HOPF bifurcation Dynamics and Persistence of Two Mutually Interdependent Predator Species for Sharing a Single Prey Species under Kolmogorov Constraints

Brahampal Singh[1], Sunita Gakkhar[2]

[1]Department of Mathematics, J.V.Jain (PG) College—Saharanpur, Saharanpur 247001, India

[2]Department of Mathematics, Indian Institute of Technology—Roorkee, Roorkee 247667, India

Abstract: ***In research paper [2] we investigated local and global stability of a model consisting of two mutually interdependent predator species feeding on a single prey species. In this paper we investigated Hopf bifurcation, quasiperiodic behavior and persistence of the nonlinear ode system [2] under the Kolmogorov conditions. Both the predator species has symbiotic interaction that is mutually beneficial [2].The existence of Hopf bifurcation is investigated and limit cycles are obtained. It is observed that the persistence is possible in the form of periodic cycle in the positive octant.***

Keywords: Food web; Hopf bifurcation; limit cycle; persistence

1. Introduction

Two prey and one predator systems are shown to have complex dynamical behavior [4]-[6]. The two predators themselves may have different types of interaction between them. In the case of two competing species, coexistence is not possible and only the fittest will survive [6]. The effect of implicit competition on the two predators sharing a common prey was investigated in [6]. There exist infinitely many non-hyperbolic equilibria lying on a straight line for a narrow choice of parameters and solution is quasi-periodic. Apart from the implicit competition, the two predators may have explicit competition between themselves [9]. Due to explicit competition, the Competitive exclusion of the weak predator is possible. In specialist and generalist prey predator models, the two predators may be in a prey-predator type of interaction [3]. In a two species system, cooperation is found to have a destabilizing effect on the stability of equilibrium. Freedman et. al. [8] investigated a three species food web considering the mutualism between two predators sharing a prey. The effect of their cooperation is considered implicitly in the functional response of the prey species. Basic Lotka-Volterra type models in which mutualism (a type of symbiosis where the two populations benefit both) is taken into account, may give unbounded solutions [1]. It is excluded such behaviour using explicit mass balances and study the consequences of symbiosis for the long-term dynamic behaviour of a three species system, two predator and one prey species in the chemostat [1].

Consider a three species food web comprised of two mutualist predators feeding on a single prey species limit [2]. The dynamical equations of this food web [2] are given as

$$\begin{aligned}
\frac{dX_1}{dT} &= rX_1\left(1-\frac{X_1}{K}\right) - F_1(X_1)X_2 - F_2(X_1)X_3 \\
\frac{dX_2}{dT} &= e_1F_1(X_1)X_2 + \beta_1X_2X_3 - d_1X_2 \qquad (1) \\
\frac{dX_3}{dT} &= e_2F_2(X_1)X_3 + \beta_2X_2X_3 - d_2X_3 \\
X_1(0) &= X_{10} \ge 0,\ X_i(0) = X_{i0} \ge 0\ \ i = 2,3\ with\ F_i(X) = a_iX/(b_i + X),\ i = 1,2
\end{aligned}$$

Where parameters, symbols, non-dimensional variables and parameters have same meanings as [2]. Accordingly, the non-dimensional system [a] is

$$\frac{d\,y_1}{d\,t}=y_1\left[(1-y_1)-\frac{y_2}{w_1+y_1}-\frac{y_3}{w_2+y_1}\right]=y_1\,F(y_1,y_2,y_3)$$
$$\frac{d\,y_2}{d\,t}=y_2\left[w_3\;f_1(y_1)+\gamma_1\,y_3-w_4\right]=y_2\,G_1(y_1,y_3) \tag{2}$$
$$\frac{d\,y_3}{d\,t}=y_3\left[w_5\;f_2(y_1)+\gamma_2\,y_2-w_6\right]=y_3\,G_2(y_1,y_2)$$
$$y_1(0)=y_{10}\geq 0,\; y_i(0)=y_{i0}\geq 0\;\; i=2,3.f_i(y)=\frac{y_1}{w_i+y_1},\; i=1,2$$

2. Boundedness

Theorem 2.1: The nonlinear dynamical system (3) has bounded solution.

Proof: is given in research paper [2].

The system (3) is divided into two subsystems. The first subsystem is obtained by assuming the absence of the second predator y_3 .

$$\frac{dy_1}{dt}=y_1\left[(1-y_1)-\frac{y_2}{w_1+y_1}\right];$$
$$\frac{dy_2}{dt}=y_2\left[w_3\,\frac{y_1}{w_1+y_1}-w_4\right] \tag{4}$$

The second subsystem is obtained when the first predator y_2 is absent.

$$\frac{dy_1}{dt}=y_1\left[(1-y_1)-\frac{y_3}{w_2+y_1}\right];$$
$$\frac{dy_3}{dt}=y_3\left[w_5\,\frac{y_1}{w_2+y_1}-w_6\right] \tag{5}$$

Theorem 2.1: The system is Kolmogorov systems [14] under the constraints:

$$w_3>w_4(1+w_1)\text{, and} \tag{6}$$
$$w_5>w_6(1+w_2). \tag{7}$$

3. Stability Analysis

Theorem 3.1: The positive equilibrium $(y_1^*,y_2^*,y_3^*),\ 0<y_1^*<1,\ y_2^*>0,\ y_3^*>0$ exists and is unique under the Kolmogorov conditions (6-7) and the condition such that

$$\frac{w_1w_4}{\gamma_1}+\frac{w_2w_6}{\gamma_2}-w_1w_2>0 \tag{8}$$

Proof: is given in research paper [2].

Theorem 3.2: The positive nonzero equilibrium (y_1^*,y_2^*,y_3^*) is locally asymptotically stable under the Kolmogorov conditions (6-7) provided

$$\min\left(d_1,\frac{ed_1+w_3\frac{1}{y_1^*}(d_1+d_2c_2+d_3c_1)}{(e+d_1+\frac{1}{y_1^*}-c_1^2c_2^2)}\right)<c_1^2c_2^2<\max\left(d_1+d_2c_2+d_3c_1,e\right)$$
$$\text{here } e=\frac{d_2c_2^2y_1^*}{a_2\gamma_2}+\frac{d_3c_1^2y_1^*}{a_1\gamma_1};\; d_1=a_1c_2+a_2c_1,d_2=\frac{w_1w_3}{\gamma_1},d_3=\frac{w_2w_5}{\gamma_2}, \tag{9}$$
$$c_1=w_1+y_1^*,c_2=w_2+y_1^*,$$
$$a_2=\frac{1}{\gamma_1}\left(w_1w_4\text{ - }y_1^*(w_3-w_4)\right)>0,a_1=\frac{1}{\gamma_2}\left(w_2w_6\text{ - }y_1^*(w_5-w_6)\right)>0$$

Proof. is given in research paper [2].
The following theorem gives the conditions for the global stability of positive nonzero equilibrium point.

Theorem 3.3 The positive equilibrium point (y_1^*,y_2^*,y_3^*) is globally asymptotically stable provided the following are satisfied:

$$y_1<\text{Min}\left\{\frac{M-c'}{2(1-y_1^*)},\frac{\alpha y_1^*-\beta}{\alpha}\right\}\text{and M is the bound of the system.}$$
$$\text{Where } \alpha=\frac{A_3l_2^*\gamma_1}{l_1^*A_2}+\gamma_2,\;\beta=\frac{A_3l_2^*\gamma_1}{A_2}+l_2^*\gamma_2,c'=(1-y_1^*)\left[(w_1+w_2)+y_1^*\right] \tag{10}$$

Proof. is given in research paper [2].

Lemma 3.4: The nonlinear dynamical system (3) may have one or more periodic solutions.

Proof: Consider the system (3) in the form of $y' = h(y) = (h_1(y), h_2(y), h_3(y))$;

$$\text{Curl } h(y) = \begin{bmatrix} i & j & k \\ \frac{\partial}{\partial y_1} & \frac{\partial}{\partial y_2} & \frac{\partial}{\partial y_3} \\ h_1 & h_2 & h_3 \end{bmatrix}$$

$$= i(\gamma_2 y_3 - \gamma_1 y_2) + j\left(\frac{w_2 w_5 y_3}{(w_2+y_1)^2} + \frac{y_1}{(w_2+y_1)}\right) + k\left(\frac{w_1 w_3 y_2}{(w_1+y_1)^2} + \frac{y_1}{(w_1+y_1)}\right) \neq 0.$$

Therefore, the nonlinear model (3) is not a gradient system [15]. Hence the system admits one or more periodic solutions.

Theorem 3.5: The non-dimensional system (3) admits limit cycle solutions in the neighborhood of positive nonzero equilibrium point at the bifurcation point γ_1^* provided the conditions (8) and the following conditions are satisfied:

$$m_3 y_1^*\left(w_1 w_3 y_2^*(w_2+y_1^*)^3 + w_2 w_5 y_3^*(w_1+y_1^*)^3\right) =$$

$$y_2^* y_3^*(w_1+y_1^*)(w_2+y_1^*)\left(w_1 w_3 \gamma_2 (w_2+y_1^*) + w_2 w_5 \gamma_1 (w_1+y_1^*)\right); \qquad (9)$$

$$m_3 = \left(1 - \frac{y_2^*}{(w_1+y_1^*)^2} - \frac{y_3^*}{(w_2+y_1^*)^2}\right) \text{. at } \gamma_1 = \gamma_1^*$$

$$\left(\frac{\partial \lambda_1}{\partial \gamma_1}\right)_{\gamma_1=\gamma_1^*} \neq 0 \qquad (10)$$

Proof. The system (3) has positive equilibrium point under conditions (8). The characteristic equation about the equilibrium is obtained as (31). It may be observed that

(i) $a_0, a_1, a_2 > 0$

(ii) At the bifurcation parameter $\gamma_1 = \gamma_1^*$, $a_0 a_1 - a_2 = 0$ i.e.

$$f(\gamma_1) = a_0 a_1 - a_2 = a_{21}(a_{11}a_{12} + a_{13}a_{32}) + a_{31}(a_{11}a_{13} + a_{12}a_{23}) = 0,$$

The characteristic polynomial can be written in the form

$$\Delta(\lambda) = (\lambda - s)(\lambda - \bar{s})(\lambda - \alpha) = \lambda^3 - (2\lambda_1 + \alpha)\lambda^2 + (|s|^2 + 2\lambda_1\alpha)\lambda - |s|^2\alpha$$

; $\lambda = \lambda_1 + i\lambda_2$

Comparing the coefficients and simplifying, we get

$$-a_2 + 2\lambda_1(a_0 + 2\lambda_1)^2 + a_1(a_0 + 2\lambda_1) = 0, \quad (11)$$

Differentiating (11) with respect to bifurcation parameter γ_1 and putting $\lambda_1(\gamma_1^*) = 0$, we get

$$\left(\frac{\partial \lambda_1}{\partial \gamma_1}\right)_{\gamma_1=\gamma_1^*} = \frac{\frac{\partial a_2}{\partial \gamma_1} - a_0\frac{\partial a_1}{\partial \gamma_1} - a_1\frac{\partial a_0}{\partial \gamma_1}}{2(a_0^2 + a_1)} \neq 0$$

The system (3) will admit Hopf bifurcation for the parameter $\gamma_1 = \gamma_1^*$ provided conditions (9) are satisfied. Thus the system admits periodic solution in the neighborhood of positive nonzero equilibrium point at the bifurcation point $\gamma_1 = \gamma_1^*$.

4. Persistence

According to Freedman and Waltman [7], the following assumptions for the system (3) are assumed to be satisfied:

$$F_1(0,0,0) > 0$$

A_1: $\frac{\partial F_1}{\partial y_1} \le 0$ provided $\frac{y_2}{(w_1+y_1)^2} + \frac{y_3}{(w_2+y_1)^2} \le 1$,

$$\frac{\partial F_1}{\partial y_2} = -(w_1+y_1)^{-1} < 0, \quad \frac{\partial F_1}{\partial y_3} = -(w_2+y_1)^{-1} < 0,$$

$$\frac{\partial G_1}{\partial y_1} = w_3 w_1 (w_1+y_1)^{-2} > 0, \quad \frac{\partial G_2}{\partial y_1} = w_2 w_5 (w_2+y_1)^{-2},$$

$G_1(0, y_2, y_3) < 0$ provided $y_3 < w_4/\gamma_1$,

$G_2(0, y_2, y_3) < 0$ provided $y_2 < w_6/\gamma_2$,

$$\frac{\partial G_1}{\partial y_2} = 0, \quad \frac{\partial G_2}{\partial y_3} = 0, \quad \frac{\partial G_1}{\partial y_3} = \gamma_1 > 0, \quad \frac{\partial G_2}{\partial y_2} = \gamma_2 > 0,$$

A_2: The prey grows to carrying capacity in the absence of predation, i.e. there exist K Such that $F_1(1,0,0) = 0, \ (K = 1)$

A_3 : There are no equilibria on the y_2 or y_3 coordinate axes and no equilibria in y_2 - y_3 plane.

A_4 : Each predator is surviving on the common prey i.e. there exists equilibrium points $E_2 = (\bar{y}_1, \bar{y}_2, 0)$ and $E_3 = (\hat{y}_1, 0, \hat{y}_3)$, $0 < \bar{y}_1, \bar{y}_2 < 1$; $0 < \hat{y}_1, \hat{y}_3 < 1$; such that

$$F_1(\bar{y}_1, \bar{y}_2, 0) = G_1(\bar{y}_1, \bar{y}_2, 0) = 0 \ \& \ F_1(\hat{y}_1, 0, \hat{y}_3) = G_2(\hat{y}_1, 0, \hat{y}_3) = 0$$

Theorem 4.1: Let $(A_1)-(A_4)$ hold and there are no limit cycles on the boundary planes then the nonlinear model (3) persists if

$$G_1(\bar{y}_1, 0, \bar{y}_3) > 0 \ \ or \ \ \left(\frac{w_3 \bar{y}_1}{w_1 + \bar{y}_1} + \gamma_1 \bar{y}_3\right) > w_4$$
$$G_2(\hat{y}_1, \hat{y}_2, 0) > 0 \ \ or \ \ \left(\frac{w_5 \hat{y}_1}{w_2 + \hat{y}_1} + \gamma_2 \hat{y}_2\right) > w_6 \qquad (12)$$

Theorem 4.2: If a finite number of limit cycles $(\hat{\varphi}(t), \hat{\psi}(t))$ of period T are allowed in $y_1 - y_2$ plane then the system (3) will persist provided the following condition is satisfied:

$$\int_0^T G_1(\hat{\phi}(t), \hat{\psi}(t), 0)dt > 0 \ \text{or} \ \frac{w_3 \hat{\phi}(t)}{w_1 + \hat{\phi}(t)} + \gamma_2 \hat{\psi}(t) > w_4 \quad (13)$$

If a finite number of limit cycles $(\bar{\varphi}(t), \bar{\psi}(t))$ of period T are allowed in $y_1 - y_3$ plane then the system (3) will persist provided the following condition is satisfied:

$$\int_0^T G_2(\bar{\phi}(t), 0, \bar{\psi}(t))dt > 0 \ \text{or} \ \frac{w_5 \bar{\phi}(t)}{w_2 + \bar{\phi}(t)} + \gamma_1 \bar{\psi}(t) > w_6 \quad (14)$$

It is concluded that with mutalist predators the persistence is possible under conditions (12) or (13) - (14) involving positive parameters γ_1 and γ_2. The persistence is possible in the form of stable nonzero equilibrium or a periodic solution in positive phase space. Due to the involvement of $(\hat{\varphi}(t), \hat{\psi}(t))$ in the conditions (12)-(14), their validation is difficult and they only give the possibility of periodic solution.

5. Numerical Simulations

The analysis does not show the behavior when the conditions are not satisfied. The numerical simulations investigate the dynamical behavior of the system in such cases. When the system allows periodic solution in any of the prey predator planes then the system (3) may persist according to conditions (13) and (14). Due to the involvement of $(\hat{\phi}(t), \hat{\psi}(t))$ in the conditions (13)-(14), their validation is difficult and they only give the possibility of periodic solution.

We fixed the biological feasible set of parameters:
Consider the variation of key parameter w_4 for the following biological feasible set of parameters:

$$w_1 = 2.1, w_2 = 2.12, w_3 = 1.8, \ w_5 = 1.9, w_6 = 0.12, \gamma_1 = 0.05, \gamma_2 = 0.05 \quad (15)$$

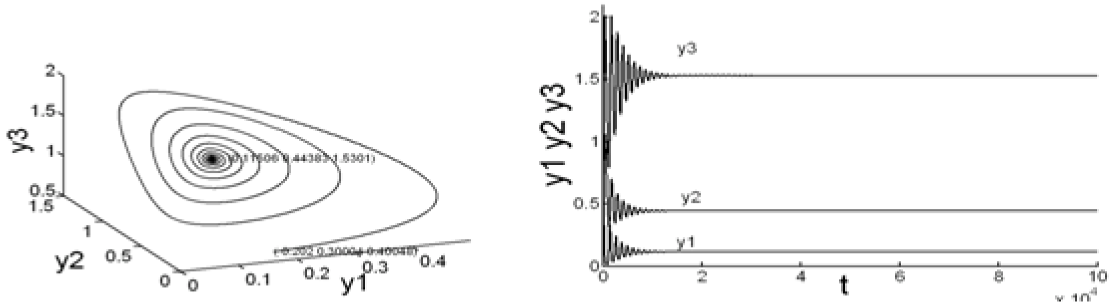
For this choice of parameters, the hopf bifurcation is found to occur in the neighborhood of $w_4^* = 0.1211$. The following values are obtained for the eigenvalues and eigenvectors at this point

-0.0001 + 0.2441i, {0.0376 - 0.2066i, 0.0376 + 0.2066i, 0.0014}

-0.0001 - 0.2441i, {-0.6347 + 0.0311i, -0.6347 - 0.0311i, -0.7034}

-0.0501, {-0.7430 , -0.7430 , 0.7108}

The transition of stability to limit cycle is shown in Fig. 4 to Fig. 6 for variation in the bifurcation parameter w_4. Thus, sub critical hopf bifurcation occurs with respect to the parameter w_4.



(a) (b)

Figure 4: For the data set (15) w4= 0.17(a) 3D behavior (b) time series

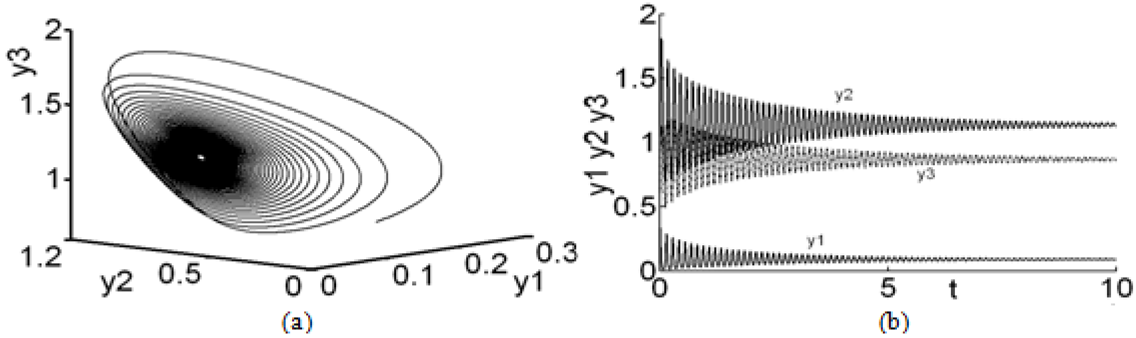


Figure 5: For the data set (15) w4= 0.13 (a) 3D behavior (b) time series

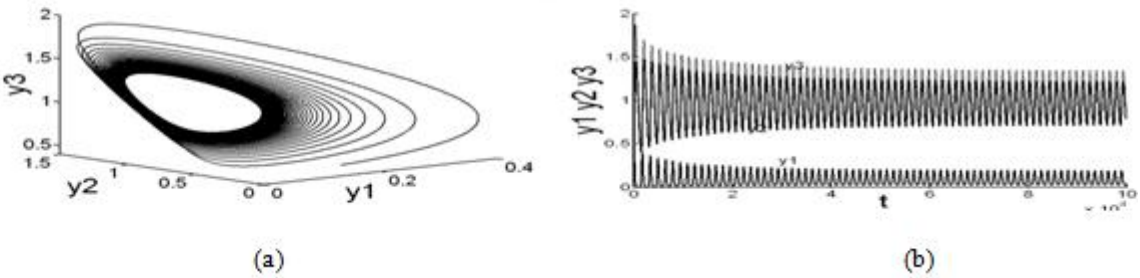


Figure 6: For the data set (15) w4=0.1211 (a) 3D behavior (b) time series

Consider the parameters

$$w_1 = 0.855, w_2 = 0.995, w_3 = 0.15, \ w_4 = 0.02, w_5 = 0.99, w_6 = 0.10, \gamma_1 = 0.011, \gamma_2 = 0.010 \quad (16)$$

It may be noted that the planar equilibriums E_2 (0.1315, 0.8568. 0) and E_3 (0.1118, 0, 0.9831) are locally stable for the perturbations in their respective planes. The eigenvalues orthogonal to their respective planes are found to be positive. Therefore the solution trajectories will stay away from the planes. Further, the positive equilibrium $(0.104739, 0.5713, 0.3300)$ is stable. The solution trajectories are shown to converge to the equilibrium in Fig. 7.

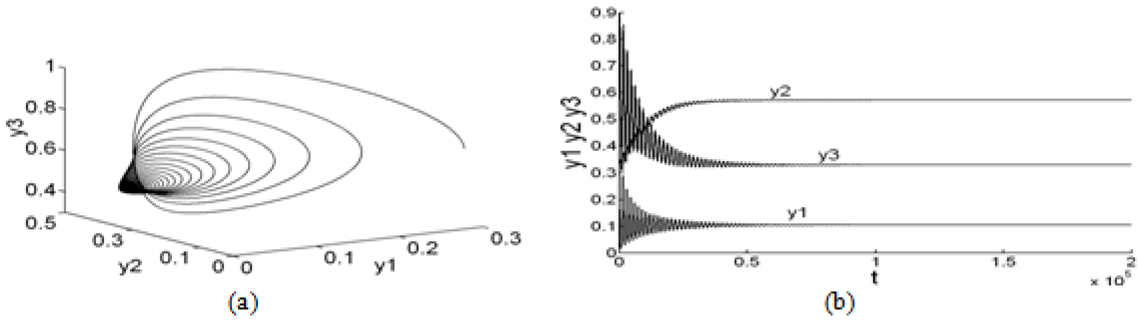


Figure 7: For the data set (16) w2= 0.995 (a) 3D behavior (b) time series

Slightly changing the parameter w_2 = 0.795, will make the equilibrium E_3 (0.0893, 0, 0.8053) and E^*(0.0867521, 0.2598, 0.5620) unstable and the global behavior of the solution is a limit cycle as shown in Fig 8. The boundary plane has a periodic solution but the persistence in the form of limit cycle is obtained in this case.

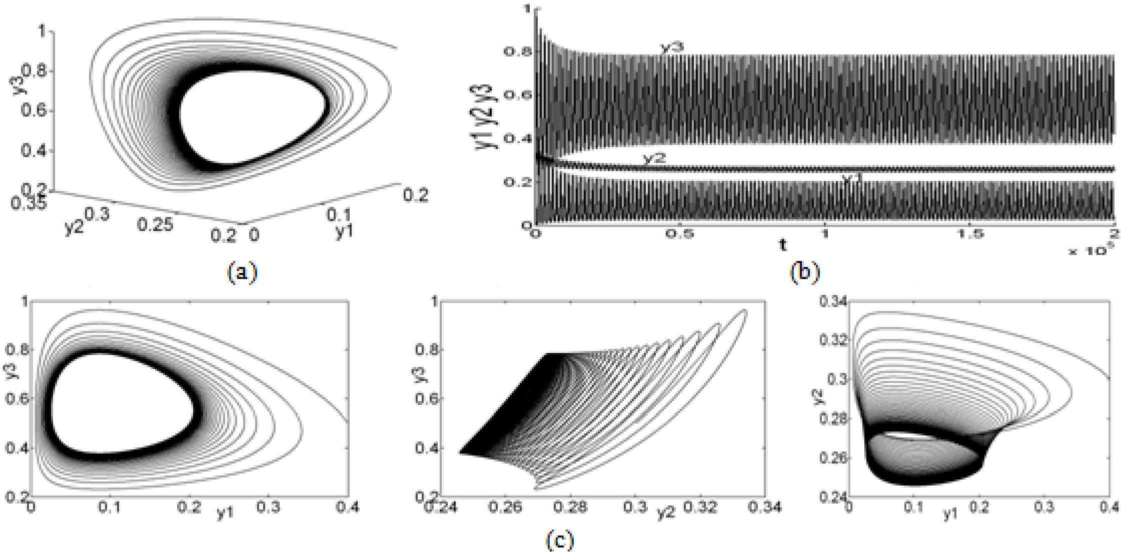


Figure 8: For the data set (16) w2=0.795 (a) 3D behavior (b) time series (c) Projection on coordinate planes

Further change in the parameter w_2 = 0.595 will destabilize the equilibrium E_2 (0.0611, 0.86, 0) also. It may be noted that the level of species will be maintained at very low level. It will not go to extinction, as the eigenvalue orthogonal to the plane is small but positive. The solution is quasi periodic See fig. 9.

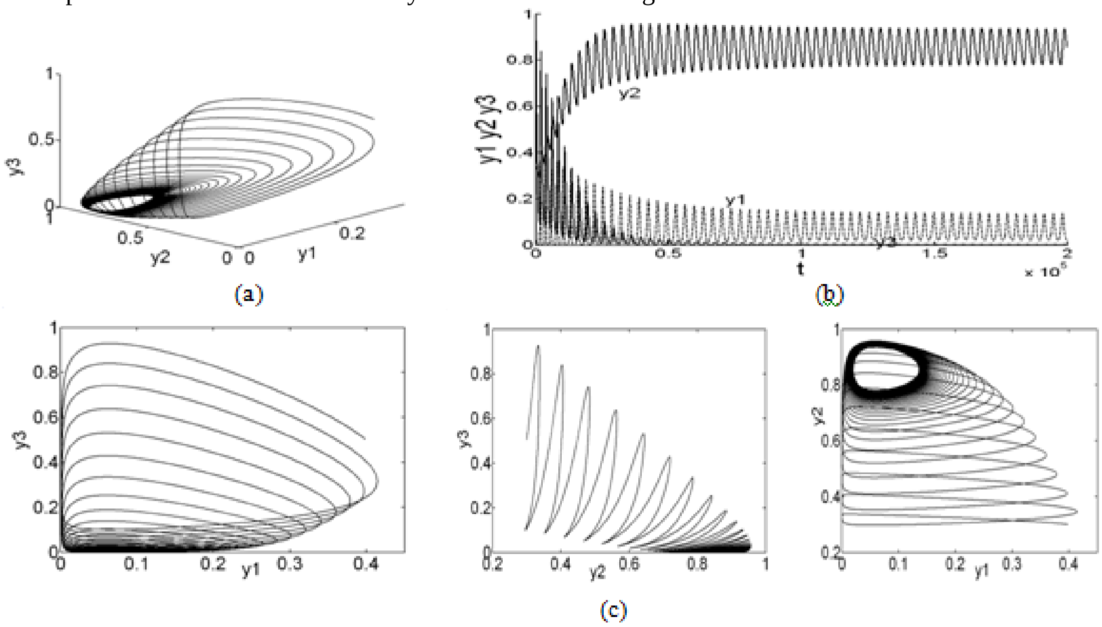


Figure 9: For the data set (16) w2=0.595 (a) 3D behavior (b) time series (c) Projection on coordinate planes

The variation with respect to w_5 is discussed for the following data:

$$w_1 = 1.1, w_2 = 1.10, w_3 = 1.1, \ w_4 = 0.1, w_6 = 0.2, \ \gamma_1 = 0.06, \gamma_2 = 0.04$$

(17)

For w_5 =2.1, the positive equilibrium exists and found to be unstable. The limit cycle is obtained in this case; see Fig 10(a). For w_5 = 2.7, 3.0 and 5.0 the behavior of solution are shown in Fig. 10(b), (c) and (d) respectively. The solution is quasi periodic in Fig.10(b) while limit cycles are obtained in all other cases.

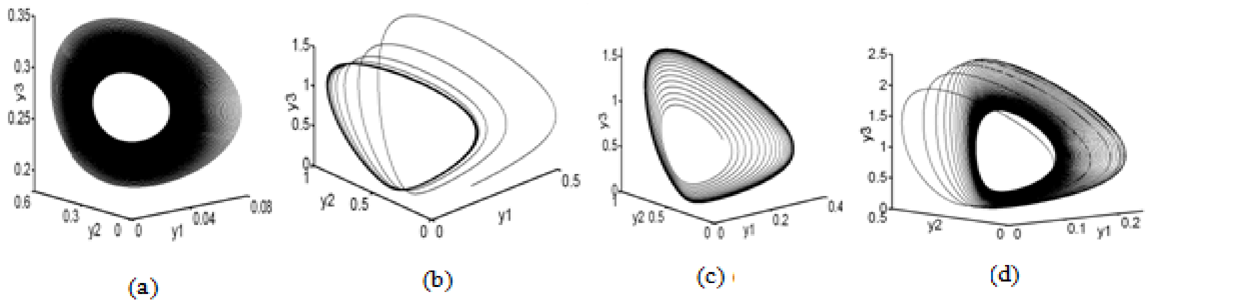


Figure 10: For the data set (17) (a) 3D behavior w5=2.1 (b) 3D behavior w5=2.7 (c) 3D behavior w5=3.0 (d) 3D behavior w5=5.0

6. Conclusions

The two predators are assumed to have mutual cooperation among them. In this paper it is analyzed numerically as well as analytically the existence of hopf bifurcation and quasiperiodic behavior of nonlinear system under the Kolmogorov conditions. The existence of limit cycle with the help of Hopf bifurcation theorem is established. The persistence of the system is possible in the presence of mutual cooperation.

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