Persistence and Extinction of One-Prey and Two-Predators System *

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Abstract. In this paper, a mathematical model is proposed and analysed to study the dynamics of one-prey two-predators system with ratio-dependent predators growth rate. Criteria for local stability, instability and global stability of the nonnegative equilibria are obtained. The permanent co-existence of the three species is also discussed. Finally, computer simulations are performed to investigate the dynamics of the system.

Keywords: ratio-dependent predator-prey model, persistence, extinction, stability.

1 Introduction

The co-existence and extinction of interacting species have been of great importance and have been studied extensively in the past. The effect of two competing predators on a single limited prey has also been studied [1–4]. In particular, Hsu [3] proposed and analysed a model of two predators competing for a single prey. He showed that if the interference coefficient is small, then the winner in purely exploitative system competes its rival successfully and if the interference coefficient is large enough, then the competition outcome depends on the initial population of predator species. Freedman and Waltman [1] considered three level food webs – two competing predators feeding on a single prey and

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a single predator feeding on two competing prey species. They obtained criteria for the system to be persistent. Cushing [5] studied a competition model of two predator species competing for a single renewable resource prey species under the assumption that the system parameters are periodic in time. Gopalsamy [6] also described a model of two consumer species and one resource species and found some sufficient conditions for the solutions of the system to converge to its equilibrium. Mitra *et al.* [4] studied the permanent co-existence and global stability of a model of a living resource supporting two competing predators. They proved that the permanent co-existence of the system depends on the threshold of the ratio between the coefficients of numerical responses of the two consumers. Dubey [7] described a mathematical model of two species utilizing a common resource and one of the species itself is an alternative resource for the other. Dubey and Das [8] proposed and analysed a mathematical model based on the dynamics of Gause-type model where the two predators are competing with interference for a limited prey.

It may be pointed out here that all the above studies are based on the traditional prey dependent models. Recently, it has been observed that in some situations, especially when predators have to search for food and therefore have to share or compete for food, a more suitable predator-prey theory should be based on the so-called ratio-dependent theory, in which the per capita predator growth rate should be function of the ratio of prey to predator abundance, and should be the so-called predator functional response [9–12]. This concept is also supported by numerous field and laboratory experiments and observations [11, 13, 14]. In prey-dependent models, predator has a vertical isocline and in ratio-dependent models, predator has a slanted isocline. There are also differences in their prey isoclines. It has been shown that the ratio-dependent models are capable of producing richer and more reasonable or acceptable dynamics [13, 15, 16]. Kuang and Beretta [17] investigated the global qualitative analysis of a ratio-dependent predator-prey system. They showed that if the positive steady state of the so-called Michaelis-Menten ratio-dependent predator-prey system is locally asymptotically stable, then the system has no nontrivial positive periodic solutions. In this paper, some important questions on the global qualitative behavior of solutions of the model were left open. These open questions and uniqueness of limit cycles are resolved by Hsu *et al.* [18]. Berezovskaya *et al.* [19] studied the stability properties and dynamic regimes of a predator-prey model in which the functional response is a function of the ratio of prey and predator abundances. They showed that there exists areas of coexistence, areas in which both the species become extinct, and the areas of conditional coexistence depending on the initial values. Xiao and Ruan [20] also investigated the qualitative behavior of a class of ratio-dependent predator-prey model, and they found that there exists numerous kinds of topological structures in a neighbourhood of the origin including the parabolic orbits, the elliptic orbits, the hyperbolic orbits, and any combination of them. It may be pointed out here that a very little attention has been paid to the qualitative analyses of food chains or multi-species interaction models based on ratio-dependent approach. Recently, Kesh *et al.* [21] proposed and analysed a mathematical model of two competing prey and one predator species where the prey species follow Lotka-Volterra dynamics and predator uptake functions are ratio-dependent. They derived conditions for the existence of different boundary equilibria and discussed their global stability. They also obtained sufficient conditions for the permanence of the system. Hsu *et al.* [18] studied the qualitative properties of a ratio dependent predator-prey model. They showed that the dynamics outcome of interactions depend upon parameter values and initial data. Hsu *et al.* [16] proposed a model to study the qualitative properties of a ratio-dependent one-prey two-predators system. But in this paper, the proposed model is not well defined at $(0, 0, 0)$. Also, in this investigation the existence of interior equilibrium, its stability behavior and persistence of the system are not discussed, which are biologically and ecologically very important. Further, no interaction has been considered between the two predators.

Keeping the above in view, in this paper, a mathematical model of one prey – two predators system in which the predator interference is of ratio-dependent is proposed and analysed. Our proposed model is well defined at the origin and the two predators are in the state of competition for the single prey. It may be pointed out here that results on one prey – two predator system with prey dependent trophic function are well known [3, 4, 8]. Here we are interested to investigate changes in the qualitative behavior of the system when the trophic function is of ratio-dependent.

2 Mathematical model

Consider an ecosystem where we wish to model the interaction of two predators competing for a single prey. It is assumed that prey species grows logistically and the predator functional response is of ratio-dependent. Let $x(t)$ be the density of prey species and $y_i(t)$ $(i = 1, 2)$ be the density of predator species that compete with each other for the prey. Then the dynamics of the system may be governed by the following system of autonomous differential equations.

$$\begin{aligned}
\frac{dx}{dt} &= rx\Big(1 - \frac{x}{K}\Big) - \frac{a_1 x y_1}{1 + b_1 x + y_1 + m y_2} - \frac{a_2 m x y_2}{1 + b_2 x + y_1 + m y_2},\\
\frac{dy_1}{dt} &= -\delta_1 y_1 - \alpha y_1 y_2 + \frac{\lambda_1 a_1 x y_1}{1 + b_1 x + y_1 + m y_2},\\
\frac{dy_2}{dt} &= -\delta_2 y_2 - \beta y_1 y_2 + \frac{\lambda_2 a_2 m x y_2}{1 + b_2 x + y_1 + m y_2},\\
x(0) &> 0, \quad y_i(0) > 0, \quad i = 1, 2.
\end{aligned} \tag{1}$$

In model (1), r is the intrinsic growth rate of prey species and K is its carrying capacity. δ_i is the mortality rate coefficient of predator species y_i and α, β are their interspecific interference coefficient. a_1, a_2 are searching efficiency constants and m is the relative predation rate of y_2 with respect to y_1. λ_i is the food conversion coefficient of the predator species y_i. a_1/b_1 and $a_2 m/b_2$ are the maximum per-capita capturing rates for y_1 and y_2 respectively.

First of all, we re-scale the variables in model (1). Let

$$\begin{aligned}
&\overline{x} = x/K, \quad \overline{y}_1 = y_1, \quad \overline{y}_2 = m y_2, \quad \overline{a}_1 = a_1, \quad \overline{a}_2 = a_2\\
&\overline{r} = r, \quad \overline{\alpha} = \alpha, \quad \overline{\beta} = \beta, \quad \overline{\delta}_1 = \delta_1, \quad \overline{\delta}_2 = \delta_2,\\
&\overline{b}_1 = b_1 K, \quad \overline{b}_2 = b_2 K, \quad \overline{\lambda}_1 = \lambda_1 K, \quad \overline{\lambda}_2 = \lambda_2 K m.
\end{aligned}$$

Using the above variables and dropping bars from the resulting equation, we obtain

$$\begin{aligned}
\frac{dx}{dt} &= rx(1 - x) - \frac{a_1 x y_1}{1 + b_1 x + y_1 + y_2} - \frac{a_2 x y_2}{1 + b_2 x + y_1 + y_2},\\
\frac{dy_1}{dt} &= -\delta_1 y_1 - \alpha y_1 y_2 + \frac{\lambda_1 a_1 x y_1}{1 + b_1 x + y_1 + y_2},\\
\frac{dy_2}{dt} &= -\delta_2 y_2 - \beta y_1 y_2 + \frac{\lambda_2 a_2 x y_2}{1 + b_2 x + y_1 + y_2},\\
x(0) &> 0, \quad y_i(0) > 0, \quad i = 1, 2.
\end{aligned} \tag{2}$$

In the next section we present the equilibrium analysis of model (2).

3 Equilibrium analysis

It can be checked that system (2) has five nonnegative equilibria, namely $E_0(0,0,0),\ E_1(1,0,0),\ E_2(\overline{x},\overline{y}_1,0),\ E_3(\widetilde{x},0,\widetilde{y}_2)$ and $E^*(x^*,y_1^*,y_2^*)$. The equilibria E_0 and E_1 obviously exist. We show the existence of other equilibria as follows.

Existence of $E_2(\overline{x},\overline{y}_1,0)$.
Here $\overline{x}$ and $\overline{y}_1$ are the positive solutions of the following algebraic equations:

$$\begin{aligned} &r(1-x)-\frac{a_1y_1}{1+b_1x+y_1}=0,\\ &-\delta_1+\frac{\lambda_1a_1x}{1+b_1x+y_1}=0. \end{aligned} \tag{3}$$

Solving (3), we get

$$\begin{aligned} \overline{x}&=L_1(1+y_1),\\ \overline{y}_1&=\frac{-B_1+\sqrt{B_1^2-4A_1C_1}}{2A_1}, \end{aligned} \tag{4}$$

where

$$\begin{aligned} L_1&=\delta_1/(\lambda_1a_1-\delta_1b_1),\\ A_1&=rL_1(1+b_1L_1),\\ B_1&=r(1+b_1L_1)[2L_1-1]+a_1,\\ C_1&=r(1+b_1L_1)[L_1-1]. \end{aligned}$$

Thus, the equilibrium E_2 exists if

$$0<L_1<1 \tag{5}$$

holds.

Existence of $E_3(\widetilde{x},0,\widetilde{y}_2)$.
As in the existence of E_2, it can be seen that

$$\begin{aligned} \widetilde{x}&=L_1(1+\widetilde{y}_2),\\ \widetilde{y}_2&=\frac{-B_2+\sqrt{B_2^2-4A_2C_2}}{2A_2}, \end{aligned} \tag{6}$$

where

$$L_2 = \delta_2/(\lambda_2 a_2 - b_2\delta_2),$$
$$A_2 = rL_2(1 + b_2L_2),$$
$$B_2 = r(1 + b_2L_2)[2L_2 - 1] + a_2,$$
$$C_2 = r(1 + b_2L_2)[L_2 - 1].$$

Thus, the equilibrium E_3 exists if

$$0 < L_2 < 1 \tag{7}$$

holds.

Existence of $E^*(x^*, y_1^*, y_2^*)$.
Here x^*, y_1^* and y_2^* is the positive solution of the system of algebraic equations given below.

$$rx(1-x) = \frac{a_1y_1}{1 + b_1x + y_1 + y_2} + \frac{a_2y_2}{1 + b_2x + y_1 + y_2}, \tag{8a}$$

$$\delta_1 + \alpha y_2 = \frac{\lambda_1 a_1 x}{1 + b_1x + y_1 + y_2}, \tag{8b}$$

$$\delta_2 + \beta y_1 = \frac{\lambda_2 a_2 x}{1 + b_2x + y_1 + y_2}. \tag{8c}$$

Solving (8b) and (8c), we get

$$\begin{aligned} f(y_1, y_2) \equiv\ & (\delta_1 + \alpha y_2)(\lambda_2 a_2 - b_2\delta_2 - b_2\beta y_1) \\ & - (\delta_2 + \beta y_1)(\lambda_1 a_1 - b_1\delta_1 - b_1\alpha y_2) = 0. \end{aligned} \tag{9}$$

Using (8b) and (8c) in (8a), we obtain

$$\begin{aligned} g(y_1, y_2) \equiv\ & r\lambda_1\lambda_2 \frac{(\delta_1+\alpha y_2)(1+y_1+y_2)}{\lambda_1 a_1 - b_1\delta_1 - b_1\alpha y_2}\left(1 - \frac{(\delta_1+\alpha y_2)(1+y_1+y_2)}{\lambda_1 a_1 - b_1\delta_1 - b_1\alpha y_2}\right) \\ & - (\delta_1 + \alpha y_2)\lambda_2 y_1 - (\delta_2 + \beta y_1)\lambda_1 y_2 = 0. \end{aligned} \tag{10}$$

From (9) we note the following: when $y_2 \to 0$, then $y_1 \to y_{1a}$, where

$$y_{1a} = \frac{L_1(\lambda_2 a_2 - b_2\delta_2) - \delta_2}{\beta(1 + b_2L_1)}. \tag{11}$$

We note that $y_{1a} > 0$ if

$$0 < L_2 < L_1. \tag{12}$$

We also have $\frac{dy_1}{dy_2} = \frac{A}{B}$, where

$$A = \alpha\big[\lambda_2 a_2 + (\delta_2 + \beta y_1)(b_1 - b_2)\big],$$
$$B = \beta\big[\lambda_1 a_1 + (\delta_2 + \alpha y_2)(b_2 - b_1)\big].$$

It is clear that $\frac{dy_1}{dy_2} > 0$ if either

$$\begin{aligned} &\text{(i) } A > 0 \quad \text{and} \quad B > 0, \quad \text{or} \\ &\text{(ii) } A < 0 \quad \text{and} \quad B < 0, \end{aligned} \tag{13}$$

hold.

Remark. *If* $b_1 = b_2$, *then* $\frac{dy_1}{dy_2} > 0$.

From (10) we note the following: when $y_2 \to 0$, then $y_1 \to y_{1b}$, where

$$y_{1b} = \frac{-B_3 + \sqrt{B_3^2 - 4A_3C_3}}{2A_3},$$
$$A_3 = r\lambda_1\lambda_2 L_1^2,$$
$$B_3 = r\lambda_1\lambda_2 L_1[2L_1 - 1] + \lambda_2\delta_1,$$
$$C_3 = r\lambda_1\lambda_2 L_1[L_1 - 1].$$

Clearly $C_3 < 0$ if inequality (5) is satisfied. We also have

$$\frac{dy_1}{dy_2} = -\frac{\partial g}{\partial y_2}\Big/\frac{\partial g}{\partial y_1}.$$

We note that $\frac{dy_1}{dy_2} < 0$ if either

$$\begin{aligned} &\text{(i) } \frac{\partial g}{\partial y_1} > 0 \quad \text{and} \quad \frac{\partial g}{\partial y_2} > 0, \quad \text{or} \\ &\text{(ii) } \frac{\partial g}{\partial y_1} < 0 \quad \text{and} \quad \frac{\partial g}{\partial y_2} < 0 \end{aligned} \tag{14}$$

hold.

From the above analysis we note that the two isoclines (9) and (10) intersect at a unique point (y_2^*, y_1^*) if in addition to conditions (5), (12)–(14), the following inequality holds:

$$y_{1a} < y_{1b}. \tag{15}$$

Knowing the values of y_1^* and y_2^*, the value of x^* can be calculated from

$$x^* = \frac{(\delta_1 + \alpha y_2^*)(1 + y_1^* + y_2^*)}{\lambda_1 a_1 - b_1 \delta_1 - b_1 \alpha y_2^*}. \tag{16}$$

It may be noted here that for x^* to be positive we must have

$$\lambda_1 a_1 > b_1(\delta_1 + \alpha y_2^*). \tag{17}$$

This completes the existence of E^*.

4 Dynamical behaviour

The dynamical behaviour of equilibria can be studied by computing the variational matrices corresponding to each equilibrium point. From these matrices and using the Routh-Hurwitz criteria, we note the following.

1. The equilibrium point E_0 is a saddle point with locally stable manifold in the $y_1 - y_2$ plane and with locally unstable manifold in the x direction.
2. (a) If inequalities (5) and (7) hold, then E_1 is a saddle point with locally stable manifold in the x direction and with locally unstable manifold in the $y_1 - y_2$ plane.

   (b) If $\lambda_i a_i < \delta_i b_i$ $(i = 1, 2)$, then equilibria E_2 and E_3 do not exist and in such a case the equilibrium point E_1 is locally asymptotically stable in the $x - y_1 - y_2$ space.
3. Let us denote

$$\begin{aligned} L_3 &= -\delta_2 - \beta \overline{y}_1 + \frac{\lambda_2 a_2 \overline{x}}{1 + b_2 \overline{x} + \overline{y}_1}, \\ L_4 &= -\delta_1 - \alpha \widetilde{y}_2 + \frac{\lambda_1 a_1 \widetilde{x}}{1 + b_1 \widetilde{x} + \widetilde{y}_2}. \end{aligned} \tag{18}$$

Then E_2 is locally stable or unstable along the y_2 direction according as $L_3 < 0$ or $L_3 > 0$ and E_3 is locally stable or unstable along the y_1 direction according as $L_4 < 0$ or $L_4 > 0$.

We now state the local dynamical behavior of planer equilibria E_2 and E_3 in the form of Theorem 1 and Theorem 2 respectively. The proofs of these two theorems follow from the Routh-Hurwitz criteria and hence omitted.

Theorem 1. (i) *If $\lambda_1 > b_1$, then E_2 is locally asymptotically stable in the $x - y_1$ plane.*

(ii) *If $\lambda_1 > b_1$ and $\lambda_2 a_2 < b_2\delta_2$, then E_2 is locally asymptotically stable in the $x - y_1 - y_2$ space.*

(iii) *If $\lambda_1 > b_1$ and $L_3 > 0$, then E_2 is a saddle point with locally stable manifold in the $x - y_1$ plane and with locally unstable manifold in the y_2 direction.*

Theorem 2. (i) *If $\lambda_2 > b_2$, then E_3 is locally asymptotically stable in the $x - y_2$ plane.*

(ii) *If $\lambda_2 > b_2$ and $\lambda_1 a_1 < b_1\delta_1$, then E_3 is locally asymptotically stable in the $x - y_1 - y_2$ space.*

(iii) *If $\lambda_2 > b_2$ and $L_4 > 0$, then E_3 is a saddle point with locally stable manifold in the $x - y_2$ plane and with locally unstable manifold in the y_1 direction.*

Remark. (a) *If $\lambda_1 a_1 < b_1\delta_1$, then the equilibrium point E_2 does not exist and in such a case $L_4 < 0$.*

(b) *If $\lambda_2 a_2 < b_2\delta_2$, then the equilibrium point E_3 does not exist and in such a case $L_3 < 0$.*

In the next two theorems we show that planer equilibria E_2 and E_3 are globally asymptotically stable under certain parametric conditions.

Theorem 3. *If $\lambda_1 > b_1$, then E_2 is globally asymptotically stable in the interior of the positive quadrant of $x - y_1$ plane.*

Proof. Let

$$
\begin{aligned}
H(x, y_1) &= \frac{1}{xy_1},\\
h_1(x, y_1) &= rx(1-x) - \frac{a_1 x y_1}{1 + b_1 x + y_1},\\
h_2(x, y_2) &= -\delta_1 y_1 + \frac{\lambda_1 a_1 x y_1}{1 + b_1 x + y_1}.
\end{aligned}
$$

Clearly, $H(x, y_1) > 0$ in the interior of the positive quadrant of $x - y_1$ plane. Then we have

$$
\Delta(x, y_1) = \frac{\partial}{\partial x}(h_1 H) + \frac{\partial}{\partial y_1}(h_2 H) = -\frac{r}{y_1} - \frac{(\lambda_1 - b_1)a_1}{(1 + b_1 x + y_1)^2} < 0.
$$

Clearly $\Delta(x, y_1)$ does not change sign and is not identically zero in the positive quadrant of $x - y_1$ plane. Therefore, by Bendixson-Dulac criterion, E_2 is globally asymptotically stable in the interior of the positive quadrant of $x - y_1$ plane. □

Similarly we can prove the following theorem.

Theorem 4. *If $\lambda_2 > b_2$, then E_3 is globally asymptotically stable in the interior of the positive quadrant of $x - y_2$ plane.*

Theorems 3 and 4 show that in ratio-dependent models, food conversion coefficients λ_i $(i = 1, 2)$ play an important role in determining the dynamics of planer equilibria.

In the next theorem we show that system (2) is uniformly persistent. By the permanence or persistence of a system, we mean that all the species are present and non of them will go to extinction. The persistence of a system have been studied by several researchers [1, 4, 22–24].

Theorem 5. *In addition to assumptions* (5) *and* (7)*, let the hypotheses of Theorem* 3 *and Theorem* 4 *hold. If*

$$
L_3 > 0, \quad L_4 > 0 \tag{19}
$$

hold, then system (2) *is uniformly persistent.*

Proof. We prove this theorem by the method of average Liapunov function [23]. Let the average Liapunov function for system (2) be

$$\sigma(X) = x^p y_1^{p_1} y_2^{p_2},$$

where p, p_1 and p_2 are positive constants. Clearly $\sigma(X)$ is a nonnegative C^1 function defined in R^3_+. Then we have

$$\begin{aligned}\psi(X) = \frac{\dot\sigma(X)}{\sigma(X)} &= p\frac{\dot x}{x} + p_1\frac{\dot y_1}{y_1} + p_2\frac{\dot y_2}{y_2}\\ &= p\left[r(1-x) - \frac{a_1 y_1}{1+b_1x+y_1+y_2} - \frac{a_2y_2}{1+b_2x+y_1+y_2}\right]\\ &\quad + p_1\left[-\delta_1 - \alpha y_2 + \frac{\lambda_1 a_1 x}{1+b_1x+y_1+y_2}\right]\\ &\quad + p_2\left[-\delta_2 - \beta y_1 + \frac{\lambda_2 a_2 x}{1+b_2x+y_1+y_2}\right].\end{aligned}$$

Since inequalities (5) and (7) hold, planer equilibria E_2 and E_3 exits. Further, hypotheses of Theorem 3 and 4 imply that there are no periodic orbits in the interior of positive quadrant of $x - y_1$ plane and $x - y_2$ plane. Thus, to prove the uniform persistence of the system, it is enough to show that $\psi(X) > 0$ for all equilibria $X \in bd\ R^3_+$, for a suitable choice of $p, p_1, p_2 > 0$ i.e., the following conditions must be satisfied for the system to be uniformly persistent.

$$\psi(E_0) = pr - p_1\delta_1 - p_2\delta_2 > 0, \tag{20a}$$

$$\psi(E_1) = p_1\left[-\delta_1 + \frac{\lambda_1 a_1}{1+b_1}\right] + p_2\left[-\delta_2 + \frac{\lambda_2 a_2}{1+b_2}\right] > 0, \tag{20b}$$

$$\psi(E_2) = p_2 L_3 > 0, \tag{20c}$$

$$\psi(E_3) = p_1 L_4 > 0. \tag{20d}$$

We note that by increasing p to sufficiently large value, $\psi(E_0)$ can be made positive. Thus, inequality (20a) holds. Equations (5) and (7) imply that (20b) holds. If inequalities in equation (19) hold, then (20c) and (20d) are satisfied. Hence the theorem follows. □

Theorem 5 shows that system (2) is permanent or uniformly persistent if prey-predator subsystems are globally asymptotically stable and death rate coefficient δ_i of predator species y_i is less than a threshold value. This threshold value depends upon the equilibrium levels of prey and predators, food conversion coefficients and capturing rates.

In the next theorem, we are able to find sufficient conditions under which the given system is not persistent.

Theorem 6. *If* $\lambda_i a_i < b_i \delta_i$ $(i = 1, 2)$, *then system* (2) *is not persistent and both predators will go to extinction.*

Proof. Under the given hypothesis we note from (20b)–(20d) that $\psi(E_1) < 0$, $\psi(E_2) < 0$ and $\psi(E_3) < 0$ for some positive constants p_1 and p_2. As stated in 2(b) of Section 4 of this article that under the given hypothesis of Theorem 6, equilibria E_2 and E_3 do not exist. Hence, distance to the boundary decreases along orbits near the fixed point E_1. Using Theorem 3 of Amann and Hofbauer [25], it follows that there is a positive invariant set $M \subset \partial R^3_+$ containing the fixed point E_1. Thus, the trajectory initiating in R^3_+ must converge to E_1. Hence, the system is not permanent and both predator species will go to extinction. $\square$

In the following theorem we show that the positive equilibrium E^* is locally asymptotically stable. In this theorem we shall use the following notations:

$$B_1^* = (1 + b_1 x^* + y_1^* + y_2^*)^2, \quad B_2^* = (1 + b_2 x^* + y_1^* + y_2^*)^2, \tag{21a}$$

$$H^* = r - a_1 b_1 y_1^*/B_1^* - a_2 b_2 y_2^*/B_2^*, \tag{21b}$$

$$c_1 = \frac{1 + b_1 x^* + y_2^*}{\lambda_1(1 + y_1^* + y_2^*)}, \quad c_2 = \frac{1 + b_2 x^* + y_1^*}{\lambda_2(1 + y_1^* + y_2^*)}. \tag{21c}$$

Theorem 7. *Let the following inequalities hold:*

$$H^* > 0, \tag{22a}$$

$$(a_2 y_2^*/B_2^*)^2 < c_1 \lambda_1 a_1 H^* x^*/B_1^*, \tag{22b}$$

$$(a_1 y_1^*/B_1^*)^2 < c_2 \lambda_2 a_2 H^* x^*/B_2^*, \tag{22c}$$

$$\begin{aligned}(c_1\alpha + c_2\beta + c_1\lambda_1 a_1 x^*/B_1^* + c_2\lambda_2 a_2 x^*/B_2^*)^2 \\ < c_1 c_2 \lambda_1 \lambda_2 a_1 a_2 x^{*2}/(B_1^* B_2^*).\end{aligned} \tag{22d}$$

Then the positive equilibrium E^* *is locally asymptotically stable.*

Proof of the theorem is deferred to Appendix A.

In the following theorem we show that the positive equilibrium is globally asymptotically stable. In order to prove this theorem we need the following lemma which establishes a region of attraction for system (2). The proof of this lemma is deferred to Appendix B.

Lemma 1. *The set*

$$\Omega = \big\{(x, y_1, y_2)\colon 0 \le x \le 1,\ 0 \le x + y_1/\lambda_1 + y_2/\lambda_2 \le y_a\big\},$$

is a region of attraction for all solutions initiating in the interior of the positive orthant, where

$$y_a = (r+\eta)\eta, \quad 0 < \eta \le \min\{\delta_1, \delta_2\}.$$

Theorem 8. *Let the following inequalities hold in the region* Ω*:*

$$G^* = r - \frac{a_1 b_1 y_1^*}{1 + b_1 x^* + y_1^* + y_2^*} - \frac{a_2 b_2 y_2^*}{1 + b_2 x^* + y_1^* + y_2^*} > 0, \tag{23a}$$

$$\left[\frac{a_2 y_2^*}{1 + b_2 x^* + y_1^* + y_2^*}\right]^2 < \frac{c_1 \lambda_1 a_1 x^* G^*}{(1 + b_1 + 2\lambda_1 y_a)(1 + b_1 x^* + y_1^* + y_2^*)}, \tag{23b}$$

$$\left[\frac{a_1 y_1^*}{1 + b_1 x^* + y_1^* + y_2^*}\right]^2 < \frac{c_2 \lambda_2 a_2 x^* G^*}{(1 + b_2 + 2\lambda_2 y_a)(1 + b_2 x^* + y_1^* + y_2^*)}, \tag{23c}$$

$$\left[c_1\alpha + c_2\beta + \frac{c_1 \lambda_1 a_1 x^*}{1 + b_1 x^* + y_1^* + y_2^*} + \frac{c_2 \lambda_2 a_2 x^*}{1 + b_2 x^* + y_1^* + y_2^*}\right]^2 < \frac{N_1}{N_2}, \tag{23d}$$

where

$$N_1 = c_1 c_2 a_1 a_2 \lambda_1 \lambda_2 x^{*2}, \tag{23e}$$

$$\begin{aligned} N_2 = {} & (1 + b_1 + 2\lambda_1 y_a)(1 + b_2 + 2\lambda_2 y_a) \\ & \times (1 + b_1 x^* + y_1^* + y_2^*)(1 + b_2 x^* + y_1^* + y_2^*), \end{aligned} \tag{23f}$$

c_1 *and* c_2 *are same as defined in* (21c).

Then the positive equilibrium E^* *is globally asymptotically stable with respect to all solutions initiating in the interior of the positive orthant* Ω*.*

Proof of this theorem is deferred to Appendix C.

Theorems 7 and 8 show that under certain parametric conditions the prey and the competing predator species settle down at its equilibrium level. Conditions (22a) and (23a) show that for system (2) to be globally asymptotically stable, the intrinsic growth rate of prey species must be grater than a threshold value.

Remark. *It may be noted here that* (23a)–(23d) ⇒ (22a)–(22d) *respectively. This ensures that global stability always implies local stability.*

5 Numerical simulations

In this section we present numerical simulations of model system (2). For this purpose, we consider the following values of parameters in model (2):

$$\begin{aligned} &r = 0.75,\ a_1 = 4,\ b_1 = 5.01,\ a_2 = 0.5,\ b_2 = 4.05, \\ &\delta_1 = 0.4,\ \alpha = 0.05,\ \lambda_1 = 1.05,\ \delta_2 = 2,\ \beta = 1.5,\ \text{and } \lambda_2 = 0.15. \end{aligned} \tag{24}$$

For the above set of parameter values, it is found that the model system (2) admits a stable limit cycle (slc) solution. Numerical simulation also shows that the dynamical outcomes of the interactions are very sensitive to parameter values and initial data. The model system (2) is solved using the ODE workbench package (AIP, New York). All the simulation are performed in the screen area $(-2 \le X \le 2) \times (-2 \le Y \le 2)$ for the initial condition $x(0) = 1,\ y_1(0) = 0.2,\ y_2(0) = 1.5$.

The main objective in this section is to show numerically that all the three species can coexist either in the form of oscillatory solution (slc) or in the form of steady state solution (stable focus) for some range of parameters and the predator species can go to extinction in some other range of parametric values. The prey species x become extinct only at the discrete point for the parameter $\delta_1 = 0.001$. The results of simulation experiments are presented in Table 1. From this table, it is found that the mortality rate coefficient of predator species y_1 (i.e. δ_1) is the only parameter which is responsible for the extinction of all the species in different parameter regimes. The predator y_1 becomes extinct in the range $[0.75, 2.65]$ but at the same time other species rests on stable focus ($y_2 \to 0$). The predator y_2 becomes extinct in the range $[0.07, 0.35]$ and other species rests on limit cycle attractor in this range. The depletion rate coefficient of prey species due to predator y_1 (i.e., a_1) and the food conversion coefficient of this predator (λ_1) are responsible for the extinction of the predator species y_1 and y_2. The predator y_1 becomes extinct in the ranges $0.1 \le a_1 \le 2.2$, $0.001 \le \lambda_1 \le 0.55$ and predator y_2 doomed to extinction in the ranges $4.3 \le a_1 \le 10$ and $1.2 \le \lambda_1 \le 4.05$. The other species rests either on limit cycle attractor or stable focus. The parameter b_1, δ_2 and β are responsible for the extinction of the predator y_2 only but at the same time other species behaves in a oscillatory manner. All the species co-exist either in the form of steady state or in the form of oscillatory solutions for the parameters r and b_2 in the range $[0.01, 10]$ and for a_2, α, λ_2 in the range $[0.001, 10]$.

The analytical condition of Theorem 6 for the parametric values given in (24) is well matched by our numerical results given in Table 1. The co-existence of the species in the form of positive steady state solution and in the form of oscillatory solutions are shown by the time trajectory in Figs. 1, 2 and 3. It is found that in no cases predator y_2 rests on stable limit cycle solution. It either rests on stable focus or goes to extinction.

Table 1. Results of simulation experiments of model system (2) with parameter values which were kept constants at limit cycle attractor are same as in (24) with the initial values $x(0) = 1.0$, $y_1(0) = 0.2$, $y_2(0) = 1.5$

Parameter Varied	Range in which Parameter Varied	Dynamical Outcome		
		x	y_1	y_2
r	0.01–0.96	Limit Cycle	Limit Cycle	Stable Focus
$0.01 \leq r \leq 10$	0.97–10	Stable Focus	Stable Focus	Stable Focus
a_1	0.1–2.2	Stable Focus	Extinct	Stable Focus
$0.1 \leq a_1 \leq 10$	2.25–3.75	Stable Focus	Stable Focus	Stable Focus
	3.8–4.25	Limit Cycle	Limit Cycle	Stable Focus
	4.3–10	Limit Cycle	Limit Cycle	Extinct
b_1	0.01–3.35	Stable Focus	Stable Focus	Stable Focus
$0.01 \leq b_1 \leq 10$	3.4–3.6	Limit Cycle	Limit Cycle	Stable Focus
	3.65–4.2	Limit Cycle	Limit Cycle	Extinct
	4.25–6.05	Limit Cycle	Limit Cycle	Stable Focus
	6.1–10	Stable Focus	Stable Focus	Stable Focus
a_2	0.001–10	Limit Cycle	Limit Cycle	Stable Focus
$0.001 \leq a_2 \leq 10$				
b_2	0.01–10	Limit Cycle	Limit Cycle	Stable Focus
$0.01 \leq b_2 \leq 10$				
δ_1	0.001	Extinct	Stable Focus	Stable Focus
$0.001 \leq \delta_1 \leq 5$	0.002–0.05	Limit Cycle	Limit Cycle	Stable Focus
	0.07–0.35	Limit Cycle	Limit Cycle	Extinct
	0.4	Limit Cycle	Limit Cycle	Stable Focus

Parameter Varied	Range in which Parameter Varied	Dynamical Outcome		
		x	y_1	y_2
δ_1	0.45–0.7	Stable Focus	Stable Focus	Stable Focus
$0.001 \leq \delta_1 \leq 5$	0.75–2.65	Stable Focus	Extinct	Stable Focus
	2.7–5	Stable Focus	Stable Focus	Extinct
α	0.001–5	Limit Cycle	Limit Cycle	Stable Focus
$0.001 \leq \alpha \leq 5$				
λ_1	0.001–0.55	Stable Focus	Extinct	Stable Focus
$0.001 \leq \lambda_1 \leq 5$	0.6–0.95	Stable Focus	Stable Focus	Stable Focus
	1–1.15	Limit Cycle	Limit Cycle	Stable Focus
	1.2–3.5	Limit Cycle	Limit Cycle	Extinct
	3.55–4.05	Stable Focus	Stable Focus	Extinct
	4.1–5	Stable Focus	Stable Focus	Stable Focus
δ_2	0.01–1.65	Limit Cycle	Limit Cycle	Extinct
$0.01 \leq \delta_2 \leq 5$	1.7–5	Limit Cycle	Limit Cycle	Stable Focus
β	0.01–0.55	Limit Cycle	Limit Cycle	Extinct
$0.01 \leq \beta \leq 5$	0.6–5	Limit Cycle	Limit Cycle	Stable Focus
λ_2	0.001–5	Limit Cycle	Limit Cycle	Stable Focus
$0.001 \leq \lambda_2 \leq 5$				

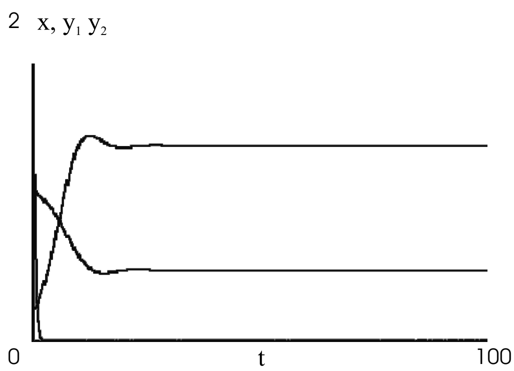

Fig. 1. This figure shows the solution of model system (2) when $r = 2$, $a_1 = 4$, $b_1 = 5$, $a_2 = 0.5$, b_2=4.05, $\delta_1 = 0.5$, $\alpha = 0.05$, $\lambda_1 = 1.25$, $\delta_2 = 2$, $\beta = 1.5$, $\lambda_2 = 0.15$, $x(0) = 1$, $y_1(0) = 0.2$, $y_2(0) = 1.5$. The solution tends to steady state. The bottom curve near the time axis depicts the predator 2, the middle curve depicts the prey species and the top curve depicts the predator 1.

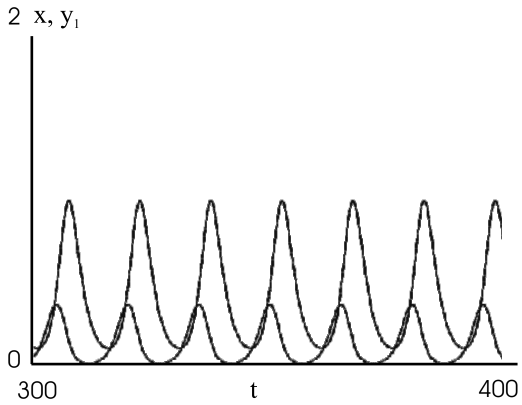

Fig. 2. This figure shows the x, y_1 components of a periodic orbit of system (2). Here initial values are $x(0) = 1$, $y_1(0) = 0.1$, $y_2(0) = 0.01$ and model parameters are $r = 0.9$, $a_1 = 4$, $b_1 = 5$, $a_2 = 0.5$, $b_2 = 4$, $\delta_1 = 0.5$, $\alpha = 0.25$, $\lambda_1 = 2.25$, $\delta_2 = 2$, $\beta = 1.5$, $\lambda_2 = 0.15$. The predator y_2 becomes extinct at this parameter space. The bottom curve depicts the prey species and the top curve depicts the predator 1.

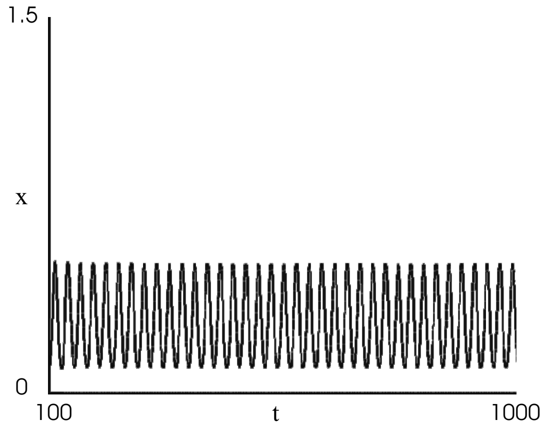

Fig. 3. This figure shows the time series of the prey species x when $r = 0.75$, $a_1 = 4$, $b_1 = 5$, $a_2 = 0.5$, $b_2 = 4.05$, $\delta_1 = 0.4$, $\alpha = 0.05$, $\lambda_1 = 1.05$, $\delta_2 = 2$, $\beta = 1.5$, $\lambda_2 = 0.15$, $x(0) = 1$, $y_1(0) = 0.2$, $y_2(0) = 1.5$.

6 Conclusions

In this paper, a mathematical model of one prey-two predator system with ratio-dependent predators growth rates has been proposed and analysed. Dynamical behavior of all feasible equilibria has been investigated. It has been shown that the role of food conversion coefficients of predators in ratio-dependent models are crucial in determining the stability behavior of planer equilibria. Sufficient conditions for the system to be uniformly persistent have been derived. It has been shown that if mortality rates of predators are less than a threshold value, then the system is uniformly persistent. However, if the mortality rate coefficients of predators increase beyond a threshold value ($\delta_i > \lambda_i a_i / b_i$), then both the predator species will be extinct and the system will not be permanent.

It may be pointed out here that in Theorem 3.4 of Hsu [3] it has been shown that the interior equilibrium of one prey-two predator system in prey-dependent case is always unstable. In fact, it is an unstable saddle point with two dimensional stable manifold through the interior equilibrium point. But in the case of ratio-dependent growth rates, the dynamics of the interior equilibrium is changed and we have found sufficient conditions under which all the three species coexist and the positive equilibrium is globally asymptotically stable.

Our numerical computations show that the dynamical outcomes of the interacting species in the ratio-dependent model are very sensitive to parameter values and initial data. An important conclusion is that the predator y_2 faces high risk of extinction depending upon the complexity of the system. The prey species find safe habitats in the complex ecosystem. Due to competitive exclusion outcome, this model is never expected to generate chaotic solution.

Appendix A: Proof of Theorem 7

We first linearize system (2) using the following transformations:

$$x = x^* + X, \quad y_1 = y_1^* + Y_1, \quad y_2 = y_2^* + Y_2, \tag{A1}$$

where X, Y_1 and Y_2 are small perturbations about E^*. Then the linear form of model (2) is given by

$$\begin{aligned}\dot{X} = -H^* x^* X &+ \left[\frac{a_2 x^* y_2^*}{B_2^*} - \frac{a_1 x^*(1 + b_1 x^* + y_2^*)}{B_1^*}\right] Y_1 \\ &+ \left[\frac{a_1 x^* y_1^*}{B_1^*} - \frac{a_2 x^*(1 + b_2 x^* + y_1^*)}{B_2^*}\right] Y_2,\end{aligned} \tag{A2}$$

$$\dot{Y}_1 = \frac{\lambda_1 a_1 y_1^*(1+y_1^*+y_2^*)}{B_1^*}X - \frac{\lambda_1 a_1 x^* y_1^*}{B_1^*}Y_1 - \left[\alpha y_1^* + \frac{\lambda_1 a_1 x^* y_1^*}{B_1^*}\right]Y_2,$$
$$\dot{Y}_2 = \frac{\lambda_2 a_2 y_2^*(1+y_1^*+y_2^*)}{B_2^*}X - \left[\beta y_2^* + \frac{\lambda_2 a_2 x^* y_2^*}{B_2^*}\right]Y_1 - \frac{\lambda_2 a_2 x^* y_2^*}{B_2^*}Y_2. \tag{A2}$$

We consider the following positive definite function,

$$U = \frac{1}{2x^*}X^2 + \frac{c_1}{2y_1^*}Y_1^2 + \frac{c_2}{2y_2^*}Y_2^2. \tag{A3}$$

Differentiating U with respect to time t along the solutions of linear model (A2) it can be seen that $\dot{U}$ is negative definite under conditions (22a)–(22d) (detail computations can be carried out similar to the proof of Theorem 8). Hence, Theorem 7 follows from Liapunov-LaSalle's invariance principle [26].

Appendix B: Proof of Lemma 1

From first equation of model (2) we have

$$\frac{dx}{dt} \le rx(1-x),$$

and hence $\limsup_{t\to\infty} x(t) \le 1$.

Define $W(t) = x(t) + y_1(t)/\lambda_1 + y_2(t)\lambda_2$. Then we have

$$\begin{aligned}\frac{dW}{dt} + \eta W &= (r+\eta)x - (\delta_1-\eta)\frac{y_1}{\lambda_1} - (\delta_2-\eta)\frac{y_2}{\lambda_2}\\ &\quad - rx^2 - \frac{\alpha y_1 y_2}{\lambda_1} - \frac{\beta y_1 y_2}{\lambda_2}\\ &\le (r+\eta) - (\delta_1-\eta)\frac{y_1}{\lambda_1} - (\delta_2-\eta)\frac{y_2}{\lambda_2}\\ &\le (r+\eta), \quad \text{since} \quad \eta \le \min(\delta_1\delta_2).\end{aligned}$$

By the theory of differential inequality [27], we have

$$0 \le W(t) \le \frac{r+\eta}{\eta}(1-e^{-\eta t}) + W(0)e^{-\eta t}.$$

When $t \to \infty$, we have $0 \le W(t) \le \frac{r+\eta}{\eta}$, proving the lemma.

Appendix C: Proof of Theorem 8

Consider the following positive definite function about E^*

$$\begin{aligned} V = &\big(x - x^* - x^* \ln(x/x^*)\big) + c_1\big(y_1 - y_1^* - y_1^* \ln(y_1/y_1^*)\big) \\ &+ c_2\big(y_2 - y_2^* - y_2^* \ln(y_2/y_2^*)\big). \end{aligned} \tag{C1}$$

Differentiating V with respect to time t along the solutions of model (2), we get

$$\dot{V} = (x - x^*)\frac{\dot{x}}{x} + c_1(y_1 - y_1^*)\frac{\dot{y}_1}{y_1} + c_2(y_2 - y_2^*)\frac{\dot{y}_2}{y_2}. \tag{C2}$$

Using system of equations (2), we get after some algebraic manipulations as

$$\begin{aligned} \dot{V} = &- \left[r - \frac{a_1 b_1 y_1^*}{M_1} - \frac{a_2 b_2 y_2^*}{M_2}\right](x - x^*)^2 \\ &- (y_1 - y_1^*)^2\left[\frac{c_1\lambda_1 a_1 x^*}{M_1}\right] - (y_2 - y_2^*)^2\left[\frac{c_2\lambda_2 a_2 x^*}{M_2}\right] \\ &+ (x - x^*)(y_1 - y_1^*)\left[- \frac{a_1(1 + b_1 x^* + y_2^*)}{M_1} \right. \\ &\qquad\qquad \left. + \frac{c_1\lambda_1 a_1(1 + y_1^* + y_2^*)}{M_1} + \frac{a_2 y_2^*}{M_2}\right] \\ &+ (x - x^*)(y_2 - y_2^*)\left[- \frac{a_2(1 + b_2 x^* + y_1^*)}{M_2} \right. \\ &\qquad\qquad \left. + \frac{c_2\lambda_2 a_2(1 + y_1^* + y_2^*)}{M_2} + \frac{a_1 y_1^*}{M_1}\right] \\ &+ (y_1 - y_1^*)(y_2 - y_2^*)\left[- c_1\alpha - c_2\beta - \frac{c_1\lambda_1 a_1 x^*}{M_1} - \frac{c_2\lambda_2 a_2 x^*}{M_2}\right], \end{aligned} \tag{C3}$$

where

$$\begin{aligned} M_1 &= (1 + b_1 x + y_1 + y_2)(1 + b_1 x^* + y_1^* + y_2^*), \\ M_2 &= (1 + b_2 x + y_1 + y_2)(1 + b_2 x^* + y_1^* + y_2^*). \end{aligned}$$

The above equation can further be written as sum of the quadratics

$$\begin{aligned} \dot{V} = &- \frac{1}{2}a_{11}(x - x^*)^2 + a_{12}(x - x^*)(y_1 - y_1^*) - \frac{1}{2}a_{22}(y_1 - y_1^*)^2 \\ &- \frac{1}{2}a_{11}(x - x^*)^2 + a_{13}(x - x^*)(y_2 - y_2^*) - \frac{1}{2}a_{33}(y_2 - y_2^*)^2 \\ &- \frac{1}{2}a_{22}(y_1 - y_1^*)^2 + a_{23}(y_1 - y_1^*)(y_2 - y_2^*) - \frac{1}{2}a_{33}(y_2 - y_2^*)^2, \end{aligned} \tag{C4}$$

where

$$a_{11} = r - \frac{a_1 b_1 y_1^*}{M_1} - \frac{a_2 b_2 y_2^*}{M_2},$$
$$a_{22} = \frac{c_1 \lambda_1 a_1 x^*}{M_1}, \quad a_{33} = \frac{c_2 \lambda_2 a_2 x^*}{M_2},$$
$$a_{12} = -\frac{a_1(1 + b_1 x^* + y_2^*)}{M_1} + \frac{c_1 \lambda_1 a_1 (1 + y_1^* + y_2^*)}{M_1} + \frac{a_2 y_2^*}{M_2},$$
$$a_{13} = -\frac{a_2(1 + b_2 x^* + y_1^*)}{M_2} + \frac{c_2 \lambda_2 a_2 (1 + y_1^* + y_2^*)}{M_2} + \frac{a_1 y_1^*}{M_1},$$
$$a_{23} = -c_1 \alpha - c_2 \beta - \frac{c_1 \lambda_1 a_1 x^*}{M_1} - \frac{c_2 \lambda_2 a_2 x^*}{M_2}.$$

Sufficient conditions for $\dot{V}$ to be negative definite are that the following inequalities hold:

$$a_{11} > 0, \tag{C5}$$
$$a_{12}^2 < a_{11} a_{22}, \tag{C6}$$
$$a_{13}^2 < a_{11} a_{33}, \tag{C7}$$
$$a_{23}^2 < a_{22} a_{33}. \tag{C8}$$

We note that (23a) ⇒ (C5), (23b) ⇒ (C6), (23c) ⇒ (C7) and (23d) ⇒ (C8). Hence V is a Liapunov function with respect to E^*, whose domain contains the region of attraction Ω, proving the theorem.

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