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Stability and Hopf bifurcation in a three-species system with feedback delays

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Abstract A kind of three-species system with Holling type II functional response and feedback delays is introduced. By analyzing the associated characteristic equation, its local stability and the existence of Hopf bifurcation are obtained. We derive explicit formulas to determine the direction of the Hopf bifurcation and the stability of periodic solution bifurcated out by using the normal-form method and center manifold theorem. Numerical simulations confirm our theoretical findings.

Keywords Stability · Hopf bifurcation · Feedback delays · Functional response

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1 Introduction

The dynamic relationship between predators and their prey has long been and will continue to be one of the dominant in both ecology and mathematical ecology. One of the oldest and most intriguing paradigms in community ecology—the competitive exclusion principle—states that at most n species can coexist on n resources [1–4], which was supported by experiments on Paramecium cultures by Gauss [3]. It was thought to hold in laboratory until Ayala [5] demonstrated experimentally that two species of Drosophila could coexist upon a single prey. Similarly, Loladze et al. [6] thought of the prey as a single species of alga and the predators as two distinct zooplankton species to explain their coexistence. Gakkhar and Najl [7] observed that complex behavior in a three-species food web consists of a prey, a specialist and a generalist predator species.

The effect of the past history on the stability of a system is an important problem in population biology. Time delays have been incorporated into population dynamic models to simulate the maturation time, capturing time, etc. In general, delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause destabilization of the equilibrium. A great deal of research has been devoted to the delay models (see [8–16] and references therein).

In 1973, May [8] first proposed and discussed briefly the delayed predator–prey system

$$\begin{cases} \dot{x}(t) = x(t)[r_1 - a_{11}x(t-\tau) - a_{12}y(t)], \\ \dot{y}(t) = y(t)[-r_2 + a_{21}x(t) - a_{22}y(t)], \end{cases} \tag{1.1}$$

where $x(t)$ and $y(t)$ can be interpreted as the population densities of prey and predator at time t, respectively; $\tau > 0$ is the feedback time delay of prey species to the growth of species itself; $r_1 > 0$ denotes intrinsic growth rate of prey and $r_2 > 0$ denotes the death rate of predator; the parameters a_{ij} $(i, j = 1, 2)$ are all positive constants. a_{11}, a_{22} are self-limitation constants. a_{12} is the capture rate of the predator and a_{21} denotes the rate of conversion of nutrients from the prey into the reproduction of predator. Recently, Yan and Li [9] incorporated the same delay τ into the population density of the predator in the second equation of system (1.1) to reflect the feedback time delay of the predator species to the growth of the species itself. They found that the unique positive equilibrium of system (1.1) will no longer be absolutely stable and the switches from stability to instability to stability disappear, which had been obtained for system (1.1) by Song and Wei [10].

Yang [11] introduced the delay into the Holling type II function in the second and third equations of system (1.2) based on the system of Ruan et al. [17], which is only referred to as the gestational period. Yang considered the local stability of the positive equilibrium and the existence of Hopf bifurcation. Meng et al. [12] considered not only the gestation period but also the growth to maturity of the second predator in the following system:

$$\begin{cases} \dot{x}(t) = rx(t)\big(1 - \frac{x(t)}{K}\big) - \frac{a_1x(t)y_1(t)}{1+b_1x(t)} - \frac{a_2x(t)y_2(t)}{1+b_2x(t)}, \\ \dot{y}_1(t) = y_1(t)\big(-d_1 + \frac{e_1x(t-\tau_1)}{1+b_1x(t-\tau_1)}\big), \\ \dot{y}_2(t) = y_2(t)\big(-d_2 - Gy_2(t-\tau_2) + \frac{e_2x(t-\tau_1)}{1+b_2x(t-\tau_1)}\big), \end{cases} \tag{1.2}$$

where $x(t)$ is the density of the prey and $y_1(t)$, $y_2(t)$ are the density of the two predators at the time t. The prey grows with intrinsic growth rate r and carrying capacity K in the absence of predation. The predators $y_1(t)$ and $y_2(t)$ compete for prey with capture rates a_1 and a_2 with Holling type II functional response and contribute to their growth with conversion rates e_1 and e_2, respectively. The constant d_1 is the death rate of the first predator, $y_1(t)$, and d_2 is the death rate of the second predator, $y_2(t)$. G is the coefficient of intra-specific competition of predator. r, a_1, a_2, b_1, b_2, d_1, d_2, e_1, e_2, τ_1, τ_2, K and G are positive constants. Meng et al. obtained some conditions of local stability and the existence of Hopf bifurcation and gave explicit formulas to determine the properties of Hopf bifurcation. In fact, when $\tau_1 = \tau_2 = 0$ and $G = b_1 = 0$, system (1.2) becomes a system, which was first proposed by Armstrong and McGehee [18] to explain Ayala's experiments. Such system with two or more delays has been studied in many works, see [11, 19–25].

In this paper, we will consider the following system with feedback delays:

$$\begin{cases} \dot{x}(t) = rx(t)\big(1 - \frac{x(t-\tau_1)}{K}\big) - \frac{a_1x(t)y_1(t)}{1+b_1x(t)} - \frac{a_2x(t)y_2(t)}{1+b_2x(t)}, \\ \dot{y}_1(t) = y_1(t)\big(-d_1 + \frac{e_1x(t)}{1+b_1x(t)}\big), \\ \dot{y}_2(t) = y_2(t)\big(-d_2 - Gy_2(t-\tau_2) + \frac{e_2x(t)}{1+b_2x(t)}\big), \end{cases} \tag{1.3}$$

where τ_1 defines the feedback time delay of the prey to the growth of the species itself, and τ_2 denotes the feedback time delay of the second predator to the growth of the species itself.

This paper is organized as follows. In Sect. 2, by analyzing the character equation of linearized system of system (1.3) at the positive equilibrium, some 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 obtained by applying the normal-form method and center manifold theory due to Hassard et al. [23] in Sect. 3. In Sect. 4, to support our theoretical predictions, some numerical simulations are included. A brief discussion is given in the last section.

2 Local stability and Hopf bifurcation

It is obvious that system (1.3) has a unique positive equilibrium $E^* = (x^*, y_1^*, y_2^*)$ defined by

$$x^* = \frac{d_1}{e_1 - b_1d_1},$$

$$y_1^* = \frac{1+b_1x^*}{a_1}\left(r - \frac{rx^*}{K} - \frac{a_2y_2^*}{1+b_2x^*}\right),$$

$$y_2^* = \frac{1}{G}\left(-d_2 + \frac{e_2d_1}{e_1+b_2d_1-b_1d_1}\right),$$

provided the following conditions are satisfied:

(H1) $r - \frac{rx^*}{K} - \frac{a_2y_2^*}{1+b_2x^*} > 0$ and
(H2) $\frac{e_1}{b_1} > d_1$, $\frac{e_2d_1}{e_1+b_2d_1-b_1d_1} > d_2$.

Note that two inequalities in (H2) simply mean that the death rates of the two competitors must be smaller than the corresponding growth rate, otherwise the competing species cannot survive and the positive steady state does not exist.

We first let $u_1(t) = x(t) - x^*$, $u_2(t) = y_1(t) - y_1^*$, $u_3(t) = y_2(t) - y_2^*$, then rewrite system (1.3) as the following system:

$$\begin{cases} \dot{u}_1(t) = a_{11}u_1(t) + a_{12}u_2(t) + a_{13}u_3(t) \\ \qquad + a_{14}u_1(t-\tau_1) \\ \qquad \times \sum_{i+j+k+l\ge 2} f_1^{(ijkl)} u_1^i u_2^j u_3^k u_1^l(t-\tau_1), \\ \dot{u}_2(t) = a_{21}u_1(t) + \sum_{i+j\ge 2} f_2^{(ij)} u_1^i u_2^j, \\ \dot{u}_3(t) = a_{31}u_1(t) + a_{32}u_3(t-\tau_2) \\ \qquad + \sum_{i+j\ge 2} f_3^{(ij)} u_1^i(t) u_3^j(t-\tau_2), \end{cases} \tag{2.1}$$

where

$$a_{11} = \frac{a_1b_1x^*y_1^*}{(1+b_1x^*)^2} + \frac{a_2b_2x^*y_2^*}{(1+b_2x^*)^2},$$

$$a_{12} = -\frac{a_1x^*}{1+b_1x^*}, \qquad a_{13} = -\frac{a_2x^*}{1+b_2x^*},$$

$$a_{14} = -\frac{rx^*}{K}, \qquad a_{21} = \frac{e_1y_1^*}{(1+b_1x^*)^2},$$

$$a_{31} = \frac{e_2y_2^*}{(1+b_2x^*)^2}, \qquad a_{32} = -Gy_2^*,$$

$$f_1^{(ijkl)} = \frac{1}{i!j!k!} \frac{\partial^{i+j+k+l} f_1}{\partial u_1^i(t)\partial u_2^j(t)\partial u_3^k(t)\partial u_1^l(t-\tau_1)}\bigg|_{(x^*,y_1^*,y_2^*)},$$

$$f_2^{(ij)} = \frac{1}{i!j!} \frac{\partial^{i+j} f_2}{\partial u_1^i(t)\partial u_2^j(t)}\bigg|_{(x^*,y_1^*,y_2^*)},$$

$$f_3^{(ij)} = \frac{1}{i!j!} \frac{\partial^{i+j} f_3}{\partial u_1^i(t)\partial u_3^j(t-\tau_2)}\bigg|_{(x^*,y_1^*,y_2^*)},$$

$$f_1 = ru_1(t)\left(1 - \frac{u_1(t-\tau_1)}{K}\right) - \frac{a_1u_1(t)u_2(t)}{1+b_1u_1(t)} - \frac{a_2u_1(t)u_3(t)}{1+b_2u_1(t)},$$

$$f_2 = u_2(t)\left(-d_1 + \frac{e_1u_1(t)}{1+b_1u_1(t)}\right),$$

$$f_3 = u_3(t)\left(-d_2 - Gu_3(t-\tau_2) + \frac{e_2u_1(t)}{1+b_2u_1(t)}\right).$$

To study the stability of the equilibrium point $E^* = (x^*, y_1^*, y_2^*)$, it is sufficient to study the stability of the origin for system (2.1). Consider the linearized system of system (2.1) at (0, 0, 0):

$$\begin{cases} \dot{u}_1(t) = a_{11}u_1(t) + a_{12}u_2(t) \\ \qquad + a_{13}u_3(t) + a_{14}u_1(t-\tau_1), \\ \dot{u}_2(t) = a_{21}u_1(t), \\ \dot{u}_3(t) = a_{31}u_1(t) + a_{32}u_3(t-\tau_2). \end{cases} \tag{2.2}$$

Then the associated characteristic equation of system (2.2) is

$$\lambda^3 + A\lambda^2 + B\lambda + C\lambda^2e^{-\lambda\tau_1} + \left(D\lambda^2 + E\lambda + F\right)e^{-\lambda\tau_2} + G\lambda e^{-\lambda(\tau_1+\tau_2)} = 0, \tag{2.3}$$

where $A = -a_{11}$, $B = -(a_{13}a_{31} + a_{12}a_{21})$, $C = -a_{14}$, $D = -a_{32}$, $E = a_{11}a_{32}$, $F = a_{12}a_{21}a_{32}$, $G = a_{14}a_{32}$. In the following, we will discuss the distribution of roots of (2.3) while τ_1 and τ_2 are different given values.

Case 1: $\tau_1 = 0$, $\tau_2 = 0$. Equation (2.3) becomes

$$\lambda^3 + (A+C+D)\lambda^2 + (B+E+G)\lambda + F = 0. \tag{2.4}$$

All roots of (2.4) have negative real parts if and only if

(H3) $A+C+D > 0$ and $(A+C+D)(B+E+G) > F$.

So the equilibrium point $E^* = (x^*, y_1^*, y_2^*)$ is locally stable when (H3) holds.

Case 2: $\tau_1 \ne 0$, $\tau_2 = 0$. For the sake of simplicity, we let $A_{22} = A + D$, $A_{21} = B + E$, $A_{20} = F$, $B_{22} = C$ and $B_{21} = G$, then (2.3) can be written in the form

$$\lambda^3 + A_{22}\lambda^2 + A_{21}\lambda + A_{20} + \left(B_{22}\lambda^2 + B_{21}\lambda\right)e^{-\lambda\tau_1} = 0. \tag{2.5}$$

We first introduce the following result which was proved by Ruan and Wei [21] using Rouch's theorem.

Lemma 2.1 *Consider the exponential polynomial*

$$\begin{aligned} &P(\lambda, e^{-\lambda\tau_1}, \dots, e^{-\lambda\tau_m}) \\ &\quad = \lambda^n + p_1^0\lambda^{n-1} + \cdots + p_{n-1}^0\lambda + p_n^0 \\ &\qquad + [p_1^1\lambda^{n-1} + \cdots + p_{n-1}^1\lambda + p_n^1]e^{-\lambda\tau_1} \\ &\qquad + \cdots + [p_1^m\lambda^{n-1} + \cdots + p_{n-1}^m\lambda + p_n^m]e^{-\lambda\tau_m}, \end{aligned} \tag{2.6}$$

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

Let $\lambda = \omega i$ $(\omega > 0)$ be the root of (2.5). We have

$$\begin{aligned} &-\omega^3 i - A_{22}\omega^2 + A_{21}\omega i + A_{20} \\ &\quad + (-B_{22}\omega^2 + B_{21}\omega i)e^{-\omega\tau_1 i} = 0. \end{aligned}$$

Separating the real and imaginary parts, we obtain

$$\begin{aligned} &-B_{22}\omega^2\cos\omega\tau_1 + B_{21}\omega\sin\omega\tau_1 = A_{22}\omega^2 - A_{20}, \\ &B_{22}\omega^2\sin\omega\tau_1 + B_{21}\omega\cos\omega\tau_1 = \omega^3 - A_{21}\omega. \end{aligned} \tag{2.7}$$

It follows that

$$\omega^6 + p\omega^4 + q\omega^2 + r = 0, \tag{2.8}$$

where $p = A_{22}^2 - 2A_{21} - B_{22}^2$, $q = A_{21}^2 - 2A_{20}A_{22} - B_{21}^2$, $r = A_{20}^2$.

Denote $v = \omega^2$, then (2.8) becomes

$$v^3 + pv^2 + qv + r = 0. \tag{2.9}$$

In the following, we need to seek conditions under which (2.9) has at least one positive root. Denote

$$f(v) = v^3 + pv^2 + qv + r. \tag{2.10}$$

Since $\lim_{v\to+\infty} f(v) = +\infty$, we conclude that if $r < 0$, then (2.9) has at least one positive root.

From (2.10), we have

$$\frac{df(v)}{dv} = 3v^2 + 2pv + q. \tag{2.11}$$

Discussion about the roots of (2.11) is similar to that in [22], so we have the following lemma.

Lemma 2.2 *For the polynomial equation (2.9), since $r \ge 0$, we have the following results:*

(i) *If $\Delta = p^2 - 3q \le 0$, then (2.9) has no positive root;*
(ii) *If $\Delta = p^2 - 3q > 0$, then (2.9) has positive roots if and only if $v_1^* = \frac{-p+\sqrt{\Delta}}{3} > 0$ and $f(v_1^*) \le 0$.*

Suppose that (2.9) has positive roots. Without loss of generality, we assume that it has three positive roots, which are denoted v_1, v_2 and v_3. Then (2.8) has three positive roots: $\omega_k = \sqrt{v_k}$, $k = 1, 2, 3$.

From (2.7), if we denote

$$\begin{aligned} \tau_k^{(j)} &= \frac{1}{\omega_k}\left\{\arccos\left(\frac{(B_{21} - A_{22}B_{22})\omega_k^2 + A_{20}B_{22} - A_{21}B_{21}}{B_{22}^2\omega_k^2 + B_{21}^2}\right) + 2j\pi\right\}, \\ &k = 1, 2, 3,\ j = 0, 1, 2, \dots, \end{aligned}$$

then $\pm i\omega_k$ are a pair of purely imaginary roots of (2.5) with $\tau_1 = \tau_k^{(j)}$.

Define

$$\tau_{10} = \tau_k^{(0)} = \min_{k\in\{1,2,3\}}\{\tau_k^{(0)}\}, \qquad \omega_0 = \omega_{k_0}.$$

Therefore, applying Lemmas 2.1 and 2.2 to (2.5), we obtain the following lemma.

Lemma 2.3 *For the third-degree exponential polynomial equation (2.5), since $r \ge 0$, we have:*

(i) *If $\Delta = p^2 - 3q \le 0$, then all roots with positive real parts of (2.5) have the same sum as those of the polynomial equation (2.4) for all $\tau_1 \ge 0$;*
(ii) *If $\Delta = p^2 - 3q > 0$, $v_1^* = \frac{-p+\sqrt{\Delta}}{3} > 0$ and $f(v_1^*) \le 0$, then all roots with positive real parts of (2.5) have the same sum as those of the polynomial equation (2.4) for all $\tau_1 \in [0, \tau_{10})$.*

Let $\lambda(\tau) = \xi(\tau) + i\omega(\tau)$ be the root of (2.5) near $\tau = \tau_{10}$ satisfying $\xi(\tau_{10}) = 0$, $\omega(\tau_{10}) = \omega_0$. Then we have the following transversality condition.

Lemma 2.4 *Suppose that $v_k = \omega_k^2$ and $f'(v_k) \ne 0$, where $f(v)$ is defined by (2.10). Then*

$$\frac{d\,\mathrm{Re}\,\lambda(\tau_{10})}{d\tau_1} \ne 0,$$

and $\frac{d\,\mathrm{Re}\,\lambda(\tau_{10})}{d\tau_1}$ and $f'(v_k)$ have the same sign.

Proof Taking the derivative of λ with respect to τ_1 in (2.5), we obtain

$$(3\lambda^2+2A_{22}\lambda+A_{21})\frac{d\lambda}{d\tau_1}+(2B_{22}\lambda+B_{21})e^{-\lambda\tau_1}\frac{d\lambda}{d\tau_1}+\left(B_{22}\lambda^2+B_{21}\lambda\right)e^{-\lambda\tau_1}\left(-\lambda-\tau_1\frac{d\lambda}{d\tau_1}\right)=0.$$

It follows that

$$\left(\frac{d\lambda}{d\tau_1}\right)^{-1}=\frac{(3\lambda^2+2A_{22}\lambda+A_{21})e^{\lambda\tau_1}}{\lambda(B_{22}\lambda^2+B_{21}\lambda)}+\frac{2B_{22}\lambda+B_{21}}{\lambda(B_{22}\lambda^2+B_{21}\lambda)}-\frac{\tau_1}{\lambda}. \tag{2.12}$$

In addition, we have

$$\left[\lambda\left(B_{22}\lambda^2+B_{21}\lambda\right)\right]_{\tau_1=\tau_k^{(j)}}=-B_{21}\omega_k^2-iB_{22}\omega_k^3, \tag{2.13}$$

$$\left[3\lambda^2+2A_{22}\lambda+A_{21}\right]_{\tau_1=\tau_k^{(j)}}=A_{21}-3\omega^2+i2A_{22}\omega_k, \tag{2.14}$$

$$[2B_{22}\lambda+B_{21}]_{\tau_1=\tau_k^{(j)}}=B_{21}+i2B_{22}\omega_k. \tag{2.15}$$

For simplicity, we define ω_k as ω and $\tau_k^{(j)}$ as τ_1. From (2.12)–(2.15) and (2.7), we obtain

$$\begin{aligned}
\left[\frac{d\,\mathrm{Re}\,\lambda(\tau_{10})}{d\tau_1}\right]^{-1}_{\tau_1=\tau_k^{(j)}}
&=\mathrm{Re}\left[\frac{(3\lambda^2+2A_{22}\lambda+A_{21})e^{-\lambda\tau_1}}{\lambda(B_{22}\lambda^2+B_{21}\lambda)}\right]_{\tau_1=\tau_k^{(j)}}
+\mathrm{Re}\left[\frac{2B_{22}\lambda+B_{21}}{\lambda(B_{22}\lambda^2+B_{21}\lambda)}\right]_{\tau_1=\tau_k^{(j)}}\\
&=\frac{-1}{\Lambda}\{[\left(A_{21}-3\omega^2\right)\cos\omega\tau_1-2A_{22}\omega\sin\omega\tau_1]B_{21}\omega^2\\
&\quad+[\left(A_{21}-3\omega^2\right)\sin\omega\tau_1-2A_{22}\omega\cos\omega\tau_1]B_{22}\omega^3\\
&\quad+B_{21}\omega^2+2B_{22}^2\omega^4\}\\
&=\frac{-1}{\Lambda}\{\left(A_{21}-3\omega^2\right)\omega[B_{21}\omega\cos\omega\tau_1\\
&\quad+B_{22}\omega^2\sin\omega\tau_1]B_{21}\omega^2\\
&\quad+2A_{22}\omega^2[-B_{21}\omega\sin\omega\tau_1+B_{22}\omega^2\sin\omega\tau_1]\\
&\quad+B_{21}\omega^2+2B_{22}^2\omega^4\}\\
&=\frac{1}{\Lambda}\{3\omega^6+2\left(A_{22}^2-2A_{21}-B_{22}^2\right)\omega^4\\
&\quad+\left(A_{21}^2-2A_{22}A_{20}-B_{21}\right)\omega^2\}\\
&=\frac{v_k}{\Lambda}\{3v_k^2+2\left(A_{22}^2-2A_{21}-B_{22}^2\right)v_k\\
&\quad+\left(A_{21}^2-2A_{22}A_{20}-B_{21}\right)\}\\
&=\frac{v_k}{\Lambda}f'(v_k),
\end{aligned}$$

where $\Lambda=B_{21}^4\omega^4+B_{22}^4\omega^8$. Thus, we have

$$\begin{aligned}
\mathrm{sign}\left[\frac{d\,\mathrm{Re}\,\lambda(\tau_{10})}{d\tau_1}\right]_{\tau_1=\tau_k^{(j)}}&=\mathrm{sign}\left[\frac{d\,\mathrm{Re}\,\lambda(\tau_{10})}{d\tau_1}\right]^{-1}_{\tau_1=\tau_k^{(j)}}\\
&=\mathrm{sign}\left[\frac{v_k}{\Lambda}f'(v_k)\right]\neq 0.
\end{aligned}$$

Furthermore, since $v_k>0$, we conclude that $[\frac{d\,\mathrm{Re}\,\lambda(\tau)}{d\tau}]_{\tau_1=\tau_k^{(j)}}$ and $f'(v_k)$ have the same sign. □

Since $r=A_{20}^2\geq 0$, by applying Lemmas 2.4 to (2.5), we have the following theorem.

Theorem 2.1 *For the third-degree exponential polynomial equation* (2.5), *we have*:

(i) *When* $\Delta=p^2-3q\leq 0$, *all roots of* (2.5) *have negative real parts for all* $\tau_1\geq 0$, *thus the zero solution of system* (1.3) *is asymptotically stable for* $\tau_1\geq 0$;

(ii) *If* $\Delta>0$, $v_1^*=\frac{-p+\sqrt{\Delta}}{3}>0$ *and* $f(v_1^*)\leq 0$ *hold, then* $f(v)$ *has at least one positive root* v_k, *and all roots of* (2.5) *have negative real parts for* $\tau_1\in[0,\tau_{10})$, *and system* (1.3) *at the equilibrium* E^* *is asymptotically stable for* $\tau_1\in[0,\tau_{10})$;

(iii) *If all the conditions as stated in (ii) and* $f'(v_k)\neq 0$ *are satisfied, then system* (1.3) *exhibits the Hopf bifurcation at the equilibrium* E^* *for* $\tau_1=\tau_k^{(j)}$ $(j=0,1,2,\ldots)$.

Case 3: $\tau_1=0$, $\tau_2\neq 0$. Since $\tau_1=0$, a_{11} of the linearized system (2.2) becomes $a_{11}=-\frac{rx^*}{K}+\frac{a_1b_1x^*y_1^*}{(1+b_1x^*)^2}+\frac{a_2b_2x^*y_2^*}{(1+b_2x^*)^2}$, a_{14} becomes $a_{14}=0$ and the others are the same as in the above Case 2. We let $A_{32}=A+C$, $A_{31}=B$, $B_{32}=D$, $B_{31}=E+G$ and $B_{30}=F$. Rewrite (2.3) as follows:

$$\lambda^3+A_{32}\lambda^2+A_{31}\lambda+\left(B_{32}\lambda^2+B_{31}\lambda+B_{30}\right)e^{-\lambda\tau_2}=0. \tag{2.16}$$

Let $\lambda = \omega i (\omega > 0)$ be the root of (2.16). We have

$$-\omega^3 i - A_{32}\omega^2 + A_{31}\omega i + \left(-B_{32}\omega^2 + B_{31}\omega i + B_{30}\right)e^{-\omega\tau_2 i} = 0.$$

Separating the real and imaginary parts, we obtain

$$\begin{aligned} &\left(B_{30} - B_{32}\omega^2\right)\cos\omega\tau_2 + B_{31}\omega\sin\omega\tau_2 = A_{32}\omega^2, \\ &-\left(B_{30} - B_{32}\omega^2\right)\sin\omega\tau_2 + B_{31}\omega\cos\omega\tau_2 = \omega^3 - A_{31}\omega. \end{aligned} \tag{2.17}$$

It follows that

$$\omega^6 + e_2\omega^4 + e_1\omega^2 + e_0 = 0, \tag{2.18}$$

where $e_2 = A_{32}^2 - 2A_{31} - B_{32}^2$, $e_1 = A_{31}^2 + 2B_{30}B_{32} - B_{31}^2$, $e_0 = -B_{30}^2$.

Define $v = \omega^2$, then (2.18) becomes

$$v^3 + e_2 v^2 + e_1 v + e_0 = 0. \tag{2.19}$$

Denote

$$g(v) = v^3 + e_2 v^2 + e_1 v + e_0.$$

Since $g(0) = e_0 = -B_{30}^2 < 0$, we conclude that (2.19) has at least one positive root. Hence (2.18) has unique positive solution ω_0^2 if $e_2 > 0$ and $e_1 > 0$.

Suppose that (2.19) has positive roots. Without loss of generality, we assume that it has three positive roots, which are denoted v_1, v_2 and v_3. Then (2.18) has three positive roots: $\omega_k = \sqrt{v_k}$, $k = 1, 2, 3$.

From (2.17), if we denote

$$\tau_k^{(j)} = \frac{1}{\omega_k}\left\{\arccos\left(\frac{(B_{31} - A_{32}B_{32})\omega^4 + (A_{32}B_{30} - A_{31}B_{31})\omega^2}{B_{32}^2\omega^4 + (B_{31}^2 - 2B_{30}B_{32})\omega^2 + B_{30}^2}\right) + 2j\pi\right\},$$
$$k = 1, 2, 3,\ j = 0, 1, \ldots,$$

then $\pm i\omega_k$ are a pair of purely imaginary roots of (2.16) with $\tau_2 = \tau_k^{(j)}$.

Define

$$\tau_{20} = \tau_k^{(0)} = \min_{k\in\{1,2,3\}}\left\{\tau_k^{(0)}\right\}, \qquad \omega_0 = \omega_{k_0}.$$

Let $\lambda(\tau) = \xi(\tau) + i\omega(\tau)$ be the root of (2.16) near $\tau_2 = \tau_{20}$ satisfying $\xi(\tau_{20}) = 0$, $\omega(\tau_{20}) = \omega_0$. Then we have the following transversality condition.

Lemma 2.5 *Suppose that* $v_k = \omega_k^2$ *and* $g'(v_k) \neq 0$. *Then*

$$\left[\frac{d\,\mathrm{Re}\,\lambda(\tau_{20})}{d\tau_2}\right]_{\tau_2 = \tau_k^{(j)}} \neq 0,$$

and $[\frac{d\,\mathrm{Re}\,\lambda(\tau_{20})}{d\tau_2}]_{\tau_2 = \tau_k^{(j)}}$ *and* $g'(v_k)$ *have the same sign.*

The proof is similar to that of Lemma 2.4, so we omit it. By applying Lemma 2.5 to (2.16), we get the following theorem.

Theorem 2.2 *As* τ_2 *increases from zero, there is a value* τ_{20} *such that the positive equilibrium* E^* *is locally asymptotically stable when* $\tau_2 \in [0, \tau_{20})$ *and unstable when* $\tau_2 > \tau_{20}$. *Further, for system* (1.3) *the positive equilibrium* E^* *undergoes a Hopf bifurcation when* $\tau_2 = \tau_{20}$.

Case 4: $\tau_1 = \tau_2 = \tau \neq 0$. All the coefficients are the same as those in Case 2. Since $A_{42} = A$, $A_{41} = B$, $B_{42} = C + D$, $B_{41} = E$, $B_{40} = F$ and $C_1 = G$, then (2.3) becomes

$$\lambda^3 + A_{42}\lambda^2 + A_{41}\lambda + \left(B_{42}\lambda^2 + B_{41}\lambda + B_{40}\right)e^{-\lambda\tau} + C_1\lambda e^{-2\lambda\tau} = 0. \tag{2.20}$$

Multiplying by $e^{\lambda\tau}$, (2.20) becomes

$$B_{42}\lambda^2 + B_{41}\lambda + B_{40} + \left(\lambda^3 + A_{42}\lambda^2 + A_{41}\lambda\right)e^{\lambda\tau} + C_1\lambda e^{-\lambda\tau} = 0. \tag{2.21}$$

Let $\lambda = \omega i (\omega > 0)$ be the root of (2.21). We get

$$-B_{42}\omega^2 + B_{41}\omega i + B_{40} + \left(-\omega^3 i - A_{42}\omega^2 + A_{41}\omega i\right)e^{\omega\tau i} + C_1\omega i e^{-\omega\tau i} = 0.$$

Separating the real and imaginary parts, we have

$$\begin{aligned} &-A_{42}\omega^2\cos\omega\tau + \left[C_1\omega - \left(A_{41}\omega - \omega^3\right)\right]\sin\omega\tau = B_{42}\omega^2 - B_{40}, \\ &-A_{42}\omega^2\sin\omega\tau + \left[C_1\omega + \left(A_{41}\omega - \omega^3\right)\right]\cos\omega\tau = -B_{41}\omega. \end{aligned} \tag{2.22}$$

It follows that

$$\begin{aligned} \sin\omega\tau &= \frac{e_2\omega^4 + e_3\omega^2 + e_4}{-\omega^5 + e_0\omega^3 + e_1\omega}, \\ \cos\omega\tau &= \frac{e_5\omega^3 + e_6\omega}{-\omega^5 + e_0\omega^3 + e_1\omega}, \end{aligned} \tag{2.23}$$

where $e_0 = 2A_{41} - A_{42}^2$, $e_1 = C_1^2 - A_{41}^2$, $e_2 = -B_{42}$, $e_3 = B_{42}C_1 + A_{41}B_{42} - A_{42}B_{41} + B_{40}$, $e_4 = -A_{41}B_{40} - B_{40}C_1$, $e_5 = A_{42}B_{42} - B_{41}$, $e_6 = A_{41}B_{41} - A_{42}B_{40} - B_{41}C_1$.

As is known, $\sin^2\omega\tau + \cos^2\omega\tau = 1$. So we have

$$\omega^{10} + f_4\omega^8 + f_3\omega^6 + f_2\omega^4 + f_1\omega^2 + f_0 = 0, \quad (2.24)$$

where $f_4 = -2e_0 - e_2^2$, $f_3 = e_0^2 - 2e_1 - 2e_2e_3 - e_5^2$, $f_2 = 2e_0e_1 - 2e_2e_4 - 2e_5e_6 - e_3^2$, $f_1 = e_1^2 - 2e_3e_4 - e_6^2$, $f_0 = -e_4^2$.

Define $v = \omega^2$, then (2.24) becomes

$$v^5 + f_4v^4 + f_3v^3 + f_2v^2 + f_1v + f_0 = 0. \quad (2.25)$$

Denote

$$h(v) = v^5 + f_4v^4 + f_3v^3 + f_2v^2 + f_1v + f_0. \quad (2.26)$$

From (2.26), we know that $h(0) = f_0 = -e_4^2 < 0$ and $h(+\infty) = +\infty$. Thus we conclude that (2.25) has at least one positive root.

Suppose that (2.25) has positive roots. Without loss of generality, we assume that it has five positive roots, which are denoted v_1, v_2, v_3, v_4 and v_5. Then (2.24) has five positive roots: $\omega_k = \sqrt{v_k}$, $k = 1, 2, 3, 4, 5$.

From (2.23), if we denote

$$\tau_k^{(j)} = \frac{1}{\omega_k}\left\{\arccos\left(\frac{e_5\omega_k^3 + e_6\omega_k}{-\omega_k^5 + e_0\omega_k^3 + e_1\omega}\right) + 2j\pi\right\},$$
$$k = 1, 2, 3, 4, 5, \quad j = 0, 1, 2, \ldots,$$

then $\pm i\omega_k$ are a pair of purely imaginary roots of (2.21) with $\tau = \tau_k^{(j)}$. Define

$$\tau_0 = \tau_k^{(0)} = \min_{k\in\{1,2,3,4,5\}}\{\tau_k^{(0)}\}, \qquad \omega_0 = \omega_{k_0}.$$

Let $\lambda(\tau) = \xi(\tau) + i\omega(\tau)$ be the root of (2.21) near $\tau = \tau_0$ satisfying $\xi(\tau_0) = 0$, $\omega(\tau_0) = \omega_0$, then we will proof the following transversality condition.

Denote

$$\begin{aligned} P &= \left[2B_{42}\lambda + B_{41} + (3\lambda^2 + 2A_{42}\lambda + A_{41})e^{\lambda\tau} + C_1e^{-\lambda\tau}\right]_{\tau=\tau_k^{(j)}} \\ &= \{[B_{41} + (A_{41} - 3\omega^2 + C_1)\cos\omega\tau - 2A_{42}\omega\sin\omega\tau] \\ &\quad + [2B_{42}\omega + (A_{41} - 3\omega^2 - C_1)\sin\omega\tau + 2A_{42}\omega\cos\omega\tau]i\} \\ &:= P_R + P_Ii, \end{aligned}$$

$$\begin{aligned} Q &= \left[\lambda(\lambda^3 + A_{42}\lambda^2 + A_{41})e^{\lambda\tau} - C_1\lambda^2e^{-\lambda\tau}\right]_{\tau=\tau_k^{(j)}} \\ &= \{[(A_{41} - 3\omega^2 + C_1)\cos\omega\tau - 2A_{42}\omega\sin\omega\tau + B_{41}] \\ &\quad + [(A_{41} - 3\omega^2 - C_1)\sin\omega\tau + 2A_{42}\omega\cos\omega\tau + 2B_{42}\omega]i\} \\ &:= Q_R + Q_Ii, \end{aligned}$$

and suppose that

(H4) $P_RQ_R + P_IQ_I \neq 0$.

Then we have the following lemma.

Lemma 2.6 *Suppose that* (H4) *holds, then*

$$\left[\frac{d\,\mathrm{Re}\,\lambda(\tau)}{d\tau}\right]_{\tau=\tau_k^{(j)}} \neq 0.$$

Proof Taking the derivative of λ with respect to τ in (2.21), we obtain

$$\begin{aligned} &(2B_{42}\lambda + B_{41})\frac{d\lambda}{d\tau} + (3\lambda^2 + 2A_{42}\lambda + A_{41})e^{\lambda\tau}\frac{d\lambda}{d\tau} \\ &\quad + (\lambda^3 + A_{42}\lambda^2 + A_{41}\lambda)e^{\lambda\tau}\left(\lambda + \tau\frac{d\lambda}{d\tau}\right) \\ &\quad + C_1e^{-\lambda\tau}\frac{d\lambda}{d\tau} + C_1\lambda e^{-\lambda\tau}\left(-\lambda - \tau\frac{d\lambda}{d\tau}\right) = 0. \end{aligned}$$

It follows that

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2B_{42}\lambda + B_{41} + (3\lambda^2 + 2A_{42}\lambda + A_{41})e^{\lambda\tau} + C_1e^{-\lambda\tau}}{-\lambda(\lambda^3 + A_{42}\lambda^2 + A_{41})e^{\lambda\tau} + C_1\lambda^2e^{-\lambda\tau}} - \frac{\tau}{\lambda}. \quad (2.27)$$

Substitute $\lambda = \omega i$ into (2.27). We have

$$\begin{aligned} \left[\frac{d\,\mathrm{Re}\,\lambda(\tau)}{d\tau}\right]^{-1}_{\tau=\tau_k^{(j)}} &= \mathrm{Re}\left[\frac{\lambda(\lambda^3 + A_{42}\lambda^2 + A_{41})e^{\lambda\tau} - C_1\lambda^2e^{-\lambda\tau}}{-\lambda(\lambda^3 + A_{42}\lambda^2 + A_{41})e^{\lambda\tau} + C_1\lambda^2e^{-\lambda\tau}}\right]_{\tau=\tau_k^{(j)}} \\ &= \frac{-1}{P_R^2 + P_I^2}(P_RQ_R + P_IQ_I). \end{aligned}$$

Thus, when (H4) holds, we obtain

$$\left[\frac{d\,\mathrm{Re}\,\lambda(\tau)}{d\tau}\right]_{\tau=\tau_k^{(j)}} \neq 0.$$

This completes the proof. □

By applying Lemma 2.6 to (2.21), we can conclude the existence of a Hopf bifurcation as stated in the following theorem.

Theorem 2.3 *Suppose* (H4) *holds. Then as* τ *increases from zero, there is a value* τ_0 *such that the positive equilibrium* E^* *is locally asymptotically stable when* $\tau \in [0, \tau_0)$ *and unstable when* $\tau > \tau_0$. *Further, system* (1.3) *undergoes a Hopf bifurcation at* E^* *when* $\tau = \tau_0$.

Case 5: $\tau_1 \neq \tau_2$, $\tau_1 > 0$ and $\tau_2 > 0$.

We consider (2.3) with τ_1 in its stable interval, regarding τ_2 as a parameter. Without loss of generality, we consider system (1.3) under Case 2. Let ωi $(\omega > 0)$ be a root of (2.3). Then we obtain

$$c_1(\omega) + 2c_2(\omega)\sin\omega\tau_1 + 2c_3(\omega)\cos\omega\tau_1 = 0, \quad (2.28)$$

where $c_1(\omega) = -\omega^6 + (D^2 + 2B - A^2 - C^2)\omega^4 + (E^2 + G^2 - B^2 - 2DF)\omega^2 + F^2$, $c_2(\omega) = C\omega^5 - (BC + DG)\omega^3 + FG\omega$, $c_3(\omega) = -AC\omega^4 + EG\omega^2$.

Suppose that

(H5) Equation (2.28) has at least finite positive roots.

If (H5) holds, the roots of (2.28) are denoted $\omega_1, \omega_2, \ldots, \omega_k$. For every fixed ω_i $(i = 1, 2, \ldots, k)$, there exists a sequence $\{\tau_{2_i}^{(j)} | j = 1, 2, \ldots\}$, such that (2.28) holds. Let $\tau_{2*} = \{\min \tau_{2_i}^{(j)} | i = 1, 2, \ldots, k, j = 1, 2, \ldots\}$. When $\tau_2 = \tau_{2*}$, (2.28) has a pair of purely imaginary roots $\pm i\omega^*$ for $\tau_1 \in [0, \tau_{10})$.

In the following, we assume that

(H6) $[\frac{d\,\mathrm{Re}\,\lambda(\tau_2)}{d\tau_2}]_{\tau_2=\tau_{2_i}^{(j)}} \neq 0$.

Therefore, by the general Hopf bifurcation theorem for FDEs in Hale [24], we have the following result on stability and bifurcation of system (1.3).

Theorem 2.4 *For system* (1.3), *suppose that* (H5) *and* (H6) *hold and* $\tau_1 \in [0, \tau_{10})$. *Then the positive equilibrium* E^* *of system* (1.3) *is asymptotically stable for* $\tau_2 \in [0, \tau_{2*})$, *and system* (1.3) *at the positive equilibrium* E^* *undergoes a Hopf bifurcation when* $\tau_2 = \tau_{2*}$. *That is, system* (1.3) *has a branch of periodic solution bifurcation from the zero solution near* $\tau_2 = \tau_{2*}$.

3 Direction and stability of the Hopf bifurcation

In this section, we shall study the direction of the Hopf bifurcation and the stability of bifurcating periodic solution of system (1.3). The approach employed here is the normal-form method and center manifold theorem introduced by Hassard et al. [23]. More precisely, we will compute the reduced system on the center manifold with the pair of conjugate complex, purely imaginary solutions of the characteristic equation (2.3). By this reduction we can determine the Hopf bifurcation direction, i.e., to answer the question of whether the bifurcation branch of periodic solution exists locally for supercritical bifurcation or subcritical bifurcation.

Without loss of generality, we assume that $\tau_1^* < \tau_2^*$, where $\tau_2^* \in [0, \tau_{20})$. We first let $u_1(t) = x(t) - x^*$, $u_2(t) = y_1(t) - y_1^*$, $u_3(t) = y_2(t) - y_2^*$, and normalize the delay with the scaling $t \to (t/\tau_1)$. Then (1.3) is transformed into an FDE in $C = C([-1, 0], R^3)$ as

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

where $u(t) = (u_1(t), u_2(t), u_3(t))^T \in R^3$, and $L_\mu : C \to R^3$, $F : R \times C \to R^3$ are given, respectively, by

$$L_\mu u_t = \tau_1\left[B(\tau_1)u_t + C(\tau_1)u\left(t - \frac{\tau_2^*}{\tau_1}\right) + D(\tau_1)u(t-1)\right], \quad (3.2)$$

and

$$F(\mu, u_t) = \tau_1(F_1, F_2, F_3)^T, \quad (3.3)$$

with

$$B(\tau_1) = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & 0 & 0 \\ a_{31} & 0 & 0 \end{pmatrix},$$

$$C(\tau_1) = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & a_{32} \end{pmatrix},$$

$$D(\tau_1) = \begin{pmatrix} a_{14} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

and

$$\begin{cases} F_1 = a_{15}\phi_1^2(0) + a_{16}\phi_1(0)\phi_2(0) \\ \qquad + a_{17}\phi_1(0)\phi_3(0) + a_{18}\phi_1(0)\phi_1(-1) \\ \qquad + a_{111}\phi_1^3(0) + a_{112}\phi_1^2(0)\phi_2(0) \\ \qquad + a_{113}\phi_1^2(0)\phi_3(0), \\ F_2 = a_{22}\phi_1^2(0) + a_{23}\phi_1(0)\phi_2(0) + a_{24}\phi_1^3(0) \\ \qquad + a_{25}\phi_1^2(0)\phi_2(0), \\ F_3 = a_{33}\phi_1^2(0) + a_{34}\phi_1(0)\phi_3(0) + a_{35}\phi_3^2\big(-\frac{\tau_1}{\tau_2^*}\big) \\ \qquad + a_{36}\phi_1^3(0) + a_{37}\phi_1^2(0)\phi_3(0). \end{cases}$$

Here $a_{11}, a_{12}, a_{13}, a_{14}, a_{21}, a_{31}, a_{32}$ are the same as in system (2.1) and

$$a_{15} = \frac{a_1 b_1 y_1^*(1-b_1x^*)}{(1+b_1x^*)^3} + \frac{a_2 b_2 y_2^*(1-b_2x^*)}{(1+b_2x^*)^3},$$

$$a_{16} = \frac{a_1 b_1 x^*}{(1+b_1x^*)^2}, \qquad a_{17} = \frac{a_2 b_2 x^*}{(1+b_2x^*)^2},$$

$$a_{18} = -\frac{r}{K},$$

$$a_{111} = \frac{2a_1 b_1 y_1^*(-2b_1 + b_1^2 x^*)}{(1+b_1x^*)^4} + \frac{a_2 b_2 y_2^*(-2b_2 + b_2^2 x^*)}{(1+b_2x^*)^4},$$

$$a_{112} = \frac{a_1 b_1(1-b_1x^*)}{(1+b_1x^*)^3}, \qquad a_{113} = \frac{a_2 b_2(1-b_2x^*)}{(1+b_2x^*)^3},$$

$$a_{22} = \frac{-2b_1 e_1 y_1^*}{(1+b_1x^*)^3}, \qquad a_{23} = \frac{e_1}{(1+b_1x^*)^2},$$

$$a_{24} = \frac{6b_1^2 e_1 y_1^*}{(1+b_1x^*)^4}, \qquad a_{25} = \frac{-b_1 e_1}{(1+b_1x^*)^3},$$

$$a_{33} = \frac{-2b_2 e_2 y_2^*}{(1+b_2x^*)^3}, \qquad a_{34} = \frac{e_2}{(1+b_2x^*)^2},$$

$$a_{35} = -G, \qquad a_{36} = \frac{6e_2 b_2^2 y_2^*}{(1+b_2x^*)^4},$$

$$a_{37} = \frac{-2b_2 e_2}{(1+b_2x^*)^3}.$$

It turning to the linear problem

$$\dot{u}(t) = L_\mu u_t,$$

by the Reisz representation theorem, there exists a 3×3 matrix-valued function $\eta(\cdot,\mu) : [-1,0] \to R^{3\times 3}$, such that

$$L_\mu(\phi) = \int_{-1}^0 d\eta(\theta,\mu)\,\phi(\theta), \quad \phi \in C. \tag{3.4}$$

In fact, we can choose

$$\eta(\theta,\mu) = \begin{cases} (\tau_{10}+\mu)(B_3+C_3+D_3), & \theta = 0, \\ (\tau_{10}+\mu)(C_3+D_3), & \theta \in \big[-\frac{\tau_2^*}{\tau_1}, 0\big), \\ (\tau_{10}+\mu)D_3, & \theta \in \big(-1, -\frac{\tau_2^*}{\tau_1}\big), \\ 0, & \theta = -1. \end{cases} \tag{3.5}$$

Then (3.4) is satisfied.

Next, for $\phi \in C([-1,0], R^3)$, we define the operator $A(\mu)$ as

$$A(\mu)\phi(\theta) = \begin{cases} \frac{d\phi}{d\theta}, & \theta \in [-1,0), \\ \int_{-1}^0 d\eta(\theta,\mu)\,\phi(\theta), & \theta = 0, \end{cases} \tag{3.6}$$

and

$$R(\mu)\phi(\theta) = \begin{cases} 0, & \theta \in [-1,0), \\ F(\mu,\phi), & \theta = 0. \end{cases} \tag{3.7}$$

Since $\frac{du_t}{d\theta} = \frac{du_t}{dt}$, then system (3.1) is equivalent to the following operator equation:

$$\dot{u}(t) = A(\mu)u_t + R(\mu)u_t, \tag{3.8}$$

where $u_t = u(t+\theta)$, for $\theta \in [-1,0]$, which is an equation of the form we desired.

For $\psi \in C'([-1,0], (R^3)^*)$, we further define the adjoint A^* of A as

$$A^*(\mu)\psi(s) = \begin{cases} -\frac{d\psi(s)}{ds}, & s \in (0,1], \\ \int_{-1}^0 \psi(-s)\,d\eta(s,\mu), & s = 0, \end{cases} \tag{3.9}$$

and in a bilinear form,

$$\langle \psi(s), \phi(\theta)\rangle = \bar{\psi}^T(0)\phi(0) - \int_{\theta=-1}^0 \int_{\xi=0}^\theta \bar{\psi}^T(\xi - s)\,d\eta(\theta)\,\phi(\xi)\,d\xi, \tag{3.10}$$

where $\eta(\theta)=\eta(\theta,0)$. Then $A(0)$ and $A^*(0)$ are adjoint operators. From the above analysis, we obtain that $\pm i\omega_0\tau_{10}$ are the eigenvalues of $A(0)$ and therefore they are also the eigenvalues of $A^*(0)$. Let $q(\theta)$ be eigenvector of $A(0)$ corresponding to $i\omega_0\tau_{10}$ and $q^*(\theta)$ be eigenvector of $A^*(0)$ corresponding to $-i\omega_0\tau_{10}$. Then we have

$$A(0)q(\theta)=i\omega_0\tau_{10}q(\theta),$$
$$A^*(0)q^*(\theta)=-i\omega_0\tau_{10}q^*(\theta).$$

By a simple computation, we can obtain

$$q(\theta)=Ve^{i\omega_0\tau_{10}\theta},\qquad q^*(s)=DV^*e^{-i\omega_0\tau_{10}s},$$

where

$$V=(1,\rho_1,\rho_2)^T,\qquad V^*=\big(1,\rho_1^*,\rho_2^*\big)^T,$$
$$\rho_1=-\frac{e_1y_2^*i}{\omega_0\tau_{10}(1+b_1x^*)^2},$$
$$\rho_2=\frac{e_2y_2^*}{i\omega_0\tau_{10}(1+b_2x^*)^2+Gy_2^*e^{-i\omega_0\frac{\tau_2^*}{\tau_{10}}}},$$
$$\rho_1^*=\frac{e_1y_1^*i}{\omega_0\tau_{10}(1+b_1x^*)^2},$$
$$\rho_2^*=\frac{e_2y_2^*}{-i\omega_0\tau_{10}(1+b_2x^*)^2+Gy_2^*e^{-i\omega_0\frac{\tau_2^*}{\tau_{10}}}},$$
$$\bar{D}=\big[1+\bar{\rho}_1^*\rho_1+\bar{\rho}_2^*\rho_2+\tau_{10}e^{-i\omega_0\tau_{10}}\big(a_{14}+a_{32}\bar{\rho}_2^*\rho_2\big)\big]^{-1}.$$

Then $\langle q^*,q\rangle=1$, $\langle q^*,\bar{q}\rangle=0$.

In the remainder of this section, by using the same notations as in Hassard et al. [23] and using a computation process similar to that in [12], we obtain the coefficients used in determining the important quantities of the periodic solution:

$$\begin{aligned}
g_{20}&=2\overline{D}\big(K_{11}+\bar{\rho}_1^*K_{21}+\bar{\rho}_2^*K_{31}\big),\\
g_{11}&=\overline{D}\big(K_{12}+\bar{\rho}_1^*K_{22}+\bar{\rho}_2^*K_{32}\big),\\
g_{02}&=2\overline{D}\big(K_{13}+\bar{\rho}_1^*K_{23}+\bar{\rho}_2^*K_{33}\big),\\
g_{21}&=2\overline{D}\big(K_{14}+\bar{\rho}_1^*K_{24}+\bar{\rho}_2^*K_{34}\big),
\end{aligned}\tag{3.11}$$

where

$$\begin{cases}
K_{11}=a_{15}+a_{16}\rho_1+a_{17}\rho_2+a_{18}e^{-i\omega_0\tau_{10}},\\
K_{12}=2a_{15}+a_{16}(\rho_1+\bar{\rho}_1)+a_{17}(\rho_2+\bar{\rho}_2)\\
\qquad +a_{18}(e^{i\omega_0\tau_{10}}+e^{-i\omega_0\tau_{10}}),\\
K_{13}=a_{15}+a_{16}\bar{\rho}_1+a_{17}\bar{\rho}_2+a_{18}e^{i\omega_0\tau_{10}},\\
K_{14}=a_{15}[2W_{11}^{(1)}(0)+W_{20}^{(1)}(0)]\\
\qquad +a_{16}\big[W_{11}^{(2)}(0)+\frac{W_{20}^{(2)}(0)}{2}+\frac{W_{20}^{(1)}(0)}{2}\bar{\rho}_1\\
\qquad +W_{11}^{(1)}(0)\rho_1\big]\\
\qquad +a_{17}\big[W_{11}^{(3)}(0)+\frac{W_{20}^{(3)}(0)}{2}+\frac{W_{20}^{(1)}(0)}{2}\bar{\rho}_2\\
\qquad +W_{11}^{(1)}(0)\rho_2\big]\\
\qquad +a_{18}\big[W_{11}^{(1)}(-1)+\frac{W_{20}^{(1)}(-1)}{2}+\frac{W_{20}^{(1)}(0)}{2}e^{i\omega_0\tau_{10}}\\
\qquad +W_{11}^{(1)}(0)e^{-i\omega_0\tau_{10}}\big]\\
\qquad +3a_{111}+a_{112}(2\rho_1+\bar{\rho}_1)+a_{113}(2\rho_2+\bar{\rho}_2),\\
K_{21}=a_{22}+a_{23}\rho_1,\\
K_{22}=2a_{22}+a_{23}(\rho_1+\bar{\rho}_1),\\
K_{23}=a_{22}+a_{23}\bar{\rho}_1,\\
K_{24}=a_{22}[2W_{11}^{(1)}(0)+W_{20}^{(1)}(0)]\\
\qquad +a_{23}\big[W_{11}^{(2)}(0)+\frac{W_{20}^{(2)}(0)}{2}+\frac{W_{20}^{(1)}(0)}{2}\bar{\rho}_1\\
\qquad +W_{11}^{(1)}(0)\rho_1\big]\\
\qquad +3a_{24}+a_{25}(2\rho_1+\bar{\rho}_1),\\
K_{31}=a_{33}+a_{34}\rho_2+a_{35}\rho_2^2e^{-i\omega_0\tau_{10}},\\
K_{32}=2a_{33}+a_{34}(\bar{\rho}_2+\rho_2)+2a_{35}\rho_2\bar{\rho}_2,\\
K_{33}=a_{33}+a_{34}\bar{\rho}_2+a_{35}\bar{\rho}_2{}^2e^{i\omega_0\tau_{10}},\\
K_{34}=a_{33}[2W_{11}^{(1)}(0)+W_{20}^{(1)}(0)]\\
\qquad +a_{34}\big[W_{11}^{(3)}(0)+\frac{W_{20}^{(3)}(0)}{2}+\frac{W_{20}^{(1)}(0)}{2}\bar{\rho}_2\\
\qquad +W_{11}^{(1)}(0)\rho_2\big]\\
\qquad +a_{35}\big[2\rho_2W_{11}^{(3)}(-\frac{\tau_2^*}{\tau_{10}})e^{-i\omega_0\tau_{10}}\\
\qquad +\bar{\rho}_2W_{20}^{(3)}(-\frac{\tau_2^*}{\tau_{10}})e^{i\omega_0\tau_{10}}\big]\\
\qquad +3a_{36}+a_{37}(2\rho_2+\bar{\rho}_2).
\end{cases}$$

However,

$$W_{20}(\theta) = \frac{ig_{20}q(0)}{\omega_0\tau_{10}}e^{i\omega_0\tau_{10}\theta} + \frac{i\overline{g}_{02}\overline{q}(0)}{3\omega_0\tau_{10}}e^{-i\omega_0\tau_{10}\theta} + E_1 e^{2i\omega_0\tau_{10}\theta}, \quad (3.12)$$

$$W_{11}(\theta) = -\frac{ig_{11}q(0)}{\omega_0\tau_{10}}e^{i\omega_0\tau_{10}\theta} + \frac{i\overline{g}_{11}\overline{q}(0)}{\omega_0\tau_{10}}e^{-i\omega_0\tau_{10}\theta} + E_2, \quad (3.13)$$

where $E_1 = (E_1^{(1)}, E_1^{(2)}, E_1^{(3)})^T$ and $E_2 = (E_2^{(1)}, E_2^{(2)}, E_2^{(3)})^T$ are both three-dimensional vectors and can be determined by

$$E_1 = 2\begin{pmatrix} 2i\omega_0 - a_{11} - a_{14}e^{-i\omega_0\tau_{10}} & -a_{12} & -a_{13} \\ -a_{21} & 2i\omega_0 & 0 \\ -a_{31} & 0 & 2i\omega_0\tau_{10} - a_{32}e^{-i\omega_0\frac{\tau_2^*}{\tau_{10}}} \end{pmatrix}^{-1} \times \begin{pmatrix} K_{11} \\ K_{21} \\ K_{31} \end{pmatrix},$$

and

$$E_2 = -\begin{pmatrix} a_{11}+a_{14} & a_{12} & a_{13} \\ a_{21} & 0 & 0 \\ a_{31} & 0 & a_{32} \end{pmatrix}^{-1} \begin{pmatrix} K_{12} \\ K_{22} \\ K_{32} \end{pmatrix}.$$

Furthermore, we can see that each g_{ij} in (3.11) is determined by parameters and delays in system (1.3). Thus, we can compute the following quantities:

$$\begin{cases} C_1(0) = \frac{i}{2\omega_0\tau_{10}}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right) + \frac{g_{21}}{2}, \\ \mu_2 = -\frac{\mathrm{Re}\{C_1(0)\}}{\mathrm{Re}\{\lambda'(\tau_{10})\}}, \\ \beta_2 = 2\,\mathrm{Re}\{C_1(0)\}, \\ T_2 = -\frac{\mathrm{Im}\{C_1(0)\}+\mu_2\,\mathrm{Im}\{\lambda'(\tau_{10})\}}{\omega_0\tau_{10}}, \end{cases} \quad (3.14)$$

which determine the properties of bifurcation periodic solutions in the center manifold at the critical value τ_{10}. By the results of Hassard et al. [23], we have the following results.

Theorem 3.1 *In* (3.14), *the following results hold*:

(i) *The sign of μ_2 determines the direction of the Hopf bifurcation*: *if $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical* (*subcritical*) *and the bifurcation periodic solutions exist for $\tau_1 > \tau_{10}$ ($\tau_1 < \tau_{10}$)*;

(ii) *The sign of β_2 determines the stability of the bifurcating periodic solution*: *the bifurcation periodic solutions are stable* (*unstable*) *if $\beta_2 < 0$ ($\beta_2 > 0$)*;

(iii) *The sign of T_2 determines the period of the bifurcating periodic solutions*: *the period increase* (*decrease*) *if $T_2 > 0$ ($T_2 < 0$).*

4 Numerical example

In this section, we give some numerical results of system (1.3) to support the analytic results obtained above. We consider the following system by taking the same coefficients as in [17]:

$$\begin{cases} \dot{x}(t) = 1.5x(t)\left(1 - \frac{x(t-\tau_1)}{3.0}\right) - \frac{0.45x(t)y_1(t)}{1+0.35x(t)} \\ \qquad - \frac{0.55x(t)y_2(t)}{1+0.35x(t)}, \\ \dot{y}_1(t) = y_1(t)\left(-0.45 + \frac{0.55x(t)}{1+0.35x(t)}\right), \\ \dot{y}_2(t) = y_2(t)\left(-0.45 - 0.1y_2(t-\tau_2) + \frac{0.65x(t)}{1+0.35x(t)}\right), \end{cases} \quad (4.1)$$

from which we get the positive equilibrium $E^* = (1.1465, 1.8859, 0.8182)$. Firstly, by computation, we have $\Delta = 0.0398 > 0$, and $\tau_{10} = 1.2740$ when $\tau_2 = 0$. From Theorem 2.1, we obtain the corresponding waveform and the phase plots are shown in Figs. 1 and 2. Similarly, we have $w_0 = 0.050109$, $\tau_{20} = 30.8121$ when $\tau_1 = 0$. From Theorem 2.2, we obtain the corresponding waveform and the phase plots are shown in Figs. 3 and 4.

Secondly, we can obtain $w_0 = 0.88240$, $\tau_0 = 1.2500$ when $\tau_1 = \tau_2 = \tau \neq 0$. That is, when τ increases from zero to the critical value τ_0, the equilibrium point E^* is asymptotically stable, then will lose its stability and a Hopf bifurcation occurs once $\tau > \tau_0 = 1.2500$ (see Figs. 5 and 6).

Finally, regard τ_2 as a parameter and let $\tau_1 = 1.20 \in (0, 1.2740)$. We can obtain that (2.28) has a root $\omega^* = 0.05096$. Furthermore, we have that $\tau_{2*} = 31.4404$. From Theorem 2.4, the equilibrium point E^* is asymptotically stable for $\tau_2 \in (0, \tau_{2*})$ and unstable for $\tau_2 > \tau_{2*}$. By algorithm (3.14) derived in

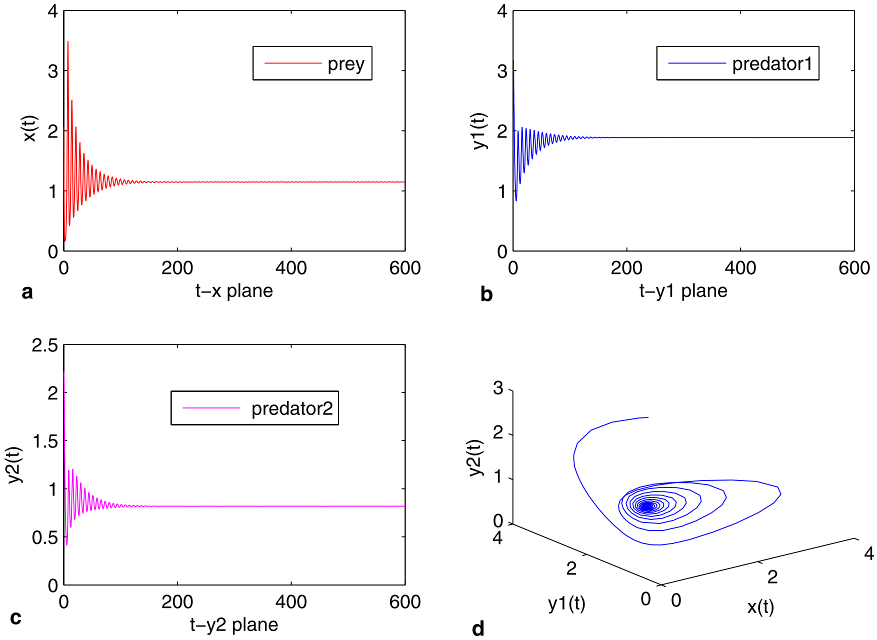

Fig. 1 When $\tau_2 = 0$, the positive equilibrium of system (4.1) is local stable for $\tau_1 = 1.20 < \tau_{10} = 1.2740$ with initial value "2.053, 3.02, 2.2"

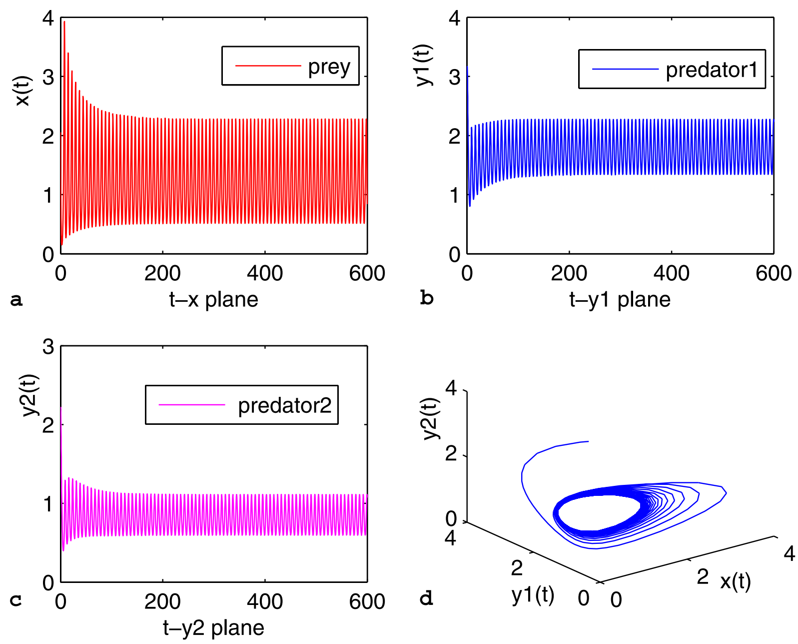

Fig. 2 When $\tau_2 = 0$, the positive equilibrium of system (4.1) undergoes a Hopf bifurcation for $\tau_1 = 1.30 > \tau_{10} = 1.2740$ with initial value "2.053, 3.02, 2.2"

Sect. 3, we have $C_1(0) = -18.9831 + 6.7294i$, then $\mu_2 = 2.5912 \times 10^5 > 0$, $\beta_2 = -37.9661 < 0$. Thus, the Hopf bifurcation is supercritical, and the bifurcating periodic solutions are asymptotically stable, as is illustrated in Figs. 7 and 8. Since $\tau_1 = 1.20$ is lower than $\tau_2 = 34.45$ and τ_1 belongs to its stable inter-

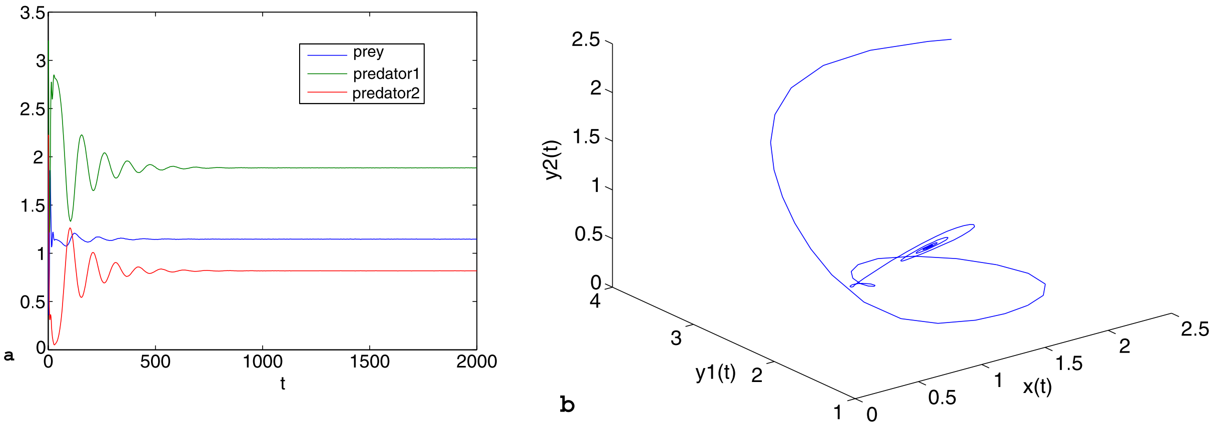

Fig. 3 Matlab simulation shows that the positive equilibrium of the system (4.1) is local stable for $\tau_2 = 25 < \tau_{20} = 30.8121$ with initial value "2.053, 3.02, 2.2"

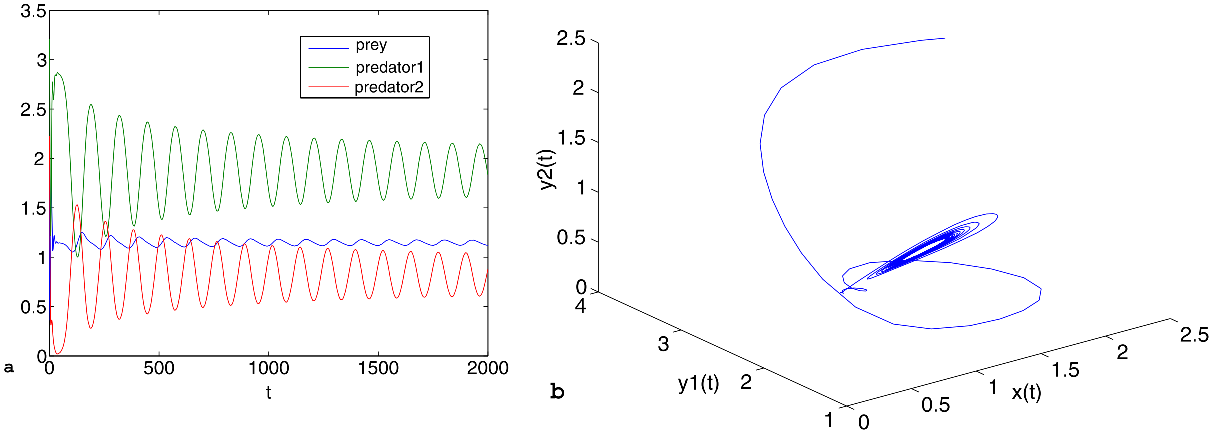

Fig. 4 Matlab simulation shows that the positive equilibrium of the system (4.1) undergoes a Hopf bifurcation for $\tau_2 = 32 > \tau_{20} = 30.8121$ when $\tau_1 = 0$ with initial value "2.053, 3.02, 2.2"

val, Fig. 8 shows that the feedback delay for the prey plays a main role at the early stage than the feedback delay for the second predator does. During this progress, the prey population oscillates about from time 80 to 160 while the predators change monotonously, which results in the small irregular and sharp curves in the phase plots of Fig. 8(b). We can see it clearly in the magnified view (see Fig. 9). If the feedback delay of the second predator increases (for example, $\tau_2 = 54.45$), the small irregular and sharp curves will disappear (see Fig. 10).

5 Discussion

While Yang [11] only considered a gestation delay for predators of system (1.2) and Meng et al. [12] investigated gestation delay and feedback delay of the second predator of system (1.2) with $\tau_1 = \tau_2$, we introduce feedback delays of the prey and the second predator to growth of the species itself in system (1.3) with different cases. By computation, we find that the feedback delays for the prey and the second predator play different role. The feedback delay for the prey is marked because the critical value of τ_1 is much

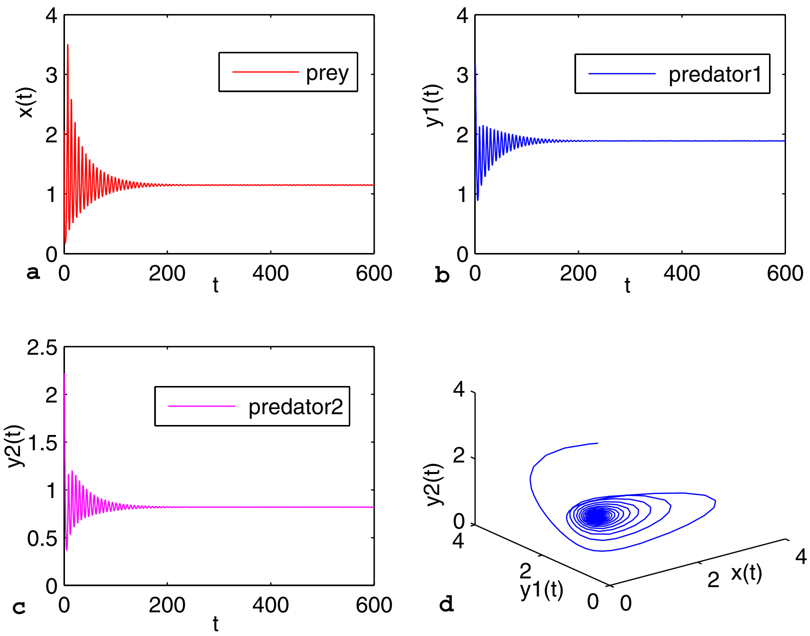

Fig. 5 Matlab simulation shows that the equilibrium point E^* is local stable for $\tau_1 = \tau_2 = \tau = 1.10 < \tau_0 = 1.2500$ with initial value "2.053, 3.02, 2.2"

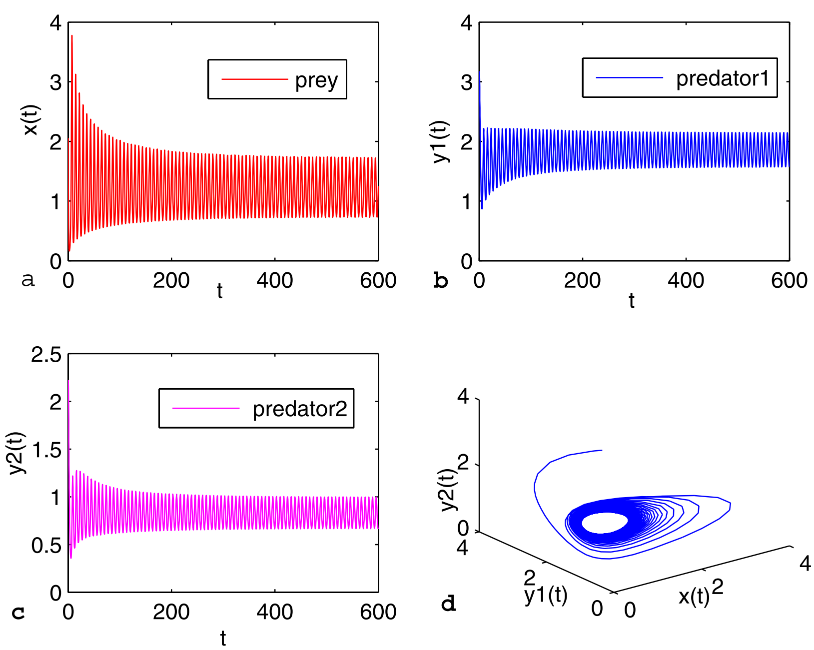

Fig. 6 Matlab simulation shows that the system (4.1) undergoes a Hopf bifurcation when $\tau_1 = \tau_2 = \tau = 1.30 > \tau_0 = 1.2500$ with initial value "2.053, 3.02, 2.2"

smaller when we only consider it. The feedback delay for the second predator is unremarkable because the critical value of τ_2 is much bigger when we omit τ_1 ($\tau_{20} = 30.8121$) or with τ_1 in its stable interval ($\tau_{2*} = 31.4404$). This is different from what is in [12] ($\tau_0 = 1.0909$). We also find that the large feedback de-

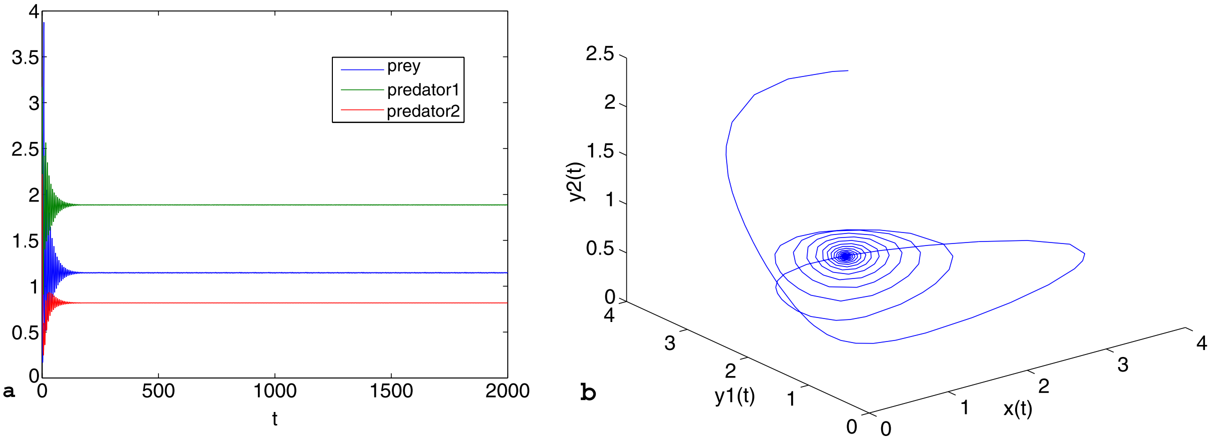

Fig. 7 Matlab simulation shows that the positive equilibrium of system (4.1) is asymptotically stable for $\tau_2 = 3.45 < \tau_{2*} = 31.4404$, $\tau_1 = 1.2$ with initial value "2.053, 3.02, 2.2"

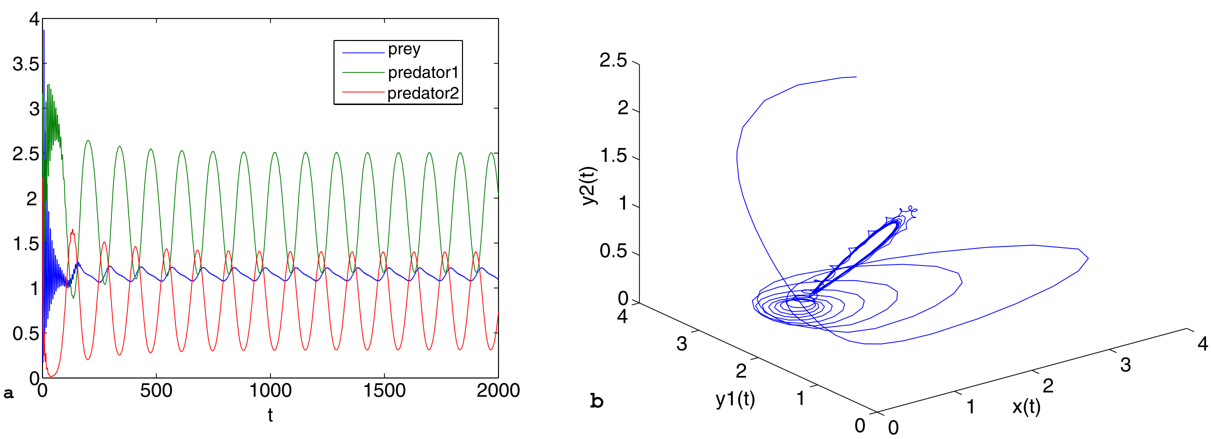

Fig. 8 Matlab simulation shows that the bifurcating periodic solutions from E^* occur and are also asymptotically stable for $\tau_2 = 34.45 > \tau_{2*} = 31.4404$, $\tau_1 = 1.2$ with initial value "2.053, 3.02, 2.2"

lay for the second predator destabilizes solutions of system (1.3). That is, the solutions of system (1.3) begin to oscillate as τ_2 increases monotonously from zero. Furthermore, Ruan et al. [17] had obtained that three species of system (1.3) without delays could coexist. However, we get that those species could also live with some available feedback delays of the prey and the second predator. This is very valuable from the view of ecology.

It is definitely an interesting future work to consider the following more general model with multiple delays:

$$\begin{cases} \dot{x}(t) = rx(t)\left(1 - \frac{x(t)}{K}\right) - \frac{a_1 x(t) y_1(t-\tau_2)}{1+b_1 x(t)} \\ \qquad - \frac{a_2 x(t) y_2(t-\tau_3)}{1+b_2 x(t)}, \\ \dot{y}_1(t) = y_1(t)\left(-d_1 + \frac{e_1 x(t-\tau_1)}{1+b_1 x(t-\tau_1)}\right), \\ \dot{y}_2(t) = y_2(t)\left(-d_2 - G y_2(t) + \frac{e_2 x(t-\tau_1)}{1+b_2 x(t-\tau_1)}\right), \end{cases} \tag{5.1}$$

where τ_1 is gestation period of the prey, and τ_2, τ_3 are the hunting delay of the first, second predator to prey, respectively. Analysis of the more complicated bifurcations is left as the future work.

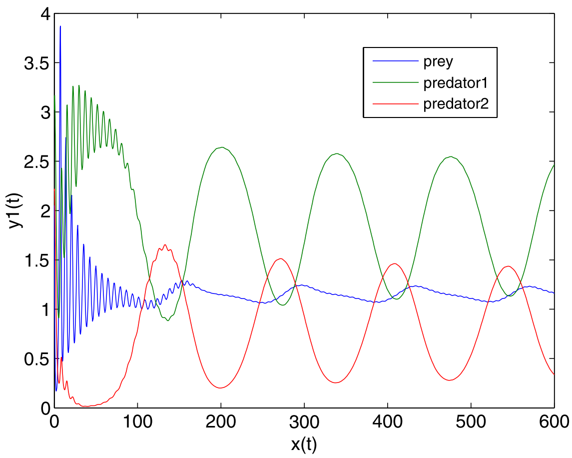

Fig. 9 Magnification of Fig. 8(a) when $0 \leq t \leq 600$

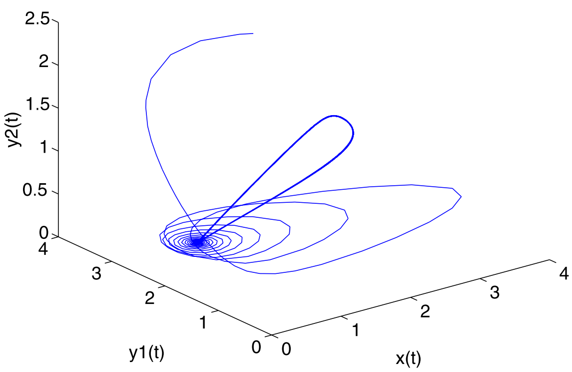

Fig. 10 Matlab simulation shows that the small irregular and sharp curves disappear for $\tau_2 = 54.45 > \tau_{2*} = 31.4404$, $\tau_1 = 1.2$ with initial value "2.053, 3.02, 2.2"

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