Strong coexistence (local and global stability) of Two Mutually Interdependent Predator Species for Sharing a Single Prey Species

Brahampal Singh, Department of Mathematics, J.V.Jain College, Saharanpur 247001, India

*Sunita Gakkhar, Department of Mathematics, Indian Institute of Technology, Roorkee 247667, India

Email: brahampal_singh@rediffmail.com; *sungkfma@iitr.ernet.in

Abstract: A model consisting of two mutually interdependent predator species feeding on a single prey species is studied. Both the predator species has symbiotic interaction that is mutually beneficial. The local stability of equilibria points is analyzed. It is observed that the persistence is possible in the form of stable non zero equilibrium point or periodic limit cycle in the positive octant. It is shown that in the case of two competing predator species feeding over a single prey species, coexistence is not possible and only the fittest will survive [7], but in the case when two predator species have mutual cooperation feeding over a single prey species, then strong coexistence (local and global stability) is possible. In this paper the mathematical model comprising two mutually interdependent predator species and a single prey species shows rich dynamics numerically as well as analytically. The effect of mutually Cooperation on the two predators feeding on a common prey was investigated.

Keywords: Mutual Cooperation among predator; prey predation; Food web; stability; limit cycle.

1. Introduction:

Many investigators have discussed three species food chains and food webs [1]-[12]. Two prey and one predator systems are shown to have complex dynamical behavior [5]-[7]. A prey and two predator system has been investigated by considering various types of interactions among the two predators. 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 [7]. It may be interesting to see the changes in the behavior of the dynamical system as the competition is added between two of the species in food webs. The effect of implicit competition on the two predators sharing a common prey was investigated in [7]. Apart

from the implicit competition, the two predators may have explicit competition between themselves [14]. 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], and due to this additional interaction a rich complex dynamics is observed. In a two species system, cooperation is found to have a destabilizing effect on the stability of equilibrium. Freedman et. al. [13] 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 [2]. 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 [2]. In this paper, we are investigating a three species food web with mutualist predators. The three species food web model has all the three types of interactions among the interacting species: prey predation, implicit competition and mutualism.

Consider a three species food web comprised of two mutualist predators feeding on a single prey species. There is an implicit competition between them due to sharing of prey. The dynamical equations of this food web are given as

$$\frac{dX_{1}}{dT} = rX_{1}\left(1 - \frac{X_{1}}{K}\right) - F_{1}(X_{1})X_{2} - F_{2}(X_{1})X_{3}$$

$$\frac{dX_{2}}{dT} = e_{1}F_{1}(X_{1})X_{2} + \beta_{1}X_{2}X_{3} - d_{1}X_{2}$$

$$\frac{dX_{3}}{dT} = e_{2}F_{2}(X_{1})X_{3} + \beta_{2}X_{2}X_{3} - d_{2}X_{3}$$

$$X_{1}(0) = X_{10} \ge 0, X_{i}(0) = X_{i0} \ge 0 \quad i = 2,3 \text{ with } F_{i}(X) = a_{i}X/(b_{i} + X), i = 1,2$$

Here X_1 , denotes the density of prey species while X_2 and X_3 are the densities of two predators, $F_i(X)$ represent the Holling type-II functional response. The model parameters r, K, a_i, b_i, d_i and e_i can assume only positive values. The parameter β_1 and β_2 represent the coefficient of cooperation between the predators. The model (1) has 12 parameters,

which are reduced to 8 by introducing the following non-dimensional variables and parameters are

t = rT;
$$y_1 = X_1/K$$
; $y_2 = a_1 X_2/rK$; and $y_3 = a_2 X_3/rK$; $\gamma_1 = \beta_1 K/a_2$;
 $\gamma_2 = \beta_2 K/a_1$; $w_1 = \frac{b_1}{K}$; $w_2 = \frac{b_2}{K}$; $w_3 = \frac{e_1 a_1}{r}$; $w_4 = \frac{d_1}{r}$; $w_5 = \frac{e_2 a_2}{r}$; $w_6 = \frac{d_2}{r}$ (2)

Accordingly, the non-dimensional system takes the form

$$\frac{d y_{1}}{d t} = y_{1} \left[(1 - y_{1}) - \frac{y_{2}}{w_{1} + y_{1}} - \frac{y_{3}}{w_{2} + y_{1}} \right] = y_{1} F(y_{1}, y_{2}, y_{3})$$

$$\frac{d y_{2}}{d t} = y_{2} \left[w_{3} f_{1}(y_{4}) + {}_{1} y_{3} G_{4} y \right] \Rightarrow {}_{2} {}_{1} {}_{1} {}_{3}$$

$$\frac{d y_{3}}{d t} = y_{3} \left[w_{5} f_{2}(y_{4}) + {}_{2} y_{2} G_{6} y \right] \Rightarrow {}_{3} {}_{2} {}_{1} {}_{2}$$

$$y_{1}(0) = y_{10} \ge 0, \ y_{i}(0) = y_{i0} \ge 0 \ i = 2, 3. f_{i}(y) = \frac{y_{1}}{w_{i} + y_{1}}, \ i = 1, 2$$
(3)

2. Boundedness:

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

Proof: Using usual comparison theorem, we get $\sup y_1 \le 1$ for sufficiently large $t \ge 0$.

Let us assume $\eta_1(t) = y_1 + \frac{1}{w_3} y_2 + y_3 / w_5$; then

$$\frac{d \eta_1(t)}{d t} = \frac{d y_1}{d t} + \frac{1}{w_3} \frac{d y_2}{d t} + \frac{1}{w_5} \frac{d y_3}{d t}.$$

$$\frac{d\eta_1}{dt} + \eta_1 \le \text{maximum}[y_1 \{ (1 - y_1) - \frac{y_2}{w_1 + y_1} - \frac{y_3}{w_2 + y_1} \} + y_2 \{ w_3 f_1(y_1) + \gamma_1 y_3 - w_4 \} + y_3 \{ w_5 f_2(y_1) + \gamma_2 y_2 - w_6 \}]$$

let
$$G(y_1, y_2, y_3) = [y_1 \{ (1 - y_1) - \frac{y_2}{w_1 + y_1} - \frac{y_3}{w_2 + y_1} \} + y_2 \{ w_3 \ f_1(y_1) + \gamma_1 \ y_3 - w_4 \}$$

 $+ y_3 \{ w_5 \ f_2(y_1) + \gamma_2 \ y_2 - w_6 \}]$

then $\frac{d\eta_1}{dt} + \eta_1 \le \text{maximum } G(y_1, y_2, y_3)$

Applying the method of maxima or minima of three variable function we get

$$\frac{d \eta_1}{d t} + \eta_1 \le \text{maximum } G(y_1, y_2, y_3) = 1 + \frac{1}{w_5 \gamma_1 + w_3 \gamma_3} [w_4 + w_6 - w_4 w_6 - 1] = C_1$$

Applying usual comparison theorem to the inequality (8) and (9), we get $\eta_1(t) \le C_1$ for sufficiently large $t \ge 0$.

This shows the bounded ness of $\eta_1(t)$ implying the bounded ness of the system (3) in the cone $R_+^3 = \{(y_1, y_2, y_3): y_1 \ge 0, y_2 \ge 0, y_3 \ge 0\}$.

Since the underlying system (3) is bounded and satisfies the Lipcshitz condition, then the solution exists and is unique.

Using the above inequality and by usual comparison theorem for $t \ge 0$ we get

$$\eta_1(t) \leq \delta - (\delta - \eta_1(0))e^{-t}$$

For given $\varepsilon > 0$ there exists $t \ge T_1 \ge 0$ such that $y_1(t) \le 1 + \frac{\varepsilon}{2}$ and $y_2(t) \le 1 + \frac{\varepsilon}{2}$, we have

$$\eta_1(t) \le \delta - \left(\delta e^{T_1} - \eta_1(T_1)e^{T_1}\right)e^{-t} \Rightarrow \eta_1(t) \le \delta - \left(\delta - \eta_1(T_1)e^{T_1}\right)e^{-t}.$$

and then for all $t \ge T_1$ we have

$$\eta_1(t) \leq \delta + \frac{\varepsilon}{2} - \left(\delta + \frac{\varepsilon}{2} - \eta_1(T_1)e^{T_1}\right)e^{-t}.$$

Consider $T_2 \ge T_1$ such that

$$\left| \left(\delta + \frac{\varepsilon}{2} - \eta_1(T_1) e^{T_1} \right) \right| e^{-t} \leq \frac{\varepsilon}{2} .$$

$$\eta_1(t) \le \delta + \varepsilon$$
 for all $t \ge T_2$.

Or
$$Sup\eta(t) \leq \delta$$
.

Therefore the system is uniformly bounded and hence dissipative in positive region $R_+^3 = \{(y_1, y_2, y_3): y_1 \ge 0, y_2 \ge 0, y_3 \ge 0\}$.

Since the solution is uniformly bounded and dissipative, it is concluded that the solution of the biological system (2) is invariant in the cone $R_+^3 = \{(y_1, y_2, y_3) : y_1 \ge 0, y_2 \ge 0, y_3 \ge 0\}$.

Theorem 2.2: The subsystem of (3) are Kolmogorov systems under the conditions:

$$w_3 > w_4(1+w_1); \quad w_5 > w_6(1+w_2).$$

Proof: 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.

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

It is observed that the two subsystems (4) and (5) are Kolmogorov systems [14] under the constraints:

$$0 < \frac{w_1 w_4}{w_3 - w_4} < 1 \text{ or } w_3 > w_4 (1 + w_1), \text{ and}$$
 (6)

$$0 < \frac{w_2 w_6}{w_5 - w_6} < 1 \text{ or } w_5 > w_6 (1 + w_2).$$
 (7)

3. Stability Analysis:

The existence and linear stability of the equilibriums are analyzed for the system (3). The following conclusions are drawn:

(i). The equilibriums $E_0 = (0,0,0)$ and $E_1 = (1,0,0)$ always exist. However, there are no equilibriums on y_2 or y_3 coordinate axes.

The variational matrices about E_0 and E_1 are obtained as

$$V_0 = \begin{bmatrix} 1, & 0, & 0 \\ 0, & -w_4, & 0 \\ 0, & 0, & -w_6 \end{bmatrix} \text{ and } V_1 = \begin{bmatrix} -1, & -1/(1+w_1), & -1/(1+w_2) \\ 0, & w_3/(1+w_1) - w_4, & 0 \\ 0, & 0, & w_5/(1+w_2) - w_6 \end{bmatrix} \text{ respectively.}$$

Thus, the equilibrium E_0 is a saddle point. Further, near E_0 the prey population grows while both the predators population decline. The equilibrium E_1 is locally asymptotically stable provided the following are satisfied

$$w_3 < w_4(1+w_1)$$
 and $w_5 < w_6(1+w_2)$ (10)

It may be observed that the conditions (10) violate the Kolmogorov conditions (6) and (7) respectively. Therefore, equilibrium E_1 is a saddle point under the Kolmogorov conditions (6) and (7) at which the prey population remains in the neighborhood of 1, while both the predators' populations increase.

(ii). In the absence of second predator, the nonnegative equilibrium point $E_2 = (\overline{y}_1, \overline{y}_2, 0)$ always exists under the condition (6) when the subsystem (4) is Kolmogorov. The expressions for \overline{y}_1 and \overline{y}_2 are given as

$$\overline{y}_1 = w_1 w_4 / (w_3 - w_4)$$
; $\overline{y}_2 = (1 - \overline{y}_1)(w_1 + \overline{y}_1)$

The equilibrium E_2 inside the plane y_1 - y_2 has the same stability behavior as that of the equilibrium $E_{20} = (\overline{y}_1, \overline{y}_2)$ of the subsystem (4). Using the Routh Hurwitz's criterion, the necessary and sufficient condition for linear stability of E_{20} is obtained as

$$\frac{1-w_1}{2} < \overline{y}_1 < 1 \tag{11}$$

The system (3) has a stable limit cycle in the y_1 - y_2 plane when the condition (11) is violated.

The eigenvalues of variational matrix about $\,E_2^{}\,$ are given as

$$\overline{\lambda}_{1} + \overline{\lambda}_{2} = \overline{y}_{1} \left[-1 + \frac{1 - \overline{y}_{1}}{w_{1} + \overline{y}_{1}} \right], \ \overline{\lambda}_{1} \ \overline{\lambda}_{2} = \frac{w_{1} \ w_{3} \ \overline{y}_{1} \left(1 - \overline{y}_{1} \right)}{\left(w_{1} + \overline{y}_{1} \right)^{2}} > 0, \ \overline{\lambda}_{3} = G_{2} \left(\overline{y}_{1}, \overline{y}_{2}, 0 \right) = \frac{w_{5} \ \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{2} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{1} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{1} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{6} = \frac{w_{1} \ w_{1} + \overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \gamma_{2} \ \overline{y}_{2} - w_{1} + \overline{y}_{2} - w_{2} -$$

Thus, the equilibrium E_2 is stable or unstable in the y_3 direction, i.e. orthogonal direction on the y_1 - y_2 plane, depending on whether $\overline{\lambda}_3$ is negative or positive respectively. The system (3) will admit a limit cycle in y_1 - y_3 plane provided

$$\overline{y}_{1} < \frac{1 - w_{1}}{2} < 1$$

$$G_{2}(\overline{y}_{1}, \overline{y}_{2}y0) = \frac{w_{5}\overline{y}_{1}}{w_{2} + \overline{y}_{1}} + \sqrt{2} - \sqrt{2} - \sqrt{6} < (13)$$

The equilibrium $E_2 = (\bar{y}_1, \bar{y}_2, 0)$ will be locally stable if (12) and (13) are satisfied.

(iii). The nonnegative equilibrium $E_3 = (\hat{y}_1, 0, \hat{y}_3)$ also exists under the condition (8) when the subsystem (5), in the absence of first predator, is Kolmogorov. The expressions for \hat{y}_1 and \hat{y}_3 are given as

$$\hat{y}_1 = w_2 w_6 / (w_5 - w_6); \ \hat{y}_3 = (1 - \hat{y}_1)(w_2 + \hat{y}_1)$$
 (14)

It is observed that the equilibrium E_3 has the same local stability behavior in the plane y_1 - y_3 as that of the equilibrium (\hat{y}_1, \hat{y}_3) of the subsystem (5) in the absence of first predator. Thus the system (3) has stable equilibrium point E_3 under the following conditions whenever the perturbations are confined in the y_1 - y_3 plane:

$$\frac{1 - w_2}{2} < \hat{y}_1 < 1 \tag{15}$$

The system will have a stable limit cycle for the perturbations in the y_1 - y_3 plane whenever the above condition (15) is violated.

The eigenvalues of the variational matrix about E_3 are given as follows

$$\hat{\lambda}_{1} + \hat{\lambda}_{3} = \hat{y}_{1} \left[-1 + \frac{1 - \hat{y}_{1}}{w_{2} + \hat{y}_{1}} \right], \hat{\lambda}_{1} \hat{\lambda}_{3} = \frac{w_{2} w_{5} \hat{y}_{1} (1 - \hat{y}_{1})}{(w_{2} + \hat{y}_{1})^{2}} > 0, \quad \hat{\lambda}_{2} = G_{1} (\hat{y}_{1}, 0, \hat{y}_{3}) = \frac{w_{3} \hat{y}_{1}}{w_{1} + \hat{y}_{1}} + \gamma_{1} \hat{y}_{3} - w_{4}$$

The equilibrium E_3 is stable or unstable in the y_2 direction, i.e. orthogonal direction on the y_1 - y_3 plane, depending on whether $\hat{\lambda}_2$ is negative or positive respectively. The system (3) will admit a limit cycle in $y_1 - y_3$ plane provided

$$\hat{\mathbf{y}}_1 < \frac{1 - w_2}{2} < 1 \tag{16}$$

$$\hat{\lambda}_2 = G_1(\hat{y}_1, 0, \hat{y}_3) = \frac{w_3 \hat{y}_1}{w_1 + \hat{y}_1} + \gamma_1 \hat{y}_3 - w_4$$
(17)

The equilibrium $E_2 = (\bar{y}_1, \bar{y}_2, 0)$ will be locally stable if (15) and (17) are satisfied.

(iv). There is no planar equilibria in the y_2 - y_3 plane since the predators cannot survive in the absence of the prey species.

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

$$\frac{w_1 w_4}{\gamma_1} + \frac{w_2 w_6}{\gamma_2} - w_1 w_2 > 0 \tag{19}$$

Proof: The positive equilibrium (y_1^*, y_2^*, y_3^*) can be obtained by solving

$$y_{1} \left[(1 - y_{1}) - \frac{y_{2}}{w_{1} + y_{1}} - \frac{y_{3}}{w_{2} + y_{1}} \right] = 0$$

$$y_{2} \left[w_{3} \ y_{1} \left(y_{1} \right) + {}_{1} \ 0_{3} - {}_{4} \right] =$$

$$y_{3} \left[w_{3} \ f_{2} \left(y_{1} \right) + {}_{2} \ 0_{2} - {}_{6} \right] =$$

$$(20)$$

Solving (21) and (22), we get

$$y_{2}^{*} = \frac{w_{2}w_{6} - y_{1}^{*}(w_{5} - w_{6})}{(w_{2} + y_{1}^{*})\gamma_{2}}; y_{3}^{*} = \frac{w_{1}w_{4} - y_{1}^{*}(w_{3} - w_{4})}{(w_{1} + y_{1}^{*})\gamma_{1}};$$
(23)

These will be positive for the conditions (18). Substituting (23) in (20) gives a cubic equation in y_1^* :

$$f(y_1) = y_1^3 + ay_1^2 - by_1 + c = 0; where a = w_1 + w_2 - 1;$$

$$b = w_1 + w_2 - w_1 w_2 + \frac{(w_3 - w_4)}{\gamma_1} + \frac{(w_5 - w_6)}{\gamma_2}; c = \frac{w_1 w_4}{\gamma_1} + \frac{w_2 w_6}{\gamma_2} - w_1 w_2.$$
(24)

It is observed that f(1) < 0 under the condition (6) and (7). Since f(0) = c, the equation (24) will have at least one positive root y_1^* of y_1 in the interval (0, 1), provided c > 0, which gives condition (19).

For uniqueness, let us first consider the case when a is positive. It can be proved that b cannot be negative in this case. There will be at most two positive roots of $f(y_1)$. The sign change for the function in the interval (0,1) suggests that the other positive root will be bigger than 1, which is not feasible.

Similarly, when a is negative there exists a unique root irrespective of the sign of b.

Hence there exists a unique biologically feasible positive root of the equation in the interval (0,1) under the conditions (18), (19).

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

$$\min \left(\frac{ed_1 + w_3 \frac{1}{y_1^*} (d_1 + d_2 c_2 + d_3 c_1)}{(e + d_1 + \frac{1}{y_1^*} - c_1^2 c_2^2)} \right) < c_1^2 c_2^2 < \max \left(d_1 + d_2 c_2 + d_3 c_1, e \right)$$

$$\text{here } e = \frac{d_2 c_2^2 y_1^*}{a_2 \gamma_2} + \frac{d_3 c_1^2 y_1^*}{a_1 \gamma_1}; \ d_1 = a_1 c_2 + a_2 c_1, d_2 = \frac{w_1 w_3}{\gamma_1}, d_3 = \frac{w_2 w_5}{\gamma_2},$$

$$c_1 = w_1 + y_1^*, c_2 = w_2 + y_1^*,$$

$$a_2 = \frac{1}{\gamma_1} \left(w_1 w_4 - y_1^* (w_3 - w_4) \right) > 0, a_1 = \frac{1}{\gamma_2} \left(w_2 w_6 - y_1^* (w_5 - w_6) \right) > 0$$

Proof. Assume $y_1 = y_1^* + u$, $y_2 = y_2^* + v$, $y_3 = y_3^* + w$ where u, v, w are small perturbations. The variational matrix about (y_1^*, y_2^*, y_3^*) is given by

$$\begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} = \begin{bmatrix} -y_1^* (1 - \frac{y_2^*}{(w_1 + y_1^*)^2} - \frac{y_3^*}{(w_2 + y_1^*)^2}) & -\frac{y_1^*}{(w_1 + y_1^*)} & -\frac{y_1^*}{(w_1 + y_1^*)} \\ \frac{w_1 w_3 y_2^*}{(w_1 + y_1^*)^2} & 0 & \gamma_1 y_2^* \\ \frac{w_2 w_5 y_3^*}{(w_2 + y_1^*)^2} & \gamma_2 y_3^* & 0 \end{bmatrix}$$
(26)

The characteristic polynomial of the variational matrix (26) is given by

$$\Delta(\lambda) = \lambda^3 + a_0 \lambda^2 + a_1 \lambda + a_2, \text{ where } a_0 = -a_{11},$$

$$a_1 = -(a_{12}a_{21} + a_{32}a_{23} + a_{13}a_{31}), a_2 = (a_{11}a_{23}a_{32} - a_{12}a_{23}a_{31} - a_{13}a_{21}a_{32})$$
(27)

According to Routh's criterion for stability, the equilibrium is locally stable if all roots of (27) have negative real parts. The equilibrium is locally stable under the following set of conditions:

$$a_{0} = y_{1}^{*} \left(1 - \frac{y_{2}^{*}}{(w_{1} + y_{1}^{*})^{2}} - \frac{y_{3}^{*}}{(w_{2} + y_{1}^{*})^{2}} \right) > 0 \Rightarrow$$

$$y_{2}^{*} (w_{2} + y_{1}^{*})^{2} + y_{3}^{*} (w_{1} + y_{1}^{*})^{2} < (w_{1} + y_{1}^{*})^{2} (w_{2} + y_{1}^{*})^{2}$$

$$a_{1} = -a_{12}a_{21} - a_{31}a_{13} - a_{23}a_{32} > 0 \Rightarrow$$

$$(w_{1} + y_{1}^{*})^{2} (w_{2} + y_{1}^{*})^{2} < \frac{w_{1}w_{3}y_{1}^{*}(w_{2} + y_{1}^{*})^{2}}{m_{2}\gamma_{2}} + \frac{w_{2}w_{5}y_{1}^{*}(w_{1} + y_{1}^{*})^{2}}{m_{1}\gamma_{1}}$$

$$where \ m_{1} = w_{2}w_{6} - y_{1}^{*}(w_{5} - w_{6}); \qquad m_{2} = w_{1}w_{4} - y_{1}^{*}(w_{3} - w_{4}).$$

Combining 30 (i) and 30 (ii) gives (25).

$$a_{2} = -a_{12}a_{23}a_{31} - a_{32}a_{13}a_{21} + a_{11}a_{23}a_{32} > 0 \Rightarrow$$

$$(\mathbf{w}_{1} + \mathbf{y}_{1}^{*})^{2}(\mathbf{w}_{2} + \mathbf{y}_{1}^{*})^{2}$$

$$< \frac{w_{1}w_{3}(\mathbf{w}_{2} + \mathbf{y}_{1}^{*})}{\gamma_{1}} + \frac{w_{2}w_{5}(\mathbf{w}_{1} + \mathbf{y}_{1}^{*})}{\gamma_{2}} + y_{2}^{*}(\mathbf{w}_{2} + \mathbf{y}_{1}^{*})^{2} + y_{3}^{*}(\mathbf{w}_{1} + \mathbf{y}_{1}^{*})^{2}$$

$$28(iii)$$

$$a_{0}a_{1} - a_{2} = a_{21}a_{11}a_{12} + a_{21}a_{13}a_{32} + a_{31}a_{11}a_{13} + a_{31}a_{12}a_{23} > 0 \Longrightarrow$$

$$\left(1 - \frac{y_{2}^{*}}{(w_{1} + y_{1}^{*})^{2}} - \frac{y_{3}^{*}}{(w_{2} + y_{1}^{*})^{2}}\right)y_{1}^{*}\left(w_{1}w_{3}y_{2}^{*}(w_{2} + y_{1}^{*})^{3} + w_{2}w_{5}y_{3}^{*}(w_{1} + y_{1}^{*})^{3}\right)$$

$$> y_{2}^{*}y_{3}^{*}(w_{1} + y_{1}^{*})(w_{2} + y_{1}^{*})\left(w_{1}w_{3}\gamma_{2}(w_{2} + y_{1}^{*}) + w_{2}w_{5}\gamma_{1}(w_{1} + y_{1}^{*})\right)$$

$$28(iv)$$

Using the new notation and 28(i-iv), we get (25)

here
$$e = \frac{d_2 c_2^2 y_1^*}{a_2 \gamma_2} + \frac{d_3 c_1^2 y_1^*}{a_1 \gamma_1}$$
; $d_1 = a_1 c_2 + a_2 c_1$, $d_2 = \frac{w_1 w_3}{\gamma_1}$, $d_3 = \frac{w_2 w_5}{\gamma_2}$, $c_1 = w_1 + y_1^*$, $c_2 = w_2 + y_1^*$, $a_2 = \frac{1}{\gamma_1} \left(w_1 w_4 - y_1^* (w_3 - w_4) \right) > 0$, $a_1 = \frac{1}{\gamma_2} \left(w_2 w_6 - y_1^* (w_5 - w_6) \right) > 0$

$$\min \left(\frac{ed_1 + w_3 \frac{1}{y_1^*} (d_1 + d_2 c_2 + d_3 c_1)}{(e + d_1 + \frac{1}{y_1^*} - c_1^2 c_2^2)} \right) < c_1^2 c_2^2 < \max \left(d_1 + d_2 c_2 + d_3 c_1, e \right)$$
(29)

Thus the nonzero positive equilibrium is locally stable under the conditions (25).

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:

$$y_{1} < \operatorname{Min}\left\{\frac{M - c^{2}}{2(1 - y_{1}^{*})}, \frac{\alpha y_{1}^{*} - \beta}{\alpha}\right\} \text{ and M is the bound of the system.}$$

$$\text{Where } \alpha = \frac{A_{3}l_{2}^{*}\gamma_{1}}{l_{1}^{*}A_{2}} + \gamma_{2}, \ \beta = \frac{A_{3}l_{2}^{*}\gamma_{1}}{A_{2}} + l_{2}^{*}\gamma_{2}, c^{2} = (1 - y_{1}^{*})\left[(w_{1} + w_{2}) + y_{1}^{*}\right]$$
(30)

Proof. Consider the small perturbations u, v, w about the positive unique equilibrium point (y_1^*, y_2^*, y_3^*) such that $y_1 = y_1^* + u$, $y_2 = y_2^* + v$, $y_3 = y_3^* + w$. Consider positive definite function for arbitrarily chosen nonzero positive constants D_1, D_2 and D_3 :

$$V(t) = D_1(u - y_1^* \log(1 + \frac{u}{y_1^*})) + D_2(v - y_2^* \log(1 + \frac{v}{y_2^*})) + D_3(w - y_3^* \log(1 + \frac{w}{y_3^*}))$$

We have,

$$\frac{dV}{d} = D_{1}u\left[\left(1 - y_{1}^{*} y_{1}\right) w \frac{y_{2}^{*} + v}{w_{1} + y_{1}^{*} + u} - \frac{y_{3}^{*} + w}{w_{2} + y_{1}^{*} + u}\right] + D_{2}v\left[\frac{w_{3}(y_{1}^{*} + u)}{w_{1} + y_{1}^{*} + u} + {}_{1}({}_{3}^{*} +) - {}_{4}\right] + D_{3}w\left[\frac{w_{5}(y_{1}^{*} + u)}{y_{2}^{*} + y_{1}^{*} + u} + {}_{2}({}_{2}^{*} +) - {}_{6}\right].$$

Putting

$$\begin{split} &A_2D_2l_2=l_2^*D_1 \ \ and \quad A_3D_3l_1 \Rightarrow d_1^*D_1^*; \ \text{where} \ \gamma Ay=wy+ \ _2 \ _2^*- \ _6, \ _3= \ _3+ \ _1 \ _3^*- \ _4, \\ &l_1=w_1+y_1, l_2=w_2+y_1, l_1^*=w_1+y_1^*, l_2^*=w_2+y_1^*, \alpha=\frac{A_3l_2^*\gamma_1}{l_1^*A_2}+\gamma_2, \ \beta=\frac{A_3l_2^*\gamma_1}{A_2}+l_2^*\gamma_2, \\ &c^*=(1-y_1^*)\Big[(w_1+w_2)+y_1^*\Big]. \end{split}$$

$$\frac{dV}{dt} = \frac{u^2 D_1}{l_1 l_2} [c' + (1 - y_1^*) y_1 - y_2 - y_3] + \frac{vw D_3}{l_2} [\alpha y_1 - \alpha y_1^* + \beta]$$

Putting

$$\alpha y_1 - \alpha y_1^* + \beta = 0$$
 and $(c' + (1 - y_1^*)y_1 - y_2 - y_3) < 0$.

$$\frac{dV}{dt} < 0$$
. When $y_1 < \min\left\{\frac{M - c}{2(1 - y_1^*)}, \frac{\alpha y_1^* - \beta}{\alpha}\right\}$ and M is the bound of the system.

Therefore, the function V is a Liapunov function

Thus, the positive nonzero equilibrium point (y_1^*, y_2^*, y_3^*) is globally asymptotically stable under the conditions (30).

4. Numerical Simulations:

Apart from the mathematical analysis for the existence of equilibria, the local and global stability are investigated, our objective is to study the dynamical behavior in the food web consisting of two mutualist predators sharing a single prey. The analysis establishes the conditions for local stability of equilibrium points and coexistence of species. The extensive

numerical simulations are carried out for various values of parameters (biologically feasible) and for different sets of initial conditions to see the global stability of the nonzero positive equilibrium point of the system (3).

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.

We fixed the biological feasible set of parameters:

$$w_1 = 2.1, w_2 = 2.12, w_3 = 1.8, w_4 = 0.11, w_5 = 1.9, w_6 = 0.12, \gamma_2 = 0.05$$
 (31)

The sign change from positive to negative for the expression a_0a_1 - a_2 is observed as the values of parameter γ_1 of cooperation are varied. The existence of Hopf bifurcation is observed in the neighborhood of $\gamma_1=0.04$. This is evident from the eigenvalues and their corresponding eigenvectors obtained at $\gamma_1^*=0.04$ as

Although, the local stability conditions for the non trivial equilibrium point are established in theorem 3.3, nothing is guaranteed for global behavior. The local stability of equilibrium point (0.10195, 0.6564, 1.3330) is predicted as the stability conditions (27) to (29) are true for data set (31) together with $\gamma_1 = 0.02$. Fig. 1(a) shows the phase space trajectories converging to the point (0.10195, 0.6564, 1.3330) for the data set (31) at $\gamma_1 = 0.02$, starting with two different initial conditions (0.20199, 0.30033, 0.40048) and (0.20095, 0.60073, 0.70184). Same result is obtained for other initial conditions also. In other words, the nontrivial equilibrium point (0.10195, 0.6564, 1.3330) is stable giving the persistence of the system for the given set of parameters. Fig 1(b) shows the time series for the initial conditions (0.20095, 0.60073, 0.60073, 0.70184).

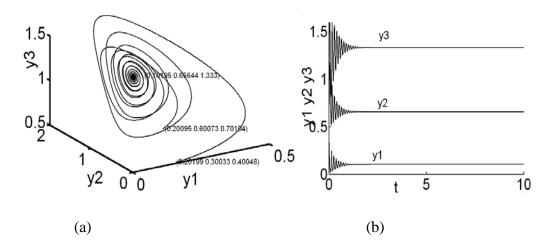


Fig 1: For the data set (31); $\gamma_1 = 0.02$ (a) 3D behavior (b) time series

Fig. 2 shows the phase space trajectories and their time series for the data set (31) at $\gamma_1 = 0.04$. The solution is quasi periodic.

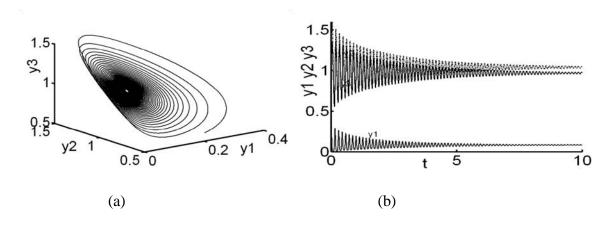
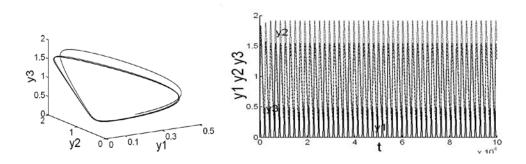


Fig. 2: For the data set (39); $\gamma_1 = 0.04$ (a) 3D behavior (b) time series

However for $\gamma_1=0.055$, there exists a limit cycle for the same set of data, as is evident from the figure:



(a) (b)

Fig 3: For the data set (39); $\gamma_1 = 0.055$ (a) 3D behavior (b) time series

5. Conclusions:

A food web model consisting of two predators sharing a common prey is analyzed. The two predators are assumed to have mutual cooperation among them. The strong coexistence (local and global stability) and limit cycle of the system is established numerically as well as analytically.

6. References:

- [1] A. Hastings, and T. Powell, Chaos in three species food chain, Ecology, 72 (1991) 896 903.
- [2] B.W. Kooi · L.D.J. Kuijper · S.A.L.M. Kooijman; Consequences of symbiosis for food web dynamics; J. Math. Biol. 49, 227–271 (2004).
- [3] K, Yodzis McCann Biological conditions for chaos in three species food chain. Ecology 75 (1994) 561-564.
- [4] S. Gakkhar, R. K. Naji, On a food web consisting of a specialist and generalist predator. Journal of biological systems Vol.11,N0.4 (2003) 365-376.
- [5] M.A Aziz-Alaoui, Study Of A Leslie Gower Type Tri-trophic Population Model., Chaos, Solitons and Fractals, 14 (2002) 1275-1293.
- [6] A. Klebanoff, and A. Hastings, Chaos in one predator two prey model: general results from bifurcation theory, Math. Biosciences 122 (1994) 221 223.
- [7] S. Gakkhar, B.Singh, Raid Kamel Naji, Dynamical behavior of two predators competing over a single prey, BioSystem, vol.90/3, page 808-817, 2007. ISSN: 0303-2647
- [8] S. Gakkhar, R. K. Naji, Existence of chaos in two-prey, one-predator system. Chaos, Solitons & fractals 17 (2003) 639-649.

- [9] S. Gakkhar, R. K. Naji, Order and chaos in a food web consisting of a predator and two independent preys. Communications Nonlinear Science And Numerical Simulations 10 (2005) 105-120.
- [10] S. Gakkhar, B.Singh, Complex dynamic behavior in a food web consisting of two preys and a predator Chaos, Solitons & fractals. 24 (2005) 789-801
- [11] Sunita Gakkhar, Brahampal Singh, Raid Kamel Naji, Dynamical behavior of two predators competing over a single prey, BioSystem, vol.90/3 (2007), 808-817.
- [13] H.I Freedman, and J.W.H So, Global stability and Persistence of simple food chain, Mathematical Bioscience, 76 (1985) 69-86.
- [14] H.I Freedman. and P. Waltman, Persistence In Models Of Three Interacting Predator-Prey Populations, Mathematical Bioscience, 68 (1984) 213-231.
- [15] Y.Takeuchi, Global dynamics properties of Lotka-Volterra systems, World Scientific (1996).
- [16] H.I.Freedman, R.Kumar, A.K.Easton and M.Singh, Mathematical models of predator mutualists Canadian Applied Mathematics Quarterly: 9(2) summer 2001
- [17] Order and Chaos of multi-species ecological systems. Ph.D. Thesis of RK Naji (2003), I I T Roorkee, (India).
- [18] H.I Freedman, Deterministic Mathematical Models in Population Ecology, Marcel Dekker, Inc, New York, USA (198).
- [19] J.D Murray, Lectures on Nonlinear-Differential-Equation Models in Biology, Clarendon Press, Walton Street, Oxford (1977).