Dynamical behaviour of an ecological system with Beddington-DeAngelis functional response

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Abstract

The objective of this paper is to study the dynamical behaviour systematically of an ecological system with Beddington-DeAngelis functional response which avoids the criticism occurred in the case of ratio-dependent functional response at the low population density of both the species. The essential mathematical features of the present model have been analyzed thoroughly in terms of the local and the global stability and the bifurcations arising in some selected situations as well. The threshold values for some parameters indicating the feasibility and the stability conditions of some equilibria are also determined. We show that the dynamics outcome of the interaction among the species are much sensitive to the system parameters and initial population volume. The ranges of the significant parameters under which the system admits a Hopf bifurcation are investigated. The explicit formulae for determining the stability, direction and other properties of bifurcating periodic solutions are also derived with the use of both the normal form and the central manifold theory (cf. Carr [1]). Numerical illustrations are performed finally in order to validate the applicability of the model under consideration.

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1 Introduction

Mathematical model is an important tool in analyzing the ecological models. Ecological problems are challenging and important issues from both the ecological and the mathematical point of view (cf. Anderson and May [2], Beretta and Kuang [3], Freedman [4], Hadeler and Freedman [5], Hethcote et al. [6], Ma and Takeuchi [7], Venturino [8], Xiao and Chen [9]). The dynamic relationship between predator and its prey has long been and will continue to be one of the dominant themes in both ecology and mathematical ecology due to its universal existence and importance. The most common method of modelling that ecological interactions consists of two differential equations with simple correspondence between the consumption of prey by the admissible predator and their population growth. The traditional predator-prey models have

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been studied extensively (cf. Cantrell and Cosner [10], Cosner et al. [11], Cui and Takeuchi [12], Huo et al. [13] and Hwang [14]), but those are questioned by several biologists. The most crucial element in these models is the “functional response” – the expression that describes the rate at which the number of prey consumed by a predator. Modifications were limited to replacing the Malthusian growth function, the predator per capita consumption of prey functions such as Holling type I, II, III functional responses or density dependent mortality rates. These functional responses depend only on the prey volume \(x\), but soon it became clear that the predator volume \(y\) can influence this function by direct interference while searching or by pseudo interference (cf. Curds and Cockburn [15], Hassell and Varley [16] and Salt [17]). A simple way of incorporating predator dependence in the functional response was proposed by Arditi and Ginzburg [18], who considered this response function as a function of the ratio \(x/y\). The ratio-dependent response function produces richer dynamics than that of all the Holling types responses, but it is often criticized that the paradox occurred at the low densities of both populations size. Normally one would expect that the population growth rate decrease when both the populations fall below some critical volume, because food-searching effort becomes very high. For some ecological interaction ratio-dependent model give the negative feedback. Thus, the Lotka-Volterra type predator-prey model with the Beddington-DeAngelis functional response has been proposed and well studied. Keeping these in mind, the proposed model can be expressed as follows:

\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1(t) \left(1 - \frac{x_1(t)}{K}\right) - \frac{c_1 x_1(t) x_2(t)}{a_1 + x_1(t) + b_1 x_2(t)} \\
\frac{dx_2}{dt} &= -\delta_1 x_2(t) + \frac{c_1 x_1(t) x_2(t)}{a_1 + x_1(t) + b_1 x_2(t)}
\end{align*}
\]  

(1.1)

with the initial conditions \(x_1(0) = x_1^0 > 0\) and \(x_2(0) = x_2^0 > 0\). The functions \(x_1(t), x_2(t)\) are the volumes of prey and predator at any time \(t\). All the system parameters are assumed to be positive and have their usual biological meanings. The functional response \(\frac{c_1 x_1(t) x_2(t)}{a_1 + x_1(t) + b_1 x_2(t)}\) in system (1.1) was introduced by Beddington [19] and DeAngelis et al. [20] as a solution of the observed problem in the classic predator-prey theory. It is similar to the well-known Holling type-II functional response but has an extra term \(b_1 x_2\) in the denominator which models mutual interference between predators. It represents the most qualitative features of the ratio-dependent models, but avoids the “low-densities problem”, which usually the source of controversy. It can be derived mechanistically from considerations of time utilization (cf. Beddington [19]) or spatial limits on predation.

The present study under consideration has been carried out sequentially in the latter sections as follows: The basic assumptions and the model formation are proposed in Section 2. Section 3 deals with some preliminary results. The equilibria and their feasibility are rightly given in Section 4. The local analyses of the system around the boundary as well as interior equilibria are discussed in Section 5. The global analysis of the system around the interior equilibrium is studied at length in Section 6. Simulation results are reported in Section 7 while a final discussion and interpretation of the results of the present study in ecological terms are rightly included in the concluding Section 8.
2 Model formulation

Firstly we replaced the logistics growth function \( r_1 x_1 (1 - \frac{x_1}{k_1}) \) of the prey species by the modified quasi-linear growth function \( r_1 x_1 (1 - \frac{x_1}{x_1 + k_1}) = r_1 \frac{k_1}{x_1 + k_1} x_1 = r_1' x_1 \) \((r' \leq r)\) in order to make the model free from any axial equilibrium. Which fits better for some special type of ecosystem, whereof environmental carrying capacity varies w.r.t. its prey volume, i.e., carrying capacity is always greater than its present prey volume. In the present model we introduce one more predator species in the model (1.1) to make it one step closure to reality. Thus, our final model is extended to the following form:

\[
\begin{align*}
\frac{dx_1}{dt} &= r_1 x_1 (1 - \frac{x_1}{x_1 + k_1}) - \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2} - \frac{c_2 x_1 x_3}{a_2 + x_1 + b_2 x_3}, \\
\frac{dx_2}{dt} &= -\delta_1 x_2 + \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2}, \\
\frac{dx_3}{dt} &= -\delta_2 x_3 + \frac{c_2 x_1 x_3}{a_2 + x_1 + b_2 x_3}
\end{align*}
\]

(2.1)

where \( x_1 \) is the population volume of the two prey species and \( x_2, x_3 \) are the population volumes of the predator species at any time \( t \). It is assumed that all the system parameters are positive constants. Here \( r \) and \( k \) are the growth rate and the half-saturation constant for the prey species, \( \delta_1, \delta_2 \) are the first and second predators death rate respectively. \( c_1, c_2 \) are the maximum number of prey that can be eaten by the first and second predator per unit time respectively; \( \frac{c_1}{a_1}, \frac{c_2}{a_2} \) being their respective half saturation rates while \( e_1, e_2 \) are the conversion factors, denoting the number of newly born first and second predator for each captured prey species respectively \((0 < e_1, e_2 < 1)\). The parameters \( b_1 \) and \( b_2 \) measure the coefficients of mutual interference among the first and second predator species respectively. The terms \( \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2} \) and \( \frac{c_2 x_1 x_3}{a_2 + x_1 + b_2 x_3} \) denote the respective predator responses on the first and second prey species. This type of predator response function is known as Beddington-DeAngelis response function (cf. Beddington [19] and DeAngelis et al. [20]).

3 Some preliminary results

3.1 Existence and positive invariance

Letting, \( x = (x_1, x_2, x_3)^T, f : \mathbb{R}^3 \rightarrow \mathbb{R}^3, F = (f_1, f_2, f_3)^T \), the system (2.1) can be rewritten as \( \dot{x} = f(x) \). Here \( f_i \in C^\infty(\mathbb{R}) \) for \( i = 1, 2, 3 \), where \( f_1 = r_1 x_1 (1 - \frac{x_1}{x_1 + k_1}) - \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2} - \frac{c_2 x_1 x_3}{a_2 + x_1 + b_2 x_3} \), \( f_2 = -\delta_1 x_2 + \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2} \) and \( f_3 = -\delta_2 x_3 + \frac{c_2 x_1 x_3}{a_2 + x_1 + b_2 x_3} \). Since the vector function \( f \) is a smooth function of the variables \((x_1, x_2, x_3)\) in the positive octant \( \Omega^0 = \{(x_1, x_2, x_3) : x_1 > 0, x_2 > 0, x_3 > 0\} \), the local existence and uniqueness of the solution of the system (2.1) hold.

3.2 Persistence

If a compact set \( D \subset \Omega^0 = \{(x_1, x_2, x_3) : x_i > 0, i = 1, 2, 3\} \) exists such that all solutions of (2.1) eventually enter and remain in \( D \), the system is called persistent.

**Proposition 3.1.** The system (2.1) is persistent if the conditions: (i) \( r > \delta_1 + \delta_2 \), (ii) \( x_{11} > \frac{a_2 b_2}{c_2 e_2 - b_2} \) (iii) \( x_{12} > \frac{a_1 b_1}{c_1 e_1 - a_1} \) are satisfied.
Hence, there always exists a positive number \(x_m\) there exists a positive constant \(\gamma\). We now prove that this function is positive at each boundary equilibrium. Let 

\[ V(x_1, x_2, x_3) = x_1^{\gamma_1} x_2^{\gamma_2} x_3^{\gamma_3}, \]

where \(\gamma_1, \gamma_2\) and \(\gamma_3\) are positive constants to be determined. We define

\[
\Pi(x_1, x_2, x_3) = \frac{\dot{V}}{V} = \gamma_1 \left( r - \frac{rx_1}{x_1 + k} - \frac{c_1x_2}{a_1 + x_1 + b_1x_2} - \frac{c_2x_3}{a_2 + x_1 + b_2x_3} \right) + \gamma_2 \left( -\delta_1 + \frac{c_1e_1x_1}{a_1 + x_1 + b_1x_2} \right) + \gamma_3 \left( -\delta_2 + \frac{c_2e_2x_1}{a_2 + x_1 + b_2x_3} \right).
\]

We now prove that this function is positive at each boundary equilibrium. Let \(\gamma_i = \gamma\), for \(i = 1, 2, 3\). In fact at \(E_0\), we have \(\Pi(0, 0, 0) = r - \delta_1 - \delta_2 > 0\) from the condition (i). Moreover, from condition (ii) and (iii), we find the values of \(\Pi\) at \(E_1\) and \(E_2\) respectively,

\[
\Pi(x_{11}, x_{21}, 0) = \gamma \left( -\delta_2 + \frac{c_2e_2x_{11}}{a_2 + x_{11}} \right) > 0,
\]

\[
\Pi(x_{12}, 0, x_{32}) = \gamma \left( -\delta_1 + \frac{c_1e_1x_{12}}{a_1 + x_{12}} \right) > 0.
\]

Hence, there always exists a positive number \(\gamma\) such that \(\Pi > 0\) at the boundary equilibria. Hence \(V\) is an average Lyapunov function and thus, the system (2.1) is persistent. \(\square\)

Since the system is uniformly persistent, there exists \(\sigma > 0\) and \(\tau > 0\) such that \(x_i(t) > \sigma\), for all \(t > \tau, i = 1, 2, 3\).

### 3.3 Boundedness

Boundedness implies that the system is consistent with biological significance. The following propositions ensure the boundedness of the system (2.1).

**Proposition 3.2.** The prey population is always bounded from above.

**Proof.** Before proving that the prey population is bounded above, we need to prove that the predator populations \(x_2\) and \(x_3\) are bounded above. To prove this result, considering the second sub equation of the system (2.1) and one can obtain the following differential inequality:

\[
\frac{dx_2}{dt} \leq -(\delta_1 - c_1e_1)x_2.
\]

Integrating the above differential inequality between the limits 0 and \(t\), we have \(x_2(t) \leq x_2(0)e^{-(\delta_1 - c_1e_1)t}\). Thus, if \(\delta_1 - c_1e_1 > 0\), then it is obviously found a positive number \(\tau_1\) there exists a positive constant \(m_1\) such that \(x_2(t) \leq m_1\), for all \(t \geq \tau_1\). By using the similar argument, one can obtain that, if \(\delta_2 - c_2e_2 > 0\), then corresponding to a positive number \(\tau_2\) there exists a positive constant \(m_2\) such that \(x_3(t) \leq m_2\), for all \(t \geq \tau_2\). Both the results can be written unitedly as \(x_i > m = \min (m_1, m_2)\) for all \(t > \tau_3 = \max (\tau_1, \tau_2), i = 2, 3\), with the additional condition \(\min (\delta_1 - c_1e_1, \delta_2 - c_2e_2) > 0\).
Now from the first sub-equation of (2.1), the following inequality is found
\[ \frac{dx_1}{dt} \leq \frac{(e_1 + e_2)\sigma - rk}{km} \left( \frac{k(rm - (e_1 + e_2)\sigma)}{(e_1 + e_2)\sigma - rk} - x_1 \right). \]
Hence, by using standard but simple argument, we have
\[ \limsup_{t \to +\infty} x_1(t) \leq \frac{krm - (e_1 + e_2)k\sigma}{(e_1 + e_2)\sigma - rk} = w, \quad \text{where} \quad \frac{rm}{e_1 + e_2} < \sigma < \frac{rk}{e_1 + e_2}. \]
\[ \square \]

**Proposition 3.3.** The solutions of (2.1) starting in \( \Omega^0 \) are uniformly bounded with an ultimate bound.

**Proof.** Considering the total environment population \( \chi = x_1 + \frac{x_2}{e_1} + \frac{x_3}{e_2} \). Using the theorem on differential inequality (cf. Birkhoff and Rota [22]) and following the steps of Haque and Venturino [23], Sarwardi et al [24], boundedness of the solution trajectories of this model is established. In particular,
\[ \limsup_{t \to +\infty} \left( x_1 + \frac{x_2}{e_1} + \frac{x_3}{e_2} \right) \leq \frac{(r + 1)k + w}{\rho} = M, \quad \text{where} \quad \rho = \min(1, \delta_1, \delta_2), \quad (3.1) \]
with the last bound is independent of the initial condition.
Hence, all the solutions of (2.1) starting in \( \mathbb{R}^3_+ \) for any \( \theta > 0 \) evolve with respect to time in the compact region
\[ \Omega = \left\{ (x_1, x_2, x_3) \in \mathbb{R}^3_+ : x_1 + \frac{x_2}{e_1} + \frac{x_3}{e_2} \leq M + \theta \right\}. \quad (3.2) \]

4 Equilibria and their feasibility

The equilibria of the dynamical system (2.1) are given as follows:
1. The trivial equilibrium point \( E_0(0, 0, 0) \) is always feasible.
2. (a) The first boundary equilibrium point is \( E_1(x_1, x_2, 0) \). The component \( x_1 \) is a root of the quadratic equation \( l_1 x_1^2 + (l_2 + l_1 k + rkb_1 e_1) x_1 + l_2 k = 0 \), where \( l_1 = (\delta_1 - c_1 e_1), l_2 = a_1 \delta_1 \). If \( l_1 < 0 \), then the quadratic equation in \( x_1 \) possesses a unique positive root and consequently \( x_2 = \frac{(c_1 e_1 - \delta_1) x_1 - a_1 \delta_1}{b_1 \delta_1} \). The feasibility of the equilibrium \( E_1 \) is maintained if the condition \( x_1 > \frac{b_1 \delta_1}{c_1 e_1 - \delta_1} \) is satisfied.
3. (b) The second boundary equilibrium point is \( E_2(x_1, 0, x_3) \). The component \( x_1 \) is the root of the quadratic equation \( m_1 x_1^2 + (m_2 + m_1 k + rkb_2 e_2) x_1 + m_2 k = 0 \), where \( m_1 = (\delta_2 - c_2 e_2), l_2 = a_2 \delta_2 \). If \( m_1 < 0 \), then the quadratic equation in \( x_1 \) possesses a unique positive root and consequently \( x_3 = \frac{(c_2 e_2 - \delta_2) x_1 - a_2 \delta_2}{b_2 \delta_2} \). The feasibility of the equilibrium \( E_2 \) is maintained if the condition \( x_1 > \frac{b_2 \delta_2}{c_2 e_2 - \delta_2} \) holds.
3. The interior equilibrium point is \( E_3(x_1, x_2, x_3) \), where the first component \( x_1 \) is the root
of the following quadratic equation:

$$n_1 x_1^2 + (n_2 + n_1 k + r k b_1 b_2 e_1 e_2) x_1 + n_2 k = 0, \quad (4.1)$$

where $n_1 = b_1 e_1 (\delta_2 - c_2 e_2) + b_2 e_2 (\delta_1 - c_1 e_1)$ and $n_2 = b_2 e_2 \delta_1 a_1 + b_1 e_1 \delta_2 a_2$.

Case I: Let $n_1 < 0$. In this case there exists exactly one positive root of the quadratic equation (4.1) irrespective of the sign of $(n_2 + n_1 k + r k b_1 b_2 e_1 e_2)$.

Case II: Let $n_1 > 0$. In this case there are two possibilities: (i) if $n_2 + n_1 k + r k b_1 b_2 e_1 e_2 > 0$, then there is no positive solution and (ii) if $n_2 + n_1 k + r k b_1 b_2 e_1 e_2 < 0$, then there exists two positive roots or no positive root.

In this present analysis we consider the Case I. Under this assumption the next two components of the interior equilibrium can be obtained as $x_{2*} = \frac{(c_1 e_1 - \delta_1) x_{1*} - a_1 \delta_1}{b_1 \delta_1 - a_2 \delta_2}$, $x_{3*} = \frac{c_2 e_2 - \delta_2 x_{1*} - a_2 \delta_2}{b_2 \delta_2}$.

The feasibility of this important equilibrium point $E_*$ is confirmed under the condition $x_{1*} > \max\left\{\frac{a_1 \delta_1}{c_1 e_1 - \delta_1}, \frac{a_2 \delta_2}{c_2 e_2 - \delta_2}\right\}$. Moreover, the positivity condition of second and third components of the interior equilibrium ensures the impossibility of the Case II.

**Remark:** The feasibility and existences conditions of both the planer equilibria $E_1$ and $E_2$ immediately implies the existence of the unique feasible interior equilibrium point $E_*$. But the existence of the unique feasible interior equilibrium point $E_*$ implies three possibilities: (i) $E_1$ exists and $E_2$ does not exist, (ii) $E_2$ exists and $E_1$ does not exist, (iii) existence of both.

## 5 Local stability and bifurcation

The Jacobian matrix $J(x)$ of the system (2.1) at any point $x = (x_1, x_2, x_3)$ is given by

$$J(x)_{3x3} = \begin{pmatrix}
\frac{r k^2}{(x_1 + k)^2} & \frac{c_1 x_2 (a_1 + b_1 x_2)}{(a_1 + x_1 + b_1 x_2)^2} - \frac{c_2 x_2 (a_2 + b_2 x_2)}{(a_2 + x_1 + b_2 x_2)^2} & -\frac{c_1 x_1 (a_1 + x_1)}{(a_1 + x_1 + b_1 x_2)^2} + \frac{c_2 x_1 (a_2 + x_1)}{(a_2 + x_1 + b_2 x_2)^2} - \delta_1 + \frac{c_2 x_2 (a_2 + x_2)}{(a_2 + x_1 + b_2 x_2)^2} \\
0 & -\delta_2 + \frac{c_2 x_2 (a_2 + x_2)}{(a_2 + x_1 + b_2 x_2)^2} & 0
\end{pmatrix}. \quad (5.1)$$

Its characteristic equation is $\Delta(\lambda) = \lambda^3 + k_1 \lambda^2 + k_2 \lambda + k_3 = 0$, where $k_1 = -\text{tr}(J)$, $k_2 = M$ and $k_3 = -\det(J)$; $M$ being the sum of the principal minors of order two of $J$.

Note that the conditions for occurrence of Hopf bifurcation are that there exists a certain bifurcation parameter $r = r_c$ such that $C_2(r_c) = k_1(r_c)k_2(r_c) - k_3(r_c) = 0$ with $k_2(r_c) > 0$ and $\frac{\partial}{\partial r} (\text{Re}(\lambda(r)))|_{r=r_c} \neq 0$, where $\lambda$ is root of the characteristic equation $\Delta(\lambda) = 0$.

### 5.1 Local analysis of the system around $E_0$, $E_1$, $E_2$

**Stability:** The eigenvalues of the Jacobian matrix $J(E_0)$ are $r$, $-\delta_1$ and $-\delta_2$. Hence $E_0$ is unstable in nature (saddle point). Let $J(E_1) = (\xi_{ij})_{3x3}$ and $J(E_2) = (\eta_{ij})_{3x3}$. Using the Routh-Hurwitz criterion, it can be easily shown that the eigenvalues of the matrices $J(E_1)$ and $J(E_2)$ will have negative real parts iff the conditions $e_1 x_{1i} + x_{2i} > \frac{k(1-b_1 e_1) - a_1}{b_1}$ and $e_2 x_{1i} + x_{3i} > \frac{k(1-b_2 e_2) - a_2}{b_2}$ respectively. Hence the equilibria $E_1$ and $E_2$ are locally asymptotically stable under
Hence the Routh-Hurwitz condition is satisfied for the matrix of
The dynamical system (2.1) undergoes Hopf bifurcation around the
Theorem 5.2. Proof. Let
Then the characteristic equation of the Jacobian matrix
Proof. Let
J_{ij})_{3 \times 3} is the Jacobian matrix at the interior equilibrium point
E_s = x_s of the system (2.1). The components of
J(x_s) are \( J_{11} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{12} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{13} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{21} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{22} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{23} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{31} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{32} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \), \( J_{33} = \frac{c_{12}x_2}{(a_1 + b_1x_1 + b_2x_2)} \).

Then the characteristic equation of the Jacobian matrix \( J(x_s) \) can be written as

\[ \lambda^3 + k_1\lambda^2 + k_2\lambda + k_3 = 0, \]  

(5.1)

where \( k_1 = -\text{tr}(J) = -(J_{11} + J_{22} + J_{33}), k_2 = M_{11} + M_{22} + M_{33} = (J_{11}J_{22} - J_{12}J_{21}) + J_{22}J_{33} + (J_{11}J_{33} - J_{13}J_{31}), k_3 = -\det(J) = -(J_{11}J_{22}J_{33} - J_{12}J_{21}J_{33} - J_{13}J_{31}J_{22}), \) and \( C_2 = k_1k_2 - k_3 = -(J_{11} + J_{22})(J_{33}(J_{11} + J_{22} + J_{33}) + (J_{11}J_{22} + J_{13}J_{31}J_{22})). \)

It is clear that \( k_1 > 0 \) if \( J_{11} < 0 \), i.e., \( k < \min \{a_1 + b_1x_2, a_2 + b_2x_3, a_3 + b_3x_1\} \) and consequently \( C_2 > 0 \). Hence the Routh-Hurwitz condition is satisfied for the matrix \( J_s \), i.e., all the characteristic roots of \( J_s \) are with negative real parts. So the system is locally asymptotically stable around \( E_s \).

**Theorem 5.2.** The dynamical system (2.1) undergoes Hopf bifurcation around the interior equilibrium point \( E_s \) whenever the critical parameter value \( r = r_c \) contained in the domain

\[ D_{HB} = \left\{ r_c \in \mathbb{R}^+ : C_2(r_c) = k_1(r_c)k_2(r_c) - k_3(r_c) = 0 \text{ with } k_2(r_c) > 0 \text{ and } \frac{dC_2}{dr}\bigg|_{r=r_c} \neq 0 \right\}. \]

**Proof.** The equation (5.1) will have a pair of purely imaginary roots if \( k_1k_2 - k_3 = 0 \) for some set of values of the system parameters. Let us now suppose that \( r = r_c \) be the value of \( r \) satisfying the condition \( k_1k_2 - k_3 = 0 \). Here only \( J_{11} \) contains \( r \) explicitly. So, we write the equation \( k_1k_2 - k_3 = 0 \) as an equation in \( J_{11} \) to find \( r_c \) as follows:

\[ h_1J_{11}^2 + h_2J_{11} + h_3 = 0, \]

(5.2)

where \( h_1 = J_{22} + J_{33}, h_2 = -J_{22}^2 + J_{33}^2 - J_{13}J_{31} - J_{12}J_{21}, h_3 = (J_{22} + J_{33})J_{22}J_{33} - J_{13}J_{31}J_{22} - J_{12}J_{21}J_{33} - J_{13}J_{31}J_{22} - J_{12}J_{21}J_{33} - J_{13}J_{31}J_{22}. \)
\( J_{12}J_{21}J_{22} \).

Thus, \( J_{11} = \frac{1}{2h_1}(-h_2 \pm \sqrt{h_2^2 - 4h_1h_3}) = J_{11}^* \).

Or,

\[
J_{11} = \frac{(x_1 + k)^2}{k^2} \left[ J_{11}^* + \frac{c_1x_2(a_1 + b_1x_2)}{(a_2 + x_1 + b_2x_2)^2} - \frac{c_2x_3(a_2 + b_2x_3)}{(a_2 + x_1 + b_2x_3)^2} \right] = r_c. \tag{5.3}
\]

Using the condition \( k_1k_2 - k_3 = 0 \), from equation (5.1) one can obtain

\[(\lambda + k_1)(\lambda^2 + k_2) = 0, \tag{5.4}\]

which has three roots \( \lambda_1 = +i\sqrt{k_2}, \lambda_2 = -i\sqrt{k_2}, \lambda_3 = -k_1 \), so there is a pair of purely imaginary eigenvalues \( \pm i\sqrt{k_2} \). For all values of \( \lambda \), the roots are, in general, of the form \( \lambda_1(r) = \xi_1(r) + i\xi_2(r), \lambda_2(r) = \xi_1(r) - i\xi_2(r), \lambda_3(r) = -k_1(r) \).

Differentiating the characteristic equation (5.1) w.r.t. \( r \), we have

\[
\frac{d\lambda}{dr} = \frac{\lambda^2\dot{k}_1 + \lambda\dot{k}_2 + \dot{k}_3}{3\lambda^2 + 2k_1\lambda + k_2} \lambda = i\sqrt{k_2}
\]

\[
\frac{\dot{k}_3 - k_2\dot{k}_1 + ik_2\sqrt{k_2}}{2(k_2 - ik_1\sqrt{k_2})}
\]

\[
\frac{\dot{k}_3 - (k_1\dot{k}_2 + k_1\dot{k}_2)}{2(k_1^2 + k_2)} + i\frac{\sqrt{k_2}(k_1\dot{k}_3 + k_2\dot{k}_2 - k_1\dot{k}_1k_2)}{2k_2(k_1^2 + k_2)}
\]

\[
\frac{\dot{dC}}{d^2} + i\left[ \frac{\sqrt{k_2}\dot{k}_2}{2k_2} \right] \right] = 0. \tag{5.5}
\]

Hence,

\[
\frac{d}{dr}(\text{Re}(\lambda(r))) \big|_{r = r_c} = -\frac{dC}{dr} \big|_{r = r_c} \neq 0. \tag{5.6}
\]

Using the monotonicity condition of the real part of the complex root \( \frac{d\text{Re}(\lambda(r))}{dr} \big|_{r = r_c} \neq 0 \) (cf. Wiggins [27], pp. 380), one can easily establish the transversality condition \( \frac{dC}{dr} \big|_{r = r_c} \neq 0 \), to ensure the existence of Hopf bifurcation around \( E_* \).

## 6 Global analysis of the system around the interior equilibrium

### 6.1 Direction of Hopf bifucation of the system (2.1) around \( E_* \)

In this Section we study on the direction of Hopf bifucation around the interior equilibrium. From the model equations (2.1), we have

\[
\dot{x} = f(x), \tag{6.1}
\]
where \( x = (x_1, x_2, x_3)^t \), \( f = (f^1, f^2, f^3)^t = \begin{pmatrix} r x_1 \left( 1 - \frac{x_1}{x_1 + k} \right) - \frac{c_1 x_2 x_3}{a_1 + x_1 + b_1 x_2} - \frac{c_2 x_1}{a_2 + x_1 + b_2 x_3} \\ -\delta_1 x_2 + \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2} \\ -\delta_2 x_3 + \frac{c_2 x_1 x_2}{a_2 + x_1 + b_2 x_3} \end{pmatrix} \).

Here, at \( x = x_* \), \( f = 0 \). Let \( y = (y_1, y_2, y_3) = (x_1 - x_1^*, x_2 - x_2^*, x_3 - x_3^*) \). Putting in equation (6.1), we have

\[
y = J(x_1^*, x_2^*, x_3^*) y + \phi, \quad (6.2)
\]

where the components of nonlinear vector function \( \phi = (\phi_1, \phi_2, \phi_3)^t \) are given by

\[
\phi_i = f^i_{x_1 x_1} y_1^2 + f^i_{x_1 x_2} y_2^2 + f^i_{x_1 x_3} y_3^2 + 2f^i_{x_1 x_2} y_1 y_2 + 2f^i_{x_1 x_3} y_1 y_3 + 2f^i_{x_1 x_2} y_2 y_3 + \text{h.o.t.}, \quad i = 1, 2, 3. \quad (6.3)
\]

The coefficients of nonlinear terms in \( y_i, i = 1, 2, 3 \) are given by

\[
\begin{align*}
f^1_{x_1 x_1} &= -\frac{2p^2}{(x_1 + k)^3} + \frac{2c_1 x_2 (a_1 + b_2 x_2)}{(a_1 + x_1 + b_1 x_2)^3}, \\
f^1_{x_1 x_2} &= -\frac{2c_1 x_2 (a_1 + b_1 x_2)}{(a_1 + x_1 + b_1 x_2)^3}, \\
f^1_{x_1 x_3} &= -\frac{2c_1 x_2 (a_1 + b_2 x_2)}{(a_1 + x_1 + b_1 x_2)^3}, \\
f^1_{x_2 x_2} &= \frac{2b_1 c_1 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_1 + x_1 + b_2 x_2)^3}, \\
f^1_{x_2 x_3} &= \frac{2b_1 c_1 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_1 + x_1 + b_2 x_2)^3}, \\
f^1_{x_3 x_3} &= \frac{2b_1 c_1 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_1 + x_1 + b_2 x_2)^3}, \\
f^2_{x_1 x_1} &= 0, \\
f^2_{x_1 x_2} &= 0, \\
f^2_{x_1 x_3} &= 0, \\
f^2_{x_2 x_2} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3}, \\
f^2_{x_2 x_3} &= 0, \\
f^2_{x_3 x_3} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3}, \\
f^3_{x_1 x_1} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3}, \\
f^3_{x_1 x_2} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3}, \\
f^3_{x_1 x_3} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3}, \\
f^3_{x_2 x_2} &= 0, \\
f^3_{x_2 x_3} &= 0, \\
f^3_{x_3 x_3} &= 0, \\
f^3_{x_1 x_2} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3}, \\
f^3_{x_1 x_3} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3}, \\
f^3_{x_2 x_3} &= \frac{2c_1 c_2 x_2 (a_1 + x_1 + b_1 x_2)^3}{(a_2 + x_1 + b_2 x_3)^3},
\end{align*}
\]

Let \( P \) be the matrix formed by the column vectors \((u_2, u_1, u_3)^t\), which are the eigenvectors corresponding to the eigenvalues \( \lambda_{1,2} = \pm i\sqrt{k_2} \) and \( \lambda_3 = -k_1 \) of \( J(x_{1^*}, x_{2^*}, x_{3^*}) \), then

\[ J(x_{1^*}, x_{2^*}, x_{3^*}) u_2 = i\sqrt{k_2} u_2, \quad J(x_{1^*}, x_{2^*}, x_{3^*}) u_1 = -i\sqrt{k_2} u_1, \quad \text{and} \quad J(x_{1^*}, x_{2^*}, x_{3^*}) u_3 = -k_1 u_3. \]

Thus,

\[
P = \begin{pmatrix}
-\frac{j_2}{j_1} & \frac{j_3}{j_1} & \frac{j_5}{j_1} \\
-\frac{j_2}{j_3} & \frac{j_6}{j_3} & \frac{j_5}{j_3} \\
-\frac{j_2}{j_5} & \frac{j_6}{j_5} & \frac{j_5}{j_5}
\end{pmatrix} = (p_{ij})_{3\times3}.
\]

Let us make use of the transformation \( y = Pz \), so as the system (6.2) is reduced to the following one

\[
\dot{z} = P^{-1} J(x_{1^*}, x_{2^*}, x_{3^*}) Pz + P^{-1} \phi = \begin{pmatrix} 0 & -i\sqrt{k_2} & 0 \\
i\sqrt{k_2} & 0 & 0 \\
0 & 0 & -k_1 \end{pmatrix} z + P^{-1} \phi. \quad (6.4)
\]

Here \( P^{-1} = \text{Adj} P \det P = (q_{ij})_{3\times3} \), where

\[
\begin{align*}
q_{11} &= \frac{1}{\det P} \left( \frac{j_2}{j_1} j_3 j_5 j_1 - \frac{j_2}{j_3} j_3 j_5 j_1 \right), \\
q_{12} &= \frac{1}{\det P} \left( \frac{j_1}{j_3} (j_5^2 + k_2) (j_3^2 + k_1) \right), \\
q_{13} &= \frac{1}{\det P} \left( \frac{j_5}{j_3} (j_3^2 + k_1) \right), \\
q_{21} &= \frac{1}{\det P} \left( \frac{j_3}{j_1} (j_5^2 + k_2) (j_2^2 + k_1) \right), \\
q_{22} &= \frac{1}{\det P} \left( \frac{j_5}{j_1} (j_3^2 + k_1) \right), \\
q_{23} &= \frac{1}{\det P} \left( \frac{j_3}{j_1} (j_3^2 + k_1) \right), \\
q_{31} &= \frac{1}{\det P} \left( \frac{j_1}{j_3} (j_5^2 + k_2) (j_3^2 + k_1) \right), \\
q_{32} &= \frac{1}{\det P} \left( \frac{j_1}{j_3} (j_5^2 + k_2) \right), \\
q_{33} &= \frac{1}{\det P} \left( \frac{j_5}{j_3} (j_3^2 + k_1) \right).
\end{align*}
\]

The system (6.4) can be written as

\[
\frac{dz_1}{dt} = \begin{pmatrix} 0 & -\sqrt{k_2} \\
\sqrt{k_2} & 0 \end{pmatrix} \begin{pmatrix} z_1 \\
z_2 \end{pmatrix} + F(z_1, z_2, z_3), \\
\frac{dz_2}{dt} = -k_1 z_3 + G(z_1, z_2, z_3)
\]

\[ d z_3 dt = -k_1 z_3 + G(z_1, z_2, z_3). \]
From the equations (6.8) and (6.6), we have

\[ \dot{z}_3 = -k_1z_3 + q_{31}\phi_1 + q_{32}\phi_2 + q_{33}\phi_3 \] (6.9)

Therefore,

\[ \dot{z}_3 = \begin{pmatrix} 0 \\ \sqrt{k_2} \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} = \sqrt{k_2}b_{12}z_1^2 + \sqrt{k_2}(b_{22} - b_{11})z_1z_2 - \sqrt{k_2}b_{12}z_2^2 \] (6.8)

Using (6.4) and (6.6), we have

\[ \dot{z}_3 = \frac{1}{2} (b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2) \] (6.7)

On the center-manifold (cf. Carr [1], Kar [28])
Comparing the coefficients of $z_1^2$, $z_1 z_2$ and $z_2^2$ from both sides, we have
\[
\sqrt{k_2} b_{12} + \frac{k_1}{2} b_{11} = \Omega_1, \quad (6.10)
\]
\[
-\sqrt{k_2} (b_{11} - b_{22}) + k_1 b_{12} = \Omega_2, \quad (6.11)
\]
\[
-\sqrt{k_2} b_{12} + \frac{k_1}{2} b_{22} = \Omega_3. \quad (6.12)
\]
From equations (6.10), (6.11) and (6.12), we have
\[
\begin{pmatrix}
\frac{1}{2}k_1 & \sqrt{k_2} & 0 \\
-k\sqrt{k_2} & k_1 & \sqrt{k_2} \\
0 & -\sqrt{k_2} & \frac{1}{2}k_1
\end{pmatrix}
\begin{pmatrix}
b_{11} \\
b_{12} \\
b_{22}
\end{pmatrix} =
\begin{pmatrix}
\Omega_1 \\
\Omega_2 \\
\Omega_3
\end{pmatrix}.
\quad (6.13)
\]
The equation (6.13) gives the coefficients $b_{11}$, $b_{12}$ and $b_{22}$ as follows:
\[
b_{11} = \frac{k_2 (\Omega_1 + \Omega_3) - \frac{k_1}{2} (\sqrt{k_2} \Omega_2 - k_1 \Omega_1)}{(\frac{k_1^2}{4} + k_1 k_2)},
\]
\[
b_{12} = \frac{k_2 \Omega_2 - k_2 \sqrt{k_2} (\Omega_3 - \Omega_1)}{(\frac{k_1^2}{4} + k_1 k_2)}.
\]
\[
b_{22} = \frac{k_2 (\Omega_1 + \Omega_3) + \frac{k_1^2 \Omega_3}{2} + \frac{k_1 \sqrt{k_2}}{2} \Omega_2}{(\frac{k_1^2}{4} + k_1 k_2)}.
\]
The flow of the central manifold is characterized by the reduced system as
\[
\frac{d}{dt} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} = \begin{pmatrix} 0 & -\sqrt{k_2} \\ \sqrt{k_2} & 0 \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} + \begin{pmatrix} F^1 \\ F^2 \end{pmatrix}, \quad (6.14)
\]
where $F^1 = q_{11}\phi_1 + q_{12}\phi_2 + q_{13}\phi_3 + h.o.t$, $F^2 = q_{21}\phi_1 + q_{22}\phi_2 + q_{23}\phi_3 + h.o.t$. The stability of the bifurcating limit cycle can be determined by the sign of the parametric expression

$$
\Pi = F^1_{111} + F^2_{112} + F^1_{122} + F^2_{222} + \frac{F^1_{12}(F^1_{11} + F^2_{12}) - F^2_{12}(F^2_{12} + F^1_{22}) - F^1_{11}F^2_{22} + F^1_{22}F^2_{12}}{\sqrt{k_2}},
$$

(6.15)

where $F_{ijk} = \frac{\partial^i F}{\partial x_i \partial x_j \partial x_k}$ at the origin. If the value of the above expression is negative, then the Hopf bifurcating limit cycle is stable and is called a supercritical Hopf bifurcation. If the value is positive, then the Hopf bifurcating limit cycle is unstable and the bifurcation is subcritical.

Here

\[
F^1_{11} = 2q_{11}\left[f_{x_1x_1}^2p_{11}^2 + f_{x_2x_2}^2p_{21}^2 + f_{x_3x_3}^2p_{31}^2 + 2f_{x_1x_2}^2p_{11}p_{31} + 2f_{x_1x_1}^2p_{11}p_{21}\right] + 2q_{12}\left[f_{x_1x_2}^2p_{12}^2 + f_{x_2x_2}^2p_{22}^2 \times p_{21}^2 + 2f_{x_1x_2}^2p_{11}p_{21}\right] + 2q_{13}\left[f_{x_1x_2}^2p_{11}^2 + f_{x_3x_3}^2p_{31}^2 + 2f_{x_1x_2}^2p_{11}p_{31}\right],
\]

\[
F^1_{12} = 2q_{11}\left[f_{x_1x_1}^2p_{11}p_{12} + f_{x_2x_2}^2p_{21}p_{22} + f_{x_3x_3}^2p_{31}p_{32} + f_{x_1x_2}^2p_{11}p_{31} + f_{x_1x_2}^2p_{11}p_{22}\right] + 2q_{12}\left[f_{x_1x_2}^2p_{11}p_{12} + f_{x_2x_2}^2p_{21}p_{22} + f_{x_1x_2}^2p_{11}p_{21} + p_{22}p_{11}\right] + 2q_{13}\left[f_{x_1x_2}^2p_{11}p_{12} + f_{x_3x_3}^2p_{31}p_{32} + f_{x_1x_2}^2p_{11}p_{31} + p_{22}p_{11}\right],
\]

\[
F^1_{22} = 2q_{11}\left[f_{x_1x_1}^2p_{22}^2 + f_{x_2x_2}^2p_{22}^2 + f_{x_3x_3}^2p_{32}^2 + 2f_{x_1x_2}^2p_{12}p_{32} + 2f_{x_1x_2}^2p_{12}p_{22}\right] + 2q_{12}\left[f_{x_1x_2}^2p_{12}^2 + f_{x_2x_2}^2p_{22}^2 + f_{x_3x_3}^2p_{32}^2 + f_{x_1x_2}^2p_{12}p_{22}\right],
\]

\[
F^1_{111} = 6q_{11}b_{11}\left[f_{x_1x_1}^2p_{11}p_{13} + f_{x_2x_2}^2p_{21}p_{23} + f_{x_3x_3}^2p_{31}p_{33} + f_{x_1x_2}^2p_{11}p_{31} + f_{x_1x_2}^2p_{11}p_{23} + p_{21}p_{13}\right] + 6q_{12}b_{11}\left[f_{x_1x_1}^2p_{11}p_{13} + f_{x_2x_2}^2p_{21}p_{23} + f_{x_3x_3}^2p_{31}p_{33} + f_{x_1x_2}^2p_{11}p_{31} + p_{13}p_{21}\right]
\]

\[
+ 6q_{13}b_{11}\left[f_{x_1x_1}^2p_{11}p_{13} + f_{x_3x_3}^2p_{31}p_{33} + f_{x_1x_2}^2p_{11}p_{33} + p_{13}p_{31}\right],
\]

\[
F^1_{122} = 2q_{11}\left[f_{x_1x_1}^2(2p_{12}p_{13}b_{12} + p_{11}p_{13}b_{22}) + f_{x_2x_2}^2(2p_{22}p_{33}b_{12} + p_{21}p_{23}b_{22}) + f_{x_3x_3}^2(2p_{32}p_{33}b_{12} + p_{31}p_{33}b_{12} + p_{21}p_{23}b_{22})\right]
\]

\[
+ f_{x_1x_2}^2(2p_{12}p_{13}b_{12} + p_{11}p_{13}b_{22} + p_{21}p_{23}b_{22} + 2p_{22}p_{33}b_{12})\right] + 2q_{12}\left[f_{x_1x_1}^2(2p_{12}p_{13}b_{12} + p_{11}p_{13}b_{22})\right]
\]

\[
+ f_{x_2x_2}^2(2p_{22}p_{33}b_{12} + p_{21}p_{23}b_{22} + 2p_{22}p_{33}b_{12} + p_{13}p_{21}b_{22})\right]
\]

\[
+ 2q_{13}\left[f_{x_3x_3}^2(2p_{32}p_{33}b_{12} + p_{31}p_{33}b_{12})\right]
\]

\[
+ f_{x_1x_2}^2(2p_{12}p_{13}b_{12} + p_{11}p_{13}b_{22} + 2p_{22}p_{33}b_{12} + p_{31}p_{33}b_{12} + 2p_{22}p_{33}b_{12} + p_{31}p_{33}b_{12} + p_{13}p_{21}b_{22}),
\]
\begin{align*}
F^2_{11} &= 2q_1[f^1_{x_1}p^3_{11} + f^1_{x_2}p^3_{21} + f^1_{x_3}p^3_{31} + 2f^1_{x_1}p_1p_{11} + 2f^1_{x_1}p_1p_{12}] + 2q_2[2f^2_{x_1}p^2_{11} + f^2_{x_2}p^2_{21}] \\
F^2_{12} &= 2q_1[f^1_{x_1}p_1p_{12} + f^1_{x_2}p_1p_{22} + f^1_{x_3}p_{11}p_{32} + f^1_{x_3}(p_{11}p_{32} + p_{12}p_{31}) + f^1_{x_1}(p_{12}p_{21} + p_{22}p_{11})] + 2q_2[f^2_{x_1}p_1p_{12} + f^2_{x_2}p_1p_{22}] + 2q_3[f^3_{x_1}p_{11}p_{12} + f^3_{x_3}p_{31}p_{32} + f^3_{x_1}(p_{11}p_{32} + p_{12}p_{31})], \\
F^2_{22} &= 2q_1[f^1_{x_1}p^2_{11} + f^1_{x_2}p^2_{21} + f^1_{x_3}p^2_{31} + 2f^1_{x_1}p_1p_{12} + 2f^1_{x_1}p_1p_{22}] + 2q_2[f^2_{x_1}p^2_{12} + 2f^2_{x_1}p_1p_{22}] + 2q_3[f^3_{x_1}p^2_{12} + f^3_{x_3}p^2_{32} + f^3_{x_1}p_1p_{22}], \\
F^2_{112} &= 2q_1[f^1_{x_1}p_1p_{12} + f^1_{x_2}p_1p_{22} + f^1_{x_3}p_{11}p_{32} + f^1_{x_3}(p_{11}p_{32} + p_{12}p_{31}) + f^1_{x_1}(p_{12}p_{21} + p_{22}p_{11})] + 2q_2[f^2_{x_1}p_1p_{12} + f^2_{x_2}p_1p_{22}] + 2q_3[f^3_{x_1}p_{11}p_{12} + f^3_{x_3}p_{31}p_{32} + f^3_{x_1}(p_{11}p_{32} + p_{12}p_{31})], \\
F^2_{222} &= 6q_2[p^1_{x_1}p_{12}p_{13} + f^1_{x_2}p_2p_{22}p_{23} + f^1_{x_3}p_{31}p_{32}p_{33} + f^1_{x_3}(p_{12}p_{33} + p_{13}p_{32}) + f^1_{x_1}(p_{12}p_{23} + p_{13}p_{22})] + 2q_2[f^2_{x_3}p_{31}p_{32} + f^2_{x_1}p_{12}p_{22}] + 2q_3[f^3_{x_3}p_{31}p_{32} + f^3_{x_1}(p_{12}p_{33} + p_{13}p_{32})].
\end{align*}

### 6.2 Global stability of the system (2.1) around $E_*$

**Theorem 6.1.** The interior equilibrium $E_*$ is globally asymptotically stable if the condition

\((i)\) \quad a_1 a_2 b_1 b_2 r k > (x_{1*} + k)(w + k)(a_1 b_1 c_2 + a_2 b_2 c_1) \quad \text{is satisfied.}\)

**Proof.** Let

\[ L(x_1, x_2, x_3) = L_1(x_1, x_2, x_3) + L_2(x_1, x_2, x_3) + L_3(x_1, x_2, x_3) \tag{6.1} \]

be a positive Lyapunov function, where

\[ L_1 = s_1(x_1 - x_{1*} - x_{1*} \ln \left( \frac{x_1}{x_{1*}} \right)), \quad L_2 = s_2(x_2 - x_{2*} - x_{2*} \ln \left( \frac{x_2}{x_{2*}} \right)), \quad \]

\[ L_3 = s_3(x_3 - x_{3*} - x_{3*} \ln \left( \frac{x_3}{x_{3*}} \right)); \]

$s_1$, $s_2$ and $s_3$ being positive real constants.

This function is well-defined and continuous in Int($R^3_+$). It can be easily verified that the function $L(x_1, x_2, x_3)$ is zero at the equilibrium point $E_*$ and is positive for all other positive values of $(x_1, x_2, x_3)$, and thus $E_*$ is the global minimum of $L(x_1, x_2, x_3)$.

Since the solutions of the system are bounded and ultimately enter the set $\Omega = \{(x_1, x_2, x_3); x_1 > 0, x_2 > 0, x_3 > 0 : x_1 + \frac{x_2}{e^1} + \frac{x_3}{e^2} \leq M + \epsilon, \forall \epsilon > 0\}$, we restrict our study in $\Omega$. The time derivative
of $L$ along with the solutions of the system (2.1) gives (cf. Sarwardi et al. [25], [29])

$$
\frac{dL}{dt} = -s_1 \left[ \frac{rk}{(x_1 + k)(x_1 + k)} - \frac{c_1x_2}{(a_1 + x_1 + b_1x_2)(a_1 + x_1 + b_1x_2)} \right] - \frac{c_2x_3}{(a_2 + x_1 + b_2x_3)(a_2 + x_1 + b_2x_3)}(x_1 - x_1^*)^2 - \frac{c_1e_1(a_1 + b_1)}{(a_1 + x_1 + b_1x_2)(a_1 + x_1 + b_1x_2)}

\times (x_2 - x_2^*)^2 - \frac{c_2e_2(a_2 + b_2)}{(a_2 + x_1 + b_2x_3)(a_2 + x_1 + b_2x_3)}(x_3 - x_3^*)^2

+ \frac{c_1(s_2b_1c_1x_2^* - s_1(a_1 + x_1^*))}{(a_1 + x_1 + b_1x_2)(a_1 + x_1 + b_1x_2^*)} - \frac{c_2(s_2b_2c_2x_3^* - s_1(a_2 + x_1^*))}{(a_2 + x_1 + b_2x_2)(a_2 + x_1 + b_2x_2^*)}

\times (x_1 - x_1^*)(x_3 - x_3^*),

(6.2)

Letting $s_1 = 1$, $s_2 = \frac{a_1^2 + x_1^*}{b_1c_1x_2^*}$ and $s_3 = \frac{a_2^2 + x_1^*}{b_2c_2x_3^*}$, we have

$$
\frac{dL}{dt} \leq - \left[ \frac{rk}{(x_1 + k)(x_1 + k)} - \frac{c_1x_2}{(a_1 + x_1 + b_1x_2)(a_1 + x_1 + b_1x_2)} \right] - \frac{c_2x_3}{(a_2 + x_1 + b_2x_3)(a_2 + x_1 + b_2x_3)}(x_1 - x_1^*)^2

< - \left[ \frac{rk}{(x_1 + k)(w + k)} - \frac{c_1}{a_1b_1} - \frac{c_2}{a_2b_2} \right] (x - x_*)^2

< 0, \text{ by condition (i)}, \quad (6.3)

along all the trajectories in the positive octant except $(x_1^*, x_2^*, x_3^*)$. Also $\frac{dL}{dt} = 0$ when $(x_1, x_2, x_3) = (x_1^*, x_2^*, x_3^*)$. The proof follows from (6.1) and Lyapunov-Lasalle invariance principle (cf. Hale [30]).

Table 1: Schematic representation of our analytical findings: LAS = Locally asymptotically stable, GAS = Globally asymptotically stable, HB = Hopf bifurcation, SHB = Subcritical Hopf bifurcation.

| Equilibria | Feasibility conditions/ parametric restrictions | Stability conditions/ parametric restrictions | Nature |
|------------|-----------------------------------------------|-----------------------------------------------|--------|
| $E_0$      | No Conditions                                 | No Conditions                                 | Unstable |
| $E_1$      | $c_1e_1 > \delta_1$, $x_{11} > \frac{b_1\delta_1}{c_1e_1 - \delta_1}$ | $e_1x_{11} + x_{21} > \frac{k(1-b_1e_1-a_1)}{b_1}$ | LAS |
| $E_2$      | $c_2e_2 > \delta_2$, $x_{12} > \frac{b_2\delta_2}{c_2e_2 - \delta_2}$ | $e_2x_{12} + x_{32} > \frac{k(1-b_2e_2-a_2)}{b_2}$ | LAS |
| $E_s$      | $x_{1s} > \max \left\{ \frac{a_1\delta_1}{c_1e_1 - \delta_1}, \frac{a_2\delta_2}{c_2e_2 - \delta_2} \right\}$ | $k < \min \{a_1 + b_1x_{2s}, a_2 + b_2x_{3s}\}$ | LAS |
| $E_s$      | .................................................. | $(i) \ r > \delta_1 + \delta_2$, $(ii) \ x_{11} > \frac{a_3b_2}{c_2e_2 - \delta_2}$, $(iii) \ x_{12} > \frac{a_2\delta_1}{c_2e_2 - \delta_2}$ | Persistence |
| $E_s$      | .................................................. | Stated in the Proposition 3.3 | Boundedness |
| $E_s$      | .................................................. | $\Pi > 0$ (cf. equation (6.15)) | SHB |
| $E_s$      | $x_{1s} > \max \left\{ \frac{a_1\delta_1}{c_1e_1 - \delta_1}, \frac{a_2\delta_2}{c_2e_2 - \delta_2} \right\}$ | $a_1a_2b_1b_2rk > (x_{1s} + k)(w + k) \times \left( a_1b_1c_2 + a_2b_2c_1 \right)$ | GAS |
Table 2: The set of system parameter (including the critical parameter \( r_c \)) values and their corresponding Figures with description.

| No. | Fixed Parameters                                      | \( r \) | Figures | Description                          |
|-----|-------------------------------------------------------|---------|---------|--------------------------------------|
| 1   | \( r = 1.37 > r_c = 1.320961640, k = 200, a_1 = 100, a_2 = 100, b_1 = 0.5, b_2 = 0.5, c_1 = 1.8, c_2 = 1.8, \delta_1 = 0.82, \delta_2 = 0.62, e_1 = 0.8143, e_2 = 0.6250 \) | 1.37    | Figs. 1: (a)-(b) | 2D view of Hopf bifurcation          |
| 2   | \( r \in [0.8, 2.0] \)                                |         | Figs. 2 | Limit cycle                          |
| 3   | \( r \in [0.8, 2.0] \)                                |         | Fig. 3  | Hopf bifurcation (growth rate \( r \) vs. population volumes) |
| 4   |                                                     | 1.4700000000 | Fig. 4  | 2D view of local stability          |
| 5   |                                                     | 1.4700000000 | Fig. 5  | 3D view of local stability          |
| 6   |                                                     | 1.4700000000 | Fig. 6  | Global stability                    |
| 7   | \( r = 1.37, k = 200, a_1 = 100, a_2 = 100, b_1 = 0.5, b_2 = 0.5, c_1 = 1.8, c_2 = 1.8, \delta_1 = 0.82, \delta_2 = 0.62, e_1 = 0.8143, e_2 = 0.6250 \) \( r_c = 1.320961640, \Pi = 1.0424314050 \) | 1.320961640 | Figs. 7  | Subcritical Hopf bifurcation        |

7 Numerical simulation

For the purpose of making qualitative analysis of the present study, numerical simulations have been carried out by making use of MATLAB-R2010a and Maple-12. The analytical findings of the present study are summarized and represented schematically in Table 1. These results are all verified by means of numerical illustrations of which some chosen ones are exhibited in the figures. Here, we have given some numerical simulations on the study of stability and bifurcation of the proposed system (2.1) around the interior equilibrium \( E^* \). We took a set of admissible parameter values: \( r = 1.7, k = 200, a_1 = a_2 = 100, b_1 = b_2 = 0.5, c_1 = c_2 = 1.8, \delta_1 = 0.82, \delta_2 = 0.62, e_1 = 0.8143, e_2 = 0.6250 \). For this set of parameter values, it is found that the system possessed an unique interior equilibrium point \( E^* = (169.1663564, 55.36073780, 62.98120968) \). The system parameter \( r \) is the growth rate of the prey population which plays a crucial role in regulating the dynamical behaviour of the proposed system. For this reason, we take this parameter as an influential parameter and try to determine the possible outcomes by varying this parameter within its feasible range. The interior equilibrium \( E^* \) is stable for the values of \( r > r_c = 1.320961640 \) (cf. Figure: 4-5 for local stability and Figure: 6 for global stability). The system (2.1) experiences Hopf bifurcation when the parameter \( r \) crosses the critical value \( r_c \) from left to right, i.e., when \( r = r_c \), all the species coexist in the form of periodic oscillation. Following the steps discussed in Subsection 6.1, we have found the value of \( \Pi = 1.0424314050 > 0 \), which indicates that the obtained Hopf bifurcation is subcritical bifurcation (cf. Figure 7).

It is observed that, if the interference coefficient \( b_1 \) (interference effect due to the presence of second predator on the first predator) increases it stabilize the system for \( b_1 = 0.7 \) while it
is unstable at \( b_1 = 0.6 \) and when the parameter \( b_1 \) exceeds its value 20, the first predator population is died out from the system, i.e., the system breakdown. Similarly, the interference effect due to the presence of first predator on the second predator, parameterized by \( b_2 \) plays an important role to stabilize the system. If the interference coefficient \( b_2 \) increases it stabilizes the system for \( b_2 = 0.6 \), while it is unstable at \( b_2 = 0.5 \). It also regulates the existence of second predator in the system. As the parameter \( b_2 \) exceeds its value 20.9, the second predator population is died out from the system.

Analogously, if the parameter \( \delta_1 \), denoting the death rate of first predator increases then the volume of the fist predator decreases as well as second predator population increases and if \( \delta_1 \) decreases, the first predator population increases and second predator population decreases. If the death rate \( \delta_1 \) is gradually increased to a certain level the first predator population goes into extinction. Similar result is observed for the case of the second predator’s death rate. The above observations ensure that the model under consideration is consistent with biological phenomenon (Figures are not reported here).

![Graphs](image)

**Figure 1:** 2D view of Hopf bifurcation around the interior equilibrium \( E_\ast \) of the system (2.1) with parameter values: \( r = 1.37 > r_c = 1.320961640, k = 200, a_1 = 100, a_2 = 100, b_1 = 0.5, b_2 = 0.5; c_1 = 1.8, c_2 = 1.8, \delta_1 = 0.82, \delta_2 = 0.62, e_1 = 0.8143, e_2 = 0.6250.**

8 **Concluding remarks**

The problem describes by the system (2.1) is well posed that \( x_1, x_2 \) and \( x_3 \) axes are invariant under the flow of the system. So far our knowledge goes this is the first attempt to study an ecological system with semilinear/bilinear growth of the prey population. Generally, researcher only studied biological model systems with logistic/linear growth of prey population. Here is the novelty of our study. One of the important observations is that the prey population becomes unbounded in absence of its admissible predator in long run of time. But in the presence of predator species the prey population can be made bounded under suitable combination of system parameters and as a consequence it is shown that the total environmental population under consideration is bounded above (cf. Subsection 3.3). Therefore, any solution starting in the interior of the first octant never leaves it. This mathematical fact is consistent with the biological interpretation of the system. Due to the inclusion of semilinear/bilinear growth of the prey population, the axial equilibrium point is driven away by the system, which is rarely found in the modern research work on Mathematical biology. Thus, the prey population alone can not survive in stable condition without their admissible predator populations. It is found that only
the mutual interference between the predators, which are parameterized by $b_1$ and $b_2$ can alone able to stabilize the prey-predator interactions even when a semilinear/bilinear intrinsic growth rate of prey population is considered in the proposed mathematical model. Whereas these parameters have much contribution in stabilizing prey-predator interactions when only linear intrinsic growth rate is considered in some mathematical models (cf. Dimitrov and Kojouharov [31]). It is observed in the study of this model system that there exist a balance between the predator’s need for food and its saturation level and in this case is likely to be expect a periodic behaviour in long run. This behaviour is neutrally stable but relatively unstable. A small change in the parameters (caused by environmental changes for instances) forces the system to stabilize around the interior equilibrium or to oscillate indefinitely around interior equilibrium (by going away from it, which causes collapse of the system or breaks the coexistence of the population). Representative numerical simulations of this case are shown in Figures: 1-3, which support our analytical findings (cf. Theorems 5.2 and 6.1). We have also established the sufficient conditions for the global stability of the coexistence equilibrium (cf. Figures: 5-6).

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Figure 3: Bifurcation diagram for all the populations with $r$ as the bifurcating parameter around the interior equilibrium $E_*$ of the system (2.1).

Figure 4: 2D view of Local asymptotic stability of the system (2.1) around the interior equilibrium $E_*$ of the system (2.1) with parameter values: $r = 1.47 > r_c = 1.320961640$, $k = 200$, $a_1 = 100$, $a_2 = 100$, $b_1 = 0.5$, $b_2 = 0.5$; $c_1 = 1.8$, $c_2 = 1.8$, $\delta_1 = 0.82$, $\delta_2 = 0.62$, $c_1 = 0.8143$, $c_2 = 0.6250$. 
Figure 5: 3D view of local asymptotic stability of the dynamical system at $E_*$ with the same parameter values used for Figure 4.

Figure 6: Solution plots with different starting points converge to the interior equilibrium point $E_* = (169.1663564, 55.36073780, 62.98120968)$, showing that the system (2.1) is global asymptotic stable. Here the same set of parameter values is used for Figure 4 except $r = 1.29$. 
Figure 7: Solution plots showing that the system (2.1) experiences subcritical Hopf bifurcation for $r > r_{\text{sub}}$. Here the set of parameter values used is mention in the last row of Table 2.

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