J. Math. Anal. Appl. 358 (2009) 389–402

Contents lists available at ScienceDirect

Journal of Mathematical Analysis and Applications

www.elsevier.com/locate/jmaa

Dynamical analysis of a delayed ratio-dependent Holling–Tanner predator–prey model

Tapan Saha [a,*], Charugopal Chakrabarti [b]

[a] Department of Mathematics, Haldia Government College, East Midnapore 721657, India
[b] Department of Applied Mathematics, University of Calcutta, Kolkata 700009, India

ARTICLE INFO

Article history:
Received 1 May 2008
Available online 3 May 2009
Submitted by P.G.L. Leach

Keywords:
Holling–Tanner model
Ratio-dependent response
Time delay
Hopf-bifurcation
Blow up transformation
Lyapunov function
Global asymptotic stability

ABSTRACT

In this paper, a delayed Holling–Tanner predator–prey model with ratio-dependent functional response is considered. It is proved that the model system is permanent under certain conditions. The local asymptotic stability and the Hopf-bifurcation results are discussed. Qualitative behaviour of the singularity $(0, 0)$ is explored by using a blow up transformation. Global asymptotic stability analysis of the positive equilibrium is carried out. Numerical simulations are presented for the support of our analytical findings.

1. Introduction

Ecological systems are open systems in which the interaction between the component parts is nonlinear and the remarkable variety of dynamical behaviours exhibited by many predator–prey species has stimulated a great interest in the development of mathematical models of ecological systems [1,2]. From a mathematical as well as biological point of view the predator–prey models can be formulated as systems of differential or difference equations and has been studied by many authors [3–10, and references therein].

Now a days attention have been paid by many authors to Holling–Tanner predator–prey model (see [11–14]). This type of model takes the form of

$$\begin{cases} \dfrac{dN}{dt} = rN(t)\left(1 - \dfrac{N(t)}{k}\right) - \dfrac{mN(t)}{N(t)+q}P(t), \\ \dfrac{dP}{dt} = P(t)\left[s\left(1 - h\dfrac{P(t)}{N(t)}\right)\right], \\ N(0) > 0, \qquad P(0) > 0. \end{cases} \tag{1.1}$$

In system (1.1), $N(t)$ and $P(t)$ stands for prey and predator density at time 't'. r, k, m, q, s, h are positive constants that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half capturing saturation constant, predator intrinsic growth rate, conversion rate of prey into predators biomass respectively.

* Corresponding author.
E-mail addresses: tsmath@rediffmail.com (T. Saha), cgc_math@rediffmail.com (C. Chakrabarti).

0022-247X/$ – see front matter
doi:10.1016/j.jmaa.2009.03.072

The local asymptotic stability of the unique positive equilibrium of (1.1) was investigated by Murray and May [2,4]. S.B. Hsu and T.W. Hwang [11] obtained results on global stability of the positive equilibrium. They showed that the local stability of the positive equilibrium implies its global stability. A. Gasull, R.E. Kooij and J. Torregrosa [12] showed that the local asymptotic stability of the positive equilibrium does not imply global stability for the model system (1.1). They obtained results under which the stable positive equilibrium of (1.1) is surrounded by two limit cycles, the innermost is unstable and the outermost is stable. E. Saez and E. Gonzalez-Olivares [13] described the bifurcation curves when the two limit cycles collapse on a semi-stable limit cycle and disappear. They also showed that local stability and global stability of the positive equilibrium are not equivalent for the model system (1.1).

Recently, there is a growing explicit biological and physiological evidences (see [15–17]) that in many situations, especially when predators have to search for food (and therefore has to share or compete for food), a more suitable general predator–prey theory should be based on the so-called ratio-dependent theory, which can be roughly states as that the per capita predator growth rate should be a function of the ratio of prey to predator abundance, and so would be so-called predator functional responses. This is supported by numerous fields and laboratory experiments and observations [18,19]. Ratio-dependent predator–prey models differs from prey dependent predator–prey models in two directions (i) equilibrium abundances are positively correlated along a gradient of enrichment (see [18]) and (ii) the "paradox of enrichment" (see [20]) either completely disappears or enrichment is linked to stability in a more complex way. For further information of ratio-dependent predator–prey model one can refer [21–26]. Generally, a ratio-dependent Holling–Tanner predator–prey model takes the form of

$$\begin{cases} \dfrac{dN}{dt} = rN(t)\left(1 - \dfrac{N(t)}{k}\right) - \dfrac{mN(t)P(t)}{N(t)+qP(t)}, \\ \dfrac{dP}{dt} = P(t)\left[s\left(1 - h\dfrac{P(t)}{N(t)}\right)\right], \\ N(0) > 0, \qquad P(0) > 0. \end{cases} \tag{1.2}$$

Z. Liang and H. Pan [27] obtained results for the global stability of the positive equilibrium of (1.2). They showed the existence of unique limit cycle for the model system (1.2). However, one of the important problems for predator–prey dynamics is to analyze the effect of time delays on the stability of the systems. In this paper we focus our attention on the delayed ratio-dependent Holling–Tanner predator–prey model where the time delay 'τ' is incorporated into the resource limitation of the prey logistic equation and this takes the form of

$$\begin{cases} \dfrac{dN}{dt} = rN(t)\left(1 - \dfrac{N(t-\tau)}{k}\right) - \dfrac{mN(t)P(t)}{N(t)+qP(t)}, \\ \dfrac{dP}{dt} = P(t)\left[s\left(1 - h\dfrac{P(t)}{N(t)}\right)\right], \end{cases} \tag{1.3}$$

with initial conditions

$$N(\theta) = \phi(\theta) \geqslant 0, \qquad P(\theta) = \psi(\theta) \geqslant 0, \quad \theta \in [-\tau, 0),\ \phi(0) > 0,\ \psi(0) > 0, \tag{1.4}$$

where $\phi(\theta)$, $\psi(\theta)$ are continuous bounded functions in the interval $[-\tau, 0]$.

The model system (1.3) is not well defined at the origin $(0,0)$ and hence cannot be linearized at $(0,0)$. In this paper, following [22,24,26] we redefine the model system (1.3) at the origin $(0,0)$ and using the terminology of Zhang et al. [28] we study the qualitative feature of the model system (1.3) around the critical point $(0,0)$ in the interior of the first quadrant. We also study the global stability results of the model system (1.3).

This paper is organized as follows. In the next section we present preliminary results including the boundedness and permanence of the system (1.3). In Section 3, we analyze the local asymptotic stability of the equilibria except the origin and it is shown that a Hopf bifurcation arises whenever the time delay 'τ' crosses a critical value 'τ_0'. In Section 4, qualitative behaviour of the singularity $(0,0)$ is discussed. In Section 5, by constructing suitable Lyapunov function we derive sufficient conditions for global stability of the positive equilibrium. Finally the paper ends with a concluding section where a comparison is made between the results obtained in [27] for the non-delayed system (1.2) and the results obtained for our delayed model system (1.3).

2. Boundedness and permanence

In this section we shall present some preliminary results including boundedness and permanence of the model system (1.3). Before proceeding further we nondimensionalize our model system (1.3) with the following scaling

$$rt \to t, \qquad \frac{N(t)}{k} \to N(t), \qquad \frac{mP(t)}{rk} \to P(t), \qquad r\tau \to \tau,$$

and this results into

$$\begin{cases} \dfrac{dN}{dt} = N(t)\big(1 - N(t-\tau)\big) - \dfrac{N(t)P(t)}{N(t) + \alpha P(t)}, \\ \dfrac{dP}{dt} = \beta P(t)\left(\delta - \dfrac{P(t)}{N(t)}\right), \end{cases} \tag{1.5}$$

where $\alpha = \frac{qr}{m}$, $\beta = \frac{sh}{m}$ and $\delta = \frac{m}{hr}$. The model system (1.5) is not defined at $(0, 0)$ and consequently we redefine the model system (1.5) as follows

$$\begin{cases} \dfrac{dN}{dt} = N(t)\big(1 - N(t-\tau)\big) - \dfrac{N(t)P(t)}{N(t) + \alpha P(t)} \equiv F(N, P), \\ \dfrac{dP}{dt} = \beta P(t)\left(\delta - \dfrac{P(t)}{N(t)}\right) \equiv G(N, P), \\ F(N, P) = G(N, P) = 0 \quad \text{when } (N, P) = (0, 0). \end{cases} \tag{1.6}$$

Lemma 2.1. *Every solution of the model system* (1.6) *with the initial conditions* (1.4) *exists in the interval* $[0, \infty)$ *and remain positive for all* $t \geqslant 0$.

Proof. The proof is similar as is presented in [6]; we omit the proof here. □

Lemma 2.2. *For any positive solution of the model system* (1.6) *there exists a* $T > 0$ *such that* $N(t) \leqslant m_1$ *and* $P(t) \leqslant m_2$ *for* $t > T$, *where* $m_1 = e^\tau$ *and* $m_2 = \delta e^\tau$.

Proof. From the first equation of (1.6), we have

$$\dot{N}(t) \leqslant N(t)\big(1 - N(t-\tau)\big).$$

This shows

$$\dot{N}(t) \leqslant N(t).$$

Integrating the above inequality from $t - \tau$ to t, we get

$$N(t) \leqslant N(t-\tau)e^\tau.$$

Hence, we have

$$\dot{N}(t) \leqslant N(t)\big(1 - N(t)e^{-\tau}\big).$$

By comparison theorem there exists a $T_1 > 0$ such that for $t > T_1 + \tau$, we have

$$N(t) \leqslant e^\tau = m_1.$$

From the second equation of the model system (1.6) for $t > T_1 + \tau$, we have

$$\dot{P}(t) \leqslant \beta P(t)\big(\delta - P(t)e^{-\tau}\big).$$

By comparison theorem there exists a $T > T_1 + \tau$ such that for $t > T$, we have

$$P(t) \leqslant \delta e^\tau = m_2.$$

The lemma is proved. □

We recall that the model system (1.6) is said to be *permanent* if there exist ξ_1, ξ_2, $0 < \xi_1 < \xi_2$, such that for all solutions of (1.6) with the initial conditions (1.4),

$$\min\Big\{\liminf_{t\to\infty} N(t), \liminf_{t\to\infty} P(t)\Big\} \geqslant \xi_1,$$

and

$$\max\Big\{\limsup_{t\to\infty} N(t), \limsup_{t\to\infty} P(t)\Big\} \leqslant \xi_2.$$

Theorem 2.1. *Suppose the condition* **(H1)**: $\alpha > 1$ *holds, then the model system* (1.6) *is* permanent.

Proof. From the first equation of the model system (1.6), we have

$$N(t)+\alpha P(t)\geqslant \alpha P(t).$$

This implies

$$\dot{N}(t)\geqslant N(t)\left(1-N(t-\tau)-\frac{1}{\alpha}\right).$$

Now by the use of Lemma 2.2, whenever $t>T$,

$$\dot{N}(t)\geqslant -N(t)e^{\tau}.$$

We then have

$$\dot{N}(t)\geqslant N(t)\left(1-N(t)e^{\tau e^{\tau}}-\frac{1}{\alpha}\right).$$

By comparison theorem there exists a $T_2>T$ such that for $t>T_2$,

$$N(t)\geqslant\left(1-\frac{1}{\alpha}\right)e^{-\tau e^{\tau}}=M_1>0\quad\text{if }\alpha>1.$$

Again from the second equation of the model system (1.6), for $t>T_2$

$$\dot{P}(t)\geqslant \beta P(t)\left(\delta-\frac{\alpha e^{\tau e^{\tau}}}{\alpha-1}P(t)\right).$$

By comparison theorem there exists a $T'>T_2$ such that for $t>T'$, we have

$$P(t)\geqslant \delta\left(1-\frac{1}{\alpha}\right)e^{-\tau e^{\tau}}=\delta M_1=M_2>0\quad\text{if }\alpha>1.$$

This shows that there exists a $T'>0$, such that for $t>T'$, $M_1\leqslant N(t)\leqslant m_1$ and $M_2\leqslant P(t)\leqslant m_2$ and the proof is completed. □

3. Local asymptotic stability

The equilibrium points for the model system (1.6) are given by (i) $E_0(0,0)$ (trivial equilibrium), (ii) $E_1(1,0)$ (axial equilibrium), and (iii) $E_*(N_*,P_*)$ (positive equilibrium), where

$$N_*=\frac{1+\alpha\delta-\delta}{1+\alpha\delta},\qquad P_*=\delta N_*. \tag{1.7}$$

The existence of most interesting equilibrium state E_*, where both prey and predator population coexist demands the condition **(H2)**: $\alpha\delta+1>\delta$ holds. To study the local stability of the equilibrium points of the model system (1.6) we are to linearize the model system (1.6) around the equilibrium points of (1.6) and then to look at the roots of the characteristic equations corresponding to the jacobian matrices of the linearized systems. In the presence of time delay 'τ', stability of the equilibrium points of the model system (1.6) carries two notions: one is absolute stability and the other corresponds to conditional stability. In case of absolute stability, the equilibrium point under consideration is asymptotically stable for all $\tau\geqslant 0$, but for conditional stability, the equilibrium point is asymptotically stable for 'τ' in some finite interval. The first one corresponds to the case that the real parts of characteristic roots are negative for all $\tau\geqslant 0$ and the second one shows an existence of critical time delay τ_0 (smallest delay) such that for $0\leqslant\tau<\tau_0$, the real parts of characteristic roots are negative and for $\tau>\tau_0$, there exists at least one root of the characteristic equation whose real part is positive.

The common approach of linearization to discuss the stability behaviour of the equilibrium point E_0 fails due to non-linearizability of the vector fields $F(N,P)$ and $G(N,P)$ at E_0. A discussion regarding this issue is provided in the next section.

The jacobian matrix at E_1 is given by

$$J_1=\begin{pmatrix}-e^{-\lambda\tau} & -1\\ 0 & \delta\beta\end{pmatrix}.$$

The characteristic equation is given by

$$G_1(\lambda,\tau)=\left(\lambda+e^{-\lambda\tau}\right)(\lambda-\delta\beta)=0. \tag{1.8}$$

Now whatever the value of τ, one root of the characteristic equation (1.8) is always positive and consequently E_1 is a saddle point.

The jacobian matrix at E_* takes the form

$$J_* = \begin{pmatrix} a_1 + a_2 e^{-\lambda\tau} & a_3 \\ b_1 & b_2 \end{pmatrix},$$

where $a_1 = \frac{\delta}{(1+\alpha\delta)^2}$, $a_2 = -N_*$, $a_3 = -\frac{1}{(1+\alpha\delta)^2}$, $b_1 = \beta\delta^2$, $b_2 = -\beta\delta$.

The characteristic equation is given by

$$G_2(\lambda, \tau) = \lambda^2 - \lambda\big(b_2 + a_1 + a_2 e^{-\lambda\tau}\big) + b_2\big(a_1 + a_2 e^{-\lambda\tau}\big) - a_3 b_1 = 0. \tag{1.9}$$

In absence of time delay τ, the characteristic equation (1.9) reduces to

$$\lambda^2 - \lambda(a_1 + a_2 + b_2) + a_2 b_2 = 0. \tag{1.10}$$

In absence of time delay τ, a detailed study of local and global asymptotic stability of E_* is presented in [27] and just for consistency of our article we state the results here:

Theorem 3.1. *Suppose the following conditions hold*

$$\mathbf{H}(\mathbf{2}):\quad \alpha\delta + 1 > \delta,$$

$$\mathbf{H}(\mathbf{3}):\quad \delta(2 + \alpha\delta) < (1 + \delta\beta)(1 + \alpha\delta)^2,$$

then the positive equilibrium E_* of the model system (1.6) *is locally asymptotically stable in absence of τ.*

In addition to this we have the following

Theorem 3.2. *Suppose the following conditions hold*

$$\mathbf{H}(\mathbf{2}):\quad \alpha\delta + 1 > \delta,$$

$$\mathbf{H}(\mathbf{4}):\quad \frac{\delta(2 + \alpha\delta)}{(1 + \alpha\delta)^2} - 1 > 0,$$

then in absence of τ, the model system (1.6) *undergoes a Hopf bifurcation around E_* whenever $\beta = \beta_* = \frac{\delta(2+\alpha\delta)}{(1+\alpha\delta)^2} - 1$.*

Let $\tau \neq 0$ and $\lambda = i\omega$, be a root of Eq. (1.9). Then by separating real and imaginary parts, we have

$$\begin{aligned} -a_2\omega \sin\omega\tau + a_2 b_2 \cos\omega\tau &= \omega^2 + a_3 b_1 - a_1 b_2, \\ a_2\omega \cos\omega\tau + a_2 b_2 \sin\omega\tau &= -\omega(a_1 + b_2). \end{aligned} \tag{1.11}$$

Squaring and adding, we get

$$\omega^4 + \big(a_1^2 + b_2^2 - a_2^2 + 2a_3 b_1\big)\omega^2 - a_2^2 b_2^2 = 0. \tag{1.12}$$

Now it follows that Eq. (1.12) has a unique positive real root, say ω_0 and consequently the phenomena switching of stability does not occur for our model system (1.6), also E_* never will be absolutely stable. The value of ω_0 is given by

$$\omega_0 = \sqrt{\frac{-(a_1^2 + b_2^2 - a_2^2 + 2a_3 b_1) + \sqrt{(a_1^2 + b_2^2 - a_2^2 + 2a_3 b_1) + 4a_2^2 b_2^2}}{2}}. \tag{1.13}$$

Putting this value of ω_0 in (1.9) and solving for τ, we obtain

$$\tau_k = \frac{1}{\omega_0} \arccos\left[\frac{-a_1\omega_0^2}{a_2(b_2^2 + \omega_0^2)}\right] + \frac{2k\pi}{\omega_0}, \quad k = 0, 1, 2, \ldots. \tag{1.14}$$

We now state the following lemma:

Lemma 3.1. *Suppose that the positive equilibrium E_* exists for the model system* (1.6)*, then for $\tau = \tau_k = \frac{1}{\omega_0}\arccos[\frac{-a_1\omega_0^2}{a_2(b_2^2+\omega_0^2)}] + \frac{2k\pi}{\omega_0}$, $k = 0, 1, 2, \ldots$, the characteristic equation* (1.9) *has a pair of imaginary roots $\pm\omega_0$, where ω_0 is given by* (1.13).

We will now study how the real parts of the roots of (1.9) changes as 'τ' varies in a small neighbourhood of τ_k. Let $\lambda = u(\tau) + i\omega(\tau)$ be a root of Eq. (1.9). Substituting $\lambda = u(\tau) + i\omega(\tau)$ in (1.9) and then separating real and imaginary parts, we get

$$H_1(u,\omega,\tau) = u^2 - (a_1 + b_2)u - \omega^2 - a_2 e^{-u\tau}(u\cos\omega\tau + \omega\sin\omega\tau) + a_2 b_2 e^{-u\tau}\cos\omega\tau + (b_2 a_1 - a_3 b_1) = 0,$$
$$H_2(u,\omega,\tau) = 2u\omega - (a_1 + b_2)\omega + a_2 e^{-u\tau}(u\sin\omega\tau - \omega\cos\omega\tau) - a_2 b_2 e^{-u\tau}\sin\omega\tau = 0.$$

Now it follows that $H_1(0,\omega_0,\tau_k) = H_2(0,\omega_0,\tau_k) = 0$. Also we have $|J|_{(0,\omega_0,\tau_k)} > 0$, where $J = \begin{pmatrix} \frac{\partial H_1}{\partial u} & \frac{\partial H_1}{\partial \omega} \\ \frac{\partial H_2}{\partial u} & \frac{\partial H_2}{\partial \omega} \end{pmatrix}$. Hence by implicit function theorem, $H_1(u,\omega,\tau) = 0 = H_2(u,\omega,\tau)$ defines u, ω as a function of τ in a neighborhood of $(0,\omega_0,\tau_k)$ such that $u(\tau_k) = 0$, $\omega_{\tau_k} = \omega_0$ and $\frac{du}{d\tau}|_{\tau=\tau_k,\omega=\omega_0} > 0$. We now state the following theorem regarding Hopf-bifurcation.

Theorem 3.3. *For the model system* (1.6)*, suppose the following conditions are satisfied*

$$\mathbf{H(2)}:\quad \alpha\delta + 1 > \delta,$$
$$\mathbf{H(3)}:\quad \delta(2 + \alpha\delta) < (1 + \delta\beta)(1 + \alpha\delta)^2,$$

then E_* is asymptotically stable whenever $0 \leqslant \tau < \tau_0$ and unstable whenever $\tau > \tau_0$. The model system (1.6) *undergoes a Hopf bifurcation at E_* for $\tau = \tau_0$.*

4. Qualitative behaviour at the origin (0, 0)

The trivial equilibrium $E_0(0,0)$ always exists for the model system (1.6). The local stability of E_0 cannot be studied by normal linearization approach as the model system (1.6) is not linearizable at E_0. To discuss the qualitative behaviour of the model system (1.6) at E_0, we perform a blow up transformation

$$N = N, \qquad P = LN \tag{1.15}$$

and this results in

$$\begin{cases} \dfrac{dN}{dt} = N(t)\big(1 - N(t-\tau)\big) - \dfrac{N(t)L(t)}{1 + \alpha L(t)}, \\ \dfrac{dL}{dt} = \beta L(\delta - L) - L\big(1 - N(t-\tau)\big) + \dfrac{L^2}{1 + \alpha L}. \end{cases} \tag{1.16}$$

The aim of this transformation is to decompose the relatively complex qualitative behaviour near a trivial equilibrium point E_0 of (1.6) into simpler topological structures of several equilibrium points of (1.16). The inverse transformation maps L-axis to E_0. Structurally, the inverse transformation leaves the pattern on the first and fourth quadrant in the (N, L) plane "qualitatively unchange", reflects the pattern in the second and third quadrant with respect to the negative axis and then the entire L-axis collapses into one point. Therefore to discuss the qualitative behaviour at E_0 of the model system (1.6) we only need to do the same around the equilibria of the model system (1.16) in the L-axis.

The trivial equilibrium $E_{00}(0,0)$ always exists for the model system (1.16). The other equilibrium points on the L-axis are given by the roots of the equation

$$\frac{L}{1 + \alpha L} - \beta L = 1 - \delta\beta. \tag{1.17}$$

We now analyze the following cases:

Case I. $1 - \delta\beta < 0$.

In this case Eq. (1.17) has only one positive real root and one negative real root, but due to biological significance we will consider the positive real root only. Let the positive real root of Eq. (1.17) be denoted by L_{01}. Then the value of L_{01} is given by

$$L_{01} = \frac{-\Delta + \Delta_1}{2\alpha\beta}, \tag{1.18}$$

where

$$\Delta = (\alpha + \beta - 1 - \alpha\beta\delta), \qquad \Delta_1 = \sqrt{\Delta^2 - 4\alpha\beta(1 - \delta\beta)}. \tag{1.19}$$

Thus it follows that the trivial equilibrium E_0 of the model system (1.6) splits into two equilibria, $E_{00}(0,0)$ and $E_{01}(0, L_{01})$ on the L-axis of the model system (1.16).

A simple calculation shows that E_{00} is an unstable node and the jacobian matrix at E_{01} is given by

$$J_{01} = \begin{pmatrix} 1 - \frac{L_{01}}{1+\alpha L_{01}} & 0 \\ L_{01} e^{-\lambda\tau} & -\beta L_{01} + \frac{L_{01}}{(1+\alpha L_{01})^2} \end{pmatrix}. \tag{1.20}$$

The equilibrium E_{01} is a stable node whenever **H(5)**: $(2\alpha\beta\delta + \Delta) - \Delta_1 < 0$. By the inverse blow up transformation (1.15) there exists a trajectory of the model system (1.6) such that it tends to $E_0(0,0)$ as $t \to \infty$.

The equilibrium E_{01} is a saddle point whenever $\mathbf{H(5)^c}$: $(2\alpha\beta\delta + \Delta) - \Delta_1 > 0$ and there exists a separatrix of this equilibrium in the first quadrant of the model system (1.16), which tends to E_{01} as $t \to -\infty$. By the inverse blow up transformation (1.15) there exists a trajectory of the model system (1.6) such that it tends to $E_0(0,0)$ as $t \to -\infty$.

Case II. $1 - \delta\beta > 0$.

In this case we also assume the condition **H(6)**: $\Delta_1 > 0, \alpha < \frac{1-\beta}{1-\beta\delta}$, so that we always have two positive equilibria on the L-axis of the model system (1.6). The equilibrium points are given by $E_0(0,0)$, $E_{01}^+(0, L_{01}^+)$ and $E_{01}^-(0, L_{01}^-)$, where the values of $L_{01}^\pm$ are given by

$$L_{01}^\pm = \frac{-\Delta \pm \Delta_1}{2\alpha\beta}. \tag{1.21}$$

The trivial equilibrium E_{00} is a saddle point and hence by the inverse blow up transformation (1.15) there exists a trajectory of the model system (1.6) such that it tends to $E_0(0,0)$ as $t \to -\infty$.

The jacobian matrices at the equilibrium points $E_{01}^\pm$ are given by

$$J_{01}^\pm = \begin{pmatrix} cc1 - \frac{L_{01}^\pm}{1+\alpha L_{01}^\pm} & 0 \\ L_{01}^\pm e^{-\lambda\tau} & -\beta L_{01}^\pm + \frac{L_{01}^\pm}{(1+\alpha L_{01}^\pm)^2} \end{pmatrix}. \tag{1.22}$$

The equilibrium E_{01}^+ is a stable node or a saddle point according as **H(5)** or $\mathbf{H(5)^c}$ holds. By the use of inverse blow up transformation (1.15), it follows that there exists a trajectory of the model system (1.6) such that it tends to $E_0(0,0)$ as $t \to \pm\infty$ according as **H(5)** or $\mathbf{H(5)^c}$ holds.

The equilibrium E_{01}^- is a saddle point or an unstable node whenever **H(7)**: $(2\alpha\beta\delta + \Delta) + \Delta_1 < 0$ or $\mathbf{H(7)^c}$: $(2\alpha\beta\delta + \Delta) + \Delta_1 > 0$ holds. Consequently it follows with the help of the inverse transformation (1.15) that there exists a trajectory of the model system (1.6) such that it tends to $E_0(0,0)$ as $t \to -\infty$ whenever **H(7)** holds.

Case III. $1 - \delta\beta = 0$.

In this case the equilibria are $E_{00}(0,0)$ and $E'_{01}(0, L'_{01})$, where the value of L'_{01} is given by

$$L'_{01} = -\frac{(\beta - 1)}{\alpha\beta}. \tag{1.23}$$

To be of biological interest we naturally assume **H(8)**: $\beta < 1$. After some lengthy computation it follows by [29] that the equilibrium E_{00} is a saddle node and the stable node part is in the first quadrant of the model system. The equilibrium point E'_{01} is a stable node whenever **H(9)**: $\alpha + \beta < 1$ holds. For both the cases it follows by the inverse blow up transformation (1.15) that there exists a trajectory of the model system (1.6) such that it tends to $E_0(0,0)$ as $t \to \infty$.

The equilibrium point E'_{01} is a saddle point whenever $\mathbf{H(9)^c}$: $\alpha + \beta > 1$ holds and by the inverse blow up transformation (1.15) there exists a trajectory of the model system (1.6) such that it tends to $E_0(0,0)$ as $t \to -\infty$.

We now state the results for the stability of the trivial equilibrium $E_0(0,0)$ of the model system (1.6) by the help of following theorems:

Theorem 4.1. *In Case* I, *suppose that the condition* **H(5)** *holds, then the positive equilibrium point E_* does not exist and there exists a trajectory of the model system* (1.6) *such that it tends to the origin* $(0,0)$ *as* $t \to \infty$.

Theorem 4.2. *In Case* II, *suppose that the conditions* **H(5)** *and* **H(6)** *hold, then the positive equilibrium point E_* may exist but unstable and there exists a trajectory of the model system* (1.6) *such that it tends to the origin* $(0,0)$ *as* $t \to \infty$.

Theorem 4.3. *In Case* III, *suppose that the conditions* **H(8)** *and* **H(9)** *hold, then the positive equilibrium point E_* does not exist and there exists a trajectory of the model system* (1.6) *such that it tends to the origin* $(0,0)$ *as* $t \to \infty$.

5. Global asymptotic stability

This has been shown in the article [27] that in absence of time delay τ the positive equilibrium E_* of the model system (1.6) is globally asymptotically stable if **H(10)**: $\alpha\delta + 1 > \max\{\delta, \frac{1}{\beta}\}$ holds. In this section we will study the same but in presence of τ. To do so we shall use Lyapunov–LaSalle's invariance principle and try to find an estimation for time delay τ. Prior to this we write the model system (1.6) as of the following form

$$\begin{cases} \dfrac{dN}{dt} = N(t)\left[\left(N_* - N(t-\tau)\right) + f\left(\dfrac{P_*}{N_*}\right) - f\left(\dfrac{P}{N}\right)\right], \\ \dfrac{dP}{dt} = \beta P(t)\left[\left(\dfrac{P_*}{N_*}\right) - \left(\dfrac{P}{N}\right)\right], \end{cases} \tag{1.24}$$

where $f(\theta) = \frac{\theta}{1+\alpha\theta}$. Now by the use of the change of variables $(N(t), P(t)) \to (N(t), L(t) = \frac{P(t)}{N(t)})$, the model system (1.24) reduces to

$$\begin{cases} \dfrac{dN}{dt} = N(t)\left[\left(N_* - N(t-\tau)\right) + f(L_*) - f(L)\right], \\ \dfrac{dP}{dt} = L(t)\left[\beta(L - L) - \left(N_* - N(t-\tau)\right) - f(L_*) + f(L)\right]. \end{cases} \tag{1.25}$$

We also introduce the following transformation

$$x = N - N_*, \qquad y = L - L_*, \tag{1.26}$$

and write the term $f(L) - f(L_*)$ in the following form

$$g(y) = f(L) - f(L_*) = \frac{y}{(1+\alpha L)(1+\alpha L_*)}. \tag{1.27}$$

Then it follows that $g(y)y \geqslant 0$ and $= 0$, when $y = 0$. We also have

$$g'(y) = \frac{1}{(1+\alpha y+\alpha L_*)^2}. \tag{1.28}$$

With the help of (1.26) and (1.27) the model system (1.25) takes the form of

$$\begin{cases} \dfrac{dx}{dt} = (x + N_*)\left[\displaystyle\int_{t-\tau}^{t} x'(s)\,ds - g(y) - x(t)\right], \\ \dfrac{dy}{dt} = (y + L_*)\left[-\beta y - \displaystyle\int_{t-\tau}^{t} x'(s)\,ds + g(y) + x(t)\right]. \end{cases} \tag{1.29}$$

The positive equilibrium E_* in (1.6) corresponds to the trivial equilibrium point of the model system (1.29) and the global asymptotic stability of this trivial equilibrium point implies the global asymptotic stability of E_*. We now state the following theorem:

Theorem 5.1. *Suppose the positive equilibrium E_* exists for the model system* (1.6), *then E_* is globally asymptotically stable if the following condition holds*

$$\mathbf{H(11)}: \quad \eta < \min\{1, \beta(1+\alpha\delta) - 1\}, \quad \textit{with } \beta(1+\alpha\delta) - 1 > 0,$$

where $\eta = \tau + m_1^2\tau$.

Proof. To prove the theorem by the help of Lyapunov–LaSalle's invariance principle, we choose the following Lyapunov functional

$$V_1\left(x(t), y(t)\right) = \left[x - N_* \log\left(\frac{x+N_*}{N_*}\right)\right] + \int_{L_*}^{L} \frac{f(s) - f(L_*)}{s}\,ds. \tag{1.30}$$

Then the time derivative of $V_1(x(t), y(t))$ along (1.29) gives

$$\dot{V}_1\left(x(t), y(t)\right) = \left(\frac{x+N_*}{N_*}\right)\dot{x} + \frac{g(y)}{L}\dot{y}. \tag{1.31}$$

By the help of (1.29), we have

$$\dot{V}_1\big(x(t), y(t)\big) = -x^2 + g^2(y) - \beta g(y)y + \big(g(y) - x\big)\int_{t-\tau}^{t} N(s)\big[g\big(y(s)\big) + x(s-\tau)\big]\,ds. \tag{1.32}$$

We now use the following inequalities

$$\begin{cases} g(y)N(s)g\big(y(s)\big) \leqslant \frac{1}{2}g^2(y) + \frac{1}{2}N^2(s)g^2\big(y(s)\big), \\ g(y)N(s)x(t-\tau) \leqslant \frac{1}{2}g^2(y) + \frac{1}{2}N^2(s)x^2(s-\tau), \\ -x(t)(y)N(s)g\big(y(s)\big) \leqslant \frac{1}{2}x^2(t) + \frac{1}{2}N^2(s)g^2\big(y(s)\big), \\ -x(t)N(s)x(s-\tau) \leqslant \frac{1}{2}x^2(t) + \frac{1}{2}N^2(s)x^2(s-\tau). \end{cases} \tag{1.33}$$

With the help of these inequalities, (1.32) reduces to

$$\dot{V}_1\big(x(t), y(t)\big) \leqslant (\tau - 1)x^2 + \tau g^2(y) - \beta g(y)y + g^2(y) + \int_{t-\tau}^{t} N^2(s)\big[g^2\big(y(s)\big) + x^2(s-\tau)\big]\,ds. \tag{1.34}$$

Owing to the structure of (1.34), we now consider the functional

$$V_2\big(x(t), y(t)\big) = V_1\big(x(t), y(t)\big) + \int_{t-\tau}^{t} d\nu \int_{\nu}^{t} N^2(s)\big[g^2\big(y(s)\big) + x^2(s-\tau)\big]\,ds. \tag{1.35}$$

The time derivative of $V_2(x(t), y(t))$ along (1.29) gives

$$\begin{aligned} \dot{V}_2\big(x(t), y(t)\big) &= \dot{V}_1\big(x(t), y(t)\big) + \tau N^2(t)\big[g^2\big(y(t)\big) + x^2(t-\tau)\big] \\ &\quad - \int_{t-\tau}^{t} N^2(s)\big[g^2\big(y(s)\big) + x^2(s-\tau)\big]\,ds. \end{aligned} \tag{1.36}$$

Hence, using (1.34), we have

$$\dot{V}_2\big(x(t), y(t)\big) \leqslant (\tau - 1)x^2 + \tau g^2(y) - \beta g(y)y + g^2(y) + \tau N^2(t)\big[g^2\big(y(t)\big) + x^2(t-\tau)\big]. \tag{1.37}$$

By Lemma 2.2, we know that there exists a $T' > 0$ such that for $t > T'$, $N(t) \leqslant m_1$. We now set $t > T'$ and obtain the following results:

$$\dot{V}_2\big(x(t), y(t)\big) \leqslant (\tau - 1)x^2 + \tau g^2(y) - \beta g(y)y + g^2(y) + \tau m_1^2 g^2(y) + \tau m_1^2 x^2(t-\tau). \tag{1.38}$$

Again looking at the structure (1.38), we consider the following Lyapunov functional

$$V\big(x(t), y(t)\big) = V_2 + m_1^2\tau \int_{t-\tau}^{t} x^2(s)\,ds. \tag{1.39}$$

We then obtain

$$\dot{V}\big(x(t), y(t)\big) \leqslant -\big(1 - \tau - m_1^2\tau\big)x^2 - g(y)y\left[\beta - \frac{\tau g(y)}{y} - \frac{m_1^2\tau g(y)}{y} - \frac{g(y)}{y}\right]. \tag{1.40}$$

We now assume $\eta = \tau + m_1^2\tau$ and get the following

$$\dot{V}\big(x(t), y(t)\big) \leqslant -(1-\eta)x^2 - g(y)y\left[\frac{\alpha(1+\alpha\delta)\beta L + \beta(1+\alpha\delta) - (1+\eta)}{(1+\alpha L)(1+\alpha L_*)}\right]. \tag{1.41}$$

We have $g(y)y > 0$ for $y \neq 0$ and $= 0$ for $y = 0$. It then follows that whenever the condition **H(10)** holds, $\dot{V}(x(t), y(t)) \leqslant 0$ except at the trivial equilibrium of (1.29). This is obvious that the condition **H(11)** coincides with the condition **H(10)** whenever time delay τ is zero. We thus complete the proof of our theorem followed by Lemma 2.2 and Lyapunov–LaSalle's invariance principle. □

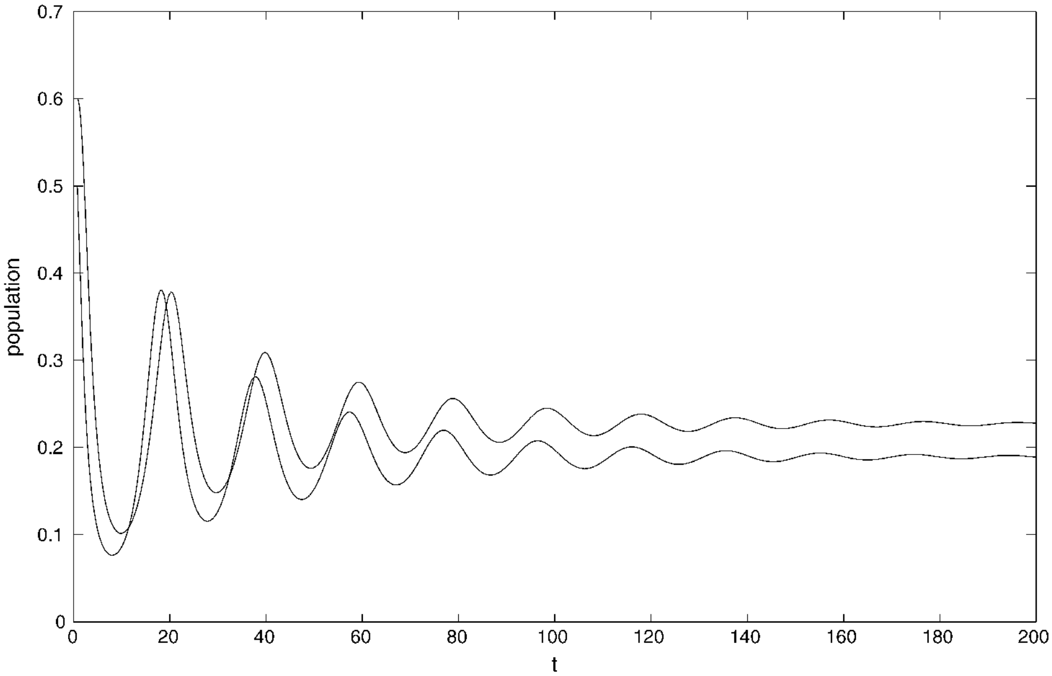

Fig. 1. The positive equilibrium point E_* of the model system (1.6) is locally asymptotically stable for $\tau < 1.48$, where $\alpha = 0.4$, $\beta = 0.4$ and $\delta = 1.2$.

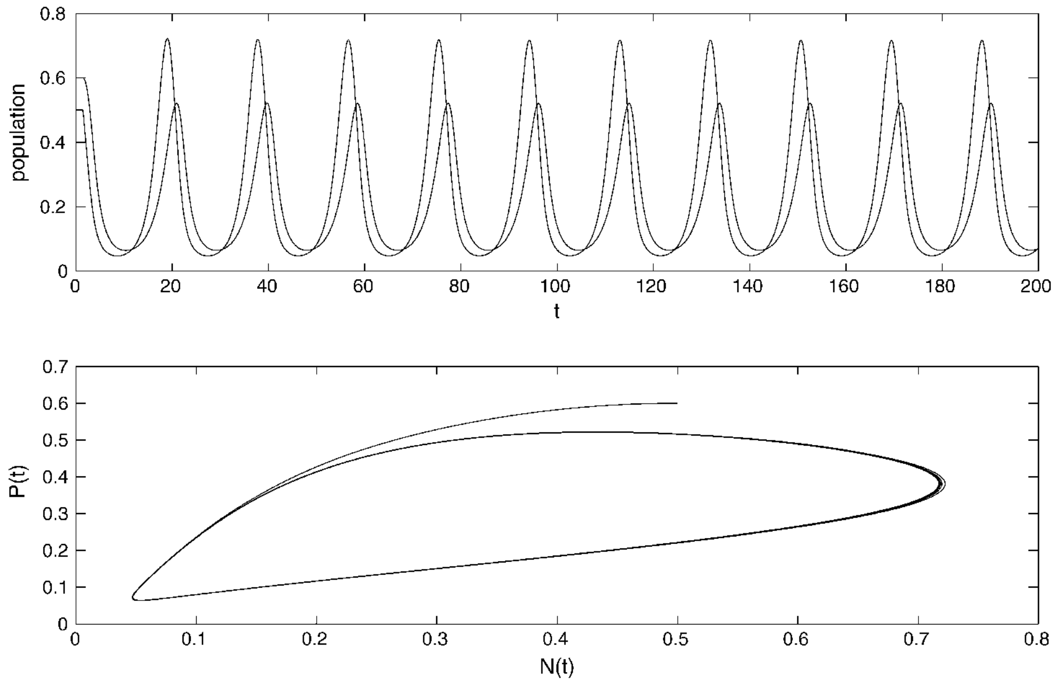

Fig. 2. The positive equilibrium point E_*, with the same parametric values bifurcates into a small amplitude periodic solution for $\tau = 1.48$.

6. Conclusions

In this paper we have considered a delayed ratio-dependent Holling–Tanner predator–prey model by redefining at the origin $(0, 0)$. Our result show that under the condition **(H1)**: $\alpha > 1$, the model system is permanent. The axial equilibrium $E_1(1, 0)$ is always a saddle point with the positive N-axis as its stable manifold. The local stability of $(0, 0)$ cannot be analyzed by normal linearization approach and to do so we used a blow up transformation given in (1.15). Under this transformation the qualitative behaviour of the given model system at the origin $(0, 0)$ remain equivalent to the qualitative

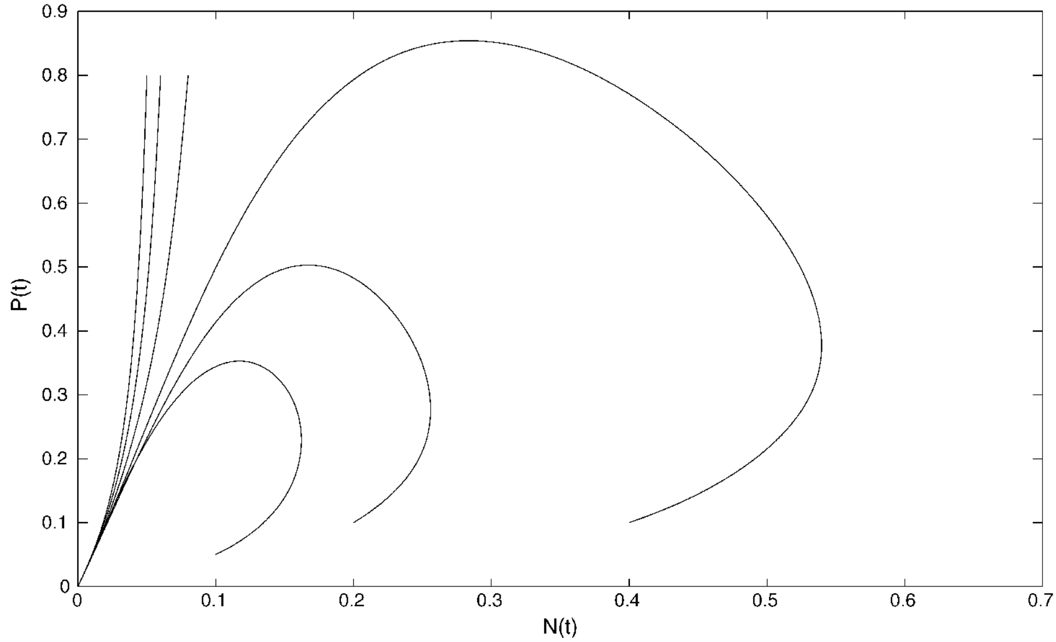

Fig. 3. The phase portrait of the model system (1.6). The origin $(0, 0)$ has a parabolic sector and an elliptic sector. The parameter values are $\alpha = 0.4$, $\beta = 0.4$, $\delta = 3$ and with these parametric restrictions the positive equilibrium point E_* does not exist (Case I).

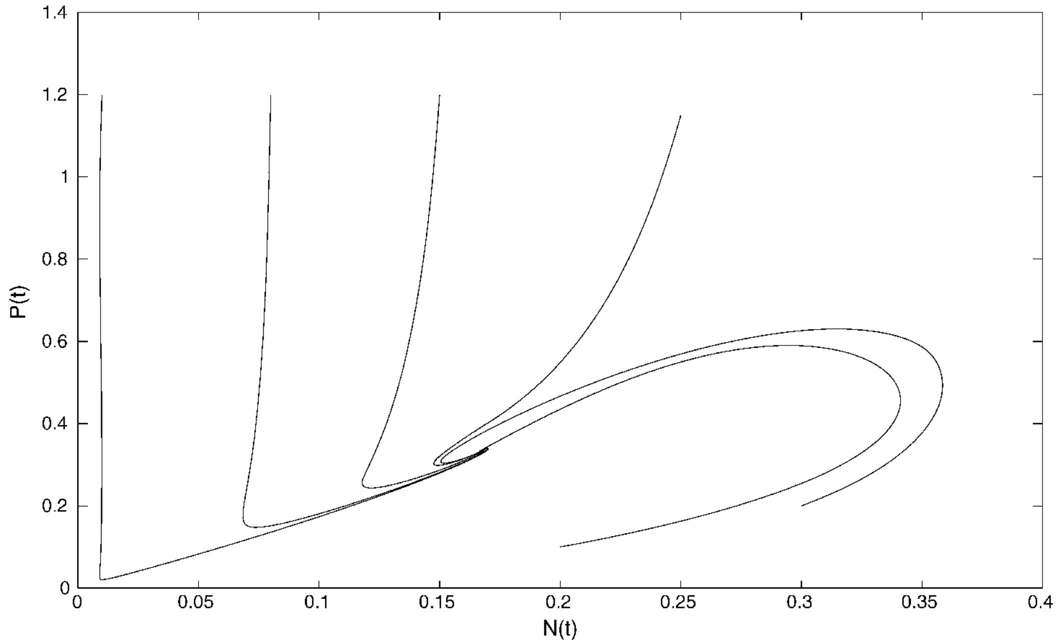

Fig. 4. The phase portrait of the model system (1.6). The origin $(0, 0)$ has a hyperbolic sector and a parabolic sector. The positive equilibrium point E_* exists and is stable for $\tau < 6.49$. Here the parameter values are $\alpha = 0.7$, $\beta = 0.6$, $\delta = 2$ (Case I).

behaviour of the equilibria on the L-axis of the transformed system. The qualitative features of the model system at the origin $(0, 0)$ are classified into the following three cases: (I) $1 - \delta\beta < 0$; (II) $1 - \delta\beta > 0$; and (III) $1 - \delta\beta = 0$. In case (I), the stability of the origin $(0, 0)$ implies the non-existence of the positive equilibrium point E_*, provided the condition **H(5)** holds (see Fig. 3). On the other hand the reverse condition $(\mathbf{H5})^{\mathbf{c}}$ implies that E_* is stable of which the stability depends on time delay 'τ' and the origin $(0, 0)$ is unstable (see Fig. 4). In Case II, the conditions **(H5)** and **(H6)** show that the positive equilibrium point E_* exist but unstable with the stability of the origin $(0, 0)$ (see Fig. 5). The reverse condition of **(H5)** implies that the origin is a saddle point (see Fig. 6). In Case III, the origin $(0, 0)$ is stable and the positive equilibrium point

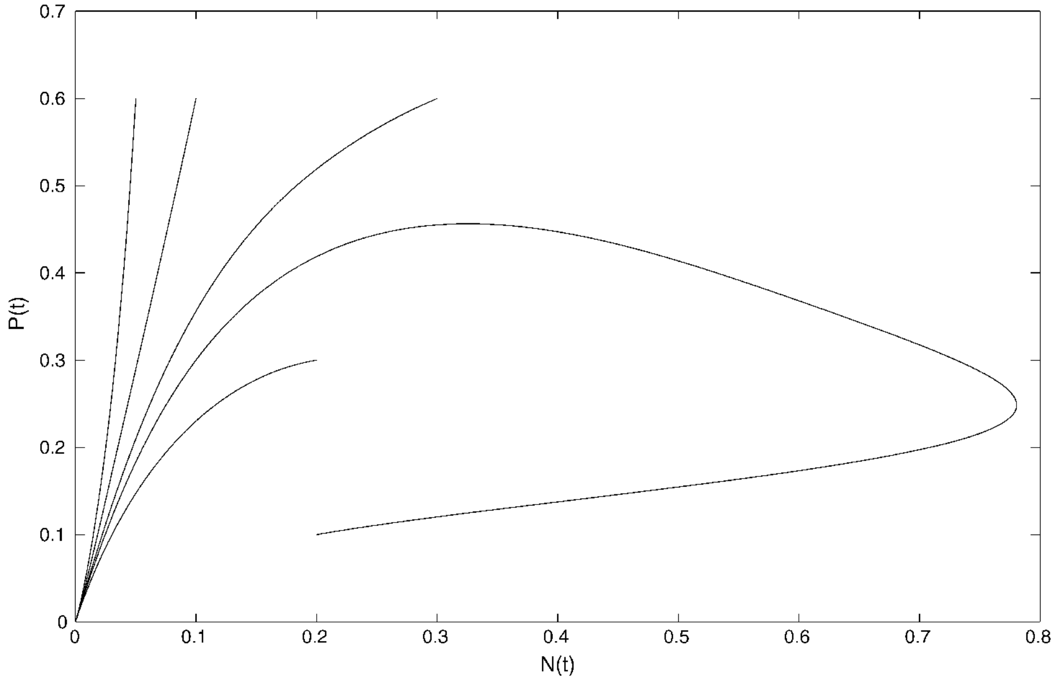

Fig. 5. The phase portrait of the model system (1.6). The origin $(0, 0)$ has a parabolic sector and an elliptic sector, the positive equilibrium point E_* exists but unstable. Here the parameter values are $\alpha = 0.4$, $\beta = 0.2$, $\delta = 1.4$ (Case II).

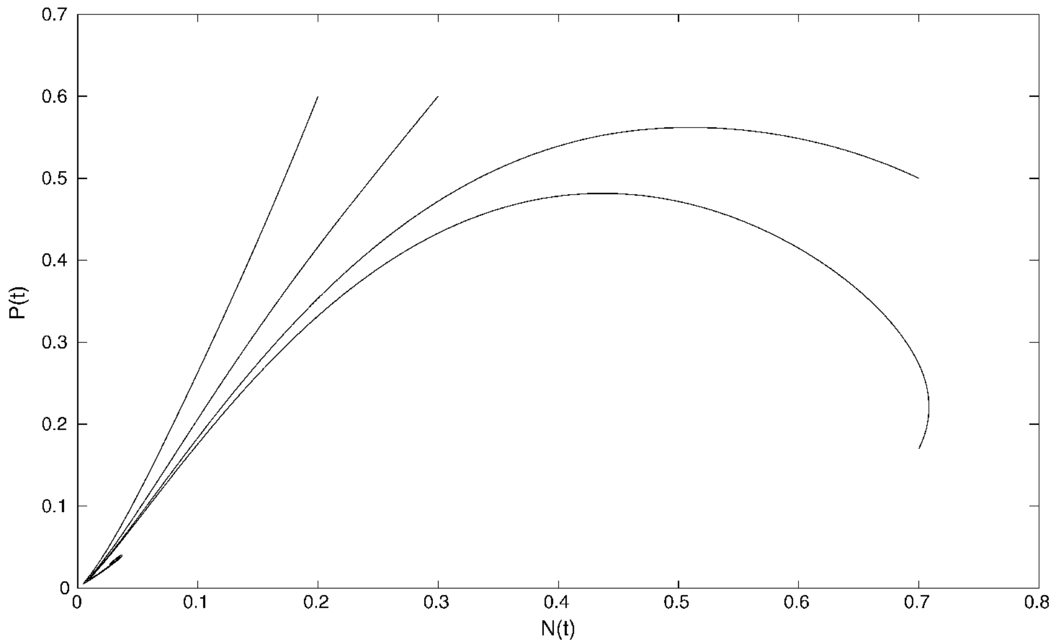

Fig. 6. The phase portrait of the model system (1.6). The origin $(0, 0)$ has a hyperbolic sector and a parabolic sector, the positive equilibrium point E_* exists and is stable for $\tau < 6.10$. Here the parameter values are $\alpha = 0.12$, $\beta = 0.9$, $\delta = 1.1$ (Case II).

E_* does not exist under the conditions **(H8)** and **(H9)** (see Figs. 7 and 8). In general it is shown for our model system (1.6) that both the prey and predator species may extinct and time delay 'τ' does not have any effect on such phenomena.

It has been shown in the article [27] that the positive equilibrium E_* is locally asymptotically stable under the conditions **H(2)**: $\alpha\delta + 1 > \delta$ and **H(3)**: $\delta(2 + \alpha\delta) < (1 + \delta\beta)(1 + \alpha\delta)^2$, but we have established here the result that time delay 'τ' can cause a stable equilibrium to become unstable. This result is stated in Theorem 3.3 showing the existence of a critical time delay value 'τ_0' such that for $\tau < \tau_0$, E_* is stable, E_* bifurcates into small amplitude periodic solution whenever τ

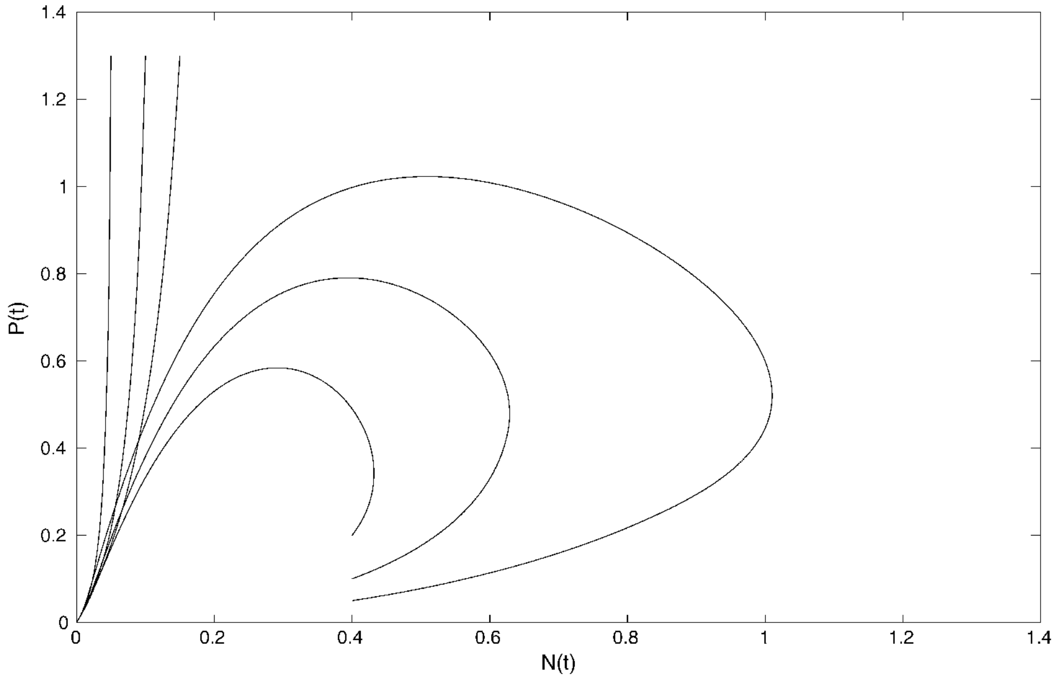

Fig. 7. The phase portrait of the model system (1.6). The origin $(0, 0)$ has a parabolic sector and an elliptic sector, the positive equilibrium point E_* does not exist. Here the parameter values are $\alpha = 0.4$, $\beta = 0.5$, $\delta = 2$ (Case III).

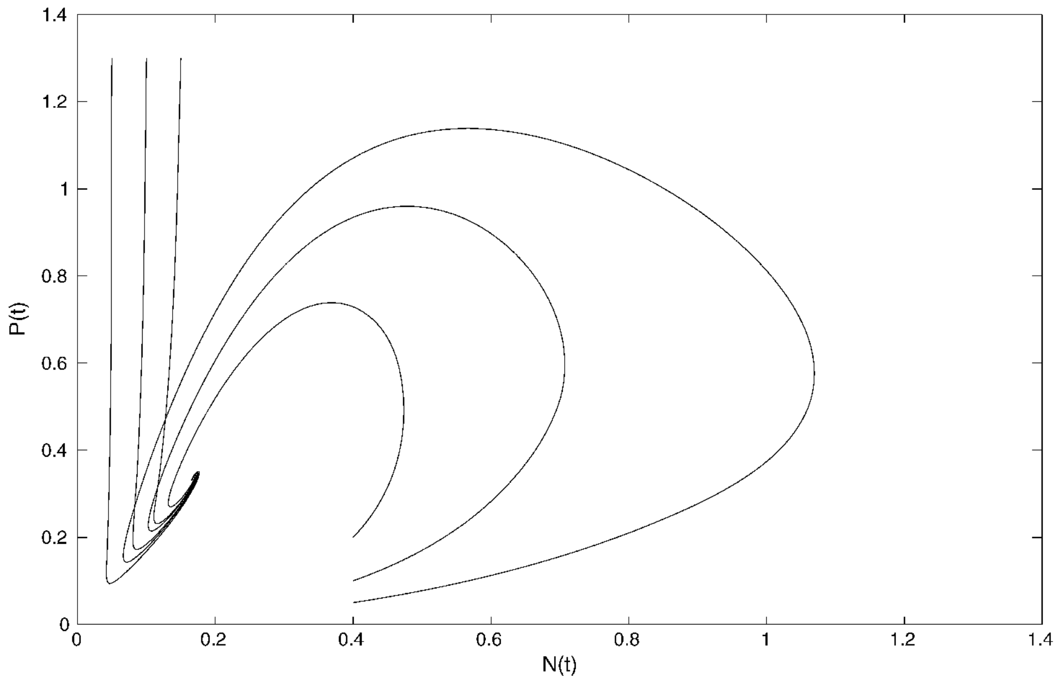

Fig. 8. The phase portrait of the model system (1.6). The origin $(0, 0)$ has a hyperbolic sector and a parabolic sector, the positive equilibrium point E_* exists and is stable for $\tau < 5.9$. Here the parameter values are $\alpha = 0.7$, $\beta = 0.5$, $\delta = 2$ (Case III).

approaches to τ_0, $\tau > \tau_0$, E_* becomes unstable (see Figs. 1 and 2). We have obtained a restriction on the length of time delay for global asymptotic stability of E_* and the result is presented in Theorem 5.1 (see Fig. 9). In other words, we have shown that time delay destabilizes E_* for the model system (1.6).

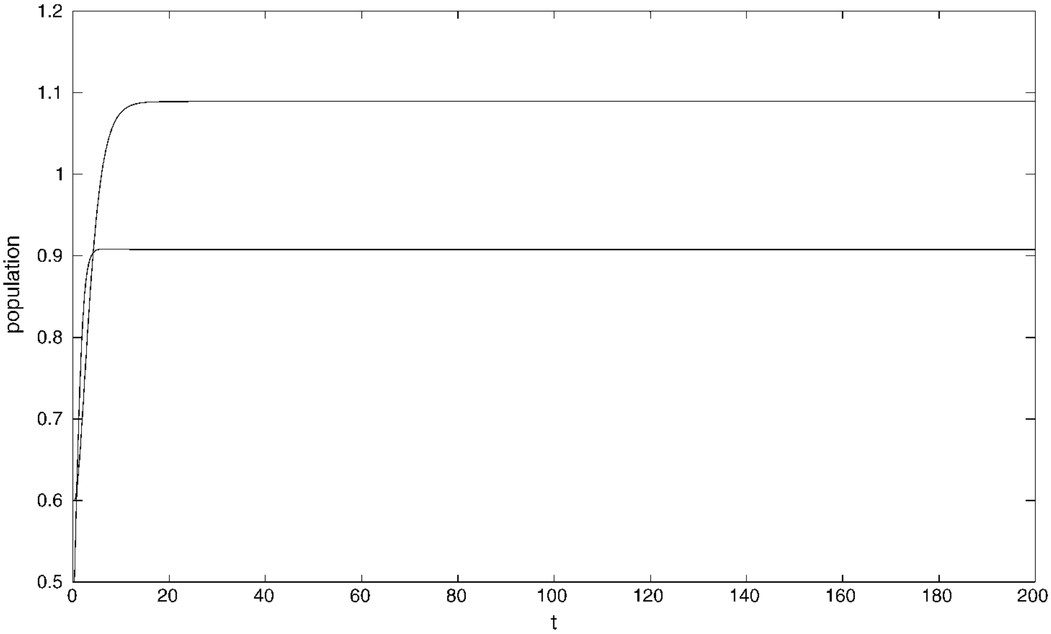

Fig. 9. The positive equilibrium point E_* is globally stable for $\tau < 0.3$, where $\alpha = 10$, $\beta = 0.4$, $\delta = 1.2$.

Acknowledgments

This work has been done under a U.P.E. project of Calcutta University. The authors are grateful to Dr. M. Bandyopadhyay, Department of Mathematics, Scottish Church College, Kolkata for his valuable comments and suggestions throughout the preparation of the paper. The authors also like to thank the referees for their careful instructions which improved the presentation of the manuscript.

References

[1] M. Kot, Elements of Mathematical Ecology, Cambridge University Press, Cambridge, 2001.
[2] J.D. Murray, Mathematical Biology, Springer-Verlag, Berlin, 1989.
[3] A.D. Bazykin, Nonlinear Dynamics of Interacting Populations, World Scientific, Singapore, 1998.
[4] R.M. May, Stability and Complexity in Ecosystems, Princeton University Press, Princeton, 2001.
[5] H.R. Thieme, Mathematics in Population Biology, Princeton University Press, Princeton, 2003.
[6] Y. Kuang, Delay Differential Equations with Applications in Population Dynamics, Academic Press, New York, 1993.
[7] H.I. Freedman, Deterministic Mathematical Models in Population Ecology, Marcel Dekker, New York, 1980.
[8] M.L. Rosenzweig, R.H. McArthur, Graphical representation and stability conditions of predator–prey interactions, Amer. Natur. 47 (1963) 209–223.
[9] C.S. Holling, The functional response of predators to prey density and its role in mimicry and population regulation, Mem. Ent. Soc. Can. 46 (1965) 1–60.
[10] J.T. Tanner, The stability and intrinsic growth rates of prey and predator populations, Ecology 56 (1975) 313–347.
[11] S.B. Hsu, T.W. Hwang, Global stability for a class of predator–prey systems, SIAM J. Appl. Math. 55 (1995) 763–783.
[12] A. Gasull, R.E. Kooij, J. Torregrosa, Limit cycles in the Holling–Tanner model, Publ. Mat. 41 (1997) 149–167.
[13] E. Saez, E. Gonzalez-Olivares, Dynamics of predator–prey model, SIAM J. Appl. Math. 59 (1999) 1867–1878.
[14] M.A. Aziz-Alaoui, M. Daher-Okiye, Boundedness and global stability for a predator–prey model with modified Leslie–Gower and Hollingtype-II schemes, Appl. Math. Lett. 16 (2003) 1069–1075.
[15] R. Arditi, H. Saiah, Empirical evidence of the role of heterogeneity in ratio-dependent consumption, Ecology 73 (1992) 1544–1551.
[16] R. Arditi, L.R. Ginzburg, H.R. Akcakaya, Variation in Plankton densities among lakes: A case for ratio-dependent models, Amer. Natur. 138 (1991) 1287–1296.
[17] A.P. Gutierrez, The physiological basis of ratio-dependent predator–prey theory: A metabolic pool model of Nicholoson's blowfies as an example, Ecology 73 (1992) 1552–1563.
[18] R. Arditi, L.R. Ginzburg, Coupling in predator–prey dynamics, ratio-dependence, J. Theoret. Biol. 139 (1989) 311–326.
[19] R. Arditi, N. Perrin, H. Saiah, Functional response and heterogeneities: An experiment test with cladocerans, OIKOS 60 (1991) 69–75.
[20] M.L. Rosenzweig, Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time, Science 171 (1971) 385–387.
[21] S.B. Hsu, T.W. Hwang, Y. Kuang, Global analysis of the Michaelis–Menten type ratio-dependent predator–prey systems, J. Math. Biol. 42 (2001) 489–506.
[22] C. Jost, O. Arino, R. Arditi, About deterministic extinction in ratio-dependent predator–prey model, Bull. Math. Biol. 61 (1999) 19–32.
[23] Y. Kuang, Rich dynamics of Gause-type ratio-dependent predator–prey systems, Fields Inst. Commun. 21 (1999) 325–337.
[24] Y. Kuang, E. Beretta, Global qualitative analysis of ratio-dependent predator–prey system, J. Math. Biol. 36 (1998) 389–406.
[25] E. Beretta, Y. Kuang, Global analysis in some delayed ratio-dependent predator–prey systems, Nonlinear Anal. 32 (3) (1998) 381–408.
[26] D. Xiao, S. Ruan, Global dynamics of a ratio-dependent predator–prey system, J. Math. Biol. 43 (2001) 268–290.
[27] Z. Liang, H. Pan, Qualitative analysis of a ratio-dependent Holling–Tanner model, J. Math. Anal. Appl. 334 (2007) 954–964.
[28] Z. Zhang, T. Ding, W. Huang, Z. Dong, Qualitative Theory of Differential Equations, Transl. Math. Monogr., vol. 101, Amer. Math. Soc., Providence, 1991.
[29] L. Perko, Differential Equations and Dynamical Systems, Texts Appl. Math., vol. 7, Springer-Verlag, 1996.