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

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Abstract The objective of this paper is to systematically study the dynamical behaviour of an ecological system with Beddington–DeAngelis functional response which avoids the criticism arising for ratio-dependent functional response at low population densities of both species. The essential mathematical features of the present model have been analyzed thoroughly: local and global stability and the bifurcations arising in some selected situations. We show that the dynamical outcomes of the interactions among the species are much sensitive to the system parameters and initial population volumes. 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 center manifold theory (cf. Carr (1981)). Numerical illustrations are performed finally in order to validate the applicability of the model under consideration.

Keywords Ecological model · Stability · Hopf bifurcation · Limit cycle · Center manifold · Numerical simulation

Mathematics Subject Classification 92D25, 92D30, 92D40

Introduction

Mathematical models are important tools for analyzing ecological models. The dynamic relationship between predator and its prey is one of the dominant themes in mathematical ecology due to its universality (cf. Anderson and May (1981), Beretta and Kuang (1998), Freedman (1990), Haderler and Freedman (1989), Hethcote et al. (2004), Ma and Takeuchi (1998), Venturino (1995), Xiao and Chen (2001)). The most common method of modelling ecological interactions consists of two differential equations with simple correspondence between the consumption of prey by the predator and the populations growth. The traditional predator–prey models have been studied extensively (cf. Cantrell and Cosner (2001), Cosner et al. (1999), Cui and Takeuchi (2006), Huo et al. (2007) and Hwang (2003)), but these studies 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 prey are consumed by a predator. Models were limited to use the Malthusian growth function, the predator per capita consumption of prey following Holling types II and 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 (1968), Hassell and Varley (1969) and Salt (1974)). A simple way of incorporating predator dependence in the functional response was proposed by Arditi and Ginzburg Arditi and Ginzburg (1989), who considered this response 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 for the paradox that occurs at low densities

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of both populations. Normally one would expect that the population growth rate decrease when both the populations fall below some critical size, because food-searching effort becomes very high. For some ecological interactions ratio-dependent model give negative feed back. The Lotka–Volterra type predator–prey model with the Beddington–DeAngelis functional response has been proposed and well studied. This proposed model can be expressed as follows:

$$\begin{cases} \frac{dx_1'}{dt} = rx_1'(1 - \frac{x_1'}{k}) - \frac{c_1 x_1' x_2'}{a_1 + x_1' + b_1 x_2'} \\ \frac{dx_2'}{dt} = -\delta_1 x_2' + \frac{c_1 e_1 x_1' x_2'}{a_1 + x_1' + b_1 x_2'} \end{cases} \quad (1.1)$$

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 sizes 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 $\frac{c_1 x_1' x_2'}{a_1 + x_1' + b_1 x_2'}$ in system (1.1) was introduced by Beddington (1975) and DeAngelis et al. (1975). 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 is the source of controversy. It can be derived mechanistically from considerations of time utilization (cf. Beddington (1975)) or spatial limits on predation.

The present study is organized as follows: The basic assumptions and the model formation are proposed in Sect. 2. Section 3 deals with some preliminary results. The equilibria and their feasibility are given in Sect. 4. The local analyses of the system around the boundary as well as interior equilibria are discussed in Sect. 5. The global analysis of the system around the interior equilibrium is studied at length in Sect. 6. Simulation results are reported in Sect. 7 while a final discussion and interpretation of the results of the present study in ecological terms appear in the concluding Sect. 8.

Model formulation

Firstly we replaced the logistic growth function $rx_1(1 - \frac{x_1}{k})$ of the prey species by the modified quasi-linear growth function $rx_1(1 - \frac{x_1}{x_1+k}) = r(\frac{k}{k+x_1})x_1 = r'x_1$ ($r' < r$) in order to make the model free from any axial equilibrium. This fits better some special type of ecosystems, where the environmental carrying capacity varies w.r.t. its prey size, i.e., the carrying capacity is always greater than its present

prey size. In the present model we introduce one more predator species in the model (1.1) to make it closer to reality. Thus, our final model is

$$\begin{cases} \frac{dx_1}{dt} = rx_1(1 - \frac{x_1}{x_1+k}) - \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2} - \frac{c_2 x_1 x_3}{a_2 + x_1 + b_2 x_3} \\ \frac{dx_2}{dt} = -\delta_1 x_2 + \frac{c_1 e_1 x_1 x_2}{a_1 + x_1 + b_1 x_2}, \\ \frac{dx_3}{dt} = -\delta_2 x_3 + \frac{c_2 e_2 x_1 x_3}{a_2 + x_1 + b_2 x_3} \end{cases} \quad (2.1)$$

where x_1 is the population size of the prey and x_2, x_3 are the population sizes 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, δ_1, δ_2 are the first and second predators death rates respectively. c_1, c_2 are the respective search rates of the first and second predator on the prey species, $\frac{c_1}{a_1}, \frac{c_2}{a_2}$ are the maximum number of prey that can be eaten by the first and second predator per unit time respectively; $\frac{1}{a_1}, \frac{1}{a_2}$ are their respective half saturation rates while e_1, e_2 are the conversion factors, denoting the number of newly born of the 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 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.

Some preliminary results

Existence and positive invariance

Letting, $x = (x_1, x_2, x_3)^t, f: \mathbf{R}^3 \rightarrow \mathbf{R}^3, f = (f_1, f_2, f_3)^t$, the system (2.1) can be rewritten as $\dot{x} = f(x)$. Here $f_i \in C^\infty(\mathbf{R})$ for $i = 1, 2, 3$, where $f_1 = rx_1(1 - \frac{x_1}{x_1+k}) - \frac{c_1 x_1 x_2}{a_1 + x_1 + b_1 x_2} - \frac{c_2 x_1 x_3}{a_2 + x_1 + b_2 x_3}$, $f_2 = -\delta_1 x_2 + \frac{c_1 e_1 x_1 x_2}{a_1 + x_1 + b_1 x_2}$ and $f_3 = -\delta_2 x_3 + \frac{c_2 e_2 x_1 x_3}{a_2 + x_1 + b_2 x_3}$. 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.

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) $x_{1_1} > \frac{a_2 \delta_2}{c_2 e_2 - \delta_2}$, (iii) $x_{1_2} > \frac{a_1 \delta_1}{c_1 e_1 - \delta_1}$ are satisfied.

Proof We use the method of average Lyapunov function (cf. Gard and Hallam (1979)), considering a function of the form

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

where γ_1, γ_2 and γ_3 are positive constants to be determined. We define

$$\begin{aligned} \Pi(x_1, x_2, x_3) &= \frac{\dot{V}}{V} \\ &= \gamma_1 \left(r - \frac{rx_1}{x_1 + k} - \frac{c_1 x_2}{a_1 + x_1 + b_1 x_2} - \frac{c_2 x_3}{a_2 + x_1 + b_2 x_3} \right) \\ &\quad + \gamma_2 \left(-\delta_1 + \frac{c_1 e_1 x_1}{a_1 + x_1 + b_1 x_2} \right) \\ &\quad + \gamma_3 \left(-\delta_2 + \frac{c_2 e_2 x_1}{a_2 + x_1 + b_2 x_3} \right). \end{aligned}$$

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

$$\begin{aligned} \Pi(x_{1_1}, x_{2_1}, 0) &= \gamma \left(-\delta_2 + \frac{e_2 c_2 x_{1_1}}{a_2 + x_{1_1}} \right) > 0, \\ \Pi(x_{1_2}, 0, x_{3_2}) &= \gamma \left(-\delta_1 + \frac{e_1 c_1 x_{1_2}}{a_1 + x_{1_2}} \right) > 0. \end{aligned}$$

Hence, there always exists a positive number γ 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 $t > \tau$, $i = 1, 2, 3$.

Boundedness

Boundedness implies that the system is biologically consistent. 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:

$$\frac{dx_2}{dt} \leq -(\delta_1 - c_1 e_1)x_2.$$

Integrating the above differential inequality between the limits 0 and t , we have $x_2(t) \leq x_2(0)e^{-(\delta_1 - c_1 e_1)t}$. Thus, if $(\delta_1 - c_1 e_1) > 0$, then a positive number τ_1 is found and there exist a positive constant m_1 such that $x_2(t) \leq m_1$, for all $t \geq \tau_1$. By using a similar argument, one can obtain that, if $(\delta_2 - c_2 e_2) > 0$, then corresponding to a positive number τ_2 there exists a positive constant m_2 such that $x_3(t) \leq m_2$, for all $t \geq \tau_2$. Both results can be written 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 $\min(\delta_1 - c_1 e_1, \delta_2 - c_2 e_2) > 0$.

Now from the first sub-equation of (2.1), the following inequality is found

$$\frac{dx_1}{dt} \leq \frac{((e_1 + e_2)\sigma - rk)x_1}{km} \left(\frac{k(rm - (e_1 + e_2)\sigma)}{(e_1 + e_2)\sigma - rk} - x_1 \right).$$

Hence, by using simple standard arguments, we have

$$\begin{aligned} \limsup_{t \rightarrow +\infty} x_1(t) &\leq \frac{krm - (e_1 + e_2)k\sigma}{(e_1 + e_2)\sigma - rk} = w, \text{ where} \\ \frac{rm}{e_1 + e_2} &< \sigma < \frac{rk}{e_1 + e_2}. \end{aligned}$$

$\square$

Proposition 3.3 The solutions of (2.1) starting in Ω^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 (1982)) and following the steps of Haque and Venturino (2006), Sarwardi et al. (2013), boundedness of the solution trajectories of this model is established. In particular,

$$\limsup_{t \rightarrow +\infty} \left(x_1 + \frac{x_2}{e_1} + \frac{x_3}{e_2} \right) \leq \frac{(r+1)k + w}{\rho} = M, \text{ where}$$

$$\rho = \min(1, \delta_1, \delta_2),$$

with the last bound independent of the initial condition.

Hence, all the solutions of (2.1) starting in $\mathbf{R}_+^3$ for any $\theta > 0$ evolve with respect to time in the compact region

$$\bar{\Omega} = \left\{ (x_1, x_2, x_3) \in \mathbf{R}_+^3 : x_1 + \frac{x_2}{e_1} + \frac{x_3}{e_2} \leq M + \theta \right\}. \quad (3.2)$$

Equilibria and their feasibility

The equilibria of the dynamical system (2.1) are:

1.

- (a) The trivial equilibrium point $E_0(0, 0, 0)$ is always feasible.

2.

- (a) The first boundary equilibrium point is $E_1(x_{1_1}, x_{2_1}, 0)$. The component x_{1_1} is a root of the quadratic equation $l_1 x_{1_1}^2 + (l_2 + l_1 k + rkb_1 e_1)x_{1_1} + l_2 k = 0$, 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_1} possesses a unique positive root and consequently $x_{2_1} = \frac{(c_1 e_1 - \delta_1)x_{1_1} - a_1 \delta_1}{b_1 \delta_1}$. The feasibility of the equilibrium E_1 is maintained if the condition $x_{1_1} > \frac{b_1 \delta_1}{c_1 e_1 - \delta_1}$ is satisfied.
- (b) The second boundary equilibrium point is $E_2(x_{1_2}, 0, x_{3_2})$. The component x_{1_2} is the root of the quadratic equation $m_1 x_{1_2}^2 + (m_2 + m_1 k + rkb_2 e_2)x_{1_2} + m_2 k = 0$, where $m_1 = (\delta_2 - c_2 e_2)$, $l_2 = a_2 \delta_2$. If $m_1 < 0$, the quadratic equation in x_{1_2} possesses a unique positive root and consequently $x_{3_2} = \frac{(c_2 e_2 - \delta_2)x_{1_2} - a_2 \delta_2}{b_2 \delta_2}$. The feasibility of the equilibrium E_2 holds if the condition $x_{1_2} > \frac{b_2 \delta_2}{c_2 e_2 - \delta_2}$ holds.

3.

- (a) The interior equilibrium point is $E_*(x_{1_*}, x_{2_*}, x_{3_*})$, where the first component x_{1_*} is the root of the following quadratic equation:

$$n_1 x_{1_*}^2 + (n_2 + n_1 k + rkb_1 b_2 e_1 e_2)x_{1_*} + n_2 k = 0, \quad (4.1)$$

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 $(n_2 + n_1 k + rkb_1 b_2 e_1 e_2)$.

Case II: Let $n_1 > 0$. In this case there are two possibilities: (i) if $n_2 + n_1 k + rkb_1 b_2 e_1 e_2 > 0$, then there is no positive solution and (ii) if $n_2 + n_1 k + rkb_1 b_2 e_1 e_2 < 0$, then there exists two positive roots or no positive root. Here we consider the Case I. Under this assumption the next two components of the interior equilibrium can be obtained as $x_{2_*} = \frac{(c_1 e_1 - \delta_1)x_{1_*} - a_1 \delta_1}{b_1 \delta_1}$, $x_{3_*} = \frac{(c_2 e_2 - \delta_2)x_{1_*} - a_2 \delta_2}{b_2 \delta_2}$. The feasibility of this equilibrium point E_* holds 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 planar 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.

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

$$J(x)_{3 \times 3} = \begin{pmatrix} \frac{rk^2}{(x_1 + k)^2} - \frac{c_1 x_2 (a_1 + b_1 x_2)}{(a_1 + x_1 + b_1 x_2)^2} - \frac{c_2 x_3 (a_2 + b_2 x_3)}{(a_2 + x_1 + b_2 x_3)^2} & -\frac{c_1 x_1 (a_1 + x_1)}{(a_1 + x_1 + b_1 x_2)^2} & -\frac{c_2 x_1 (a_2 + x_1)}{(a_2 + x_1 + b_2 x_3)^2} \\ \frac{c_1 e_1 x_2 (a_1 + b_1 x_2)}{(a_1 + x_1 + b_1 x_2)^2} & -\delta_1 + \frac{c_1 e_1 x_1 (a_1 + x_1)}{(a_1 + x_1 + b_1 x_2)^2} & 0 \\ \frac{c_2 e_2 x_3 (a_2 + b_2 x_3)}{(a_2 + x_1 + b_2 x_3)^2} & 0 & -\delta_2 + \frac{c_2 e_2 x_1 (a_2 + x_1)}{(a_2 + x_1 + b_2 x_3)^2} \end{pmatrix}. \quad (5.1)$$

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 $k_3 = -\det(J)$; where M is the sum of the principal minors of order two of J .

Note that a Hopf bifurcation occurs if there exist 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 $\frac{d}{dr}(\text{Re}(\lambda(r)))|_{r=r_c} \neq 0$, where λ is root of the characteristic equation $\Delta(\lambda) = 0$.

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 $J(E_1) = (\xi_{ij})_{3 \times 3}$ and $J(E_2) = (\eta_{ij})_{3 \times 3}$. Using the Routh-Hurwitz criterion, it can be easily shown that the eigenvalues of the matrices $J(E_1)$ and $J(E_2)$ have negative real parts iff the conditions $e_1x_{11} + x_{21} > \frac{k(1-b_1e_1)-a_1}{b_1}$ and $e_2x_{12} + x_{32} > \frac{k(1-b_2e_2)-a_2}{b_2}$ are satisfied. Hence the equilibria E_1 and E_2 are locally asymptotically stable under the above conditions (cf. Sect. 4 of Sarwardi et al. (2012)).

Bifurcation Since the equilibrium point E_0 is a saddle, there is no Hopf bifurcation around it. In order to have Hopf bifurcation around the equilibria E_1, E_2 , it is sufficient to show that the coefficient of λ in the quadratic factor of the characteristic polynomial of $J(E_k)$ ($k = 1, 2$) is zero and the constant term is positive. The conditions for which annihilation of the linear terms in the quadratic factors of the characteristic polynomials of $J(E_1)$ and $J(E_2)$ can be made possible are $\xi_{11} + \xi_{22} = 0$ and $\eta_{11} + \eta_{33} = 0$. For a detailed analysis, interested readers are referred to Appendix A of Haque and Venturino (2006). The parametric regions where Hopf bifurcations occur around E_1 and E_2 are respectively established by the equality constraints $e_1x_{11} + x_{21} = \frac{k(1-b_1e_1)-a_1}{b_1}$ and $e_2x_{12} + x_{32} = \frac{k(1-b_2e_2)-a_2}{b_2}$.

Local analysis of the system around the interior equilibrium

Proposition 5.1 The system (2.1) around E_* is locally asymptotically stable if the condition (i) $k < \min\{a_1 + b_1x_{2*}, a_2 + b_2x_{3*}\}$ is satisfied.

Proof Let $J(x_*) = (J_{ij})_{3 \times 3}$ be the Jacobian matrix at the interior equilibrium point $E_* = x_*$ of the system (2.1). The components of $J(x_*)$ are

$$J_{11} = \frac{c_1x_{1*}x_{2*}(k - (a_1 + b_1x_{2*}))}{(x_{1*} + k)(a_1 + x_{1*} + b_1x_{2*})} + \frac{c_2x_{1*}x_{3*}(k - (a_2 + b_2x_{3*}))}{(x_{1*} + k)(a_2 + x_{1*} + b_2x_{3*})},$$

$$J_{12} = -\frac{c_1x_{1*}(a_1 + x_{1*})}{(a_1 + x_{1*} + b_1x_{2*})^2} < 0, \quad J_{13} = -\frac{c_2x_{1*}(a_2 + x_{1*})}{(a_2 + x_{1*} + b_2x_{3*})^2} < 0,$$

$$J_{21} = \frac{c_1e_1x_{2*}(a_1 + b_1x_{2*})}{(a_1 + x_{1*} + b_1x_{2*})^2} > 0, \quad J_{22} = -\frac{b_1c_1e_1x_{1*}x_{2*}}{(a_1 + x_{1*} + b_1x_{2*})^2} < 0, \quad J_{23} = 0,$$

$$J_{31} = \frac{c_2e_2x_{3*}(a_2 + b_2x_{3*})}{(a_2 + x_{1*} + b_2x_{3*})^2} > 0, \quad J_{32} = 0, \quad J_{33} = -\frac{b_2c_2e_2x_{1*}x_{3*}}{(a_2 + x_{1*} + b_2x_{3*})^2} < 0.$$

Then the characteristic equation of the Jacobian matrix $J(x_*)$ can be written as

$$\lambda^3 + k_1\lambda^2 + k_2\lambda + k_3 = 0, \quad (5.2)$$

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

It is clear that $k_1 > 0$ if $J_{11} < 0$, i.e., $k < \min\{a_1 + b_1x_{2*}, a_2 + b_2x_{3*}\}$ and consequently $C_2 > 0$. Hence the Routh-Hurwitz condition is satisfied for the matrix J_* , i.e., all the characteristic roots of J_* have negative real parts. So the system is locally asymptotically stable around E_* .

Theorem 5.2 The dynamical system (2.1) undergoes a Hopf bifurcation around the interior equilibrium point E_* whenever the critical parameter r attains the value $r = r_c$ in the domain

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

Proof The equation (5.2) 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 $r = r_c$ is 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:

$$h_1J_{11}^2 + h_2J_{11} + h_3 = 0, \quad (5.3)$$

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

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

Or,

$$r = \frac{(x_{1*} + k)^2}{k^2} \times \left[J_{11}^* + \frac{c_1x_{2*}(a_1 + b_1x_{2*})}{(a_1 + x_{1*} + b_1x_{2*})^2} - \frac{c_2x_{3*}(a_2 + b_2x_{3*})}{(a_2 + x_{1*} + b_2x_{3*})^2} \right] = r_c. \quad (5.4)$$

Using the condition $k_1k_2 - k_3 = 0$, from equation (5.2) one can obtain

$$(\lambda + k_1)(\lambda^2 + k_2) = 0, \quad (5.5)$$

which has three roots $\lambda_1 = +i\sqrt{k_2}$, $\lambda_2 = -i\sqrt{k_2}$, $\lambda_3 = -k_1$. Thus, there is a pair of purely imaginary eigenvalues

$\pm i\sqrt{k_2}$. For all values of λ , 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 (5.2) w.r.t. r , we have

$$\begin{aligned} \frac{d\lambda}{dr} &= -\frac{\lambda^2 \dot{k}_1 + \lambda \dot{k}_2 + \dot{k}_3}{3\lambda^2 + 2k_1\lambda + k_2} \Big|_{\lambda=i\sqrt{k_2}} \\ &= \frac{\dot{k}_3 - k_2\dot{k}_1 + i\dot{k}_2\sqrt{k_2}}{2(k_2 - ik_1\sqrt{k_2})} \\ &= \frac{\dot{k}_3 - (\dot{k}_1k_2 + k_1\dot{k}_2)}{2(k_1^2 + k_2)} + i \frac{\sqrt{k_2}(k_1\dot{k}_3 + k_2\dot{k}_2 - k_1\dot{k}_1k_2)}{2k_2(k_1^2 + k_2)} \\ &= -\frac{\frac{dC_2}{dr}}{2(k_1^2 + k_2)} + i \left[\frac{\sqrt{k_2}\dot{k}_2}{2k_2} - \frac{k_1\sqrt{k_2}\frac{dC_2}{dr}}{2k_2(k_1^2 + k_2)} \right]. \end{aligned} \quad (5.6)$$

Hence,

$$\frac{d}{dr}(\operatorname{Re}(\lambda(r))) \Big|_{r=r_c} = -\frac{\frac{dC_2}{dr}}{2(k_1^2 + k_2)} \Big|_{r=r_c} \neq 0. \quad (5.7)$$

Using the monotonicity condition of the real part of the complex root $\frac{d(\operatorname{Re}(\lambda(r)))}{dr} \Big|_{r=r_c} \neq 0$ (cf. Wiggins (2003), pp. 380), one can easily establish the transversality condition $\frac{dC_2}{dr} \Big|_{r=r_c} \neq 0$, to ensure the existence of Hopf bifurcation around E_* .

Global analysis of the system around the interior equilibrium

Direction of Hopf bifurcation of the system (2.1) around E_*

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

$$\dot{x} = f(x), \quad (6.1)$$

$$\text{where } x = (x_1, x_2, x_3)^t, f = (f^1, f^2, f^3)^t = \begin{pmatrix} rx_1(1 - \frac{x_1}{x_1 + k}) - \frac{c_1x_1x_2}{a_1 + x_1 + b_1x_2} - \frac{c_2x_1x_3}{a_2 + x_1 + b_2x_3} \\ -\delta_1x_2 + \frac{c_1e_1x_1x_2}{a_1 + x_1 + b_1x_2} \\ -\delta_2x_3 + \frac{c_2e_2x_1x_3}{a_2 + x_1 + b_2x_3} \end{pmatrix}.$$

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

$$\dot{y} = J(x_1^*, x_2^*, x_3^*)y + \phi, \quad (6.2)$$

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

$$\begin{aligned} \phi_i &= f_{x_1x_1}^i y_1^2 + f_{x_2x_2}^i y_2^2 + f_{x_3x_3}^i y_3^2 + 2f_{x_2x_3}^i y_2y_3 + 2f_{x_3x_1}^i y_3y_1 \\ &\quad + 2f_{x_1x_2}^i y_1y_2 + \text{h.o.t.}, i = 1, 2, 3. \end{aligned} \quad (6.3)$$

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

$$\begin{aligned} f_{x_1x_1}^1 &= -\frac{2rk^2}{(x_1 + k)^3} + \frac{2c_1x_2(a_1 + b_1x_2)}{(a_1 + x_1 + b_1x_2)^3} + \frac{2c_2x_3(a_2 + b_2x_3)}{(a_2 + x_1 + b_2x_3)^3}, \\ f_{x_2x_2}^1 &= \frac{2b_1c_1x_1(a_1 + x_1)}{(a_1 + x_1 + b_1x_2)^3}, f_{x_3x_3}^1 = \frac{2b_2c_2x_1(a_2 + x_1)}{(a_2 + x_1 + b_2x_3)^3}, \\ f_{x_2x_3}^1 &= 0, f_{x_1x_2}^1 = -\frac{c_1a_1(a_1 + x_1 + b_1x_2) + 2b_1c_1x_1x_2}{(a_1 + x_1 + b_1x_2)^3}, \\ f_{x_3x_1}^1 &= -\frac{c_2a_2(a_2 + x_1 + b_2x_3) + 2b_2c_2x_3x_1}{(a_2 + x_1 + b_2x_3)^3}; \\ f_{x_1x_1}^2 &= -\frac{2c_1e_1x_2(a_1 + b_1x_2)}{(a_1 + x_1 + b_1x_2)^3}, f_{x_2x_2}^2 = -\frac{2b_1c_1e_1x_1(a_1 + x_1)}{(a_1 + x_1 + b_1x_2)^3}, \\ f_{x_3x_3}^2 &= 0, f_{x_1x_2}^2 = \frac{a_1c_1e_1(a_1 + x_1 + b_1x_2) + 2b_1c_1e_1x_1x_2}{(a_1 + x_1 + b_1x_2)^3}, \\ f_{x_2x_3}^2 &= 0, f_{x_3x_1}^2 = 0; f_{x_1x_1}^3 = -\frac{2c_2e_2x_3(a_2 + b_2x_3)}{(a_2 + x_1 + b_2x_3)^3}, \\ f_{x_2x_2}^3 &= 0, f_{x_3x_3}^3 = -\frac{2b_2c_2e_2x_1(a_2 + x_1)}{(a_2 + x_1 + b_2x_3)^3}, \\ f_{x_2x_3}^3 &= 0, f_{x_3x_1}^3 = \frac{a_2c_2e_2(a_2 + x_1 + b_2x_3) + 2b_2c_2e_2x_1x_3}{(a_2 + x_1 + b_2x_3)^3}, \\ f_{x_1x_2}^3 &= 0. \end{aligned}$$

Let P be the matrix formed by the column vectors $(\mathbf{u}_2, \mathbf{u}_1, \mathbf{u}_3)$, 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 $J(x_1^*, x_2^*, x_3^*)\mathbf{u}_2 = i\sqrt{k_2}\mathbf{u}_2$, $J(x_1^*, x_2^*, x_3^*)\mathbf{u}_1 = -i\sqrt{k_2}\mathbf{u}_1$, and $J(x_1^*, x_2^*, x_3^*)\mathbf{u}_3 = -k_1\mathbf{u}_3$.

Thus,

$$P = \begin{pmatrix} 0 & 1 & 1 \\ \frac{-J_{21}\sqrt{k_2}}{J_{22}^2 + k_2} & \frac{-J_{21}J_{22}}{J_{22}^2 + k_2} & \frac{-J_{21}}{J_{22} + k_1} \\ \frac{-J_{31}\sqrt{k_2}}{J_{33}^2 + k_2} & \frac{-J_{31}J_{33}}{J_{33}^2 + k_2} & \frac{-J_{31}}{J_{33} + k_1} \end{pmatrix} = (p_{ij})_{3 \times 3}.$$

Let us make use of the transformation $\mathbf{y} = P\mathbf{z}$, so that the system (6.2) is reduced to the following one

$$\begin{aligned} \dot{\mathbf{z}} &= P^{-1}J(x_1^*, x_2^*, x_3^*)P\mathbf{z} + P^{-1}\phi \\ \phi &= \begin{pmatrix} 0 & -i\sqrt{k_2} & 0 \\ i\sqrt{k_2} & 0 & 0 \\ 0 & 0 & -k_1 \end{pmatrix} \mathbf{z} + P^{-1}\phi. \end{aligned} \quad (6.4)$$

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

$$q_{11} = \frac{1}{\det P} \left(\frac{J_{21}J_{22}J_{31}}{(J_{22}^2 + k_2)(J_{33} + k_1)} - \frac{J_{21}J_{33}J_{31}}{(J_{22}^2 + k_2)(J_{22} + k_1)} \right),$$

$$q_{12} = \frac{1}{\det P} \left(\frac{J_{31}}{J_{33}^2 + k_1} - \frac{J_{31}J_{33}}{J_{33}^2 + k_2} \right),$$

$$q_{13} = \frac{1}{\det P} \left(\frac{-J_{21}}{J_{21} + k_1} + \frac{J_{21}J_{22}}{J_{22}^2 + k_2} \right),$$

$$q_{21} = \frac{1}{\det P} \left(\frac{J_{21}\sqrt{k_2}J_{31}}{(J_{22}^2 + k_2)(J_{22} + k_1)} - \frac{J_{21}\sqrt{k_2}J_{31}}{(J_{33}^2 + k_2)(J_{22} + k_1)} \right),$$

$$q_{22} = \frac{1}{\det P} \frac{\sqrt{k_2}J_{31}}{(J_{33}^2 + k_2)}, \quad q_{23} = \frac{1}{\det P} \frac{-\sqrt{k_2}J_{31}}{(J_{33}^2 + k_2)},$$

$$q_{31} = \frac{1}{\det P} \left(\frac{J_{21}\sqrt{k_2}J_{31}J_{33}}{(J_{22}^2 + k_2)(J_{33}^2 + k_2)} - \frac{J_{21}\sqrt{k_2}J_{31}J_{22}}{(J_{33}^2 + k_2)(J_{22}^2 + k_2)} \right),$$

$$q_{32} = \frac{1}{\det P} \frac{-\sqrt{k_2}J_{21}}{(J_{22}^2 + k_2)}, \quad q_{33} = \frac{1}{\det P} \frac{\sqrt{k_2}J_{21}}{(J_{22}^2 + k_2)}.$$

The system (6.4) can be written as

$$\frac{d}{dt} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} = \begin{pmatrix} 0 & -\sqrt{k_2} \\ \sqrt{k_2} & 0 \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} + F(z_1, z_2, z_3), \quad (6.5)$$

$$\frac{dz_3}{dt} = -k_1 z_3 + G(z_1, z_2, z_3). \quad (6.6)$$

On the center-manifold (cf. Carr (1981), Kar et al. (2012))

$$z_3 = \frac{1}{2} (b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2) \quad (6.7)$$

Therefore,

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

Using (6.4) and (6.6), we have

$$\dot{z}_3 = -k_1 z_3 + q_{31}\phi_1 + q_{32}\phi_2 + q_{33}\phi_3 \quad (6.9)$$

From the Eqs. (6.8) and (6.9), we have

$$\begin{aligned} &\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 \\ &= -\frac{1}{2}k_1(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2) + q_{31}[f_{x_1x_1}^1\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 \\ &\quad + f_{x_2x_2}^1\{p_{21}z_1 + p_{22}z_2 + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 + f_{x_3x_3}^1\{p_{31}z_1 + p_{32}z_2 + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 \\ &\quad + 2f_{x_3x_1}^1\{p_{31}z_1 + p_{32}z_2 + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\} \\ &\quad + 2f_{x_1x_2}^1\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}\{p_{21}z_1 + p_{22}z_2 + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}] \\ &\quad + q_{32}[f_{x_1x_1}^2\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 \\ &\quad + f_{x_2x_2}^2\{p_{21}z_1 + p_{22}z_2 \\ &\quad + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 + f_{x_3x_3}^2\{p_{31}z_1 + p_{32}z_2 + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 \\ &\quad + 2f_{x_2x_3}^2\{p_{21}z_1 + p_{22}z_2 + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}\{p_{31}z_1 + p_{32}z_2 + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\} \\ &\quad + 2f_{x_3x_1}^2\{p_{31}z_1 + p_{32}z_2 + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\} \\ &\quad + 2f_{x_1x_2}^2\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\} \times \{p_{21}z_1 + p_{22}z_2 + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}] \\ &\quad + q_{33}[f_{x_1x_1}^3\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 + f_{x_2x_2}^3\{p_{21}z_1 + p_{22}z_2 + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 \\ &\quad + f_{x_3x_3}^3\{p_{31}z_1 + p_{32}z_2 + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}^2 + 2f_{x_2x_3}^3\{p_{21}z_1 + p_{22}z_2 \\ &\quad + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}\{p_{31}z_1 + p_{32}z_2 + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\} + 2f_{x_3x_1}^3\{p_{31}z_1 + p_{32}z_2 \\ &\quad + p_{33}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}\{p_{11}z_1 + p_{12}z_2 + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\} + 2f_{x_1x_2}^3\{p_{11}z_1 + p_{12}z_2 \\ &\quad + p_{13}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}\{p_{21}z_1 + p_{22}z_2 + p_{23}\frac{1}{2}(b_{11}z_1^2 + 2b_{12}z_1z_2 + b_{22}z_2^2)\}]. \end{aligned}$$

Comparing the coefficients of z_1^2 , $z_1 z_2$ and z_2^2 from both sides, we have

$$\begin{aligned} & \sqrt{k_2} b_{12} + \frac{k_1}{2} b_{11} \\ &= q_{31} \left[f_{x_1 x_1}^1 p_{11}^2 + f_{x_2 x_2}^1 p_{21}^2 + f_{x_3 x_3}^1 p_{31}^2 + 2f_{x_2 x_3}^1 p_{21} p_{31} + 2f_{x_3 x_1}^1 p_{31} p_{11} + 2f_{x_1 x_2}^1 p_{11} p_{21} \right] \\ &+ q_{32} \left[f_{x_1 x_1}^2 p_{11}^2 + f_{x_2 x_2}^2 p_{21}^2 + f_{x_3 x_3}^2 p_{31}^2 + 2f_{x_2 x_3}^2 p_{21} p_{31} + 2f_{x_3 x_1}^2 p_{31} p_{11} + 2f_{x_1 x_2}^2 p_{11} p_{21} \right] \\ &+ q_{33} \left[f_{x_1 x_1}^3 p_{11}^2 + f_{x_2 x_2}^3 p_{21}^2 + f_{x_3 x_3}^3 p_{31}^2 + 2f_{x_2 x_3}^3 p_{21} p_{31} + 2f_{x_3 x_1}^3 p_{31} p_{11} + 2f_{x_1 x_2}^3 p_{11} p_{21} \right] \\ &= \Omega_1, \end{aligned} \quad (6.10)$$

$$\begin{aligned} & -\sqrt{k_2}(b_{11} - b_{22}) + k_1 b_{12} \\ &= 2q_{31} [f_{x_1 x_1}^1 p_{11} p_{12} + f_{x_2 x_2}^1 p_{21} p_{22} + f_{x_3 x_3}^1 p_{31} p_{32} + f_{x_2 x_3}^1 (p_{21} p_{32} + p_{22} p_{31}) + f_{x_3 x_1}^1 (p_{11} p_{32} \\ &+ p_{12} p_{31}) + f_{x_1 x_2}^1 (p_{11} p_{22} + p_{12} p_{21})] + q_{32} [f_{x_1 x_1}^2 p_{11} p_{12} + f_{x_2 x_2}^2 p_{21} p_{22} + f_{x_3 x_3}^2 p_{31} p_{32} + f_{x_2 x_3}^2 \\ &\times (p_{21} p_{32} + p_{22} p_{31}) + f_{x_3 x_1}^2 (p_{11} p_{32} + p_{12} p_{31}) + f_{x_1 x_2}^2 (p_{11} p_{22} + p_{12} p_{21})] + q_{33} [f_{x_1 x_1}^3 p_{11} p_{12} \\ &+ f_{x_2 x_2}^3 p_{21} p_{22} + f_{x_3 x_3}^3 p_{31} p_{32} + f_{x_2 x_3}^3 (p_{21} p_{32} + p_{22} p_{31}) + f_{x_3 x_1}^3 (p_{11} p_{32} + p_{12} p_{31}) \\ &+ f_{x_1 x_2}^3 (p_{11} p_{22} + p_{12} p_{21})] = \Omega_2, \end{aligned} \quad (6.11)$$

and

$$\begin{aligned} & -\sqrt{k_2} b_{12} + \frac{k_1}{2} b_{22} \\ &= q_{31} \left[f_{x_1 x_1}^1 p_{12}^2 + f_{x_2 x_2}^1 p_{22}^2 + f_{x_3 x_3}^1 p_{32}^2 + 2f_{x_2 x_3}^1 p_{22} p_{32} + 2f_{x_3 x_1}^1 p_{31} p_{12} + 2f_{x_1 x_2}^1 p_{12} p_{22} \right] \\ &+ q_{32} \left[f_{x_1 x_1}^2 p_{12}^2 + f_{x_2 x_2}^2 p_{22}^2 + f_{x_3 x_3}^2 p_{32}^2 + 2f_{x_2 x_3}^2 p_{22} p_{32} + 2f_{x_3 x_1}^2 p_{31} p_{12} + 2f_{x_1 x_2}^2 p_{12} p_{22} \right] \\ &+ q_{33} \left[f_{x_1 x_1}^3 p_{12}^2 + f_{x_2 x_2}^3 p_{22}^2 + f_{x_3 x_3}^3 p_{32}^2 + 2f_{x_2 x_3}^3 p_{22} p_{32} + 2f_{x_3 x_1}^3 p_{31} p_{12} + 2f_{x_1 x_2}^3 p_{12} p_{22} \right] \\ &= \Omega_3. \end{aligned} \quad (6.12)$$

From equations (6.10), (6.11) and (6.12), we have

$$\begin{pmatrix} \frac{1}{2} k_1 & \sqrt{k_2} & 0 \\ -\sqrt{k_2} & k_1 & \sqrt{k_2} \\ 0 & -\sqrt{k_2} & \frac{1}{2} k_1 \end{pmatrix} \begin{pmatrix} b_{11} \\ b_{12} \\ b_{22} \end{pmatrix} = \begin{pmatrix} \Omega_1 \\ \Omega_2 \\ \Omega_3 \end{pmatrix}. \quad (6.13)$$

The equation (6.13) gives the coefficients b_{11} , b_{12} and b_{22} as follows:

$$\begin{aligned} b_{11} &= \frac{k_2(\Omega_1 + \Omega_3) - \frac{k_1}{2}(\sqrt{k_2}\Omega_2 - k_1\Omega_1)}{\left(\frac{k_1^3}{4} + k_1 k_2\right)}, \\ b_{12} &= \frac{\frac{k_1^2 \Omega_2}{4} - \frac{k_1 \sqrt{k_2}}{2}(\Omega_3 - \Omega_1)}{\left(\frac{k_1^3}{4} + k_1 k_2\right)}, \\ b_{22} &= \frac{k_2(\Omega_1 + \Omega_3) + \frac{k_1^2 \Omega_3}{2} + \frac{k_1 \sqrt{k_2}}{2}\Omega_2}{\left(\frac{k_1^3}{4} + k_1 k_2\right)}. \end{aligned}$$

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

$$\Pi = F_{111}^1 + F_{112}^1 + F_{122}^1 + F_{222}^1 + \frac{F_{12}^1(F_{11}^1 + F_{22}^1) - F_{12}^2(F_{11}^2 + F_{22}^2) - F_{11}^1F_{11}^2 + F_{22}^1F_{22}^2}{\sqrt{k_2}}, \quad (6.15)$$

where $F_{ijk} = \frac{\partial^3 F}{\partial z_i \partial z_j \partial z_k}$ at the origin. If the value of the above expression is negative, then the Hopf bifurcating limit cycle is stable and we have a supercritical Hopf bifurcation. If the value is positive, then the Hopf bifurcating limit cycle is unstable and the bifurcation is subcritical.

Here

$$\begin{aligned} F_{11}^1 &= 2q_{11}[f_{x_1x_1}^1p_{11}^2 + f_{x_2x_2}^1p_{21}^2 + f_{x_3x_3}^1p_{31}^2 + 2f_{x_1x_2}^1p_{11}p_{31} + 2f_{x_1x_3}^1p_{11}p_{21}] \\ &\quad + 2q_{12}[f_{x_1x_1}^2p_{11}^2 + f_{x_2x_2}^2p_{21}^2 + f_{x_3x_3}^2p_{31}^2 + 2f_{x_1x_2}^2p_{11}p_{31} + 2f_{x_1x_3}^2p_{11}p_{21}] \\ &\quad + 2q_{13}[f_{x_1x_1}^3p_{11}^2 + f_{x_2x_2}^3p_{21}^2 + f_{x_3x_3}^3p_{31}^2 + 2f_{x_1x_2}^3p_{11}p_{31} + 2f_{x_1x_3}^3p_{11}p_{21}], \\ F_{12}^1 &= 2q_{11}[f_{x_1x_1}^1p_{11}p_{12} + f_{x_2x_2}^1p_{21}p_{22} + f_{x_3x_3}^1p_{31}p_{32} + f_{x_1x_2}^1(p_{11}p_{32} + p_{12}p_{31}) \\ &\quad + f_{x_1x_3}^1(p_{11}p_{32} + p_{12}p_{31})] + 2q_{12}[f_{x_1x_1}^2p_{11}p_{12} + f_{x_2x_2}^2p_{21}p_{22} + f_{x_3x_3}^2p_{31}p_{32} \\ &\quad + f_{x_1x_2}^2(p_{11}p_{32} + p_{12}p_{31}) + f_{x_1x_3}^2(p_{11}p_{32} + p_{12}p_{31})] + 2q_{13}[f_{x_1x_1}^3p_{11}p_{12} + f_{x_2x_2}^3p_{21}p_{22} + f_{x_3x_3}^3p_{31}p_{32} \\ &\quad + f_{x_1x_2}^3(p_{11}p_{32} + p_{12}p_{31}) + f_{x_1x_3}^3(p_{11}p_{32} + p_{12}p_{31})], \end{aligned}$$

$$\begin{aligned} F_{22}^1 &= 2q_{11}[f_{x_1x_1}^1p_{12}^2 + f_{x_2x_2}^1p_{22}^2 + f_{x_3x_3}^1p_{32}^2 + 2f_{x_1x_2}^1p_{12}p_{32} + 2f_{x_1x_3}^1p_{12}p_{22}] \\ &\quad + 2q_{12}[f_{x_1x_1}^2p_{12}^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_3}^2p_{12}p_{22}] + 2q_{13} \\ &\quad [f_{x_1x_1}^3p_{12}^2 + f_{x_2x_2}^3p_{22}^2 + f_{x_3x_3}^3p_{32}^2 + 2f_{x_1x_2}^3p_{12}p_{32} + 2f_{x_1x_3}^3p_{12}p_{22}], \\ F_{111}^1 &= 6q_{11}b_{11}[f_{x_1x_1}^1p_{11}p_{13} + f_{x_2x_2}^1p_{21}p_{23} + f_{x_3x_3}^1p_{31}p_{33} + f_{x_1x_2}^1(p_{11}p_{33} + p_{13}p_{31}) \\ &\quad + f_{x_1x_3}^1(p_{11}p_{33} + p_{13}p_{31})] + 6q_{12}b_{11}[f_{x_1x_1}^2p_{11}p_{13} + f_{x_2x_2}^2p_{21}p_{23} + f_{x_3x_3}^2p_{31}p_{33} \\ &\quad + f_{x_1x_2}^2(p_{11}p_{33} + p_{13}p_{31}) + f_{x_1x_3}^2(p_{11}p_{33} + p_{13}p_{31})] + 6q_{13}b_{11}[f_{x_1x_1}^3p_{11}p_{13} + f_{x_2x_2}^3p_{21}p_{23} + f_{x_3x_3}^3p_{31}p_{33} \\ &\quad + f_{x_1x_2}^3(p_{11}p_{33} + p_{13}p_{31}) + f_{x_1x_3}^3(p_{11}p_{33} + p_{13}p_{31})], \\ F_{122}^1 &= 2q_{11}[f_{x_1x_1}^1(2p_{12}p_{13}b_{12} + p_{11}p_{13}b_{22}) + f_{x_2x_2}^1(2p_{22}p_{23}b_{12} + p_{21}p_{23}b_{22}) \\ &\quad + f_{x_3x_3}^1(2p_{32}p_{33}b_{12} + p_{31}p_{33}b_{22}) + f_{x_1x_2}^1(2p_{13}p_{32}b_{12} + p_{11}p_{33}b_{22} + p_{13}p_{32}b_{22} + 2p_{12}p_{33}b_{12}) \\ &\quad + f_{x_1x_3}^1(2p_{12}p_{23} \times b_{12} + p_{13}p_{21}b_{22} + p_{11}p_{23}b_{22} + 2p_{22}p_{13}b_{12})] \\ &\quad + 2q_{12}[f_{x_1x_1}^2(2p_{12}p_{13}b_{12} + p_{11}p_{13}b_{22}) + f_{x_2x_2}^2 \times (2p_{22}p_{23}b_{12} + p_{21}p_{23}b_{22}) \\ &\quad + f_{x_3x_3}^2(2p_{12}p_{23}b_{12} + p_{11}p_{23}b_{22} + 2p_{13}p_{22}b_{12} + p_{13}p_{21}b_{22})] \\ &\quad + 2q_{13}[f_{x_1x_1}^3(2p_{13}p_{12}b_{12} + p_{11}p_{13}b_{22}) + f_{x_2x_2}^3(2p_{22}p_{23}b_{12} + p_{21}p_{23}b_{22}) \\ &\quad + f_{x_3x_3}^3(2p_{32}p_{33}b_{12} + p_{31}p_{33}b_{22}) + f_{x_1x_2}^3(2p_{13}p_{32}b_{12} + p_{11}p_{33}b_{22} + p_{13}p_{32}b_{22} + 2p_{12}p_{33}b_{12}) \\ &\quad + f_{x_1x_3}^3(2p_{12}p_{23}b_{12} + p_{11}p_{23}b_{22} + 2p_{13}p_{22}b_{12} + p_{13}p_{21}b_{22})], \end{aligned}$$

$$\begin{aligned} F_{11}^2 &= 2q_{21}[f_{x_1x_1}^1p_{11}^2 + f_{x_2x_2}^1p_{21}^2 + f_{x_3x_3}^1p_{31}^2 + 2f_{x_1x_2}^1p_{11}p_{31} + 2f_{x_1x_3}^1p_{11}p_{21}] \\ &\quad + 2q_{22}[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_3}^2p_{11}p_{21}] \\ &\quad + 2q_{23}[f_{x_1x_1}^3p_{11}^2 + f_{x_2x_2}^3p_{21}^2 + f_{x_3x_3}^3p_{31}^2 + 2f_{x_1x_2}^3p_{11}p_{31} + 2f_{x_1x_3}^3p_{11}p_{21}], \\ F_{12}^2 &= 2q_{21}[f_{x_1x_1}^1p_{11}p_{12} + f_{x_2x_2}^1p_{21}p_{22} + f_{x_3x_3}^1p_{31}p_{32} + f_{x_1x_2}^1(p_{11}p_{32} + p_{12}p_{31}) \\ &\quad + f_{x_1x_3}^1(p_{11}p_{32} + p_{12}p_{31})] + 2q_{22}[f_{x_1x_1}^2p_{11}p_{12} + f_{x_2x_2}^2p_{21}p_{22} + f_{x_3x_3}^2p_{31}p_{32} \\ &\quad + f_{x_1x_2}^2(p_{11}p_{32} + p_{12}p_{31}) + f_{x_1x_3}^2(p_{11}p_{32} + p_{12}p_{31})] + 2q_{23}[f_{x_1x_1}^3p_{11}p_{12} + f_{x_2x_2}^3p_{21}p_{22} + f_{x_3x_3}^3p_{31}p_{32} \\ &\quad + f_{x_1x_2}^3(p_{11}p_{32} + p_{12}p_{31}) + f_{x_1x_3}^3(p_{11}p_{32} + p_{12}p_{31})], \\ F_{22}^2 &= 2q_{21}[f_{x_1x_1}^1p_{12}^2 + f_{x_2x_2}^1p_{22}^2 + f_{x_3x_3}^1p_{32}^2 + 2f_{x_1x_2}^1p_{12}p_{32} + 2f_{x_1x_3}^1p_{12}p_{22}] \\ &\quad + 2q_{22}[f_{x_1x_1}^2p_{12}^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_3}^2p_{12}p_{22}] \\ &\quad + 2q_{23}[f_{x_1x_1}^3p_{12}^2 + f_{x_2x_2}^3p_{22}^2 + f_{x_3x_3}^3p_{32}^2 + 2f_{x_1x_2}^3p_{12}p_{32} + 2f_{x_1x_3}^3p_{12}p_{22}], \\ F_{112}^2 &= 2q_{21}[f_{x_1x_1}^1(2p_{11}p_{13}b_{12} + p_{12}p_{13}b_{11}) + f_{x_2x_2}^1(2p_{21}p_{23}b_{12} + p_{22}p_{23}b_{11}) \\ &\quad + f_{x_3x_3}^1(2p_{31}p_{33}b_{12} + p_{32}p_{33}b_{11}) + f_{x_1x_2}^1(2p_{11}p_{33}b_{12} + p_{13}p_{32}b_{11} + p_{12}p_{33}b_{11}) \\ &\quad + 2p_{13}p_{31}b_{12}) + f_{x_1x_3}^1(2p_{13}p_{21} \times b_{12} + p_{12}p_{23}b_{11} + 2p_{11}p_{23}b_{12} + p_{22}p_{13}b_{11})] \\ &\quad + 2q_{22}[f_{x_1x_1}^2(2p_{11}p_{13}b_{12} + p_{12}p_{13}b_{11}) + f_{x_2x_2}^2 \times (2p_{21}p_{23}b_{12} + p_{22}p_{23}b_{11}) \\ &\quad + f_{x_3x_3}^2(2p_{11}p_{23}b_{12} + p_{12}p_{23}b_{11} + 2p_{13}p_{21}b_{12} + p_{13}p_{22}b_{11})] + 2q_{23}[f_{x_1x_1}^3(2p_{11}p_{13}b_{12} + p_{12}p_{13}b_{11}) \\ &\quad + f_{x_2x_2}^3 \times (2p_{21}p_{23}b_{12} + p_{22}p_{23}b_{11}) + f_{x_3x_3}^3(2p_{31}p_{33}b_{12} + p_{32}p_{33}b_{11}) \\ &\quad + f_{x_1x_2}^3(2p_{13}p_{31}b_{12} + p_{32}p_{33}b_{11}) + f_{x_1x_3}^3(2p_{31}p_{13}b_{12} + p_{33}p_{12}b_{11} + 2p_{11}p_{33}b_{12} + p_{32}p_{13}b_{11})], \\ F_{222}^2 &= 6q_{21}b_{22}[f_{x_1x_1}^1p_{12}p_{13} + f_{x_2x_2}^1p_{22}p_{23} + f_{x_3x_3}^1p_{32}p_{33} + f_{x_1x_2}^1(p_{12}p_{33} + p_{13}p_{32}) \\ &\quad + f_{x_1x_3}^1(p_{12}p_{33} + p_{13}p_{32})] + 6q_{22}b_{22}[f_{x_1x_1}^2p_{12}p_{13} + f_{x_2x_2}^2p_{22}p_{23} + f_{x_3x_3}^2p_{32}p_{33} \\ &\quad + f_{x_1x_2}^2(p_{12}p_{33} + p_{13}p_{32}) + f_{x_1x_3}^2(p_{12}p_{33} + p_{13}p_{32})] + 6q_{23}b_{22}[f_{x_1x_1}^3p_{12}p_{13} + f_{x_2x_2}^3p_{22}p_{23} + f_{x_3x_3}^3p_{32}p_{33} \\ &\quad + f_{x_1x_2}^3(p_{12}p_{33} + p_{13}p_{32}) + f_{x_1x_3}^3(p_{12}p_{33} + p_{13}p_{32})]. \end{aligned}$$

Global stability of the system (2.1) around E_*

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

- (i) $a_1a_2b_1b_2rk > (x_{1*} + k)(w + k)(a_1b_1c_2 + a_2b_2c_1)$ is satisfied.

Proof Let

$$L(x_1, x_2, x_3) = L_1(x_1, x_2, x_3) + L_2(x_1, x_2, x_3) + L_3(x_1, x_2, x_3) \quad (6.16)$$

be a positive Lyapunov function, where

$$\begin{aligned} L_1 &= s_1(x_1 - x_{1*} - x_{1*} \ln(\frac{x_1}{x_{1*}})), L_2 = s_2(x_2 - x_{2*} - x_{2*} \ln(\frac{x_2}{x_{2*}})), \\ L_3 &= s_3(x_3 - x_{3*} - x_{3*} \ln(\frac{x_3}{x_{3*}})); \end{aligned}$$

s_1, s_2 and s_3 being positive real constants.

This function is well-defined and continuous in $\text{Int}(R_+^3)$. 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 Ω . The time derivative of L along with the solutions of the system (2.1) gives (cf. Sarwardi et al. (2010), Sarwardi et al. (2012))

$$\begin{aligned} \frac{dL}{dt} = & -s_1 \left[\frac{rk}{(x_{1*} + k)(x_1 + k)} - \frac{c_1 x_{2*}}{(a_1 + x_1 + b_1 x_2)(a_1 + x_{1*} + b_1 x_{2*})} \right. \\ & \left. - \frac{c_2 x_{3*}}{(a_2 + x_1 + b_2 x_3)(a_2 + x_{1*} + b_2 x_{3*})} \right] (x_1 - x_{1*})^2 \\ & - s_2 \left[\frac{c_1 e_1 (a_1 + b_1)}{(a_1 + x_1 + b_1 x_2)(a_1 + x_{1*} + b_1 x_{2*})} \right] \\ & \times (x_2 - x_{2*})^2 - s_3 \left[\frac{c_2 e_2 (a_2 + b_2)}{(a_2 + x_1 + b_2 x_3)(a_2 + x_{1*} + b_2 x_{3*})} \right] \\ & (x_3 - x_{3*})^2 \\ & + \frac{c_1 (s_2 b_1 e_1 x_{2*} - s_1 (a_1 + x_{1*})) (x_1 - x_{1*}) (x_2 - x_{2*})}{(a_1 + x_1 + b_1 x_2)(a_1 + x_{1*} + b_1 x_{2*})} \\ & + \frac{c_2 (s_3 b_2 e_2 x_{3*} - s_1 (a_2 + x_{1*}))}{(a_2 + x_1 + b_2 x_3)(a_2 + x_{1*} + b_2 x_{3*})} \\ & \times (x_1 - x_{1*}) (x_3 - x_{3*}). \end{aligned} \quad (6.17)$$

Letting $s_1 = 1$, $s_2 = \frac{a_1 + x_{1*}}{b_1 e_1 x_{2*}}$ and $s_3 = \frac{a_2 + x_{1*}}{b_2 e_2 x_{3*}}$, we have

$$\begin{aligned} \frac{dL}{dt} \leq & - \left[\frac{rk}{(x_{1*} + k)(x_1 + k)} - \frac{c_1 x_{2*}}{(a_1 + x_1 + b_1 x_2)(a_1 + x_{1*} + b_1 x_{2*})} \right. \\ & \left. - \frac{c_2 x_{3*}}{(a_2 + x_1 + b_2 x_3)(a_2 + x_{1*} + b_2 x_{3*})} \right] (x_1 - x_{1*})^2 \\ & < - \left[\frac{rk}{(x_{1*} + k)(w + k)} - \frac{c_1}{a_1 b_1} - \frac{c_2}{a_2 b_2} \right] (x - x_*)^2 \\ & < 0, \text{ by condition (i),} \end{aligned} \quad (6.18)$$

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 (6.16) and Lyapunov-Lasalle's invariance principle (cf. Hale (1989)).

Numerical simulations

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 Tables 1 and 2. These results are all verified by means of numerical illustrations of which some chosen ones are shown in the figures. 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, the system possessed a unique interior equilibrium point $E_* = (169.1663564, 55.36073780, 62.98120968)$.

The system parameter r is the growth rate of the prey population. It plays a crucial role in regulating the dynamical behaviour of the proposed system. For this reason, we try to determine the system's possible outcomes by varying this parameter within its feasible range. The interior equilibrium E_* is stable for $r > r_c = 1.320961640$ (cf. Figs. 4, 5 for local stability and Fig. 6 for global stability). The system (2.1) experiences a 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 oscillating. Following the steps discussed in Subsect. 6.1, we have found the value of $\Pi = 1.042431405 > 0$, which indicates that the obtained Hopf bifurcation is a subcritical bifurcation (cf. Fig. 7).

It is observed that, if the interference coefficient b_1 (interference effect on the first predator due to the presence of the second predator) increases it stabilizes the system for $b_1 = 0.7$, while it is unstable at $b_1 = 0.6$. When the parameter b_1 exceeds its value 20, the first predator population disappears from the system. Similarly, the interference on the second predator due to the presence of first predator, parameterized by b_2 also 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 20.9, the second predator population gets extinguished.

Analogously, if the parameter δ_1 , denoting the death rate of the first predator increases then the size of the first predator decreases as well as the second predator population increases. If δ_1 decreases, the first predator population increases and second predator population decreases. If the death rate δ_1 is gradually increased to a certain level the first predator population goes to extinction. A 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 observations (Figures are not reported here).

Concluding remarks

The problem described by the system (2.1) is well posed. The x_1, x_2 and x_3 axes are invariant under the flow of the system. To our knowledge this is the first attempt to study an ecological system with quasi-linear/bilinear growth of the prey population. Generally, researchers only studied biological model systems with logistic/linear growth of prey population. One of the important results is that the prey population becomes unbounded in absence of its admissible predator in the long run. But in the presence of predator the prey population can be bounded under

Table 1 Schematic representation of our analytical findings

Equilibria	Feasibility conditions/parametric restrictions	Stability conditions/parametric restrictions	Nature
E_0	No conditions	No conditions	Unstable
E_1	$c_1 e_1 > \delta_1, x_{11} > \frac{b_1 \delta_1}{c_1 e_1 - \delta_1}$	$e_1 x_{11} + x_{21} > \frac{k(1-b_1 e_1) - a_1}{b_1}$	LAS
E_2	$c_2 e_2 > \delta_2, x_{12} > \frac{b_2 \delta_2}{c_2 e_2 - \delta_2}$	$e_2 x_{12} + x_{32} > \frac{k(1-b_2 e_2) - a_2}{b_2}$	LAS
E_*	$x_{1*} > \max \left\{ \frac{a_1 \delta_1}{c_1 e_1 - \delta_1}, \frac{a_2 \delta_2}{c_2 e_2 - \delta_2} \right\}$	$k < \min \{a_1 + b_1 x_{2*}, a_2 + b_2 x_{3*}\}$	LAS
E_*		$(i) r > \delta_1 + \delta_2, (ii) x_{11} > \frac{a_2 \delta_2}{c_2 e_2 - \delta_2}, (iii) x_{12} > \frac{a_1 \delta_1}{c_1 e_1 - \delta_1}$	Persistence
E_*		Stated in the Proposition 3.3	Boundedness
E_*		$\Pi > 0$ (cf. equation (6.15))	SHB
E_*	$x_{1*} > \max \left\{ \frac{a_1 \delta_1}{c_1 e_1 - \delta_1}, \frac{a_2 \delta_2}{c_2 e_2 - \delta_2} \right\}$	$a_1 a_2 b_1 b_2 r k > (x_{1*} + k)(w + k) \times (a_1 b_1 c_2 + a_2 b_2 c_1)$	GAS

LAS locally asymptotically stable, GAS globally asymptotically stable, HB Hopf bifurcation, SHB subcritical Hopf bifurcation

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	Fig. 1: (a)-(b)	2D view of Hopf bifurcation
2		1.320961640	Fig. 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	$r = 1.37, k = 200$, $a_1 = 100, a_2 = 100$, $b_1 = 0.5; b_2 = 0.5$, $c_1 = 1.8, c_2 = 1.8$, $\delta_1 = 0.82, \delta_2 = 0.62$, $e_1 = 0.8143, e_2 = 0.6250$	$r_c = 1.320961640$, $\Pi = 1.0424314050$	Fig. 7	Subcritical Hopf bifurcation

suitable combinations of system parameters. As a consequence the total environmental population is bounded above (cf. Subsect. 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 quasi-linear/bilinear growth of the prey population, the axial equilibrium point is driven away by the system, a fact

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

Fig. 2 Limit cycle behaviour of the dynamical system at E_* with the same parameter values used for Fig. 1

which is rarely found in the modern research work on mathematical biology. Thus, the prey population alone cannot survive in stable condition without the predator populations. Only the mutual interference between the predators, which are parameterized by b_1 and b_2 can alone stabilize the prey–predator interactions even when a quasi-linear/bilinear intrinsic growth rate of prey population is considered in the proposed mathematical model. These parameters contribute in stabilizing prey–predator interactions when only linear intrinsic growth rate is considered in some mathematical models (cf. Dimitrov and Kojouharov (2005)). There exist a balance between the predator’s need

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

for food and its saturation level. In this case a periodic behaviour is expected. 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 it (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 Figs. 1, 2 and 3,

Fig. 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: $r = 1.47 > r_c = 1.320961640$, $k = 200$, $a_1 = 100$, $a_2 = 100$, $b_1 = 0.5$, $b_2 = 0.5$; $c_1 = 1.8$, $c_2 = 1.8$, $\delta_1 = 0.82$, $\delta_2 = 0.62$, $e_1 = 0.8143$, $e_2 = 0.6250$

Fig. 5 3D view of local asymptotic stability of the dynamical system at E_* with the same parameter values used for Fig. 4

Fig. 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 Fig. 4 except $r = 1.29$

Fig. 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

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. Figs. 5, 6).

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