Stability and bifurcation analysis for a delayed Lotka–Volterra predator–prey system

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Abstract

The present paper deals with a delayed Lotka–Volterra predator–prey system. By linearizing the equations and by analyzing the locations on the complex plane of the roots of the characteristic equation, we find the necessary conditions that the parameters should verify in order to have the oscillations in the system. In addition, the normal form of the Hopf bifurcation arising in the system is determined to investigate the direction and the stability of periodic solutions bifurcating from these Hopf bifurcations. To verify the obtained conditions, a special numerical example is also included.

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1. Introduction

In recent years, population models in various fields of mathematical biology have been proposed and studied extensively. In order to reflect that the dynamical behaviors of models that depend on the past history of the system, it is often necessary to incorporate time-delays into the models. Suppose that in a certain environment there are the prey and predator species with respective population densities \( x(t) \) and \( y(t) \) at time \( t \), if the predator species need time \( \tau_1 \) to possess the ability of predation after it was born and it captures only the adult prey species with maturation time \( \tau_2 \). Then in this case, the model two species interaction can be described by the following differential difference equations with two discrete delays:

\[
\begin{align*}
\dot{x}(t) &= x(t)[r_1 - a_{11}x(t) - a_{12}y(t - \tau_1)], \\
\dot{y}(t) &= y(t)[-r_2 + a_{21}x(t - \tau_2) - a_{22}y(t)],
\end{align*}
\]

where \( \tau_1 \geq 0 \) is called the hunting delay and \( \tau_2 \geq 0 \) is the maturation time of the prey species; \( r_1 > 0 \) denotes intrinsic growth rate of prey species and \( r_2 > 0 \) denotes the death rate of predator species; the parameters \( a_{12} \) and \( a_{21} \) are positive constants, and \( a_{11} \) and \( a_{22} \) are nonnegative constants. Also, system (1.1) shows that, in the absence of predator species,
the prey species is governed by the well-known logistic equation \( \dot{x}(t) = x(t)[r_1 - a_{11}x(t)] \) and the predator species will decrease in the absence of the prey species.

Systems similar to (1.1) and with some constants vanishing (most of the literatures consider \( \tau_1 = a_{22} = 0 \)) or with some more constraints on the constants or with distributed delays have been widely studied. There is an extensive literature about the studies of the dynamics of systems similar to (1.1), including the boundedness of solutions, persistence, local and global stabilities of equilibria, and existence of nonconstant periodic solutions (e.g., [1,5,6,9,10,12,16] and references therein).

In general, time delays in competitive and Lotka–Volterra type predator–prey systems are harmless for the boundedness and persistence in the sense that, if the solutions of the non-delayed systems are uniformly bounded and persistent eventually, then the solutions of the corresponding systems with delays are also uniformly bounded and persistent eventually (see, for example, [13] for delayed predator–prey systems and [10] for delayed competitive systems). However, the other dynamical behaviors such as periodic phenomenon, bifurcation and so on are even richer and more complicated.

It is well known that the studies on dynamical systems not only include a discussion of stability, attractivity and persistence, but also include many dynamical behaviors such as periodic phenomenon, bifurcation and chaos. In particular, the properties of periodic solutions appearing through the Hopf bifurcation in delayed systems are of great interest, see Hale [7], Liu and Yuan [11], Wei and Li [14] and Wei and Ruan [15].

Recently, Faria [3] investigated system (1.1) and obtained the stability of positive equilibrium, the existence of local Hopf bifurcation and the properties such as the stability and the direction of periodic solutions bifurcating from local Hopf bifurcation by regarding \( \tau_2 > 0 \) as a bifurcation parameter. In addition, in view of the difficulty of computation, Faria gave only the normal form of the Hopf bifurcations for the special case of system (1.1) such as \( a_{11} = a_{22} = 0 \). However, for the general case of system (1.1), the abstract formulae were presented while not resolved.

In this paper, we investigate again the effects of delay on solutions of (1.1). That is to say, we shall take the sum of the two delays, \( \tau = \tau_1 + \tau_2 \), as a parameter and show that when \( \tau \) passes through a certain critical value, the positive equilibrium loses its stability and a Hopf bifurcation occurs. Furthermore, when \( \tau \) takes a sequence of critical values, system (1.1) undergoes a Hopf bifurcation near positive equilibrium and at critical values of \( \tau \). By following the procedure of deriving normal form due to Faria and Magalhães [4], the normal form of the Hopf bifurcations is given for the general case of system (1.1). In addition, a numerical example is also included to illustrate the theoretical prediction.

### 2. Stability of positive equilibrium and local Hopf bifurcation

It is obvious that system (1.1) has three boundary equilibria \( O(0, 0) \), \( A(r_1/a_{11}, 0) \), \( B(0, -r_2/a_{22}) \) and a unique positive equilibrium \( E_*(x^*, y^*) \) provided that the condition (H) \( r_1a_{21} - r_2a_{11} > 0 \) holds, where

\[
x^* = \frac{r_1a_{22} + r_2a_{12}}{a_{11}a_{22} + a_{12}a_{21}}, \quad y^* = \frac{r_1a_{21} - r_2a_{11}}{a_{11}a_{22} + a_{12}a_{21}}.
\]

Since \( x(t) \) and \( y(t) \) denote the densities of prey and predator species, respectively, the non-negative solutions are significative and the positive solutions of system (1.1) are of interest. Therefore, system (1.1) has only three feasible equilibria \( O(0, 0) \), \( A(r_1/a_{11}, 0) \) and \( E_*(x^*, y^*) \) under condition (H).

The linearized systems of system (1.1) near the equilibria \( O(0, 0) \) and \( A(r_1/a_{11}, 0) \) are, respectively

\[
\begin{align*}
\dot{x}(t) &= r_1 x(t), \\
\dot{y}(t) &= -r_2 y(t),
\end{align*}
\]

and

\[
\begin{align*}
\dot{x}(t) &= -r_1 x(t) - \frac{r_1a_{12}}{a_{11}} y(t - \tau_2), \\
\dot{y}(t) &= \frac{r_1a_{21} - r_2a_{11}}{a_{11}} y(t).
\end{align*}
\]

From the two linear systems, it is easy to see that the characteristic equation of the linearized system of system (1.1) at the original point \( O(0, 0) \) has two real roots \( r_1 > 0 \) and \( -r_2 < 0 \). Therefore, \( O(0, 0) \) is a saddle point of system (1.1). The equilibrium \( A(r_1/a_{11}, 0) \) is a saddle point, higher order equilibrium, stable node of system (1.1) when condition (H), \( r_1a_{21} - r_2a_{11} = 0, r_1a_{21} - r_2a_{11} < 0 \) holds, respectively, since the characteristic equation of the linearized system of system (1.1) at the equilibrium \( A(r_1/a_{11}, 0) \) has two real roots \( -r_1 < 0 \) and \( (r_1a_{21} - r_2a_{11})/a_{11} \).
Under hypothesis (H), let \( u_1(t) = x(t) - x^* \), \( u_2(t) = y(t) - y^* \), then system (1.1) can be rewritten as the following equivalent system:

\[
\begin{align*}
\dot{u}_1(t) &= (u_1(t) + x^*)(-a_{11}u_1(t) - a_{12}u_2(t - \tau_1)), \\
\dot{u}_2(t) &= (u_2(t) + y^*)(a_{21}u_1(t - \tau_2) - a_{22}u_2(t)).
\end{align*}
\]

(2.1)

Thus, the linearized system of system (1.1) near the equilibrium \( E_*(x^*, y^*) \) given by the following linear system:

\[
\begin{align*}
\dot{u}_1(t) &= -a_{11}x^*u_1(t) - a_{12}x^*u_2(t - \tau_1), \\
\dot{u}_2(t) &= a_{21}y^*u_1(t - \tau_2) - a_{22}y^*u_2(t)
\end{align*}
\]

(2.2)

with characteristic equation

\[
\lambda^2 + p\lambda + q + re^{-\lambda\tau} = 0,
\]

(2.3)

where \( \tau = \tau_1 + \tau_2, p = a_{11}x^* + a_{22}y^* \geq 0, q = a_{11}a_{22}x^*y^* > 0, r = a_{12}a_{21}x^*y^* > 0 \). The stability of trivial solution of system (2.2) depends on the locations of the roots of the characteristic equation (2.3). When all roots of Eq. (2.3) locate in the left half of complex plane, the trivial solution of system (2.2) is stable; otherwise, it is instable. In the following, we will investigate the distribution of roots of Eq. (2.3).

For Eq. (2.3), we first have the following result.

**Lemma 2.1.** The two roots of Eq. (2.3) with \( \tau = 0 \) have always negative real parts.

In addition, \( i\omega(\omega > 0) \) is a root of Eq. (2.3) if and only if \( \omega \) satisfies the following equation:

\[
-\omega^2 + q + ip\omega + r(\cos \omega\tau - \sin \omega\tau) = 0.
\]

(2.4)

Separating the real and imaginary parts of Eq. (2.4) gives the following equations:

\[
\begin{align*}
-\omega^2 + q + r \cos \omega\tau &= 0, \\
p\omega - r \sin \omega\tau &= 0,
\end{align*}
\]

(2.5)

which implies that

\[
\omega^4 + (p^2 - 2q)\omega^2 + q^2 - r^2 = 0.
\]

(2.6)

Noting that \( p^2 \geq 4q \), we can easily see that Eq. (2.6) has no positive root if \( q \geq r \) and only one positive root \( \omega_0 = ((-p^2 - 2q) + \sqrt{(p^2 - 4q)p^2 + 4r^2})/2)^{1/2} \) provided that \( q < r \). Consequently, when \( q < r \) if we define

\[
\tau^{(j)} = \frac{1}{\omega_0} \left( \arccos \left( \frac{\omega_0^2 - q}{r} \right) + 2j\pi \right), \quad j = 0, 1, 2, \ldots,
\]

(2.7)

then Eq. (2.3) with \( \tau = \tau^{(j)} \) has a pair of purely imaginary roots \( \pm i\omega_0 \).

Summarizing the above remarks and combining Lemma 2.1, we have the following result on the distribution of roots of Eq. (2.3).

**Lemma 2.2.** (i) If \( q \geq r \), then all roots of Eq. (2.3) have negative real parts for all \( \tau \geq 0 \).

(ii) If \( q < r \), then when \( \tau \in [0, \tau^{(0)}] \), all roots of Eq. (2.3) have strictly negative real parts, while when \( \tau = \tau^{(0)} \), all roots of Eq. (2.3) except \( \pm i\omega_0 \) have strictly negative real parts.

(iii) If \( q < r \), then Eq. (2.3) with \( \tau = \tau^{(j)} \) has a simple pair of purely imaginary roots \( \pm i\omega_0 \).

Let \( \lambda(\tau) = \alpha(\tau) \pm i\omega(\tau) \) be the root of Eq. (2.3) near \( \tau = \tau^{(j)} \) satisfying \( \alpha(\tau^{(j)}) = 0, \omega(\tau^{(j)}) = \omega_0 \) (\( j = 0, 1, 2, \ldots \)).

**Lemma 2.3.** If \( q < r \), then the transversality conditions \( d\Re \lambda(\tau)/d\tau|_{\tau=\tau^{(j)}} > 0 \) (\( j = 0, 1, 2, \ldots \)) hold.
Theorem 2.5. For system

\[
\frac{d\lambda}{d\tau} = r\lambda e^{-\lambda \tau},
\]
which implies

\[
\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda + p)e^{\lambda \tau}}{r\lambda} - \frac{\tau}{\lambda}.
\]

Noting that \(\lambda = \pm i\omega_0\) when \(\tau = \tau^{(j)}\) and \(\tau^{(j)}, \omega_0\) satisfy (2.5), therefore, we have

\[
\text{Re}\left(\left(\frac{d\lambda}{d\tau}\right)^{-1}\right)_{\tau = \tau^{(j)}} = \frac{1}{\tau^2} \sqrt{(p^2 - 4q)p^2 + 4r^2} > 0.
\]

It follows that \(d\text{Re} \lambda(\tau)/d\tau|_{\tau = \tau^{(j)}} > 0\) and the proof is complete. □

From Lemma 2.3, we have the following result.

Lemma 2.4. If \(\tau > \tau^{(0)}\), then Eq. (2.3) has at least one root with strictly positive real part.

By Lemmas 2.2–2.4, we have the following result on stability and bifurcation of system (1.1).

Theorem 2.5. For system (1.1), the following statements are true:

(i) If \(q \geq r\), then the positive equilibrium \(E_0(x^*, y^*)\) of system (1.1) is asymptotically stable for any \(\tau \geq 0\); if \(q < r\), then when \(\tau \in [0, \tau^{(0)}]\), the positive equilibrium \(E_0(x^*, y^*)\) of system (1.1) is asymptotically stable.

(ii) If \(\tau > \tau^{(0)}\), then the equilibrium \(E_0(x^*, y^*)\) of system (1.1) is unstable.

(iii) \(\tau \in \{\tau^{(j)}\}, j = 0, 1, 2, \ldots\), are Hopf bifurcation values for system (1.1).

3. Direction and stability of the Hopf bifurcation

In the previous section, we have already obtained some conditions ensuring that system (1.1) undergoes a Hopf bifurcation at the positive equilibrium \(E_0(x^*, y^*)\) when \(\tau\) takes some critical values \(\tau^{(j)}(j = 0, 1, 2, \ldots)\). In this section, we shall study the direction and stability of the Hopf bifurcation by applying the normal form theory due to Faria and Magalhães [4].

For fixed \(j \in \{0, 1, 2, \ldots\}\), let \(\mu = \tau - \tau^{(j)}\). Then \(\mu = 0\) is the Hopf bifurcation value of system (1.1). Under hypothesis (H), let \(z_1(t) = x(t - \tau_2) - x^*, z_2(t) = y(t) - y^*\) and \(\tau = \tau_1 + \tau_2\). Then system (1.1) can be transformed into the following equivalent system:

\[
\begin{align*}
\dot{z}_1(t) &= (z_1(t) + x^*)[-a_{11}z_1(t) - a_{12}z_2(t - \tau)], \\
\dot{z}_2(t) &= (z_2(t) + y^*)[a_{21}z_1(t) - a_{22}z_2(t)].
\end{align*}
\]

Let \(u_1(t) = z_1(\tau t), u_2(t) = z_2(\tau t)\), then the above system can be rewritten an functional differential equation in \(C([-1, 0], \mathbb{R}^2)\) as

\[
\begin{align*}
\dot{u}_1(t) &= \tau(u_1(t) + x^*)[-a_{11}u_1(t) - a_{12}u_2(t - 1)], \\
\dot{u}_2(t) &= \tau(u_2(t) + y^*)[a_{21}u_1(t) - a_{22}u_2(t)].
\end{align*}
\]

Let \(u = (u_1, u_2)^T\). Then system (3.1) can further be written as

\[
\dot{u}(t) = L(\tau)(u_t) + F(u_t, \tau),
\]
where
\[ L(\tau)(\phi) = \tau \begin{pmatrix} -a_{11}x^*\phi_1(0) - a_{12}x^*\phi_2(-1) \\ a_{21}y^*\phi_1(0) - a_{22}y^*\phi_2(0) \end{pmatrix}, \]
and
\[ F(\phi, \tau) = \tau \begin{pmatrix} -a_{11}\phi_1^2(0) - a_{12}\phi_1(0)\phi_2(-1) \\ a_{21}\phi_1(0)\phi_2(0) - a_{22}\phi_2^2(0) \end{pmatrix}, \]
here \( \phi = (\phi_1, \phi_2)^T \in C([-1, 0], \mathbb{R}^2). \)

Obviously, \( L(\tau) \) is a continuous linear function mapping \( C([-1, 0], \mathbb{R}^2) \) into \( \mathbb{R}^2 \). By the Riesz representation theorem, there exists a 2 \( \times \) 2 matrix function \( \eta(\theta, \tau), -1 \leq \theta \leq 0 \), whose elements are of bounded variation such that
\[
L(\tau)(\phi) = \int_{-1}^{0} d\eta(\theta, \tau) \phi(\theta) \quad \text{for} \quad \phi \in C([-1, 0], \mathbb{R}^2). \tag{3.3}
\]

In fact, we can choose
\[
\eta(\theta, \tau) = \tau \begin{pmatrix} -a_{11}x^* & 0 \\ a_{21}y^* & -a_{22}y^* \end{pmatrix} \delta(\theta) - \tau \begin{pmatrix} 0 & -a_{12}x^* \\ 0 & 0 \end{pmatrix} \delta(\theta + 1), \tag{3.4}
\]
where \( \delta(\theta) \) denotes delta function. Then (3.3) is satisfied.

If \( \phi \) is an any given function in \( C([-1, 0], \mathbb{R}^2) \) and \( u(\phi) \) is the unique solution of the linearized equation \( \dot{u}(t) = L(\tau)u_t \) of Eq. (3.2) with the initial function \( \phi \) at zero, then the solution operator \( T(t) : C([-1, 0], \mathbb{R}^2) \rightarrow C([-1, 0], \mathbb{R}^2) \) is defined by
\[
T(t)\phi = u_t(\phi), \quad t \geq 0. \tag{3.5}
\]

From Lemma 7.1.1 in Hale \cite{7}, we know that \( T(t), t \geq 0 \), is a strongly continuous semigroup of linear transformation on \([0, \infty)\) and the infinitesimal generator \( A(\tau) \) of \( T(t), t \geq 0 \) is given by
\[
A(\tau)\phi(\theta) = \dot{\phi}(\theta) + X_0(\theta)[L(\tau)(\phi) - \dot{\phi}(0)] \quad \text{for} \quad \phi \in C^1([-1, 0], \mathbb{R}^2), \tag{3.6}
\]
where
\[
X_0(\theta) = \begin{cases} 0, & -1 \leq \theta < 0, \\ I, & \theta = 0. \end{cases}
\]

For \( \psi \in C^1([0, 1], (\mathbb{R}^2)^*) \), define
\[
A^*\psi(s) = -\dot{\psi}(s) + X_0(-s) \int_{-1}^{0} \psi(-t) \, d\eta(t, \tau^{(j)}) + \dot{\psi}(0) \tag{3.7}
\]
and a bilinear inner product
\[
\langle \psi(s), \phi(\theta) \rangle = \psi(0)\phi(0) - \int_{-1}^{0} \int_{\xi=0}^{\theta} \psi(\xi - \theta) \, d\eta(\theta) \phi(\xi) \, d\xi, \tag{3.8}
\]
where \( \eta(\theta) = \eta(\theta, \tau^{(j)}) \) and \( (\mathbb{R}^2)^* \) is two-dimensional real vector space of row vectors. Then, we know that \( A(\tau^{(j)}) \) and \( A^* \) are adjoint operators.

From the discussion in Section 2, we know that \( A(\tau^{(j)}) \) have a pair of simple purely imaginary roots \( \pm i\omega_0\tau^{(j)} \). They are also eigenvalues of \( A^* \). Let \( A = \{-i\omega_0\tau^{(j)}, \ i\omega_0\tau^{(j)} \} \) and denote by \( P \) the invariant space of \( A(\tau^{(j)}) \) associated with \( A \), where the dimension of \( P \) equals to 2. Now, we can decompose the space \( C := C([-1, 0], \mathbb{R}^2) \) as \( C = P \oplus Q \) by applying the formal adjoint theory for functional differential equations in \cite{7}. Considering complex coordinates and still denoting \( C([-1, 0], \mathbb{C}^2) \) as \( C \). Suppose that \( \Phi_1, \Phi_2 \) are the eigenvectors of the operator \( A(\tau^{(j)}) \) corresponding to eigenvalues \( i\omega_0\tau^{(j)} \), \( -i\omega_0\tau^{(j)} \), respectively. Then \( \Phi = (\Phi_1, \Phi_2) \) is a basis of \( P \) and \( \Phi_1(\theta) = e^{i\omega_0\tau^{(j)}\theta}(1, \xi)^T, \ \Phi_2(\theta) = \overline{\Phi_1(\theta)}, -1 \leq \theta \leq 0, \) where \( \xi = -((a_{11}x^* + i\omega_0)/a_{12}x^*)e^{i\omega_0\tau^{(j)}} \). Also, the two eigenvectors \( \Psi_1, \Psi_2 \) of \( A^* \) corresponding respectively to
eigenvalues $i\omega_0\tau^{(j)}$, $-i\omega_0\tau^{(j)}$ construct a basis $\Psi = (\Psi_1, \Psi_2)^T$ of the adjoint space $P^*$ of $P$ and $\Psi_1 = D(1, \zeta)e^{-i\omega_0\tau^{(j)}}, \Psi_2(\theta) = \Psi_1(\theta), 0 \leq s \leq 1$, where $\zeta = (a_{11}x^* + i\omega_0)/a_{21}y^*$ and

$$D = \frac{a_{22}y^* + i\omega_0}{[1 + \tau^{(j)}(a_{11}x^* + i\omega_0)](a_{22}y^* + i\omega_0) + a_{11}x^* + i\omega_0}.$$ 

Thus $(\Psi, \Phi) = ((\Psi_j, \Phi_j), i, j = 1, 2) = I_2$, second order identical matrix. It is known that $\hat{\Phi} = \Phi B$, where

$$B = \begin{pmatrix} i\omega_0\tau^{(j)} & 0 \\ 0 & -i\omega_0\tau^{(j)} \end{pmatrix}.$$ 

Take the enlarged phase space $C$ by considering the space $BC := \{\phi : [-1, 0] \to \mathbb{C}^2 | \phi$ is continuous on $[-1, 0]$ and $\lim_{\theta \to 0^-} \phi(\theta)$ exists$\}$ is replaced by $\pi : BC \to P$ such that $\pi(\phi + X_0x) = \Phi[(\Psi, \phi) + \Psi(0)x]$, where $x \in \mathbb{C}^2$.

Thus, we have the decomposition $BC = P \oplus \ker \pi$. Using the decomposition $u_t = \Phi x(t) + y_t, x(t) \in \mathbb{C}^2, y_t \in \ker \pi \cap C^1 = Q^1$, from Theorem 7.6.1 in [7], we can decompose (3.2) as

$$\begin{align*}
\dot{x} &= Bx + \Psi(0)F_0(\Phi x + y, \mu), \\
\frac{dy}{dt} &= A(\tau^{(j)})|_Q 1y + (I - \pi)x_0F_0(\Phi x + y, \mu),
\end{align*}$$

where $F_0(\phi, \mu) = L(\mu)(\phi) + F(\phi, \tau^{(j)} + \mu)$. In view of Taylor expansion, we denote, respectively, $\Psi(0)F_0(\Phi x + y, \mu)$ and $(I - \pi)x_0F_0(\Phi x + y, \mu)$ as

$$\begin{align*}
\Psi(0)F_0(\Phi x + y, \mu) &= \frac{1}{2}f_1^1(x, y, \mu) + \frac{1}{3!}f_1^3(x, y, \mu) + \cdots, \\
(I - \pi)x_0F_0(\Phi x + y, \mu) &= \frac{1}{2}f_2^1(x, y, \mu) + \frac{1}{3!}f_2^3(x, y, \mu) + \cdots,
\end{align*}$$

where $f_j^1(x, y, \mu)$ and $f_j^2(x, y, \mu)$ are homogeneous polynomials in $(x, y, \mu)$ of degree $j, j = 2, 3, \ldots$, with coefficients in $\mathbb{C}^2$ and $\ker \pi$, respectively. The normal form method gives a normal form on the center manifold of the origin for (3.9) as

$$\dot{x} = Bx + \frac{1}{2}g_2^1(x, 0, \mu) + \frac{1}{3!}g_3^1(x, 0, \mu) + \cdots, \tag{3.10}$$

where $g_j^1(x, 0, \mu)$ are homogeneous polynomials in $(x, \mu)$ of degree $j, j = 2, 3, \ldots$.

In what follows, we first define the operators $M_1^j$ as

$$M_1^j(p)(x, \mu) = D_\lambda p(x, \mu)Bx - Bp(x, \mu), \quad j \geq 2.$$ 

In particular, $M_1^j(\mu^l x^q e_k) = i\omega_0\tau^{(j)}(q_1 - q_2 + (-1)^k)\mu^l x^q e_k, l + q_1 + q_2 = j, k = 1, 2$, for $j = 2, 3, q = (q_1, q_2) \in \mathbb{N}_0^2, l \in \mathbb{N}_0$ and $\{e_1, e_2\}$ the canonical basis for $\mathbb{C}^2$. Therefore, we have

$$\ker (M_1^j) = \text{span} \left\{ \begin{pmatrix} x_1^\mu \\ 0 \\ x_2^\mu \end{pmatrix}, \begin{pmatrix} 0 \\ x_1^\mu \\ 0 \end{pmatrix} \right\}.$$ 

For (3.9), we have

$$f_2^1(x, y, \mu) = 2\Psi(0)[L(\mu)(\Phi x + y) + F(\Phi x + y, \tau^{(j)})]. \tag{3.11}$$

Note that $L(\mu) = (\mu/\tau^{(j)})L(\tau^{(j)})$, we have

$$f_2^1(x, 0, \mu) = \begin{pmatrix} 2A_1x_1^\mu + 2A_2x_1x_2 + b_{20}x_1^2 + b_{21}x_1x_2 + b_{02}x_2^2 \\ 2A_1x_2^\mu + 2A_2x_1x_2 + b_{20}x_2^2 + b_{21}x_1x_2 + b_{02}x_1^2 \end{pmatrix}, \tag{3.12}$$

where $A_1, A_2, B_{ij}$ are constants.
where

\[
A_1 = i\omega_0 D(1 + \zeta), \\
A_2 = -i\omega_0 D(1 + \overline{\zeta}), \\
b_{20} = 2D \tau^{(j)} [(a_{21} - a_{22}) \bar{\eta} \zeta - (a_{11} + a_{12} \bar{\eta} e^{-i\omega_0 \tau^{(j)}})], \\
b_{11} = 4D \tau^{(j)} [(a_{11} \text{Re} \zeta) - a_{22} |\zeta|^2 \zeta - (a_{11} + a_{12} \text{Re} \{\zeta e^{-i\omega_0 \tau^{(j)}}\})], \\
b_{02} = 2D \tau^{(j)} [(a_{21} - a_{22} \bar{\eta}) \bar{\zeta} \bar{\eta} - (a_{11} + a_{12} \overline{\eta} e^{i\omega_0 \tau^{(j)}})].
\]

(3.13)

Since the second order terms in \((\mu, x)\) on the center manifold are given by

\[
\frac{1}{2} g_1^1(x, 0, \mu) = \frac{1}{2} \text{Proj}_{\text{Ker}(M_2^1)} f_2^1(x, 0, \mu),
\]

it follows that

\[
\frac{1}{2} g_1^1(x, 0, \mu) = \left( \frac{A_1 x_1 \mu}{A_1 x_2 \mu} \right),
\]

(3.14)

where \(A_1\) defined by (3.13).

In the following, we shall compute the cubic term \(g_3^1(x, 0, \mu)\). First, we note that

\[
g_3^1(x, 0, \mu) \in \text{Ker}(M_2^1) = \text{span} \left\{ \left( \begin{array}{c} x_1^3 x_2 \\ 0 \\ x_1 x_2^2 \end{array} \right), \left( \begin{array}{c} x_1^2 x_2 \\ 0 \\ x_1 x_2^2 \end{array} \right), \left( \begin{array}{c} 0 \\ x_1^2 x_2 \\ x_1 x_2^2 \end{array} \right), \left( \begin{array}{c} 0 \\ 0 \\ x_1 x_2^2 \end{array} \right) \right\}.
\]

However, the terms \(O(|x| \mu^2)\) are irrelevant to determine the generic Hopf bifurcation. Hence, it is only needed to compute the coefficients of

\[
\left( \begin{array}{c} x_1^3 x_2 \\ 0 \\ x_1 x_2^2 \end{array} \right) \quad \text{and} \quad \left( \begin{array}{c} 0 \\ x_1^2 x_2 \\ x_1 x_2^2 \end{array} \right).
\]

Let

\[
s := \text{span} \left\{ \left( \begin{array}{c} x_1^3 x_2 \\ 0 \\ x_1 x_2^2 \end{array} \right), \left( \begin{array}{c} 0 \\ x_1^2 x_2 \\ x_1 x_2^2 \end{array} \right) \right\},
\]

then we have

\[
\frac{1}{3} g_3^1(x, 0, \mu) = \frac{1}{3} \text{Proj}_{\text{Ker}(M_1^1)} f_3^1(x, 0, \mu) = \frac{1}{3} \text{Proj}_{s} f_3^1(x, 0, 0) + O(|x| \mu^2),
\]

where

\[
f_3^1(x, 0, 0) = f_2^1(x, 0, 0) + \frac{3}{2} ((D_x f_2^1) U_1^2 - (D_x U_2^2) g_2^1)|_{(x, 0, 0)} + \frac{3}{2} ((D_y f_2^1) h)|_{(x, 0, 0)}
\]

is the third order term of the equation which is obtained after computing the second order terms of the normal form, \(U_2^2(x, 0)\) the solution of equation \(M_2^1 U_2^2(x, 0) = f_2^1(x, 0, 0)\) and \(h = (h^1, h^2)^T\) is a second order homogeneous polynomial in \((x_1, x_2, \mu)\) with coefficients in \(Q_1^1\).

From (3.1), (3.2) and (3.14) we can easily see that \(f_2^1(x, 0, 0) = 0\) and \(g_2^1(x, 0, 0) = 0\). Therefore, we have \([(D_x f_2^1) g_2^1]|_{(x, 0, 0)} = 0\) and thus we only need to compute \(f_2^1(x, 0, 0)\) and \(h(x)(\theta)\).

From (3.12), we have

\[
f_2^1(x, 0, 0) = \left( \begin{array}{c} b_{20} x_1^2 + 2b_{11} x_1 x_2 + b_{02} x_2^2 \\ b_{02} x_1^2 + 2b_{11} x_1 x_2 + b_{20} x_2^2 \end{array} \right).
\]

In view of the definition of \(M_2^1\), the equation \(M_2^1 U_2^1(x, 0) = f_2^1(x, 0, 0)\) can be written as the following partial differential equations:

\[
\begin{cases}
1 x_1 \frac{\partial u_1}{\partial x_1} - x_2 \frac{\partial u_1}{\partial x_2} - u_1 = \frac{1}{i\omega_0 \tau^{(j)}} (b_{20} x_1^2 + 2b_{11} x_1 x_2 + b_{02} x_2^2), \\
1 x_1 \frac{\partial u_2}{\partial x_1} - x_2 \frac{\partial u_2}{\partial x_2} + u_2 = \frac{1}{i\omega_0 \tau^{(j)}} (b_{02} x_1^2 + 2b_{11} x_1 x_2 + b_{20} x_2^2).
\end{cases}
\]

(3.15)
Thus, we know that

$$
U_2^1(x, 0) = \begin{pmatrix}
\frac{1}{i\omega_0\tau(j)}(b_{20}x_1^2 - 2b_{11}x_1x_2 - \frac{1}{3}b_{02}x_2^2) \\
\frac{1}{i\omega_0\tau(j)}(\frac{1}{3}b_{02}x_1^2 + 2b_{11}x_1x_2 - \bar{b}_{20}x_2^2)
\end{pmatrix}.
$$

Thus, we know that

$$
\text{Proj}_s[[D_yf_2^1]U_2^1]_{(x, 0, 0)} = \begin{pmatrix}
\frac{2i}{\omega_0\tau(j)}(b_{20}b_{11} - 2|b_{11}|^2 - \frac{1}{3}|b_{02}|^2)x_1x_2 \\
\frac{-2i}{\omega_0\tau(j)}(\bar{b}_{20}\bar{b}_{11} - 2|b_{11}|^2 - \frac{1}{3}|b_{02}|^2)x_1x_2
\end{pmatrix}.
$$

In the following, we shall compute \(\text{Proj}_s[[D_yf_2^1]h]_{(x, 0, 0)}\). From (3.11), we know

$$
f_2^1(x, y, 0) = 2\Psi(0) F(\Phi x + y, \tau(j)) = 2\tau(j) \begin{pmatrix}
D([a_{21}c_1d_1 - a_{22}d_1^2]\zeta - (a_{11}c_1^2 + a_{12}c_1d_2)) \\
\bar{D}([a_{21}c_1d_1 - a_{22}d_1^2]\bar{\zeta} - (a_{11}c_1^2 + a_{12}c_1d_2))
\end{pmatrix},
$$

where

\[
\begin{align*}
c_1 &= x_1 + x_2 + y_1(0), \\
d_1 &= x_1\zeta + x_2\bar{\zeta} + y_2(0), \\
d_2 &= x_1\zeta e^{-i\omega_0\tau(j)} + x_2\bar{\zeta} e^{i\omega_0\tau(j)} + y_2(-1).
\end{align*}
\]

Since \(h = (h^{(1)}, h^{(2)})^T\) is a second order homogeneous polynomial in \((x_1, x_2, \mu)\) with coefficients in \(Q^1\). Hence, we can let

\[
h = h_{110}x_1x_2 + h_{101}x_1\mu + h_{011}x_2\mu + h_{200}x_1^2 + h_{020}x_2^2 + h_{002}\mu^2.
\]

Thus, we from (3.16) have

\[
[(D_yf_2^1)h]_{(x, 0, 0)} = 2\tau(j) \begin{pmatrix}
D([a_{21}[h^{(1)}(0)d_1^0 + h^{(2)}(0)c_1^0]\zeta - 2a_{22}d_1^0h^{(2)}(0)\zeta] \\
-2a_{11}c_1^0h^{(1)}(0) - a_{12}[h^{(1)}(0)d_2^0 + h^{(2)}(0)c_1^0]) \\
\bar{D}([a_{21}[h^{(1)}(0)d_1^0 + h^{(2)}(0)c_1^0]\bar{\zeta} - 2a_{22}d_1^0h^{(2)}(0)\bar{\zeta}]
\end{pmatrix},
\]

where

\[
\begin{align*}
c_1^0 &= x_1 + x_2, \\
d_1^0 &= x_1\zeta + x_2\bar{\zeta}, \\
d_2^0 &= x_1\zeta e^{-i\omega_0\tau(j)} + x_2\bar{\zeta} e^{i\omega_0\tau(j)}.
\end{align*}
\]

Therefore,

\[
\text{Proj}_s[[D_yf_2^1]h]_{(x, 0, 0)} = \begin{pmatrix}
2c_3x_1^2x_2^2 \\
2\overline{c_3}x_1x_2^2
\end{pmatrix}
\]

where

\[
 c_3 = D\tau(j)[a_{21}[h_{110}^1(0)\zeta + h_{200}^1(0)\bar{\zeta} + h_{110}^2(0) + h_{200}^2(0)]\zeta \\
-2a_{22}[h_{110}^2(0)\zeta + h_{200}^2(0)\bar{\zeta}]\zeta - 2a_{11}[h_{110}^1(0) + h_{200}^1(0)] \\
- a_{12}[h_{110}^1(0)e^{-i\omega_0\tau(j)}\zeta + h_{200}^1(0)\bar{\zeta} e^{i\omega_0\tau(j)} + h_{110}^2(-1) + h_{200}^2(-1))].
\]

Since \(h_{110}(\theta)\) and \(h_{200}(\theta)\) for \(\theta \in [-1, 0]\) appear in \(c_3\) and \(c_4\), we still need to compute them.
Following [4], we know that \( h = h(\theta; x_1, x_2, \mu) \) is the unique solution in the linear space of homogeneous polynomials of degree 2 in 3 real variables \((x, \mu) = (x_1, x_2, \mu)\) of the equation

\[
(M_2^2 h)(x, \mu) = 2(I - \pi)X_0[L(\mu)(\Phi x) + F(\Phi x, \tau^{(j)})].
\]

Since

\[
(M_2^2 h)(x, \mu) = D_x h(x, \mu)Bx - A(\tau^{(j)})\big|_{\hat{\gamma}}(h(x, \mu)).
\]

Combining definition (3.6) of the operator \( A(\tau) \), we can obtain

\[
D_x h(x, \mu)Bx - \hat{h}(x, \mu) - X_0(\theta)[L(\tau)(h(x, \mu)) - \hat{h}(x, \mu)(0)] = 2(I - \pi)X_0[L(\mu)(\Phi x) + F(\Phi x, \tau^{(j)})].
\]

For the sake of simplicity, let

\[
h_0 = h_{110}(0)x_1x_2 + h_{200}(0)x_1^2 + h_{020}(0)x_2^2.
\]

Then \( h_0 \) can be evaluated by the system

\[
\begin{align*}
\dot{h}_{110} & = 2(b_{11} \Phi_1 + \tilde{b}_{11} \Phi_2), \\
\dot{h}_{110}(0) - L(\tau^{(j)})(h_{110}) & = 2\tau^{(j)} \left( -a_{11} - a_{12} \text{Re}\{\xi e^{-i\omega_0 \tau^{(j)}}\} \right),
\end{align*}
\]

(3.20)

\[
\begin{align*}
\dot{h}_{200} - 2i\omega_0 \tau^{(j)}h_{200} & = b_{20} \Phi_1 + \tilde{b}_{20} \Phi_2, \\
\dot{h}_{200}(0) - L(\tau^{(j)})(h_{200}) & = \tau^{(j)} \left( -a_{11} - a_{12} \xi e^{-i\omega_0 \tau^{(j)}} \right).
\end{align*}
\]

(3.21)

Respectively, solving Eqs. (3.20) and (3.21), we have

\[
h_{110}(\theta) = \frac{2}{i\omega_0 \tau^{(j)}}(b_{11} \Phi_1 - \tilde{b}_{11} \Phi_2) + c',
\]

\[
h_{200}(\theta) = \frac{b_{20}}{i\omega_0 \tau^{(j)}} \Phi_1 - \frac{\tilde{b}_{20}}{3i\omega_0 \tau^{(j)}} \Phi_2 + c'' e^{2i\omega_0 \tau^{(j)}\theta},
\]

where \( c', c'' \) are, respectively, the solution of the following linear algebra equations

\[
\begin{bmatrix}
-a_{11}x^* & -a_{12}x^* \\
a_{21}y^* & -a_{22}y^*
\end{bmatrix} c' = -2 \begin{bmatrix}
-a_{11} - a_{12} \text{Re}\{\xi e^{-i\omega_0 \tau^{(j)}}\} \\
a_{21} \text{Re}\{\xi\} - a_{22} |\xi|^2
\end{bmatrix}.
\]

(3.22)

\[
\begin{bmatrix}
2i\omega_0 + a_{11}x^* & a_{12}x^* e^{2i\omega_0 \tau^{(j)}} \\
-a_{21}y^* & 2i\omega_0 + a_{22}y^*
\end{bmatrix} c'' = \begin{bmatrix}
-a_{11} - a_{12} \xi e^{-i\omega_0 \tau^{(j)}} \\
a_{21} \xi - a_{22} \xi^2
\end{bmatrix}.
\]

(3.23)
Thus, we know that
\[
\frac{1}{3!} g^3_3(x, 0, 0) = \left( \frac{A_3 x_1^2 x_2}{A_3 x_1 x_2^2} \right),
\]
where \( A_3 = (i/2 \omega_0 \tau^{(j)})(b_{20} b_{11} - 2 |b_{11}|^2 - \frac{1}{3} |b_{02}|^2) + \frac{1}{2} c_3 \). Accordingly, the normal form (3.10) of (3.9) has the form
\[
\dot{x} = B x + \frac{1}{2} g^2_2(x, 0, \mu) + \frac{1}{3!} g^3_3(x, 0, \mu) + \cdots
\]
\[
= B x + \left( \frac{A_1 x_1 \mu}{A_1 x_2 \mu} \right) + \left( \frac{A_3 x_1^2 x_2}{A_3 x_1 x_2^2} \right) + O(|x| \mu^2 + |x|^4).
\]
The formal form (3.10) relative to \( P \) can be written in real coordinates \((w_1, w_2)\) through the change of variables \( x_1 = w_1 - i w_2, x_2 = w_1 + i w_2 \). Setting \( w_1 = \rho \cos \nu, w_2 = \rho \sin \nu \), this form becomes
\[
\begin{align*}
\dot{\rho} &= k_1 \rho \mu + k_2 \rho^3 + O(\mu^2 \rho + |(\rho, \mu)|^4), \\
\dot{\nu} &= -\sigma_k + O(|(\rho, \mu)|),
\end{align*}
\]
where \( k_1 = \text{Re}(A_1), k_2 = \text{Re}(A_3) \). Following [2], we know that the sign of \( k_1 k_2 \) determines the direction of the bifurcation and the sign of \( k_2 \) determines the stability of the nontrivial periodic solution bifurcating from Hopf bifurcation. Summarizing the above discussion, we can obtain the following result.

**Theorem 3.1.** The flow of Eq. (3.2) on the center manifold of the origin at \( \mu = 0 \) is given by (3.24). If \( k_1 k_2 < 0 \), Hopf bifurcation is supercritical, and subcritical if \( k_1 k_2 > 0 \). If \( k_2 < 0 \), the nontrivial periodic solution is stable, and unstable if \( k_2 > 0 \).

4. Numerical simulations

As a example, we consider system (1.1) with \( r_1 = r_2 = 1, a_{11} = 1, a_{12} = 1, a_{21} = 2, a_{22} = 1 \), that is,
\[
\begin{align*}
\dot{x}(t) &= x(t)[1 - x(t) - y(t - \tau_1)], \\
\dot{y}(t) &= y(t)[1 - 2x(t - \tau_2) - y(t)],
\end{align*}
\]
which has also a positive equilibrium \( E_\ast = (\xi, \frac{1}{3}) \). For system (4.1), since \( q = 0.2222 < r = 0.4444 \), it follows from the discussion in Section 2 that \( \omega_0 = 0.4437 \) and hence \( \tau_0 = 3.6686 \). From Theorem 2.5, we know that the positive equilibrium \( E_\ast = (\xi, \frac{1}{3}) \) is asymptotically stable when \( \tau_1 + \tau_2 \in [0, 3.6686] \) and is unstable when \( \tau_1 + \tau_2 > 3.6686 \). The numerical simulations for \( \tau_1 = 1.7 \) and \( \tau_2 = 1.8 \) are shown in Figs. 1–3.

By means of software Matlab6.5, we can compute the following values:
\[
\begin{align*}
\zeta &= 0.7215 - 0.9604i, & \bar{\zeta} &= 1.0000 + 0.6656i, & D &= 0.1968 - 0.0470i, \\
B_{20} &= 3.6470 + 1.2031i, & B_{11} &= 0, & B_{02} &= 2.5285 + 1.0713i, \\
A_1 &= 0.0912 + 0.1962i, & C_3 &= -0.8385 + 2.5604i.
\end{align*}
\]
It follows that \( A_3 = -0.4192 + 0.5081i \) and so \( k_1 = 0.0912, k_2 = -0.4192 \). Therefore, from Theorem 3.1, we know that system (4.1) with \( \tau_1 + \tau_2 = \tau_0 = 3.6686 \) has a supercritical Hopf bifurcation and the nontrivial periodic solution bifurcating from Hopf bifurcation of (4.1) with \( \tau_1 + \tau_2 = \tau_0 = 3.6686 \) is stable in the center manifold. In addition, all roots of Eq. (2.4) with \( \tau_1 + \tau_2 = \tau_0 = 3.6686 \), except \( \pm 0.4437 \), have negative real parts. Thus, the center manifold theory implies that the stability of the periodic solutions projected in the center manifold coincide with the stability of the periodic solutions in the whole phase space. The numerical simulations for \( \tau_1 = 1.8 \) and \( \tau_2 = 1.9 \) are shown in Figs. 4–6.
Fig. 1. The trajectory graph on $t-x$ plane of system (4.1) with $\tau_1 = 1.7, \tau_2 = 1.8$.

Fig. 2. The trajectory graph on $t-y$ plane of system (4.1) with $\tau_1 = 1.7, \tau_2 = 1.8$.

Fig. 3. The phase graph of system (4.1) with $\tau_1 = 1.7, \tau_2 = 1.8$.

Fig. 4. The trajectory graph in $t-x$ plane of system (4.1) with $\tau_1 = 1.8, \tau_2 = 1.9$. 
5. Biological explanations and conclusions

5.1. Biological explanations

From the discussion in Section 2, we know that the original point O(0, 0) is a saddle point and the equilibrium $A(r_1/a_{11}, 0)$ is a stable node of system (1.1) for any delays $\tau_1 \geq 0$ and $\tau_2 \geq 0$ and system (1.1) has no positive equilibrium when $r_1a_{12} - r_2a_{11} < 0$. This shows that, in this case, the predator species will tend to extinction and the prey species will tend to stabilization, and this fact is not influenced by the hunting delay $\tau_2$ and the maturation time $\tau_1$ of the prey species.

When assumption (H) holds, we know that the boundary equilibria O(0, 0) and $A(r_1/a_{11}, 0)$ of system (1.1) are the saddle points for any delays $\tau_1 \geq 0$ and $\tau_2 \geq 0$ and system (1.1) has a unique positive equilibrium $E_*(x^*, y^*)$. For the positive equilibrium $E_*(x^*, y^*)$, Theorem 2.5 implies that it is stable for any delay $\tau = \tau_1 + \tau_2 \geq 0$ if $q \geq r$. Therefore, in this case if the species densities of prey and predator population are all greater than zero, then the two species will reach gradually a natural balance state and stabilize at the positive equilibrium level. But if $q < r$, then the two species will also stabilize at the positive equilibrium level when $\tau \in [0, \tau^{(0)})$. When $\tau$ crosses through the critical value $\tau^{(0)}$, the positive equilibrium $E_*(x^*, y^*)$ loses stability and a Hopf bifurcation occurs. If the periodic solution bifurcating from the Hopf bifurcation is stable, then this shows that the predator and the prey species may coexist in an oscillatory mode. From the analysis in Section 2, we know that the unique positive equilibrium $E_*(x^*, y^*)$ is always unstable when $\tau > \tau_0$. Therefore, if the above bifurcating periodic solution is unstable, then it is at least semi-stable (stable inside and unstable outside) and hence the two species with the initial species densities near the positive equilibrium will coexist in an oscillatory mode.

5.2. Conclusions

As nonlinear dynamical system, Lotka–Volterra predator–prey systems are complex while the dynamics of the delayed Lotka–Volterra predator–prey systems are even richer and more complicated. Lotka–Volterra predator–prey systems with delays can exhibit very rich dynamics.
In general, in the investigating on a delay model, linearization of the system at its steady state gives us a transcendental characteristic equation or called an exponential polynomial equation. It is well known that the steady state is stable if all eigenvalues of the corresponding transcendental characteristic equation have negative real parts, and unstable if at least one root has positive real part. For the locations on the complex plane of roots of an exponential polynomial equation, there are two possibilities:

(a) Under certain assumptions, the real parts of all eigenvalues remain negative for all values of the delay; that is, independent of the delay. In this case, the corresponding delay system is called absolutely stable (see, for example, [8]). A general result in [8] says that a delay system is absolutely stable if and only if the corresponding ODE system is asymptotically stable and the characteristic equation has no purely imaginary roots.

(b) If the assumptions in (a) are not satisfied, then there is an eigenvalue changing the real part from negative to zero and to positive (i.e., the steady state changes from stability to instability). Thus, a Hopf bifurcation occurs.

In particular, the stability and direction of periodic solutions bifurcating from Hopf bifurcations are of great interest. However, it is very complex and difficult to determine the normal form of the Hopf bifurcation in order to investigate the properties of bifurcating periodic solutions.

In the present paper, we consider the sum of two delays \( \tau_1 \) and \( \tau_2 \), \( \tau = \tau_1 + \tau_2 \), as a bifurcation parameter and find that system (1.1) is absolutely stable when \( q \geq r \). When \( q < r \), there are a sequence of critical values \( \tau^{(j)} (j = 0, 1, 2, \ldots) \) of \( \tau \) such that the positive equilibrium \( E^*_n(x^*, y^*) \) is stable when \( \tau \in [0, \tau^{(0)}) \), a Hopf bifurcation occurs when \( \tau = \tau^{(0)} \), the positive equilibrium \( E^*_n(x^*, y^*) \) is always unstable when \( \tau > \tau_0 \) and there is always a Hopf bifurcation near the positive equilibrium \( E^*_n(x^*, y^*) \) when \( \tau \) takes the critical values \( \tau^{(j)} (j = 0, 1, 2, \ldots) \). For these Hopf bifurcations, the explicit formulae determining the stability and the direction are given by using the normal form theory and then center manifold theorem due to Faria and Magalhães [4]. A numerical example verifying our theoretical results is also included.

References