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Global Hopf bifurcation for three-species ratio-dependent predator-prey system with two delays

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Abstract

In this paper, the effect of the two different delays on the dynamics of a three-species ratio-dependent predator-prey food-chain model is considered. By regarding the delay as the bifurcation parameter, the local stability of the positive equilibrium and the existence of Hopf bifurcation are investigated. Explicit formulas determining the properties of a Hopf bifurcation are obtained by using the normal form method and the center manifold theorem. Special attention is paid to the global continuation of local Hopf bifurcation when the delay $\tau_1 \neq \tau_2$. Finally, several numerical simulations supporting the theoretical analysis are also given.

Keywords: predator-prey system; ratio-dependent; two delays; Hopf bifurcation; global Hopf bifurcation

1 Introduction

There has been great interest in dynamical characteristics of population models during the last few decades, among these models, predator-prey systems play an important role in population dynamics. Ratio-dependent predator-prey systems have received much attention as more suitable ones for predator-prey interactions where predation involves searching process. Many theoreticians and experimentalists have concentrated on a ratio-dependent predator-prey system. The general form of the ratio-dependent model is

$$\begin{cases} \dot{x} = xf(x) - yp(\frac{x}{y}), \\ \dot{y} = cyq(\frac{x}{y}) - dy, \end{cases} \tag{1.1}$$

where x, y, respectively, denote the prey and predator density. The functions $p(z)$ (the so-called predator functional response) and $q(z)$ satisfy the usual properties such as being nonnegative and increasing, and being equal to zero at zero. Arditi and Ginzburg [1] proposed the following ratio-dependent predator-prey model with a Michaelis-Menten-type or Holling-type II functional response:

$$\begin{cases} \dot{x} = ax(1 - \frac{x}{K}) - \frac{cxy}{my+x}, \\ \dot{y} = y(-d + \frac{fx}{my+x}), \end{cases} \tag{1.2}$$

where a, K, c, m, f, d are positive constants that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half capturing saturation constant, conversion rate, predator death rate, respectively.

It is well known that time delays in an ecological system can have a considerable influence on the qualitative behavior of these systems. The ratio-dependent predator-prey models with time delays have been studied by many researchers recently and rich dynamics has been observed (see, for example, [2–9] and references cited therein). In [7], Xu and Chen incorporate time delay due to gestation into the ratio-dependent predator-prey system and investigate the following n-species ratio-dependent predator-prey food-chain model with a Michaelis-Menten-type functional response:

$$\begin{cases} \frac{dx_1}{dt} = x_1(t)[a_1 - a_{11}x_1(t) - \frac{a_{12}x_2(t)}{m_{12}x_2(t)+x_1(t)}], \\ \dots, \\ \frac{dx_i}{dt} = x_i(t)[-a_i + \frac{a_{i,i-1}x_{i-1}(t-\tau_{i-1})}{m_{i-1,i}x_i(t-\tau_{i-1})+x_{i-1}(t-\tau_{i-1})} - \frac{a_{i,i+1}x_{i+1}(t)}{m_{i,i+1}x_{i+1}(t)+x_i(t)}], \quad i = 2, \dots, n-1, \\ \dots, \\ \frac{dx_n}{dt} = x_n(t)[-a_n + \frac{a_{n,n-1}x_{n-1}(t-\tau_{n-1})}{m_{n-1,n}x_n(t-\tau_{n-1})+x_{n-1}(t-\tau_{n-1})}], \end{cases} \tag{1.3}$$

where $x_i(t)$ represents the density of the ith population, respectively, $i = 1, 2, \dots, n$. a_i, a_{ij} $(i, j = 1, 2, \dots, n)$ and $m_{i,i+1}$ $(i = 1, 2, \dots, n-1)$ are positive constants. $\tau_i \geq 0$ $(i = 1, 2, \dots, n-1)$ are constant delays due to gestation. Xu and Chen showed that the system is permanent under some appropriate conditions, and sufficient conditions are obtained for the global stability of the positive equilibrium of the system.

Periodic solutions bifurcating from Hopf bifurcations in delayed differential equations are generally local. However, it is an important subject to investigate if these nonconstant periodic solutions which are obtained through local Hopf bifurcations exist globally due to theoretical and practical significance. In this paper, let $n = 3$ and make use of sufficient conditions of the global stability of the positive equilibrium of system (1.3) in [7], we investigate the Hopf bifurcation and global periodic solutions of three-species ratio-dependent predator-prey model with two delays:

$$\begin{cases} \frac{dx_1}{dt} = x_1(t)[a_1 - a_{11}x_1(t) - \frac{a_{12}x_2(t)}{m_{12}x_2(t)+x_1(t)}], \\ \frac{dx_2}{dt} = x_2(t)[-a_2 + \frac{a_{21}x_1(t-\tau_1)}{m_{12}x_2(t-\tau_1)+x_1(t-\tau_1)} - \frac{a_{23}x_3(t)}{m_{23}x_3(t)+x_2(t)}], \\ \frac{dx_3}{dt} = x_3(t)[-a_3 + \frac{a_{32}x_2(t-\tau_2)}{m_{23}x_3(t-\tau_2)+x_2(t-\tau_2)}], \end{cases} \tag{1.4}$$

with initial conditions

$$x_i(t) = \phi_i(t), \quad t \in [-\tau, 0], \qquad \phi_i(0) > 0, \quad i = 1, 2, 3, \tag{1.5}$$

where $x_1(t)$, $x_2(t)$, and $x_3(t)$ denote the densities of the prey, predator and top predator population, respectively; a_1, a_2 and a_3 are the intrinsic growth rate of prey, death rates of predator and top predator, respectively; a_{12}, a_{21}, a_{23} and a_{32} stand for the conversion rates, m_{12} and m_{23} stand for the half capturing saturations. τ_1, τ_2, are constant delays due to gestation, that is, mature adult preys can only contribute to the production of predator biomass. $\tau = \max\{\tau_1, \tau_2\}$. $\phi_i(t)$ $(i = 1, 2, 3)$ are continuous bounded functions in the interval $[-\tau, 0]$.

We would like to point out that many works investigated the dynamical behaviors of the system with two delays under the assumption $\tau_1 + \tau_2 = \tau$ or $\tau_1 = \tau_2 = \tau$. It is important to deal with the effect of the different delays on the dynamics of system (1.4), and it is also a mathematical subject to investigate whether the nontrivial periodic solutions which are obtained through local Hopf bifurcations exist globally. Recently, a great deal of research has been devoted to the topics [10–16]. To the best of our knowledge, there are few works which deal with global Hopf bifurcation of system with different two delays. In this paper, we investigate the stability and bifurcation of model (1.4) with the different delays τ_1 and τ_2, and the existence of the global Hopf bifurcation of system (1.4) is studied.

This paper is organized as follows: In Section 2, by analyzing the characteristic equation of the linearized system of system (1.4) at positive equilibrium, the sufficient conditions ensuring the local stability of the positive equilibrium and the existence of Hopf bifurcation are obtained. Some explicit formulas determining the direction and stability of periodic solutions bifurcating from Hopf bifurcations are demonstrated by applying the normal form method and center manifold theory in Section 3. In Section 4, we consider the global existence of the bifurcating periodic solutions. A brief discussion is given in the last section.

2 Stability of the positive equilibrium and local Hopf bifurcations

In this section, we first study the existence and local stability of the positive equilibrium, and then we investigate the effect of delay and the conditions for the existence of Hopf bifurcations.

$\widetilde{E} = (\tilde{x}_1, \tilde{x}_2, 0)$ is a nonnegative equilibrium if $a_{21} - a_2 > 0$, $a_1 - \frac{a_{12}(a_{21}-a_2)}{m_{12}a_{21}} > 0$.

$E^* = (x_1^*, x_2^*, x_3^*)$ is a unique positive equilibrium point if and only if the following conditions are true:

$$
\begin{aligned}
(\mathrm{H}_1)\quad & a_{32} > a_3, \\
& a_{21} - \left(a_2 + \frac{a_{23}}{a_{32}m_{23}}(a_{32} - a_3)\right) > 0, \\
& a_1 - \frac{a_{12}}{a_{21}m_{12}}\left[a_{21} - \left(a_2 + \frac{a_{23}}{a_{32}m_{23}}(a_{32} - a_3)\right)\right] > 0,
\end{aligned}
$$

where

$$
\begin{aligned}
\tilde{x}_1 &= \frac{1}{a_{11}}\left[a_1 - \frac{a_{12}(a_{21} - a_2)}{m_{12}a_{21}}\right], \qquad \tilde{x}_2 = \frac{a_{21} - a_2}{a_2 m_{12}}\tilde{x}_1, \\
x_1^* &= \frac{1}{a_{11}}\left\{a_1 - \frac{a_{12}}{m_{12}a_{21}}\left[a_{21} - \left(a_2 + \frac{a_{23}}{m_{23}a_{32}}(a_{32} - a_3)\right)\right]\right\}, \\
x_2^* &= \frac{1}{m_{12}[a_2 + \frac{a_{23}(a_{32}-a_3)}{m_{23}a_{32}}]}\left[a_{21} - \left(a_2 + \frac{a_{23}}{a_{32}m_{23}}(a_{32} - a_3)\right)\right]x_1^*, \\
x_3^* &= \frac{a_{32} - a_3}{a_3 m_{23}}x_2^*.
\end{aligned}
$$

Let $E = (x_{10}, x_{20}, x_{30})$ be the arbitrary equilibrium, and let $u_1(t) = x_1(t) - x_{10}$, $u_2(t) = x_2(t) - x_{20}$, $u_3(t) = x_3(t) - x_{30}$, then the linearized system of the corresponding equations at E is as follows:

$$\dot{u}(t) = Bu(t) + Cu(t-\tau_1) + Du(t-\tau_2), \tag{2.1}$$

where

$$\begin{aligned}
&u(t) = \bigl(u_1(t), u_2(t), u_3(t)\bigr)^T, \qquad B = (b_{ij})_{3\times 3}, \qquad C = (c_{ij})_{3\times 3}, \qquad D = (d_{ij})_{3\times 3},\\
&b_{11} = a_1 - 2a_{11}x_{10} - \frac{a_{12}m_{12}x_{20}^2}{(m_{12}x_{20}+x_{10})^2}, \qquad b_{12} = -\frac{a_{12}x_{10}^2}{(m_{12}x_{20}+x_{10})^2},\\
&b_{22} = -a_2 + \frac{a_{21}x_{10}}{m_{12}x_{20}+x_{10}} - \frac{a_{23}m_{23}x_{30}^2}{(m_{23}x_{30}+x_{20})^2},\\
&b_{23} = -\frac{a_{23}x_{20}^2}{(m_{23}x_{30}+x_{20})^2}, \qquad b_{33} = -a_3 + \frac{a_{32}x_{20}}{m_{23}x_{30}+x_{20}},\\
&c_{21} = \frac{a_{21}m_{12}x_{20}^2}{(m_{12}x_{20}+x_{10})^2}, \qquad c_{22} = -\frac{a_{21}m_{12}x_{10}x_{20}}{(m_{12}x_{20}+x_{10})^2},\\
&d_{32} = \frac{a_{32}m_{23}x_{30}^2}{(m_{23}x_{30}+x_{20})^2}, \qquad d_{33} = -\frac{a_{32}m_{23}x_{20}x_{30}}{(m_{23}x_{30}+x_{20})^2},
\end{aligned}$$

all the other a_{ij}, b_{ij}, and c_{ij} are 0.

The characteristic equation for system (2.1) is

$$\begin{aligned}
&\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + \bigl(q_2\lambda^2 + q_1\lambda + q_0\bigr)e^{-\lambda\tau_1}\\
&\quad + \bigl(r_2\lambda^2 + r_1\lambda + r_0\bigr)e^{-\lambda\tau_2} + (m_1\lambda + m_0)e^{-\lambda(\tau_1+\tau_2)} = 0,
\end{aligned} \tag{2.2}$$

where

$$\begin{aligned}
&p_2 = -(b_{11} + b_{22} + b_{33}), \qquad p_1 = b_{11}b_{22} + b_{22}b_{33} + b_{11}b_{33}, \qquad p_0 = -b_{11}b_{22}b_{33},\\
&q_2 = -c_{22}, \qquad q_1 = b_{33}c_{22} + b_{11}c_{22} - b_{12}c_{21}, \qquad q_0 = b_{12}c_{21}b_{33} - b_{11}b_{33}c_{22},\\
&r_2 = -d_{33}, \qquad r_1 = b_{22}b_{33} - b_{23}d_{32} + b_{11}d_{33}, \qquad r_0 = b_{11}b_{23}d_{32} - b_{11}b_{22}d_{33},\\
&m_1 = c_{22}d_{33}, \qquad m_0 = b_{12}c_{21}d_{33} - b_{11}c_{22}d_{33}.
\end{aligned}$$

The characteristic equation of system (2.1) at E_3 reduces to

$$(\lambda - b_{33})\bigl[\lambda^2 - b_{11}\lambda + e^{-\lambda\tau_1}(-c_{22}\lambda + b_{11}c_{22} - b_{12}c_{21})\bigr] = 0.$$

We can easily see that E_3 is unstable if $b_{33} = a_{32} - a_3 > 0$.

In the following, we study local stability of the positive equilibrium E^* by analyzing the distribution of the roots of equation (2.2). We consider four cases.

Case (a) $\tau_1 = \tau_2 = 0$.

The associated characteristic equation of system (1.4) is

$$\lambda^3 + (p_2 + q_2 + r_2)\lambda^2 + (p_1 + q_1 + r_1 + m_1)\lambda + (p_0 + q_0 + r_0 + m_0) = 0. \tag{2.3}$$

Let

$$(\mathrm{H}_2)\quad p_2+q_2+r_2>0,\qquad (p_2+q_2+r_2)(p_1+q_1+r_1+m_1)-(p_0+q_0+r_0+m_0)>0,$$
$$p_0+q_0+r_0+m_0>0.$$

By the Routh-Hurwitz criterion, we have the following.

Theorem 1 *Assume that* (H_1), (H_2) *hold, then when* $\tau_1=\tau_2=0$, *the positive equilibrium* $E^*(x_1^*,x_2^*,x_3^*)$ *of system* (1.4) *is locally asymptotically stable.*

Case (b) $\tau_1=0$, $\tau_2>0$.

The associated characteristic equation of system (1.4) is

$$\lambda^3+(p_2+q_2)\lambda^2+(p_1+q_1)\lambda+(p_0+q_0)+\bigl[r_2\lambda^2+(r_1+m_1)\lambda+(r_0+m_0)\bigr]e^{-\lambda\tau_2}=0. \quad (2.4)$$

We want to determine if the real part of some root increases to reach zero and eventually becomes positive as τ_2 varies. Let $\lambda=i\omega$ ($\omega>0$) be a root of equation (2.4), then we have

$$\begin{aligned}&-i\omega^3-(p_2+q_2)\omega^2+i(p_1+q_1)\omega+(p_0+q_0)\\&\quad+\bigl[-r_2\omega^2+(r_1+m_1)\omega i+(r_0+m_0)\bigr](\cos\omega\tau_2-i\sin\omega\tau_2)=0.\end{aligned}$$

Separating the real and imaginary parts, we have

$$\begin{cases}\omega^3-(p_1+q_1)\omega=[r_2\omega^2-(r_0+m_0)]\sin\omega\tau_2+(r_1+m_1)\omega\cos\omega\tau_2,\\-(p_2+q_2)\omega^2+(p_0+q_0)=[r_2\omega^2-(r_0+m_0)]\cos\omega\tau_2-(r_1+m_1)\omega\sin\omega\tau_2.\end{cases} \quad (2.5)$$

It follows that

$$\omega^6+m_{12}\omega^4+m_{11}\omega^2+m_{10}=0, \quad (2.6)$$

where $m_{12}=(p_2+q_2)^2-2(p_1+q_1)-r_2^2$, $m_{11}=(p_1+q_1)^2-2(p_2+q_2)(p_0+q_0)+2(r_0+m_0)r_2-(r_1+m_1)^2$, $m_{10}=(p_0+q_0)^2-(r_0+m_0)^2$.

Denote $z=\omega^2$, (2.6) becomes

$$z^3+m_{12}z^2+m_{11}z+m_{10}=0. \quad (2.7)$$

Let

$$h_1(z)=z^3+m_{12}z^2+m_{11}z+m_{10}. \quad (2.8)$$

By (2.8), we have

$$\frac{dh_1(z)}{dz}=3z^2+2m_{12}z+m_{11}.$$

If $m_{10}=(p_0+q_0)^2-(r_0+m_0)^2<0$, then $h_1(0)<0$, $\lim_{z\to+\infty}h_1(z)=+\infty$. We can know that equation (2.7) has at least one positive root.

If $m_{10} = (p_0 + q_0)^2 - (r_0 + m_0)^2 \geq 0$, we see that when $\triangle_1 = m_{12}^2 - 3m_{11} \leq 0$, equation (2.7) has no positive root for $z \in [0, +\infty)$. On the other hand, when $\triangle_1 = m_{12}^2 - 3m_{11} > 0$, the equation

$$3z^2 + 2m_{12}z + m_{11} = 0$$

has two real roots: $z_{11}^* = \frac{-m_{12}+\sqrt{\triangle_1}}{3}$, $z_{12}^* = \frac{-m_{12}-\sqrt{\triangle_1}}{3}$. Because of $h_1''(z_{11}^*) = 2\sqrt{\triangle_1} > 0$, $h_1''(z_{12}^*) = -2\sqrt{\triangle_1} < 0$, z_{11}^* and z_{12}^* are the local minimum and the local maximum of $h_1(z)$, respectively. By the above analysis, we immediately obtain the following.

Lemma 1

(1) *If* $m_{10} \geq 0$ *and* $\triangle_1 = m_{12}^2 - 3m_{11} \leq 0$, *equation* (2.7) *has no positive roots for* $z \in [0, +\infty)$.
(2) *If* $m_{10} \geq 0$ *and* $\triangle_1 = m_{12}^2 - 3m_{11} > 0$, *equation* (2.7) *has at least one positive root if and only if* $z_{11}^* = \frac{-m_{12}+\sqrt{\triangle}}{3} > 0$ *and* $h_1(z_{11}^*) \leq 0$.
(3) *If* $m_{10} < 0$, *equation* (2.7) *has at least one positive root.*

Without loss of generality, we assume that (2.7) has three positive roots, defined by z_{11}, z_{12}, z_{13}, respectively. Then (2.6) has three positive roots

$$\omega_{11} = \sqrt{z_{11}}, \qquad \omega_{12} = \sqrt{z_{12}}, \qquad \omega_{13} = \sqrt{z_{13}}.$$

From (2.5) we have

$$\begin{aligned} \cos\omega_{1k}\tau_{2_{1k}} = {} & \frac{[(r_1 + m_1) - r_2(p_2 + q_2)]\omega_{1k}^4}{[r_2\omega_{1k}^2 - (r_0 + m_0)]^2 + (r_1 + m_1)^2\omega_{1k}^2} \\ & + \frac{[(p_2 + q_2)(r_0 + m_0) + r_2(p_0 + q_0) - (q_1 + p_1)(r_1 + m_1)]\omega_{1k}^2}{[r_2\omega_{1k}^2 - (r_0 + m_0)]^2 + (r_1 + m_1)^2\omega_{1k}^2} \\ & - \frac{(q_0 + p_0)(r_0 + m_0)}{[r_2\omega_{1k}^2 - (r_0 + m_0)]^2 + (r_1 + m_1)^2\omega_{1k}^2}. \end{aligned}$$

Thus, if we denote

$$\begin{aligned} \tau_{2_{1k}}^{(j)} = {} & \frac{1}{\omega_{1k}}\left\{\arccos\left(\frac{[(r_1 + m_1) - r_2(p_2 + q_2)]\omega_{1k}^4}{[r_2\omega_{1k}^2 - (r_0 + m_0)]^2 + (r_1 + m_1)^2\omega_{1k}^2}\right.\right. \\ & + \frac{[(p_2 + q_2)(r_0 + m_0) + r_2(p_0 + q_0) - (q_1 + p_1)(r_1 + m_1)]\omega_{1k}^2}{[r_2\omega_{1k}^2 - (r_0 + m_0)]^2 + (r_1 + m_1)^2\omega_{1k}^2} \\ & \left.\left. - \frac{(q_0 + p_0)(r_0 + m_0)}{[r_2\omega_{1k}^2 - (r_0 + m_0)]^2 + (r_1 + m_1)^2\omega_{1k}^2}\right) + 2j\pi\right\}, \end{aligned} \tag{2.9}$$

where $k = 1, 2, 3$; $j = 0, 1, 2, \ldots$, then $\pm i\omega_{1k}$ is a pair of purely imaginary roots of (2.4) corresponding to $\tau_{2_{1k}}^{(j)}$. Define

$$\tau_{2_{10}} = \tau_{2_{1k_0}}^{(0)} = \min_{k=1,2,3}\{\tau_{2_{1k}}^{(0)}\}, \qquad \omega_{10} = \omega_{1k_0}.$$

Let $\lambda(\tau_2) = \alpha(\tau_2) + i\omega(\tau_2)$ be the root of equation (2.4) near $\tau_2 = \tau_{2_{1k}}^{(j)}$ satisfying

$$\alpha(\tau_{2_{1k}}^{(j)}) = 0, \qquad \omega(\tau_{2_{1k}}^{(j)}) = \omega_{1k}.$$

Substituting $\lambda(\tau_2)$ into (2.4) and taking the derivative with respect to τ_2, we have

$$\begin{aligned}
&\big\{3\lambda^2 + 2(p_2+q_2)\lambda + (p_1+q_1) + \big[2r_2\lambda + (r_1+m_1)\big]e^{-\lambda\tau_2} \\
&\quad - \tau_2\big[r_2\lambda^2 + (r_1+m_1)\lambda + (r_0+m_0)\big]e^{-\lambda\tau_2}\big\}\frac{d\lambda}{d\tau_2} \\
&= \lambda\big[r_2\lambda^2 + (r_1+m_1)\lambda + (r_0+m_0)\big]e^{-\lambda\tau_2}.
\end{aligned}$$

Therefore,

$$\begin{aligned}
\left[\frac{d\lambda}{d\tau_2}\right]^{-1} &= \frac{[3\lambda^2 + 2(p_2+q_2)\lambda + (p_1+q_1)]e^{\lambda\tau_2}}{\lambda[r_2\lambda^2 + (r_1+m_1)\lambda + (r_0+m_0)]} \\
&\quad + \frac{2r_2\lambda + (r_1+m_1)}{\lambda[r_2\lambda^2 + (r_1+m_1)\lambda + (r_0+m_0)]} - \frac{\tau_2}{\lambda}.
\end{aligned} \tag{2.10}$$

When $\tau_2 = \tau_{21k}^{(j)}$, $\lambda(\tau_{21k}^{(j)}) = i\omega_{1k}$ $(k = 1, 2, 3)$,

$$\begin{aligned}
&\big\{\lambda\big[r_2\lambda^2 + (r_1+m_1)\lambda + (r_0+m_0)\big]\big\}\big|_{\tau_2=\tau_{21k}^{(j)}} = -(r_1+m_1)\omega_{1k}^2 + i\big[(r_0+m_0)\omega_{1k} - r_2\omega_{1k}^3\big], \\
&\big\{\big[3\lambda^2 + 2(p_2+q_2)\lambda + (p_1+q_1)\big]e^{\lambda\tau_2}\big\}\big|_{\tau_2=\tau_{21k}^{(j)}} \\
&\quad = \big\{\big[-3\omega_{1k}^2 + (p_1+q_1)\big]\cos\big(\omega_{1k}\tau_{21k}^{(j)}\big) - 2(p_2+q_2)\omega_{1k}\sin\big(\omega_{1k}\tau_{21k}^{(j)}\big)\big\} \\
&\qquad + i\big\{2(p_2+q_2)\omega_{1k}\cos\big(\omega_{1k}\tau_{21k}^{(j)}\big) + \big[-3\omega_{1k}^2 + (p_1+q_1)\big]\sin\big(\omega_{1k}\tau_{21k}^{(j)}\big)\big\}, \\
&\big\{2r_2\lambda + (r_1+m_1)\big\}\big|_{\tau_2=\tau_{21k}^{(j)}} = (r_1+m_1) + i2r_2\omega_{1k}.
\end{aligned}$$

According to (2.10), we have

$$\begin{aligned}
&\left[\frac{\operatorname{Re} d(\lambda(\tau_2))}{d\tau_2}\right]^{-1}_{\tau_2=\tau_{21k}^{(j)}} \\
&\quad = \operatorname{Re}\left[\frac{[3\lambda^2 + 2(p_2+q_2)\lambda + (p_1+q_1)]e^{\lambda\tau_2}}{\lambda[r_2\lambda^2 + (r_1+m_1)\lambda + (r_0+m_0)]}\right]_{\tau_2=\tau_{21k}^{(j)}} \\
&\qquad + \operatorname{Re}\left[\frac{2r_2\lambda + (r_1+m_1)}{\lambda[r_2\lambda^2 + (r_1+m_1)\lambda + (r_0+m_0)]}\right]_{\tau_2=\tau_{21k}^{(j)}} \\
&\quad = \frac{1}{\Lambda_1}\big\{-\big[-3\omega_{1k}^2 + (p_1+q_1)\big]\omega_{1k}\big[\big[r_2\omega_{1k}^2 - (r_0+m_0)\big]\sin\omega_{1k}\tau_{21k}^{(j)} \\
&\qquad + (r_1+m_1)\omega_{1k}\cos\omega_{1k}\tau_{21k}^{(j)}\big] \\
&\qquad - 2(p_2+q_2)\omega_{1k}^2\big[\big[r_2\omega_{1k}^2 - (r_0+m_0)\big]\cos\omega_{1k}\tau_{21k}^{(j)} - (r_1+m_1)\omega_{1k}\sin\omega_{1k}\tau_{21k}^{(j)}\big] \\
&\qquad - (r_1+m_1)^2\omega_{1k}^2 + 2\omega_{1k}r_2\big[(r_0+m_0)\omega_{1k} - r_2\omega_{1k}^3\big]\big\} \\
&\quad = \frac{1}{\Lambda_1}\big\{3\omega_{1k}^6 + 2\big[(p_2+q_2)^2 - 2(p_1+q_1) - r_2^2\big]\omega_{1k}^4 \\
&\qquad + \big[(p_1+q_1)^2 - 2(p_2+q_2)(p_0+q_0) \\
&\qquad + 2(r_0+m_0)r_2 - (r_1+m_1)^2\big]\omega_{1k}^2\big\}
\end{aligned}$$

$$= \frac{1}{\Lambda_1}\{z_{1k}(3z_{1k}^2 + 2m_{12}z_{1k} + m_{11})\}$$
$$= \frac{1}{\Lambda_1} z_{1k}h_1'(z_{1k}),$$

where $\Lambda_1 = (r_1 + m_1)^2\omega_{1k}^4 + [(r_0 + m_0)\omega_{1k} - r_2\omega_{1k}^3]^2 > 0$. Notice that $\Lambda_1 > 0$, $z_{1k} > 0$,

$$\operatorname{sign}\left\{\left[\frac{\operatorname{Re} d(\lambda(\tau_2))}{d\tau_2}\right]_{\tau_2=\tau_{21k}^{(j)}}\right\} = \operatorname{sign}\left\{\left[\frac{\operatorname{Re} d(\lambda(\tau_2))}{d\tau_2}\right]^{-1}_{\tau_2=\tau_{21k}^{(j)}}\right\},$$

then we have the following lemma.

Lemma 2 *Suppose that $z_{1k} = \omega_{1k}^2$ and $h_1'(z_{1k}) \neq 0$, where $h_1(z)$ is defined by* (2.8), *then $\frac{d(\operatorname{Re}\lambda(\tau_{21k}^{(j)}))}{d\tau_2}$ has the same sign with $h_1'(z_{1k})$.*

Here we also need the following lemma [17].

Lemma 3 *Consider the exponential polynomial*

$$\begin{aligned} P(\lambda, e^{-\lambda\tau_1}, \ldots, e^{-\lambda\tau_m}) = {} & \lambda^n + p_1^{(0)}\lambda^{n-1} + \cdots + p_{n-1}^{(0)}\lambda + p_n^{(0)} \\ & + [p_1^{(1)}\lambda^{n-1} + \cdots + p_{n-1}^{(1)}\lambda + p_n^{(1)}]e^{-\lambda\tau_1} + \cdots \\ & + [p_1^{(m)}\lambda^{n-1} + \cdots + p_{n-1}^{(m)}\lambda + p_n^{(m)}]e^{-\lambda\tau_m}, \end{aligned}$$

where $\tau_i \geq 0$, $i = 1, 2, \ldots, m$, and $p_j^{(i)}$ $(i = 0, 1, \ldots, m;\ j = 1, 2, \ldots, n)$ are constants. As $(\tau_1, \tau_2, \ldots, \tau_m)$ vary, the sum of the orders of the zeros of $P(\lambda, e^{-\lambda\tau_1}, \ldots, e^{-\lambda\tau_m})$ in the open right half plane can change only if a zero appears on or crosses the imaginary axis.

From Lemmas 1, 2, 3, and Theorem 1, we can easily obtain the following theorem.

Theorem 2 *For $\tau_1 = 0$, $\tau_2 > 0$, suppose that* (H_1), (H_2) *hold, then*:

(i) *If $m_{10} \geq 0$ and $\triangle_1 = m_{12}^2 - 3m_{11} \leq 0$, then all roots of equation* (2.4) *have negative real parts for all $\tau_2 \geq 0$, and the positive equilibrium E^* is locally asymptotically stable for all $\tau_2 \geq 0$.*

(ii) *If either $m_{10} < 0$ or $m_{10} \geq 0$, $\triangle_1 = m_{12}^2 - 3m_{11} > 0$, $z_{11}^* > 0$ and $h_1(z_{11}^*) \leq 0$, then $h_1(z)$ has at least one positive roots, and all roots of equation* (2.4) *have negative real parts for $\tau_2 \in [0, \tau_{210})$, and the positive equilibrium E^* is locally asymptotically stable for $\tau_2 \in [0, \tau_{210})$.*

(iii) *If* (ii) *holds and $h_1'(z_{1k}) \neq 0$, then system* (1.4) *undergoes Hopf bifurcations at the positive equilibrium E^* for $\tau_2 = \tau_{21k}^{(j)}$ $(k = 1, 2, 3; j = 0, 1, 2, \ldots)$.*

Case (c) $\tau_1 > 0$, $\tau_2 = 0$.

The associated characteristic equation of system (1.4) is

$$\begin{aligned} & \lambda^3 + (p_2 + r_2)\lambda^2 + (p_1 + r_1)\lambda + (p_0 + r_0) \\ & \quad + [q_2\lambda^2 + (q_1 + m_1)\lambda + (q_0 + m_0)]e^{-\lambda\tau_1} = 0. \end{aligned} \tag{2.11}$$

We want to determine if the real part of some root increases to reach zero and eventually becomes positive as τ_1 varies. Let $\lambda = i\omega$ ($\omega > 0$) be a root of equation (2.11), then we have

$$\begin{aligned}&-i\omega^3 - (p_2 + r_2)\omega^2 + i(p_1 + r_1)\omega + (p_0 + r_0)\\&\quad + \bigl[-q_2\omega^2 + (q_1 + m_1)\omega i + (q_0 + m_0)\bigr](\cos\omega\tau_1 - i\sin\omega\tau_1) = 0.\end{aligned}$$

Separating the real and imaginary parts, we have

$$\begin{cases}\omega^3 - (p_1 + r_1)\omega = [q_2\omega^2 - (q_0 + m_0)]\sin\omega\tau_1 + (q_1 + m_1)\omega\cos\omega\tau_1,\\ -(p_2 + r_2)\omega^2 + (p_0 + r_0) = [q_2\omega^2 - (q_0 + m_0)]\cos\omega\tau_1 - (q_1 + m_1)\omega\sin\omega\tau_1.\end{cases} \tag{2.12}$$

It follows that

$$\omega^6 + m_{22}\omega^4 + m_{21}\omega^2 + m_{20} = 0, \tag{2.13}$$

where $m_{22} = (p_2 + r_2)^2 - 2(p_1 + r_1) - q_2^2$, $m_{21} = (p_1 + r_1)^2 - 2(p_2 + r_2)(p_0 + r_0) + 2(q_0 + m_0)q_2 - (q_1 + m_1)^2$, $m_{20} = (p_0 + r_0)^2 - (q_0 + m_0)^2$.

Denote $z = \omega^2$, (2.13) becomes

$$z^3 + m_{22}z^2 + m_{21}z + m_{20} = 0. \tag{2.14}$$

Let

$$h_2(z) = z^3 + m_{22}z^2 + m_{21}z + m_{20}. \tag{2.15}$$

By (2.15), we have

$$\frac{dh_2(z)}{dz} = 3z^2 + 2m_{22}z + m_{21}.$$

If $m_{20} = (p_0 + r_0)^2 - (q_0 + m_0)^2 < 0$, then $h_2(0) < 0$, $\lim_{z\to+\infty} h_2(z) = +\infty$. We can know that equation (2.14) has at least one positive root.

If $m_{20} = (p_0 + r_0)^2 - (q_0 + m_0)^2 \geq 0$, we see that when $\triangle_2 = m_{12}^2 - 3m_{11} \leq 0$, equation (2.14) has no positive roots for $z \in [0, +\infty)$. On the other hand, when $\triangle_2 = m_{22}^2 - 3m_{21} > 0$, the equation

$$3z^2 + 2m_{22}z + m_{21} = 0$$

has two real roots: $z_{21}^* = \frac{-m_{22}+\sqrt{\triangle_2}}{3}$, $z_{22}^* = \frac{-m_{22}-\sqrt{\triangle_2}}{3}$. Because of $h_2''(z_{21}^*) = 2\sqrt{\triangle_2} > 0$, $h_2''(z_{22}^*) = -2\sqrt{\triangle_2} < 0$, z_{21}^* and z_{22}^* are the local minimum and the local maximum of $h_2(z)$, respectively. By the above analysis, we immediately obtain the following.

Lemma 4

(1) *If* $m_{20} \geq 0$ *and* $\triangle_2 = m_{22}^2 - 3m_{21} \leq 0$, *equation* (2.14) *has no positive root for* $z \in [0, +\infty)$.

(2) *If* $m_{20} \geq 0$ *and* $\triangle_2 = m_{22}^2 - 3m_{21} > 0$, *equation* (2.14) *has at least one positive root if and only if* $z_{21}^* = \frac{-m_{22}+\sqrt{\triangle}}{3} > 0$ *and* $h_2(z_{21}^*) \leq 0$.

(3) *If* $m_{20} < 0$, *equation* (2.14) *has at least one positive root.*

Without loss of generality, we assume that (2.14) has three positive roots, defined by z_{21}, z_{22}, z_{23}, respectively. Then (2.13) has three positive roots,

$$\omega_{21} = \sqrt{z_{21}}, \qquad \omega_{22} = \sqrt{z_{22}}, \qquad \omega_{23} = \sqrt{z_{23}}.$$

From (2.12) we have

$$\begin{aligned} \cos \omega_{2k}\tau_{1_{2k}} = {} & \frac{[(q_1+m_1) - q_2(p_2+r_2)]\omega_{2k}^4}{[q_2\omega_{2k}^2 - (q_0+m_0)]^2 + (q_1+m_1)^2\omega_{2k}^2} \\ & + \frac{[(p_2+r_2)(q_0+m_0) + q_2(p_0+r_0) - (r_1+p_1)(q_1+m_1)]\omega_{2k}^2}{[q_2\omega_{2k}^2 - (q_0+m_0)]^2 + (q_1+m_1)^2\omega_{2k}^2} \\ & - \frac{(r_0+p_0)(q_0+m_0)}{[q_2\omega_{2k}^2 - (q_0+m_0)]^2 + (q_1+m_1)^2\omega_{2k}^2}. \end{aligned}$$

Thus, if we denote

$$\begin{aligned} \tau_{1_{2k}}^{(j)} = {} & \frac{1}{\omega_{2k}} \biggl\{ \arccos \biggl(\frac{[(q_1+m_1) - q_2(p_2+r_2)]\omega_{2k}^4}{[q_2\omega_{2k}^2 - (q_0+m_0)]^2 + (q_1+m_1)^2\omega_{2k}^2} \\ & + \frac{[(p_2+r_2)(q_0+m_0) + q_2(p_0+r_0) - (r_1+p_1)(q_1+m_1)]\omega_{2k}^2}{[q_2\omega_{2k}^2 - (q_0+m_0)]^2 + (q_1+m_1)^2\omega_{2k}^2} \\ & - \frac{(r_0+p_0)(q_0+m_0)}{[q_2\omega_{2k}^2 - (q_0+m_0)]^2 + (q_1+m_1)^2\omega_{2k}^2} \biggr) + 2j\pi \biggr\}, \end{aligned} \tag{2.16}$$

where $k = 1,2,3$; $j = 0,1,2,\ldots$, then $\pm i\omega_{2k}$ is a pair of purely imaginary roots of (2.11) corresponding to $\tau_{1_{2k}}^{(j)}$. Define

$$\tau_{1_{20}} = \tau_{1_{2k_0}}^{(0)} = \min_{k=1,2,3} \bigl\{ \tau_{1_{2k}}^{(0)} \bigr\}, \qquad \omega_{20} = \omega_{2k_0}.$$

Let $\lambda(\tau_1) = \alpha(\tau_1) + i\omega(\tau_1)$ be the root of equation (2.11) near $\tau_1 = \tau_{1_{2k}}^{(j)}$ satisfying

$$\alpha\bigl(\tau_{1_{2k}}^{(j)}\bigr) = 0, \qquad \omega\bigl(\tau_{1_{2k}}^{(j)}\bigr) = \omega_{2k}.$$

Substituting $\lambda(\tau_1)$ into (2.11) and taking the derivative with respect to τ_1, we have

$$\begin{aligned} & \bigl\{ 3\lambda^2 + 2(p_2+r_2)\lambda + (p_1+r_1) + \bigl[2q_2\lambda + (q_1+m_1)\bigr]e^{-\lambda\tau_1} \\ & \quad - \tau_1\bigl[q_2\lambda^2 + (q_1+m_1)\lambda + (q_0+m_0)\bigr]e^{-\lambda\tau_1} \bigr\} \frac{d\lambda}{d\tau_1} \\ & = \lambda\bigl[q_2\lambda^2 + (q_1+m_1)\lambda + (q_0+m_0)\bigr]e^{-\lambda\tau_1}. \end{aligned}$$

Therefore,

$$\begin{aligned} \left[\frac{d\lambda}{d\tau_1}\right]^{-1} = {} & \frac{[3\lambda^2 + 2(p_2+r_2)\lambda + (p_1+r_1)]e^{\lambda\tau_1}}{\lambda[q_2\lambda^2 + (q_1+m_1)\lambda + (q_0+m_0)]} \\ & + \frac{2q_2\lambda + (q_1+m_1)}{\lambda[q_2\lambda^2 + (q_1+m_1)\lambda + (q_0+m_0)]} - \frac{\tau_1}{\lambda}. \end{aligned} \tag{2.17}$$

When $\tau_1 = \tau_{1_{2k}}^{(j)}$, $\lambda(\tau_{1_{2k}}^{(j)}) = i\omega_{2k}$ $(k = 1, 2, 3)$,

$$\begin{aligned}
&\bigl\{\lambda\bigl[q_2\lambda^2 + (q_1 + m_1)\lambda + (q_0 + m_0)\bigr]\bigr\}\big|_{\tau_1=\tau_{1_{2k}}^{(j)}} = -(q_1 + m_1)\omega_{2k}^2 + i\bigl[(q_0 + m_0)\omega_{2k} - q_2\omega_{2k}^3\bigr], \\
&\bigl\{\bigl[3\lambda^2 + 2(p_2 + r_2)\lambda + (p_1 + r_1)\bigr]e^{\lambda\tau_1}\bigr\}\big|_{\tau_1=\tau_{1_{2k}}^{(j)}} \\
&\quad = \bigl\{\bigl[-3\omega_{2k}^2 + (p_1 + r_1)\bigr]\cos\bigl(\omega_{2k}\tau_{1_{2k}}^{(j)}\bigr) - 2(p_2 + r_2)\omega_{2k}\sin\bigl(\omega_{2k}\tau_{1_{2k}}^{(j)}\bigr)\bigr\} \\
&\qquad + i\bigl\{2(p_2 + r_2)\omega_{2k}\cos\bigl(\omega_{2k}\tau_{1_{2k}}^{(j)}\bigr) + \bigl[-3\omega_{2k}^2 + (p_1 + r_1)\bigr]\sin\bigl(\omega_{2k}\tau_{1_{2k}}^{(j)}\bigr)\bigr\}, \\
&\bigl\{2q_2\lambda + (q_1 + m_1)\bigr\}\big|_{\tau_1=\tau_{1_{2k}}^{(j)}} = (q_1 + m_1) + i2q_2\omega_{2k}.
\end{aligned}$$

According to (2.17), we have

$$\begin{aligned}
&\left[\frac{\operatorname{Re} d(\lambda(\tau_1))}{d\tau_1}\right]^{-1}_{\tau_1=\tau_{1_{2k}}^{(j)}} \\
&\quad = \operatorname{Re}\left[\frac{[3\lambda^2 + 2(p_2 + r_2)\lambda + (p_1 + r_1)]e^{\lambda\tau_1}}{\lambda[q_2\lambda^2 + (q_1 + m_1)\lambda + (q_0 + m_0)]}\right]_{\tau_1=\tau_{2_{2k}}^{(j)}} \\
&\qquad + \operatorname{Re}\left[\frac{2q_2\lambda + (q_1 + m_1)}{\lambda[q_2\lambda^2 + (q_1 + m_1)\lambda + (q_0 + m_0)]}\right]_{\tau_1=\tau_{1_{2k}}^{(j)}} \\
&\quad = \frac{1}{\Lambda_2}\bigl\{-\bigl[-3\omega_{2k}^2 + (p_1 + r_1)\bigr]\omega_{2k}\bigl[\bigl[q_2\omega_{2k}^2 - (q_0 + m_0)\bigr]\sin\omega_{2k}\tau_{1_{2k}}^{(j)} \\
&\qquad + (q_1 + m_1)\omega_{2k}\cos\omega_{2k}\tau_{1_{2k}}^{(j)}\bigr] \\
&\qquad - 2(p_2 + r_2)\omega_{2k}^2\bigl[\bigl[q_2\omega_{2k}^2 - (q_0 + m_0)\bigr]\cos\omega_{2k}\tau_{1_{2k}}^{(j)} - (q_1 + m_1)\omega_{2k}\sin\omega_{2k}\tau_{1_{2k}}^{(j)}\bigr] \\
&\qquad - (q_1 + m_1)^2\omega_{2k}^2 + 2\omega_{2k}q_2\bigl[(q_0 + m_0)\omega_{2k} - q_2\omega_{2k}^3\bigr]\bigr\} \\
&\quad = \frac{1}{\Lambda_2}\bigl\{3\omega_{2k}^6 + 2\bigl[(p_2 + r_2)^2 - 2(p_1 + r_1) - q_2^2\bigr]\omega_{2k}^4 + \bigl[(p_1 + r_1)^2 - 2(p_2 + r_2)(p_0 + r_0) \\
&\qquad + 2(q_0 + m_0)q_2 - (q_1 + m_1)^2\bigr]\omega_{2k}^2\bigr\} \\
&\quad = \frac{1}{\Lambda_2}\bigl\{z_{2k}\bigl(3z_{2k}^2 + 2m_{22}z_{2k} + m_{21}\bigr)\bigr\} \\
&\quad = \frac{1}{\Lambda_2}z_{2k}h_2'(z_{2k}),
\end{aligned}$$

where $\Lambda_2 = (q_1 + m_1)^2\omega_{2k}^4 + [(q_0 + m_0)\omega_{2k} - q_2\omega_{2k}^3]^2 > 0$. Notice that $\Lambda_2 > 0$, $z_{2k} > 0$,

$$\operatorname{sign}\left\{\left[\frac{\operatorname{Re} d(\lambda(\tau_1))}{d\tau_1}\right]_{\tau_1=\tau_{1_{2k}}^{(j)}}\right\} = \operatorname{sign}\left\{\left[\frac{\operatorname{Re} d(\lambda(\tau_1))}{d\tau_1}\right]^{-1}_{\tau_1=\tau_{1_{2k}}^{(j)}}\right\},$$

then we have the following lemma.

Lemma 5 *Suppose that* $z_{2k} = \omega_{2k}^2$ *and* $h_2'(z_{2k}) \neq 0$, *where* $h_2(z)$ *is defined by* (2.15), *then* $\frac{d(\operatorname{Re}\lambda(\tau_{1_{2k}}^{(j)}))}{d\tau_1}$ *has the same sign as* $h_2'(z_{2k})$.

From Lemmas 3, 4, 5 and Theorem 1, we can easily obtain the following theorem.

Theorem 3 *For* $\tau_1 > 0$, $\tau_2 = 0$, *suppose that* (H_1), (H_2) *hold, then*:

(i) *If* $m_{20} \geq 0$ *and* $\triangle_2 = m_{22}^2 - 3m_{21} \leq 0$, *then all roots of equation* (2.11) *have negative real parts for all* $\tau_1 \geq 0$, *and the positive equilibrium* E^* *is locally asymptotically stable for all* $\tau_1 \geq 0$.

(ii) *If either* $m_{20} < 0$ *or* $m_{20} \geq 0$, $\triangle_2 = m_{22}^2 - 3m_{21} > 0$, $z_{21}^* > 0$ *and* $h_2(z_{21}^*) \leq 0$, *then* $h_2(z)$ *has at least one positive roots, and all roots of equation* (2.11) *have negative real parts for* $\tau_1 \in [0, \tau_{1_{20}})$, *and the positive equilibrium* E^* *is locally asymptotically stable for* $\tau_1 \in [0, \tau_{1_{20}})$.

(iii) *If* (ii) *holds and* $h_2'(z_{2k}) \neq 0$, *then system* (1.4) *undergoes Hopf bifurcations at the positive equilibrium* E^* *for* $\tau_1 = \tau_{1_{2k}}^{(j)}$ $(k = 1, 2, 3; j = 0, 1, 2, \ldots)$.

Case (d) $\tau_1 > 0$, $\tau_2 > 0$, $\tau_1 \neq \tau_2$.

The associated characteristic equation of system (1.4) is

$$\begin{aligned} &\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + \left(q_2\lambda^2 + q_1\lambda + q_0\right)e^{-\lambda\tau_1} \\ &\quad + \left(r_2\lambda^2 + r_1\lambda + r_0\right)e^{-\lambda\tau_2} + (m_1\lambda + m_0)e^{-\lambda(\tau_1+\tau_2)} = 0. \end{aligned} \tag{2.18}$$

We consider (2.18) with $\tau_2 = \tau_2^*$ in its stable interval $[0, \tau_{2_{10}})$. Regard τ_1 as a parameter.

Let $\lambda = i\omega$ $(\omega > 0)$ be a root of equation (2.18), then we have

$$\begin{aligned} &-i\omega^3 - p_2\omega^2 + ip_1\omega + p_0 + \left(-q_2\omega^2 + iq_1\omega + q_0\right)(\cos\omega\tau_1 - i\sin\omega\tau_1) \\ &\quad + \left(-r_2\omega^2 + r_0 + ir_1\omega\right)\left(\cos\omega\tau_2^* - i\sin\omega\tau_2^*\right) \\ &\quad + (im_1\omega + m_0)\left(\cos\omega\left(\tau_1 + \tau_2^*\right) - i\sin\omega\left(\tau_1 + \tau_2^*\right)\right) = 0. \end{aligned}$$

Separating the real and imaginary parts, we have

$$\begin{cases} \omega^3 - p_1\omega - r_1\omega\cos\omega\tau_2^* + (-r_2\omega^2 + r_0)\sin\omega\tau_2^* \\ \quad = q_1\omega\cos\omega\tau_1 - (-q_2\omega^2 + q_0)\sin\omega\tau_1 \\ \qquad + m_1\omega\cos\omega(\tau_1 + \tau_2^*) - m_0\sin\omega(\tau_1 + \tau_2^*), \\ p_2\omega^2 - p_0 - (-r_2\omega^2 + r_0)\cos\omega\tau_2^* - r_1\omega\sin\omega\tau_2^* \\ \quad = (-q_2\omega^2 + q_0)\cos\omega\tau_1 + q_1\omega\sin\omega\tau_1 \\ \qquad + m_0\cos\omega(\tau_1 + \tau_2^*) + m_1\omega\sin\omega(\tau_1 + \tau_2^*). \end{cases} \tag{2.19}$$

It follows that

$$\omega^6 + m_{34}\omega^4 + m_{33}\omega^2 + m_{32} + m_{31}\cos\omega\tau_2^* + m_{30}\sin\omega\tau_2^* = 0, \tag{2.20}$$

where

$$\begin{aligned} &m_{34} = p_2^2 - 2p_1 - q_2^2 + r_2^2, \qquad m_{33} = p_1^2 - 2p_0p_2 + r_1^2 - 2r_2r_0 - q_1^2 + 2q_2q_0 - m_1^2, \\ &m_{32} = p_0^2 + r_0^2 - m_0^2 - q_0^2, \\ &m_{31} = -2(r_1 + r_2p_2)\omega^4 + 2(r_1p_1 - p_0r_2 - p_2r_0 - q_1m_1 + q_2m_0)\omega^2 + 2(p_0r_0 - q_0m_0), \\ &m_{30} = -2r_2\omega^5 + 2(p_1r_2 + r_0 - p_2r_1 + q_2m_1)\omega^3 + 2(-r_0p_1 + p_0r_1 - q_1m_0 - q_0m_1)\omega. \end{aligned}$$

Denote $F(\omega) = \omega^6 + m_{34}\omega^4 + m_{33}\omega^2 + m_{32} + m_{31}\cos\omega(\tau_1 + \tau_2^*) + m_{30}\sin\omega(\tau_1 + \tau_2^*)$. If $(p_0 + r_0)^2 - (m_0 + q_0)^2 < 0$, then

$$F(0) < 0, \qquad \lim_{\omega\to+\infty} F(\omega) = +\infty.$$

We can see that (2.20) has at most six positive roots $\omega_1, \omega_2, \ldots, \omega_6$. For every fixed ω_k, $k = 1, 2, \ldots, 6$, there exists a sequence $\{\tau_{1k}^{(j)} | j = 0, 1, 2, 3, \ldots\}$, such that (2.19) holds.

Let

$$\tau_{10} = \min\bigl\{\tau_{1k}^{(j)} | k = 1, 2, \ldots, 6; j = 0, 1, 2, 3, \ldots\bigr\}. \tag{2.21}$$

When $\tau_1 = \tau_{1k}^{(j)}$, equation (2.18) has a pair of purely imaginary roots $\pm i\omega_{1k}^{(j)}$ for $\tau_2^* \in [0, \tau_{2_{10}})$.

In the following, we assume that

$$(\mathrm{H}_3) \quad \frac{d\,\mathrm{Re}(\lambda)}{d\tau_1}\bigg|_{\lambda=\pm i\omega_{1k}^{(j)}} \neq 0.$$

Then we have the following result on the stability and Hopf bifurcation in system (1.4).

Theorem 4 *For $\tau_1 > 0$, $\tau_2 > 0$, $\tau_1 \neq \tau_2$, suppose that (H_1)-(H_3) are satisfied. If $p_0 + r_0 - q_0 - m_0 < 0$ and $\tau_2^* \in [0, \tau_{2_{10}}]$, then the positive equilibrium E^* is locally asymptotically stable for $\tau_1 \in [0, \tau_{10})$. System* (1.4) *undergoes Hopf bifurcations at the positive equilibrium E^* for $\tau_1 = \tau_{1k}^{(j)}$.*

3 Direction and stability of the Hopf bifurcation

In Section 2, we obtain the conditions under which system (1.4) undergoes the Hopf bifurcation at the positive equilibrium E^*. In this section, we consider direction and stability of the Hopf bifurcation with $\tau_2 = \tau_2^* \in [0, \tau_{2_{10}})$ regarding τ_1 as a parameter. We will derive the explicit formulas determining the direction, stability, and period of these periodic solutions bifurcating from equilibrium E^* at the critical values τ_1, by using the normal form and the center manifold theory developed by Hassard *et al.* [18]. Without loss of generality, denote any one of these critical values $\tau_1 = \tau_{1k}^{(j)}$ $(k = 1, 2, \ldots, 6; j = 0, 1, 2, \ldots)$ by $\tilde{\tau}_1$, at which equation (2.18) has a pair of purely imaginary roots $\pm i\omega$ and system (1.4) undergoes Hopf bifurcation from E^*.

Throughout this section, we always assume that $\tau_2^* < \tau_{10}$. Let $u_1 = x_1 - x_1^*$, $u_2 = x_1 - x_2^*$, $u_3 = x_2 - x_3^*$, $t = \tau_1 t$ and $\mu = \tau_1 - \tilde{\tau}_1$, $\mu \in \mathcal{R}$. Then $\mu = 0$ is the Hopf bifurcation value of system (1.4) may be written as a functional differential equation in $\mathcal{C}([-1, 0], \mathcal{R}^3)$,

$$\dot{u}(t) = L_\mu(u_t) + f(\mu, u_t), \tag{3.1}$$

where $u = (u_1, u_2, u_3)^T \in \mathcal{R}^3$, and

$$L_\mu(\phi) = (\tilde{\tau}_1 + \mu)B \begin{bmatrix} \phi_1(0) \\ \phi_2(0) \\ \phi_3(0) \end{bmatrix} + (\tilde{\tau}_1 + \mu)C \begin{bmatrix} \phi_1(-1) \\ \phi_2(-1) \\ \phi_3(-1) \end{bmatrix} + (\tilde{\tau}_1 + \mu)D \begin{bmatrix} \phi_1(-\frac{\tau_2^*}{\tau_1}) \\ \phi_2(-\frac{\tau_2^*}{\tau_1}) \\ \phi_3(-\frac{\tau_2^*}{\tau_1}) \end{bmatrix}, \tag{3.2}$$

$$f(\mu,\phi) = (\tilde{\tau}_1 + \mu)\begin{bmatrix} f_1 \\ f_2 \\ f_3 \end{bmatrix}, \tag{3.3}$$

where $\phi = (\phi_1, \phi_2, \phi_3)^T \in \mathcal{C}([-1,0], \mathcal{R}^3)$, and

$$B = \begin{bmatrix} b_{11} & b_{12} & 0 \\ 0 & b_{22} & b_{23} \\ 0 & 0 & b_{33} \end{bmatrix}, \qquad C = \begin{bmatrix} 0 & 0 & 0 \\ c_{21} & c_{22} & 0 \\ 0 & 0 & 0 \end{bmatrix}, \qquad D = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & d_{32} & d_{33} \end{bmatrix},$$

$$\begin{aligned}
f_1 &= (-a_{11} + l_1)\phi_1^2(0) - l_2\phi_1(0)\phi_2(0) + l_3\phi_2^2(0) + \cdots, \\
f_2 &= -l_4\phi_1^2(-1) + l_5\phi_2^2(-1) + l_6\phi_1(-1)\phi_2(-1) + l_7\phi_1(-1)\phi_2(0) - l_8\phi_2(-1)\phi_2(0) \\
&\quad + l_9\phi_1^2(0) - l_{10}\phi_1(0)\phi_2(0) + l_{11}\phi_2^2(0) + \cdots, \\
f_3 &= -l_{12}\phi_2^2\left(-\frac{\tau_2^*}{\tau_1}\right) + l_{13}\phi_3^2\left(-\frac{\tau_2^*}{\tau_1}\right) + l_{14}\phi_2\left(-\frac{\tau_2^*}{\tau_1}\right)\phi_3(0) + l_{15}\phi_2\left(-\frac{\tau_2^*}{\tau_1}\right)\phi_3\left(-\frac{\tau_2^*}{\tau_1}\right) \\
&\quad - l_{16}\phi_3\left(-\frac{\tau_2^*}{\tau_1}\right)\phi_3(0) + \cdots, \\
l_1 &= \frac{a_{12}m_{12}x_2^{*2}}{(m_{12}x_2^* + x_1^*)^3}, \qquad l_2 = \frac{a_{12}m_{12}x_1^*x_2^*}{(m_{12}x_2^* + x_1^*)^3}, \qquad l_3 = \frac{a_{12}m_{12}x_1^{*2}}{(m_{12}x_2^* + x_1^*)^3}, \\
l_4 &= \frac{a_{21}m_{12}x_2^{*2}}{(m_{12}x_2^* + x_1^*)^3}, \qquad l_5 = \frac{a_{21}m_{12}^2x_1^*x_2^*}{(m_{12}x_2^* + x_1^*)^3}, \qquad l_6 = \frac{a_{21}m_{12}x_1^*x_2^* - a_{21}m_{12}^2x_2^{*2}}{(m_{12}x_2^* + x_1^*)^3}, \\
l_7 &= \frac{a_{21}m_{12}x_2^*}{(m_{12}x_2^* + x_1^*)^2}, \qquad l_8 = \frac{a_{21}m_{12}x_1^*}{(m_{12}x_2^* + x_1^*)^2}, \qquad l_9 = \frac{a_{23}m_{23}x_3^{*2}}{(m_{23}x_3^* + x_2^*)^3}, \\
l_{10} &= \frac{2a_{23}m_{23}x_2^*x_3^*}{(m_{23}x_3^* + x_2^*)^3}, \qquad l_{11} = \frac{a_{23}m_{23}x_2^{*2}}{(m_{23}x_3^* + x_2^*)^3}, \qquad l_{12} = \frac{a_{32}m_{23}x_3^{*2}}{(m_{23}x_3^* + x_2^*)^3}, \\
l_{13} &= \frac{a_{32}m_{23}^2x_2^*x_3^*}{(m_{23}x_3^* + x_2^*)^3}, \qquad l_{14} = \frac{a_{32}m_{23}x_3^*}{(m_{23}x_3^* + x_2^*)^2}, \\
l_{15} &= \frac{a_{32}m_{23}x_2^*x_3^* - a_{32}m_{23}^2x_3^{*2}}{(m_{23}x_3^* + x_2^*)^3}, \qquad l_{16} = \frac{a_{32}m_{23}x_2^*}{(m_{23}x_3^* + x_2^*)^2}.
\end{aligned}$$

Obviously, $L_\mu(\phi)$ is a continuous linear function mapping $\mathcal{C}([-1,0], \mathcal{R}^3)$ into $\mathcal{R}^3$. By the Riesz representation theorem, there exists a 3×3 matrix function $\eta(\theta,\mu)$ $(-1 \leq \theta \leq 0)$, whose elements are of bounded variation such that

$$L_\mu(\phi) = \int_{-1}^0 d\eta(\theta,\mu)\phi(\theta), \quad \text{for } \phi \in \mathcal{C}\bigl([-1,0], \mathcal{R}^3\bigr). \tag{3.4}$$

In fact, we can choose

$$d\eta(\theta,\mu) = (\tilde{\tau}_1 + \mu)\left[B\delta(\theta) + C\delta(\theta+1) + D\delta\left(\theta + \frac{\tau_2^*}{\tau_1}\right)\right], \tag{3.5}$$

where δ is the Dirac delta function. For $\phi \in \mathcal{C}([-1,0], \mathcal{R}^3)$, define

$$A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \theta \in [-1,0), \\ \int_{-1}^0 d\eta(s,\mu)\phi(s), & \theta = 0 \end{cases}$$

and

$$R(\mu)\phi = \begin{cases} 0, & \theta \in [-1,0), \\ f(\mu,\phi), & \theta = 0. \end{cases}$$

Then when $\theta = 0$, system (3.1) is equivalent to

$$\dot{x_t} = A(\mu)x_t + R(\mu)x_t, \tag{3.6}$$

where $x_t(\theta) = x(t+\theta)$, $\theta \in [-1,0]$. For $\psi \in \mathcal{C}^1([0,1],(\mathcal{R}^3)^*)$, define

$$A^*\psi(s) = \begin{cases} -\frac{d\psi(s)}{ds}, & s \in (0,1], \\ \int_{-1}^{0} d\eta^T(t,0)\psi(-t), & s = 0, \end{cases}$$

and a bilinear inner product

$$\bigl\langle \psi(s),\phi(\theta)\bigr\rangle = \bar{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{\xi=0}^{\theta} \bar{\psi}(\xi-\theta)\,d\eta(\theta)\phi(\xi)\,d\xi, \tag{3.7}$$

where $\eta(\theta) = \eta(\theta,0)$. Let $A = A(0)$, then A and A^* are adjoint operators. By the discussion in Section 2, we know that $\pm i\omega\tilde{\tau}_1$ are eigenvalues of A. Thus, they are also eigenvalues of A^*. We first need to compute the eigenvector of A and A^* corresponding to $i\omega\tilde{\tau}_1$ and $-i\omega\tilde{\tau}_1$, respectively. Suppose that $q(\theta) = (1,\alpha,\beta)^T e^{i\theta\omega\tilde{\tau}_1}$ is the eigenvector of A corresponding to $i\omega\tilde{\tau}_1$. Then $Aq(\theta) = i\omega\tilde{\tau}_1 q(\theta)$. From the definition of A, $L_\mu(\phi)$ and $\eta(\theta,\mu)$, we can easily obtain $q(\theta) = (1,\alpha,\beta)^T e^{i\theta\omega\tilde{\tau}_1}$, where

$$\alpha = \frac{i\omega - b_{11}}{b_{12}}, \qquad \beta = \frac{d_{32}(i\omega - b_{11})e^{-i\omega\tau_2^*}}{b_{12}(i\omega - b_{33} - d_{33}e^{-i\omega\tau_2^*})},$$

and $q(0) = (1,\alpha,\beta)^T$. Similarly, let $q^*(s) = D(1,\alpha^*,\beta^*)e^{is\omega\tilde{\tau}_1}$ be the eigenvector of A^* corresponding to $-i\omega\tilde{\tau}_1$. By the definition of A^*, we can compute

$$\alpha^* = \frac{-i\omega - b_{11}}{c_{21}e^{i\omega\tilde{\tau}_1}}, \qquad \beta^* = \frac{b_{23}(-i\omega - b_{11})}{c_{21}(-i\omega - b_{33} - d_{33}e^{i\omega\tau_2^*})e^{i\omega\tilde{\tau}_1}}.$$

From (3.7), we have

$$\begin{aligned} &\bigl\langle q^*(s),q(\theta)\bigr\rangle \\ &\quad = \bar{D}\bigl(1,\bar{\alpha}^*,\bar{\beta}^*\bigr)(1,\alpha,\beta)^T - \int_{-1}^{0}\int_{\xi=0}^{\theta} \bar{D}\bigl(1,\bar{\alpha}^*,\bar{\beta}^*\bigr)e^{-i\omega\tilde{\tau}_1(\xi-\theta)}\,d\eta(\theta)(1,\alpha,\beta)^T e^{i\omega\tilde{\tau}_1\xi}\,d\xi \\ &\quad = \bar{D}\bigl\{1 + \alpha\bar{\alpha}^* + \beta\bar{\beta}^* + \tilde{\tau}_1\bigl(c_{21}\bar{\alpha}^* + c_{22}\alpha\bar{\alpha}^*\bigr)e^{-i\omega\tilde{\tau}_1} + \tau_2^*\bigl(d_{32}\alpha\bar{\beta}^* + d_{33}\beta\bar{\beta}^*\bigr)e^{-i\omega\tau_2^*}\bigr\}. \end{aligned}$$

Thus, we can choose

$$\bar{D} = \bigl\{1 + \alpha\bar{\alpha}^* + \beta\bar{\beta}^* + \tilde{\tau}_1\bigl(c_{21}\bar{\alpha}^* + c_{22}\alpha\bar{\alpha}^*\bigr)e^{-i\omega\tilde{\tau}_1} + \tau_2^*\bigl(d_{32}\alpha\bar{\beta}^* + d_{33}\beta\bar{\beta}^*\bigr)e^{-i\omega\tau_2^*}\bigr\}^{-1},$$

such that $\langle q^*(s),q(\theta)\rangle = 1$, $\langle q^*(s),\bar{q}(\theta)\rangle = 0$.

In the remainder of this section, we follow the ideas in Hassard *et al.* [18] using the same notations as there to compute the coordinates describing the center manifold C_0 at $\mu = 0$. Let x_t be the solution of equation (3.1) when $\mu = 0$. Define

$$z(t) = \langle q^*, x_t \rangle, \qquad W(t,\theta) = x_t(\theta) - 2\operatorname{Re}\{z(t)q(\theta)\}. \tag{3.8}$$

On the center manifold C_0, we have

$$W(t,\theta) = W\bigl(z(t),\bar{z}(t),\theta\bigr) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + W_{30}(\theta)\frac{z^3}{6} + \cdots,$$

where z and $\bar{z}$ are local coordinates for center manifold C_0 in the direction of q and $\bar{q}$. Note that W is real if x_t is real. We consider only real solutions. For the solution $x_t \in C_0$ of (3.1), since $\mu = 0$, we have

$$\begin{aligned}
\dot{z} &= i\omega\tilde{\tau}_1 z + \bigl\langle q^*(\theta), f\bigl(0, W\bigl(z(t),\bar{z}(t),\theta\bigr) + 2\operatorname{Re}\bigl\{z(t)q(\theta)\bigr\}\bigr)\bigr\rangle \\
&= i\omega\tilde{\tau}_1 z + \bar{q}^*(0)f\bigl(0, W\bigl(z(t),\bar{z}(t),0\bigr) + 2\operatorname{Re}\bigl\{z(t)q(0)\bigr\}\bigr) \\
&= i\omega\tilde{\tau}_1 z + \bar{q}^*(0)f_0(z,\bar{z}) \triangleq i\omega\tilde{\tau}_1 z + g(z,\bar{z}),
\end{aligned} \tag{3.9}$$

where

$$g(z,\bar{z}) = \bar{q}^*(0)f_0(z,\bar{z}) = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots. \tag{3.10}$$

By (3.8), we have $x_t(\theta) = (x_{1t}(\theta), x_{2t}(\theta), x_{3t}(\theta))^T = W(t,\theta) + zq(\theta) + \bar{z}\bar{q}(\theta)$. It follows from this, together with (3.3), that

$$\begin{aligned}
g(z,\bar{z}) &= \bar{q}^*(0)f_0(z,\bar{z}) \\
&= \bar{D}\tilde{\tau}_1\bigl(1,\bar{\alpha}^*,\bar{\beta}^*\bigr)\bigl(f_1^{(0)}f_2^{(0)}f_3^{(0)}\bigr)^T \\
&= \bar{D}\tilde{\tau}_1\Biggl\{\bigl[(-a_{11}+l_1)\phi_1^2(0) - l_2\phi_1(0)\phi_2(0) + l_3\phi_2^2(0) + \cdots\bigr] \\
&\quad + \bar{\alpha}^*\bigl[-l_4\phi_1^2(-1) + l_5\phi_2^2(-1) \\
&\quad + l_6\phi_1(-1)\phi_2(-1) + l_7\phi_1(-1)\phi_2(0) - l_8\phi_2(-1)\phi_2(0) \\
&\quad + l_9\phi_1^2(0) - l_{10}\phi_1(0)\phi_2(0) + l_{11}\phi_2^2(0) + \cdots\bigr] \\
&\quad + \bar{\beta}^*\Biggl[-l_{12}\phi_2^2\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr) + l_{13}\phi_3^2\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr) + l_{14}\phi_2\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)\phi_3(0) \\
&\quad + l_{15}\phi_2\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)\phi_3\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr) - l_{16}\phi_3\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)\phi_3(0) + \cdots\Biggr]\Biggr\}.
\end{aligned}$$

Comparing the coefficients with (3.10), we have

$$\begin{aligned}
g_{20} = \bar{D}\tilde{\tau}_1\bigl\{&\bigl[2(-a_{11}+l_1) - 2l_2\alpha + 2l_3\alpha^2\bigr] + \bar{\alpha}^*\bigl[-2l_4e^{-2i\omega\tilde{\tau}_1} + 2l_5\alpha^2e^{-2i\omega\tilde{\tau}_1} + 2l_6\alpha e^{-2i\omega\tilde{\tau}_1} \\
&+ 2l_7\alpha e^{-i\omega\tilde{\tau}_1} - 2l_8\alpha^2e^{-i\omega\tilde{\tau}_1} + 2l_9 - 2l_{10}\alpha + 2l_{11}\alpha^2\bigr] + \bar{\beta}^*\bigl[-2l_{12}\alpha^2e^{-2i\omega\tau_2^*} \\
&+ 2l_{13}\beta^2e^{-2i\omega\tau_2^*} + 2l_{14}\alpha\beta e^{-i\omega\tau_2^*} + 2l_{15}\alpha\beta e^{-2i\omega\tau_2^*} - 2l_{16}\beta^2e^{-i\omega\tau_2^*}\bigr]\bigr\},
\end{aligned}$$

$$
\begin{aligned}
g_{11} = {} & \bar{D}\tilde{\tau}_1\bigl\{\bigl[2(-a_{11}+l_1) - l_2(\alpha+\bar{\alpha}) + 2al_3\alpha\bar{\alpha}\bigr] + \bar{\alpha}^*\bigl[-2l_4 + 2l_5\alpha\bar{\alpha} + l_6(\alpha+\bar{\alpha}) \\
& + l_7\bigl(\bar{\alpha}e^{-i\omega\tilde{\tau}_1} + \alpha e^{i\omega\tilde{\tau}_1}\bigr) - l_8\bigl(\alpha\bar{\alpha}e^{-i\omega\tilde{\tau}_1} + \alpha\bar{\alpha}e^{i\omega\tilde{\tau}_1}\bigr) + 2l_9 - l_{10}(\alpha+\bar{\alpha}) + 2l_{11}\alpha\bar{\alpha}\bigr] \\
& + \bar{\beta}^*\bigl[-2l_{12}\alpha\bar{\alpha} + 2l_{13}\beta\bar{\beta} + l_{14}\bigl(\alpha\bar{\beta}e^{-i\omega\tau_2^*} + \beta\bar{\alpha}e^{i\omega\tau_2^*}\bigr) \\
& + l_{15}(\alpha\bar{\beta} + \bar{\alpha}\beta) - l_{16}\beta\bar{\beta}\bigl(e^{i\omega\tau_2^*} + e^{-i\omega\tau_2^*}\bigr)\bigr]\bigr\}, \\
g_{02} = {} & \bar{D}\tilde{\tau}_1\bigl\{\bigl[2(-a_{11}+l_1) - 2l_2\bar{\alpha} + 2l_3\bar{\alpha}^2\bigr] + \bar{\alpha}^*\bigl[-2l_4e^{2i\omega\tilde{\tau}_1} + 2l_5\bar{\alpha}^2e^{2i\omega\tilde{\tau}_1} + 2l_6\bar{\alpha}e^{2i\omega\tilde{\tau}_1} \\
& + 2l_7\bar{\alpha}e^{i\omega\tilde{\tau}_1} - 2l_8\bar{\alpha}^2e^{i\omega\tilde{\tau}_1} + 2l_9 - 2l_{10}\bar{\alpha} + 2l_{11}\bar{\alpha}^2\bigr] + \bar{\beta}^*\bigl[-2l_{12}\bar{\alpha}^2e^{2i\omega\tau_2^*} + 2l_{13}\bar{\beta}^2e^{2i\omega\tau_2^*} \\
& + 2l_{14}\bar{\alpha}\bar{\beta}e^{i\omega\tau_2^*} + 2l_{15}\bar{\alpha}\bar{\beta}e^{2i\omega\tau_2^*} - 2l_{16}\bar{\beta}^2e^{i\omega\tau_2^*}\bigr]\bigr\}, \\
g_{21} = {} & \bar{D}\tilde{\tau}_1\Biggl\{\bigl[(-a_{11}+l_1)\bigl(2W_{20}^{(1)}(0) + 4W_{11}^{(1)}(0)\bigr) \\
& - l_2\bigl(2\alpha W_{11}^{(1)}(0) + \bar{\alpha}W_{20}^{(1)}(0) + W_{20}^{(2)}(0) + 2W_{11}^{(2)}(0)\bigr) \\
& + l_3\bigl(4\alpha W_{11}^{(2)}(0) + 2\bar{\alpha}W_{20}^{(2)}(0)\bigr)\bigr] + \bar{\alpha}^*\bigl[-l_4\bigl(4W_{11}^{(1)}(-1)e^{-i\omega\tilde{\tau}_1} + 2W_{20}^{(1)}(-1)e^{i\omega\tilde{\tau}_1}\bigr) \\
& + l_5\bigl(2\bar{\alpha}W_{20}^{(2)}(-1)e^{i\omega\tilde{\tau}_1} + 4\alpha W_{11}^{(2)}(-1)e^{-i\omega\tilde{\tau}_1}\bigr) + l_6\bigl(2W_{11}^{(2)}(-1)e^{-i\omega\tilde{\tau}_1} + W_{20}^{(2)}(-1)e^{i\omega\tilde{\tau}_1} \\
& + \bar{\alpha}W_{20}^{(1)}(-1)e^{i\omega\tilde{\tau}_1} + 2\alpha W_{11}^{(2)}(-1)e^{-i\omega\tilde{\tau}_1}\bigr) + l_7\bigl(2\alpha W_{11}^{(1)}(-1) + \bar{\alpha}W_{20}^{(1)}(-1) \\
& + W_{20}^{(2)}(0)e^{i\omega\tilde{\tau}_1} + 2W_{11}^{(2)}(0)e^{-i\omega\tilde{\tau}_1}\bigr) - l_8\bigl(2\alpha W_{11}^{(2)}(-1) + \bar{\alpha}W_{20}^{(2)}(-1) + \bar{\alpha}W_{20}^{(2)}(0)e^{i\omega\tilde{\tau}_1} \\
& + 2\alpha W_{11}^{(2)}(0)e^{-i\omega\tilde{\tau}_1}\bigr) + l_9\bigl(4W_{11}^{(1)}(0) + 2W_{20}^{(1)}(0)\bigr) - l_{10}\bigl(2W_{11}^{(2)}(0) + W_{20}^{(2)}(0) \\
& + \bar{\alpha}W_{20}^{(1)}(0) + 2\alpha W_{11}^{(1)}(0)\bigr) + l_{11}\bigl(4\alpha W_{11}^{(2)}(0) + 2\bar{\alpha}W_{20}^{(2)}(0)\bigr)\bigr] \\
& + \bar{\beta}^*\Biggl[-l_{12}\Biggl(4\alpha W_{11}^{(2)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{-i\omega\tau_2^*} + 2\bar{\alpha}W_{20}^{(2)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{i\omega\tau_2^*}\Biggr) \\
& + l_{13}\Biggl(2\bar{\beta}W_{20}^{(3)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{i\omega\tau_2^*} + 4\beta W_{11}^{(3)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{-i\omega\tau_2^*}\Biggr) \\
& + l_{14}\Biggl(2\alpha W_{11}^{(3)}(0)e^{-i\omega\tau_2^*} + \bar{\alpha}W_{20}^{(3)}(0)e^{i\omega\tau_2^*} + \bar{\beta}W_{20}^{(2)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr) + 2\beta W_{11}^{(2)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)\Biggr) \\
& + l_{15}\Biggl(2\alpha W_{11}^{(3)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{-i\omega\tau_2^*} + \bar{\alpha}W_{20}^{(3)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{i\omega\tau_2^*} \\
& + \bar{\beta}W_{20}^{(2)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{i\omega\tau_2^*} + 2\beta W_{11}^{(2)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)e^{-i\omega\tau_2^*}\Biggr) \\
& - l_{16}\Biggl(2\beta W_{11}^{(3)}(0)e^{-i\omega\tau_2^*} + \bar{\beta}W_{20}^{(3)}(0)e^{i\omega\tau_2^*} + \bar{\beta}W_{20}^{(3)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr) + 2\beta W_{11}^{(3)}\biggl(-\frac{\tau_2^*}{\tilde{\tau}_1}\biggr)\Biggr)\Biggr]\Biggr\},
\end{aligned}
$$

where

$$
\begin{aligned}
W_{20}(\theta) &= \frac{ig_{20}}{\omega\tilde{\tau}_1}q(0)e^{i\omega\tilde{\tau}_1\theta} + \frac{i\bar{g}_{02}}{3\omega\tilde{\tau}_1}\bar{q}(0)e^{-i\omega\tilde{\tau}_1\theta} + E_1e^{2i\omega\tilde{\tau}_1\theta}, \\
W_{11}(\theta) &= -\frac{ig_{11}}{\omega\tilde{\tau}_1}q(0)e^{i\omega\tilde{\tau}_1\theta} + \frac{i\bar{g}_{11}}{\omega\tilde{\tau}_1}\bar{q}(0)e^{-i\omega\tilde{\tau}_1\theta} + E_2,
\end{aligned}
$$

and

$$
E_1 = 2\begin{bmatrix} 2i\omega - b_{11} & -b_{12} & 0 \\ -c_{21}e^{-2i\omega\tilde{\tau}_1} & 2i\omega - b_{22} - c_{22}e^{-2i\omega\tilde{\tau}_1} & -b_{23} \\ 0 & -d_{32}e^{-2i\omega\tau_2^*} & 2i\omega - b_{33} - d_{33}e^{-2i\omega\tau_2^*} \end{bmatrix}^{-1} \cdot \begin{bmatrix} M_1 \\ M_2 \\ M_3 \end{bmatrix},
$$

$$E_2 = 2\begin{bmatrix} -b_{11} & -b_{12} & 0 \\ -c_{21} & -b_{22}-c_{22} & -b_{23} \\ 0 & -d_{32} & -b_{33}-d_{33} \end{bmatrix}^{-1} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \end{bmatrix},$$

where

$$\begin{aligned}
M_1 &= 2(-a_{11}+l_1) - 2l_2\alpha + 2l_3\alpha^2, \\
M_2 &= -2l_4 e^{-2i\omega\tilde{\tau}_1} + 2l_5\alpha^2 e^{-2i\omega\tilde{\tau}_1} + 2l_6\alpha e^{-2i\omega\tilde{\tau}_1} + 2l_7\alpha e^{-i\omega\tilde{\tau}_1} - 2l_8\alpha^2 e^{-i\omega\tilde{\tau}_1} \\
&\quad + 2l_9 - 2l_{10}\alpha + 2l_{11}\alpha^2, \\
M_3 &= -2l_{12}\alpha^2 e^{-2i\omega\tau_2^*} + 2l_{13}\beta^2 e^{-2i\omega\tau_2^*} + 2l_{14}\alpha\beta e^{-i\omega\tau_2^*} + 2l_{15}\alpha\beta e^{-2i\omega\tau_2^*} - 2l_{16}\beta^2 e^{-i\omega\tau_2^*}, \\
N_1 &= 2(-a_{11}+l_1) - l_2(\alpha+\bar{\alpha}) + 2l_3\alpha\bar{\alpha}, \\
N_2 &= -2l_4 + 2l_5\alpha\bar{\alpha} + l_6(\alpha+\bar{\alpha}) + l_7\bigl(\bar{\alpha}e^{-i\omega\tilde{\tau}_1} + \alpha e^{i\omega\tilde{\tau}_1}\bigr) - l_8\bigl(\alpha\bar{\alpha}e^{-i\omega\tilde{\tau}_1} + \alpha\bar{\alpha}e^{i\omega\tilde{\tau}_1}\bigr) \\
&\quad + 2l_9 - l_{10}(\alpha+\bar{\alpha}) + 2l_{11}\alpha\bar{\alpha}, \\
N_3 &= -2l_{12}\alpha\bar{\alpha} + 2l_{13}\beta\bar{\beta} + l_{14}\bigl(\alpha\bar{\beta}e^{-i\omega\tau_2^*} + \beta\bar{\alpha}e^{i\omega\tau_2^*}\bigr) + l_{15}(\alpha\bar{\beta} + \bar{\alpha}\beta) \\
&\quad - l_{16}\beta\bar{\beta}\bigl(e^{i\omega\tau_2^*} + e^{-i\omega\tau_2^*}\bigr).
\end{aligned}$$

Thus, we can determine $W_{20}(\theta)$ and $W_{11}(\theta)$. Furthermore, we can determine each g_{ij} by the parameters and delay in (1.3). Thus, we can compute the following values:

$$\begin{aligned}
c_1(0) &= \frac{i}{2\omega\tilde{\tau}_1}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{1}{2}g_{21}, \qquad \mu_2 = -\frac{\operatorname{Re}\{c_1(0)\}}{\operatorname{Re}\{\lambda'(\tilde{\tau}_1)\}}, \\
T_2 &= -\frac{\operatorname{Im}\{c_1(0)\} + \mu_2 \operatorname{Im}\{\lambda'(\tilde{\tau}_1)\}}{\omega\tilde{\tau}_1}, \qquad \beta_2 = 2\operatorname{Re}\bigl\{c_1(0)\bigr\},
\end{aligned}$$

which determine the quantities of bifurcating periodic solutions in the center manifold at the critical value $\tilde{\tau}_1$. Suppose $\operatorname{Re}\{\lambda'(\tilde{\tau}_1)\} > 0$. μ_2 determines the directions of the Hopf bifurcation: if $\mu_2 > 0$ (< 0), then the Hopf bifurcation is supercritical (subcritical) and the bifurcation exist for $\tau > \tilde{\tau}_1$ ($< \tilde{\tau}_1$); β_2 determines the stability of the bifurcation periodic solutions: the bifurcating periodic solutions are stable (unstable) if $\beta_2 < 0$ (> 0); and T_2 determines the period of the bifurcating periodic solutions: the period increases (decreases) if $T_2 > 0$ (< 0).

4 Global continuation of local Hopf bifurcations

In this section, we study the global continuation of periodic solutions bifurcating from the positive equilibrium. Throughout this section, we follow closely the notations in [19] and assume that $\tau_2 = \tau_2^* \in [0, \tau_{2_{10}})$ regarding τ_1 as a parameter. For simplification of notations, setting $z_t(t) = (x_{1t}, x_{2t}, x_{3t})^T$, we may rewrite system (1.4) as the following functional differential equation:

$$\dot{z}(t) = F(z_t, \tau_1, p), \tag{4.1}$$

where $z_t(\theta) = (x_{1t}(\theta), x_{2t}(\theta), x_{3t}(\theta))^T = (x_1(t+\theta), x_2(t+\theta), x_3(t+\theta))^T$ for $t \geq 0$ and $\theta \in [-\tau_1, 0]$. Since $x_1(t)$, $x_2(t)$, and $x_3(t)$ denote the densities of the prey, the first predator, and the second predator, respectively, the positive solution of system (1.4) is of interest and its periodic solutions only arise in the first quadrant. Thus, we consider system (1.4) only in the domain $R_+^3 = \{(x_1, x_2, x_3) \in R^3, x_1 > 0, x_2 > 0, x_3 > 0\}$. It is obvious that (4.1) has a unique positive equilibrium $E^*(x_1^*, x_2^*, x_3^*)$ in R_+^3 under the assumption (H_1). Following the work of [19], we define

$$\begin{aligned} &X = C\big([-\tau_1, 0], R_+^3\big), \\ &\Gamma = Cl\big\{(z, \tau_1, p) \in \mathbf{X} \times \mathbf{R} \times \mathbf{R}^+; z \text{ is a } p\text{-periodic solution of system (4.1)}\big\}, \\ &\mathcal{N} = \big\{(\bar{z}, \bar{\tau}_1, \bar{p}); F(\bar{z}, \bar{\tau}_1, \bar{p}) = 0\big\}. \end{aligned}$$

Let $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_{1k}^{(j)}})}$ denote the connected component passing through $(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_{1k}^{(j)}})$ in Γ, where $\tau_{1k}^{(j)}$ is defined by (2.20). We know that $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_{1k}^{(j)}})}$ through $(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_{1k}^{(j)}})$ is nonempty.

Lemma 6 *If the conditions* (H_1) *hold, then all nontrivial periodic solutions of system* (4.1) *with initial conditions*

$$\begin{aligned} &x_1(\theta) = \varphi(\theta) \geq 0, \qquad x_2(\theta) = \psi(\theta) \geq 0, \qquad x_3(\theta) = \phi(\theta) \geq 0, \quad t \in [-\tau_1, 0); \\ &\varphi(0) > 0, \qquad \psi(0) > 0, \qquad \phi(0) > 0, \end{aligned}$$

are uniformly bounded.

Proof Suppose that $(x_1(t), x_2(t), x_3(t))$ are nonconstant periodic solutions of system (1.4) and define

$$\begin{aligned} &x_1(\xi_1) = \min\big\{x_1(t)\big\}, \qquad x_1(\eta_1) = \max\big\{x_1(t)\big\}, \\ &x_2(\xi_2) = \min\big\{x_2(t)\big\}, \qquad x_2(\eta_2) = \max\big\{x_2(t)\big\}, \\ &x_3(\xi_3) = \min\big\{x_3(t)\big\}, \qquad x_3(\eta_3) = \max\big\{x_3(t)\big\}. \end{aligned} \tag{4.2}$$

It follows from system (1.4) that

$$\begin{aligned} &x_1(t) = x_1(0)\exp\left\{\int_0^t \left[a_1 - a_{11}x_1(s) - \frac{a_{12}x_2(s)}{m_1 + x_1(s)}\right] ds\right\}, \\ &x_2(t) = x_2(0)\exp\left\{\int_0^t \left[-a_2 + \frac{a_{21}x_1(s-\tau_1)}{m_1 + x_1(s-\tau_1)} - a_{22}x_2(s) - \frac{a_{23}x_3(s)}{m_2 + x_2(s)}\right] ds\right\}, \\ &x_3(t) = x_3(0)\exp\left\{\int_0^t \left[-a_3 + \frac{a_{32}x_2(s-\tau_2^*)}{m_2 + x_2(s-\tau_2^*)} - a_{33}x_3(s)\right] ds\right\}, \end{aligned}$$

which implies that the solutions of system (1.4) cannot cross the x_i-axis ($i = 1, 2, 3$). Thus, the nonconstant periodic orbits must be located in the interior of each quadrant. It follows from the initial data of system (1.4) that $x_1(t) > 0$, $x_2(t) > 0$, $x_3(t) > 0$ for $t \geq 0$.

From the first equation of system (1.4), we can get

$$0 = a_1 - a_{11}x_1(\eta_1) - \frac{a_{12}x_2(\eta_1)}{m_{12}x_2(\eta_1) + x_1(\eta_1)} \leq a_1 - a_{11}x_1(\eta_1),$$

thus, we have

$$x_1(\eta_1) \le \frac{a_1}{a_{11}}. \tag{4.3}$$

From the second equation of system (1.4), we obtain

$$\begin{aligned} 0 &= -a_2 + \frac{a_{21}x_1(\eta_2 - \tau_1)}{m_{12}x_2(\eta_2 - \tau_1) + x_1(\eta_2 - \tau_1)} - \frac{a_{23}x_3(\eta_2)}{m_{23}x_3(\eta_2) + x_2(\eta_2)} \\ &\le -a_2 + \frac{a_{21}x_1(\eta_2 - \tau_1)}{m_{12}x_2(\eta_2 - \tau_1) + x_1(\eta_2 - \tau_1)}, \end{aligned}$$

therefore, one gets

$$x_2(\eta_2 - \tau_1) \le \frac{a_1(a_{21} - a_2)}{a_2 a_{11} m_{12}}.$$

From the second equation of system (1.4), we obtain

$$\dot{x}_2(t) \le (a_{21} - a_2)x_2(t),$$

when $t > \tau_1$, $x_2(t) \le x_2(t - \tau_1)e^{(a_{21}-a_2)\tau_1}$.

Then we have

$$x_2(\eta_2) \le \frac{a_1(a_{21} - a_2)}{a_2 a_{11} m_{12}} e^{(a_{21}-a_2)\tau_1} \doteq Q. \tag{4.4}$$

Applying the third equation of system (1.4), we know

$$\begin{aligned} 0 &= -a_3 + \frac{a_{32}x_2(\eta_3 - \tau_2^*)}{m_{23}x_3(\eta_3 - \tau_2^*) + x_2(\eta_3 - \tau_2^*)} \\ &\le -a_3 + \frac{a_{32}Q}{m_{23}x_3(\eta_3 - \tau_2^*) + Q}. \end{aligned}$$

It follows that

$$x_3(\eta_3) \le \frac{(a_{32} - a_3)Q}{a_3 m_{23}} e^{(a_{32}-a_3)\tau_2}. \tag{4.5}$$

This shows that the nontrivial periodic solution of system (1.4) is uniformly bounded and the proof is complete. □

Lemma 7 *If the conditions* (H_1) *and*

$$\begin{aligned} (\mathrm{H}_4) \quad & \frac{a_{21}m_{23}}{a_{23}}\left(a_{21} - \frac{a_{12}}{m_{12}}\right) - \frac{1}{2}a_{32}a_{21}m_{23}\tau_2^* > 0, \\ & a_{32} - \frac{a_{23}}{m_{23}} - \frac{a_{32}\tau_2^*}{2m_{23}}\left(a_{21} + \frac{a_{23}}{m_{23}} + a_{32}\right) - \frac{1}{2}a_{32}a_{23}\tau_2^* - \frac{1}{2}a_{32}^2 m_{23}\tau_2^* > 0, \end{aligned}$$

hold, then system (1.4) *has no nontrivial* τ_1*-periodic solution.*

Proof Suppose for a contradiction that system (1.4) has nontrivial periodic solution with period τ_1. Then the system (4.6) has nontrivial periodic solution:

$$\begin{cases} \frac{dx_1}{dt} = x_1(t)[a_1 - a_{11}x_1(t) - \frac{a_{12}x_2(t)}{m_{12}x_2(t)+x_1(t)}], \\ \frac{dx_2}{dt} = x_2(t)[-a_2 + \frac{a_{21}x_1(t)}{m_{12}x_2(t)+x_1(t)} - \frac{a_{23}x_3(t)}{m_{23}x_3(t)+x_2(t)}], \\ \frac{dx_3}{dt} = x_3(t)[-a_3 + \frac{a_{32}x_2(t-\tau_2^*)}{m_{23}x_3(t-\tau_2^*)+x_2(t-\tau_2^*)}], \end{cases} \tag{4.6}$$

which has the same equilibria to system (1.4), *i.e.*,

$$\widetilde{E} = (\tilde{x}_1, \tilde{x}_2, 0), \qquad E^* = (x_1^*, x_2^*, x_3^*).$$

Note that the x_i-axis ($i = 1,2,3$), the invariable manifold of system (4.6), and the orbits of system (4.6) do not intersect each other. Thus, there are no solutions crossing the coordinate axes. On the other hand, note the fact that if system (4.6) has a periodic solution, then there must be the equilibrium in its interior, and that $\widetilde{E}$ are located on the coordinate axis. Thus, we conclude that the periodic orbit of system (4.6) must lie in the first quadrant. If (H_4) holds, it is well known that the positive equilibrium E^* is global asymptotically stable in the first quadrant (see [7, 8]). Thus, there is no periodic orbit in the first quadrant. The above discussion means that (4.6) has no nontrivial periodic solution. It is a contradiction. Therefore, Lemma 7 is confirmed. □

Theorem 5 *Suppose the conditions of Theorem* 4 *and* (H_4) *hold, let ω_k and $\tau_{1k}^{(j)}$ be defined in Section* 2, *then when $\tau_1 > \tau_{1k}^{(j)}$, $j = 1,2,3,\ldots$, system* (1.4) *has at least $j-1$ periodic solutions.*

Proof It is sufficient to prove that the projection of $\ell_{(E^*,\tau_{1k}^{(j)},\frac{2\pi}{\omega_k})}$ onto τ_1-space is $[\bar{\tau}_1, +\infty)$ for each $j \geq 1$, where $\bar{\tau}_1 \leq \tau_{1k}^{(j)}$.

In the following we prove that the hypotheses (A1)-(A4) in [19] hold.

(1) From system (1.4) we easily see that the following conditions hold:

(A1) $\widehat{F} \in C^2(R_+^3 \times R_+ \times R_+)$, where $\widehat{F} = F|_{R_+^3\times R_+\times R_+} \to R_+^3$.

(A3) $F(\phi, \tau_1, p)$ is differential with respect to ϕ.

(2) It follows from system (1.4) that

$$D_z\widehat{F}(z,\tau_1,p) = \begin{bmatrix} a_1 - 2a_{11}x_1 - \frac{a_{12}m_{12}x_2^2}{(m_{12}x_2+x_1)^2} & -\frac{a_{12}x_1^2}{(m_{12}x_2+x_1)^2} & 0 \\ \frac{a_{21}m_{12}x_2^2}{(m_{12}x_2+x_1)^2} & -a_2 + \frac{a_{21}x_1^2}{(m_{12}x_2+x_1)^2} - \frac{a_{23}m_{23}x_3^2}{(m_{23}x_3+x_2)^2} & -\frac{a_{23}x_3^2}{(m_{23}x_3+x_2)^2} \\ 0 & \frac{a_{32}m_{23}x_3^2}{(m_{23}x_3+x_2)^2} & -a_3 + \frac{a_{32}x_2^2}{(m_{23}x_3+x_2)^2} \end{bmatrix}. \tag{4.7}$$

Then under the assumption (H_1)-(H_3), we have

$$\begin{aligned} \det D_z\widehat{F}(z^*,\tau_1,p) &= \det \begin{bmatrix} -a_{11}x_1^* + \frac{a_{12}x_1^*x_2^*}{(m_{12}x_2^*+x_1^*)^2} & \frac{a_{12}x_1^{*2}}{(m_{12}x_2^*+x_1^*)^2} & 0 \\ \frac{a_{21}m_{12}x_2^{*2}}{(m_{12}x_2^*+x_1^*)^2} & \frac{a_{23}x_2^*x_3^*}{(m_{12}x_2^*+x_1^*)^2} - \frac{a_{21}m_{12}x_1^*x_2^*}{(m_{12}x_2^*+x_1^*)^2} & -\frac{a_{23}x_2^{*2}}{(m_{23}x_3^*+x_2^*)^2} \\ 0 & \frac{a_{32}m_{23}x_3^{*2}}{(m_{23}x_3^*+x_2^*)^2} & \frac{a_{32}m_{23}x_2^*x_3^*}{(m_{23}x_3^*+x_2^*)^2} \end{bmatrix} \\ &= -\frac{a_{11}a_{21}m_{12}x_1^{*2}x_2^{*2}x_3^*}{(m_{12}x_2^*+x_1^*)^2(m_{23}x_3^*+x_2^*)^2} < 0. \end{aligned} \tag{4.8}$$

From (4.8), we know that the hypothesis (A2) in [19] is satisfied.

(3) The characteristic matrix of equation (4.1) at a stationary solution $(\bar{z}, \tau_0, p_0)$, where $\bar{z} = (\bar{z}^{(1)}, \bar{z}^{(2)}, \bar{z}^{(3)}) \in R^3$, takes the following form:

$$\triangle(\bar{z}, \tau_1, p)(\lambda) = \lambda Id - D_\phi F(\bar{z}, \bar{\tau}_1, \bar{p})\big(e^{\lambda \cdot} I\big), \tag{4.9}$$

that is,

$$\begin{aligned}&\triangle(\bar{z}, \tau_1, p)(\lambda)\\ &\quad = \begin{bmatrix} \lambda - a_1 + 2a_{11}\bar{z}^{(1)} + \frac{a_{12}m_{12}\bar{z}^{(2)2}}{(m_{12}\bar{z}^{(2)}+\bar{z}^{(1)})^2} & \frac{a_{12}\bar{z}^{(1)2}}{(m_{12}\bar{z}^{(2)}+\bar{z}^{(1)})^2} & 0 \\ -\frac{a_{21}m_{12}\bar{z}^{(2)2}}{(m_{12}\bar{z}^{(2)}+\bar{z}^{(1)})^2}e^{-\lambda\tau_1} & \lambda + a_2 + G_1 & \frac{a_{23}\bar{z}^{(3)2}}{(m_{23}\bar{z}^{(3)}+\bar{z}^{(2)})^2} \\ 0 & -\frac{a_{32}m_{23}\bar{z}^{(3)2}}{(m_{23}\bar{z}^{(3)}+\bar{z}^{(2)})^2}e^{-\lambda\tau_2^*} & \lambda + a_3 + G_2 \end{bmatrix},\end{aligned} \tag{4.10}$$

where

$$\begin{aligned} G_1 &= -\frac{a_{21}\bar{z}^{(1)}}{(m_{12}\bar{z}^{(2)} + \bar{z}^{(1)})} + \frac{a_{23}m_{23}\bar{z}^{(3)2}}{(m_{23}\bar{z}^{(3)} + \bar{z}^{(2)})^2} - \frac{a_{21}\bar{z}^{(1)2}}{(m_{12}\bar{z}^{(2)} + \bar{z}^{(1)})^2}e^{-\lambda\tau_1}, \\ G_2 &= -\frac{a_{32}\bar{z}^{(2)}}{m_{23}\bar{z}^{(3)} + \bar{z}^{(2)}} + \frac{a_{32}\bar{z}^{(2)2}}{(m_{23}\bar{z}^{(3)} + \bar{z}^{(2)})^2}e^{-\lambda\tau_2^*}. \end{aligned}$$

A stationary solution $(\bar{z}, \bar{\tau}_1, \bar{p})$ of (4.1) is called a center if $F(\bar{z}, \bar{\tau}_1, \bar{p}) = 0$ and $\det\triangle(\bar{z}, \bar{\tau}_1, \bar{p})(\frac{2\pi i}{p}) = 0$. A center $(\bar{z}, \bar{\tau}_1, \bar{p})$ is said to isolated if it is the only center in some neighborhood of $(\bar{z}, \bar{\tau}_1, \bar{p})$.

From (4.10), we have

$$\begin{aligned} \det\big(\triangle\big(E^*, \tau_1, p\big)(\lambda)\big) &= \lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + \big(q_2\lambda^2 + q_1\lambda + q_0\big)e^{-\lambda\tau_1} \\ &\quad + \big(r_2\lambda^2 + r_1\lambda + r_0\big)e^{-\lambda\tau_2} + (m_1\lambda + m_0)e^{-\lambda(\tau_1+\tau_2)}. \end{aligned} \tag{4.11}$$

Note that the above equation is the same as (2.18), from the discussion in Section 2 about the local Hopf bifurcation, it is easy to verify that $(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})$ is an isolated center, and there exist $\epsilon > 0$, $\delta > 0$ and a smooth curve $\lambda : (\tau_{1k}^{(j)} - \delta, \tau_{1k}^{(j)} + \delta) \to \mathcal{C}$ such that $\det(\triangle(\lambda(\tau_1))) = 0$, $|\lambda(\tau_1) - \omega_k| < \epsilon$ for all $\tau_1 \in [\tau_{1k}^{(j)} - \delta, \tau_{1k}^{(j)} + \delta]$ and

$$\lambda\big(\tau_{1k}^{(j)}\big) = \omega_k i, \qquad \frac{d\,\mathrm{Re}\,\lambda(\tau_1)}{d\tau_1}\bigg|_{\tau_1=\tau_{1k}^{(j)}} > 0.$$

Let

$$\Omega_{\epsilon, \frac{2\pi}{\omega_k}} = \left\{(\eta, p); 0 < \eta < \epsilon, \left|p - \frac{2\pi}{\omega_k}\right| < \epsilon\right\}.$$

It is easy to verify that on $[\tau_{1k}^{(j)} - \delta, \tau_{1k}^{(j)} + \delta] \times \partial\Omega_{\epsilon, \frac{2\pi}{\omega_k}}$,

$$\det\left(\triangle\big(E^*, \tau_1, p\big)\left(\eta + \frac{2\pi}{p}i\right)\right) = 0 \quad \text{if and only if}$$

$$\eta = 0, \qquad \tau_1 = \tau_{1k}^{(j)}, \qquad p = \frac{2\pi}{\omega_k}, \quad k = 1,2,3; j = 0,1,2,\ldots.$$

Therefore, the hypothesis (A4) in [19] is satisfied.

If we define

$$H^{\pm}\left(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k}\right)(\eta, p) = \det\left(\triangle\left(E^*, \tau_{1k}^{(j)} \pm \delta, p\right)\left(\eta + \frac{2\pi}{p} i\right)\right),$$

then we have the crossing number of the isolated center $(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})$ as follows:

$$\begin{aligned}\gamma\left(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k}\right) &= \deg_B\left(H^-\left(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k}\right), \Omega_{\epsilon, \frac{2\pi}{\omega_k}}\right) \\ &\quad - \deg_B\left(H^+\left(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k}\right), \Omega_{\epsilon, \frac{2\pi}{\omega_k}}\right) \\ &= -1.\end{aligned}$$

Thus, we have

$$\sum_{(\bar{z}, \bar{\tau}_1, \bar{p}) \in C_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}} \gamma(\bar{z}, \bar{\tau}_1, \bar{p}) < 0,$$

where $(\bar{z}, \bar{\tau}_1, \bar{p})$ has all or parts of the form $(E^*, \tau_{1j}^{(k)}, \frac{2\pi}{\omega_k})$ $(j = 0,1,\ldots)$. It follows from Theorem 3.3 in [19] that the connected component $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$ through $(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})$ is unbounded for each center (z^*, τ_1, p) $(j = 0,1,\ldots)$. From the discussion in Section 2, one can get $\frac{2\pi}{\omega_k} \leq \tau_{1k}^{(j)}$ for $j \geq 1$.

Now we prove that the projection of $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$ onto τ_1-space is $[\bar{\tau}_1, +\infty)$, where $\bar{\tau}_1 \leq \tau_{1k}^{(j)}$. Clearly, it follows from the proof of Lemma 7 that system (1.4) with $\tau_1 = 0$ has no nontrivial periodic solution. Hence, the projection of $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$ onto τ_1-space is away from zero.

For a contradiction, we suppose that the projection of $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$ onto τ_1-space is bounded, this means that the projection of $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$ onto τ_1-space is included in an interval $(0, \tau^*)$. Noticing $\frac{2\pi}{\omega_k} < \tau_{1k}^{j}$ and applying Lemma 6 we have $p < \tau^*$ for $(z(t), \tau_1, p)$ belonging to $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$. This implies that the projection of $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$ onto p-space is bounded. Then applying Lemma 6 we see that the connected component $\ell_{(E^*, \tau_{1k}^{(j)}, \frac{2\pi}{\omega_k})}$ is bounded. This contradiction completes the proof. □

5 Numerical simulations

In this section, we present some numerical results of system (1.1) to verify the analytical predictions obtained in the previous section. As an example, we consider the following system:

$$\begin{cases} \frac{dx_1}{dt} = x_1(t)[2 - 0.5x_1(t) - \frac{0.2x_2(t)}{x_2(t)+x_1(t)}], \\ \frac{dx_2}{dt} = x_2(t)[-0.15 + \frac{0.3x_1(t-\tau_1)}{x_2(t-\tau_1)+x_1(t-\tau_1)} - \frac{0.1x_3(t)}{x_3(t)+x_2(t)}], \\ \frac{dx_3}{dt} = x_3(t)[-0.2 + \frac{0.25x_2(t-\tau_2)}{x_3(t-\tau_2)+x_2(t-\tau_2)}]. \end{cases} \tag{5.1}$$

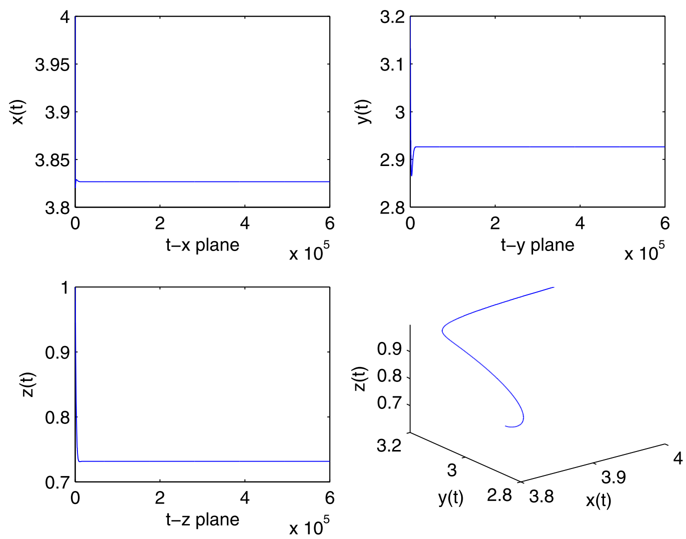

Figure 1 The trajectories of system (5.1) with $\tau_1 = 0$, $\tau_2 = 1.1 < \tau_{2_{10}} = 31.1328$. The positive equilibrium E^* is asymptotically stable. The initial value is $(4, 3.2, 1)$.

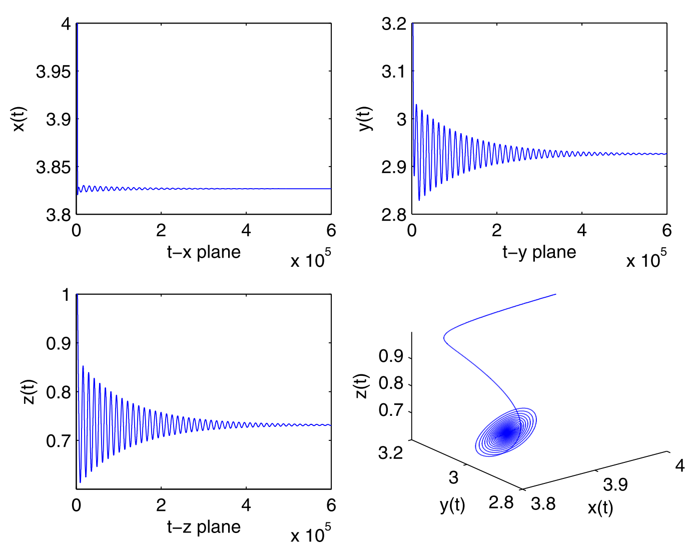

Figure 2 The trajectories of system (5.1) with $\tau_1 = 0$, $\tau_2 = 30 < \tau_{2_{10}} = 31.1328$. The positive equilibrium E^* is asymptotically stable. The initial value is $(4, 3.2, 1)$.

From the coefficients of system (5.1), we can easily see that

$$\begin{aligned}
&a_{32} - a_3 = 0.0500, \\
&a_{21} - \left(a_2 + \frac{a_{23}}{a_{32}m_{23}}(a_{32} - a_3)\right) = 0.1300 > 0, \\
&a_1 - \frac{a_{12}}{a_{21}m_{12}}\left[a_{21} - \left(a_2 + \frac{a_{23}}{a_{32}m_{23}}(a_{32} - a_3)\right)\right] = 1.9133 > 0, \\
&p_2 + q_2 + r_2 = 1.9619 > 0,
\end{aligned}$$

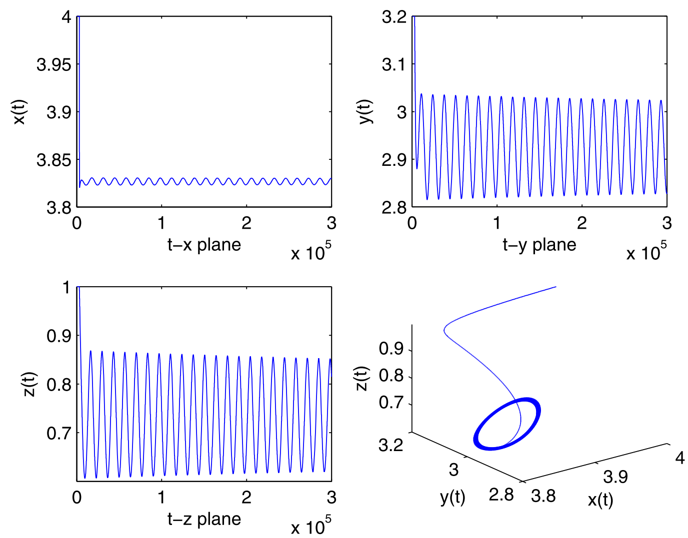

Figure 3 The trajectories of system (5.1) with $\tau_1 = 0$, $\tau_2 = 31.14 > \tau_{2_{10}} = 31.1328$. A Hopf bifurcation occurs from the positive equilibrium E^*. The initial value is $(4, 3.2, 1)$.

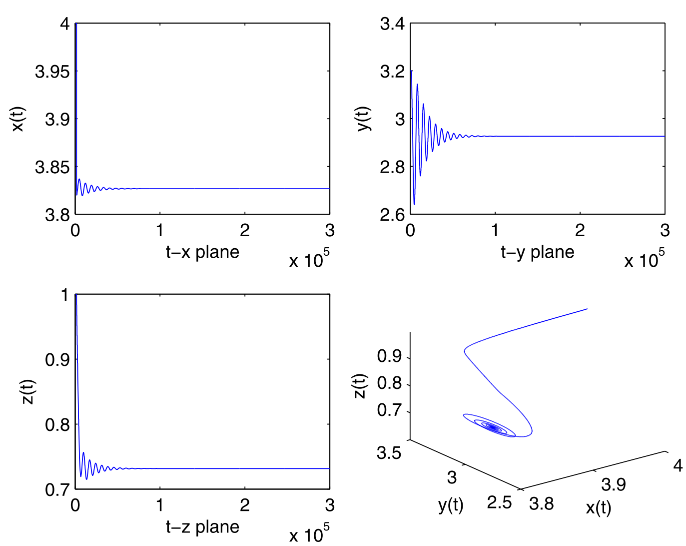

Figure 4 The trajectories of system (5.1) with $\tau_1 = 15$, $\tau_2 = 1.1$. The positive equilibrium E^* is asymptotically stable. The initial value is $(4, 3.2, 1)$.

$$(p_2 + q_2 + r_2)(p_1 + q_1 + r_1 + m_1) - (p_0 + q_0 + r_0 + m_0) = 0.3657 > 0,$$

$$p_0 + q_0 + r_0 + m_0 = 0.0056 > 0.$$

Then the conditions (H_1)-(H_4) are satisfied. $E^* = (3.8267, 2.9263, 0.7316)$ is a unique positive equilibrium of system (5.1).

When $\tau_1 = 0$, by some computations by means of Matlab 7.0, we have $m_{10} = -3.1789\text{e}{-005} < 0$, $\omega_{10} = 0.0470$, $\tau_{2_{10}} = 31.1328$. From Theorem 2, we know that the positive equilibrium E^* is asymptotically stable for $\tau_2 < \tau_{2_{10}} = 31.1328$ and unstable for

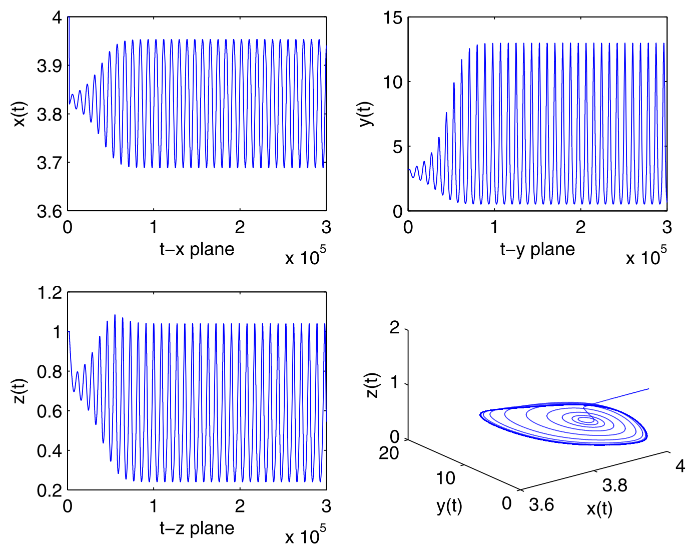

Figure 5 System (5.1) undergoes a Hopf bifurcation when $\tau_1 = 20$, $\tau_2 = 1.1$. A Hopf bifurcation occurs from the positive equilibrium E^*. The initial value is $(4, 3.2, 1)$.

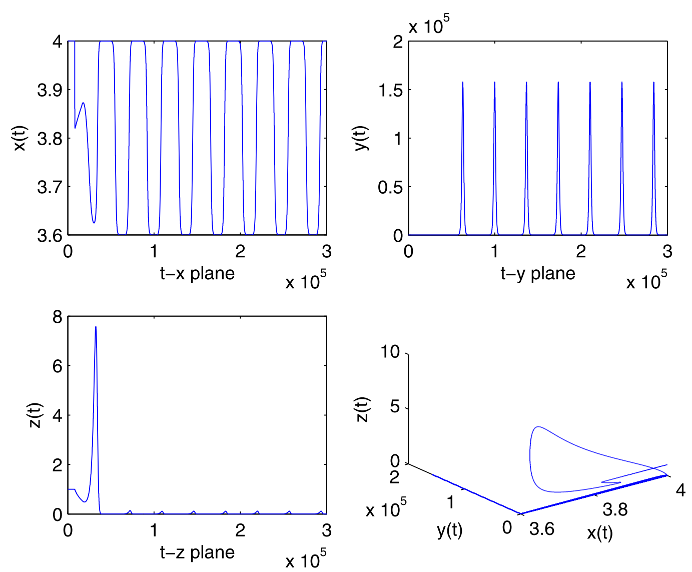

Figure 6 System (5.1) undergoes a Hopf bifurcation when $\tau_1 = 80$, $\tau_2 = 1.1$. The initial value is $(4, 3.2, 1)$.

$\tau_2 > \tau_{2_{10}} = 31.1328$, which is shown in Figures 1-3. When $\tau_2 = 31.14$, system (5.1) undergoes a Hopf bifurcation at the positive equilibrium E^*.

Let $\tau_2 = 1.1 \in (0, 31.1328)$ and choose τ_1 as a parameter. Theorem 5 is satisfied. By the computer simulations, we have $\tau_{10} \approx 20$. Then the positive equilibrium E^* is asymptotically stable when $\tau_1 \in [0, 20)$. A Hopf bifurcation occurs from positive equilibrium E^* when $\tau_1 = 20$. The top predator is in danger of extinction when $\tau_1 = 80$. These numerical simulations, mentioned above, are shown in Figures 4-6.

6 Conclusion

In this paper, we devoted our attention to the stability and bifurcation analysis of a delayed two predator-one prey system. We obtained some conditions for local stability and Hopf bifurcation occurring. Specially, when $\tau_1 \neq \tau_2$, we derived the explicit formulas to determine the properties of periodic solutions by the normal form method and center manifold theorem. In addition, the global existence results of periodic solutions bifurcating from Hopf bifurcations were established by using a global Hopf bifurcation result due to [19]. Finally, a numerical example supporting our theoretical predications was given.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
All authors contributed equally to the writing of this paper. All authors read and approved the final manuscript.

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