^{3} \), with suitable choices for the constants \( \pi_{11} = \pi_{12} = \gamma \), and because of well known conditions and properties of the functional responses and specific growth rate functions [56,27,61], \( (u, v, w) \) is positive in the region defined by: \( 0 < u < u', 0 < v' < v < \xi_{1}, 0 < w < \xi_{2} \), where \( \xi_{1} \) and \( \xi_{2} \) are positive constants. Thus, the Lyapunov function reduces to:

\[
V(u, v, w) = [\gamma(p(u, w) - p(u', w')) + \gamma(q(u, v) - q(u', v'))] \left[ \frac{uf(u)}{p(u, w)} - \frac{vp(u, w)}{q(u, v)} - w \right] +\ (v - v')[-g(v) + \gamma p(u, w)] + w[-h(w) + \gamma q(u, v)].
\]

At \( E_{2}(u', v', 0) \), the system (13)–(15) reduces to:

\[
u' f(u') - v' p(u') = 0,
\]

\[
u' p(u') + g(v') = 0.
\]

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

\[
\frac{dV}{dt} = \left[ \gamma(p(u, w) - p(u')) + \gamma \frac{p(u, w)}{q(u, v)} (q(u, v) - q(u')) \right] \left[ \frac{uf(u)}{p(u, w)} - \frac{uf(u')}{p(u')} \right] + \left( v - v' \right) \left[ \gamma \frac{q(u, v)}{q(u')} (p(u') - p(u, w)) + (h(0) - h(w)) \right] < 0.
\]

Hence, global asymptotic stability of \( E_{2}(u', v', 0) \) follows if and only if \( \frac{dV}{dt} < 0 \), and this leads to the following lemma.

Lemma 2.2. If in the neighbourhood of \( E_{2}(u', v', 0) \) in the positive cone, the function \( \frac{uf(u)}{p(w, w)} \) is strictly decreasing, then the equilibrium point \( E_{2}(u', v', 0) \) is globally asymptotically stable.

Lemma 2.3. Without loss of generality, the global asymptotic stability of \( E_{3}(u', 0, w') \) follows in a similar fashion.

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

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

The permanence and global stability of the model (7)–(9) depends essentially on local stability, i.e., on the eigenvalues of the Jacobian evaluated at a steady state, of the coexistence equilibrium \( E_{3}(u', v', w') \). The variational matrices evaluated at all equilibrium points give eigenvalues with non-zero real parts i.e., hyperbolic solutions.

2.6. Periodicity and species’ dispersal

Within the game park, prey and predator species diffuse (random movements) and disperse (synchronised motion in defined direction destined to known locations). For example, dispersal rates between female social units of kudus were studied and averaged to 0.5% per individual per year [43]. Thus, a dimensionless migration coefficient \( m = \frac{\partial m}{\partial p} \), where \( m_{p} \) and \( m_{a} \) are migration coefficients of prey and predators, respectively, is incorporated to the reaction–diffusion system (13)–(15), and as defined earlier, \( D = \frac{\partial m}{\partial p} \) remains the relative dispersal coefficient of prey to predators where \( D_{p} \) is the dispersal rate of prey and \( D_{p} \) is the synchronized dispersal rate of the predators. This leads to the advection–reaction–diffusion system:

\[
\frac{\partial u}{\partial t} = D \nabla^{2} u - m \nabla u + f(u, v, w), \tag{19}
\]

\[
\frac{\partial v}{\partial t} = \nabla^{2} v - \nabla v + g(u, v, w), \tag{20}
\]
\[
\frac{\partial w}{\partial t} = \nabla^2 w - \nabla w + \bar{h}(u,v,w),
\]
(21)

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

Using the methods of limit cycle perturbations on Burgers equation \((\frac{\partial}{\partial t} u(x,t) + u(x,t) \frac{\partial}{\partial x} u(x,t) = \sigma \frac{\partial^2}{\partial x^2} u(x,t) + f(x,t))\), the dynamical properties of phase waves in reaction–diffusion equations have been assiduously studied \[38,66,50,48,49,55\]. In the sampled literature, the limit cycle perturbation method has been predominantly used in the analysis of one or two interacting quantities (chemicals and/or populations) in which one or two equation mathematical models have been studied. A variety of qualitative dynamics have been deduced from the generic reaction–diffusion Brusselator model using such limit cycle perturbation methods (cf. Section (2.4)). Other approaches, for example, the time-dependent wave packet approach used \[39\] for analysing qualitatively the quantum dynamics of the Schrödinger equation \((\hbar \frac{\partial}{\partial t} \psi = \hat{H}\psi)\) may also apply to a variety of ecological predator–prey models.

A limit cycle solution is a closed trajectory in the predator–prey space which is not a member of a continuous family of closed trajectories \[61\]. A stable limit cycle trajectory is such that any small perturbation from the trajectory decays to zero. Both prey and predator populations undergo constant oscillations whose amplitudes bear no relationship to the biology of the species involved but only to the initial sizes of their populations, which is quite arbitrary \[3,61\].

**Theorem 2.4** (Poincaré–Bendixson theorem (i); \[4\]). Let the reaction (external force) functions \(f(u,v,w), g(u,v,w)\) and \(h(u,v,w)\) have continuous first partial derivatives in a domain \(\Omega\) of the \(uvw\)-space. Further, let \(\Omega\) be a bounded sub-domain in \(\Omega\), and let \(S\) be the region that consists of \(\Omega\) together with its boundary, i.e., all points of \(S\) are in \(\Omega\). In addition, suppose that \(S\) contains no critical point for system (19)–(21). If there exists a constant \(\tau_0\) such that \(u = \phi(\tau), v = \psi(\tau)\) and \(w = \phi(\tau)\) is a solution to system (19)–(21) that exists and stays in \(S\) for all \(\tau \geq \tau_0\), then system (19)–(21) allows a periodic solution in \(S\); i.e., either \(u = \phi(\tau), v = \psi(\tau)\) and \(w = \phi(\tau)\) is a periodic solution (closed trajectory), or \(u = \phi(\tau), v = \psi(\tau)\) and \(w = \phi(\tau)\) spirals toward a closed trajectory as \(\tau \to \infty\).

**Theorem 2.5** (Poincaré–Bendixson theorem (ii); \[61\]). A bounded semi-orbit that does not approach any singular point is either a closed periodic orbit or approaches a closed periodic orbit.

**Theorem 2.6** (Consequence to Green’s theorem; \[4\]). Let \(f(u,v)\) and \(g(u,v)\) be any two reaction (external force) functions for a two equation framework model. Suppose further that \(f(u,v)\) and \(g(u,v)\) have continuous first partial derivatives in a simply connected domain \(\Omega\) of the \(uv\)-plane. If \(f(u,v) + g(u,v)\) has the same sign throughout \(\Omega\), then there is no closed trajectory lying entirely in \(\Omega\) for the model system of the interacting variables.

By assuming that the advection–reaction–diffusion model (19)–(21) admits a limit cycle with frequency \(\phi_0\), and employing vector notation, the vector of species’ reaction (external force for Burgers’ equation) \(f(u,v) = [f,g,h]^T\), vector of interacting species \(u_0 = [u_0,v_0,w_0]^T\) such that for an initial periodic solution \(u = u_0(\tau)\) for \(\tau = \phi_0t\) for some periods \(T_h\) and \(T_p\). These descriptions yield:

\[
\frac{\partial u_0}{\partial \tau} = f(u_0) \text{ for } u_0(\tau) = \partial u_0(\tau + T_h, T_p).
\]
(22)

As shown by \[38,66,49,55\], with \(\theta = \theta(G,0)\) and any small parameter \(\epsilon\), with the introduction of the following multiple scales:

\[
G = \sqrt{\epsilon} \exp(\phi_0 \sqrt{\epsilon}t), \quad \theta = \epsilon t \exp(\phi_0 \epsilon t), \quad \tau = \epsilon t \exp(\phi_0 \epsilon t), \quad i \in \mathbb{N} \quad \epsilon, \phi_0 > 0
\]

into the advection–reaction–diffusion system (19)–(21) leads to the following linear equations:

\[
\frac{\partial u_0}{\partial \tau} = f(u_0) \text{ where } f(u_0) = \left[f(u_0,v_0,w_0), g(u_0,v_0,w_0), h(u_0,v_0,w_0)\right]^T
\]
(23)

and

\[
[a_{ij}] = [P_{\chi}]^T \quad \text{for } i,j = 1,2,3.
\]

where

\[
\begin{align*}
\alpha_{11} &= \phi_0 \frac{\partial}{\partial u_0} - \frac{\partial}{\partial v_0}(u_0,v_0,w_0), \\
\alpha_{12} &= -\frac{\partial}{\partial u_0}(u_0,v_0,w_0), \\
\alpha_{13} &= -\frac{\partial}{\partial u_0}(u_0,v_0,w_0), \\
\alpha_{21} &= -\frac{\partial}{\partial u_0}(u_0,v_0,w_0), \\
\alpha_{22} &= \phi_0 \frac{\partial}{\partial u_0} - \frac{\partial}{\partial v_0}(u_0,v_0,w_0), \\
\alpha_{23} &= -\frac{\partial}{\partial u_0}(u_0,v_0,w_0), \\
\alpha_{31} &= -\frac{\partial}{\partial u_0}(u_0,v_0,w_0), \\
\alpha_{32} &= -\frac{\partial}{\partial u_0}(u_0,v_0,w_0), \\
\alpha_{33} &= \phi_0 \frac{\partial}{\partial u_0} - \frac{\partial}{\partial v_0}(u_0,v_0,w_0)
\end{align*}
\]

are the entries of the non-adiabatic potential matrix, the superscript \(T\) denotes the usual transpose operation and \(P_{\chi}\)'s are the heterogeneous terms of the nth order equation. By considering a first order situation, i.e., \(\chi = 1\):

\[
P_{\chi} = -u_0 \frac{\partial}{\partial u_0} m_i u_0 \nabla \theta + D_2 \left(u_0 \nabla \theta^2 + u_0 \nabla^2 \theta\right), \quad i = 1,2,3; \quad \chi = b \text{ for } u_0, \quad \text{otherwise } \chi = p.
\]

Furthermore, as shown by \[66,5\], we define the direct tensor (outer) products: \(\zeta_0 \otimes \phi_0 = [u_0,v_0,w_0]^T, \zeta_1 \otimes \phi_1 = [u_1,v_1,w_1]^T, \zeta_2 \otimes \phi_2 = [u_2,v_2,w_2]^T\), while \(\zeta_1 \otimes \zeta_2 = [u, v, w]^T\) is the non-trivial periodic solution to the adjoint differential equa-
tion \( \tilde{\Gamma} \zeta_0 \otimes \zeta_0 = 0 \), where \( \tilde{\Gamma} = [\tilde{a}_0] \) for which: \( \tilde{a}_{11} = -\varphi_0 \frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{12} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{13} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{21} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{22} = -\varphi_0 \frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{23} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{31} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{32} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), and \( \tilde{a}_{33} = -\varphi_0 \frac{\partial }{\partial n} (u_0, v_0, w_0) \).

The phase wave periodic solvability condition for \( \zeta_i \) and \( \zeta_i \) as used by [38,66], gives:

\[
\begin{align*}
\langle \zeta, \zeta, \zeta \rangle \frac{\partial \Theta}{\partial \Theta} &= \langle \zeta, \zeta, \zeta \rangle \nabla \theta + \langle \zeta, \zeta, \zeta \rangle \nabla^2 \theta + \langle \zeta, \zeta, \zeta \rangle |\nabla \theta|^2 , \\
\Rightarrow \frac{\partial \Theta}{\partial \Theta} &= \hat{\Phi}_1 \frac{\partial \Theta}{\partial \Theta} + \hat{\Phi}_2 \frac{\partial^2 \Theta}{\partial \Theta^2} + \hat{\Phi}_3 |\nabla \Theta|^2 ,
\end{align*}
\]

where \( \hat{\Phi}_1 = [\langle \zeta, \zeta, \zeta \rangle] \), \( \hat{\Phi}_2 \), \( \hat{\Phi}_3 \), being evaluated in accordance to the Poincaré–Bendixon theorem [4,6] over the composite region \( \mathfrak{R}: \zeta_1 = \{ -m_p u_0, -m_p v_0, -m_p w_0 \}^T \), \( \zeta_2 = \{ D_h u_0, D_h v_0, D_h w_0 \}^T \) and \( \zeta_3 = \{ D_d u_0, D_d v_0, D_d w_0 \}^T \) and the periodic solvability condition of \( \zeta_i \) and \( \zeta_i \) as suggested by [50] and motivated by [38]:

\[
\langle \zeta, \zeta, \zeta \rangle = \int_0^{T_p} \int_0^{T_p} \langle \zeta, \zeta, \zeta \rangle d\tau_s d\tau_p
\]

leads to:

\[
\sum_{s-bp} \int_0^{T_p} \int_0^{T_p} \left[ -u_0 \frac{\partial \Theta}{\partial \Theta} - m_p u_0 \nabla \theta + D_p \left( u_0 \nabla \theta + u_0 \nabla^2 \theta \right) \right] d\tau_s d\tau_p = 0 ; \quad \varphi = b \text{ for } u_0 ,
\]

otherwise \( \varphi = p \), where:

\[
\varphi_0 \left[ \frac{\partial \Theta}{\partial \Theta} \right] = [\tilde{a}_0] \tilde{u} , \quad \tilde{u} = [\tilde{u}, \tilde{v}, \tilde{w}]^T ,
\]

for which: \( \tilde{a}_{11} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{12} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{13} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{21} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{22} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{23} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{31} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{32} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \), \( \tilde{a}_{33} = -\frac{\partial }{\partial n} (u_0, v_0, w_0) \) and \( T \) being the matrix/vector transpose. With \( \Theta = \varphi d + \theta \), Eq. (24) becomes:

\[
\frac{\partial \Theta}{\partial \Theta} = \varphi_0 + \hat{\Phi}_1 \nabla \Theta + \hat{\Phi}_2 \nabla^2 \Theta + \hat{\Phi}_3 |\nabla \Theta|^2 .
\]

The species’ dispersal relationships are determined from Eqs. (25) and (26) by using the standard wave characteristics [38,50,49], \( \varphi = \frac{\partial \Theta}{\partial \Theta} \) and \( \kappa = \nabla \Theta \):

\[
\varphi = \varphi_0 + \hat{\Phi}_1 \kappa + \hat{\Phi}_2 \kappa^2.
\]

Using Eqs. (24) and (25), and defining:

\[
\tilde{I}_{\text{Migration}} = \int_0^{T_p} \int_0^{T_p} \left[ \tilde{u}(-m_p u_0) + \tilde{v}(-m_p v_0) + \tilde{w}(-m_p w_0) \right] d\tau_s d\tau_p ,
\]

\[
\tilde{I}_{\text{Diffusion}} = \int_0^{T_p} \int_0^{T_p} \left[ \tilde{u}D_h u_0 + \tilde{v}D_h v_0 + \tilde{w}D_h w_0 \right] d\tau_s d\tau_p ,
\]

\[
\tilde{I}_{\text{Periodicity}} = \int_0^{T_p} \int_0^{T_p} \left[ \tilde{u}u_0 + \tilde{v}v_0 + \tilde{w}w_0 \right] d\tau_s d\tau_p
\]

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

\[
\tilde{\Phi}_1 = \frac{\tilde{I}_{\text{Migration}}}{\tilde{I}_{\text{Periodicity}}} \quad \text{and} \quad \tilde{\Phi}_3 = \frac{\tilde{I}_{\text{Diffusion}}}{\tilde{I}_{\text{Periodicity}}} .
\]

3. Biological interpretation

Due to an overlap in dietary niche, models for the dynamics of interspecific interference of two predators whose activity feeding pattern is regulated by additional food have been analytically analysed for stability, dissipativity, permanence, periodicity and persistence. Group vigilance of the prey and predator interference have been modelled by the so-called Beddington–DeAngelis functional and numerical responses. The effect of additional food on the dispersal trends of the dynamics of
the model has been shown to be of some significance. In particular, the wave number \( k \), and relative diffusion of the species \( D \), whose magnitudes are determined by the nutritional value of additional food, have been shown to provide the necessary stability conditions for analysed equilibrium points. The analytical results show that avoidance of out-competition of one of the interfering predators can be achieved via a given choice of additional predator food. The positivity conditions on the wave number \( k \), is in agreement with prey preference of most predators and hence a deviation from the notion of “meat is meat” to a predator [22,18,23].

The dispersal properties of the species can be tracked from a clear knowledge of the dispersal rate \( (\varphi) \), which is determined from values of periodic solutions \( (\Phi_1, \Phi_2) \) for various estimates of the wave numbers \( (\kappa) \). Furthermore, erratic dynamics and more conspicuous heterogeneous patterns arise as a result of an increase in the wave number (amplitude of underlying oscillations) which in turn leads to unstable periodic solutions. Such heterogeneities, as observed by [47], often result in constant regions of the “boom-and-bust type” in predator–prey ecosystems. The results of the phase wave dynamics that have been deduced from Eq. (24) are related to the Schrödinger equation results [39] for a particle moving in any potential gradient, where the velocity (frequency) of such a particle is assumed to be proportional to the potential gradient. The periodic solutions \( \Phi_1 \) and \( \Phi_2 \), which regulate the species dispersal frequency can be controlled when the right choice of additional food to the interfering predators is established. Basing on the formulated model, the underlying governing principle to the right quality and/or quantity of such additional predator food are the \( I_{\text{Migration}} \) and \( I_{\text{Diffusion}} \) results. Limited movement of species due to additional food to predators can regulate the populations and prevent population annihilation. Hence, this result helps in resolving the Rosenzweig’s paradox of enrichment within species’ spatial interactions. Furthermore, as noted by [44], perturbations in kudu populations due to predation, disease and extreme weather depress populations below half of the mean density set by food limitations. Such perturbations can be regulated by the dispersal rate \( \varphi \) i.e., limit-cycle frequency \( \varphi_0 \), periodic solutions \( \Phi_1 \) and \( \Phi_2 \), and wave numbers \( \kappa \), which has been shown to depend implicitly on both migration and diffusion rates of the interacting species. Besides other parameters, it has been shown (see Section 2.4) that diffusion of the interacting species is regulated by quality of additional food to predators and this gives a basis in dictating species’ dispersal trends.

Despite initially being proposed as a model of turbulent flow analysis and later becoming well known in nonlinear studies [66,5,49], we have carried out a study by formulating a mathematically plausible ecological model equivalent to Burger’s equation to account for both density–dependent migrations and diffusion. Burger’s equation being an advection–reaction–diffusion type, indeed accounts for the species’ dispersal [62]. Solutions of traveling wave fronts that arise from biological invasion have been deduced from the large-time asymptotic results. Advection–reaction–diffusion equations have been identified as efficient tools for addressing questions relating to species’ dispersal, spatial patterning and biological invasions [38,66,62,47,49,5]. This study has addressed the challenges that come along with predator interference and additional food which has led to both unstable and stable equilibria, periodicity and species’ dispersal patterns. This suggests that any attempt by man to enrich the ecosystem aimed at increasing food yield should be well formulated, otherwise it may result in the so-called paradox of enrichment. Such results ecologically suggest that mathematical modelling provide a useful tool to investigate the consequences for a particular ecological system. As observed by [38,50,48,49,55], since analytical methods seem to be rather tedious in solving the advection–reaction–diffusion partial differential type of models, a great deal of analysis of such models has been carried out [38,66,50,49,5] and references in them using numerical methods which are somehow handy per se. Indeed as revealed by [38], the theoretical (qualitative/analytical analyses) results concur with the numerically quantitative results.

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

4. Numerical simulation/quantitative results

Reliability and resolution of demographic and environmental data involves quite some challenges making it difficult to numerically integrate and accommodate most of the influencing factors in population models. In this section, we give numerical demonstrations for the dynamics and pattern of the species by numerically integrating model systems (13)–(14) and (19)–(21) using the solver, pdepe, that uses both finite difference and finite element methods [59]. The Matlab solver, pdepe, is efficient for solving systems of non-linear partial differential equations and solves initial-boundary value problems for systems of parabolic-elliptic PDEs in the one space variable \( x \) and time \( t \) [26,59].

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

4.1. Parameter estimates

Density-dependent changes in both adult kudu survival and juvenile kudu recruitment come into effect when kudu populations exceed about half of the mean density which is dictated by resource (food) limitations [44]. Because annual survival rates of particular age classes (social units) of the kudu species depend on resource availability (annual rainfall), the effective carrying capacity \( K_b \) is a dynamic variable that depends on rainfall [43]. Using a rainfall-driven model, [43] predicted a density of 2.4 kudus per square kilometer which appeared to be higher than the observed density of 1.5 kudus per square kilometer. Basing on the size of AENP’s main camp (approximately 134 km\(^2\)) and the predicted population density of kudu (i.e., 2.4 kudus per square kilometer), the effective carrying capacity \( K_b \) is numerically varied at 320.

### Table 1
Parameter descriptions and their base value estimates.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Numerical value</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \mu_h ), ( \mu_l )</td>
<td>Natural mortality rate</td>
<td>0.0833 &amp; 0.0625</td>
<td>[32,45,46,64]</td>
</tr>
<tr>
<td>( \alpha_h ), ( \alpha_l )</td>
<td>Predation rates</td>
<td>0.1054 &amp; 0.1690</td>
<td>[16], AENP*</td>
</tr>
<tr>
<td>( \psi_h ), ( \psi_l )</td>
<td>Interspecific interference coefficients</td>
<td>0.02365 &amp; 0.0153</td>
<td>[16,17,22]</td>
</tr>
<tr>
<td>( F_h ), ( F_l )</td>
<td>Additional food biomass</td>
<td>0.2500 &amp; 0.5000</td>
<td>Estimate</td>
</tr>
<tr>
<td>( r_s )</td>
<td>Intrinsic growth rate</td>
<td>0.84</td>
<td>[43,44], AENP*</td>
</tr>
<tr>
<td>( K_b )</td>
<td>Carrying capacity for prey species</td>
<td>320</td>
<td>[43,44]</td>
</tr>
<tr>
<td>( c_h ), ( c_l )</td>
<td>Fertility factors due to predation</td>
<td>0.001054 &amp; 0.001690</td>
<td>Estimate</td>
</tr>
<tr>
<td>( c_h ), ( c_l )</td>
<td>Fertility factors due to added food</td>
<td>0.002500 &amp; 0.005000</td>
<td>Estimate</td>
</tr>
<tr>
<td>( \frac{1}{k_h} ), ( \frac{1}{k_l} )</td>
<td>Half saturation constants</td>
<td>10.54 &amp; 16.90</td>
<td>[16]</td>
</tr>
</tbody>
</table>

* Unpublished data.

![Fig. 1. Space–time evolution of species density for model system (13)–(15) when predators face a high interspecific interference as a result of overlap of activity patterns (i.e., \( \psi_h = 0.02365 \times 10^3 \) and \( \psi_l = 0.0153 \times 10^3 \)). \( D_h = 4 \times 10^{-1} \), \( D_p = 9 \times 10^{-1} \). The initial population density chosen as: \( B(0) = 19.0 \), \( H(0) = 6.0 \) and \( L(0) = 3.0 \).](image-url)
Fig. 2. The effect of high predation rates (i.e., \( a_h = 0.1054 \times 10^3 \) and \( a_l = 0.1690 \times 10^3 \)) at high fertility gain (i.e., \( c_5 = 0.001054 \times 10^3 \) and \( c_7 = 0.001690 \times 10^3 \)) when a steady additional food input is maintained. Perturbations have both positive and negative small values around the equilibrium state.

Fig. 3. Contour snapshots of approximate species densities corresponding to parameter values for the respective surface plots in Fig. 1 for model system \((13)-(15)\) i.e., when predators face a high interspecific interference. In all plots; \( \Delta t = 0.02, \Delta h = 0.01, x = 2 \) and \( t = 3 \), and for any initial population and perturbations about the steady state tends to the steady state asymptotically.
Fig. 4. Snapshots of approximate species densities corresponding to parameter values for the respective surface plots in Fig. 2 i.e., high predation rates that results in high fertility gain. Any initial population and perturbations about the steady state tends to the steady state asymptotically.

Fig. 5. Space–time evolution of species density for model system (19)-(21) when predators face a high interspecific interference as a result of overlap of activity patterns, same as Fig. 1 (i.e., $w_h = 0.02365 \times 10^2$ and $w_i = 0.0153 \times 10^2$). Dispersal rates: $D_b = 4 \times 10^{-1}$, $D_p = 9 \times 10^{-1}$, $m_b = 6.5 \times 10^{-1}$ and $m_p = 3.5 \times 10^{-1}$. 
On average, female lions in the wild live up to 17 years and the males live up to 15 years \[46,32\]. Due to less stress of defending their territories and hunting, lions living in captivity have longer life spans (25 years) than when in the wild (game parks). Beyond the first few years of life, mortality threats for lions appear due to fighting amongst males, starvation, and poaching/killing by humans \[32,65\]. Less than 10% of male lions reach old-age as a result of these factors. Only a small percentage of lions die of natural causes, whereas 75% of lions die by being caught in snares, shot by poachers, or killed in fights with rival lions \[32,65\]. Various studies show that females give birth to a litter of 1–6 cubs (average 3 cubs) after a gestation period of 110–120 days (approximately 4 months) \[46,32,45\]. According to \[32,45\], the mortality rate of lions is high (more than half do not survive the first year) and only 20% of cubs reach the age of 2 years. Demographic computation of life expectancy of a species being \(\mu^{-1}\), we estimate mortality rates \(\mu_l = \frac{1}{16} \approx 0.0625\) for lions and \(\mu_h = \frac{1}{12} \approx 0.0833\) for spotted hyaenas.

Based on regression analysis results, various functional forms of annual survival rates \(S = f(R/H)\) that are related to the law of diminishing returns and the satiation effects have been proposed and studied \[43\]. Kudu mortality which involves both pre- and post-natal losses combined with female infertility, is estimated from the calf to cow ratio and normally about half of the annual calf mortality occurs shortly after birth \[44,43\].

Despite evidence of fluctuations in mortality that depend on nutritional well-being as influenced by rainfall relative to kudu density, predation is responsible for a background mortality level of 5–10% per annum in most animals \[44\]. Because rarely do 2-year old female kudus give birth to calves that survive for more than a few weeks \[44\], in kudus, juvenile survival estimates incorporate conception failures and prenatal mortality. Although infertility cases occur, adult female kudus can give birth annually \[44\]. Because newly born kudus lie out and only move with groups after 2–3 months of age, it is difficult to determine kudu natality rates \[44\]. Annual rainfall dictates the survival rates of the various social units of kudus \[44\]. With a sex ratio of 0.5, an adult female kudu (aged more than 3 years) gives birth to 1 calf per year \[43\].

Being alternative prey to lions and spotted hyaenas, kudus are vulnerable to prey switching. In the absence of predation, and at high population density, malnutrition, disease outbreaks, habitat conditions and other weather effects become the major cause of kudu's mortality \[43\]. Unpublished data of AENP show that on average a female lion eats 5 kg whereas a male lion consumes 7.5 kg of prey biomass per day. This gives 6.25 kg as the average lion’s daily prey biomass requirement. A spotted hyaena need 3.8–4.0 kg of meat daily to maintain its conditions \[16\]. Because the kudu has an average adult body mass of 135 kg, it is estimated that on average a lion predate upon 16.90 adult kudus’ biomass per year and a spotted

![Fig. 6](image-url)

**Fig. 6.** The effect of high predation rates (i.e., \(a_h = 0.1054 \times 10^3\) and \(a_l = 0.1690 \times 10^3\)) at high fertility gain, same as Fig. 2 (i.e., \(e_h = 0.001054 \times 10^2\) and \(e_l = 0.001690 \times 10^3\)) when a steady additional food input is maintained. Perturbations have both positive and negative small values around the equilibrium state.
hyaena consumes approximately 10.54 adult kudus’ biomass per year. Considering predation as the number (biomass) of prey killed/eaten per predator per year (unit time) and after rescaling, we estimate \( \chi_t = 0.1690 \text{ yr}^{-1} \) and \( \chi_b = 0.1054 \text{ yr}^{-1} \) as base values. Basing on the offspring production per year after prey biomass consumption, the fertility factors are estimated as a percentage of the respective predation rates and additional food biomass consumption (i.e., \( \epsilon_h = \frac{\chi_t}{100}, \epsilon_l = \frac{\chi_t}{100}, \epsilon_f = \frac{\chi_b}{100} \)).

As in [57], using the “inverse method,” we compute/estimate some of the biological parameters that could not be estimated in accordance with the stability analysis and/or from ecological literature on predator–prey dynamics. Approximations on fine meshes and small time steps are compared for model system (13)–(15) i.e., \( \Delta t = 0.02, \Delta h = 0.01 \). \( x = 2 \) and \( t = 3 \) whereas for model system (19)–(21)\( ; \Delta t = 0.5, \Delta h = 0.005 \). \( x = 1 \) and \( t = 4 \) are considered. With the initial set of data and parameter values as summarised in Table 1, numerical simulations are carried out to examine the behaviour of the model systems due to variations in predator additional food, interspecific interference coefficients, predator fertility rate as a result of predation and feeding on additional food.

5. Discussion

The primary interest, from an ecological point of view, is the situation that involves oscillatory densities of predators and prey. In the numerical experiments, we chose parameter sets that guarantee stable oscillatory dynamics of the system i.e., stable limit cycles, spirals and nodes in the reaction kinetics surrounding an unstable steady state \((u^*, v^*, w^*)\). The numerical solutions reflect the intrinsic properties of the system. Such properties are important in revealing how the system responds to parameter variations. In Figs. 1 and 2, surface numerical results of model system (13)–(15) alongside their analogous contour snapshots (Figs. 3 and 4) are presented. In Figs. 5 and 6, we present the surface plots for model system (19)–(21) that correspond to the parameter values of Figs. 1 and 2, respectively.

A typical response resulting from a steady food input is observed in Figs. 2, 4 and 6. In the absence of additional food supply, starvation gives rise to an unstable stationary state. Thus, a stationary and uniform source of food input leads to a stationary steady state of the system. However, as shown in Figs. 1, 3 and 5, at high interspecific interference as a result of overlap of activity patterns, predators nearly obtain a saturation value under minimal starvation conditions. Availability of food leads to the ordered component of food intake to give a saturation shift towards a saturation level (Figs. 2 and 4). This can arise from neglecting the saturation decline force that emanates from high predator fertility factors. The saturation spread is smaller for high food concentrations and high predation rates than for low cases. This spread as shown in Figs. 3 and 4 eventually reduce as species dispersal rates are increased further. When the food supply is constant in both space and time, the high predator fertility factor arising from the food intake at high predation rates evokes both the “linear conjecture” and the ecological principle of competitive exclusion among the interfering predators (Figs. 1, 5 and 6).

Long periods of damped oscillations behind the invasion front are observed in Fig. 4. High predation rates that results in high fertility gain coupled with high interspecific interference among predators lead to longer temporal dynamical convergence to the stable equilibrium state resulting into long periods of damped oscillations (Figs. 3 and 4). Spatio-temporal heterogeneity is temporarily observed within the interfering predators, however, this does not persist at later times. The stability of the primary steady state has a fundamental impact on the spatio-temporal dynamics of the interacting species (Figs. 3 and 4). Stable travelling waves of the interfering predators exhibit increasingly irregular periodic travelling wave behaviour when key parameter values are increased beyond their baseline values. Such irregular periodic travelling waves, as observed by [47], often result in heterogeneous spatio-temporal patterns of prey (host) and predator (parasitoid) abundance. The generation of such heterogeneous patterns have various ecological implications [47].

From the numerical experimental results, it is noted that spatial dispersal of the predators does not damp out population fluctuations in predator–prey systems involving additional food supply. The heterogeneous patterns continue to evolve over time and a fixed spatial distribution does not arise. This suggests that temporally and spatially fixed niches will not arise in dispersive predator–prey systems that are provided with additional food. Thus, dispersal amplifies the impact of temporal oscillations on the population dynamics leading to the quasi-chaotic heterogeneous spatio-temporal patterns as observed by [47]. The results of this study highlight the value of further investigation of predator–prey interactions that are; provided with additional food, involving predator interference and modelled by reaction–diffusion equations. Furthermore, the results reveal the behaviour of such interactions, while also suggesting ways of improving the models under this study. The many open questions regarding multi–species predator–prey interactions in a spatial setting which have remained unanswered call for more similar/related studies.

Acknowledgements

The authors are grateful for the financial support of the Nelson Mandela Metropolitan University (NMMU) and the South African National Parks service (SANParks) for allowing them not only to use AENP data but also to contact their technical staff. We would like to thank Professor R.J. Naudé who is a Research Associate at NMMU (Department of Biochemistry and Microbiology) for carefully and critically reading the first draft manuscript.