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A DELAYED PREDATOR-PREY MODEL WITH PREY POPULATION GUIDED ANTI-PREDATOR BEHAVIOUR AND STAGE STRUCTURE*

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Abstract We consider a predator-prey model with stage structure for the prey and anti-predator behaviour such that the adult prey can attack vulnerable predators. In which a time delay due to the gestation of the predator is incorporated into this model. By analyzing corresponding characteristic equations, the local stability of each of feasible equilibria and the existence of Hopf bifurcations at the positive equilibrium are established, respectively. By using Lyapunov functionals and LaSalle's invariance principle, sufficient conditions are obtained for the global stability of the trivial equilibrium, the predator-extinction equilibrium and the positive equilibrium, respectively. Numerical simulations are performed to illustrate the theoretical results.

Keywords Predator-prey model, anti-predator behaviour, stage structure, time delay, Hopf bifurcation, stability.

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1. Introduction

Predator-prey model is an essential tool in mathematical ecology and specifically for our understanding of interacting populations in the natural environment. Although biologists routinely label the animals as predator or prey, there is sometimes no obvious winner as prey can sometimes inflict harm on their predators, which indicates that cyclic dominance is also important for predator-prey interactions [13,18]. Anti-predator behavior is an evolutionary adaptation developed over time, which assists prey organisms in their constant struggle against their predators. Indeed, role reversals between predator and prey (i.e. anti-predator behaviour) often occur. Experiments show that anti-predator behaviour of prey populations is realized in terms of (a) morphological changes or through changes in behaviour [8, 11, 14], or (b) the prey attack their predators [2, 6, 19]. To model anti-predator behaviour (b), Biao Tang and Yanni Xiao [19] proposed a predator-prey model to describe

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anti-predator behaviour as follows:

$$\begin{aligned}\dot{x}(t) &= rx\left(1 - \frac{x}{k}\right) - \frac{\beta xy}{a + x^2},\\ \dot{y}(t) &= \frac{\mu\beta xy}{a + x^2} - dy - \eta xy,\end{aligned} \tag{1.1}$$

where $x(t)$ and $y(t)$ are the densities of the prey and the predator at time t, respectively. All the parameters are positive constants in which r is the intrinsic growth rate of the prey, k is the carrying capacity of the environment, β is the capture rate of the predator, μ is the conversion rate of the prey into predator, d is the natural death rate of the predator population, and η is the rate of anti-predator behaviour of prey to the predator population. In [19], numerical studies showed that anti-predator behaviour not only makes the coexistence of the prey and predator populations less likely, but also damps the predator-prey oscillations.

Time delays of one type or another have been incorporated into biological models by many researchers(see, for example, [1, 7, 9, 21–23]). In general, delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause the population to fluctuate. Therefore, more realistic models of population interactions should take into account the effect of time delays. Time delay due to the gestation is a common example, because generally the consumption of prey by the predator throughout its past history governs the present birth rate of the predator.

Motivated by Refs. [1, 10, 15, 22, 23] in the resent study, our objective of this paper is to investigate and analyze a predator-prey model which consists of a prey population which is divided into two subpopulations, one is juvenile prey and other is adult prey. Based on above discussions, in this paper, we study the following differential equations

$$\begin{aligned}\dot{x}_1(t) &= rx_2(t) - (r_1 + d_1)x_1(t),\\ \dot{x}_2(t) &= r_1x_1(t) - d_2x_2(t) - ax_2^2(t) - a_1x_2(t)y(t),\\ \dot{y}(t) &= a_2x_2(t-\tau)y(t-\tau) - by^2(t) - d_3y(t) - \eta x_2(t)y(t),\end{aligned} \tag{1.2}$$

where $x_1(t)$ and $x_2(t)$ represent the densities of the juvenile and the adult prey population at time t, respectively; $y(t)$ is the density of the predator at time t. The parameters $a, a_1, a_2, b, d_1, d_2, d_3, r, r_1$ and η are positive constants, in which the birth rate r of the prey is proportional to the existing adult population; a and b are the intra-specific competition rates of the adult prey and the predator, respectively; d_1, d_2 and d_3 are the natural death rates of the juvenile prey, adult prey and the predator, respectively; r_1 is the transformation rate from the juvenile individuals to adult individuals for the prey; a_1 is the capturing rate of the predator, a_2/a_1 is the conversion rate of nutrients into the reproduction of the predator, η is the rate of anti-predator behaviour of prey to the predator population. $\tau \geq 0$ is a constant delay due to the gestation of the predator.

In real world natural ecological system, it is seen that the juvenile members of a species may not be able to direct predation. Basically, they are dependent on the adult members. In system (1.2), we have considered that only the adult members of prey are captured by the predators. Note that here anti-predator behaviour does not directly benefit the prey population but reduces the growth of the predator population since the prey population does not feed chiefly on the predator population. It is reasonable to assume that $a_2 > \eta$.

The initial conditions for system (1.2) take the form

$$x_1(\theta) = \varphi_1(\theta) \geq 0, \;\; x_2(\theta) = \varphi_2(\theta) \geq 0, \;\; y(\theta) = \phi_1(\theta) \geq 0, \;\; \varphi_1(0) > 0,$$
$$\varphi_2(0) > 0, \;\; \phi_1(0) > 0, \;\; (\varphi_1(\theta), \varphi_2(\theta), \phi_1(\theta)) \in C([-\tau, 0], R^3_{+0}), \;\; \theta \in [-\tau, 0), \quad (1.3)$$

where $R^3_{+0} = \{(z_1, z_2, z_3) : z_i \geq 0, i = 1, 2, 3\}$.

The rest of the paper is organized as follows. In Section 2, we discuss the boundedness of solutions of the system (1.2). In Section 3, by using the theory on characteristic equation of delay differential equations developed by [7], we discuss the local stability of the positive equilibrium of system (1.2). We establish the existence of Hopf bifurcations at the positive equilibrium. By means of Lyaponov functionals and LaSalle's invariance principle, we obtain sufficient conditions for the global stability of the positive equilibrium. In Section 4, we obtain sufficient conditions for the local and the global stability of each of boundary equilibria of system (1.2). In Section 5, some numerical simulations are presented to illustrate the theoretical results. The paper ends with a discussion in Section 6.

2. Positivity and boundedness of solutions

It is well known by the fundamental theory of functional differential equations [4] that system (1.2) has a unique solution $(x_1(t), x_2(t), y(t))$ satisfying initial conditions (1.3). In this section, we show the positivity and the boundedness of solutions of system (1.2)–(1.3).

Lemma 2.1. *Solutions of system (1.2) corresponding to initial conditions (1.3) are defined on* $[0, +\infty)$ *and remain positive for all* $t \geq 0$.

Proof. Let $(x_1(t), x_2(t), y(t))$ be a solution of system (1.2) with initial conditions (1.3). First, we show that $x_2(t) > 0$ for all $t > 0$. Notice $x_2(0) > 0$, hence if there exists a t_0 such that $x_2(t_0) = 0$, then $t_0 > 0$. Assume that t_0 is the first such time that $x_2(t) = 0$, that is $t_0 = \inf\{t > 0 : x_2(t_0) = 0\}$. By the second equation of system (1.2), we obtain $\dot{x}_2(t_0) = r_1 x_1(t_0) \leq 0$. Hence $x_1(t_0) \leq 0$. By the first equation of system (1.2), we have

$$x_1(t) = [x_1(0) + r \int_0^t x_2(s) e^{(r_1+d_1)s} ds] e^{-(r_1+d_1)t}. \tag{2.1}$$

By the definition of t_0, $x_2(t) \geq 0$ for $t \in [0, t_0]$. Thus, we have $x_1(t_0) > 0$. This contradiction shows that $x_2(t) > 0$ for all $t > 0$. By (2.1), we have $x_1(t) > 0$ for all $t > 0$.

Now, we show that $y(t) > 0$ for all $t > 0$. Let us consider $y(t)$ for $t \in [0, \tau]$. Since $\phi_1(\theta) \geq 0$ for $\theta \in [-\tau, 0]$, we derive from the third equation of system (1.2) that

$$\dot{y}(t) \geq -(d_3 + \eta x_2(t)) y(t).$$

A standard comparison argument shows that

$$y(t) \geq y(0) \exp\left\{-\int_0^t (d_3 + \eta x_2(s)) ds\right\} > 0,$$

i.e. $y(t) > 0$ for $t \in [0, \tau]$. In a similar way, we treat the intervals $[\tau, 2\tau], \ldots, [n\tau, (n+1)\tau], n \in N$. Thus, we have $y(t) > 0$ for all $t > 0$. $\square$

Lemma 2.2. *There are positive constants M_1, M_2 and M_3 such that for any positive solution $(x_1(t), x_2(t), y(t))$ of system (1.2) with initial conditions (1.3),*

$$\limsup_{t\to+\infty} x_1(t) \le M_1,\ \limsup_{t\to+\infty} x_2(t) \le M_2,\ \limsup_{t\to+\infty} y(t) \le M_3.$$

Proof. Let $(x_1(t), x_2(t), y(t))$ be any positive solution of system (1.2) with initial conditions (1.3). By the first and second equations of system (1.2), we can obtain

$$\begin{aligned}\dot{x}_1(t) &= rx_2(t) - (r_1 + d_1)x_1(t),\\ \dot{x}_2(t) &\le r_1x_1(t) - d_2x_2(t) - ax_2^2(t),\end{aligned}$$

which yields

$$\limsup_{t\to+\infty} x_1(t) \le \frac{r|rr_1 - d_2(r_1+d_1)|}{a(r_1+d_1)^2} := M_1,\ \limsup_{t\to+\infty} x_2(t) \le \frac{|rr_1 - d_2(r_1+d_1)|}{a(r_1+d_1)} := M_2.$$

By the third equation of system (1.2), for t sufficiently large, we have

$$\dot{y}(t) \le a_2M_2y(t-\tau) - by^2(t) - d_3y(t).$$

Consider the following auxiliary equation

$$\dot{u}(t) = a_2M_2u(t-\tau) - bu^2(t) - d_3u(t).$$

By Lamma 3.1 in [17], we derive that

$$\lim_{t\to\infty} u(t) = \frac{|a_2M_2 - d_3|}{b}.$$

By comparison, it follows that

$$\limsup_{t\to\infty} y(t) \le \frac{|a_2M_2 - d_3|}{b} := M_3.$$

□

Lemma 2.3. *For any positive solution $(x_1(t), x_2(t), y(t))$ of system (1.2) with initial conditions (1.3), we have*

$$\liminf_{t\to+\infty} x_2(t) \ge \frac{rr_1 - (r_1+d_1)(d_2 + a_1M_3)}{a(r_1+d_1)} := \underline{x}_2,$$

where M_3 is defined in Lemma 2.2.

Proof. Let $(x_1(t), x_2(t), y(t))$ be any positive solution of system (1.2) with initial conditions (1.3). By Lemma 2.2, it follows that $\limsup_{t\to+\infty} y(t) \le M_3$. Hence, for $\varepsilon > 0$ being sufficiently small, there is a $T_0 > 0$ such that if $t > T_0$, $y(t) < M_3 + \varepsilon$. Accordingly, for $\varepsilon > 0$ being sufficiently small, we derive from the first and the second equations of system (1.2) that, for $t > T_0$,

$$\begin{aligned}\dot{x}_1(t) &= rx_2(t) - (r_1 + d_1)x_1(t),\\ \dot{x}_2(t) &\ge r_1x_1(t) - d_2x_2(t) - ax_2^2(t) - a_1(M_3+\varepsilon)x_2(t),\end{aligned} \tag{2.2}$$

which leads to

$$\liminf_{t\to+\infty} x_2(t) \ge \frac{rr_1 - (r_1+d_1)(d_2 + a_1M_3)}{a(r_1+d_1)} := \underline{x}_2. \tag{2.3}$$

□

3. Stability analysis of the positive equilibrium and Hopf bifurcations

In this section, we discuss the stability of the positive equilibrium of system (1.2). Firstly, we consider the existence of the non-negative equilibrium of system (1.2).

System (1.2) always has a trivial equilibrium $E_0(0,0,0)$. If $rr_1 > d_2(r_1+d_1)$, then system (1.2) has a predator-extinction equilibrium $E_1(x_1^0, x_2^0, 0)$, where

$$x_1^0 = \frac{r[rr_1 - d_2(r_1+d_1)]}{a(r_1+d_1)^2},\quad x_2^0 = \frac{rr_1 - d_2(r_1+d_1)}{a(r_1+d_1)}.$$

If the following condition holds:

$$(H_1)\ \ (a_2-\eta)x_2^0 > d_3,$$

then system (1.2) has a positive equilibrium $E_*(x_1^*, x_2^*, y^*)$, where

$$x_1^* = \frac{r(abx_2^0 + a_1d_3)}{(r_1+d_1)[ab + a_1(a_2-\eta)]},\quad x_2^* = \frac{abx_2^0 + a_1d_3}{ab + a_1(a_2-\eta)},\quad y^* = \frac{a(a_2-\eta)x_2^0 - ad_3}{a_1(a_2-\eta)+ab}.$$

The Jacobian matrix at the positive equilibrium E_* is given by

$$J_{E_*} = \begin{pmatrix} -(r_1+d_1) & r & 0 \\ r_1 & -(\frac{rr_1}{r_1+d_1} + ax_2^*) & -a_1x_2^* \\ 0 & -\eta y^* + a_2y^*e^{-\lambda\tau} & -(a_2x_2^* + by^*) + a_2x_2^*e^{-\lambda\tau} \end{pmatrix}.$$

Then the characteristic equation of system (1.2) at the equilibrium E_* is of the form

$$\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + (q_2\lambda^2 + q_1\lambda + q_0)e^{-\lambda\tau} = 0, \tag{3.1}$$

where

$$\begin{aligned}
p_2 &= r_1 + d_1 + \frac{rr_1}{r_1+d_1} + (a+a_2)x_2^* + by^*,\\
p_1 &= (r_1+d_1)[(a+a_2)x_2^* + by^*] + (a_2x_2^* + by^*)(\frac{rr_1}{r_1+d_1} + ax_2^*) - a_1\eta x_2^*y^*,\\
p_0 &= (r_1+d_1)[ax_2^*(a_2x_2^* + by^*) - a_1\eta x_2^*y^*],\\
q_2 &= -a_2x_2^*,\\
q_1 &= -a_2x_2^*(r_1 + d_1 + \frac{rr_1}{r_1+d_1} + ax_2^* - a_1y^*),\\
q_0 &= -a_2x_2^*(r_1+d_1)(ax_2^* - a_1y^*).
\end{aligned}$$

When $\tau = 0$, equation (3.1) becomes

$$\lambda^3 + (p_2+q_2)\lambda^2 + (p_1+q_1)\lambda + p_0 + q_0 = 0. \tag{3.2}$$

Direct calculation yields

$$\triangle_1 = p_2 + q_2 = r_1 + d_1 + \frac{rr_1}{r_1+d_1} + ax_2^* + by^* > 0,$$

$$\begin{aligned}\triangle_2 =&(p_2+q_2)(p_1+q_1)-(p_0+q_0) = x_2^*y^*[a_1(a_2-\eta)+ab](\frac{rr_1}{r_1+d_1}+ax_2^*+by^*)\\ &+[ax_2^*(r_1+d_1)+by^*(r_1+d_1+\frac{rr_1}{r_1+d_1})](p_2+q_2)>0,\\ \triangle_3 =&(p_0+q_0)\triangle_3 = x_2^*y^*(r_1+d_1)[a_1(a_2-\eta)+ab]\triangle_3>0.\end{aligned}$$

Then, by the Routh-Hurwitz criterion, the equilibrium E_* is locally asymptotically stable when $\tau = 0$.

When $\tau > 0$, then the roots of (3.1) can only enter the right-half plane in the complex plane by crossing the imaginary axis as the delay τ increases. Let $\lambda = i\omega(\omega > 0)$ be a root of Eq.(3.1). Substituting $\lambda = i\omega$ into Eq.(3.1) and separating the real and imaginary parts, one obtains

$$\begin{aligned}(q_2\omega^2-q_0)\sin\omega\tau+q_1\omega\cos\omega\tau &= \omega^3-p_1\omega,\\ (q_2\omega^2-q_0)\cos\omega\tau-q_1\omega\sin\omega\tau &= -p_2\omega^2+p_0.\end{aligned}\tag{3.3}$$

Squaring and adding the two equations of (3.3), we derive that

$$\omega^6+h_2\omega^4+h_1\omega^2+h_0=0,\tag{3.4}$$

where

$$\begin{aligned}h_2 &= p_2^2-2p_1-q_2^2\\ &= (r_1+d_1+\frac{rr_1}{r_1+d_1})^2+ax_2^*(ax_2^*+2\frac{rr_1}{r_1+d_1})+by^*(by^*+2a_2x_2^*)+2a_1x_2^*\eta y^*>0,\\ h_1 &= p_1^2-2p_0p_2-q_1^2+2q_0q_2,\\ h_0 &= p_0^2-q_0^2\\ &= (p_0-q_0)x_2^*y^*(r_1+d_1)[a_1(a_2-\eta)+ab].\end{aligned}$$

Let $z=\omega^2$, then equation (3.4) can be rewritten as

$$z^3+h_2z^2+h_1z+h_0=0.\tag{3.5}$$

If $h_1 > 0$ and $p_0 > q_0$, then Eq.(3.5) has always no positive roots. Hence, under these conditions, Eq.(3.4) has no purely imaginary roots for any $\tau > 0$ and accordingly, the equilibrium E_* is locally asymptotically stable for all $\tau \ge 0$.

If $h_1 > 0$ and $p_0 < q_0$, then Eq.(3.5) has always one positive root z_0. Accordingly, Eq.(3.4) has a pair of purely imaginary roots $\pm i\omega_0$ given by

$$\tau_k = \frac{2k\pi}{\omega_0}+\frac{1}{\omega_0}\arccos\frac{q_1\omega_0(\omega_0^3-p_1\omega_0)-(p_2\omega_0^2-p_0)(q_2\omega_0^2-q_0)}{(q_1\omega_0)^2+(q_2\omega_0^2-q_0)^2},\quad k=0,1,2,\cdots.$$

Differentiating the two sides of (3.1) with respect to τ, it follows that

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{3\lambda^2+2p_2\lambda+p_1}{-\lambda(\lambda^3+p_2\lambda^2+p_1\lambda+p_0)}+\frac{2q_2\lambda+q_1}{\lambda(q_2\lambda^2+q_1\lambda+q_0)}-\frac{\tau}{\lambda}.$$

After some algebra, one obtains that

$$sgn\left\{\frac{dRe\lambda}{d\tau}\right\}_{\tau=\tau_k} = sgn\left\{Re\left(\frac{d\lambda}{d\tau}\right)^{-1}\right\}_{\tau=\tau_k} = sgn\left\{\frac{h'(z_k)}{(q_1\omega_0)^2+(q_2\omega_0^2-q_0)^2}\right\}.$$

Based on the theory of characteristic equation of delay differential equations with delay-dependent parameters developed by [7], one can obtain the following results.

Theorem 3.1. *For system (1.2), assume that* (H_1) *holds and* $h_1 > 0$*, we have*

(i) If $p_0 > q_0$*, then the equilibrium* E_* *is locally asymptotically stable.*

(ii) If $p_0 < q_0$*, then the equilibrium* E_* *is locally asymptotically stable for* $\tau \in [0, \tau_0)$ *and unstable for* $\tau > \tau_0$*. System (1.2) undergoes a Hopf bifurcation at* E_* *when* $\tau = \tau_0$*.*

Theorem 3.2. *Assume that* (H_1) *holds,* $h_1 > 0$ *and* $p_0 > q_0$*, then the equilibrium* E_* *is globally asymptotically stable provided that*

$$(H_2)\ \underline{x_2} > \frac{a_2[(a_2-\eta)x_2^0 - d_3]}{k_2[a_1(a_2-\eta)+ab]}.$$

Here, $\underline{x_2}$ *is the persistency constant for* $x_2(t)$ *as defined in Lemma 2.3.*

Proof. By Theorem 3.1, we see that if (H_1) holds, $h_1 > 0$ and $p_0 > q_0$, then E_* is locally asymptotically stable. Hence, we only prove that all positive solutions of system (1.2) with initial conditions (1.3) converge to E_*. Let $(x_1(t), x_2(t), y(t))$ be any positive solution of system (1.2) with initial conditions (1.3). System (1.2) can be rewritten as

$$\begin{aligned}
\dot{x}_1(t) &= \frac{r}{x_1^*}[-x_2(t)(x_1(t)-x_1^*) + x_1(t)(x_2(t)-x_2^*)],\\
\dot{x}_2(t) &= \frac{r_1}{x_2^*}[-x_1(t)(x_2(t)-x_2^*) + x_2(t)(x_1(t)-x_1^*)] + x_2(t)[-a(x_2(t)-x_2^*)]\\
&\quad + a_1y^*x_2(t) - a_1x_2(t)y(t), \qquad (3.6)\\
\dot{y}(t) &= a_2x_2(t-\tau)y(t-\tau) - d_3y(t) - by^2(t) - \eta x_2(t)y(t).
\end{aligned}$$

Define

$$V(t) = k_1\Big(x_1 - x_1^* - x_1^*\ln\frac{x_1}{x_1^*}\Big) + k_2\Big(x_2 - x_2^* - x_2^*\ln\frac{x_2}{x_2^*}\Big) + y - y^* - y^*\ln\frac{y}{y^*},$$

where $k_1 = r_1x_1^*/(rx_2^*),\ k_2 = (a_2-\eta)/(a_1)$.

Calculating the derivative of $V(t)$ along positive solutions of system (1.2), it follows that

$$\begin{aligned}
\dot{V}(t) =& k_1\frac{x_1(t)-x_1^*}{x_1(t)}\dot{x}_1(t) + k_2\frac{x_2(t)-x_2^*}{x_2(t)}\dot{x}_2(t) + \frac{y(t)-y^*}{y(t)}\dot{y}(t)\\
=& -\frac{r_1k_2}{x_2^*}\left[\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t)-x_1^*) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t)-x_2^*)\right]^2 - ak_2(x_2(t)-x_2^*)^2\\
&+ a_2y^*(x_2(t)-x_2^*) - a_2x_2(t)y(t) + a_2x_2(t-\tau)y(t-\tau)\\
&- a_2\frac{y^*}{y(t)}x_2(t-\tau)y(t-\tau) - b(y(t)-y^*)^2 + a_2x_2^*y^*. \qquad (3.7)
\end{aligned}$$

Define

$$V_*(t) = V(t) + a_2\int_{t-\tau}^{t}\left[x_2(u)y(u) - x_2^*y^* - x_2^*y^*\ln\frac{x_2(u)y(u)}{x_2^*y^*}\right]du.$$

Direct calculation shows that

$$\dot{V}_*(t) = -\frac{r_1k_2}{x_2^*}\left[\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t)-x_1^*) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t)-x_2^*)\right]^2 - b(y(t)-y^*)^2$$

$$-a_2x_2^*y^*\left[\frac{x_2(t-\tau)y(t-\tau)}{x_2^*y(t)}-1-\ln\frac{x_2(t-\tau)y(t-\tau)}{x_2^*y(t)}\right]$$
$$-a_2x_2^*y^*\left[\frac{x_2^*}{x_2(t)}-1-\ln\frac{x_2^*}{x_2(t)}\right]-(x_2(t)-x_2^*)^2\left[ak_2-\frac{a_2y^*}{x_2(t)}\right]. \quad (3.8)$$

Note that the function $g(x)=x-1-\ln x$ is always non-negative for any $x>0$, and $g(x)=0$ if and only if $x=1$. Hence, if (H_2) hols, we have $x_2(t)>\frac{a_2y^*}{ak_2}$ for $t\geq T$. Thus $\dot{V}_*(t)\leq 0$ with equality if and only if $x_1(t)=x_1^*, x_2(t)=x_2(t-\tau)=x_2^*$ and $y(t)=y(t-\tau)=y^*$. Hence, the only invariant set in M is $\Lambda=\{(x_1^*,x_2^*,y^*)\}$. Therefore, the global attractiveness of E_* follows from LaSalle invariant principle for delay differential systems. □

4. Stability analysis of the boundary equilibria

In this section, we discuss the stability of the trivial equilibrium E_0 and the predator-extinction equilibrium E_1 of system (1.2).

Now we consider the local stability of the E_0 and E_1. The Jacobian matrix at the equilibrium E_0 is given by

$$J_{E_0}=\begin{pmatrix}-(r_1+d_1) & r & 0\\ r_1 & -d_2 & 0\\ 0 & 0 & -d_3\end{pmatrix}.$$

So, the characteristic equation of system (1.2) at E_0 takes the form

$$(\lambda+d_3)[\lambda^2+(r_1+d_1+d_2)\lambda+d_2(r_1+d_1)-rr_1]=0. \quad (4.1)$$

Obviously, Eq. (4.1) always has a negative real root: $\lambda=-d_3$. If $rr_1<d_2(r_1+d_1)$, then all roots of Eq. (4.1) are negative. If $rr_1>d_2(r_1+d_1)$, then Eq. (4.1) has a positive real root. Hence, E_0 is locally asymptotically stable when $rr_1<d_2(r_1+d_1)$ and unstable when $rr_1>d_2(r_1+d_1)$.

The Jacobian matrix at the equilibrium E_1 is given by

$$J_{E_1}=\begin{pmatrix}-(r_1+d_1) & r & 0\\ r_1 & -(d_2+2ax_2^0) & -a_1x_2^0\\ 0 & 0 & -(d_3+\eta x_2^0)+a_2x_2^0e^{-\lambda\tau}\end{pmatrix}.$$

Hence, the corresponding characteristic equation of the above Jacobian matrix is

$$(\lambda+d_3+\eta x_2^0-a_2x_2^0e^{-\lambda\tau})[\lambda^2+(r_1+d_1+d_2+2ax_2^0)\lambda+rr_1-d_2(r_1+d_1)]=0. \quad (4.2)$$

Clearly, all the roots of the following equation

$$\lambda^2+(r_1+d_1+d_2+2ax_2^0)\lambda+rr_1-d_2(r_1+d_1)=0$$

are negative as $rr_1>d_2(r_1+d_1)$. Other roots of Eq (4.2) are determined by the following equation:

$$f_1(\lambda):=\lambda+d_3+\eta x_2^0-a_2x_2^0e^{-\lambda\tau}=0. \quad (4.3)$$

If $(a_2-\eta)x_2^0 > d_3$, for λ real, it is easy to show that,

$$f_1(0) = d_3 - (a_2-\eta)x_2^0 < 0, \quad f_1'(\lambda) = 1 + \tau a_2 x_2^0 e^{-\lambda\tau} > 0.$$

Hence, $f_1(\lambda) = 0$ has at least one positive real root in this case. If $(a_2-\eta)x_2^0 < d_3$, one has

$$Re(\lambda) = a_2 x_2^0 \cos(\tau Im\lambda) - (d_3 + \eta x_2^0) \le (a_2-\eta)x_2^0 - d_3 < 0.$$

Accordingly, by Theorem 3.4.1 in Kuang [7], we see that if $(a_2-\eta)x_2^0 < d_3$, the equilibrium E_1 is locally asymptotically stable. If $(a_2-\eta)x_2^0 > d_3$, the equilibrium E_1 is unstable.

From above discussions, we have the following theorem.

Theorem 4.1. *For system (1.2), we have the following:*

(i) If $rr_1 < d_2(r_1+d_1)$, then the equilibrium E_0 is locally asymptotically stable; if $rr_1 > d_2(r_1+d_1)$, then E_0 is unstable;

(ii) Assume that $rr_1 > d_2(r_1+d_1)$. If $(a_2-\eta)x_2^0 < d_3$, then the equilibrium E_1 is locally asymptotically stable; if $(a_2-\eta)x_2^0 > d_3$, then E_1 is unstable.

Now, we study the global stability of the equilibria E_0 and E_1, respectively. The strategy of proofs is to use Lyapunov functions and LaSalle's invariance principle.

Theorem 4.2. *If $rr_1 < d_2(r_1+d_1)$, then the trivial equilibrium E_0 of system (1.2)is globally asymptotically stable.*

Proof. Based on Theorem 4.1, it is seen that E_0 is locally asymptotically stable when $rr_1 < d_2(r_1+d_1)$. Hence, we only prove that all positive solutions of system (1.2) with initial conditions (1.3) converge to E_0. Let $(x_1(t), x_2(t), y(t))$ be any positive solution of system (1.2) with initial conditions (1.3). Define

$$V_0(t) = \frac{r_1(a_2-\eta)}{a_1(r_1+d_1)}x_1(t) + \frac{a_2-\eta}{a_1}x_2(t) + y(t) + a_2\int_{t-\tau}^{t} x_2(u)y(u)du.$$

Calculating the derivative of $V_0(t)$ along positive solutions of system (1.2), it follows that

$$\dot{V}_0(t) = -\frac{(a_2-\eta)[d_2(r_1+d_1)-rr_1]}{a_1(r_1+d_1)}x_2(t) - \frac{a(a_2-\eta)}{a_1}x_2^2(t) - d_3y(t) - by^2(t). \tag{4.4}$$

If $rr_1 < d_2(r_1+d_1)$, it then follows from (4.4) that $\dot{V}_0(t) \le 0$. By Theorem 5.3.1 in [4], solutions limit to Λ, the largest invariant subset of $\{\dot{V}_0(t) = 0\}$. Clearly, we see from (4.4) that $\dot{V}_0(t) = 0$ if and only if $x_2(t) = 0$ and $y(t) = 0$. Noting that Λ is invariant, for each element in Λ, we have $x_2(t) = 0$. It therefore follows from the second equation of system (1.2) that

$$0 = \dot{x}_2(t) = rx_1(t),$$

which yields $x_1(t) = 0$. Hence, $\dot{V}_0(t) = 0$ if and only if $(x_1(t), x_2(t), y(t)) = (0,0,0)$. Accordingly, the global asymptotic stability of E_0 follows from LaSalle's invariant principle for delay differential systems. □

Theorem 4.3. *Assume that $rr_1 > d_2(r_1 + d_1)$ holds. If $(a_2 - \eta)x_2^0 < d_3$, then the predator-extinction equilibrium $E_1(x_1^0, x_2^0, 0)$ of system (1.2) is globally asymptotically stable.*

Proof. By Theorem 4.1, we see that if $(a_2 - \eta)x_2^0 < d_3$, then E_1 is locally asymptotically stable. Hence, we only prove that all positive solutions of system (1.2) with initial conditions (1.3) converge to E_1. Let $(x_1(t), x_2(t), y(t))$ be any positive solution of system (1.2) with initial conditions (1.3). System (1.2) can be rewritten as

$$
\begin{aligned}
\dot{x}_1(t) &= \frac{r}{x_1^0}[-x_2(t)(x_1(t) - x_1^0) + x_1(t)(x_2(t) - x_2^0)],\\
\dot{x}_2(t) &= \frac{r_1}{x_2^0}[-x_1(t)(x_2(t) - x_2^0) + x_2(t)(x_1(t) - x_1^0)] + x_2(t)[-a(x_2(t) - x_2^0)]\\
&\quad - a_1 x_2(t)y(t),\\
\dot{y}(t) &= a_2 x_2(t-\tau)y(t-\tau) - d_3 y(t) - by^2(t) - \eta x_2(t)y(t).
\end{aligned}
\tag{4.5}
$$

Define

$$
V_{11}(t) = c_1\left(x_1 - x_1^0 - x_1^0 \ln\frac{x_1}{x_1^0}\right) + c_2\left(x_2 - x_2^0 - x_2^0\ln\frac{x_2}{x_2^0}\right) + y(t),
$$

where $c_1 = r_1 x_1^0/(r x_2^0)$, $c_2 = (a_2 - \eta)/a_1$. Calculating the derivative of $V_{11}(t)$ along positive solutions of (4.5), it follows that

$$
\begin{aligned}
\dot{V}_{11}(t) =& c_1\frac{x_1(t) - x_1^0}{x_1(t)}\dot{x}_1(t) + c_2\frac{x_2(t) - x_2^0}{x_2(t)}\dot{x}_2(t) + \dot{y}(t)\\
=& -\frac{r}{x_2^0}\left(\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t) - x_1^0) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t) - x_2^0)\right)^2 - ac_2(x_2(t) - x_2^0)^2\\
&- a_2x_2(t)y(t) + a_2x_2(t-\tau)y(t-\tau) - [d_3 - (a_2 - \eta)x_2^0]y(t) - by^2(t).
\end{aligned}
\tag{4.6}
$$

Define

$$
V_1(t) = V_{11}(t) + a_2\int_{t-\tau}^{t} x_2(u)y(u)du.
$$

By calculation, we have that

$$
\begin{aligned}
\dot{V}_1(t) =& -\frac{r_1}{x_2^0}\left(\sqrt{\frac{x_2(t)}{x_1(t)}}(x_1(t) - x_1^0) - \sqrt{\frac{x_1(t)}{x_2(t)}}(x_2(t) - x_2^0)\right)^2 - ac_2(x_2(t) - x_2^0)^2\\
&- [d_3 - (a_2 - \eta)x_2^0]y(t) - by^2(t).
\end{aligned}
\tag{4.7}
$$

If $(a_2 - \eta)x_2^0 < d_3$, it then follows from (4.7) that $\dot{V}_2(t) \le 0$. By Theorem 5.3.1 in [4], solutions limit to Λ, the largest invariant subset of $\{\dot{V}_2(t) = 0\}$. Clearly, we see from (4.7) that $\dot{V}_2(t) = 0$ if and only if $x_1(t) = x_1^0, x_2(t) = x_2^0$ and $y(t) = 0$. Hence, the only invariant set $\Lambda = \{(x_1^0, x_2^0, 0)\}$. Using LaSalle's invariant principle for delay differential systems, the global asymptotic stability of E_1 follows. □

5. Numerical simulations

In this section, we give some examples to illustrate the main results in this paper.

Example 5.1. In system (1.2), let $a = 1, a_1 = 1, a_2 = 1.2, b = 1, d_1 = 0.8, d_2 = 0.8, d_3 = 0.5, r = 1, r_1 = 0.7$ and $\eta = 1$. System (1.2) always has a trivial equilibrium $E_0(0, 0, 0)$. It is easy to show that $rr_1 < d_2(r_1 + d_1)$. By Theorem 4.1, we see that the equilibrium E_0 is locally asymptotically stable. Numerical simulation illustrates this fact (see Fig.1).

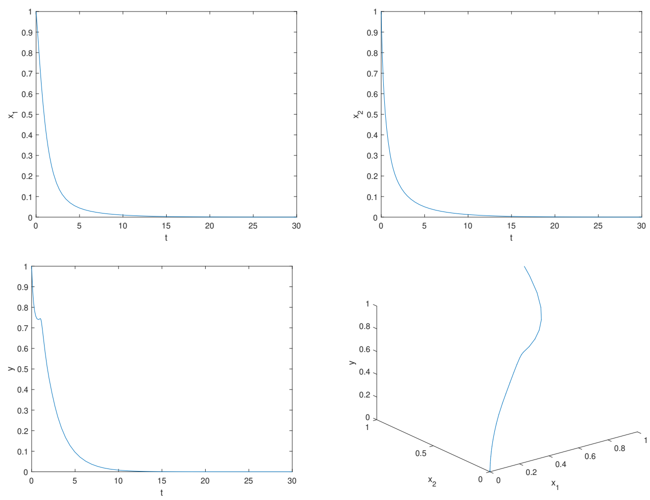

Figure 1. The temporal solution found by numerical integration of system (1.2) with $\tau = 0.5$ and $(\varphi_1(0), \varphi_2(0), \phi(0)) = (1, 1, 1)$

Example 5.2. In system (1.2), let $a = 1, a_1 = 1, a_2 = 1.2, b = 1, d_1 = 0.5, d_2 = 0.5, d_3 = 0.5, r = 2, r_1 = 0.8$ and $\eta = 1$. By calculation, we obtain $rr_1 > d_2(r_1 + d_1)$ and therefore, system (1.2) has a predator-extinction equilibrium $E_1(1.1243, 0.7308, 0)$. By Theorem 4.1, we see that the equilibrium E_1 is locally asymptotically stable. Numerical simulation illustrates this fact (see Fig.2).

Example 5.3. In (1.2), let $a = 1, a_1 = 0.5, a_2 = 1.5, b = 0.1, d_1 = 0.5, d_2 = 0.5, d_3 = 0.1, r = 3, r_1 = 0.8$ and $\eta = 1$. By calculation, we obtain system (1.1) has a unique coexistence equilibrium $E^*(0.0536, 0.0121, 0.0735, 0.8263)$. By calculation, we have

$$(p_2 + q_2)(p_3 + q_3) - (p_1 + q_1) = 50.6392 > 0,$$

$$(p_2 + q_2)(p_3 + q_3)(p_1 + q_1) - (p_1 + q_1)^2 - (p_0 + q_0)(p_3 + q_3)^2 = 20.7950 > 0,$$

$$2\alpha(r_1 + d_1) - 2rr_1 - (r_1 + d_1)\frac{a_1 y_2^*}{(1 + mx_2^*)^2} = -4.2142 < 0,$$

$$\tau_0 \approx 2.3147.$$

By Theorem 2.1, E^* is locally asymptotically stable if $0 < \tau < \tau_0$ and is unstable if $\tau > \tau_0$, and system (1.1) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$. Numerical simulation illustrates this fact(see Fig.3 and Fig.4).

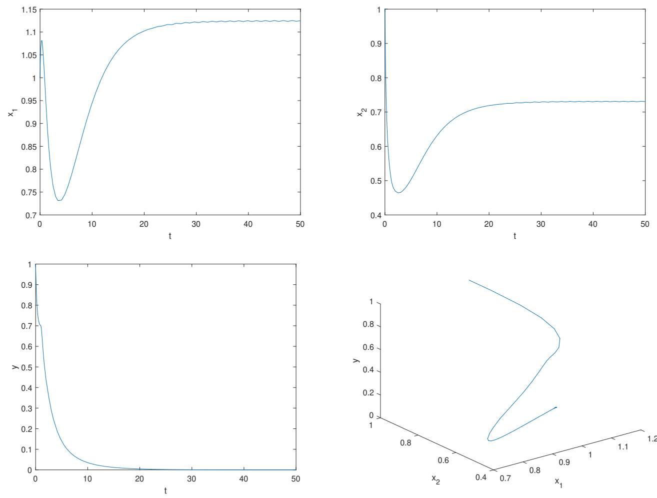

Figure 2. The temporal solution found by numerical integration of system (1.2) with $\tau = 0.5$ and $(\varphi_1(0), \varphi_2(0), \phi(0)) = (1, 1, 1)$

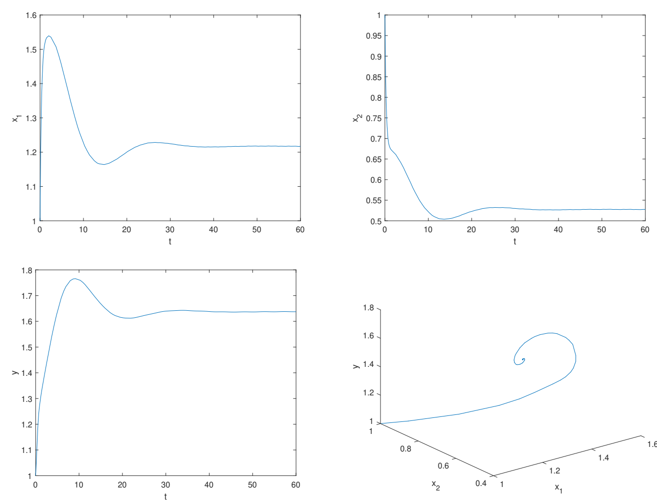

Figure 3. The temporal solution found by numerical integration of system (1.2) with $\tau = 0.5$ and $(\varphi_1(0), \varphi_2(0), \phi(0)) = (1, 1, 1)$

6. Discussion

In this paper, we have investigated the stability of a predator-prey model with stage structure for the prey and anti-predator behaviour. By analyzing the corresponding characteristic equation, the local stability of the trivial equilibrium, the predator-extinction equilibrium and the positive equilibrium has been established. It has been shown that, under some conditions, the time delay due to gestation of the predators may destabilize the positive equilibrium of system (1.2) and cause the population to fluctuate. From Theorem 2.1, we see that there is a threshold τ_0 for the time

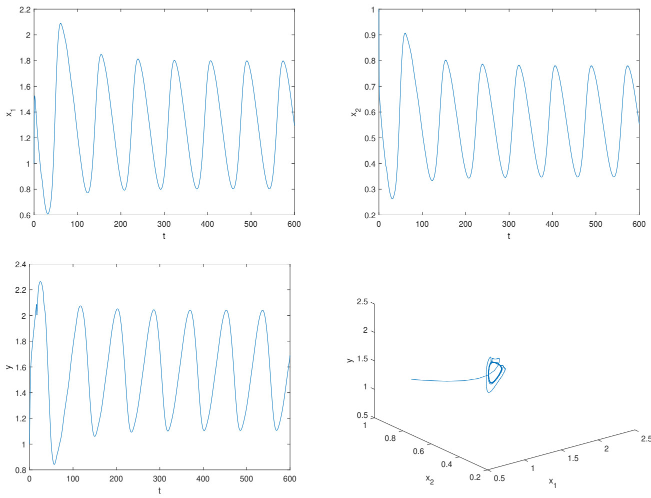

Figure 4. The temporal solution found by numerical integration of system (1.2) with $\tau = 15.706$ and $(\varphi_1(0), \varphi_2(0), \phi(0)) = (1, 1, 1)$

delay such that below it the positive equilibrium is stable, but if the delay is greater than the threshold, sustained oscillations arise. By means of Lyapunov functionals and LaSalle's invariant principle, sufficient conditions were obtained for the global stability of the the trivial equilibrium, the predator-extinction equilibrium and the positive equilibrium of system (1.2).

References

[1] W. G. Aiello and H. I. Freedman, *A time delay model of single species growth with stage-structure,* Math. Biosci., 1990, 101, 139–156.

[2] Y. Choh, M. Lgnacio, M. W. Sabelis and A. Janssen, *Predator-prey role reversals, juvenile experience and adult antipredator behaviour,* Scientific Reports, 2012, 2, 728.

[3] S. Gourley and Y. Kuang, *A stage structured predator-prey model and its dependence on maturation delay and death rate,* J. Math. Biol., 2004, 49, 188–200.

[4] J. Hale, *Theory of Functional Differential Equation,* Springer Heidelberg, 1977.

[5] J. Huang, S. Ruan and J. Song, *Bifurcations in a predator-prey system of Leslie type with generalized Holling type III functional response,* J Diff. Equations, 2014, 257(6), 1721–1752.

[6] A. Janssen, F. Faraji, T. V. D. Hammen, S. Magalhaes and M. W. Sabelis, *Interspecific infanticide deters predators,* Ecology Letters, 2002, 5, 490–494.

[7] Y. Kuang, *Delay Differential Equation with Application in Population Synamics,* Academic Press, New York, 1993.

[8] S. L. Lima, *Stress and decision-making under the risk of predation: recent developments from behavioral reproductive, and ecological perspectives,* Advances in the Study of Behavior, 1998, 27, 215–290.

[9] C. Liu, S. Li and Y. Yan, *Hopf bifurcation analysis of a density predator-prey model with crowley-martin functional response and two time delays,* Journal of Applied Analysis and Computation, 2019, 9(4), 1589–1605

[10] S. G. Mortoja, P. Panja and S. K. Mondal, *Dynamics of a predator-prey model with stage-structure on both species and anti-predator behavior,* Informatics in Medicine Unlocked, 2018, 10, 50–57.

[11] A. Pallina, A. Jaassen and M. W. Sabelis, *Predators induce interspecific herbivore competition for food in refuge space,* Ecology Letters, 2010, 1, 171–177.

[12] P. Panja and S. Mondal, *Stability analysis of coexistence of three species prey-predator model,* Nonlinear Dynam., 2015, 81, 373–82.

[13] M. Perc and P. Grigolini, *Collective behavior and evolutionary games -An introduction,* Chaos, Solitons & Fractals, 2013, 56, 1–5.

[14] R. A. Relvea, *How prey response to combined predators: a review and an empirical test,* Ecology, 2003, 84, 1827–1839.

[15] Y. Song, T. Yin and H. Shu, *Dynamics of a ratio-dependent stage-structured predator-pery model with delay,* Mathematical Methods in the Applied Sciences, 2017, 1–17.

[16] X. Sun, Y. Li and Y. Xiao, *A predator-prey model with prey population guided anti-predator behavior,* International Journal of Bifurcation and Chaos, 2017, 27, 1750099–1–40.

[17] X. Song and L. Chen, *Optimal harvesting and stability for a two-species competetive system with stage structure,* Math. Biosci., 2001, 170, 173–186.

[18] A. Szolnoki, M. Mobilia, L. Jiang, B. Szczesny, A. M. Rucklidge and M. Perc, *Cyclic dominance in evolutionary games: a review,* Journal of the Royal Society Interface, 2014, 11, 20140735.

[19] B. Tang and Y. Xiao, *Bifurcation analysis of a predator-prey model with anti-predator behaviour,* Chaos, Solitons & Fractals, 2015, 70, 58–68.

[20] S. Wang, *Research on the suitable living environment of the Rana temporaria chensinensis larva,* Chinese, J. Zool., 1997, 31, 38–41.

[21] C. Xu and Y. Yu, *Stability analysis of time delay fraction order predator-prey system with crowley-martin functional response,* Journal of Applied Analysis and Computation, 2019, 9(3), 928–942.

[22] R. Xu and Z. Ma, *The effect of stage-structure on the permanence of a predator-prey system with time delay,* Appl. Math. Comput., 2007, 189, 1164–1177.

[23] R. Xu and Z. Ma, *Stability and Hopf bifurcation in a predator-prey model with stage structure for the predator,* Nonlinear Analysis: Real World Applications, 2008, 9(4), 1444–1460.

[24] R. Yang and J. Ma, *Analysis of a diffusive predator-prey system with anti-predator behaviour and maturation delay,* Chaos, Solitons and Fractals, 2018, 109, 128–139.