

The Dynamics of Food Web Model with Defensive Switching Property

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Abstract. In this paper, a food web model consisting of two-predator one-prey with the defensive switching of predation avoidance is proposed and analyzed. It is assumed that the prey growth logistically in the absence of predators and defends itself from relatively abundant predator species by switching to another habitat with relatively rare predator species. Sufficient conditions for the stability of the non-trivial equilibrium point are obtained. The Lyapunov function is constructed to establish the global asymptotic stability of the non-trivial equilibrium point when the intensity of defensive switching equal one. Numerical simulations for different sets of parameter values and for different sets of initial conditions are carried out. It has been shown that the system has a globally asymptotically stable non-trivial point when the two predators have the same mortality rates.

Keywords: food web, prey-predator, defensive switching property, stability, Lyapunov function.

1 Introduction

In predator-prey environment, there is variety of ways in which potential prey attempts to avoid predators; these anti-predator behaviors include habitat selection, vigilance and other types of behaviors [1–4]. The anti-predator behavior, when a prey is shared by two or more predator species, may be classified as specific or non-specific. It is known as predator-specific defense when the prey defense is effective against only one predator species. However, if each of the different behaviors is equally effective against all predator species then it is perfectly non-specific defense [5].

Although many of the studies in literature have been focused on the observed patterns in anti-predator behavior in terms of costs and benefits of different levels of prey investment, little attention had been given to the influence of these anti-predator behaviors on the population dynamics of predator prey system [6–10]. The effects of adaptive switching on the Lotka-Volterra population dynamics have been studied later on by Krivan [11–13], Krivan and Sikder [14] and Krivan and Eisner [15]. It has been observed that the

optimal behavior of animals leads to persistence of predator-prey systems and reduction of oscillations in population densities. The effect of invading species in food chains has been discussed in Kooi et al. [16] and Kooi and Kooijman [17]. Recently, Aggelis et al. [18] studied the effect of the facultative predation strategy on one-prey one-facultative predator dynamic model. It is assumed that both prey and predator populations grow together in a chemostat that fed with medium containing the necessary nutrients for saprophytic growth of both populations. However, Vayenas et al. [19] was introduced and studied a novel regulatory mechanism, called catabolic repression control-like mode (CRCL), in the classical one-predator-two-prey dynamic model. The two prey populations (desirable and alternative) grow in the same chemostat together with their predator, while the desirable prey population represses the attack of the predator on the alternative prey through CRCL. Bifurcation analysis was used to study the effect of switching, as regulated by CRCL, on the dynamics and survival of both prey and predator populations.

The phenomena of change of habitats from one to other due to prey guards itself against the abundant predator, is called defensive switching. Later on, Saleem et al. [5] analyzed a mathematical model consisting of two-predator feeding on a single prey has defensive switching property for predation avoidance. They assumed that the prey is growing exponentially in the absence of predators. It is observed that, the system is asymptotically settles to a Volterra's oscillation in the three dimensional space when the intensity of defensive switching equals one and the two predators have the same mortality rates. In this paper the food web model given by Saleem et al. [5] is modified to be more realistic so that the prey is growing logistically in the absence of predators. The effect of prey's defensive switching on the dynamical behavior of the food web model is investigated theoretically as well as numerically.

2 The mathematical model

Consider the food web model consisting of two-predator one-prey in which the prey species growth logistically in the absence of predators, while the predators decay exponentially in the absence of prey species. The simplest set of differential equations, which describes the dynamics of such food web, can be written in the Volterra framework as follows:

$$\begin{aligned}\frac{dX}{dT} &= -\alpha_1 X + A_1 X Z, & X(0) &\geq 0, \\ \frac{dY}{dT} &= -\alpha_2 Y + A_2 Y Z, & Y(0) &\geq 0, \\ \frac{dZ}{dT} &= \alpha_3 Z \left(1 - \frac{Z}{K}\right) - A_1 X Z - A_2 Y Z, & Z(0) &\geq 0,\end{aligned}\tag{1}$$

where $X(T)$, $Y(T)$ and $Z(T)$ denote, respectively, the population densities of two kinds of predator's species and a prey species at time T respectively. $\alpha_1, \alpha_2, \alpha_3, K, A_1, A_2$ are positive constants and they standing for mortality rates of first and Second predator respectively; the intrinsic growth rate of the prey species; the carrying capacity; and the

respective predation rates of the first and second predator respectively. Obviously, in system (1) the predator species, which has greater value of, α_i/A_i , $i = 1, 2$ will face extinction, and hence system (1); reduce to a simple predator-prey Volterra's system.

The effect of prey defensive switching on the dynamical behavior of system (1) can be considered through replacing the constant predatory rates A_1 and A_2 by the following nonlinear functions of X and Y respectively [20].

$$A_1 = \frac{aY^n}{X^n + Y^n} = \frac{a}{(X/Y)^n + 1}, \quad A_2 = \frac{bX^n}{X^n + Y^n} = \frac{b}{1 + (Y/X)^n}, \quad (2)$$

where a and b are positive constants that stand for the predation coefficients of the first and second predator respectively, $n \geq 0$ is the intensity of prey defensive switching. Clearly, equation (2) has a characteristic property of a prey defensive switching mechanism. Indeed, the predatory rate decreases when the population of that species becomes large compared with the population of another predator species. Obviously this property is much amplified for large value of n , see Fig 1. Clearly when the population of predator becomes large the prey defends itself against it and switches to another predator species habitat with a relatively smaller population in order to avoid too much predation of individuals.

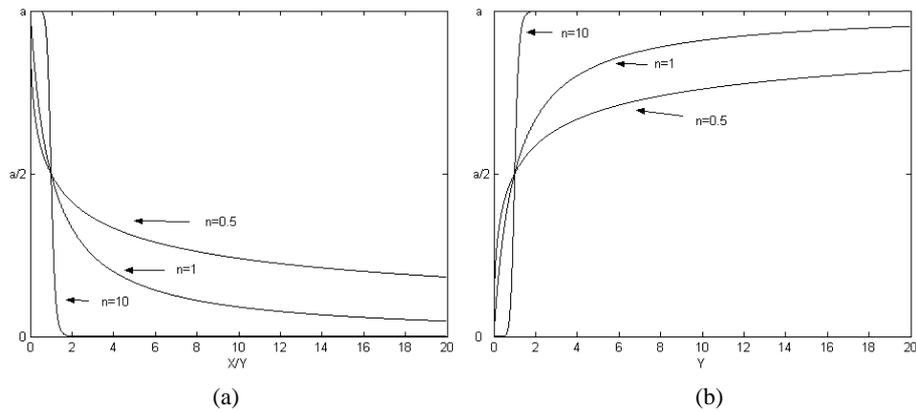


Fig. 1. The predator rate function $A_1(X, Y)$ (a) A_1 as a function of X/Y ; (b) A_1 as a function of Y with fixed value of $X = 1.0$.

Consequently, the two-predators, one-prey system, in which the prey species exhibits defensive switching, can be written in the form:

$$\begin{aligned} \frac{dX}{dT} &= X \left[-\alpha_1 + c_1 a \frac{ZY^n}{X^n + Y^n} \right], \quad X(0) > 0, \\ \frac{dY}{dT} &= Y \left[-\alpha_2 + c_2 b \frac{ZX^n}{X^n + Y^n} \right], \quad Y(0) > 0, \\ \frac{dZ}{dT} &= Z \left[\alpha_3 \left(1 - \frac{Z}{K} \right) + \frac{aXY^n + bYX^n}{X^n + Y^n} \right], \quad Z(0) > 0, \end{aligned} \quad (3)$$

where α_i ($i = 1, 2, 3$), K , c_j ($j = 1, 2$), a and b are positive constants, in which the parameters c_1, c_2 are the conversion rates of a prey Z to predators X and Y respectively.

Now in order to avoid the analysis difficulty of system (3) due to the existence of the non-linear terms given in (2) and the eight control parameters, the following dimensionless variables and parameters are used.

$$\begin{aligned} x &= \frac{c_1 a}{\alpha_1} X, & y &= \frac{c_1 a}{\alpha_1} Y, & z &= \frac{c_1 a}{\alpha_1} Z, & t &= \alpha_1 T, \\ w_1 &= \frac{c_2 b}{c_1 a}, & w_2 &= \frac{\alpha_2}{\alpha_1}, & w_3 &= \frac{\alpha_1}{c_1 a K}, & w_4 &= \frac{b}{a}, & w_5 &= \frac{\alpha_3}{\alpha_1}. \end{aligned}$$

Accordingly, the dimensionless system is

$$\begin{aligned} \frac{dx}{dt} &= x \left[-1 + \frac{zy^n}{x^n + y^n} \right] = x f_1(x, y, z) = F_1(x, y, z), \\ \frac{dy}{dt} &= y \left[-w_2 + \frac{w_1 z x^n}{x^n + y^n} \right] = y f_2(x, y, z) = F_2(x, y, z), \\ \frac{dz}{dt} &= z \left[w_5(1 - w_3 z) - \frac{xy^n + w_4 y x^n}{c_1(x^n + y^n)} \right] = z f_3(x, y, z) = F_3(x, y, z). \end{aligned} \tag{4}$$

Note that, the interaction functions F_i , $i = 1, 2, 3$ of system (4) are C^2 on the domain $Int.R_+^3 = \{(x, y, z) : x > 0, y > 0, z > 0\}$. Thus, the solution to the initial value problem under consideration exists uniquely at least for some positive time. Further, the interaction functions F_i , $i = 1, 2, 3$ of system (4), are assumed to have a finite values at the point $(0, 0, 0)$ that is:

$$\lim_{(x,y,z) \rightarrow (0,0,0)} F_i(x, y, z) = F_i(0, 0, 0) = 0, \quad i = 1, 2, 3.$$

Hence, these functions are continuous on the extended domain

$$R_+^3 = \{(x, y, z) : x \geq 0, y \geq 0, z \geq 0\}.$$

In fact, they are Lipschitz on R_+^3 . Accordingly the solution of the system (4) with non-negative initial condition exists and is unique. Therefore, the interior of R_+^3 is invariant for model (4). Further, the boundedness of the solution of system (4) is given in the following theorem.

Theorem 1. *All the solutions of system (4), which initiate in R_+^3 , are uniformly bounded.*

Proof. From the third equation of system (4), we observe that

$$\frac{dz}{dt} = w_5 z(1 - w_3 z) - \frac{xy^n z + w_4 y x^n z}{c_1(x^n + y^n)} \leq w_5 z - w_3 w_5 z^2.$$

Thus by using the theory of differential inequality (see Hall [21]), we get

$$z(t) \leq \frac{w_5}{w_3 w_5 - k e^{-w_5 t}},$$

where k is the constant of integration. Letting $t \rightarrow \infty$, we get

$$z(t) \leq \frac{1}{w_3}. \tag{5}$$

Consider $\omega = \frac{x}{c_1} + \frac{w_4 y}{c_1 w_1} + z$, then from system (4) we get

$$\begin{aligned} \frac{d\omega}{dt} &= w_5(1 - w_3 z)z - \frac{w_2 w_4}{c_1 w_1} y - \frac{x}{c_1} \\ &\leq w_5 z - \frac{w_2 w_4}{c_1 w_1} y - \frac{x}{c_1} \leq w_5 z - N \left[\frac{w_4 y}{c_1 w_1} + \frac{x}{c_1} \right], \\ &= (w_5 + N)z - N \left[z + \frac{w_4 y}{c_1 w_1} + \frac{x}{c_1} \right] = (w_5 + N)z - N\omega, \end{aligned}$$

where $N = \min(1, w_2)$.

Thus by using equation (5), we obtain

$$\frac{d\omega}{dt} + N\omega \leq \frac{w_5 + N}{w_3}.$$

Again, by applying the theory of differential inequality, we obtain

$$\omega(t) = \frac{1}{c_1} x(t) + \frac{w_4}{c_1 w_1} y(t) + z(t) \leq \frac{w_5 + N}{N w_3} (1 - e^{-Nt}).$$

Therefore, for all t sufficiently large, we obtain

$$\omega(t) \leq \frac{w_5 + N}{N w_3}.$$

Hence the proof of theorem is complete. □

Note that, the ecological system is said to be dissipative if the solution of system, which initiate in R_+^3 , are uniformly bounded as $t \rightarrow \infty$. Thus system (4) is dissipative.

3 The stability analysis

The food web system (4) has at most three nonnegative equilibrium points, namely $E_0 = (0, 0, 0)$, $E_1 = (0, 0, 1/w_3)$, $E_2 = (x^*, y^*, z^*)$ with $x^* > 0$, $y^* > 0$ and $z^* > 0$. The boundary points E_0 and E_1 are always exist, however the positive equilibrium points E_2 exists if and only if there is a positive solution to the following set of algebraic equations.

$$x^n + y^n = z y^n, \tag{6a}$$

$$w_2(x^n + y^n) = w_1 z x^n, \tag{6b}$$

$$c_1 w_5(1 - w_3 z)(x^n + y^n) = x y^n + w_4 y x^n. \tag{6c}$$

Clearly, equation (6a) and equation (6b) gives

$$y^* = \left(\frac{w_1}{w_2}\right)^{1/n} x^*. \quad (6d)$$

Substituting equation (6d) in (6a) yields

$$z^* = 1 + \frac{w_2}{w_1}. \quad (6e)$$

Using equation (6d) and (6e) in equation (6c) we get

$$x^* = c_1 w_5 \left(1 - w_3 - \frac{w_2 w_3}{w_1}\right) \left(1 + \frac{w_1}{w_2}\right) / \left(\frac{w_1}{w_2} + w_4 \left(\frac{w_1}{w_2}\right)^{1/n}\right). \quad (6f)$$

Obviously, the point E_2 is positive if and only if the following condition holds

$$w_3 < \frac{w_1}{w_1 + w_2} \quad (7)$$

Now, in order to study the stability at the above equilibrium points, the Variation matrix G of system (4) at point (x, y, z) is computed.

$$G(x, y, z) = \begin{bmatrix} b_{11} & b_{12} & b_{13} \\ b_{21} & b_{22} & b_{23} \\ b_{31} & b_{32} & b_{33} \end{bmatrix},$$

where

$$\begin{aligned} b_{11} &= f_1 - \frac{nx^n y^n z}{A^2}, & b_{12} &= \frac{nx^{n+1} y^{n-1} z}{A^2}, & b_{13} &= \frac{xy^n}{A}, \\ b_{21} &= \frac{nw_1 x^{n-1} y^{n+1} z}{A^2}, & b_{22} &= f_2 - \frac{nw_1 x^n y^n z}{A^2}, & b_{23} &= \frac{w_1 x^n y}{A}, \\ b_{31} &= \frac{nx^n y^n z}{c_1 A^2} - \frac{nw_4 x^{n-1} y^{n+1} z}{c_1 A^2} - \frac{y^n z}{c_1 A}, \\ b_{32} &= \frac{-nx^{n+1} y^{n-1} z}{c_1 A^2} + \frac{nw_4 x^n y^n z}{c_1 A^2} - \frac{w_4 x^n z}{c_1 A}, \\ b_{33} &= f_3 - w_3 w_5 z, \end{aligned}$$

where f_i ($i = 1, 2, 3$) is given by equation (4).

Let G_i , ($i = 0, 1, 2$) denotes the variational matrix G at the points E_0, E_1 and E_2 respectively. Then

$$G_0 = \begin{bmatrix} -1 & 0 & 0 \\ 0 & -w_2 & 0 \\ 0 & 0 & w_5 \end{bmatrix}, \quad G_1 = \begin{bmatrix} -1 & 0 & 0 \\ 0 & -w_2 & 0 \\ 0 & 0 & -w_5 \end{bmatrix}, \quad G_2 = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix},$$

where

$$\begin{aligned}
 a_{11} &= \frac{-nw_2}{w_1 + w_2}, & a_{12} &= \frac{n}{(w_1/w_2)^{1/n}(1 + (w_1/w_2))}, & a_{13} &= \frac{w_1 x^*}{w_1 + w_2}, \\
 a_{21} &= \frac{nw_1(w_1/w_2)^{1/n}}{1 + (w_1/w_2)}, & a_{22} &= \frac{-nw_1}{1 + (w_1/w_2)}, & a_{23} &= \frac{w_1(w_1/w_2)^{1/n} x^*}{1 + (w_1/w_2)}, \\
 a_{31} &= \frac{-1}{c_1(w_1 + w_2)} [w_2(1 - n) + w_1 + nw_2 w_4 (w_1/w_2)^{1/n}], \\
 a_{32} &= \frac{-w_2}{c_1 w_1 (w_1 + w_2)} [w_1 w_4 (1 - n) + w_2 w_4 + n w_1 (w_1/w_2)^{-1/n}], \\
 a_{33} &= -w_3 w_5 \left(1 + \frac{w_2}{w_1}\right).
 \end{aligned}$$

Accordingly, the following observations are made:

- The eigenvalues of G_0 are $\mu_{01} = -1 < 0$, $\mu_{02} = -w_2 < 0$ and $\mu_{03} = w_5 > 0$. Thus the point E_0 is unstable saddle point with locally stable manifold in the $x - y$ plane and with locally unstable manifold in the z direction.
- The eigenvalues of G_1 are $\mu_{11} = -1 < 0$, $\mu_{12} = -w_2 < 0$ and $\mu_{13} = -w_5 < 0$. Therefore E_1 is locally asymptotically stable point.
- However, the local stability analysis of the positive equilibrium point E_2 is investigated in the following theorem.

Theorem 2. *Suppose that the positive equilibrium E_2 of system (4) exists. Then it is locally asymptotically stable if the following set of sufficient conditions holds:*

$$0 < n < \frac{w_1 + w_2}{w_2(1 - w_4(w_1/w_2)^{1/n})} \quad \text{or} \quad 0 < n < \frac{(w_1 + w_2)w_4(w_1/w_2)^{1/n}}{w_2(w_4(w_1/w_2)^{1/n} - 1)}, \quad (8)$$

$$w_2 = 1 \quad \text{or} \quad 0 < n < \frac{w_3 w_5 (w_1 + w_2)^2}{w_1^2 (1 - w_2)} \quad \text{or} \quad 0 < n < \frac{w_3 w_5 (w_1 + w_2)^2}{w_1 w_2 (w_2 - 1)}. \quad (9)$$

Proof. It is easy to verify that, the characteristic equation of the variational matrix G_2 of E_2 is:

$$\mu^3 + b_1 \mu^2 + b_2 \mu + b_3 = 0, \quad (10)$$

where

$$\begin{aligned}
 b_1 &= -(a_{11} + a_{22} + a_{33}), \\
 b_2 &= a_{11} a_{33} + a_{22} a_{33} - a_{13} a_{31} - a_{23} a_{32}, \\
 b_3 &= a_{13} a_{31} a_{22} + a_{23} a_{32} a_{11} - a_{12} a_{23} a_{31} - a_{13} a_{21} a_{32}.
 \end{aligned}$$

Therefore, according to Routh-Hurwitz criteria all the roots of equation (10) have negative real parts and that E_2 is local asymptotically stable if and only if $b_1 > 0$, $b_3 > 0$ and $b_1 b_2 - b_3 > 0$. Now, straightforward computation shows that:

$$b_1 = \frac{nw_1 w_2 + nw_1^2 w_2 + w_3 w_5 (w_1 + w_2)^2}{w_1 (w_1 + w_2)} > 0,$$

$$b_3 = -\frac{nw_1 w_2 x^*}{w_1 + w_2} a_{31} - \frac{nw_1 w_2 (w_1/w_2)^{1/n} x^*}{w_1 + w_2} a_{32}.$$

Clearly, the sign of b_3 is completely depends on the sign of a_{31} and a_{32} . Thus, substituting the values of a_{31} and a_{32} in b_3 and then rearranging the resulting terms yield:

$$b_3 = \frac{nw_1 w_2 x^*}{c_1 (w_1 + w_2)^2} \left[(w_1 + w_2) + nw_2 \left(w_4 \left(\frac{w_1}{w_2} \right)^{1/n} - 1 \right) \right]$$

$$+ \frac{nw_1 w_2^2 (w_1/w_2)^{1/n} x^*}{c_1 w_1 (w_1 + w_2)^2} \left[(w_1 + w_2) w_4 + nw_1 \left(\frac{w_1}{w_2} \right)^{1/n} \left(1 - w_4 \left(\frac{w_1}{w_2} \right)^{1/n} \right) \right].$$

Thus, condition (8) represents the sufficient condition for $b_3 > 0$.

Now, expand $b_1 b_2$ and calculate $b_1 b_2 - b_3$, we get

$$b_1 b_2 - b_3 = -a_{33} (a_{11} + a_{22}) [a_{11} + a_{22} + a_{33}]$$

$$+ [(a_{11} + a_{33}) a_{13} + a_{12} a_{23}] a_{31} + [(a_{22} + a_{33}) a_{23} + a_{13} a_{21}] a_{32}.$$

According to the values of the coefficients a_{ij} , ($i, j = 1, 2, 3$) we obtain

$$b_1 b_2 - b_3 = B_1 + B_2 + B_3,$$

where

$$B_1 = \frac{nw_2 w_3 w_5 (1 + w_1)}{w_1^2 (w_1 + w_2)} [nw_1 w_2 (1 + w_1) + w_3 w_5 (w_1 + w_2)^2] > 0,$$

$$B_2 = -\frac{a_{31} x^*}{(w_1 + w_2)^2} [nw_1 w_2 (1 - w_2) + w_3 w_5 (w_1 + w_2)^2],$$

$$B_3 = -\frac{a_{32} w_2 (w_1/w_2)^{1/n} x^*}{(w_1 + w_2)^2} [nw_1^2 (w_2 - 1) + w_3 w_5 (w_1 + w_2)^2].$$

Note that, since (8) represents the sufficient condition for $a_{31} < 0$ and $a_{32} < 0$ also. Thus, condition (9) is the sufficient condition for $b_1 b_2 - b_3 > 0$. Hence, according to Routh-Hurwitz criteria, the above set of conditions represents the sufficient conditions for the local stability of E_2 and then the proof is complete. \square

Clearly, the local stability conditions given by Theorem 2 do not seem to be simple for general values of n . Therefore, in the following we shall discuss those conditions for a special value of n . It is clear from the form of a_{31} and a_{32} that:

- For $n < 1$, it is easy to verify that condition (8) is automatically satisfied. Hence the local stability conditions of the positive equilibrium point E_2 will be reducing to satisfying condition (9) only.
- For $n = 1$, rewriting the value of $b_1b_2 - b_3$ after substituting the values of a_{31} , a_{32} and x^* yields the following result:

$$\begin{aligned} b_1b_2 - b_3 &= B_1 + B_2 + B_3 \\ &= \frac{w_2w_3w_5(1+w_1)}{w_1^2(w_1+w_2)} [w_1w_2(1+w_1) + w_3w_5(w_1+w_2)^2] \\ &\quad + \frac{w_5(w_1-w_3(w_1+w_2))}{w_1(w_1+w_2)^2} [w_1w_2(1-w_2) + w_3w_5(w_1+w_2)^2] \\ &\quad + \frac{w_2^2w_5(w_1-w_3(w_1+w_2))}{w_1^2(w_1+w_2)^2} [w_1^2(w_2-1) + w_3w_5(w_1+w_2)^2]. \end{aligned}$$

So,

$$\begin{aligned} b_1b_2 - b_3 &= \frac{w_2w_3w_5(1+w_1)}{w_1^2(w_1+w_2)} [w_1w_2(1+w_1) + w_3w_5(w_1+w_2)^2] \\ &\quad + \frac{w_2w_5[w_1-w_3(w_1+w_2)]}{(w_1+w_2)^2} (1-w_2) + \frac{w_3w_5^2}{w_1} [w_1-w_3(w_1+w_2)] \\ &\quad + \frac{w_2^2w_5[w_1-w_3(w_1+w_2)]}{(w_1+w_2)^2} (w_2-1) + \frac{w_2^2w_3w_5^2}{w_1^2} [w_1-w_3(w_1+w_2)], \end{aligned}$$

$$\begin{aligned} b_1b_2 - b_3 &= \frac{w_2w_3w_5(1+w_1)}{w_1^2(w_1+w_2)} [w_1w_2(1+w_1) + w_3w_5(w_1+w_2)^2] \\ &\quad + \frac{w_2w_5}{w_1+w_2} \left[\frac{w_1}{w_1+w_2} - w_3 \right] (1-w_2) \\ &\quad + \frac{w_3w_5^2}{w_1} (w_1+w_2) \left[\frac{w_1}{w_1+w_2} - w_3 \right] \\ &\quad - \frac{w_2^2w_5}{w_1+w_2} \left[\frac{w_1}{w_1+w_2} - w_3 \right] (1-w_2) \\ &\quad + \frac{w_2^2w_3w_5^2}{w_1^2} (w_1+w_2) \left[\frac{w_1}{w_1+w_2} - w_3 \right], \end{aligned}$$

$$\begin{aligned} b_1b_2 - b_3 &= \frac{w_2w_3w_5(1+w_1)}{w_1^2(w_1+w_2)} [w_1w_2(1+w_1) + w_3w_5(w_1+w_2)^2] \\ &\quad + \frac{w_2w_5}{w_1+w_2} \left[\frac{w_1}{w_1+w_2} - w_3 \right] (1-w_2)^2 \\ &\quad + \frac{w_3w_5^2}{w_1} (w_1+w_2) \left[\frac{w_1}{w_1+w_2} - w_3 \right] \left(1 + \frac{w_2^2}{w_1} \right). \end{aligned}$$

Now, according to existence condition (7) of the positive equilibrium point E_2 , we get $b_1b_2 - b_3 > 0$ is true always. Therefore, when the intensity of prey defensive switching equal one ($n = 1$), it has been proved that system (4) generally has a locally asymptotically stable coexisting equilibrium point E_2 . Moreover, the global asymptotic stability of E_2 is given in the following theorem.

Theorem 3. *If $n = 1$, then the positive equilibrium point E_2 is a globally asymptotically stable with respect to all solutions initiate in the $Int.R_+^3$.*

Proof. Consider the following positive definite function

$$L(x, y, z) = \alpha \int_{x^*}^x \frac{u - x^*}{u} du + \beta \int_{y^*}^y \frac{v - y^*}{v} dv + \gamma \int_{z^*}^z \frac{w - z^*}{w} dw, \quad (11)$$

where α, β and γ are positive constants to be determined. Differentiating L with respect to time t along the solution of system (4), we get

$$\begin{aligned} \frac{dL}{dt} &= \alpha(x - x^*) \left[-1 + \frac{yz}{x + y} \right] + \beta(y - y^*) \left[-w_2 + \frac{w_1xz}{x + y} \right] \\ &\quad + \gamma(z - z^*) \left[w_5(1 - w_3z) - \frac{(1 + w_4)xy}{c_1(x + y)} \right] \\ &= \alpha(x - x^*) \left[\frac{yz}{x + y} - \frac{y^*z^*}{x^* + y^*} \right] + \beta(y - y^*) \left[\frac{w_1xz}{x + y} - \frac{w_1x^*z^*}{x^* + y^*} \right] \\ &\quad + \gamma(z - z^*) \left[-w_3w_5(z - z^*) - \left(\frac{(1 + w_4)xy}{c_1(x + y)} - \frac{(1 + w_4)x^*y^*}{c_1(x^* + y^*)} \right) \right] \\ &= \alpha(x - x^*) \left[\frac{(z - z^*)y}{x + y} - \frac{(x - x^*)y^*z^*}{(x + y)(x^* + y^*)} + \frac{(y - y^*)x^*z^*}{(x + y)(x^* + y^*)} \right] \\ &\quad + \beta(y - y^*) \left[\frac{w_1(z - z^*)x}{x + y} - \frac{w_1(y - y^*)x^*y^*}{(x + y)(x^* + y^*)} + \frac{w_1(x - x^*)y^*z^*}{(x + y)(x^* + y^*)} \right] \\ &\quad + \gamma(z - z^*) \left[-w_3w_5(z - z^*) - \frac{(1 + w_4)(y - y^*)xx^*}{c_1(x + y)(x^* + y^*)} - \frac{(1 + w_4)(x - x^*)yy^*}{(x + y)(x^* + y^*)} \right]. \end{aligned}$$

Therefore,

$$\begin{aligned} \frac{dL}{dt} &= - \left[\frac{\alpha y^* z^*}{(x + y)(x^* + y^*)} \right] (x - x^*)^2 - \left[\frac{\beta w_1 x^* z^*}{(x + y)(x^* + y^*)} \right] (y - y^*)^2 \\ &\quad - \gamma w_3 w_5 (z - z^*)^2 + \left[\beta w_1 x - \frac{\gamma(1 + w_4)xx^*}{c_1(x^* + y^*)} \right] \frac{(y - y^*)(z - z^*)}{x + y} \\ &\quad + [\beta w_1 y^* z^* + \alpha x^* z^*] \frac{(x - x^*)(y - y^*)}{(x + y)(x^* + y^*)} \\ &\quad + \left[\alpha y - \frac{\gamma(1 + w_4)yy^*}{c_1(x^* + y^*)} \right] \frac{(x - x^*)(z - z^*)}{x + y}. \end{aligned}$$

Choose the positive constants as follows:

$$\alpha = \frac{(1 + w_4)y^*}{c_1(x^* + y^*)}, \quad \beta = \frac{(1 + w_4)x^*}{c_1w_1(x^* + y^*)}, \quad \gamma = 1.$$

Then, we obtain

$$\begin{aligned} \frac{dL}{dt} = & -\frac{M_1y^{*2}z^*}{M_2}(x - x^*)^2 - \frac{M_1x^{*2}z^*}{M_2}(y - y^*)^2 \\ & - w_3w_5(z - z^*)^2 + \frac{2M_1x^*y^*z^*}{M_2}(x - x^*)(y - y^*). \end{aligned}$$

Hence

$$\frac{dL}{dt} = -\frac{M_1z^*}{M_2}[y^*(x - x^*) - x^*(y - y^*)]^2 - w_3w_5(z - z^*)^2,$$

where $M_1 = 1 + w_4$ and $M_2 = c_1(x + y)(x^* + y^*)^2$. Clearly $\frac{dL}{dt} < 0$ and $\frac{dL}{dt} = 0$ if and only if $x = x^*$, $y = y^*$ and $z = z^*$. So, L is a Lyapunov function with respect to E_2 , and hence E_2 is a globally asymptotically stable.

4 Numerical simulation

In order to better understand the dynamics of the proposed model, given in equation (4), in three-dimensional system we turn to numerical simulations. Extensive numerical simulations were carried out for different sets of parameter values and for different sets of initial conditions. We first consider the following values of parameters:

$$w_1 = 1.0, \quad w_3 = 0.2, \quad w_4 = 0.5, \quad w_5 = 2.0, \quad c_1 = 1.0, \quad n = 1. \quad (12)$$

For the above set of parameter values with $w_2 = 0.1, 1, 2$; it is found that the model system (4) admits a globally asymptotically stable point. Further, the computer simulation, as given in Fig. 2, of system (4) at the above set of data insures this analytical behavior.

Clearly, Fig. 2(a) shows that, system (4) for $w_2 = 0.1$ with other parameter values fixed as in equation (12) converges to the equilibrium point (1.14, 11.44, 1.1) in the $Int.R_+^3$ from two different sets of initial data, Fig. 2(b) shows that, for $w_2 = 1$ with other parameter values fixed as in equation (12), the system (4) has a globally asymptotically stable point (1.6, 1.6, 2). However, it is converging to another equilibrium point (1.6, 0.8, 3) for $w_2 = 2$ keeping other parameter as in equation (12).

Now, consider the following set of parameter values:

$$w_1 = 1.0, \quad w_3 = 0.2, \quad w_4 = 0.5, \quad w_5 = 2.0, \quad c_1 = 1.0, \quad n = 0.5. \quad (13)$$

According to the analytical behavior the system (4) with $w_2 = 0.1, 1, 2$ has a locally asymptotically stable point. Numerical simulations of system (4) for $w_2 = 0.1, 1, 2$ keeping other parameter fixed as in equation (13) have been down in Fig. 3(a)–(c) respectively.

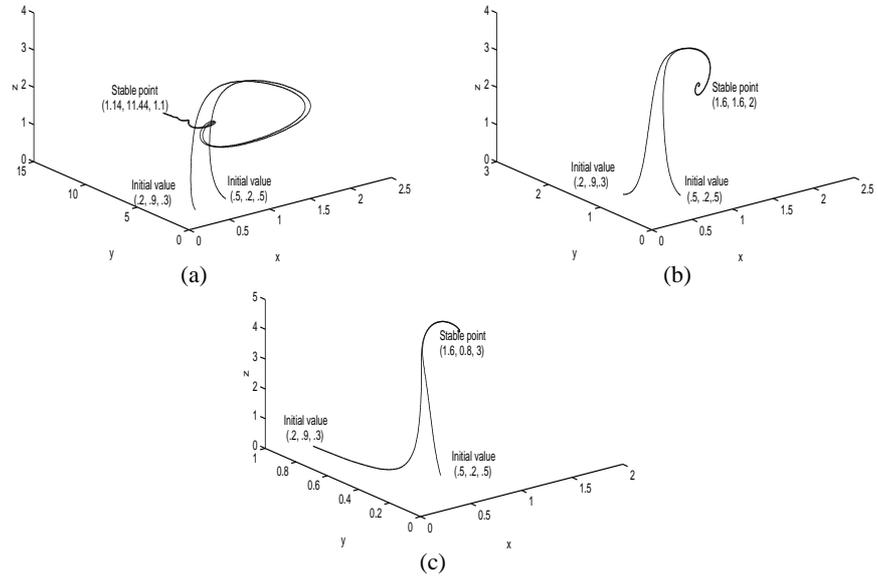


Fig. 2. Trajectories of system (4), for the data given by equation (12) starting from two different initial data: (a) stable point (1.14, 11.44, 1.1) for $w_2 = 0.1$; (b) stable point (1.6, 1.6, 2) for $w_2 = 1$; (c) stable point (1.6, 0.8, 3) for $w_2 = 2$.

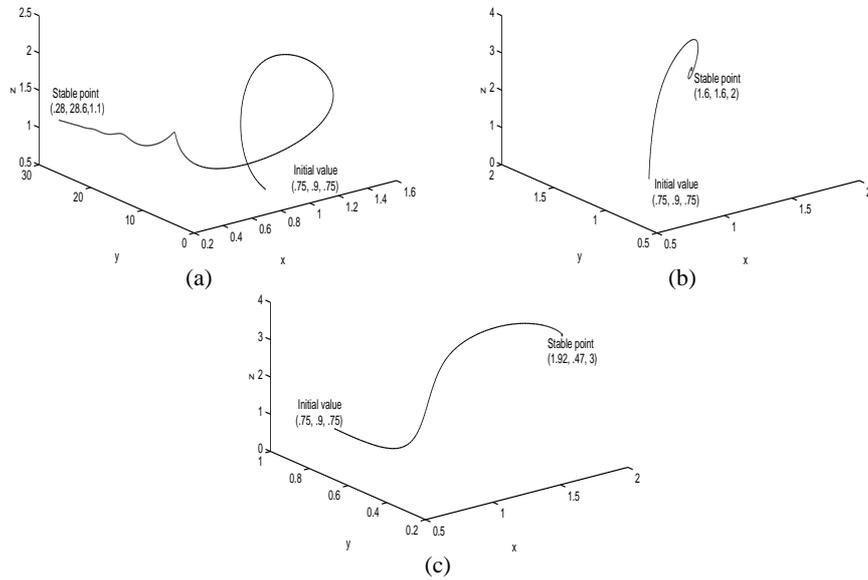


Fig. 3. Trajectories of system (4), for the data given by equation (13) starting from initial data: (a) stable point (0.28, 28.6, 1.1) for $w_2 = 0.1$; (b) stable point (1.6, 1.6, 2) for $w_2 = 1$; (c) stable point (1.92, 0.47, 3) for $w_2 = 2$.

Obviously, the three computer simulations in Fig. 3(a)–(c) present a stable case. Finally, for the following set of parameter values, the sufficient conditions for the locally asymptotically stable of E_2 , which are given by Theorem 2, are not satisfied.

$$w_1 = 1.0, \quad w_3 = 0.2, \quad w_4 = 0.5, \quad w_5 = 2.0, \quad c_1 = 1.0, \quad n = 10 \quad (14)$$

with $w_2 = 0.1, 1.0, 2$ respectively.

Note that the numerical simulation given by Fig. 4(a)–(c), for the system (4) of the above set of data with $w_2 = 0.1, 1, 2$ respectively, also shows the coexistence of stable equilibrium points.

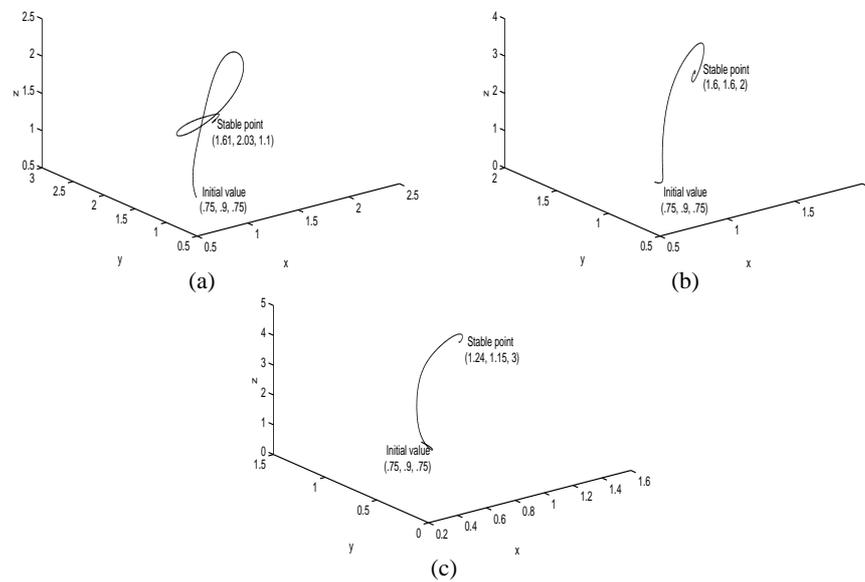


Fig. 4. Trajectories of system (4), for the data given by equation (14) starting from initial data: (a) stable point (1.61, 2.03, 1.1) for $w_2 = 0.1$; (b) stable point (1.6, 1.6, 2) for $w_2 = 1$; (c) stable point (1.24, 1.15, 3) for $w_2 = 2$.

5 Discussion and conclusions

In the last two decades number of papers have been done on the effects of switching mechanism of prey and / or predator, due to variety of biological concepts, on the behavior of population dynamics [11–18]. The effect of optimal diet choice in two-prey-one-predator population dynamic model is investigated in Krivan [11]. It is observed that a system consisting of predators, which specialize on the more profitable prey only may be stable, while the same system with predators following the rule of optimal diet choice may not have a stable equilibrium. In addition, he showed that optimal foraging might lead to

permanence of the predator-prey system. The effects of various host-feeding patterns on host-parasitoid population dynamic are studied in Krivan [12]. He obtained that while the destructive type of host-feeding does not qualitatively influence host-parasitoid population dynamics, non-destructive host-feeding has strong effect on population dynamics since it leads either to a stable equilibrium or it reduces the amplitude of maximal fluctuations in population densities. The influence of individual behavior on the Lotka-Volterra predator-prey dynamics in two-patch environment is also examined by Krivan see [13]. It is assumed that the individuals behave to maximize their fitness measured by the instantaneous per capita growth rate. Two cases are investigated in detail: In the first case its assumed that only predators are free to move between patches whereas in the second both predators and prey move freely between patches. It is concluded that the optimal behavior of animals leads to persistence of predator-prey systems and reduction of oscillations in population densities. Further investigations of optimal foraging behavior of predators on two-prey-one-predator population dynamic model were done in Krivan and Sikder [14] and Krivan and Eisner [15]. These studies showed that, in case of logistic description of prey growth the optimal foraging behavior of predators might promote coexistence in predator-prey systems [14], while it is leads to persistence of prey-predator systems and reduction of oscillations in population densities when the model assumes the exponential growth of prey [15].

The effect of invading species in food chain models with Holling type-II functional response have been studied by Kooi et al. [16] and Kooi and Kooijman [17]. They have found that when a fast grown top predator is introduced in a food chain, the resulting system becomes more resistant to further invasion [16]. However, they concluded that, since the growth rate decreases with the trophic level, this enable short food chains to be resistant to invaders. Moreover, it is observed that the invasion of a competitor of the prey can stabilize an oscillatory nutrient-prey-predator bi-trophic food chain [17].

The facultative predation strategy in one-prey-one-facultative-predator dynamic model is investigated by Aggelis et al. in [18]. It is assumed that both prey and predator populations grow together in a chemostat, which is fed with medium containing the necessary nutrients for saprophytic growth of both populations. The attack of the facultative predator on the prey population is regulated by the abundance of the common resource for saprophytic growth, via a catabolic repression mechanism. The common substrate for saprophytic growth of both populations acted as repressor on the attack of predators on the prey population. It is observed that the catabolic repression control favors domination of the prey over the predator and, under certain circumstances (when the predator has the competitive advantage at high substrate concentration) coexistence of both prey and predator populations. In a similar manner Vayenas et al. [19] studied the strategy of alternative prey (switching), regulated by a catabolic repression control-like mode (CRCL), in a two-prey-one-predator chemostat model. It is observed that, when the alternative prey has no competitive advantage for the common substrate over the desirable prey, its survival depends on the protection offered by the desirable prey via CRCL, and hence CRCL allows the coexistence of both desirable and alternative prey and predator populations. However, when the alternative prey has the competitive advantage over the desirable prey, CRCL negatively affects both the state of survival of the desirable prey

and the coexistence state.

Keeping the above in view, a three species food web model consisting of two-predator feeding on the logistic prey species is considered in case of existence of defensive switching behavior. Further, in order to better understand the effect of the prey's defensive property, the food web model (1) in case of there is no defensive switching behavior is also investigated. It has been observed that system (1) has a non-hyperbolic positive equilibrium point in interior of positive octant and hence all types of dynamics such as stable point, periodic, quasiperiodic, and even chaotic in the interior of R_+^3 are possible. However, the analysis of section (3) shows that, the food web model with defensive switching behavior generally has a stable three species coexisting equilibrium state. Moreover, in the special case when the intensity of defensive switch equals one the system has a globally asymptotically stable coexisting equilibrium state. Accordingly, it is concluded that adding the defensive switching behavior to the food web system under consideration have a stabilizing effect on the dynamical behavior.

It may be pointed out here that the analysis of Saleem et al. [5] shown that the food web system, which is consisting of two-predator feeding on an exponential prey species with defensive switching property, is asymptotically settles to a Volterra's oscillation in the three dimensional space when the intensity of defensive switching equals one and the two predators have the same mortality rates. In contrast when we using logistic prey species instead of an exponential prey species, the dynamics of the interior equilibrium is changed and we have obtained sufficient conditions under which the food web system is a globally asymptotically stable in the interior of positive octant.

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References

1. D. F. Eraser, F. A. Huntingford, Feeding and avoiding predation hazard: the behavioral response of the prey, *Ethology*, **73**, pp. 56–70, 1986.
2. D. W. Lendrem, Predation risk and vigilance in the blue tit (*Parus caeruleus*), *Behav. Ecol. Sociobiol.*, **14**, pp. 9–20, 1983.
3. M. Milinski, R. Heller, Influence of a predator on the optimal foraging behavior of sticklebacks. *Gasterosteus aculeatus*, *Nature*, **275**, pp. 642–650, 1978.
4. A. Sih, Stability and prey behavioral responses to predator density, *J. Anim. Ecol.*, **48**, pp. 79–85, 1979.
5. M. Saleem, A. K. Tripathi, A. H. Sadiyal, Coexistence of species in a defensive switching model, *Mathematical Biosciences*, **181**, pp. 145–164, 2003.

6. M. P. Hassell, R. M. May, From individual behavior to population dynamics, in: *Behavioral Ecology: Ecological Consequences of Adaptive Behavior*, R. M. Sibly, R. H. Smith (Eds.), Blackwell, Oxford, P. 3, 1985.
7. H. P. Matsuda, A. Abrams, M. Hori, The effect of adaptive anti-predator behavior on exploitative competition and mutualism between predators, *Oikos*, **68**, pp. 549–595, 1993.
8. J. N. McNair, The effects of refuges on predator-prey interactions: a reconsideration, *Theor. Popul.*, **29**, pp. 38–63, 1986.
9. G. A. Parker, Population consequences of evolutionarily stable strategies, in: *Behavioral Ecology: Ecological Consequences of Adaptive Behavior*, R. M. Sibly, R. H. Smith (Eds.), Blackwell, Oxford, P. 33, 1985.
10. S. Takahashi, M. Hori, Unstable evolutionarily stable strategy and oscillation: a model of lateral asymmetry in scale-eating cichlids, *Am. Nat.*, **144**, pp. 1001–1020, 1994.
11. V. Krivan, Optimal foraging and predator-prey dynamic, *Theor. Popul. Biol.*, **49**, pp. 265–290, 1996.
12. V. Krivan, Dynamic ideal free distribution: effect of optimal patch choice on predator-prey dynamic, *Am. Nat.*, **149**, pp. 164–178, 1997.
13. V. Krivan, Dynamical consequence of optimal host-feeding on host-parasitoid population dynamic, *Bull. Math. Biol.*, **59**, pp. 809–831, 1997.
14. V. Krivan, A. Sikder, Optimal foraging and predator-prey dynamics II, *Theor. Popul. Biol.*, **55**, pp. 111–126, 1999.
15. V. Krivan, J. Eisner, Optimal foraging and predator-prey dynamics III, *Theor. Popul. Biol.*, **63**, pp. 269–279, 2003.
16. B. W. Kooi, M. P. Boer, S. A. L. M. Kooijman, Resistance of a food chain to invasion by a top predator, *Math. Biosci.*, **157**, pp. 217–236, 1999.
17. B. W. Kooi, S. A. L. M. Kooijman, Invading species can stabilize simple trophic systems, *Ecol. Model.*, **133**, pp. 57–2, 2000.
18. G. Aggeli, D. V. Vayena, V. Tsagou, S. Pavlou, Prey-predator dynamic with predator switching regulated by a catabolic repression control mode, *Ecol. Model.*, **183**, pp. 453–464, 2005.
19. D. V. Vayena, G. Aggeli, V. Tsagou, S. Pavlou, Dynamic of a two-prey-one-predator system with predator switching regulated by a catabolic repression control-like mode, *Ecol. Model.*, **186**, pp. 345–357, 2005.
20. M. Tansky, switching effect in prey-predator system, *J. Theor. Biol.*, **70**, pp. 263–271, 1978.
21. J. K. Hale, *Ordinary differential equation*, New York, Wiley-Interscience, 1969.