

Effect of prey refuge in a tri-trophic food chain model with Monod-Haldane type response function

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ABSTRACT

The present paper deals with the control of a constant proportion of prey refuge in the presence of intra-specific competition among adult predator species of a continuous time food chain model. Dynamic behaviour of the model close to the biologically meaningful feasible equilibria is examined in detail. The preliminary results such as positivity and boundedness of the proposed system are well-recognized. Stability analysis together with the local and global stability of the equilibria has been carried out in order to scrutinize the behaviour of the system. The Hopf-bifurcation analysis of the model with respect to the significant parameter has been explored both analytically and numerically. The effects of the prey refuge parameters on the dynamical behaviour of the system are displayed through a number of valid figures. Also, effects of intra-specific competition among adult predators on the system are exposed by different diagrams. Such outcomes can be exercised to recover ecological decision-making on species protection.

Keywords: Nonlinear dynamics, Mathematical biology, Dynamical systems in biology, Numerical simulation.

2010 Mathematics Subject Classification: 34A34, 34G20, 35F25, 37N25, 92Bxx, 92D25.

JEL Classification Number: C02, C62, C63.

1 Introduction

The natural world, dynamical behaviour exhibited by various ecological systems is very complicated. Predator-prey communities are embedded in complex food webs. These webs are related by trophic (predation) as well as non-trophic interactions (e.g., competition, mutualism and interference). Predator mainly depends on prey species for continuous survival. Basically, prey species provide an important food source for predators. Predator-prey interacting system has some biological phenomenon and relationship between predator and prey in the real world that play a crucial role in mathematics and have been extensively considered in many ways by many researchers (Hu and Li, 2010), (Song, Peng

and Wei, 2008), (Qu and Wei, 2007), (Xiao and Ruan, 2001), (May, 1972), (Medvinsky, Petrovskii, Tikhonova, Malchow and Li, 2002), (Bhattacharya and Martcheva, 2010), (Bhattacharya, Martcheva and Li, 2014), (Wu, Li and Wang, 2008), (Sambath and Gokila, 2019). To study the system dynamics of our proposed model, we will use specific topics and techniques from the dynamical systems (Layek, 2015). The construction of deterministic and stochastic models and their qualitative analysis is an important area in population biology since the famous Lotka-Volterra equation. A lot of predator-prey models have been studied extensively in the last few decades (Ali, Mondal, Guin and Chakravarty, 2018), (Ali, Sarkar and Guin, 2019a), (Ali, Sarkar and Guin, 2019b), (Ganguli and Kar, 2019), (Guin, Das and Sambath, 2020), (Han, Guin and Dai, 2020). A most crucial element in these interacting species models is the 'functional response', the function that describes per unit time that is Functional response is the number of prey successfully attacked by a predator as a function of prey density. It describes the way a predator responds to the changing density of its prey species. In mathematical ecology, many factors can affect functional responses, for example predator hunting ability, prey escape ability, structure of the prey habitat etc. Holling type IV functional response is a kind of important functional responses and can enrich the system dynamics of predator-prey system. There are several types of functional response, Holling type I (linear), type II (hyperbolic), type III (sigmoid), type IV, Beddington-DeAngelis type, Crowley-Martin type, Hassel-Verrely type, Ivlev type, ratio type etc. Holling type IV functional response is relatively less investigated in the theoretical ecology. In 1930, it was first introduced by Haldane (Haldane, 1965) in enzymology. Later, Sokol and Howell (Sokol and Howell, 1981) derived a simplified Monod-Haldane functional response.

While one goes through the literature review of the dynamical complexity scenario on the predator-prey interaction in addition to prey refuge / intra-specific competition among the predator species, we have noticed that there are much research works on the dynamics of predators and their functional responses. Haque et al. (Haque, Ali and Chakravarty, 2013) offered a detailed mathematical analysis of the food chain model by incorporating intra-specific competition among predators to illustrate some of the significant results that had been arisen from the interplay of deterministic ecological phenomena and processes. Also, Haque et al. (Haque et al., 2013) established that intra-specific competitions have a potential role in controlling the chaotic dynamics of the system. Ali and Chakravarty (Ali and Chakravarty, 2014) investigate the interactions between predator and prey species by incorporating constant proportion of prey refuge in presence of intra-specific competition among predator species through a system of ordinary differential equations, and they examined that their model admits oscillatory behaviour and a stable limit cycle appears at the bifurcating point. In the proposed model system with Holling type IV response function, we incorporate some extension of a mathematical model, which is a proposed research article of Khajanchi (Khajanchi, 2017). He analyzed predator-prey interaction scenario via Monod-Haldane type functional response in his model. Holling type IV functional response is relatively. Now, the model has been updated through the incorporation of a prey refuge and intra-specific competition among adult predators in (Khajanchi, 2017). Many prey individuals have developed defense mechanisms against predation. Here, it is assumed that a constant proportion of prey species is taking refuge and the remaining portion is exposed to predation. Moreover, the intra-specific competition among adult predator species also plays an important role in determining the eventual state of the ecosystem. Here, our aim is to investigate the interactive effects of prey refuge and intra-specific competition among adult predator species on the platform of temporal dynamics.

The research manuscript is organized as follows: in Section 2 we have proposed our model system. Section 3 contains the idea of positive invariance of the solution. Section 4 contains the boundedness of the whole model system. We have divided Section 5 into some subsections and discussed briefly the three types of equilibria and obtained their stability analysis one by one. Also, we have analyzed Hopf - bifurcation with respect to the significant parameters with fulfilling exact criteria. In Section 6 we have discussed our model system numerically by choosing various parameter values and performed

their respective stability diagram. The paper ends with a discussion in Section 7.

2 The model formulation

Khajanchi (Khajanchi, 2017) used a Monod-Haldane type functional response in a tri-trophic food chain model is of the form

$$\frac{dx}{dt} = ax\left(1 - \frac{x}{K}\right) - \frac{bxz}{p + cx^2}, \quad (2.1a)$$

$$\frac{dy}{dt} = \frac{ebxz}{p + cx^2} - (r - d_1)y, \quad (2.1b)$$

$$\frac{dz}{dt} = ry - d_2z, \quad (2.1c)$$

$$x(0) = x_0 \geq 0, \quad y(0) = y_0 \geq 0, \quad z(0) = z_0 \geq 0. \quad (2.1d)$$

where all the system parameters are positive and defined in Table 1.

Sl. No.	Variable and Parameter	Description
1	$x(t)$	Density of prey population.
2	$y(t)$	Density of juvenile predator population.
3	$z(t)$	Density of adult predator population.
4	a	Intrinsic growth rate of prey population.
5	K	Environmental carrying capacity of prey.
6	b	Predation coefficient.
7	p	Half saturation constant.
8	c	Inverse measure of inhibiting effect.
9	e	Predator's efficiency.
10	r	Transition rate on the evolution of the Juvenile to adult predators.
11	d_1	Natural death rate of Juvenile predators.
12	d_2	Natural death rate of adult predators.

Table 1: The set of model parameters and variables and their biological description.

The juvenile predators have no ability to attack prey species and fully dependent on adult predators. Adult predators have the ability to attack prey species and have reproductive capability. In our present model, an attempt has been made to update the model (2.1) incorporating prey refuges proportional to the prey density mx from the adult predator species where $m \in [0, 1)$ and consequently $(1 - m)x$ is only prey available to predator for predation. We also consider the density-dependent death factor of the adult predator representing the term $(d_2 + hz)z$ and the environment is supposed to be uniform, that is, the system parameters do not depend on space and time. Thus, one may obtain the following system

$$\frac{dx}{dt} = ax\left(1 - \frac{x}{K}\right) - \frac{b(1 - m)xz}{p + c(1 - m)^2x^2}, \quad (2.2a)$$

$$\frac{dy}{dt} = \frac{eb(1 - m)xz}{p + c(1 - m)^2x^2} - (r - d_1)y, \quad (2.2b)$$

$$\frac{dz}{dt} = ry - d_2z - hz^2, \quad (2.2c)$$

$$x(0) = x_0 \geq 0, \quad y(0) = y_0 \geq 0, \quad z(0) = z_0 \geq 0, \quad (2.2d)$$

where all the system parameters are defined earlier and m and h are prey refuge parameter and intra-specific competition factor among adult predators respectively with $0 \leq m < 1$ and $h \geq 0$.

3 Positive invariance

Consider the model system (2.2) and put in the vector form,

$$\dot{Y}(t) = \mathcal{G}(Y(t)) \quad (3.1)$$

where $Y(t) = (y_1, y_2, y_3)^T = (x(t), y(t), z(t))^T$, $Y(0) = (x(0), y(0), z(0))^T \in \mathbb{R}_+^3$ and

$$\mathcal{G}(Y(t)) = \begin{pmatrix} \mathcal{G}_1(Y(t)) \\ \mathcal{G}_2(Y(t)) \\ \mathcal{G}_3(Y(t)) \end{pmatrix} = \begin{pmatrix} ax(t) \left(1 - \frac{x(t)}{k}\right) - \frac{b(1-m)x(t)z(t)}{p + c(1-m)^2x^2(t)} \\ \frac{eb(1-m)x(t)z(t)}{p + c(1-m)^2x^2(t)} - (r + d_1)y(t) \\ ry(t) - d_2z(t) - hz^2(t) \end{pmatrix}. \quad (3.2)$$

It is easy to verify that $\mathcal{G}_i(Y(t))|_{y_i=0} \geq 0$. (for $i = 1, 2, 3$). Due to Nagumo's theorem (Nagumo, 1942), any solution of (3.1) with initial condition $Y(0) = Y_0 \in \mathbb{R}_+^3$, say $Y(t) = Y(t : Y_0)$ in such a way that $Y(t) \in \mathbb{R}_+^3$ for all $t > 0$, that is, remain positive throughout the region $\mathbb{R}_+^3$.

4 Boundedness of the model system (2.2)

Proposition 1: The solutions of the model system (2.2) which originate from $\mathbb{R}_+^3$ are uniformly bounded.

Proof: Using the above positiveness of the solutions, we can write from the first equation of (2.2)

$$\begin{aligned} \frac{dx}{dt} &\leq ax \left(1 - \frac{x}{K}\right) \\ \Rightarrow \limsup x(t) &\leq K \quad \forall t. \end{aligned}$$

Let us consider a function $S(t) = ex(t) + y(t) + z(t)$. The time derivative of this function along the solution of the system (2.2) is

$$\frac{dS(t)}{dt} = e \frac{dx}{dt} + \frac{dy}{dt} + \frac{dz}{dt}.$$

Now for each $\eta > 0$, and taking $\eta > d_1$ we have

$$\frac{dS(t)}{dt} + \eta S(t) \leq \frac{e(\eta K + aK)^2}{4ak} + \frac{(\eta - d_2)^2}{4h}.$$

Thus $\exists \sigma > 0$, such that

$$\begin{aligned} \frac{dS(t)}{dt} + \eta S(t) &\leq \sigma, \\ \Rightarrow 0 < S(t) &\leq \frac{\sigma}{\eta}, \text{ as } t \rightarrow \infty. \end{aligned}$$

Hence, all the solutions of system (2.2) which initiating in $\mathbb{R}_+^3$ are confined in the compact region

$$\Omega = \left\{ (x, y, z) \in \mathbb{R}_+^3 : 0 < x(t) \leq K, 0 \leq ex(t) + y(t) + z(t) \leq \frac{\sigma}{\eta} \right\}. \quad (4.1)$$

5 Equilibria and their stability analysis

In this section, we wish to determine all possible non-negative equilibria of the system (2.2) and then analyze the stability criteria around those ecologically meaningful equilibria.

5.1 Equilibria

The system (2.2) possesses three equilibrium points, namely

(i) The trivial equilibrium point, $E_0(0, 0, 0)$,

(ii) The axial equilibrium point, $E_1(K, 0, 0)$,

and (iii) The interior equilibrium point $E_2(x^*, y^*, z^*)$, which is getting by solving the three equations

$$a\left(1 - \frac{x}{K}\right) - \frac{b(1-m)z}{p+c(1-m)^2x^2} = 0,$$

$$\frac{eb(1-m)xz}{p+c(1-m)^2x^2} - (r+d_1)y = 0,$$

$$ry - d_2z - hc^2 = 0.$$

For co-existence equilibrium point, one can easily obtain $y^* = \frac{d_2z^* + hc^{*2}}{r}$, $z^* = a\left(1 - \frac{x^*}{K}\right)\left(\frac{p+c(1-m)^2x^{*2}}{b(1-m)}\right)$ and x^* be a root of the fifth degree equation

$$(ah(p+c(1-m)^2x^{*2})\left(1 - \frac{x^*}{K}\right) + d_2)(p+c(1-m)^2x^{*2}) - \frac{erb(1-m)x^*}{(r+d_1)} = 0.$$

Among all the ecologically meaningful equilibria of the system (2.2); mainly we pay our attention only for unique coexistence equilibrium point $E_2(x^*, y^*, z^*)$, for the sake of brevity. We set the values of system parameters in such a way that the coexistence equilibrium point $E_2(x^*, y^*, z^*)$ exists uniquely with the implementation of Descartes' rule of sign.

5.2 Linear stability analysis of system (2.2)

In this section, we deal with local stability, global stability and Hopf-bifurcation of the given model system (2.2). The presence of the stability behaviour and bifurcations are the subject of interest. Now, we discuss about the dynamical behaviour of the system around the equilibrium points $E_0(0, 0, 0)$, $E_1(K, 0, 0)$ and $E_2(x^*, y^*, z^*)$. The variational matrix or the stability matrix or the Jacobian matrix J of the system (2.2) is

$$J = \begin{bmatrix} a\left(1 - \frac{x}{K}\right) - \frac{ax}{K} - \frac{b(1-m)z}{p+c(1-m)^2x^2} + \frac{2b(1-m)^3x^2zc}{(p+c(1-m)^2x^2)^2} & 0 & -\frac{b(1-m)x}{p+c(1-m)^2x^2} \\ \frac{eb(1-m)z}{p+c(1-m)^2x^2} - \frac{2eb(1-m)^3x^2zc}{(p+c(1-m)^2x^2)^2} & -r-d & \frac{eb(1-m)x}{p+c(1-m)^2x^2} \\ 0 & r & -2hz - d_2 \end{bmatrix}. \quad (5.1)$$

5.2.1 Dynamical behaviour around $E_0(0, 0, 0)$

Proposition 2: Around the trivial equilibrium point $E_0(0, 0, 0)$, the model system (2.2) is unstable in nature.

Proof: From the (5.1), the Jacobian matrix of system (2.2) around $E_0(0, 0, 0)$ is

$$J_{E_0} = \begin{bmatrix} a & 0 & 0 \\ 0 & -(r + d_1) & 0 \\ 0 & r & -d_2 \end{bmatrix}.$$

Since all the parameters are positive, the eigenvalues of J_{E_0} are $\lambda_1 = a > 0$, $\lambda_2 = -(r + d_1) < 0$ and $\lambda_3 = -d_2 < 0$.

Thus the equilibrium point $E_0(0, 0, 0)$ is a saddle point. More precisely the system has a 1-dimensional unstable manifold and 2-dimensional stable manifold around $E_0(0, 0, 0)$. Overall the system (2.2) is unstable at $E_0(0, 0, 0)$.

5.2.2 Dynamical behaviour around $E_1(K, 0, 0)$

Proposition 3: The system (2.2) is locally asymptotically stable around $E_1(K, 0, 0)$ if $\frac{d_2(r + d_1)(p + c(1 - m)^2 K^2)}{rb(1 - m)K} > e$ and unstable if $\frac{d_2(r + d_1)(p + c(1 - m)^2 K^2)}{rb(1 - m)K} < e$.

Proof: The Jacobian matrix at $E_1(K, 0, 0)$ is given by

$$J_{E_1} = \begin{bmatrix} -a & 0 & -\frac{b(1 - m)K}{p + c(1 - m)^2 K^2} \\ 0 & -r - d_1 & \frac{eb(1 - m)K}{p + c(1 - m)^2 K^2} \\ 0 & r & -d_2 \end{bmatrix}.$$

One eigenvalue of J_{E_1} is $\lambda_1 = -a < 0$ and other two eigenvalues λ_2 and λ_3 are the roots of the characteristic equation

$$\lambda^2 + \psi_1 \lambda + \psi_2 = 0$$

of the $2D$ matrix

$$\begin{bmatrix} -r - d_1 & \frac{eb(1 - m)K}{p + c(1 - m)^2 K^2} \\ r & -d_2 \end{bmatrix},$$

where $\psi_1 = (r + d_1 + d_2)$, $\psi_2 = (d_2(r + d_1) - \frac{reb(1 - m)K}{p + c(1 - m)^2 K^2})$. Thus the system (2.2) will be a locally asymptotically stable system at $E_1(K, 0, 0)$ if $\lambda_2 < 0$ and $\lambda_3 < 0$ that is if $\frac{d_2(r + d_1)(p + c(1 - m)^2 K^2)}{rb(1 - m)K} > e$ and the system will be unstable at $E_1(K, 0, 0)$ if $\frac{d_2(r + d_1)(p + c(1 - m)^2 K^2)}{rb(1 - m)K} < e$.

5.2.3 Dynamical behaviour around the co-existence equilibrium point $E_2(x^*, y^*, z^*)$

Proposition 4: The model system (2.2) is locally asymptotically stable around the interior equilibrium point $E_2(x^*, y^*, z^*)$ if

$$(i) \ a > \frac{1}{[p + c(1 - m)^2 x^{*2}]^2} \max \{ 2Kcb(1 - m)^3 x^* z^*,$$

$$Kb(1-m)^2 \left(2c(1-m)x^* + \frac{re(p-c(1-m)^2x^{*2})}{(p+c(1-m)^2x^{*2})(r+d_1+d_2+2hz^*)} \right),$$

$$(ii) p > \max \left\{ c(1-m)^2x^{*2}, \frac{reb(1-m)x^*}{(r+d_1)(d_2+2hz^*)} - c(1-m)^2x^{*2} \right\}.$$

Proof: The Jacobian or variational matrix of system (2.2) around the interior equilibrium point $E_2(x^*, y^*, z^*)$ is given by

$$J_{E_2} = \begin{bmatrix} \tau_{11} & \tau_{12} & \tau_{13} \\ \tau_{21} & \tau_{22} & \tau_{23} \\ \tau_{31} & \tau_{32} & \tau_{33} \end{bmatrix},$$

where,

$$\tau_{11} = -\frac{ax^*}{K} + \frac{2cb(1-m)^3x^{*2}z^*}{[p+c(1-m)^2x^{*2}]^2},$$

$$\tau_{12} = 0,$$

$$\tau_{13} = -\frac{b(1-m)x^*}{p+c(1-m)^2x^{*2}},$$

$$\tau_{21} = \frac{eb(1-m)z^*[p-c(1-m)^2x^{*2}]}{[p+c(1-m)^2x^{*2}]^2},$$

$$\tau_{22} = -(r+d_1),$$

$$\tau_{23} = \frac{eb(1-m)x^*}{p+c(1-m)^2x^{*2}},$$

$$\tau_{31} = 0,$$

$$\tau_{32} = r,$$

$$\tau_{33} = -d_2 - 2hz^*.$$

The eigenvalues of J_{E_2} are the roots of the following characteristic equation:

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0, \quad (5.2)$$

where,

$$A_1 = -\text{trace of } J_{E_2} = (r+d_1+d_2+2hz^*) + x^* \left(\frac{a}{K} - \frac{2cb(1-m)^3x^{*2}z^*}{[p+c(1-m)^2x^{*2}]^2} \right),$$

$$A_2 = \text{Sum of three principal minors of } J_{E_2}$$

$$= (r+d_1+d_2+2hz^*)x^* \left(\frac{a}{K} - \frac{2cb(1-m)^3x^{*2}z^*}{[p+c(1-m)^2x^{*2}]^2} \right) + \left((r+d_1)(d_2+2hz^*) - \frac{reb(1-m)x^*}{p+c(1-m)^2x^{*2}} \right),$$

$$A_3 = -\text{Determinant of } J_{E_2}$$

$$= x^* \left(\frac{a}{K} - \frac{2cb(1-m)^3x^{*2}z^*}{[p+c(1-m)^2x^{*2}]^2} \right) \left((r+d_1)(d_2+2hz^*) - \frac{reb(1-m)x^*}{p+c(1-m)^2x^{*2}} \right) + \frac{reb^2(1-m)^2x^{*2}z^*(p-c(1-m)^2x^{*2})}{[p+c(1-m)^2x^{*2}]^3}.$$

One can evaluate $A_1A_2 - A_3$ as follows :

$$\begin{aligned} A_1A_2 - A_3 &= \left((r + d_1 + d_2 + 2hz^*) + x^* \left(\frac{a}{K} - \frac{2cb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2} \right) \right) \left((r + d_1 + d_2 + 2hz^*)x^* \left(\frac{a}{K} - \frac{2cb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2} \right) \right. \\ &\quad \left. + \left((r + d_1)(d_2 + 2hz^*) - \frac{reb(1-m)x^*}{p + c(1-m)^2x^{*2}} \right) - \left(x^* \left(\frac{a}{K} - \frac{2cb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2} \right) \left((r + d_1)(d_2 + 2hz^*) - \frac{reb(1-m)x^*}{p + c(1-m)^2x^{*2}} \right) \right. \right. \\ &\quad \left. \left. + \frac{reb^2(1-m)^2x^*z^*(p - c(1-m)^2x^{*2})}{[p + c(1-m)^2x^{*2}]^3} \right) \right), \\ &= \left(\frac{a}{K} - \frac{2cb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2} \right)^2 x^{*2}(r + d_1 + d_2 + 2hz^*) + (r + d_1 + d_2 + 2hz^*) \left((r + d_1)(d_2 + 2hz^*) - \frac{reb(1-m)x^*}{p + c(1-m)^2x^{*2}} \right) \\ &\quad + \left[\left(\frac{a}{K} - \frac{2cb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2} \right) x^*(r + d_1 + d_2 + 2hz^*)^2 - \frac{reb^2(1-m)^2x^*z^*(p - c(1-m)^2x^{*2})}{[p + c(1-m)^2x^{*2}]^3} \right]. \end{aligned}$$

Now, the system satisfy the well known Routh-Hurwitz criteria if $A_1 > 0$, $A_3 > 0$ and $A_1A_2 - A_3 > 0$, which implies that

$$\begin{aligned} (i) \quad &\frac{a}{K} > \frac{2cb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2}, \text{ that is, } a > \frac{2Kcb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2}, \\ (ii) \quad &(r + d_1)(d_2 + 2hz^*) > \frac{reb(1-m)x^*}{p + c(1-m)^2x^{*2}}, \text{ that is } p > \frac{reb(1-m)x^*}{(r + d_1)(d_2 + 2hz^*)} - c(1-m)^2x^{*2}, \\ (iii) \quad &p > c(1-m)^2x^{*2}, \\ (iv) \quad &\left(\frac{a}{K} - \frac{2cb(1-m)^3x^*z^*}{[p + c(1-m)^2x^{*2}]^2} \right) x^*(r + d_1 + d_2 + 2hz^*)^2 > \frac{reb^2(1-m)^2x^*z^*(p - c(1-m)^2x^{*2})}{[p + c(1-m)^2x^{*2}]^3}, \text{ which} \\ &\text{can be written as } a > \frac{Kb(1-m)^2}{[p + c(1-m)^2x^{*2}]^2} \left(2c(1-m)x^* + \frac{reb(p - c(1-m)^2x^{*2})}{(p + c(1-m)^2x^{*2})(r + d_1 + d_2 + 2hz^*)^2} \right). \end{aligned}$$

Combining these four results we will get the conditions of the said proposition.

5.2.4 Global stability analysis around $E_2(x^*, y^*, z^*)$

Let us define a function $L(x, y, z) = L_1(x, y, z) + L_2(x, y, z) + L_3(x, y, z)$.

where,

$$L_1(x, y, z) = \xi_1 \int_{x^*}^x \left(\frac{x - x^*}{x} \right) dx, \quad L_2(x, y, z) = \xi_2 \int_0^{y-y^*} \eta d\eta, \quad L_3(x, y, z) = \xi_3 \int_0^{z-z^*} \gamma d\gamma$$

It is to be showed that L is a Lyapunav function. L vanishes at $E_2(x^*, y^*, z^*)$ and it is positive for all $x, y, z > 0$. Now taking time derivative of L we have

$$\begin{aligned} \frac{dL}{dt} &= -\xi_1 \frac{a}{K} (x - x^*)^2 - \xi_2 (r + d_1)(y - y^*)^2 - \xi_3 (d_2 + z + z^*)(z - z^*)^2 + \frac{\xi_2 eb(1-m)z^*[p - c(1-m)^2x^{*2}]}{(p + c(1-m)^2x^{*2})(p + c(1-m)^2x^{*2})} (x - x^*)(y - y^*) \\ &\quad + \left(\xi_3 a + \frac{\xi_2 eb(1-m)x}{(p + c(1-m)^2x^{*2})} \right) (y - y^*)(z - z^*) - \frac{\xi_1 b(1-m)}{(p + c(1-m)^2x^{*2})} (z - z^*)(x - x^*). \end{aligned}$$

In quadratic form

$$\begin{aligned} \frac{dL}{dt} &= - \left(A(x - x^*)^2 + B(y - y^*)^2 + C(z - z^*)^2 + 2H(x - x^*)(y - y^*) + 2F(y - y^*)(z - z^*) + 2G(z - z^*)(x - x^*) \right), \\ &= -v^T Q v. \end{aligned}$$

where $v = \left((x - x^*), (y - y^*), (z - z^*) \right)^T$.

In matrix form

$$Q = \begin{bmatrix} A & H & G \\ H & B & F \\ G & F & C \end{bmatrix},$$

where,

$$A = \xi_1 \frac{a}{K}, \quad B = \xi_2(r + d_1), \quad C = \xi_3(d_2 + z + z^*), \quad H = -\frac{1}{2} \frac{\xi_2 eb(1-m)z^*[p - c(1-m)^2xx^*]}{(p + c(1-m)^2x^2)(p + c(1-m)^2x^{*2})},$$

$$F = -\frac{1}{2} \left(\xi_3 a + \frac{\xi_2 eb(1-m)x}{(p + c(1-m)^2x^2)} \right), \quad G = \frac{1}{2} \frac{\xi_1 b(1-m)}{(p + c(1-m)^2x^{*2})}.$$

Proposition 5: The co-existence equilibrium point $E_2(x^*, y^*, z^*)$ is globally asymptotically stable if $M_1 > 0$, $M_2 > 0$, $P_3 > 0$ where $M_1 = A$, $M_2 = AB - H^2$ and $P_3 = ABC + 2FGH - AF^2 - BG^2 - CH^2 = C(AB - H^2) + G(FH - BG) + F(GH - AF)$ that is if $p > c(1-m)^2xx^*$ and $\frac{e(p - c(1-m)^2xx^*)}{p + c(1-m)^2x^2} \left(\xi_3 a + \frac{\xi_2 eb(1-m)x}{(p + c(1-m)^2x^2)} \right) > \xi_1(r + d_1)$.

5.2.5 Hopf - bifurcation analysis at $E_2(x^*, y^*, z^*)$

When the conversion coefficient e (conversion of prey population to juvenile predators) exceeds threshold value $e = e^{[HB]}$, the system (2.2) undergoes Hopf - bifurcation around the non-negative interior equilibrium point $E_2(x^*, y^*, z^*)$. The necessary and sufficient conditions for Hopf - bifurcation is that there exists $e = e^{[HB]}$ varies over $\mathbb{R}$, such that

- I. $A_i(e^{[HB]}) > 0$ for $i = 1, 2, 3$,
- II. $H(e = e^{[HB]}) = A_1(e^{[HB]})A_2(e^{[HB]}) - A_3(e^{[HB]}) = 0$,
- III. $\frac{d}{de}[\text{Re}(\lambda(e))]_{e=e^{[HB]}} \neq 0$,

where λ is the roots of the characteristic equation around to the interior equilibrium point $E_2(x^*, y^*, z^*)$.

Due to the property of continuity of the roots of $H(e = e^{[HB]})$, there exists an open interval $(e^{[HB]} - \epsilon, e^{[HB]} + \epsilon)$ (say) for some positive ϵ . Thus, for $e \in (e^{[HB]} - \epsilon, e^{[HB]} + \epsilon)$ the characteristic equation (5.2) has no roots whose real parts are negative.

Therefore, for $e = e^{[HB]}$, we have

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0, \quad (5.3)$$

which can be written as $(\lambda^2 + A_2)(\lambda + A_1) = 0$.

Now (5.3) has three roots, namely, $\lambda_{1,2} = \pm i\sqrt{A_2}$ and $\lambda_3 = -A_1$ at $e = e^{[HB]}$.

For $e^{[HB]} \in (e^{[HB]} - \epsilon, e^{[HB]} + \epsilon)$, the roots can be written as

$$\lambda_1(e) = \phi_1(e) + i\phi_2(e),$$

$$\lambda_2(e) = \phi_1(e) - i\phi_2(e),$$

$$\lambda_3(e) = -\phi_1(e).$$

Now, we verify the transversality condition

$$\frac{d}{de} [\operatorname{Re}(\lambda_j(e))]_{e=e^{[HB]}} \neq 0 \text{ for } j = 1, 2, 3.$$

Substituting $\lambda_1(e) = \phi_1(e) + i\phi_2(e)$ and $\lambda_1(e) = \phi_1(e) - i\phi_2(e)$ into the characteristic equation (5.3) and calculating the derivative, then separating the real and imaginary parts, we have

$$M_1(e)\phi_1'(e) - M_2(e)\phi_2'(e) + N_1(e) = 0,$$

$$M_2(e)\phi_1'(e) + M_1(e)\phi_2'(e) + N_2(e) = 0,$$

where

$$M_1(e) = 3\phi_1^2(e) + A_2(e) + 2A_1(e)\phi_1(e) - 3\phi_2^2(e),$$

$$M_2(e) = 2A_1(e)\phi_2(e) + 6\phi_1(e)\phi_2(e),$$

$$N_1(e) = A_2'(e)\phi_1(e) + A_1'(e)\phi_1^2(e) + A_3'(e) - A_1'(e)\phi_2^2(e),$$

$$N_2(e) = A_2'(e)\phi_2(e) + 2A_1'(e)\phi_1(e)\phi_2(e).$$

Notice that, $\phi_1(e^{[HB]}) = 0, \phi_2(e^{[HB]}) = \sqrt{A_2(e^{[HB]})}$, then we have $M_1(e^{[HB]}) = -2A_2(e^{[HB]})$,

$$M_2(e^{[HB]}) = 2A_1(e^{[HB]})\sqrt{A_2(e^{[HB]})}, \quad N_1(e^{[HB]}) = A_3'(e^{[HB]}) - A_1'(e^{[HB]})A_2'(e^{[HB]}) \text{ and } N_2(e^{[HB]}) = A_2'(e^{[HB]})\sqrt{A_2(e^{[HB]})}$$

Now,

$$\begin{aligned} \frac{d}{de} [\operatorname{Re}(\lambda(e))]_{e=e^{[HB]}} &= -\frac{M_2(e^{[HB]})N_2(e^{[HB]}) + M_1(e^{[HB]})N_1(e^{[HB]})}{M_1^2(e^{[HB]}) + N_1^2(e^{[HB]})} \\ &= -\frac{2A_1(e^{[HB]})\sqrt{A_2(e^{[HB]})} \times A_2'(e^{[HB]})\sqrt{A_2(e^{[HB]})}}{(-2A_2(e^{[HB]}))^2 + (2A_1(e^{[HB]})\sqrt{A_2(e^{[HB]})})^2} \\ &\quad - \frac{(-2A_2(e^{[HB]})) \times (A_3'(e^{[HB]}) - A_1'(e^{[HB]})A_2'(e^{[HB]}))}{(-2A_2(e^{[HB]}))^2 + (2A_1(e^{[HB]})\sqrt{A_2(e^{[HB]})})^2} \\ &= -\frac{2A_2(e^{[HB]})[A_1(e^{[HB]})A_2'(e^{[HB]}) - A_3'(e^{[HB]}) + A_1'(e^{[HB]})A_2(e^{[HB]})]}{4A_2(e^{[HB]})[A_2(e^{[HB]}) + (A_1(e^{[HB]})^2)]} \\ &= -\frac{2A_2(e^{[HB]})[A_1(e^{[HB]})A_2'(e^{[HB]}) - A_3'(e^{[HB]}) + A_1'(e^{[HB]})A_2(e^{[HB]})]}{4A_2(e^{[HB]})[A_2(e^{[HB]}) + (A_1(e^{[HB]})^2)]} \\ &= -\frac{A_1(e^{[HB]})A_2'(e^{[HB]}) - A_3'(e^{[HB]}) + A_1'(e^{[HB]})A_2(e^{[HB]})}{2(A_2(e^{[HB]}) + (A_1(e^{[HB]})^2))} \\ &\neq 0, \quad \text{when } A_1(e^{[HB]})A_2'(e^{[HB]}) - A_3'(e^{[HB]}) + A_1'(e^{[HB]})A_2(e^{[HB]}) \neq 0 \end{aligned}$$

and $\lambda_3(e^{[HB]}) = -A_1(e^{[HB]}) \neq 0$.

Therefore, the transversality condition holds. We can now state the results in the following proposition:

Proposition 6: When the conversion coefficient e crosses the threshold value $e = e^{[HB]}$, the system (2.2) undergoes Hopf - bifurcation around the interior equilibrium point $E_2(x^*, y^*, z^*)$.

6 Numerical simulation and discussion

This section deals with the relationship between the graphical representations and the theoretical analysis. Here, we perform numerical simulation to validate our analytical findings of the previous sections by making use of the computing software MATLAB R2015a and Maple 16. We consider the following set of parameter values:

$$a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, e = .52, r = 0.1, d_1 = 0.5, d_2 = 0.05, h = 0.01.$$

Now, putting this parameter values in the model system (2.2) and we obtain an axial equilibrium point $E_1(1.71, 0, 0)$ and a unique positive interior equilibrium point $E_2(0.155235, 0.184709, 0.345539)$. When there is only prey species in the system that is the predator free or axial equilibrium point $E_1(1.71, 0, 0)$ is unstable for the above set of parameter values. If we choose $e = 0.035$, then the axial equilibrium point $E_1(1.71, 0, 0)$ is locally asymptotically stable. Which is shown by Fig. 1. For interior equilibrium point $E_2(0.155235, 0.184709, 0.345539)$ we have to check the Routh-Hurwitz criteria. We see that $A_1 = 0.7914816916 > 0$, $A_3 = 0.04423222095 > 0$ and $A_1A_2 - A_3 = 0.02737669129 > 0$ i.e. the Routh-Hurwitz criteria satisfied and hence the model system (2.2) is locally asymptotically stable around interior equilibrium point E_2 for $e = 0.52$, which is shown in Fig. 2.

Moreover, the chosen set of parameter values satisfies the condition of global stability as mentioned in subsection 5.2.4 and hence the global stability of the system (2.2) around $E_2(0.155235, 0.184709, 0.345539)$ is ensured which has been depicted in Fig. 3. Now if we gradually increase the value of e , the model system (2.2) undergoes stable limit cycle oscillations for $e \approx 0.77$ from its stable position and the transversality condition satisfied. Thus the model system (2.2) experiences a Hopf - bifurcation with respect to the conversion coefficient e at the threshold value $e = e^{[HB]} \approx 0.77$ (see Fig. 4). For lower threshold value ($e < e^{[HB]} \approx 0.77$), the system is stable and for the upper threshold value ($e > e^{[HB]} \approx 0.77$) the system (2.2) shows oscillation with large amplitude which is shown in Fig. 6.

We also plot the bifurcation diagram of the model system (2.2) with respect to the transition rate r on the evolution of the juvenile predators to adult predators (see Fig. 7), where the value of e is fixed at the point 0.65 and other parameter values are same as previous ($a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, e = 0.65, d_1 = 0.5, d_2 = 0.05, h = 0.01$). From the bifurcation diagram Fig. 7, it can be observed that the model system (2.2) changes stability from the local asymptotically stability to limit cycle oscillations as the bifurcation parameter or transition rate r increases through bifurcation threshold value $r = r^{[HB]} \approx 0.13$. For $r < r^{[HB]} \approx 0.13$, the model system exhibits asymptotically stable and the system undergoes limit cycle oscillations for $r > r^{[HB]} \approx 0.13$ with large amplitude via Hopf - bifurcation.

If we gradually increase the value of the refuge parameter then the system (2.2) goes to stable position stepwise from its unstable position. If we consider the previous set of parameters with $m = 0.28$ then we will show that the system is stable (see Fig. 8).

(A) (B)

Figure 1: (A) The time diagram and (B) phase portrait show that the axial equilibrium point E_1 is locally asymptotically stable. The corresponding parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, r = 0.1, d_1 = 0.5, d_2 = 0.05, h = 0.01$ and $e = 0.035$. The initial values are $x(0) = 0.8, y(0) = 1.0, z(0) = 0.9$.

7 Conclusion

In this paper, we have studied a three-tier model of prey-juvenile predator-adult predator, in which adult predators have the ability to attack prey species and have reproductive capability. Also, they provide

(A) (B)

Figure 2: (A) The time diagram and (B) phase portrait show that the interior equilibrium point E_2 is locally asymptotically stable for the choosing parameter values with $e = 0.52$ and the other parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, r = 0.1, d_1 = 0.5, d_2 = 0.05, h = 0.01$ with the initial values $x(0) = 0.1, y(0) = 0.2, z(0) = 0.5$.

Figure 3: The diagram shows that the phase portrait starting from various initial points goes to interior equilibrium point E_2 globally. Here, the parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, e = 0.52, r = 0.1, d_1 = 0.5, d_2 = 0.05, h = 0.01$.

Figure 4: The bifurcation diagram of the system (2.2) corresponding to the bifurcating parameter $e = e^{[HB]} \approx 0.77$, where other parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, r = 0.1, d_1 = 0.5, d_2 = 0.05, h = 0.01$.

(A) (B)

Figure 5: (A) The time series and (B) phase-portrait diagram of the system (2.2) for limit cycle oscillation. The parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, r = 0.1, d_1 = 0.5, d_2 = 0.05, h = 0.01$ with $e = 0.9$. The initial condition is $x(0) = 0.0246, y(0) = 0.0293, z(0) = 0.2832$.

(A) (B)

Figure 6: (A) The time series plot and (B) 3D phase-portrait diagram of the system (2.2) around interior equilibrium point E_2 for $e = 0.85$. The phase-portrait shows that the system (2.2) is unstable when $e = 0.85$, the other parameter values remain same as in Fig. 5.

(A) (B) (C)

Figure 7: (A) The time series plot, (B) emergence of Hopf - bifurcation of prey, juvenile predators and adult predators with respect to the parameter r and (C) the 3D phase-portrait diagram representing stable limit point cycle. $r = r^{[HB]} \approx 0.13$. The other parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, m = 0.151, e = 0.65, d_1 = 0.5, d_2 = 0.05, h = 0.01$.

(A) (B) (C) (D) (E) (F)

Figure 8: The figure shows that the system (2.2) changes from unstable dynamics to a stable dynamics when refuge m is increased from 0 to 0.4 via 0.2. Here (A), (C), (E) represents the time series plot and (B), (D), (F) represents 3D phase-portrait diagram for $m = 0.0, 0.2, 0.4$ respectively, where other parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, c = 0.02, e = 0.65, r = 0.13, d_1 = 0.5, d_2 = 0.05, h = 0.01$.

(A) (B) (C) (D) (E) (F)

Figure 9: The figure shows that the system (2.2) changes from unstable dynamics to a stable dynamics when intra-specific among adult predators h is increased from 0 to 0.08 via 0.02. Here (A), (C), (E) represents the time series plot and (B), (D), (F) represents 3D phase-portrait diagram for $h = 0.0, 0.02, 0.08$ respectively, where other parameter values are $a = 1.51, b = 1.78, K = 1.71, p = 0.38, m = 0.2, c = 0.02, e = 0.65, r = 0.13, d_1 = 0.5, d_2 = 0.05$.

resources for both juvenile and adult predators, whereas juvenile predators have no ability to attack prey species, and they are fully dependent on their parents (adult predators). The model is realistic because we introduce the prey refuge and intra-specific competition among adult predators to remain under control to keep the ecological balance. The dynamical behaviour of the proposed model (2.2) in the vicinity of co-existence equilibrium point $E_2(x^*, y^*, z^*)$ is very significant as all the three species persist about E_2 . The co-existence equilibrium point $E_2(x^*, y^*, z^*)$ is rather difficult to assess explicitly. Therefore, we explore its existence and stability numerically; for the specific set of system parameter values.

Firstly, the predator-prey model is studied analytically and then for better understanding we have plotted their respective time diagram, phase-portrait, bifurcation diagram using numerical simulations. We have showed the positivity and boundedness of the system (2.2). Determining equilibrium points, we showed their local stability by Routh-Hurwitz criteria (see Fig. 1 and Fig. 2). We have also studied global stability at a positive interior equilibrium point and plotted a phase-portrait diagram using various initial conditions. Furthermore, analytical results for a Hopf-bifurcation at the co-existence equilibrium point are determined. Numerical evidence supports this finding. We have plotted a bifurcation diagram with respect to two different parameters one is the conversion coefficient e from the prey species to the juvenile predators (see Fig. 4) and the other one is the transition rate r from juvenile predators to adult predators (see Fig. 7). To understand the real world situation better, one may interpret such type of phenomena in the following way: the conversion coefficient e increases for some of its threshold level, then the number of prey species decline slowly, and the number of juvenile predators increases primarily because of the accessibility of sufficient resource but after that the curve decline because of inaccessibility of the prey species. This exhibit the stochastic effects may lead to the catastrophe of the ecological system dynamics.

We pay attention to the system dynamics by varying the key parameters m and h . For the variation of the refuge parameter m , we have examined different limit cycles and stable focus. It is perceived that the model system settles down into a stable focus through different nonlinear behaviour. In addition, we have examined that the role of intra-specific competition factor among adult predators h on the system dynamics. Consequently, one may conclude that refugia and intra-specific competition factor among adult predators play a vital function in controlling system dynamics and giving a sustained eco-system where all species survive smoothly, and it can assist to sustain ecological balance.

We have added a prey refuge and intra-specific competition among adult predators in this model. When the level of refuge is of 0%, that is, there is no prey refuge in the system, the system is unstable. When we gradually increase the level of refuge from 0% to 20% and 20% to 40% we observe that the system goes to a stable dynamics from an unstable limit cycle and a stable of small amplitude oscillation from a stable of large amplitude oscillation (see Fig. 8). Similarly, when there is no intra-specific competition among adult predators, the system (2.2) shows unstable behaviour. If we increase the competitive effect in the system, the system (2.2) goes from an unstable system to a stable system (see Fig. 9) and this type of effects we can see among predator-prey in the real world. Based on the results of the prey refuge and the impact on the trajectory blueprints for the predator-prey interaction, ecologists must be careful in giving predictions of the interaction between the prey and predator in the case of the intra-specific competition among predators, where the credibility of this result can be affected by the dynamic behaviour.

Acknowledgments

We are thankful to the anonymous referees for their invaluable remarks, which contributed to the improvement in the presentation of the paper. The first author of this research manuscript thankfully acknowledges the financial support in part from Special Assistance Programme (SAP-III) sponsored by

the University Grants Commission (UGC), New Delhi, India (Grant No. F.510 / 3 / DRS-III / 2015 (SAP-I)). The third author is thankful to UGC(BSR)-Start Up Grant (Grant No.F.30-361/2017(BSR)), University Grants Commission, New Delhi

References

- Ali, N. and Chakravarty, S. 2014. Consequence of prey refuge in a tri-trophic prey-dependent food chain model with intra-specific competition, *Journal of Applied Nonlinear Dynamics* **3**(1): 1–6.
- Ali, N., Mondal, B., Guin, L. N. and Chakravarty, S. 2018. Dynamics of species in a two preys-one predator model system with help, *International Journal of Mathematics and Computation* **29**(1): 106–121.
- Ali, N., Sarkar, K. and Guin, L. N. 2019a. A predator-prey model with Crowley-Martin response for predation, *International Journal of Ecological Economics & Statistics* **40**(2): 38–48.
- Ali, N., Sarkar, K. and Guin, L. N. 2019b. Ratio-dependent predator-prey model with Qiwu's growth for prey, *International Journal of Ecological Economics & Statistics* **40**(3): 50–58.
- Bhattacharya, S. and Martcheva, M. 2010. Oscillations in a size-structured prey-predator model, *Mathematical Biosciences* **228**(1): 31–44.
- Bhattacharya, S., Martcheva, M. and Li, X.-Z. 2014. A predator-prey disease model with immune response in infected prey, *Journal of Mathematical Analysis and Applications* **411**(1): 297–313.
- Ganguli, C. and Kar, T. 2019. Maintenance of yield maximization and species conservation perspective in a three species food chain model, *International Journal of Ecological Economics & Statistics* **40**(1): 95–117.
- Guin, L. N., Das, E. and Sambath, M. 2020. Pattern formation scenario through Turing instability in interacting reaction-diffusion systems with both refuge and nonlinear harvesting, *Journal of Applied Nonlinear Dynamics* **9**(1): 1–21.
- Haldane, J. 1965. *Enzymes*, Reprint by MIT, Cambridge.
- Han, R., Guin, L. N. and Dai, B. 2020. Cross-diffusion-driven pattern formation and selection in a modified Leslie-Gower predator-prey model with fear effect, *Journal of Biological Systems* **28**(01): 27–64.
- Haque, M., Ali, N. and Chakravarty, S. 2013. Study of a tri-trophic prey-dependent food chain model of interacting populations, *Mathematical Biosciences* **246**(1): 55–71.
- Hu, G.-P. and Li, W.-T. 2010. Hopf bifurcation analysis for a delayed predator-prey system with diffusion effects, *Nonlinear Analysis: Real World Applications* **11**(2): 819–826.
- Khajanchi, S. 2017. Modeling the dynamics of stage-structure predator-prey system with Monod–Haldane type response function, *Applied Mathematics and Computation* **302**: 122–143.
- Layek, G. 2015. *An Introduction to Dynamical Systems and Chaos*, Springer.
- May, R. M. 1972. Limit cycles in predator-prey communities, *Science* **177**(4052): 900–902.
- Medvinsky, A. B., Petrovskii, S. V., Tikhonova, I. A., Malchow, H. and Li, B.-L. 2002. Spatiotemporal complexity of plankton and fish dynamics, *SIAM Review* **44**(3): 311–370.
- Nagumo, M. 1942. Über die lage der integralkurven gewöhnlicher differentialgleichungen, *Proceedings of the Physico-Mathematical Society of Japan; 3rd Series* **24**: 551–559.

- Qu, Y. and Wei, J. 2007. Bifurcation analysis in a time-delay model for prey-predator growth with stage-structure, *Nonlinear Dynamics* **49**(1-2): 285–294.
- Sambath, M. and Gokila, C. 2019. Stability and bifurcation analysis of three species predator-prey model with Holling Type II, *Discontinuity, Nonlinearity, and Complexity* **8**: 127–144.
- Sokol, W. and Howell, J. 1981. Kinetics of phenol oxidation by washed cells, *Biotechnology and Bio-engineering* **23**(9): 2039–2049.
- Song, Y., Peng, Y. and Wei, J. 2008. Bifurcations for a predator-prey system with two delays, *Journal of Mathematical Analysis and Applications* **337**(1): 466–479.
- Wu, X., Li, J. and Wang, Z. 2008. Existence of positive periodic solutions for a generalized prey-predator model with harvesting term, *Computers & Mathematics with Applications* **55**(8): 1895–1905.
- Xiao, D. and Ruan, S. 2001. Multiple bifurcations in a delayed predator-prey system with nonmonotonic functional response, *Journal of Differential Equations* **176**(2): 494–510.