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A delayed predator-prey system with modified Holling-Tanner response

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Abstract
The paper deals with a delayed prey predator model with the incorporation of modified Holling- *Tanner functional response. The model highlights the loss in prey population via migration and the natural death rate due to age factor and other reasons such as prenatal death, infection etc. The model also considers the significance of delay in the predator population which is taken as a parameter of bifurcation. Local stability analysis is done in the paper and it is examined that delay is important in attaining stability of the system. Hopf bifurcation has been discussed in brief and stability of bifurcated periodic solutions using normal form theory and central manifold theorem has been applied. Numerical simulations asserts the theory at the end of the paper.*
Key words: *Predator-prey, Migration, Local Stability.*

1. Introduction

The analysis of prey-predator models has gained momentum from many ecologists and biologists. Various types of models are proposed for the study of prey predator interaction. The incorporation of delay in differential equations is significant to describe the dynamics. Many delay version of the models are available in literature.

In[**1**], Leslie type of predator prey system with the inclusion of Holling type II functional response is investigated which has the following form;

$$\begin{cases} \frac{dx}{dt} = rx\left(1-\frac{x}{k}\right) - \frac{mx}{A+x}y, \\ \frac{dy}{dt} = y\left[s\left(1-h\frac{y}{x}\right)\right], \end{cases} \tag{1.1}$$

Where, x and y are prey and predator population density. System (1.1) has been studied thoroughly in literature [**1**]. System (1.1) is modified further by incorporating Beddington-DeAngelis functional response in [**2**] which is of the following form;

$$\begin{cases} \frac{dx}{dt} = rx\left(1-\frac{x}{k}\right) - \frac{\alpha xy}{a+bx+cy}, \\ \frac{dy}{dt} = y\left[s\left(1-h\frac{y(t-\tau)}{x(t-\tau)}\right)\right], \end{cases} \tag{1.2}$$

where x and y denote the prey and predator densities respectively. The expression $\frac{\alpha xy}{a+bx+cy}$ is known as Beddington-DeAngelis functional response.

The system (1.2) is written in dimensionless form by taking $\tilde{t} = rt$, $\tilde{x} = \frac{x(t)}{K}$, $\tilde{y} = \frac{\alpha y(t)}{rK}$, and ignoring the tildes, we get as,

$$\begin{cases}\frac{dx}{dt} = x(1-x) - \frac{xy}{a_1+bx+c_1y}, \\ \frac{dy}{dt} = y\left[\left(\delta - \beta\frac{y(t-\tau)}{x(t-\tau)}\right)\right],\end{cases} \tag{1.3}$$

Where, $\delta = \frac{s}{r}, \beta = \frac{sh}{\alpha}$, $a_1 = \frac{a}{K}, c_1 = \frac{cr}{\alpha}, \tilde{\tau} = r\tau.$ System (1.3) is studied from the perspectives of local and global stability of the equilibrium[**2**]. Model (1.3) is investigated further in [**3**] and the stability of positive equilibrium and Hopf bifurcation are examined along with the study of direction of Hopf bifurcation and stability of bifurcated periodic solutions.

Moreover, the model (1.3) is considered to study the significance of refuge in the system [**4**]. Main aspect of the study is the incorporation of prey refuge in the system (1.3) and the model takes the form as;

$$\begin{cases}\frac{dx}{dt} = x(1-x) - \frac{(1-m)xy}{a_1+bx+c_1y}, \\ \frac{dy}{dt} = y\left[\left(\delta - \beta\frac{y(t-\tau)}{x(t-\tau)} + (1-m)x\right)\right],\end{cases} \tag{1.4}$$

where x and y are the prey and predator densities. The parameter m represents the prey refuge with range as $0 < m < 1.$ Initial values are $x(0) > 0, y(0) > 0.$ $a_1, b, c_1, \delta, \beta$ are the positive constants.

Prey predator relationship is studied well in literature which reflects the role of migration using Holling type IV functional response in [**5**]. The system is defined as below;

$$\begin{cases}\frac{dx}{dt} = x(1-x) - \frac{(1-m)xy}{a_1+bx+c_1x^2} - m_1x, \\ \frac{dy}{dt} = y\left[\left(\delta - \varepsilon\frac{y(t-\tau)}{x(t-\tau)}\right)\right] - m_2y,\end{cases} \tag{1.5}$$

Where, m_1, m_2 denote the migration in prey and predator population.

In this paper, we modify the above system by incorporating ratio dependent functional response along with time delay factor and the system becomes as;

$$\begin{cases}\frac{dx}{dt} = rx\left(1-\frac{x}{k}\right) - \frac{(1-m)xy}{a'y+x} - dx - m'_1x, \\ \frac{dy}{dt} = y\left[s\left(1 - h\frac{y(t-\tau)}{x(t-\tau)}\right)\right],\end{cases}$$

Now by using , $\tilde{t} = rt, \delta = \frac{s}{r}, \tilde{x} = \frac{x(t)}{K}, \tilde{y} = \frac{y(t)}{rK}, a'r = a,\ \tilde{\tau} = r\tau,\ m_1 = \frac{d+m'_1}{r},,\ hr = \varepsilon$

The system becomes as,

$$\begin{cases}\frac{dx}{dt} = x(1-x) - \frac{(1-m)xy}{ay+x} - m_1x, \\ \frac{dy}{dt} = y\left[\left(\delta - \varepsilon\frac{y(t-\tau)}{x(t-\tau)}\right)\right],\end{cases} \tag{1.6}$$

Where, m_1 denote the loss in prey population due to migration and other factors such as prenatal death, adult death due to some infection etc. Rest of the parameters same as above.

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In the paper, the stability of positive equilibrium along with the Hopf bifurcation process is discussed in a precise way.
The rest of the paper is as follows. In Section 2, stability of positive equilibrium and the existence of Hopf bifurcation are discussed. Section 3 comprises of the direction of Hopf bifurcation and stability of bifurcated periodic solutions are investigated. The theory has been verified by numerical simulation in Section 4 and Section 5 provides the conclusion.

2. Stability of positive equilibrium and Hopf bifurcation

The system (1.6) has unique positive equilibrium say $E^*(x^*, y^*)$, where x^* and y^* are given as;

$$x^* = \frac{(1-m_1)(a(\delta-m_2)+\delta\varepsilon)-(1-m)(\delta-m_2)}{(a(\delta-m_2)+\delta\varepsilon)}, \quad y^* = \frac{(\delta-m_2)x^*}{\delta\varepsilon}$$

Initially, we examine the dynamics of the system without delay.
The variational matrix has the following form as,

$$J=\begin{pmatrix}\alpha_{11} & \alpha_{12}\\ \alpha_{21} & \alpha_{22}\end{pmatrix},$$

Where,
$\alpha_{11} = 1-2x^* - \frac{(1-m)ay^{*2}}{(x^*+ay^*)^2} - m_1$ $\alpha_{12} = \frac{-(1-m)x^{*2}}{(x^*+ay^*)^2}$, $\alpha_{21} = \frac{\delta\varepsilon {y^*}^2}{x^{*2}} - m_2$, $\alpha_{22} = \delta - \frac{2\delta\varepsilon y^*}{x^*} - m_2$ and the characteristic equation is a quadratic equation is given by
$\lambda^2 - (Tr.\ J)\lambda + (Det.J) = 0$ or $\lambda^2 - (\alpha_{11}+\alpha_{22})\lambda + (\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}) = 0.$
Using Routh-Hurwitz criteria for determining the stability of the system under consideration. We have,
$Det.J = \alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} = [1-2x^* - \frac{(1-m)ay^{*2}}{(ay^*+x^*)^2} - m_1][\delta - \frac{2\delta\varepsilon y^*}{x^*} - m_2] + [\frac{-(1-m)x^{*2}}{(x^*+ay^*)^2}][\frac{\delta\varepsilon {y^*}^2}{x^{*2}} - m_2] > 0,$
and
$traceJ = \alpha_{11} + \alpha_{22} < 0.$

The condition $(\alpha_{11}+\alpha_{22}) < 0$ is required for the asymptotically stability of the model without delay. Hence, we can state the following Theorem.

Theorem 2.1. *Equilibrium $E^*(x^*, y^*)$ of System (1.6) without delay is locally asymptotically stable if the following conditions are satisfied:*
(H_1) $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$
(H_2) $(\alpha_{11}+\alpha_{22}) < 0.$

Now, we investigate the condition for Hopf bifurcation as done in [**3**]. The linearalized form of the model (1.6) is as follows,

$$\begin{cases} u_1'(t) = \alpha_{11}u_1(t) + \alpha_{12}u_2(t), \\ u_2'(t) = \alpha_{21}u_1(t-\tau) + \alpha_{22}u_2(t-\tau). \end{cases} \tag{2.1}$$

The characteristics equation may be written as

$\lambda^2 - (\alpha_{11} + \alpha_{22})\lambda + (-\beta_{22}\lambda + \alpha_{11}\beta_{22} - \beta_{21}\alpha_{21})e^{-\lambda\tau} + \alpha_{11}\alpha_{22} - \alpha_{21}\alpha_{12} = 0$
(2.2)

Where, $\beta_{22} = \frac{-\delta\varepsilon y^*}{x^*}$ and , $\beta_{21} = \frac{\delta\varepsilon y^{*2}}{x^{*2}}$

Now, put $\lambda = i\omega$ in Eq. (2.2), we get,

$-\omega^2 + (\alpha_{11}\alpha_{22} - \alpha_{12}\beta_{21})\cos\omega\tau - \beta_{22}\omega\sin\omega\tau + \alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} + i\{-\beta_{22}\omega\cos\omega\tau - (\alpha_{11}\beta_{22} - \beta_{21}\alpha_{21})\sin\omega\tau - \alpha_{11}\omega - \alpha_{22}\omega\} = 0 + i0.$

Separating real and imaginary parts, we get,

$$-\omega^2 + (\alpha_{11}\alpha_{22} - \alpha_{12}\beta_{21})\cos\omega\tau - \beta_{22}\omega\sin\omega\tau + \alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} = 0 \qquad (2.3)$$

$$\{-\beta_{22}\omega\cos\omega\tau - (\alpha_{11}\beta_{22} - \beta_{21}\alpha_{21})\sin\omega\tau - \alpha_{11}\omega - \alpha_{22}\omega\} = 0 \qquad (2.4)$$

Squaring and adding Eq. (2.3) & (2.4), we get,

$$\omega^4 + \left({\alpha_{11}}^2 + {\alpha_{22}}^2 - \beta_{22}^2 - 2\alpha_{21\alpha_{12}}\right)\omega^2 + (2\alpha_{11}\alpha_{22}\alpha_{21}\beta_{21}) + (\alpha_{21}\alpha_{12})^2 + \alpha_{21}^2\beta_{21}^2 - 2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12} = 0. \qquad (2.5)$$

If we put $z = \omega^2$, we get,

$$z^2 + \left({\alpha_{11}}^2 + {\alpha_{22}}^2 - \beta_{22}^2 - 2\alpha_{21\alpha_{12}}\right)z + (2\alpha_{11}\alpha_{22}\alpha_{21}\beta_{21}) + (\alpha_{21}\alpha_{12})^2 + \alpha_{21}^2\beta_{21}^2 - 2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12} = 0. \qquad (2.6)$$

which is a quadratic equation, hence the roots are

$$z = -\frac{\left({\alpha_{11}}^2+{\alpha_{22}}^2-\beta_{22}^2-2\alpha_{21\alpha_{12}}\right) \pm \sqrt{\left({\alpha_{11}}^2+{\alpha_{22}}^2-\beta_{22}^2-2\alpha_{21\alpha_{12}}\right)2+4(\alpha_{21}^2\beta_{21}^2-2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12+-2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12}}}}{2}. \qquad (2.7)$$

Taking the positive root only.

Denoting positive roots by $\omega_{pos.}$, therefore , we have,

$$\omega_{pos.} = \sqrt{\frac{\left({\alpha_{11}}^2+{\alpha_{22}}^2-\beta_{22}^2-2\alpha_{21\alpha_{12}}\right)+\sqrt{\left({\alpha_{11}}^2+{\alpha_{22}}^2-\beta_{22}^2-2\alpha_{21\alpha_{12}}\right)2+4(\alpha_{21}^2\beta_{21}^2-2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12+-2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12}}}}{2}}. \qquad (2.8)$$

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Now solving Eq. (2.3) & (2.4), we get the values of τ say critical value(s) of the form

$$\tau_j = \frac{1}{\omega_{pos}} \cos^{-1} \frac{\omega_{pos}^2(\alpha_{11}\alpha_{22-}\beta_{21}\alpha_{21} - \alpha_{11}\beta_{22} - \alpha_{22}\beta_{22}) - \alpha_{11}\alpha_{22}\omega_{pos}}{(\alpha_{11}\alpha_{22} - \alpha_{12}\beta_{21})^2 + \beta_{22}^2\omega_{pos}^2} + \frac{2\pi j}{\omega_{pos}},$$

where $j = 0,1,2, \ldots.$

Denote one of the set of critical value of τ as τ_{cr} and we get,

$$\tau_{cr} = \frac{1}{\omega_{pos}} \cos^{-1} \frac{\omega_{pos}^2(\alpha_{11}\alpha_{22-}\beta_{21}\alpha_{21} - \alpha_{11}\beta_{22} - \alpha_{22}\beta_{22}) - \alpha_{11}\alpha_{22}\omega_{pos}}{(\alpha_{11}\alpha_{22} - \alpha_{12}\beta_{21})^2 + \beta_{22}^2\omega_{pos}^2}.$$

Now, we can state the following lemma by the above discussion and using Rouche's theorem, similar to J.-F Zhang [**3**];

Lemma 2.2: *Assume that positive equilibrium point of system (1.4) without delay is locally asymptotically stable. Then at*

$$\tau_j = \frac{1}{\omega_{pos}} \cos^{-1} \frac{\omega_{pos}^2(\alpha_{11}\alpha_{22-}\beta_{21}\alpha_{21} - \alpha_{11}\beta_{22} - \alpha_{22}\beta_{22}) - \alpha_{11}\alpha_{22}\omega_{pos}}{(\alpha_{11}\alpha_{22} - \alpha_{12}\beta_{21})^2 + \beta_{22}^2\omega_{pos}^2} + \frac{2\pi j}{\omega_{pos}},$$

($j = 0,1,2 \ldots$), system (2.5) has a pair of pair of conjugate purely imaginary roots $\pm i\omega_{pos}$, where

$$\omega_{pos.} = \sqrt{\frac{({\alpha_{11}}^2+{\alpha_{22}}^2-\beta_{22}^2-2\alpha_{21\alpha_{12}})+\sqrt{({\alpha_{11}}^2+{\alpha_{22}}^2-\beta_{22}^2-2\alpha_{21\alpha_{12}})2+4(\alpha_{21}^2\beta_{21}^2-2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12+-2\alpha_{11}\alpha_{22}\alpha_{21}\alpha_{12}}}}{2}}.$$

Furthermore, we have the following results

(i) *If $\tau \in [0, \tau_{cr})$, then all roots of system (1.6) have negative real parts.*

(ii) *If $\tau = \tau_{cr}$, system (1.6) has a pair of conjugate purely imaginary roots $\pm i\omega_{pos}$, and all other roots have negative real parts.*

Let $\lambda = \nu(\tau) + i\omega(\tau)$ be the root of the characteristic equation (2.2) with the condition that when $\tau = \tau_{cr}$,

$$\begin{cases} \nu(\tau_{cr}) = 0, \\ \omega(\tau_{cr}) = \omega_{pos.} \end{cases}$$

After differentiating (2.2) with respect to τ, and after simplifying, we get

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda - \alpha_{11} - \alpha_{22}e^{-\lambda\tau})}{(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} - \alpha_{22}\lambda)} - \frac{\tau}{\lambda}. \qquad (2.9)$$

Therefore,

$$\left[Re\left(\frac{d\lambda}{d\tau}\right)^{-1}\right]_{i\omega_{pos}} = \frac{\omega_{pos}^2}{(\alpha_{22}^2\omega_{pos}^4 + (\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})^2\omega_{pos}^2)}\sqrt{({\alpha_{11}}^2 - {\alpha_{22}}^2)^2 + 4(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})^2}$$

now $(\alpha_{22}^2\omega_{pos}^4 + (\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})^2\omega_{pos}^2) > 0$, thus, we have,

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$$\left[Re\ \left(\frac{d\lambda}{d\tau}\right)^{-1}\right]_{i\omega_{pos}} > 0, \tag{2.10}$$

therefore the transversality condition is proved. Now we can state the bifurcation theorem for the proposed system (1.6);

Theorem 2.2. *Suppose the condition of Theorem 2.1 holds.*

(i) *If* $\tau \in [0, \tau_{cr})$, *the positive equilibrium* $E^*(x^*, y^*)$ *of system (1.6) is asymptotically stable.*

(ii) *If* $\tau > \tau_{cr}$, *the positive equilibrium* $E^*(x^*, y^*)$ *of system (1.6) is unstable.*

(iii) *System (1.6) observe Hopf bifurcation at the positive equilibrium* $E^*(x^*, y^*)$ *when* $\tau = \tau_j$, *where*

$$\tau_j = \frac{1}{\omega_{pos}} \cos^{-1} \frac{\omega_{pos}^2(\alpha_{11}\alpha_{22} - \beta_{21}\alpha_{21} - \alpha_{11}\beta_{22} - \alpha_{22}\beta_{22}) - \alpha_{11}\alpha_{22}\omega_{pos}}{(\alpha_{11}\alpha_{22} - \alpha_{12}\beta_{21})^2 + \beta_{22}^2\omega_{pos}^2} + \frac{2\pi j}{\omega_{pos}}$$

$$j = 0,1,2, \ldots.$$

3. Direction of Hopf bifurcation

In this section, we discuss in brief about the direction of Hopf bifurcation and stability of bifurcated periodic solutions by the application of normal form theory and central manifold reduction theorem which has been introduced by Hassard et al.[**7**]. Many theories of this perspective have also been studied in literature. It is observed by Theorem 2.2 that system (1.6) undergoes a Hopf bifurcation at some specified values of τ, these values are denoted by τ_j. As a matter of generalization, we denote any one such value by $\bar{\tau}$ and at $\bar{\tau}$ the characteristic equation has a pair of imaginary roots $\pm i\omega_{pos}$. As the procedure being discussed in Hassard et al. [**7**], we proceed in a similar manner. For the reduction of system (1.6) a system of functional differential equation is used. Moreover, we denote such delay τ as $\tau = \bar{\tau} + \mu$, where μ is an element of the set of real numbers. Further $\mu = 0$ is the value of Hopf bifurcation of system (1.6). On rescaling the time by $\rightarrow \frac{t}{\tau}$. System (1.6) takes the form

$$u'(t) = L_\mu u_t + F(u_t, \mu), \tag{3.1}$$

in the Banach space $\mathbb{C}([-1, 0], \mathbb{R}^2)$, where $u = \binom{u_1}{u_2} \in \mathbb{C}$, and $L_\mu: \mathbb{C} \rightarrow \mathbb{R}$, $F: \mathbb{R} \times \mathbb{C} \rightarrow \mathbb{R}$ has been obtained in J.-F Zhang[**3,6,7**]. We proceed in a similar way as in [**3,6,7**] and we can obtain the following values (with usual symbols as obtained in [**3**]):

$$C_1(0) = \frac{i}{2\omega_{pos}\bar{\tau}}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2},$$

$$\mu_2 = \frac{Re\{C_1(0)\}}{Re\{\lambda'(\bar{\tau})\}} \text{ and } \beta_2 = 2Re\{C_1(0)\}.$$

Now we can state the following theorem:

Theorem 3.1.

(i) μ_2 determines the directions of Hopf bifurcation. If $\mu_2 > 0 (< 0)$, the Hopf bifurcation is supercritical(subcritical);

(ii) β_2 determines the stability of bifurcated periodic solutions. If $\beta_2 > 0(< 0)$, the bifurcated periodic solutions are stable (unstable).

4. Numerical simulations

We studied effect of delay and refuge on the modified Holling-Tanner predator-prey model with loss in population factor but as there is a limitation of the real parameters. So, theoretical results are affirmed by taking hypothetical set of parameters as in [**3,4,5**]. We consider the following numerical example as:

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{0.4xy}{3y+x} - 0.5x, \\ \dfrac{dy}{dt} = y\left[3.5 - 2\dfrac{y(t-\tau)}{x(t-\tau)}\right] - 0.5y. \end{cases} \tag{4.1}$$

By taking $(1-m) = 0.4$ and it is observed that system (4.1) has a positive equilibrium $E^*(2.6,\ 0.4)$. By lemma 2.1, we calculate $\omega_{pos} = 2.846$ and $\tau_{cr} = 0.39$. It is to be remarked that $\alpha_{11} + \alpha_{22} < 0$, hence $E^*(2.6,\ 0.4)$ of the system (4.1) is locally stable without the delay term τ. By theorem, it may be concluded that $E^*(2.6,\ 0.4)$ is asymptotically stable if $\tau \in [0,0.39)$ and unstable if $\tau > 0.39$. It is to observed that, Hopf bifurcation occurs at $\tau = 0.39$. Solution curves of (4.1) for $\tau = \tau_{cr} = 0.39$, 0.43 $(> \tau_{cr})$ and 0.21 $(< \tau_{cr})$ respectively are given in Fig. (1-3). It is to be noticed that the graphs are accordance with the theoretical formulation of the results. System shows Hopf bifurcation at some specific value of delay at the positive equilibrium which determines that delay has a significance effect on the dynamics. Furthermore, effect of refuge is examined which depicts that refuge in prey will ultimately effect the predator population so ultimately system changes if much refuge is present .

(a) (b)

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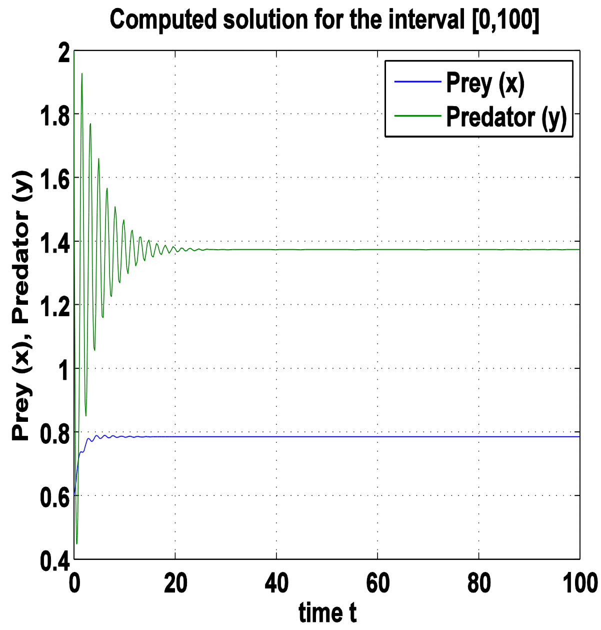

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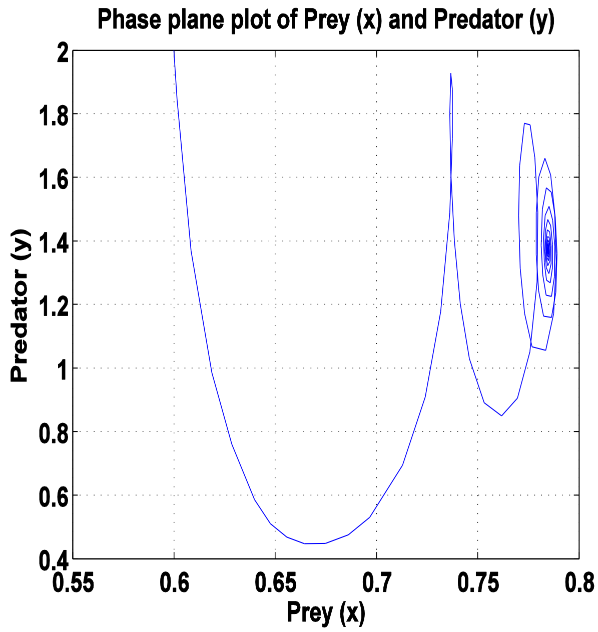

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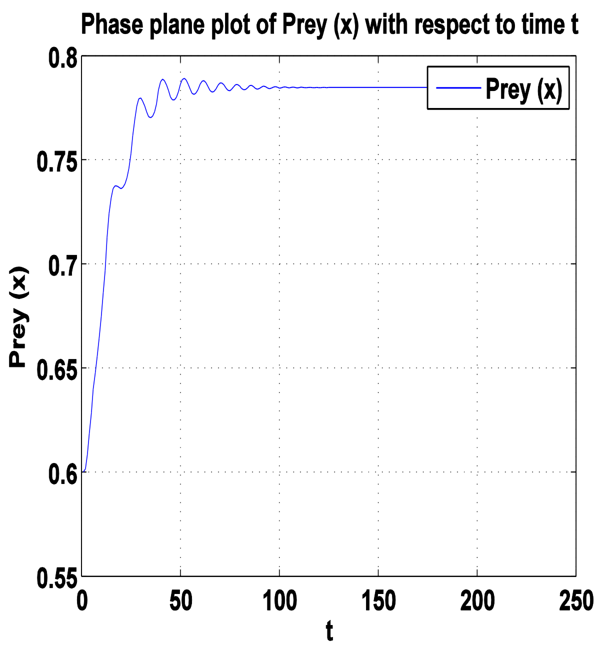

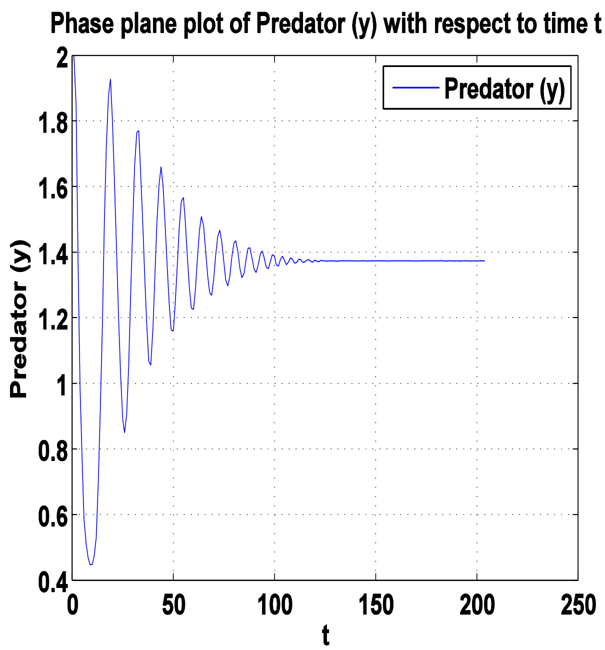

Fig. 1. Solution curves of System (4.1) with $(1-m) = 0.4$ and $\tau = 0.39$ computed over the interval [0,100].

(a) (b)

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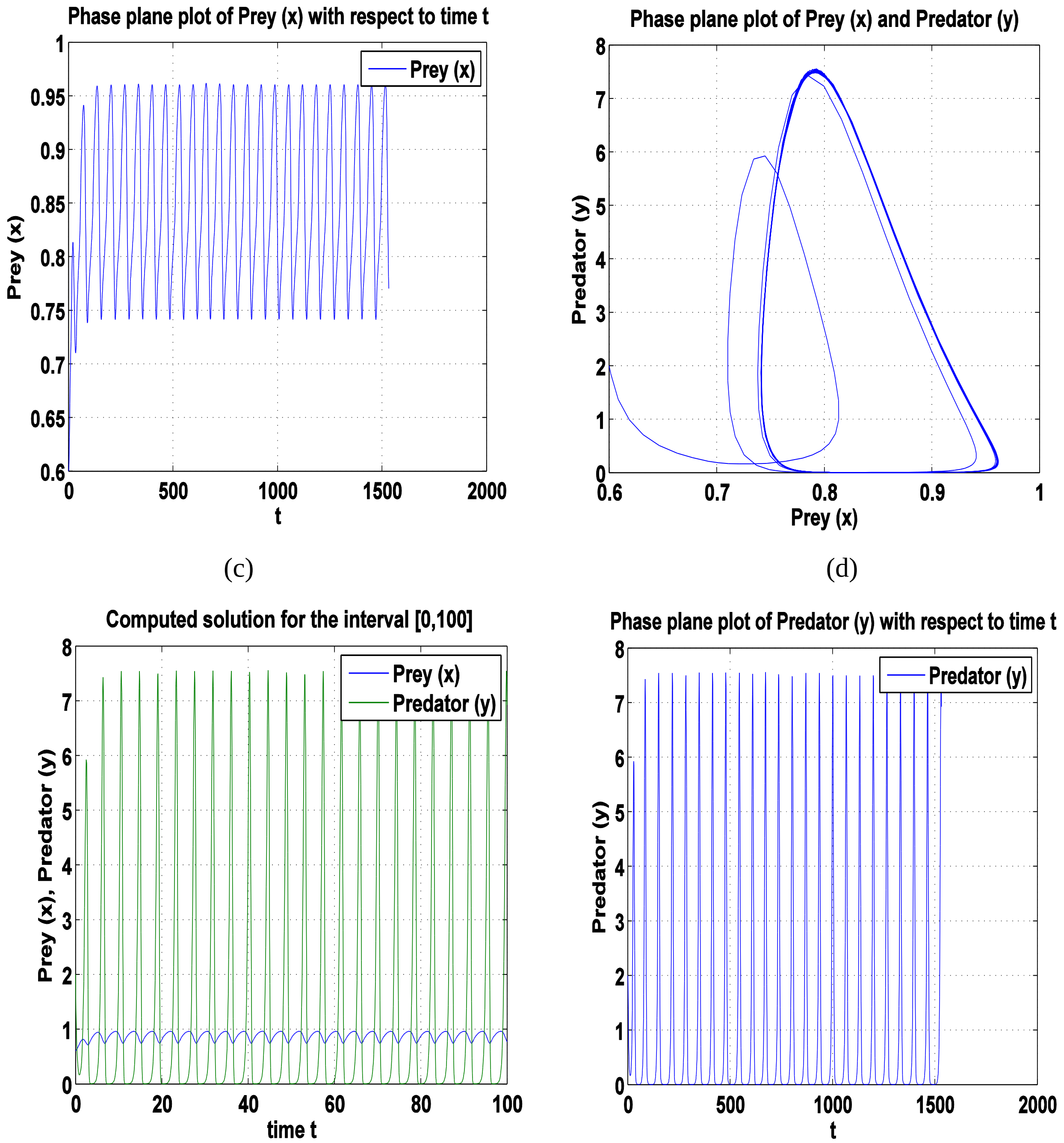

Fig. 2. Solution curves of System (4.1) with $(1-m) = 0.4$ and $\tau = 0.43 > \tau_{cr} = 0.38$ computed over the interval [0,100].

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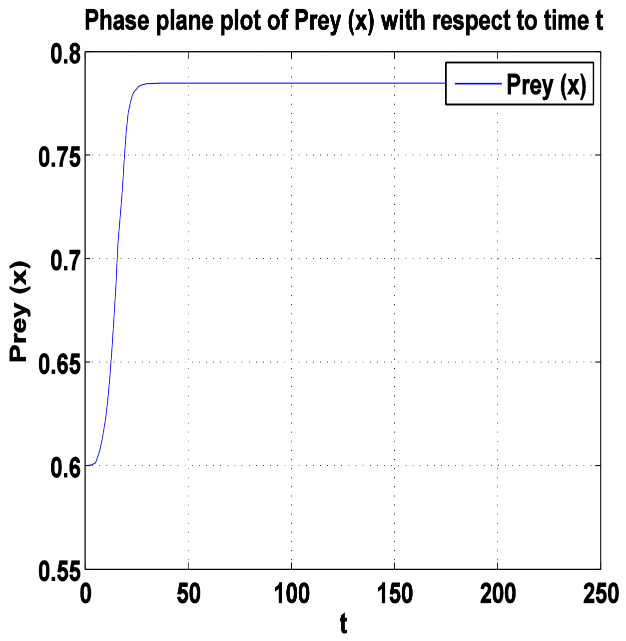
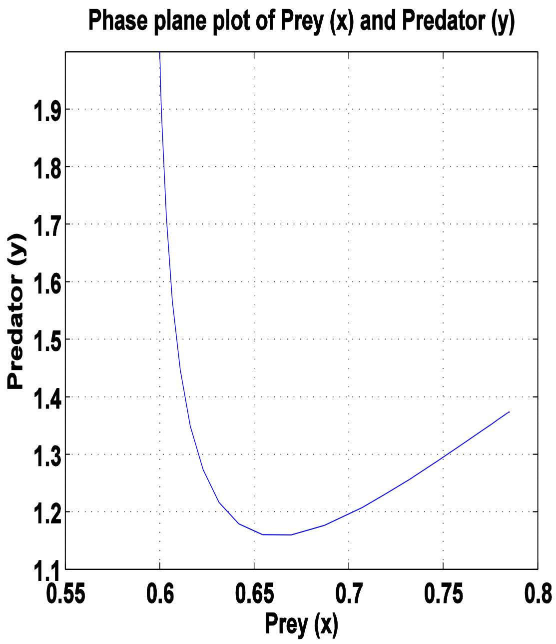
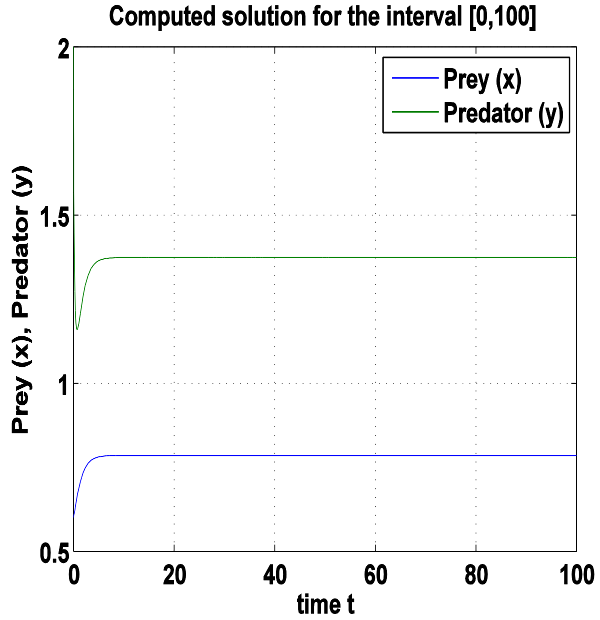
(a)



(b)



(c)



(d)

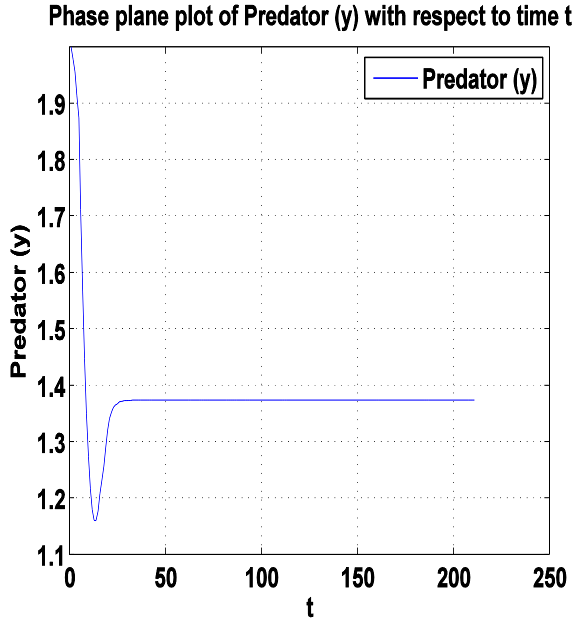


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Fig. 3. Solution curves of System (4.1) with $(1-m) = 0.4$ and $\tau = 0.21 < \tau_{cr} = 0.39$ computed over the interval [0,100].

(a) (b)

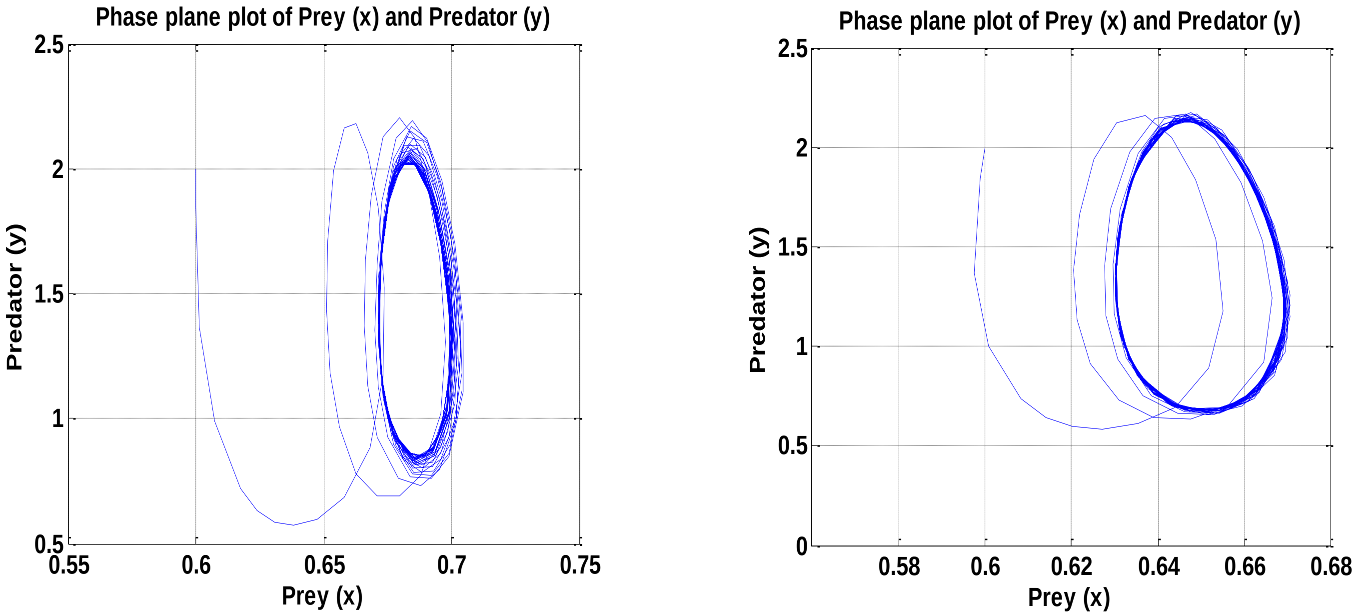

Fig. 4.Solution curve of System (4.1) with (a) (1-m) = 0.7, (b)=0.9 and $\tau = \tau_{cr} = 0.39$ computed over the interval [0,100] for both (a) & (b)

5. Discussion

In this paper, we have analysed a delayed prey-predator system with modified Holling-Tanner functional response and also the interaction between prey and predator is governed by ratio dependent functional response[**8,9**]. If we consider $m = 0$ in (1.6), then system has no role of refuge and a simple version of ratio dependent model is obtained. Also, model [**3**] is a particular case of system (1.4) . Limitations of our study is the non availability of real parameters. Even though a numerical example is provided in section 4 to validate the theory. Also, for the different values of m(refuge), system is analysed which depicts that as the value of refuge is changing i.e. more refuge to prey means less predation, so ultimately it will result in decrease predator density. Therefore, interaction among prey population leads to an unstable system of the existent stable system.

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