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Control of chaos due to additional predator in the Hastings–Powell food chain model

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ABSTRACT

A three species Hastings and Powell (HP) food chain model involving another predator of top prey is proposed and studied. The modified food web model is analyzed to obtain the different conditions for which system exhibits stability around the biological feasible equilibrium points. The permanence is established and global stability of boundary equilibrium point E_x is discussed. It is observed through numerical simulations, that four-dimensional model may show stable dynamics in contrast to chaotic dynamics that occurred in three species food chain. Varieties of dynamical behaviors in the food web are possible depending upon the sharing of food between the two predators of the top prey. The results demonstrate that the additional predator play the crucial role in reducing the complexity in the dynamical behavior of the system.

1. Introduction

Unpredictability is ubiquitous in ecological system. It is argued whether this unpredictability is due to deterministic chaos or stochastic environmental disturbances. Although Hassell et al. [1] found no evidence of chaotic behavior in any field of population, the notion that populations fluctuations in nature may be caused by deterministic chaos has persisted. Berryman and Millstein [2] observed that chaos is frequently described but rarely explained. It was discussed that although every ecological system has seeds of chaos but also pointed out the ecological reasons due to which ecosystem fail to exhibit chaos frequently. According to them chaos may be driven by human actions that increase growth rates or induce delays in the regulatory process. Rai [3] explained one of the reason for non-occurrence of chaos lies in the organization of the ecological system. The chaotically fluctuating population are prone to extinction, with consequence that group selection acts to eliminate species and chaos disappears. Apart from that class of model are identified which lies on the edge of chaos.

Deterministic chaos is currently an interesting area of research in ecological, mathematical and physical sciences. The ecological systems contain the ingredients (positive feed back) for possible occurrence of chaos. The pioneering work done by Hastings and Powell [4] has emerged as a subject of interest to ecologists. Hastings and Powell proposed three species food chain system and chaos is obtained for biologically reasonable choices of parameters [4]. The three species food chain model is a coupled system of nonlinear equations. Hastings and Powell numerically simulated the behavior of the model and established the occurrence of chaos for the realistic parametric values. The behavior of solution is sensitive to initial conditions as well as the specific model parameter with respect to which chaos is observed. The small change in any of these will change the behavior all together. As such the chaotic systems are not robust in contrast to ecological systems. Probably, nature has its own ways to counter the complexity of the system.

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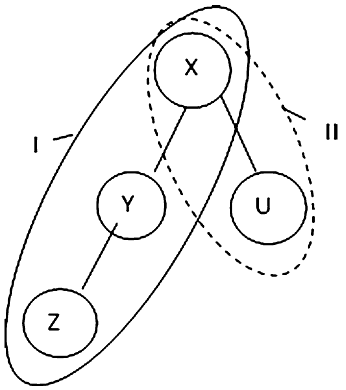

Fig. 1. Food web model.

Several investigations have reported the complex dynamical behavior of multi-species food chains/food webs of variable lengths [5–8] is explored by several researchers for various ecological interests [9–11]. As appearance of chaos is rare in the natural populations. Several investigators made efforts to replace this chaotic dynamics by stability and oscillatory behavior. Thus, since last decade stabilizing the chaos has become a new aspect in ecological modeling.

Scrutinizing the HP model formulation, it is observed that the three species forming food chain are assumed to live in isolation with other species of the habitat. In other words, either only three species forming food chain live in the habitat or food chain is not affected by the presence of other species. As such, the effects of other species living in the habitat have been largely ignored. Here is an effort to analyze the influence of additional predator to top prey on the Hastings–Powell food chain. The possibility to reduce the complexity of original HP model is being investigated and attempt is made to bring order in otherwise chaotic system.

2. Mathematical formulation

Let the density of top prey be X. The two predator species having densities Y and U share food on the top prey species. Due to difference in predation capabilities of two predators, let the fraction m_1 of total prey density is exposed to the first predator and the fraction of food $m_2(m_1 + m_2 = 1)$ is available for predation to the second predator i.e. the fraction m_1 of prey X is available for predation by first predator Y and m_2X is predated by second predator. The other interpretation may be that a prey is predated by first predator with probability m_1 and the probability that it is predated by second predator is m_2. There is an inherent competition between two predators. Let there be a third predator having density Z and first predator be its prey. The combined four-dimensional food web model is schematically shown in Fig. 1. Accordingly, the following mathematical model is proposed for the dynamics of the combined system:

$$\begin{aligned}
\frac{dX}{dT} &= RX\left(1 - \frac{X}{K}\right) - C_1F_1(m_1X)Y - C_2F_2(m_2X)U \\
\frac{dY}{dT} &= F_1(m_1X)Y - F_3(Y)Z - D_1Y \\
\frac{dZ}{dT} &= C_3F_3(Y)Z - D_2Z \\
\frac{dU}{dT} &= F_2(m_2X)U - D_3U, \qquad F_i(V) = \frac{A_iV}{B_i + V}, \quad i = 1, 2, 3.
\end{aligned} \tag{1}$$

In the model, the function $F_i(V)$ represents the Holling type II functional response. R, K, C_i and D_i are model parameters assuming only positive values and are defined as follows:

> R is the growth rate of prey X, K measures the carrying capacity of prey species and D_i $(i = 1, 2, 3)$ describes the loss of predator population in absence of food. C_i^{-1} $(i = 1, 2)$ represents the conversion rate of common prey into predators Y and U, whereas C_3 is the conversion rate of Y into Z. It may be observed that the model (1) transforms to the Hastings–Powell food chain when $m_2 = 0$.

The food web has two subsystems I and II. The subsystem I is the usual HP food chain with common prey, first predator and third predator, while subsystem II consists of common prey and second predator.

The model (1) has 13 parameters which are reduced to 10 by introducing the following non-dimensional variables and parameters:

$$t = RT, \quad x = \frac{X}{K}, \quad y = \frac{C_1 Y}{K}, \quad z = \frac{C_1 Z}{C_3 K}, \quad u = \frac{C_2 U}{K}$$
$$a = \frac{A_1 K}{R B_1}, \quad b = \frac{K}{B_1}, \quad c = \frac{K A_3 C_3}{R B_3 C_1}, \quad d = \frac{K}{B_3 C_1}, \quad e = \frac{A_2 K}{R B_2}$$
$$g = \frac{K}{B_2}, \quad l = \frac{D_1}{R}, \quad n = \frac{D_2}{R}, \quad p = \frac{D_3}{R}.$$

Accordingly, the non-dimensional system takes the form

$$\begin{aligned}
\frac{dx}{dt} &= x(1-x) - \frac{am_1xy}{1+bm_1x} - \frac{em_2xu}{1+gm_2x}\\
\frac{dy}{dt} &= \frac{am_1xy}{1+bm_1x} - \frac{cyz}{1+dy} - ly\\
\frac{dz}{dt} &= \frac{cyz}{1+dy} - nz\\
\frac{du}{dt} &= \frac{em_2xu}{1+gm_2x} - pu.
\end{aligned} \tag{2}$$

The non-negative initial conditions are associated with system (2):

$$x(0) \geqslant 0, \quad y(0) \geqslant 0, \quad z(0) \geqslant 0, \quad \text{and} \quad u(0) \geqslant 0. \tag{3}$$

In order to explore the survival/extinction of species/sub-systems and control of chaos, the model (2) system is analyzed in the next section.

3. Some preliminary results

In the following section, positivity and boundedness for the system (2) are established. Since the state variables x, y, z, u represent populations, positivity insures that they never become negative and population always survive. The boundedness may be interpreted as a natural restriction to growth as a consequence of limited resources.

3.1. Positive invariance

The model system (2) can be put into the matrix form $\dot{\bar{X}} = G(\bar{X})$ with $\bar{X}(0) = \bar{X}_0 \in R^4_+$, where $\bar{X} = (x, y, z, u)^T \in R^4$. $G(\bar{X})$ is given by

$$G(\bar{X}) = \begin{pmatrix} G_1(\bar{X}) \\ G_2(\bar{X}) \\ G_3(\bar{X}) \\ G_4(\bar{X}) \end{pmatrix} = \begin{pmatrix} x(1-x) - \frac{am_1xy}{1+bm_1x} - \frac{em_2xu}{1+gm_2x} \\ \frac{am_1xy}{1+bm_1x} - \frac{cyz}{1+dy} - ly \\ \frac{cyz}{1+dy} - nz \\ \frac{em_2xu}{1+gm_2x} - pu \end{pmatrix}$$

where $G : C_+ \to R^4$ and $G \in C^\infty(R^4)$.

It can be seen, whenever $\bar{X}(0) \in R^4_+$ such that $\bar{X}_i = 0$ then $G_i(\bar{X})|_{\bar{X}_i(0)} \geqslant 0$ $(i = 1, 2, 3, 4)$. Now any solution of $\dot{\bar{X}} = G(\bar{X})$ with $\bar{X}_0 \in R^4_+$, say $\bar{X}(t) = \bar{X}(t, \bar{X}_0)$, is such that $\bar{X}(t) \in R^4_+$ for all $t > 0$ [12].

3.2. Boundedness

Theorem 3.1. *All the solutions of the model system* (2) *with initial conditions* (3) *that initiate in* R^4_+ *are uniformly bounded.*

Proof. Let

$$W = x + y + z + u.$$

The time derivative along a solution of (2) is

$$\frac{dW}{dt} = x(1-x) - ly - nz - pu.$$

Introducing positive L and rewriting gives

$$\frac{dW}{dt} + LW = \big((1-x)+L\big)x - (l-L)y - (n-L)z - (p-L)u.$$

Choosing $L = min\{l, n, p\}$, yields

$$\frac{dW}{dt} + LW \leqslant -\left(x - \frac{1+L}{2}\right)^2 + \frac{(1+L)^2}{4} \quad \text{or}$$
$$\frac{dW}{dt} + LW \leqslant \frac{(1+L)^2}{4}.$$

Applying the theory of differential inequality[13], it is obtained

$$0 < W(x,y,z,u) \leqslant \frac{(1+L)^2}{4L}\big(1-e^{-Lt}\big) + W\big(x(0),y(0),z(0),u(0)\big)e^{-Lt}.$$

For $t \to \infty$, $0 < W \leqslant \frac{(1+L)^2}{4L}$. Hence, all solutions of (2) that initiate in R^4_+ are confined in the region

$$B = \left\{(x,y,z,u) \in R^4_+ \colon 0 < W \leqslant \frac{(1+L)^2}{4L} + \phi, \ \text{for any}\ \phi > 0\right\}.$$

This proves the theorem. □

3.3. Existence of equilibrium points

System (2) has the following equilibrium points:
The trivial equilibrium point $E_0 = (0,0,0,0)$ always exists.
The axial equilibrium point is $E_x = (1,0,0,0)$.
The planar equilibrium point $E_{xy} = (\tilde{x}, \tilde{y}, 0, 0) = (\frac{l}{(a-bl)m_1}, \frac{(a-bl)m_1 - l}{((a-bl)m_1)^2}, 0, 0)$ exists provided

$$(a-bl)m_1 > l. \tag{4}$$

Another planar equilibrium point is

$$E_{xu} = (\tilde{\tilde{x}}, 0, 0, \tilde{\tilde{u}}) = \left(\frac{p}{(e-gp)m_2}, 0, 0, \frac{(e-gp)m_2 - p}{((e-gp)m_2)^2}\right); \quad m_2 \neq 0,$$

and its existence condition is

$$(e-gp)m_2 > p. \tag{5}$$

The equilibrium point $(\bar{x}, \bar{y}, 0, \bar{u})$ lies on intersection of the following planes:

$$\begin{aligned}
&(1-x) - \frac{am_1 y}{1+bm_1 x} - \frac{em_2 u}{1+gm_2 x} = 0\\
&\frac{am_1 x}{1+bm_1 x} - l = 0\\
&\frac{em_2 x}{1+gm_2 x} - p = 0.
\end{aligned} \tag{6}$$

The system is consistent when

$$\bar{x} = \frac{l}{(a-bl)m_1} = \frac{p}{(e-gp)m_2}.$$

But it is not realistic to impose such a restriction in the ecological context. In rare cases, if it is so then equilibrium points lie on the plane:

$$\frac{am_1\bar{y}}{1+bm_1\bar{x}} - \frac{em_2\bar{u}}{1+m_2 g\bar{x}} + \bar{x} - 1 = 0. \tag{7}$$

The following theorems give the existence of other equilibrium points.

Theorem 3.2. *Let*

$$\hat{x} = \frac{-(1-bm_1) + \sqrt{(1+bm_1)^2 - \frac{4bm_1^2 an}{c-nd}}}{2bm_1}, \qquad \hat{y} = \frac{n}{(c-nd)},$$
$$\hat{z} = \frac{1}{(c-nd)}\left(\frac{am_1\hat{x}}{1+bm_1\hat{x}} - l\right), \qquad \hat{u} = 0. \tag{8}$$

The equilibrium point $E_{HP} = (\hat{x}, \hat{y}, \hat{z}, 0)$ *exists when*

$$c > (am_1 + d)n, \qquad \hat{x} > \tilde{x}. \tag{9}$$

Proof. Equilibrium point is obtained from solving equations

$$(1-\hat{x}) - \frac{am_1\hat{y}}{1+bm_1\hat{x}} = 0$$
$$\frac{am_1\hat{x}}{1+bm_1\hat{x}} - \frac{c\hat{z}}{1+d\hat{y}} - l = 0$$
$$\frac{c\hat{z}}{1+d\hat{y}} - n = 0. \tag{10}$$

Solution of the third equation of (10) gives $\hat{y}$ positive for $c > nd$.

From the second equation, $\hat{z}$ positive is obtained for $\hat{x} > \tilde{x}$.

$\hat{x}$ is obtained from the quadratic equation

$$bm_1\hat{x}^2 + (1-bm_1)\hat{x} - \left(1 - \frac{am_1 n}{c-nd}\right) = 0. \tag{11}$$

It may be observed that $\hat{x}$ positive will be unique provided $c > (am_1 + d)n$.

Hence the result. □

Note. Two positive values of $\hat{x}$ exist if

$$c < (am_1 + d)n, \qquad bm_1 > 1, \qquad (bm_1 + 1)^2 > \frac{4abm_1^2 n}{c-nd}.$$

For the subsequent part of this paper, the parameters choice are restricted by conditions (9) for unique positive equilibrium point.

Remark 1. Since top prey is source of the food for both y and z species, the equilibrium level prey density $\hat{x}$ for HP model should be greater than the prey density at E_{xy}.

Theorem 3.3. *Consider*

$$x^* = \tilde{\tilde{x}} = \frac{p}{m_2(e-gp)}, \qquad y^* = \frac{n}{c-nd}, \qquad z^* = \frac{1}{(c-nd)}\left(\frac{am_1x^*}{1+bm_1x^*} - l\right),$$
$$u^* = \frac{1+gm_2x^*}{em_2}\left\{(1-x^*) - \frac{am_1 n}{(c-nd)(1+bm_1x^*)}\right\}. \tag{12}$$

The positive interior equilibrium point $E^* = (x^*, y^*, z^*, u^*)$ *exists provided*

$$(e-gp)m_2 > p, \qquad c > nd, \qquad x^* > \tilde{x}. \tag{13}$$

Proof. The interior equilibrium point is the solution of the following system of equations:

$$(1-x) - \frac{am_1y}{1+bm_1x} - \frac{em_2u}{1+gm_2x} = 0$$
$$\frac{am_1x}{1+bm_1x} - \frac{cz}{1+dy} - l = 0$$
$$\frac{cy}{1+dy} - n = 0$$
$$\frac{em_2x}{1+gm_2x} - p = 0. \tag{14}$$

The solution is obtained as (12). For positive equilibrium point

$$e > gp, \qquad c > nd, \qquad x^* > \tilde{x}, \qquad x^*(1-x^*) > \frac{nl}{c-nd}.$$

Clearly for $c > nd$, last condition simplifies to $(e-gp)m_2 > p$. Hence the result. □

Remark 2. To satisfy (13), the equilibrium level of prey density to support all species at E^* must be higher than the equilibrium level of prey density at E_{xy}. Further, when interior equilibrium point E^* exists then the planar equilibrium point E_{xu} will always exist.

4. Local stability analysis

The Jacobian matrix $V(x,y,z,u)$ for the system (2) at any point (x,y,z,u) is given by

$$\begin{pmatrix} 1-2x-\frac{am_1y}{(1+bm_1x)^2}-\frac{em_2u}{(1+gm_2x)^2} & -\frac{am_1x}{1+bm_1x} & 0 & -\frac{em_2x}{1+gm_2x} \\ \frac{am_1y}{(1+bm_1x)^2} & \frac{am_1x}{1+bm_1x}-\frac{cz}{(1+dy)^2}-l & -\frac{cy}{1+dy} & 0 \\ 0 & \frac{cz}{(1+dy)^2} & \frac{cy}{1+dy}-n & 0 \\ \frac{em_2u}{(1+gm_2x)^2} & 0 & 0 & \frac{em_2x}{1+gm_2x}-p \end{pmatrix}. \tag{15}$$

Remark 3. The eigenvalues about E_0 are $1, -l, -n, -p$. Hence E_0 is a saddle point and has unstable manifold along x-axis.

Theorem 4.1. *The equilibrium point $E_x(1,0,0,0)$ is stable if*

$$(a-bl)m_1 < l \quad \textit{and} \quad (e-gp)m_2 < p. \tag{16}$$

Proof. The eigenvalues of the variational matrix about the equilibrium point $E_x(1,0,0,0)$ are -1, $\frac{(a-bl)m_1-l}{(1+bm_1)}$, $-n$, $\frac{(e-gp)m_2-p}{1+m_2g}$. Accordingly, E_x is stable under (16). □

Therefore, the equilibrium point E_x is a saddle point when either of $(a-bl)m_1 < l$ or $(e-gp)m_2 < p$ is violated. Further, it is observed that the stability of this equilibrium point rules out the existence of E_{xy}, E_{xu} and E^*.

Theorem 4.2. *The equilibrium point $E_{xy}(\tilde{x}, \tilde{y}, 0, 0)$ is asymptotically stable provided*

$$\tilde{x} < x^*, \qquad \tilde{y} < y^*, \qquad (a+bl) > (a-bl)bm_1. \tag{17}$$

Proof. The variational matrix about E_{xy} gives

$$\lambda_1 = \frac{elm_2}{(a-bl)m_1+glm_2} - p, \qquad \lambda_2 = \frac{c(am_1-blm_1-l)}{(a-bl)^2m_1^2+d(am_1-blm_1-l)} - n \quad \text{and}$$

$$am_1(a-bl)\lambda^2 + l\big[(a+bl)-(a-bl)bm_1\big]\lambda + l\big((a-bl)m_1-l\big)(a-bl) = 0.$$

Accordingly, λ_1 and λ_2 will be negative for

$$p(a-bl)m_1 < l(e-gp)m_2 \quad \text{and} \quad (c-nd)\big((a-bl)m_1-l\big) < n(a-bl)^2m_1^2$$

respectively or $\tilde{x} < x^*$, $\tilde{y} < y^*$.

The remaining two eigenvalues will be negative if $(a+bl) > (a-bl)bm_1$.

Combining these, with existence condition (4) gives the asymptotic stability of E_{xy} under conditions (17). □

Theorem 4.3. *The equilibrium point $E_{xu}(\tilde{\tilde{x}}, 0, 0, \tilde{\tilde{u}})$ is locally asymptotically stable provided*

$$l(e-gp)m_2 > p(a-bl)m_1 \quad \textit{and} \quad g(e-gp)m_2 < (e+gp). \tag{18}$$

Proof. The eigenvalues of variational matrix around the equilibrium point E_{xu} are obtained from the following characteristic equation:

$$(\lambda+n)\left(\lambda - \frac{p(a-bl)m_1-l(e-gp)m_2}{(e-gp)m_2+bm_1p}\right)$$
$$\left(\lambda^2 - \frac{g(e-gp)m_2-(e+gp)}{e(e-gp)m_2}p\lambda + \frac{((e-gp)m_2-p)p}{em_2}\right) = 0.$$

The quadratic factor gives eigenvalues with negative real parts provided

$$g(e-gp)m_2 < (e+gp).$$

From the linear factors, the eigenvalues will be negative provided

$$l(e-gp)m_2 > p(a-bl)m_1 \quad \text{or} \quad \tilde{x} > x^*.$$

Hence, the equilibrium point is locally asymptotically stable under conditions (18). □

Remark 4. The stability of E_{xu} violates the stability of E_{xy} as well as the existence of E^*.

The characteristic equation around the equilibrium point $E_{HP}(\hat{x}, \hat{y}, \hat{z}, 0)$ is

$$\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0 \tag{19}$$

where

$$\begin{aligned}
A_1 &= -1 + p + s - m(v-l) - w + 2\hat{x}\\
A_2 &= (v-l)\big[n(1-m) + m(1-s-2\hat{x}+w-p)\big] + vs + (-1+s+2\hat{x})(p-w)\\
A_3 &= n(1-m)(v-l)(-1+p+s+w+2\hat{x}) - vs(p-w) - (p-w)m(-1+s+2\hat{x})(v-l)\\
A_4 &= n(1-m)(v-l)(p-w)(-1+s+2\hat{x})\\
m &= \frac{nd}{c}, \qquad v = \frac{am_1\hat{x}}{1+bm_1\hat{x}}, \qquad s = \frac{am_1 n}{(c-nd)(1+bm_1\hat{x})^2}, \qquad w = \frac{em_2\hat{x}}{1+gm_2\hat{x}}.
\end{aligned} \tag{20}$$

The conditions for local stability are given in the following theorem.

Theorem 4.4. *The equilibrium point $E_{HP}(\hat{x}, \hat{y}, \hat{z}, 0)$ is locally stable when*

$$A_i > 0, \qquad A_1A_2 > A_3, \qquad A_3(A_1A_2 - A_3) - A_4A_1^2 > 0. \tag{21}$$

Similarly, the characteristic equation around the equilibrium point $E^* = (x^*, y^*, z^*, u^*)$ is

$$\lambda^4 + B_1\lambda^3 + B_2\lambda^2 + B_3\lambda + B_4 = 0 \tag{22}$$

where

$$\begin{aligned}
B_1 &= -1 + p + q + 2x^* - w - m(v-l)\\
B_2 &= rw + sv + m(v-l)\big(1-p-q-n-2x^*+w\big) + n(v-l) + (w-p)\big(1-q-2x^*\big)\\
B_3 &= n(1-m)(v-l)\big(-1+p+q-w+2x^*\big) - wm\big(1+r-q-2x^*\big)(v-l) - vs(w-p)\\
&\quad + p\big(-1+q+2x^*\big)(lm-vs)\\
B_4 &= n(1-m)(v-l)\big[(w-p)\big(-1+q-2x^*\big) + wr\big]\\
q &= \frac{am_1nx^*(gm_2-bm_1)}{(c-nd)(1+bm_1x^*)^2(1+gm_2x^*)} + \frac{1-x^*}{1+gm_2x^*}, \qquad m = \frac{nd}{c}, \qquad v = \frac{am_1x^*}{1+bm_1x^*},\\
s &= \frac{am_1n}{(c-nd)(1+bm_1x^*)^2}, \qquad w = \frac{em_2x^*}{1+gm_2x^*}, \qquad r = \frac{(1-x^*) - \frac{am_1n}{(1+bm_1x^*)(c-nd)}}{\{1+gm_2x^*\}^2}.
\end{aligned} \tag{23}$$

The conditions for local stability are given in the following theorem.

Theorem 4.5. *The positive interior equilibrium point $E^* = (x^*, y^*, z^*, u^*)$ is stable when*

$$B_i > 0, \qquad B_1B_2 > B_3, \qquad B_3(B_1B_2 - B_3) - B_4B_1^2 > 0. \tag{24}$$

5. Permanence and global stability

From biological point of view, persistence of a system means the long term survival of all populations of the system, no matter what the initial populations are. Mathematically, persistence of a system means that strictly positive solutions do not have omega limit points on the boundary of the non-negative cone.

Theorem 5.1. *If $(a - bl)m_1 > l$, $(e - gp)m_2 > p$, $\tilde{x} > x^*$, $g(e - gp)m_2 < (e + gp)$ hold and there exists a finite number of periodic solutions (say, k) $x = \phi_i(t)$, $u = \psi_i$, $i = 1, 2, 3, \ldots, k$ in the x–u plane. Then the system* (2) *is uniformly persistent provided for each periodic solution of period T,*

$$\eta_i = -l + \frac{1}{T}\int_0^T \frac{am_1\phi_i}{1 + bm_1\phi_i} > 0, \quad i = 1, 2, \ldots, k.$$

Proof. Let x be a point in the positive octant and $o(x)$ be the orbit through x and $\Omega(x)$ be the omega limit set of the orbit $o(x)$. Note that $\Omega(x)$ is bounded.

First, it is claimed that $E_0 \notin \Omega(x)$. If $E_0 \in \Omega(x)$ then by Butler–McGehee lemma [14] there exists a point P in $\Omega(x) \cap W^s(E_0)$ where $W^s(E_0)$ denotes the stable manifold of E_0. Since $o(P)$ lies in $\Omega(x)$ and $W^s(E_0)$ is the y–z–u space. It can be concluded that $o(P)$ is unbounded, which is a contradiction.

Next $E_x \notin \Omega(x)$, for otherwise, since E_x is a saddle point (whenever $(a - bl)m_1 > l$, $(e - fp)m_2 > p$, i.e. existence conditions of E_{xy} and E_{xu}), by the Butler–McGehee lemma there exists a point P in $\Omega(x) \cap W^s(E_x)$. Now $W^s(E_x)$ is the x–z plane implies that an unbounded orbit lies in $\Omega(x)$, which is contrary to the boundedness of the system.

Next $E_{xy} \notin \Omega(x)$. If $E_{xy} \in \Omega(x)$, the condition $\tilde{x} > x^*$ implies that E_{xy} is saddle point. $W^s(E_{xy})$ is the x–y–z space and hence the orbits in this space emanate from either E_0 or E_1 or an unbounded lies in $\Omega(x)$, again a contradiction. In the same way it can be shown that $E_{HP} \notin \Omega(x)$ for under those conditions on which Routh–Hurwitz criterion is not satisfied.

Lastly it is shown that no periodic orbit in x–u plane or $E_{xu} \in \Omega(x)$. Let γ_i, $i = 1, 2, \ldots, k$ denote the closed orbit of the periodic solution $(\phi_i(t), \psi_i(t))$ in x–u plane such that γ_i lies inside γ_{i-1}. The variational matrix $V_i(\phi_i(t), 0, 0, \psi_i(t))$ corresponding to γ_i is given by

$$V_i = \begin{pmatrix} 1 - 2\phi_i - \frac{em_2\psi_i}{(1+gm_2\psi_i)^2} & -\frac{am_1\phi_i}{1+bm_1\phi_i} & 0 & -\frac{em_2\phi_i}{1+gm_2\phi_i} \\ 0 & \frac{am_1\phi_i}{1+bm_1\phi_i} - l & 0 & 0 \\ 0 & 0 & -n & 0 \\ \frac{em_2\psi_i}{(1+gm_2\phi_i)^2} & 0 & 0 & \frac{em_2\phi_i}{1+gm_i\phi_i} - p \end{pmatrix}.$$

Computing the fundamental matrix of the linear periodic system

$$M' = V_i(t)M, \qquad M(0) = M_0.$$

It can be noticed that the Floquet multiplier in the y direction is $e^{\eta_i}T$. Then by Kumar and Freedman [15], it can be concluded that no γ_i lies on $\Omega(x)$. Thus $\Omega(x)$ lies in the positive quadrant and system (2) is persistent. Finally, since only the closed orbits and the equilibria form the omega limit set of the solutions on the boundary of R_+^4 and the system in (2) is dissipative. By main theorem of Butler et al. [16], system (2) is uniformly persistent. □

Corollary 1. *If*

$$(a - bl)m_1 > l, \qquad (e - gp)m_2 > p, \qquad \tilde{x} > x^*, \qquad g(e - gp)m_2 < (e + gp), \qquad \frac{am_1\tilde{\tilde{x}}}{1 + bm_1\tilde{\tilde{x}}} > l \tag{25}$$

hold then if there are no limit cycles in the x–u plane, the system (2) *is uniformly persistent.*

Proof. Proof is obvious and hence omitted. □

Theorem 5.2. *Let $(a - bl)m_1 > l$, $(e - gp)m_2 > p$. If the condition $\tilde{x} < x^*$ holds, then the system* (2) *is impermanent.*

Proof. If conditions $(a - bl)m_1 > l$, $(e - gp)m_2 > p$ hold, the equilibrium points E_{xy} and E_{xu} exist. The given condition $\tilde{x} < x^*$ implies that E_{xy} is strictly a saturated equilibrium point on the boundary. Hence, there exists at least one orbit in the interior that converges to the boundary [17]. Consequently the system (2) is impermanent [18]. □

As discussed in Section 4, E_0 is a saddle point (see Remark 3) and E_x is stable under the condition (16) according to Theorem 4.1. It is noticed that the stability of E_x rules out the existence of E_{xy}, E_{xu} as well as E^*.

The global stability of E_x for system (2) is established here using Li and Muldowney approach, which is outlined as follows [19].

Let the map $\mathbf{x} \mapsto f(\mathbf{x})$ from an open subset $\mathcal{D} \subset \mathcal{R}^n$ to $\mathcal{R}^n$ be such that the solution $\mathbf{x}(t)$ to the differential equation

$$\dot{\mathbf{x}} = f(\mathbf{x}) \tag{26}$$

is uniquely determined by its initial value $\mathbf{x}(0) = \mathbf{x}_0$ and this solution is denoted by $\mathbf{x}(t, \mathbf{x}_0)$. It is assumed that

(H_1) $\mathcal{D}$ is simply connected;
(H_2) $\bar{\mathbf{x}}$ is the only equilibrium point of (26) in $\mathcal{D}$; and
(H_3) there is compact absorbing set $\mathcal{K} \subset \mathcal{D}$.

A set $\mathcal{K}$ is called absorbing in $\mathcal{D}$ for system (26) if $\mathbf{x}(t, F) \subset \mathcal{K}$ for each component set $F \subset \mathcal{D}_1 \subset \mathcal{D}$ ($\mathcal{D}_1$ is an open set) for sufficiently large $t > 0$.

For a square matrix B, the Lozinskiĭ measure (or logarithmic norm) μ with respect to induced matrix norm $\|\cdot\|$ is defined by [20]

$$\mu(B) = \lim_{h \to 0} \frac{\|I + hB\| - 1}{h}. \tag{27}$$

For $\mathbf{x} \in \mathcal{D}$, consider a nonsingular ${}^nC_2 \times {}^nC_2$ matrix valued C^1 function $\mathbf{x} \to M(\mathbf{x})$ and it is defined

$$B = M_f M^{-1} + M J^{[2]} M^{-1}.$$

Here M_f is the matrix obtained by replacing each entry m_{ij} in M by its directional derivative in the direction of f, and $M^{[2]}$ is the second additive compound matrix [21] of Jacobian matrix M of the system (26).

For Lozinskiĭ measure μ on $R^{{}^nC_2 \times {}^nC_2}$, define a quantity $\bar{q}_2$ as

$$\bar{q}_2 = \limsup_{t \to \infty} \sup_{\mathbf{x}_0 \in \mathcal{K}} \frac{1}{t} \int_0^t \mu\big(B\big(\mathbf{x}(s, \mathbf{x}_0)\big)\big)\, ds. \tag{28}$$

Consider $\mathbf{x} = (x, y, z, u)^T$ and

$$f(\mathbf{x}) = \begin{pmatrix} x(1-x) - \frac{am_1xy}{1+bm_1x} - \frac{em_2xu}{1+gm_2x} \\ \frac{am_1xy}{1+bm_1x} - \frac{cyz}{1+dy} - ly \\ \frac{cyz}{1+dy} - nz \\ \frac{em_2xu}{1+gm_2x} - pu \end{pmatrix}$$

for the system (2). $\bar{\mathbf{x}} = E_x$ is the unique equilibrium point in $\mathcal{D}$. Let the assumptions (H_1)–(H_3) hold.

Theorem 5.3. *The equilibrium point $E_x(1, 0, 0, 0)$ is globally asymptotically stable provided*

$$p - \frac{em_2}{1 + gm_2} < n, \quad l < 1, \quad p < n \quad \text{and} \quad p < 1 \tag{29}$$

if there exist a function $M(\mathbf{x})$ and a Lozinskiĭ μ such that $\bar{q_2} < 0$.

Proof. The Jacobian matrix of system (2) around equilibrium point E_x is

$$J(E_x) = \begin{pmatrix} -1 & -\delta - l & 0 & -\nu - p \\ 0 & \delta & 0 & 0 \\ 0 & 0 & -n & 0 \\ 0 & 0 & 0 & \nu \end{pmatrix}; \quad \delta = \frac{am_1}{1 + bm_1} - l, \ \nu = \frac{em_2}{1 + gm_2} - p$$

whose second additive compound matrix $J^{[2]}$ is

$$J^{[2]}(E_x) = \begin{pmatrix} -1+\delta & 0 & 0 & 0 & \nu+p & 0 \\ 0 & -(1+n) & 0 & -\delta-l & 0 & \nu+p \\ 0 & 0 & -1+\nu & 0 & -\delta-l & 0 \\ 0 & 0 & 0 & \delta-n & 0 & 0 \\ 0 & 0 & 0 & 0 & \delta+\nu & 0 \\ 0 & 0 & 0 & 0 & 0 & \nu-n \end{pmatrix}.$$

Set the following diagonal matrix

$$M(x, y, z, u) = \operatorname{diag}(x, x, 1, 1, 1, 1).$$

Then $M_f M^{-1} = \operatorname{diag}(\frac{\dot{x}}{x}, \frac{\dot{x}}{x}, 1, 1, 1, 1)$ where f is vector field of (2).

Therefore, the matrix

$$B = M_f M^{-1} + M J^{[2]} M^{-1} = \left(\begin{array}{c|c|c|ccc} \frac{\dot{x}}{x} - 1 + \delta & 0 & 0 & 0 & (\nu+p)x & 0 \\ \hline 0 & \frac{\dot{x}}{x} - (1+n) & 0 & -(\delta+l)x & 0 & (\nu+p)x \\ \hline 0 & 0 & -1+\nu & 0 & -(\delta+l) & 0 \\ \hline 0 & 0 & 0 & \delta-n & 0 & 0 \\ 0 & 0 & 0 & 0 & \delta+\nu & 0 \\ 0 & 0 & 0 & 0 & 0 & \nu-n \end{array}\right)$$

or

$$B = \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix}$$

where

$$B_{11} = \left(\frac{\dot{x}}{x} - 1 + \delta\right), \qquad B_{12} = \begin{pmatrix} 0 & 0 & 0 & (\nu+p)x & 0 \end{pmatrix}, \qquad B_{21} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

and

$$B_{22} = \begin{pmatrix} \frac{\dot{x}}{x} - (1+n) & 0 & -(\delta+l)x & 0 & (\nu+p)x \\ 0 & -1+\nu & 0 & -(\delta+l) & 0 \\ 0 & 0 & \delta-n & 0 & 0 \\ 0 & 0 & 0 & \delta+\nu & 0 \\ 0 & 0 & 0 & 0 & \nu-n \end{pmatrix}.$$

The Lozinskiĭ measure $\mu(B)$ with respect to $\|\cdot\|$ can be estimated as follows

$$\mu(B) \leqslant \max\{g_1, g_2\} \tag{30}$$

where $g_1 = \mu(B_{11}) + \|B_{12}\|$ and $g_2 = \|B_{21}\| + \mu(B_{22})$ ($\|B_{12}\|$ and $\|B_{21}\|$ are with respect to one-norm).

Now,

$$g_1 = \frac{\dot{x}}{x} - 1 + \delta + (\nu+p)x, \qquad g_2 = \mu(B_{22})$$

$$\mu(B) \leqslant \max\left\{\frac{\dot{x}}{x} - 1 + \delta + (\nu+p)x, \mu\big((B_{22})_{5\times5}\big)\right\}.$$

Using successive partitioning as in matrix, the Lozinskiĭ measure $\mu(B)$ is computed as

$$\mu(B_{22})_{5\times5} \leqslant \max\big\{C_{11} + \big\|(C_{12})_{1\times4}\big\|, \big\|(C_{21})_{4\times1}\big\| + \mu(C_{22})_{4\times4}\big\}$$

$$\mu(C_{22})_{4\times4} \leqslant \max\big\{D_{11} + \big\|(D_{12})_{1\times3}\big\|, \big\|(D_{21})_{3\times1}\big\| + \mu(D_{22})_{3\times3}\big\}$$

$$\mu(D_{22})_{3\times3} \leqslant \max\big\{E_{11} + \big\|(E_{12})_{1\times2}\big\|, \big\|(E_{21})_{2\times1}\big\| + \mu(E_{22})_{2\times2}\big\}$$

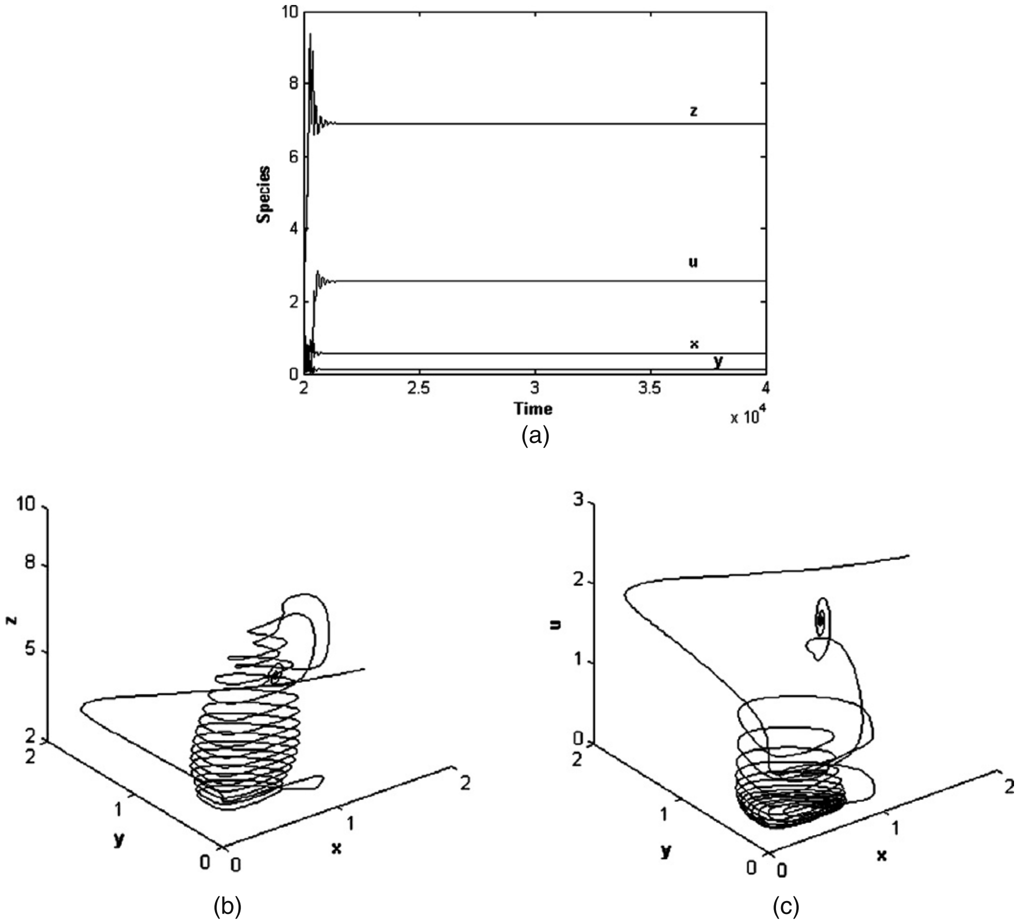

Fig. 2. (a) Time series. (b) Phase portrait in x–y–z plane. (c) Phase portrait in x–y–u plane depicting stable behavior of the system at $m_1 = 0.8$.

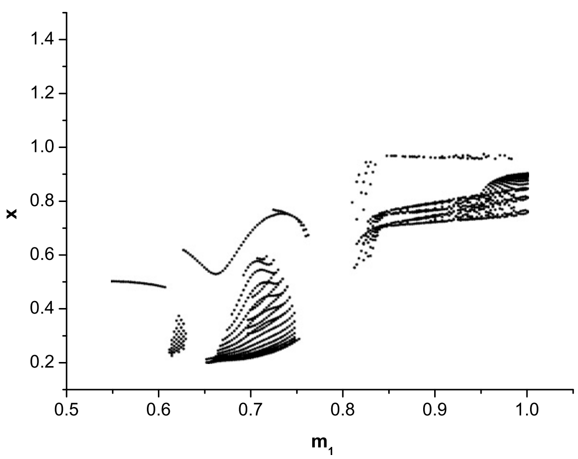

Fig. 3. Bifurcation diagram with respect to m_1.

$$\mu(E_{22})_{2\times 2} \leqslant \max\{\delta + \nu, \nu - n\}$$
$$\mu(E_{22})_{2\times 2} \leqslant \delta + \nu \quad \text{since } -\delta < n$$
$$\mu(D_{22})_{3\times 3} \leqslant \max\{\delta - n, \delta + \nu\}$$
$$\mu(D_{22})_{3\times 3} \leqslant \delta + \nu \quad \text{since } -\nu < n$$

Table 1
Study of system (2) for fixed parameter values $a = 5.0$, $b = 3.0$, $c = 0.1$, $d = 2.0$, $l = 0.4$, $n = 0.01$, $e = 0.5$, $g = 1.0$, $p = 0.05$.

m_1	Dynamical behavior of the system	
0.0	System reduces to Prey–Predator model, y and z extinct, only x and u survive, stable behavior	Fig. 4
0.3	y and z extinct, only x and u survive, stable behavior	Fig. 5
0.54	All four species, oscillate, limit cycle	Fig. 6
0.7	All species survive Long periodic solution with multiple periodicity	Fig. 7
0.8	All four species coexist, stable behavior	Fig. 2
0.9	u extinct, chaotic behavior	Fig. 8
1.0	HP model, tea cup attractor	Fig. 9

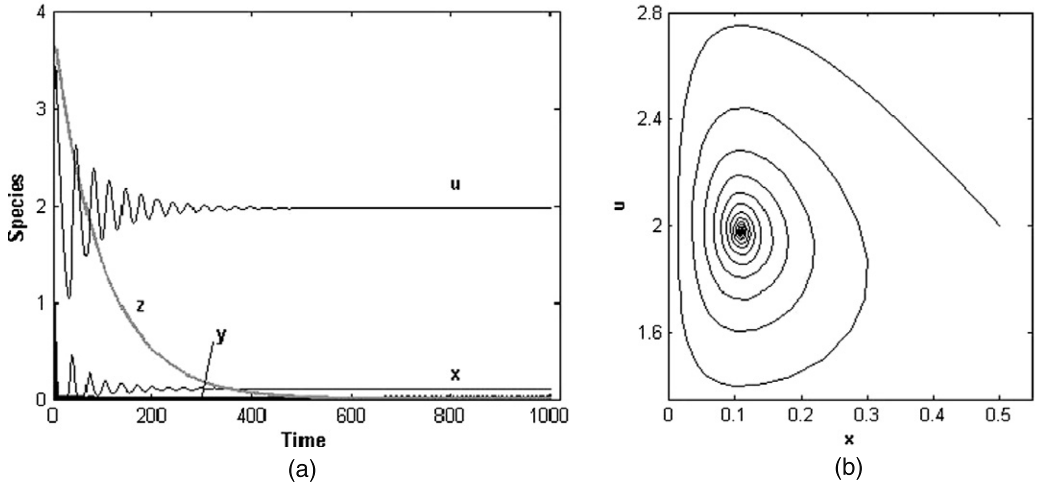

Fig. 4. (a) Time series. (b) Phase portrait in x–u plane depicting stability in the system at $m_1 = 0.0$.

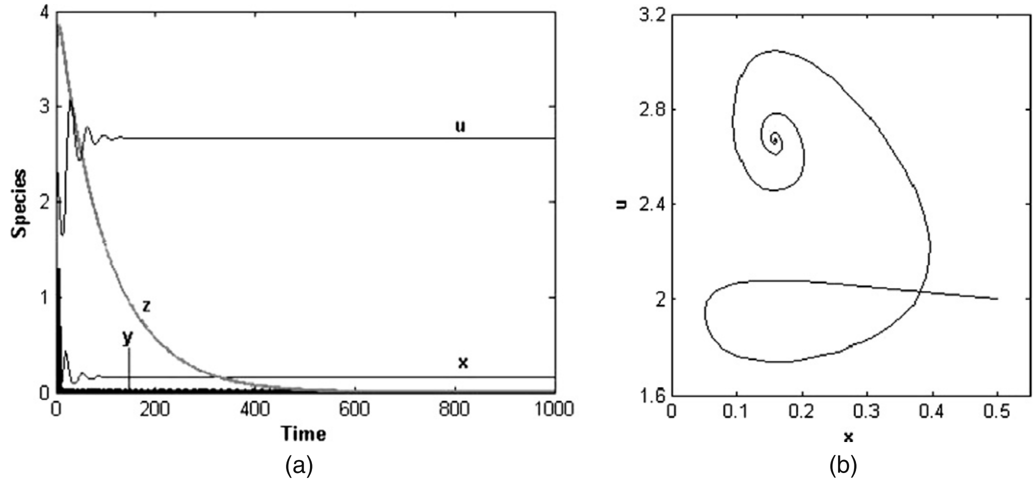

Fig. 5. (a) Time series. (b) Phase portrait in x–u plane depicting stability in the system at $m_1 = 0.3$.

$$\mu(C_{22})_{4\times 4} \leqslant \delta + \nu \quad \text{if } l < 1$$

$$\mu(B_{22})_{5\times 5} \leqslant \frac{\dot{x}}{x} + \delta + \nu \quad \text{if } p < n.$$

Finally,

$$\mu(B) \leqslant \frac{\dot{x}}{x} + \delta + \nu \quad \text{since } p < 1.$$

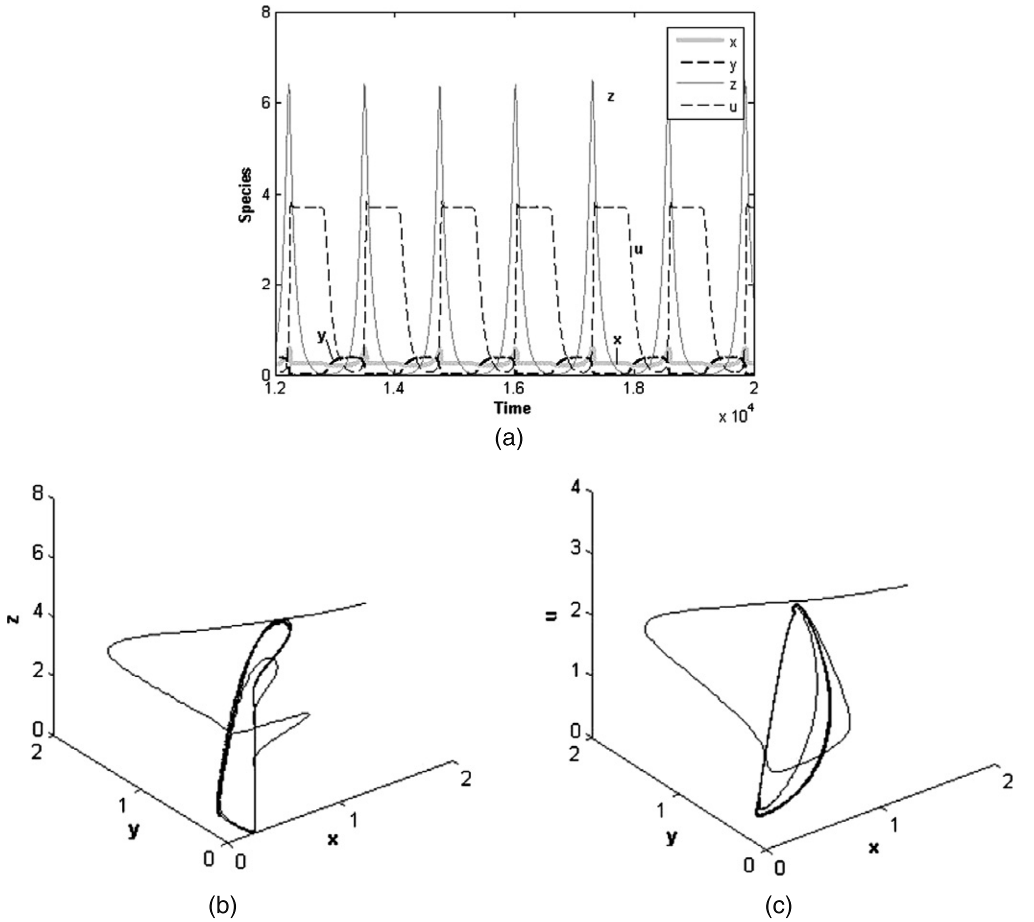

Fig. 6. (a) Time series. (b) Phase portrait in x–y–z plane. (c) Phase portrait in x–y–u plane depicting limit cycle in the system at $m_1 = 0.54$.

As $\delta + \nu < 0$, say $\delta + \nu = -\omega$, then

$$\mu(B) \leqslant \frac{\dot{x}}{x} - \omega.$$

Now, let $E_x(1, 0, 0, 0)$ be any solution starting in the compact absorbing set $\mathcal{K} \subset \mathcal{D}$ and let T be sufficiently large such that $E_x \in \mathcal{K}$ for all $t > T$. Since the system is uniformly persistent under (25), then for $c > 0$

$$x(t) \geqslant c, \qquad \frac{1}{t} \log x(t) < \frac{\omega}{2} \tag{31}$$

for all $x(0), y(0), z(0), u(0) \in \mathcal{K}$. Then along each solution of $E_x \subset \mathcal{K}$, it is obtained for $t > T$

$$\frac{1}{t} \int_0^t \mu(B)\, dt < \log x(t) - \omega < -\frac{\omega}{2} \tag{32}$$

for all $x(0), y(0), z(0), u(0) \in \mathcal{K}$. Therefore, $\bar{q}_2 < 0$ on $\mathcal{K}$, completing the proof. □

The system (2) attain Poincar'e–Andronov–Hopf (Hopf-steady state) bifurcation (PAHB) around E_{HP} equilibrium point [22].

6. Numerical explorations

In this section, numerical experiments are performed to investigate the dynamics of the system (2). Hastings and Powell [4] has studied food chain model which is a subsystem of system (2) under the following choice of parameters:

$$a = 5.0, \qquad b = 3.0, \qquad c = 0.1, \qquad d = 2.0, \qquad l = 0.4, \qquad n = 0.01. \tag{33}$$

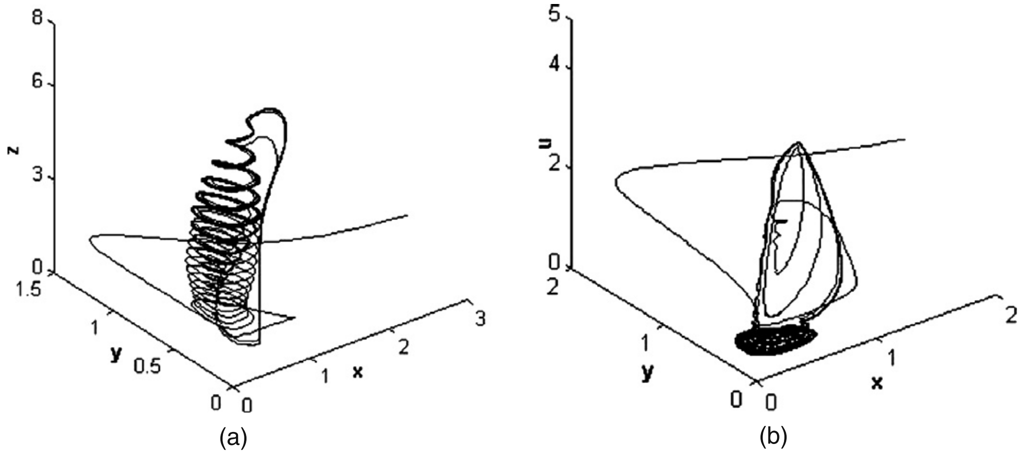

Fig. 7. (a) Quasi-periodic attractor in x–y–z plane. (b) Quasi-periodic attractor in x–y–u plane at $m_1 = 0.7$.

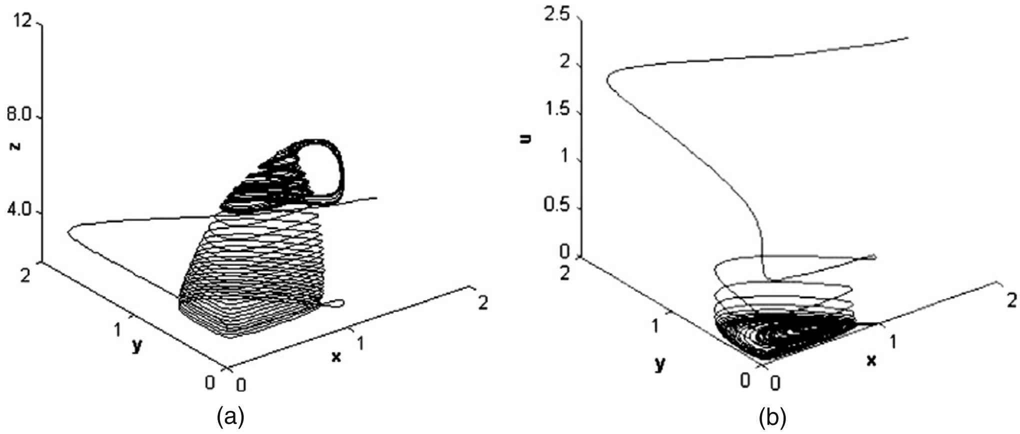

Fig. 8. (a) Chaotic attractor in x–y–z plane. (b) Chaotic attractor in x–y–u plane at $m_1 = 0.9$.

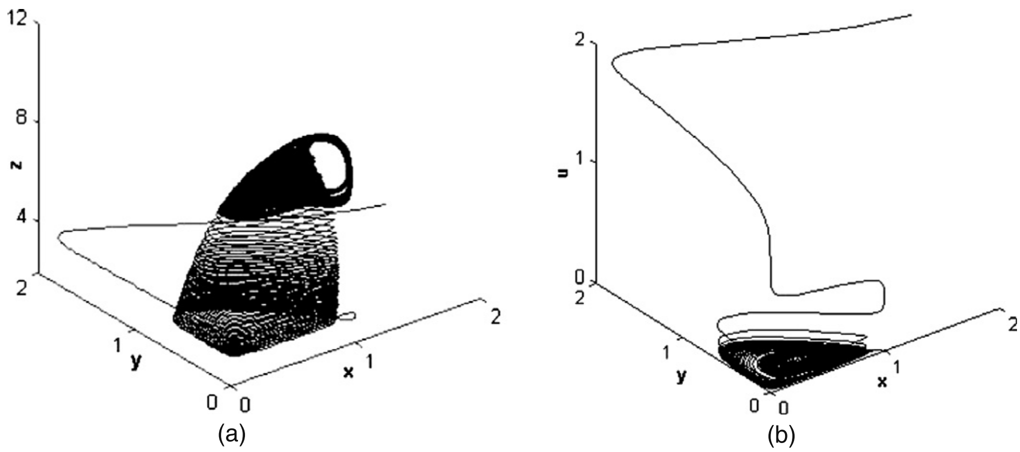

Fig. 9. (a) Tea cup attractor in x–y–z plane. (b) Chaotic attractor in x–y–u plane at $m_1 = 1.0$.

For this choice of parameters, HP model has chaotic dynamics. These parameters are kept fixed throughout the numerical simulations, while the remaining four parameters are varied. Consider the following typical parametric choice

$$e = 0.5, \qquad g = 1.0, \qquad m_1 = 0.8, \qquad p = 0.05. \tag{34}$$

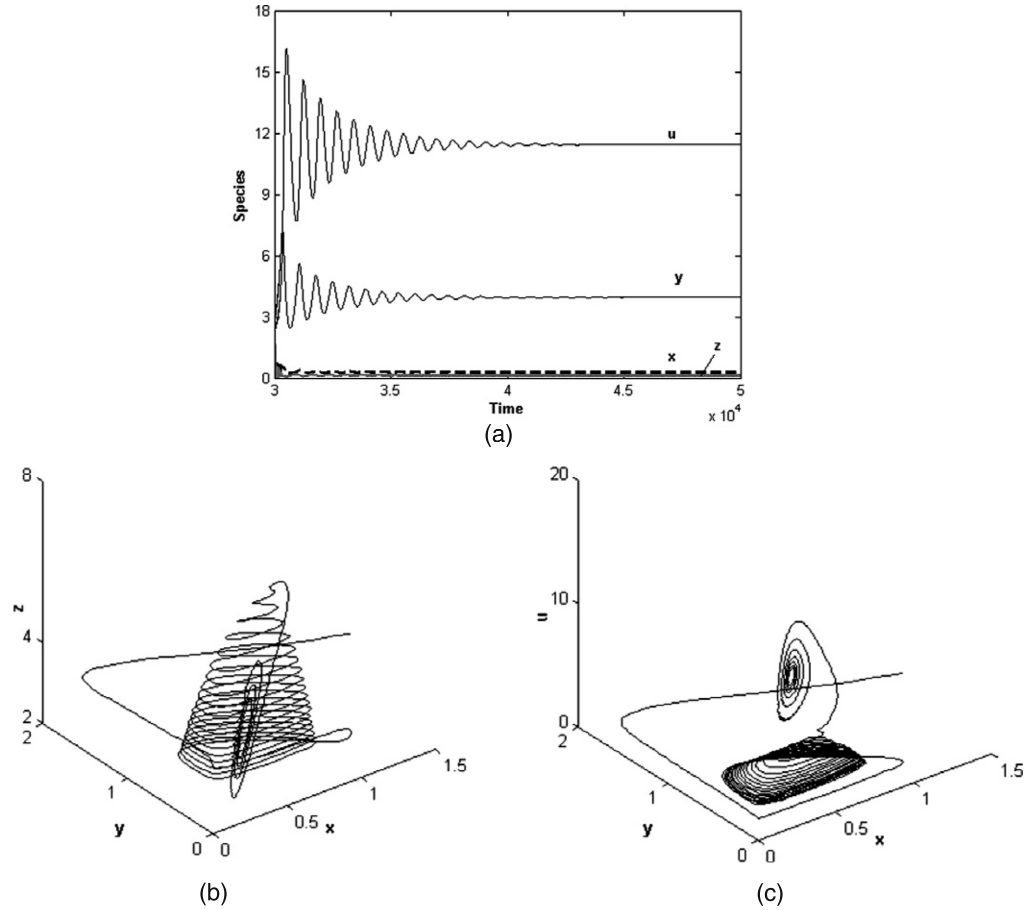

Fig. 10. (a) Time series. (b) Phase portrait in x–y–z plane. (c) Phase portrait in x–y–u plane depicting stable behavior of the system at $p = 0.01$, $m_1 = 0.9$.

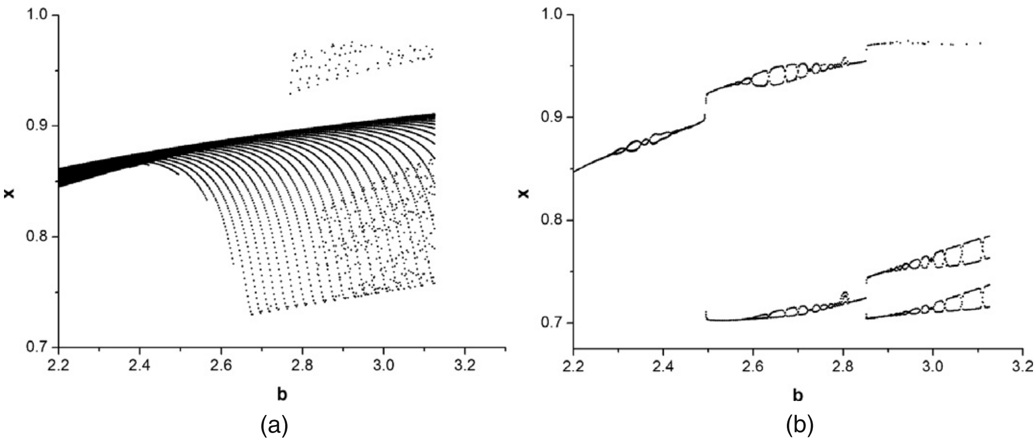

Fig. 11. Bifurcation diagram with respect to half saturation constant b for (a) HP model, (b) four-dimensional model.

The necessary conditions (29) for the stability of the positive equilibrium point E_x are satisfied for this choice of parameters which means that the system (2) is locally asymptotically stable around positive equilibrium point E_x. Fig. 2 displays the stable dynamics of the system. The solution converges to stable interior equilibrium point $E^*(0.556, 0.125, 6.905, 2.558)$ showing the coexistence of all the four species. Thus, the three species Hastings–Powell food chain which was chaotic turned out to have stable dynamics when another predator is added to the top prey.

Similar results are obtained for sets of parameters other than (34). It may be interesting to note that the HP food chain gets major share of food while the additional predator is getting small amount from the top prey.

Bifurcation diagram is plotted with respect to key parameter m_1 for above set of parameters in Fig. 3. The system exhibits stability up to $m_1 = 0.5$. The system has periodic solution in the region $(0.54, 0.6)$. More complex periodic solutions are observed in the domain $(0.6, 0.78)$. A stable window is also visible in the region $(0.78, 0.81)$. The system exhibits chaotic behavior in the region $(0.81, 1.0)$.

The system dynamics is further explored for different values of m_1 while others parameters kept fixed. The observations are summarized in Table 1.

Further decreasing the mortality rate p of additional predator may lead to stable coexistence of all the species at higher value of m_1 (lower value of m_2). For $m_1 = 0.9$, $p = 0.01$ system exhibits stable dynamics, see Fig. 10.

Bifurcation diagrams are plotted with respect to half saturation constant b for original HP model (data as (33)) and proposed four-dimensional model (2) (for data (33) and (34)) in Fig. 11. The HP model (Fig. 11(a)) system exhibits chaos in the system whereas the complexity is reduced in the proposed model (Fig. 11(b)).

7. Discussion

In the present paper an additional predator to the top prey is introduced in HP model and resulting dynamics of four-dimensional model has been explored. The top prey is now being shared between the two predators. The parameters m_1 and m_2 represent the availability of food for the two predators y and u respectively. Hastings and Powell observed various behaviors like stability, limit cycle and chaos in his proposed food chain at different values of half saturation constant. The introduction of additional predator to the top prey, changes the dynamics of system. The complexity of HP model is reduced in the sense that the chaotic behavior of original system may show the limit cycle or stability for suitable combination of parameters. An interesting thing to be noted is that all the four species may coexist while dependence of additional second predator on the top prey is very low. The assumption of ignoring additional prey may lead to HP model and the solution is predicted to be chaotic. This may not be true and inclusion of an additional predator in the system may bring order to the system in the form of stable coexistence of all the four species. These findings clearly indicate that considering additional predator for top prey is the key factor for disappearance of chaotic dynamics observed in HP model. This serves as an explanation to why chaos is not detected frequently in the natural population.

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