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Bifurcation analysis of a delayed predator-prey system with stage structure and Holling-II functional response

Juan Liu[*]

[*]Correspondence:
liujuan7216@163.com
Department of Mathematics and
Physics, Bengbu College, Bengbu,
233030, China

Abstract

This paper is concerned with a stage-structured predator-prey system with Holling-II functional response and two delays. Choosing a possible combination of the two delays as the bifurcation parameter, the existence of the Hopf bifurcation of the system is discussed. Furthermore, the properties of the Hopf bifurcation such as the direction and the stability are determined by using the normal form method and center manifold theorem. Finally, some numerical simulations are presented to justify the theoretical results.

Keywords: predator-prey system; stage-structured; periodic solution; delays; Hopf bifurcation

1 Introduction

It is well known that there are many species whose individual members have a life history that takes them through an immature stage and a mature stage. Based on this fact, stage-structured predator-prey systems have been investigated by many authors in recent years [1–8]. In [5], Xu considered the global stability and permanence of a predator-prey system with a stage structure for the predator:

$$\begin{cases} \frac{dx(t)}{dt} = rx(t) - ax^2(t) - \frac{a_1 x(t) y_2(t)}{1+mx(t)}, \\ \frac{dy_1(t)}{dt} = \frac{a_2 x(t-\tau) y_2(t-\tau)}{1+mx(t-\tau)} - r_1 y_1(t) - Dy_1(t), \\ \frac{dy_2(t)}{dt} = Dy_1(t) - r_2 y_2(t), \end{cases} \tag{1}$$

where $x(t)$ represents the density of the prey at time t. $y_1(t)$ and $y_2(t)$ represent the densities of the immature predator and the mature predator at time t, respectively. In [7], Li and Li investigated the Hopf bifurcation problem of a predator-prey system with stage structure for the prey:

$$\begin{cases} \frac{dx_1(t)}{dt} = ax_2(t) - r_1 x_1(t) - bx_1(t), \\ \frac{dx_2(t)}{dt} = bx_1(t) - r_2 x_2(t) - b_1 x_2^2(t) - \frac{a_1 x_2^2(t) y(t)}{1+mx_2^2(t)}, \\ \frac{dy(t)}{dt} = \frac{a_2 x_2^2(t-\tau) y(t-\tau)}{1+mx_2^2(t-\tau)} - ry(t), \end{cases} \tag{2}$$

where $x_1(t)$ and $x_2(t)$ represent the densities of the immature prey and the mature prey at time t, respectively. $y(t)$ represents the density of the predator at time t.

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Obviously, all the above researchers consider predator-prey systems with stage structure only for the predator or the prey. Since both predator and prey have a life history that takes them through an immature stage and a mature stage, it is reasonable to consider the predator-prey system with a stage structure for both the predator and the prey. Based on this consideration, Wang and Feng [9] proposed a predator-prey system with a stage structure for both the predator and the prey:

$$
\begin{cases}
\frac{dx_1(t)}{dt} = rx_2(t) - r_1 x_1(t) - d_1 x_1(t), \\
\frac{dx_2(t)}{dt} = r_1 x_1(t) - d_2 x_2(t) - a x_2^2(t) - \frac{a_1 x_2(t) y_2(t)}{1 + m x_2(t)}, \\
\frac{dy_1(t)}{dt} = \frac{a_2 x_2(t) y_2(t)}{1 + m x_2(t)} - r_2 y_1(t) - d_3 y_1(t), \\
\frac{dy_2(t)}{dt} = r_2 y_1(t) - d_4 y_2(t),
\end{cases}
\tag{3}
$$

where $x_1(t)$ and $x_2(t)$ represent the densities of the immature prey and the mature prey at time t, respectively. $y_1(t)$ and $y_2(t)$ represent the densities of the immature predator and the mature predator at time t, respectively. a is the intra-specific competition rate among the mature prey; a_1 is the predation rate of the mature predator; a_2 is the conversion factor from the mature prey to the immature predator; d_1, d_2, d_3, and d_4 are the death rates of the immature prey, mature prey, immature predator, and mature predator, respectively. r_1 (r_2) is the transformation rate from the immature prey (predator) to the mature prey (predator). r is the birth rate of the immature prey and m is the half saturation rate of the mature predator. Wang and Feng [9] studied the local and global stability of system (3).

As is well known, it is necessary to incorporate time delay into dynamical systems in order to reflect the dynamics of the systems depending on the past history of the systems. Dynamical systems with time delay have been investigated by many authors [10–13]. Ferrara *et al.* [10] investigated the properties of the Hopf bifurcation of a delayed continuous-time growth model with a special mound-shaped production function. Bianca *et al.* [12] studied the existence and properties of Hopf bifurcations in a delayed-energy-based model of capital accumulation. There are also some dynamical systems with two or multiple delays that have been studied by some scholars [14–21]. In [14], Bianca *et al.* studied the Hopf bifurcation of an economic growth model with two delays. In [16], Cui and Yan investigated a three-species Lotka-Volterra food chain system with two delays by taking the sum of the two delays as the bifurcation parameter and showed the effects of the two delays on the dynamical behaviors of the system. In [17], Meng *et al.* considered a two-competitor, one-prey system with two feedback delays and they investigated the Hopf bifurcation problem by choosing the possible combination of the two delays as the bifurcation parameter. They also discussed the direction of the Hopf bifurcation and stability of the bifurcating periodic solutions by using a center manifold theorem and the normal form method. To the best of our knowledge, there are few papers on the effect of time delays on system (3). Based on this and motivated by the work above, in the present paper, we incorporate the feedback delay of the mature prey and the time delay due to the gestation of the mature predator into system (3) and investigate the Hopf bifurcation of the following delayed system:

$$
\begin{cases}
\frac{dx_1(t)}{dt} = rx_2(t) - r_1 x_1(t) - d_1 x_1(t), \\
\frac{dx_2(t)}{dt} = r_1 x_1(t) - d_2 x_2(t) - a x_2(t) x_2(t - \tau_1) - \frac{a_1 x_2(t) y_2(t)}{1 + m x_2(t)}, \\
\frac{dy_1(t)}{dt} = \frac{a_2 x_2(t - \tau_2) y_2(t - \tau_2)}{1 + m x_2(t - \tau_2)} - r_2 y_1(t) - d_3 y_1(t), \\
\frac{dy_2(t)}{dt} = r_2 y_1(t) - d_4 y_2(t),
\end{cases}
\tag{4}
$$

where τ_1 is the feedback delay of the mature prey and τ_2 is the time delay due to the gestation of the mature predator.

This paper is organized as follows. In Section 2, we discuss the local stability of the positive equilibrium and the existence of local Hopf bifurcation of system (4). In Section 3, the properties of the Hopf bifurcation such as the direction and stability are determined by using the normal form method and center manifold theorem. Some numerical simulations are performed to illustrate the theoretical results in Section 4. In Section 5, we derive some concluding remarks concerning the whole analysis.

2 Local stability of positive equilibrium and existence of Hopf bifurcation

It is easy to show that if $a_2 r_2 > m d_4 (r_2 + d_3)$ and $\frac{r r_1}{r_1 + d_1} > d_2 + \frac{a d_4 (r_2 + d_3)}{a_2 r_2 - m d_4 (r_2 + d_3)}$, then system (4) has a unique positive equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$, where

$$x_1^* = \frac{r x_2^*}{r_1 + d_1}, \qquad x_2^* = \frac{d_4 (r_2 + d_3)}{a_2 r_2 - m d_4 (r_2 + d_3)},$$

$$y_1^* = \frac{d_4 y_2^*}{r_2}, \qquad y_2^* = \frac{(1 + m x_2^*)(r_1 x_1^* - d_2 x_2^* - a(x_2^*)^2)}{a_1 x_2^*}.$$

Let $\bar{x}_1(t) = x_1(t) - x_1^*$, $\bar{x}_2(t) = x_2(t) - x_2^*$, $\bar{y}_1(t) = y_1(t) - y_1^*$, $\bar{y}_2(t) = y_2(t) - y_2^*$. Dropping the bars for convenience, system (4) gets the following form:

$$
\begin{cases}
\frac{dx_1(t)}{dt} = a_{11} x_1(t) + a_{12} x_2(t), \\
\frac{dx_2(t)}{dt} = a_{21} x_1(t) + a_{22} x_2(t) + a_{24} y_2(t) + b_{22} x_2(t - \tau_1) + f_2, \\
\frac{dy_1(t)}{dt} = a_{33} y_1(t) + c_{32} x_2(t - \tau_2) + c_{34} y_2(t - \tau_2) + f_3, \\
\frac{dy_2(t)}{dt} = a_{43} y_1(t) + a_{44} y_2(t),
\end{cases}
\tag{5}
$$

where

$$a_{11} = -(d_1 + r_1), \qquad a_{12} = r, \qquad a_{21} = r_1, \qquad a_{22} = -d_2 - a x_2^* - \frac{a_1 y_2^*}{(1 + m x_2^*)^2},$$

$$a_{24} = -\frac{a_1 x_2^*}{1 + m x_2^*}, \qquad a_{33} = -(d_3 + r_2), \qquad a_{43} = r_2, \qquad a_{44} = -d_4,$$

$$b_{22} = -a x_2^*, \qquad c_{32} = \frac{a_2 y_2^*}{(1 + m x_2^*)^2}, \qquad c_{34} = \frac{a_2 x_2^*}{1 + m x_2^*},$$

and

$$
\begin{aligned}
f_2 ={}& a_{25} x_2^2(t) + a_{26} x_2(t) y_2(t) + a_{27} x_2(t) x_2(t - \tau_1) \\
& + a_{28} x_2^2(t) y_2(t) + a_{29} x_2^3(t) + \cdots, \\
f_3 ={}& a_{34} x_2^2(t - \tau_2) + a_{35} x_2(t - \tau_2) y_2(t - \tau_2) \\
& + a_{36} x_2^2(t - \tau_2) y_2(t - \tau_2) + a_{37} x_2^3(t - \tau_2) + \cdots,
\end{aligned}
$$

with

$$a_{25} = \frac{m a_1 y_2^*}{(1 + m x_2^*)^3}, \qquad a_{26} = -\frac{a_1}{(1 + m x_2^*)^2}, \qquad a_{27} = -a,$$

$$a_{28} = \frac{ma_1}{(1 + mx_2^*)^3}, \qquad a_{29} = -\frac{m^2 a_1 y_2^*}{(1 + mx_2^*)^4},$$

$$a_{34} = -\frac{ma_2 y_2^*}{(1 + mx_2^*)^3}, \qquad a_{35} = \frac{a_2}{(1 + mx_2^*)^2},$$

$$a_{36} = -\frac{ma_2}{(1 + mx_2^*)^3}, \qquad a_{37} = \frac{m^2 a_2 y_2^*}{(1 + mx_2^*)^4}.$$

The linearized system of (5) is

$$\begin{cases} \frac{dx_1(t)}{dt} = a_{11}x_1(t) + a_{12}x_2(t), \\ \frac{dx_2(t)}{dt} = a_{21}x_1(t) + a_{22}x_2(t) + a_{24}y_2(t) + b_{22}x_2(t - \tau_1), \\ \frac{dy_1(t)}{dt} = a_{33}y_1(t) + c_{32}x_2(t - \tau_2) + c_{34}y_2(t - \tau_2), \\ \frac{dy_2(t)}{dt} = a_{43}y_1(t) + a_{44}y_2(t). \end{cases} \tag{6}$$

The characteristic equation of system (6) at the positive equilibrium E^* is of the form

$$\lambda^4 + A_3\lambda^3 + A_2\lambda^2 + A_1\lambda + A_0 + \left(B_3\lambda^3 + B_2\lambda^2 + B_1\lambda + B_0\right)e^{-\lambda\tau_1}$$

$$+ \left(C_2\lambda^2 + C_1\lambda + C_0\right)e^{-\lambda\tau_2} + (D_1\lambda + D_0)e^{-\lambda(\tau_1 + \tau_2)} = 0, \tag{7}$$

where

$$A_0 = (a_{11}a_{22} - a_{12}a_{21})a_{33}a_{44},$$

$$A_1 = (a_{12}a_{21} - a_{11}a_{22})(a_{33} + a_{44}) - a_{33}a_{44}(a_{11} + a_{22}),$$

$$A_2 = a_{11}a_{22} + a_{33}a_{44} - a_{12}a_{21} + (a_{11} + a_{22})(a_{33} + a_{44}),$$

$$A_3 = -(a_{11} + a_{22} + a_{33} + a_{44}),$$

$$B_0 = a_{11}a_{33}a_{44}b_{22}, \qquad B_1 = -(a_{11}a_{33} + a_{11}a_{44} + a_{33}a_{44})b_{22},$$

$$B_2 = (a_{11} + a_{33} + a_{44})b_{22}, \qquad B_3 = -b_{22},$$

$$C_0 = (a_{12}a_{21} - a_{11}a_{22})a_{43}c_{34} + a_{11}a_{24}a_{43}c_{32},$$

$$C_1 = a_{43}c_{34}(a_{11} + a_{22}) - a_{24}a_{43}c_{32}, \qquad C_2 = -a_{43}c_{34},$$

$$D_0 = -a_{11}a_{43}b_{22}c_{34}, \qquad D_1 = a_{43}b_{22}c_{34}.$$

Case 1. $\tau_1 = \tau_2 = 0$. Equation (7) becomes

$$\lambda^4 + A_{13}\lambda^3 + A_{12}\lambda^2 + A_{11}\lambda + A_{10} = 0, \tag{8}$$

where

$$A_{10} = A_0 + B_0 + C_0 + D_0,$$

$$A_{11} = A_1 + B_1 + C_1 + D_1,$$

$$A_{12} = A_2 + B_2 + C_2, \qquad A_{13} = A_3 + B_3.$$

Obviously, $\det_1 = A_{13} = d_1 + d_2 + d_3 + d_4 + r_1 + r_2 + 2ax_2^* + \frac{a_1 y_2^*}{(1+mx_2^*)^2} > 0$. Thus, all roots of (8) have negative real parts if the condition (H$_1$): (9) is satisfied. We have

$$\det_2 = \begin{vmatrix} A_{13} & 1 \\ A_{11} & A_{12} \end{vmatrix} > 0, \qquad \det_3 = \begin{vmatrix} A_{13} & 1 & 0 \\ A_{11} & A_{12} & A_{13} \\ 0 & A_{10} & A_{11} \end{vmatrix} > 0,$$

$$\det_4 = \begin{vmatrix} A_{13} & 1 & 0 & 0 \\ A_{11} & A_{12} & A_{13} & 1 \\ 0 & A_{10} & A_{11} & A_{12} \\ 0 & 0 & 0 & A_{10} \end{vmatrix} > 0. \tag{9}$$

Thus, the positive equilibrium of system (4) without delay is locally asymptotically stable under the condition (H$_1$): (9) holds.

Case 2. $\tau_1 > 0$, $\tau_2 = 0$.

When $\tau_2 = 0$, (7) becomes

$$\lambda^4 + A_{23}\lambda^3 + A_{22}\lambda^2 + A_{21}\lambda + A_{20} + \left(B_{23}\lambda^3 + B_{22}\lambda^2 + B_{21}\lambda + B_{20}\right)e^{-\lambda\tau_1} = 0, \tag{10}$$

where

$$A_{20} = A_0 + C_0, \qquad A_{21} = A_1 + C_1, \qquad A_{22} = A_2 + C_2, \qquad A_{23} = A_3,$$

$$B_{23} = B_3, \qquad B_{22} = B_2, \qquad B_{21} = B_1 + D_1, \qquad B_{20} = B_0 + D_0.$$

Let $\lambda = i\omega_1$ ($\omega_1 > 0$) be a root of (10). Then

$$\begin{cases} (B_{21}\omega_1 - B_{23}\omega_1^3)\sin\omega_1\tau_1 + (B_{20} - B_{22}\omega_1^2)\cos\omega_1\tau_1 = A_{22}\omega_1^2 - \omega_1^4 - A_{20}, \\ (B_{21}\omega_1 - B_{23}\omega_1^3)\cos\omega_1\tau_1 - (B_{20} - B_{22}\omega_1^2)\sin\omega_1\tau_1 = A_{23}\omega_1^3 - A_{21}\omega_1, \end{cases}$$

from which it follows that

$$\omega_1^8 + e_{23}\omega_1^6 + e_{22}\omega_1^4 + e_{21}\omega_1^2 + e_{20} = 0, \tag{11}$$

where

$$e_{20} = A_{20}^2 - B_{20}^2, \qquad e_{21} = A_{21}^2 - B_{21}^2 - 2A_{20}A_{22} + 2B_{20}B_{22},$$

$$e_{22} = A_{22}^2 - B_{22}^2 + 2A_{20} - 2A_{21}A_{23} + 2B_{21}B_{23}, \qquad e_{23} = A_{23}^2 - B_{23}^2 - 2A_{22}.$$

Let $\omega_1^2 = v_1$, then (11) becomes

$$v_1^4 + e_{23}v_1^3 + e_{22}v_1^2 + e_{21}v_1 + e_{20} = 0. \tag{12}$$

Discussion of the roots of (12) is similar to that in [22]. Denote

$$f_1(v_1) = v_1^4 + e_{23}v_1^3 + e_{22}v_1^2 + e_{21}v_1 + e_{20}. \tag{13}$$

Clearly, if $e_{20} < 0$, then (12) has at least one positive root. From (13), one can get

$$f_1'(v_1) = 4v_1^3 + 3e_{23}v_1^2 + 2e_{22}v_1 + e_{21}.$$

Set

$$4v_1^3 + 3e_{23}v_1^2 + 2e_{22}v_1 + e_{21} = 0. \tag{14}$$

Let $y_1 = v_1 + \frac{3e_{23}}{4}$. Then (14) becomes

$$y_1^3 + p_1 y_1 + q_1 = 0,$$

where

$$p_1 = \frac{e_{22}}{2} - \frac{3}{16}e_{23}^2, \qquad q_1 = \frac{e_{23}^3}{32} - \frac{e_{22}e_{23}}{8} + e_{21}.$$

Define

$$\alpha_1 = \left(\frac{q_1}{2}\right)^2 + \left(\frac{p_1}{3}\right)^3, \qquad \beta_1 = \frac{-1 + \sqrt{3}i}{2},$$

$$y_{11} = \sqrt[3]{-\frac{q_1}{2} + \sqrt{\alpha_1}} + \sqrt[3]{-\frac{q_1}{2} - \sqrt{\alpha_1}},$$

$$y_{12} = \sqrt[3]{-\frac{q_1}{2} + \sqrt{\alpha_1}}\beta_1 + \sqrt[3]{-\frac{q_1}{2} - \sqrt{\alpha_1}}\beta_1^2,$$

$$y_{13} = \sqrt[3]{-\frac{q_1}{2} + \sqrt{\alpha_1}}\beta_1^2 + \sqrt[3]{-\frac{q_1}{2} - \sqrt{\alpha_1}}\beta_1,$$

$$v_{1i} = y_{1i} - \frac{3e_{23}}{4}, \quad i = 1, 2, 3.$$

Then we have the following results according to the Lemma 2.2 in [22].

Lemma 1 *For* (12),

(i) *if $e_{20} \geq 0$ and $\alpha_1 \geq 0$, then* (12) *has positive roots if and only if $v_{11} > 0$ and $f_1(v_{11}) < 0$;*

(ii) *if $e_{20} \geq 0$ and $\alpha_1 < 0$, then* (12) *has positive roots if and only if there exists at least one $v_{1*} \in \{v_{11}, v_{12}, v_{13}\}$, such that $v_{1*} > 0$ and $f_1(v_{1*}) \leq 0$.*

In what follows, we assume that we have (H_{21}): the coefficients in $f_1(v_1)$ satisfy one of the following conditions in (α)-(γ): (α) $e_{20} < 0$; (β) $e_{20} \geq 0$, $\alpha_1 \geq 0$, $v_{11} > 0$, and $f_1(v_{11}) < 0$; (γ) $e_{20} \geq 0$, $\alpha_1 < 0$, and there exists at least one $v_{1*} \in \{v_{11}, v_{12}, v_{13}\}$, such that $v_{1*} > 0$ and $f_1(v_{1*}) \leq 0$.

If the condition (H_{21}) holds, (11) has at least one positive root ω_{10} such that (10) has a pair of purely imaginary roots $\pm i\omega_{10}$ and the corresponding critical value of the delay is

$$\tau_{1k} = \frac{1}{\omega_{10}} \arccos\left\{ \frac{(B_{22} - A_{23}B_{23})\omega_{10}^6 + (A_{21}B_{23} + A_{23}B_{21} - A_{22}B_{22} - B_{20})\omega_{10}^4}{(B_{20} - B_{22}\omega_{10}^2)^2 + (B_{21}\omega_{10} - B_{23}\omega_{10}^3)^2} \right.$$

$$\left. + \frac{(A_{20}B_{22} + A_{22}B_{20} - A_{21}B_{21})\omega_{10}^2 - A_{20}B_{20}}{(B_{20} - B_{22}\omega_{10}^2)^2 + (B_{21}\omega_{10} - B_{23}\omega_{10}^3)^2} \right\} + \frac{2k\pi}{\omega_{10}}, \quad k = 0, 1, 2, \dots.$$

Differentiating the two sides of (10), we can get

$$\left[\frac{d\lambda}{d\tau_1}\right]^{-1} = -\frac{4\lambda^3 + 3A_{23}\lambda^2 + 2A_{22}\lambda + A_{21}}{\lambda(\lambda^4 + A_{23}\lambda^3 + A_{22}\lambda^2 + A_{21}\lambda + A_{20})} + \frac{3B_{23}\lambda^2 + 2B_{22}\lambda + B_{21}}{\lambda(B_{23}\lambda^3 + B_{22}\lambda^2 + B_{21}\lambda + B_{20})} - \frac{\tau_1}{\lambda}.$$

Thus,

$$\mathrm{Re}\left[\frac{d\lambda}{d\tau_1}\right]^{-1}_{\tau_1=\tau_{10}} = \frac{f_1'(v_1^*)}{(B_{20} - B_{22}\omega_{10}^2)^2 + (B_{21}\omega_{10} - B_{23}\omega_{10}^3)^2},$$

where $v_1^* = \omega_{10}^2$. Obviously, if the condition (H$_{22}$): $f_1'(v_1^*) \neq 0$ holds, then $\mathrm{Re}[\frac{d\lambda}{d\tau_1}]^{-1}_{\tau_1=\tau_{10}} \neq 0$. In conclusion, we have the following results according to the Hopf bifurcation theorem in [23].

Theorem 1 *Suppose that the conditions* (H$_{21}$)-(H$_{22}$) *hold. The positive equilibrium* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *of system* (4) *is asymptotically stable for* $\tau_1 \in [0, \tau_{10})$ *and system* (4) *undergoes a Hopf bifurcation at* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *when* $\tau_1 = \tau_{10}$.

Case 3. $\tau_2 > 0$, $\tau_1 = 0$.
Substitute $\tau_1 = 0$ into (7) and we have

$$\lambda^4 + A_{33}\lambda^3 + A_{32}\lambda^2 + A_{31}\lambda + A_{30} + \left(B_{32}\lambda^2 + B_{31}\lambda + B_{30}\right)e^{-\lambda\tau_2} = 0, \tag{15}$$

where

$$A_{30} = A_0 + B_0, \qquad A_{31} = A_1 + B_1, \qquad A_{32} = A_2 + B_2,$$

$$A_{33} = A_3 + B_3, \qquad B_{32} = C_2, \qquad B_{31} = C_1 + D_1, \qquad B_{30} = C_0 + D_0.$$

Let $\lambda = i\omega_2$ $(\omega_2 > 0)$ be the root of (15). Then

$$\begin{cases} B_{31}\omega_2 \sin\omega_2\tau_2 + (B_{30} - B_{32}\omega_2^2)\cos\omega_2\tau_2 = A_{32}\omega_2^2 - \omega_2^4 - A_{30}, \\ B_{31}\omega_2 \cos\omega_2\tau_2 - (B_{30} - B_{32}\omega_2^2)\sin\omega_2\tau_2 = A_{33}\omega_2^3 - A_{31}\omega_2, \end{cases}$$

from which it follows that

$$\omega_2^8 + e_{33}\omega_2^6 + e_{32}\omega_2^4 + e_{31}\omega_2 + e_{30} = 0, \tag{16}$$

where

$$e_{30} = A_{30}^2 - B_{30}^2, \qquad e_{31} = A_{31}^2 - B_{31}^2 - 2A_{30}A_{32} + 2B_{30}B_{32},$$

$$e_{32} = A_{32}^2 - B_{32}^2 + 2A_{30} - 2A_{31}A_{33}, \qquad e_{33} = A_{33}^2 - 2A_{32}.$$

Let $\omega_2^2 = v_2$, then (16) becomes

$$v_2^4 + e_{33}v_2^3 + e_{32}v_2^2 + e_{31}v_2 + e_{30} = 0. \tag{17}$$

Define

$$f_2(v_2) = v_2^4 + e_{33}v_2^3 + e_{32}v_2^2 + e_{31}v_2 + e_{30}.$$

Then

$$f_2'(v_2) = 4v_2^3 + 3e_{33}v_2^2 + 2e_{32}v_2 + e_{31}.$$

Set

$$4v_2^3 + 3e_{33}v_2^2 + 2e_{32}v_2 + e_{31} = 0. \tag{18}$$

Let $y_2 = v_2 + \frac{3e_{33}}{4}$. Then (18) becomes

$$y_2^3 + p_2 y_2 + q_2 = 0,$$

where

$$p_2 = \frac{e_{32}}{2} - \frac{3}{16}e_{33}^2, \qquad q_2 = \frac{e_{33}^3}{32} - \frac{e_{32}e_{33}}{8} + e_{31}.$$

Define

$$\alpha_2 = \left(\frac{q_2}{2}\right)^2 + \left(\frac{p_2}{3}\right)^3, \qquad \beta_2 = \frac{-1 + \sqrt{3}i}{2},$$

$$y_{21} = \sqrt[3]{-\frac{q_2}{2} + \sqrt{\alpha_2}} + \sqrt[3]{-\frac{q_2}{2} - \sqrt{\alpha_2}},$$

$$y_{22} = \sqrt[3]{-\frac{q_2}{2} + \sqrt{\alpha_2}}\beta_2 + \sqrt[3]{-\frac{q_2}{2} - \sqrt{\alpha_2}}\beta_2^2,$$

$$y_{23} = \sqrt[3]{-\frac{q_2}{2} + \sqrt{\alpha_2}}\beta_2^2 + \sqrt[3]{-\frac{q_2}{2} - \sqrt{\alpha_2}}\beta_2,$$

$$v_{2i} = y_{2i} - \frac{3e_{33}}{4}, \quad i = 1, 2, 3.$$

According to Lemma 1, we can conclude that if we may consider the condition (H_{31}): the coefficients in $f_2(v_2)$ satisfy one of the following conditions in (α')-(γ'): (α') $e_{30} < 0$; (β') $e_{30} \geq 0$, $\alpha_2 \geq$, $v_{21} > 0$, and $f_2(v_{21}) < 0$; (γ') $e_{30} \geq 0$, $\alpha_2 < 0$, and there exists at least one $v_{2*} \in \{v_{21}, v_{22}, v_{23}\}$, such that $v_{2*} > 0$ and $f_2(v_{2*}) \leq 0$.

If the condition (H_{31}) holds, (16) has at least one positive root ω_{20} such that (15) has a pair of purely imaginary roots $\pm i\omega_{20}$ and the corresponding critical value of the delay is

$$\tau_{2k} = \frac{1}{\omega_{20}} \arccos\left\{ \frac{B_{32}\omega_{20}^6 + (A_{33}B_{31} - A_{32}B_{32} - B_{30})\omega_{20}^4}{B_{31}^2\omega_{20}^2 + (B_{30} - B_{32}\omega_{20}^2)^2} \right.$$

$$\left. + \frac{(A_{30}B_{32} + A_{32}B_{30} - A_{31}B_{31})\omega_{20}^2 - A_{30}B_{30}}{B_{31}^2\omega_{20}^2 + (B_{30} - B_{32}\omega_{20}^2)^2} \right\} + \frac{2k\pi}{\omega_{20}}, \quad k = 0, 1, 2, \ldots.$$

Similar as in Case 2, if the condition (H_{32}): $f_2'(v_2^*) \neq 0$ holds, where $v_2^* = \omega_{20}^2$, then $\text{Re}[\frac{d\lambda}{d\tau_2}]^{-1}_{\tau_2 = \tau_{20}} \neq 0$. In conclusion, we have the following results according to the Hopf bifurcation theorem in [23].

Theorem 2 *Suppose that the conditions* (H_{31})-(H_{32}) *hold. The positive equilibrium* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *of system* (4) *is asymptotically stable for* $\tau_2 \in [0, \tau_{20})$ *and system* (4) *undergoes a Hopf bifurcation at* $E^*E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *when* $\tau_2 = \tau_{20}$.

Case 4. $\tau_1 = \tau_2 = \tau > 0$.

Substitute $\tau_1 = \tau_2 = \tau$ into (7); then (7) becomes

$$\lambda^4 + A_{43}\lambda^3 + A_{42}\lambda^2 + A_{41}\lambda + A_{40} + \left(B_{43}\lambda^3 + B_{42}\lambda^2 + B_{41}\lambda + B_{40}\right)e^{-\lambda\tau}$$
$$+ (C_{41}\lambda + C_{40})e^{-2\lambda\tau} = 0, \tag{19}$$

where

$$A_{40} = A_0, \qquad A_{41} = A_1, \qquad A_{42} = A_2, \qquad A_{43} = A_3,$$
$$B_{40} = B_0 + C_0, \qquad B_{41} = B_1 + C_1, \qquad B_{42} = B_2 + C_2,$$
$$B_{43} = B_3, \qquad C_{40} = D_0, \qquad C_{41} = D_1.$$

Multiplying (19) by $e^{\lambda\tau}$, then (19) becomes

$$B_{43}\lambda^3 + B_{42}\lambda^2 + B_{41}\lambda + B_{40} + \left(\lambda^4 + A_{43}\lambda^3 + A_{42}\lambda^2 + A_{41}\lambda + A_{40}\right)e^{\lambda\tau}$$
$$+ (C_{41}\lambda + C_{40})e^{-\lambda\tau} = 0. \tag{20}$$

Let $\lambda = i\omega$ ($\omega > 0$) be the root of (20), then

$$\begin{cases} (\omega^4 - A_{42}\omega^2 + A_{40} + C_{40})\cos\tau\omega + (A_{43}\omega^3 - A_{41}\omega + C_{41}\omega)\sin\tau\omega = B_{42}\omega^2 - B_{40}, \\ (\omega^4 - A_{42}\omega^2 + A_{40} - C_{40})\sin\tau\omega - (A_{43}\omega^3 - A_{41}\omega - C_{41}\omega)\cos\tau\omega = B_{43}\omega^3 - B_{41}\omega, \end{cases}$$

from which it follows that

$$\sin(\tau\omega) = \frac{g_7\omega^7 + g_5\omega^5 + g_3\omega^3 + g_1\omega}{\omega^8 + h_6\omega^6 + h_4\omega^4 + h_2\omega^2 + h_0},$$

$$\cos(\tau\omega) = \frac{g_6\omega^6 + g_4\omega^4 + g_2\omega^2 + g_0}{\omega^8 + h_6\omega^6 + h_4\omega^4 + h_2\omega^2 + h_0},$$

where

$$g_0 = (C_{40} - A_{40})B_{40}, \qquad g_1 = (A_{41} + C_{41})B_{40} - (A_{40} + C_{40}),$$
$$g_2 = A_{40}B_{42} + A_{42}B_{40} + B_{41}C_{41} - A_{41}B_{41} - B_{42}C_{40},$$
$$g_3 = A_{40}B_{43} + A_{42}B_{41} + B_{43}C_{40} - A_{41}B_{42} - A_{43}B_{40} - B_{42}C_{41},$$
$$g_4 = A_{41}B_{43} + A_{43}B_{41} - A_{42}B_{42} - B_{43}C_{41} - B_{40},$$
$$g_5 = A_{43}B_{42} - A_{42}B_{43} - B_{41}, \qquad g_6 = B_{42} - A_{43}B_{43}, \qquad g_7 = B_{43},$$
$$h_0 = A_{40}^2 - C_{40}^2, \qquad h_2 = A_{41}^2 - C_{41}^2 - 2A_{40}A_{42},$$
$$h_4 = A_{42}^2 + 2A_{40} - 2A_{41}A_{43}, \qquad h_6 = A_{43}^2 - 2A_{42}.$$

Then we can obtain

$$\omega^{16} + e_{47}\omega^{14} + e_{46}\omega^{12} + e_{45}\omega^{10} + e_{44}\omega^8 + e_{43}\omega^6 + e_{42}\omega^4 + e_{41}\omega^2 + e_{40} = 0, \tag{21}$$

where

$$e_{40} = h_0^2 - g_0^2, \qquad e_{41} = 2h_0h_2 - 2g_0g_2 - g_1^2,$$

$$e_{42} = h_2^2 - g_2^2 + 2h_0h_4 - 2g_1g_3 - 2g_0g_4,$$

$$e_{43} = 2h_0h_6 + 2h_2h_4 - g_3^2 - 2g_0g_6 - 2g_1g_5 - 2g_2g_4,$$

$$e_{44} = h_4^2 + 2h_0 + 2h_2h_6 - g_4^2 - 2g_1g_7 - 2g_2g_6 - 2g_3g_5,$$

$$e_{45} = 2h_2 + 2h_4h_6 - g_5^2 - 2g_3g_5 - 2g_4g_6,$$

$$e_{46} = h_6^2 - g_6^2 + 2h_4 - 2g_5g_7, \qquad e_{47} = 2h_6 - g_7^2.$$

Let $\omega^2 = v$, then (21) becomes

$$v^8 + e_{47}v^7 + e_{46}v^6 + e_{45}v^5 + e_{44}v^4 + e_{43}v^3 + e_{42}v^2 + e_{41}v + e_{40} = 0. \tag{22}$$

If the coefficients of system (4) are given, the roots of (22) can be obtained by the Matlab software package. Therefore, we make the following assumption in order to get the main results in this paper.

Suppose that (H_{41}): (22) has at least one positive root.

If the condition (H_{41}) holds, without loss of generality, we assume that (22) has eight positive roots which are denoted by $v_1, v_2, \ldots, v_8$, respectively. Then (21) has eight positive roots $\omega_k = \sqrt{v_k}$, $k = 1, 2, \ldots, 8$. For every ω_k, the corresponding critical value of the time delay is

$$\tau_k^{(j)} = \frac{1}{\omega_k} \arccos \frac{g_6\omega_k^6 + g_4\omega_k^4 + g_2\omega_k^2 + g_0}{\omega_k^8 + h_6\omega_k^6 + h_4\omega_k^4 + h_2\omega_k^2 + h_0} + \frac{2j\pi}{\omega_k}, \quad k = 1, 2, 3, \ldots, 8; j = 0, 1, 2, \ldots.$$

Let

$$\tau_0 = \min\{\tau_k^{(0)}\}, \quad k = 1, 2, \ldots, 8, \omega_0 = \omega_k|_{\tau = \tau_0}.$$

Thus, when $\tau = \tau_0$, (20) has a pair of purely imaginary roots $\pm i\omega_0$.

Differentiating both sides of (20) with respect to τ, we get

$$\left[\frac{d\lambda}{d\tau}\right]^{-1} = -\frac{(4\lambda^3 + 3A_{43}\lambda^2 + 2A_{42}\lambda + A_{41})e^{\lambda\tau} + C_{41}e^{-\lambda\tau} + 3B_{43}\lambda^2 + 2B_{42}\lambda + B_{41}}{\lambda[(\lambda^4 + A_{43}\lambda^3 + A_{42}\lambda^2 + A_{41}\lambda + A_{40})e^{\lambda\tau} - (C_{41}\lambda + C_{40})e^{-\lambda\tau}]} - \frac{\tau}{\lambda}.$$

Then we have

$$\operatorname{Re}\left[\frac{d\lambda}{d\tau}\right]^{-1}_{\tau = \tau_0} = \frac{P_{41}Q_{41} + P_{42}Q_{42}}{Q_{41}^2 + Q_{42}^2},$$

where

$$P_{41} = \left(A_{41} + C_{41} - 3A_{43}\omega_0^2\right)\cos\tau_0\omega_0 - \left(2A_{42}\omega_0 - 4\omega_0^3\right)\sin\tau_0\omega_0 - 3B_{43}\omega_0^2 + B_{41},$$

$$P_{42} = \left(A_{41} - C_{41} - 3A_{43}\omega_0^2\right)\sin\tau_0\omega_0 + \left(2A_{42}\omega_0 - 4\omega_0^3\right)\cos\tau_0\omega_0 + 2B_{42}\omega_0,$$

$$Q_{41} = \left(A_{43}\omega_0^4 - A_{41}\omega_0^2 - C_{41}\omega_0^2\right)\cos\tau_0\omega_0 - \left(\omega_0^5 - A_{42}\omega_0^3 + A_{40}\omega_0 + C_{40}\omega_0\right)\sin\tau_0\omega_0,$$

$$Q_{42} = \left(A_{43}\omega_0^4 - A_{41}\omega_0^2 + C_{41}\omega_0^2\right)\sin\tau_0\omega_0 + \left(\omega_0^5 - A_{42}\omega_0^3 + A_{40}\omega_0 - C_{40}\omega_0\right)\cos\tau_0\omega_0.$$

Obviously, if the condition (H_{42}): $P_{41}Q_{41} + P_{42}Q_{42} \neq 0$ holds, then $\mathrm{Re}[\frac{d\lambda}{d\tau}]^{-1}_{\tau=\tau_0} \neq 0$. Thus, according to the Hopf bifurcation theorem in [23], we have the following results.

Theorem 3 *Suppose that the conditions* (H_{41})-(H_{42}) *hold. The positive equilibrium* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *of system (4) is asymptotically stable for* $\tau_1 \in [0, \tau_0)$ *and system (4) undergoes a Hopf bifurcation at* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *when* $\tau = \tau_0$.

Case 5. $\tau_2 > 0$ and $\tau_1 \in (0, \tau_{10})$. We consider (7) with τ_1 in its stable interval and τ_2 is considered as a parameter.

Let $\lambda = i\omega_2'$ ($\omega_2' > 0$) be the root of (7). Then we get

$$\begin{cases} \Delta_{51}\sin\tau_2\omega_2' + \Delta_{52}\cos\tau_2\omega_2' = \Delta_{53}, \\ \Delta_{51}\cos\tau_2\omega_2' - \Delta_{52}\sin\tau_2\omega_2' = \Delta_{54}, \end{cases}$$

where

$$\Delta_{51} = C_1\omega_2' - D_0\sin\tau_1\omega_2' + D_1\omega_2'\cos\tau_1\omega_2',$$

$$\Delta_{52} = C_0 - C_2\left(\omega_2'\right)^2 + D_0\cos\tau_1\omega_2' + D_1\omega_2'\sin\tau_1\omega_2',$$

$$\Delta_{53} = \left(B_2\left(\omega_2'\right)^2 - B_0\right)\cos\tau_1\omega_2' + \left(\left(\omega_2'\right)^3 - B_1\omega_2'\right)\sin\tau_1\omega_2' - \left(\omega_2'\right)^4 + A_2\left(\omega_2'\right)^2 - A_0,$$

$$\Delta_{54} = \left(B_0 - B_2\left(\omega_2'\right)^2\right)\sin\tau_1\omega_2' + \left(\left(\omega_2'\right)^3 - B_1\omega_2'\right)\cos\tau_1\omega_2' + A_3\left(\omega_2'\right)^3 - A_1\omega_2'.$$

It follows that

$$e_{50}\left(\omega_2'\right) + e_{51}\left(\omega_2'\right)\cos\tau_1\omega_2' + e_{52}\left(\omega_2'\right)\sin\tau_1\omega_2' = 0, \tag{23}$$

where

$$\begin{aligned}
e_{50}\left(\omega_2'\right) = {}& \left(\omega_2'\right)^8 + \left(A_3^2 + B_3^2 - 2A_2\right)\left(\omega_2'\right)^6 \\
& + \left(A_2^2 + B_2^2 - C_2^2 + 2A_0 - 2A_1A_3 - 2B_1B_3\right)\left(\omega_2'\right)^4 \\
& + \left(A_1^2 + B_1^2 - C_1^2 - D_1^2 - 2A_0A_2 - 2B_0B_2 + 2C_0C_2\right)\left(\omega_2'\right)^2 \\
& + A_0^2 + B_0^2 - C_0^2 - D_0^2, \\
e_{51}\left(\omega_2'\right) = {}& 2(A_3B_3 - B_2)\left(\omega_2'\right)^6 + 2(A_2B_2 + B_0 - A_3B_1 - A_1B_3)\left(\omega_2'\right)^4 \\
& + 2(A_1B_1 - A_0B_2 - A_2B_0 - C_1D_1 + C_2D_0)\left(\omega_2'\right)^2 + 2(A_0B_0 - C_0D_0), \\
e_{52}\left(\omega_2'\right) = {}& -2B_3\left(\omega_2'\right)^7 + 2(A_2B_3 - A_3B_2 + B_1)\left(\omega_2'\right)^5 \\
& + 2(A_3B_0 + A_1B_2 - A_0B_3 - A_2B_1 + C_2D_1)\left(\omega_2'\right)^3 \\
& + 2(A_0B_1 - A_1B_0 + C_1q_D - C_0D_1)\omega_2^*.
\end{aligned}$$

Suppose that we have (H_{51}): (23) has at least finite positive roots. We denote the positive roots of (23) as $\omega'_{21}, \omega'_{22}, \ldots, \omega'_{2k}$. Then, for every fixed ω'_{2i} ($i = 1, 2, \ldots, k$), the corresponding critical value of time delay is

$$\tau_{2i}^{(j)'} = \frac{1}{\omega'_{2i}} \arccos\left\{ \frac{\Delta_{51}\Delta_{54} + \Delta_{52}\Delta_{53}}{\Delta_{51}^2 + \Delta_{52}^2} \bigg|_{\omega'_2 = \omega'_{2i}} \right\} + \frac{2j\pi}{\omega'_{2i}},$$

with $i = 1, 2, \ldots, k$; $j = 0, 1, 2, \ldots$.

Let $\tau_{20}^* = \min\{\tau_{2i}^{(0)'} | i = 1, 2, \ldots, k\}$. When $\tau_2 = \tau_{20}^*$, (7) has a pair of purely imaginary roots $\pm i\omega_2^*$ for $\tau_1 \in (0, \tau_{10})$. Differentiating (7) with respect to τ_2, one can obtain

$$\left[\frac{d\lambda}{d\tau_2}\right]^{-1} = \frac{p_0(\lambda) + p_1(\lambda)e^{-\lambda\tau_1} + p_2(\lambda)e^{-\lambda\tau_2} + p_3(\lambda)e^{-\lambda(\tau_1+\tau_2)}}{q_1(\lambda)e^{-\lambda\tau_2} + q_2(\lambda)e^{-(\lambda_1+\lambda_2)}} - \frac{\tau_2}{\lambda},$$

with

$$p_0(\lambda) = 4\lambda^3 + 3A_3\lambda^2 + 2A_2\lambda + A_1,$$

$$p_1(\lambda) = -\tau_1 B_3\lambda^3 + (3B_3 - \tau_1 B_2)\lambda^2 + (2B_2 - \tau_1 B_1)\lambda + B_1 - \tau_1 B_0,$$

$$p_2(\lambda) = 2C_2\lambda + C_1, \qquad p_3(\lambda) = D_1,$$

$$q_1(\lambda) = C_2\lambda^3 + C_1\lambda^2 + C_0\lambda, \qquad q_2(\lambda) = D_1\lambda^2 + D_0\lambda.$$

Hence,

$$\mathrm{Re}\left[\frac{d\lambda}{d\tau_2}\right]^{-1}_{\tau=\tau_{20}^*} = -\frac{P_{51}Q_{51} - P_{52}Q_{52}}{Q_{51}^2 + Q_{52}^2},$$

where

$$\begin{aligned}
P_{51} = {} & \left(2C_2\omega_2^* - D_1\sin\tau_1\omega_2^*\right)\sin\tau_{20}^*\omega_2^* + \left(C_1 + D_1\cos\tau_1\omega_2^*\right)\cos\tau_{20}^*\omega_2^* \\
& + \left(\tau_1 B_3\left(\omega_2^*\right)^3 + (2B_2 - \tau_1 B_1)\omega_2^*\right)\sin\tau_1\omega_2^* \\
& + \left((\tau_1 B_2 - 3B_3)\left(\omega_2^*\right)^2 + B_1 - \tau_1 B_0\right)\cos\tau_1\omega_2^* - 3A_3\left(\omega_2^*\right)^2 + A_1, \\
P_{52} = {} & \left(2C_2\omega_2^* - D_1\sin\tau_1\omega_2^*\right)\cos\tau_{20}^*\omega_2^* - \left(C_1 + D_1\cos\tau_1\omega_2^*\right)\sin\tau_{20}^*\omega_2^* \\
& + \left(\tau_1 B_3\left(\omega_2^*\right)^3 + (2B_2 - \tau_1 B_1)\omega_2^*\right)\cos\tau_1\omega_2^* \\
& - \left((\tau_1 B_2 - 3B_3)\left(\omega_2^*\right)^2 + B_1 - \tau_1 B_0\right)\sin\tau_1\omega_2^* - 4\left(\omega_2^*\right)^3 + 2A_2\omega_2^*, \\
Q_{51} = {} & \left(C_2\left(\omega_2^*\right)^3 - C_0\omega_2^* - D_1\left(\omega_2^*\right)^2\sin\tau_1\omega_2^* - D_0\omega_2^*\cos\tau_1\omega_2^*\right)\sin\tau_{20}^*\omega_2^* \\
& + \left(C_1\left(\omega_2^*\right)^2 + D_1\left(\omega_2^*\right)^2\cos\tau_1\omega_2^* - D_0\omega_2^*\sin\tau_1\omega_2^*\right)\cos\tau_{20}^*\omega_2^*, \\
Q_{52} = {} & \left(C_2\left(\omega_2^*\right)^3 - C_0\omega_2^* - D_1\left(\omega_2^*\right)^2\sin\tau_1\omega_2^* - D_0\omega_2^*\cos\tau_1\omega_2^*\right)\cos\tau_{20}^*\omega_2^* \\
& - \left(C_1\left(\omega_2^*\right)^2 + D_1\left(\omega_2^*\right)^2\cos\tau_1\omega_2^* - D_0\omega_2^*\sin\tau_1\omega_2^*\right)\sin\tau_{20}^*\omega_2^*.
\end{aligned}$$

Obviously, if the condition (H_{52}): $P_{51}Q_{51} \neq P_{52}Q_{52}$ holds, then $\mathrm{Re}[\frac{d\lambda}{d\tau_2}]^{-1}_{\tau=\tau_{20}^*} \neq 0$. Namely, if the condition (H_{52}) holds, the transversality condition is satisfied. Thus, according to the Hopf bifurcation theorem in [23], we have the following results.

Theorem 4 *If the conditions* (H_{51})-(H_{52}) *hold and* $\tau_1 \in (0, \tau_{10})$, *then the positive equilibrium* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *of system* (4) *is asymptotically stable for* $\tau_2 \in [0, \tau_{20}^*)$ *and system* (4) *undergoes a Hopf bifurcation at* $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ *when* $\tau_2 = \tau_{20}^*$.

3 Stability of bifurcating periodic solutions

In this section, we shall derive the explicit formulas determining the direction and stability of the bifurcating periodic solutions with respect to τ_2 for $\tau_1 \in (0, \tau_{10})$. Throughout this section, we assume that $\tau_{1*} < \tau_{20}^*$ where $\tau_{1*} \in (0, \tau_{10})$.

Let $\tau_2 = \mu + \tau_{20}^*$, $u_1(t) = x_1(t) - x_1^*$, $u_2(t) = x_2(t) - x_2^*$, $u_3(t) = y_1(t) - y_1^*$, $u_4(t) = y_2(t) - y_2^*$, and rescale the time delay $t \to (t/\tau_2)$, then system (4) can be rewritten as

$$\dot{u}(t) = L_\mu u_t + F(\mu, u_t), \tag{24}$$

where

$$L_\mu \phi = \left(\tau_{20}^* + \mu\right)\left(A'\phi(0) + B'\phi\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right) + C'\phi(-1)\right)$$

and

$$F(\mu, \phi) = \left(\tau_{20}^* + \mu\right)(0, F_2, F_3, 0)^T,$$

with

$$\phi(\theta) = \left(\phi_1(\theta), \phi_2(\theta), \phi_3(\theta), \phi_4(\theta)\right)^T \in C\left([-1, 0], R^4\right),$$

$$A' = \begin{pmatrix} a_{11} & a_{12} & 0 & 0 \\ a_{21} & a_{22} & 0 & a_{24} \\ 0 & 0 & a_{33} & 0 \\ 0 & 0 & a_{43} & a_{44} \end{pmatrix}, \qquad B' = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & b_{22} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

$$C' = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & c_{32} & 0 & c_{34} \\ 0 & 0 & 0 & 0 \end{pmatrix},$$

$$F_2 = a_{25}\phi_2^2(0) + a_{26}\phi_2(0)\phi_4(0) + a_{27}\phi_2(0)\phi_2\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right)$$

$$+ a_{28}\phi_2^2(0)\phi_4(0) + a_{29}\phi_2^3(0) + \cdots,$$

$$F_3 = a_{34}\phi_2^2(-1) + a_{35}\phi_2(-1)\phi_4(-1) + a_{36}\phi_2^2(-1)\phi_4(-1) + a_{37}\phi_2^3(-1) + \cdots.$$

Therefore, according to the Riesz representation theorem, there exists a 4×4 matrix function $\eta(\theta, \mu) : [-1, 0] \to R^4$ whose elements are of bounded variation such that

$$L_\mu \phi = \int_{-1}^0 d\eta(\theta, \mu)\phi(\theta), \quad \phi \in C\left([-1, 0], R^4\right).$$

In fact, we choose

$$\eta(\theta, \mu) = \begin{cases} (\tau_{20}^* + \mu)(A' + B' + C'), & \theta = 0, \\ (\tau_{20}^* + \mu)(B' + C'), & \theta \in [-\frac{\tau_{1*}}{\tau_{20}^*}, 0), \\ (\tau_{20}^* + \mu)C', & \theta \in (-1, -\frac{\tau_{1*}}{\tau_{20}^*}), \\ 0, & \theta = -1. \end{cases}$$

For $\phi \in C([-1, 0], R^4)$, we define

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

and

$$R(\mu)\phi = \begin{cases} 0, & -1 \le \theta < 0, \\ F(\mu, \phi), & \theta = 0. \end{cases}$$

Then system (24) can be transformed into the following operator equation:

$$\dot{u}(t) = A(\mu)u_t + R(\mu)u_t, \tag{25}$$

where $u_t = u(t + \theta) = (u_1(t + \theta), u_2(t + \theta), u_3(t + \theta), u_4(t + \theta))$ for $\theta \in [-1, 0]$.

For $\varphi \in C^1([0, 1], (R^4)^*)$, where $(R^4)^*$ is the 4-dimensional space of row vectors, we define the adjoint operator A^* of A:

$$A^*(\varphi) = \begin{cases} -\frac{d\varphi(s)}{ds}, & 0 < s \le 1, \\ \int_{-1}^{0} d\eta^T(s, 0)\varphi(-s), & s = 0, \end{cases}$$

and a bilinear inner product:

$$\langle \varphi(s), \phi(\theta) \rangle = \bar{\varphi}(0)\phi(0) - \int_{\theta=-1}^{0} \int_{\xi=0}^{\theta} \bar{\varphi}(\xi - \theta) \, d\eta(\theta)\phi(\xi) \, d\xi, \tag{26}$$

where $\eta(\theta) = \eta(\theta, 0)$.

Let $q(\theta) = (1, q_2, q_3, q_4)^T e^{i\omega_2^* \tau_{20}^* \theta}$ be the eigenvectors of $A(0)$ corresponding to the eigenvalue $+i\omega_2^* \tau_{20}^*$ and $q^*(s) = D(1, q_2^*, q_3^*, q_4^*)e^{i\omega_2^* \tau_{20}^* s}$ be the eigenvectors of $A^*(0)$ corresponding to the eigenvalue $-i\omega_2^* \tau_{20}^*$. It is not difficult to verify that

$$q_2 = \frac{i\omega_2^* - a_{11}}{a_{12}}, \qquad q_3 = \frac{c_{32}q_2 + c_{34}q_4}{(i\omega_2^* - a_{33})e^{i\omega_2^* \tau_{20}^*}},$$

$$q_4 = \frac{(i\omega_2^* - a_{11})(i\omega_2^* - a_{22} - b_{22}e^{-i\omega_2^* \tau_{1*}}) - a_{12}a_{21}}{a_{12}a_{24}},$$

$$q_2^* = -\frac{i\omega_2^* + a_{11}}{a_{21}}, \qquad q_4^* = \frac{a_{24}q_2^* + c_{34}e^{i\omega_2^* \tau_{20}^*}}{i\omega_2^* + a_{44}},$$

$$q_3^* = \frac{(i\omega_2^* + a_{11})(a_{22} + b_{22}e^{i\omega_2^* \tau_{1*}}) - a_{12}a_{21}}{a_{21}(i\omega_2^* + c_{32}e^{i\omega_2^* \tau_{20}^*})}.$$
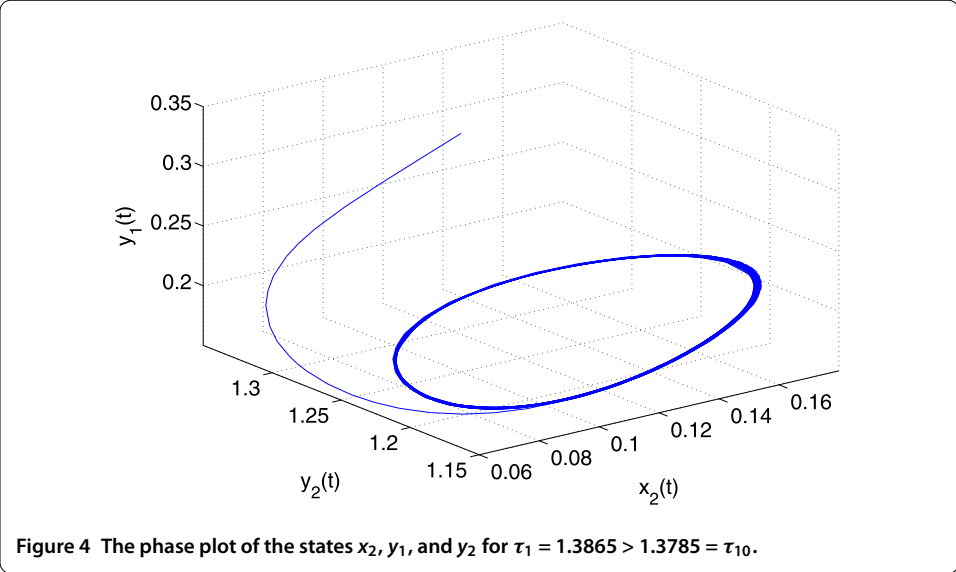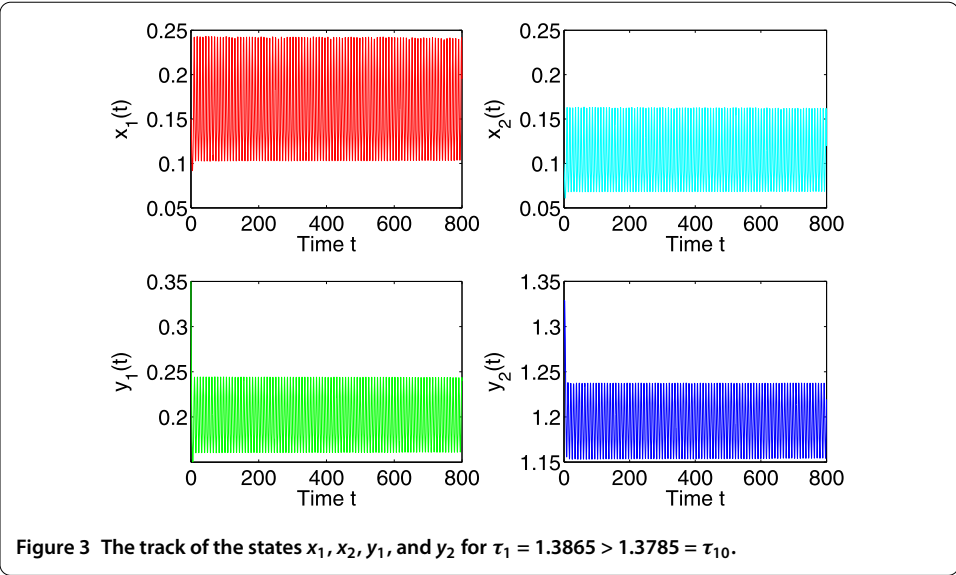
Figure 1 The track of the states x_1, x_2, y_1, and y_2 for $\tau_1 = 1.3500 < 1.3785 = \tau_{10}$.

Figure 2 The phase plot of the states x_2, y_1, and y_2 for $\tau_1 = 1.3500 < 1.3785 = \tau_{10}$.
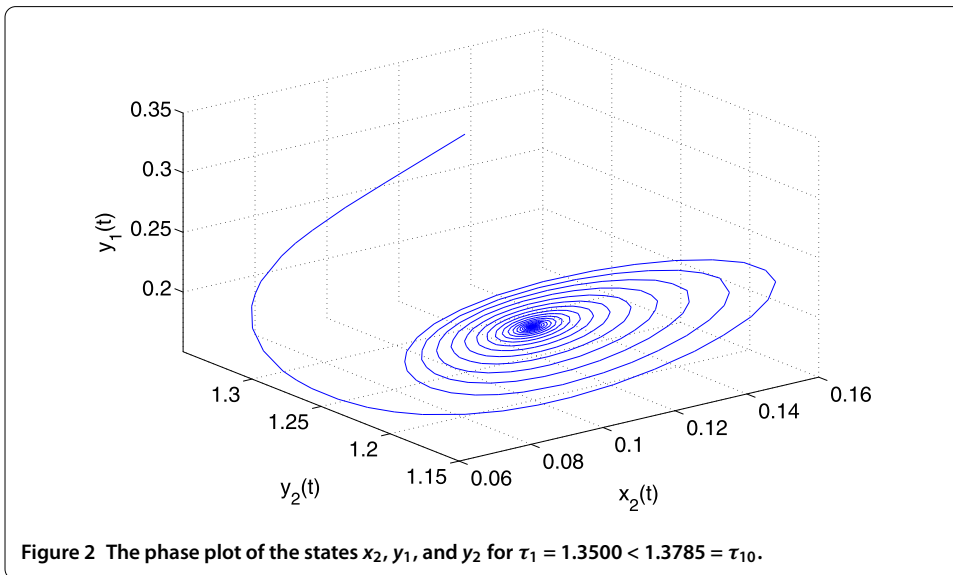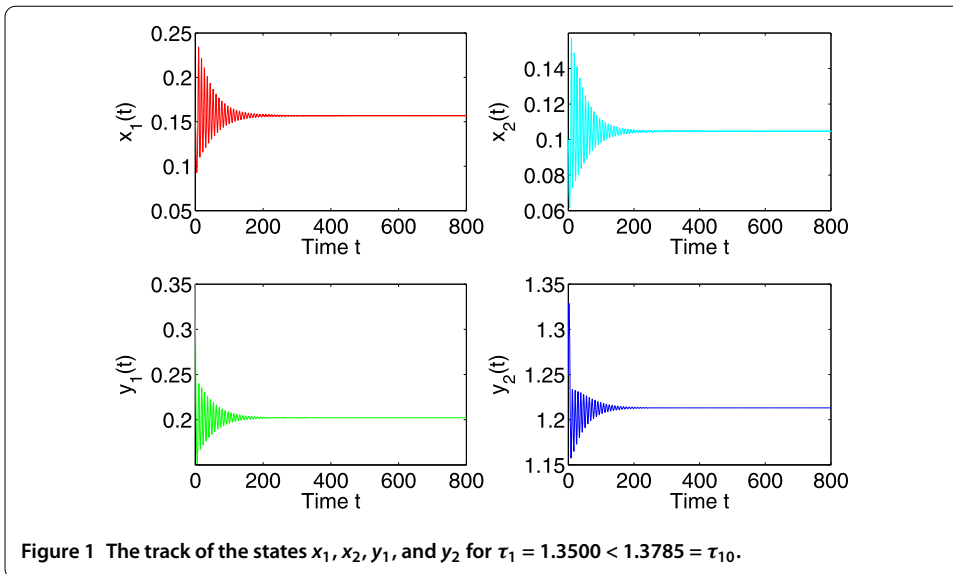
From (26), we choose

$$\bar{D} = \left[1 + q_2\bar{q}_2^* + q_3\bar{q}_3^* + q_4\bar{q}_4^* + q_2\left(\tau_{1*}b_{22}\bar{q}_2^*e^{-i\omega_2^*\tau_{1*}} + \tau_{20}^*c_{32}\bar{q}_3^*e^{-i\omega_2^*\tau_{20}}\right) \right.$$
$$\left. + \tau_{20}^*c_{34}q_4\bar{q}_4^*e^{-i\omega_2^*\tau_{20}^*} \right]^{-1},$$

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

In the remainder of this section, we obtain the coefficients that can determine direction of the Hopf bifurcation and stability of the bifurcating periodic solutions by using the algorithms given in [23] and using the computation process which is similar to that in [14]:

$$g_{20} = 2\tau_{20}^*\bar{D}\left[\bar{q}_2^*\left(a_{25}\left(q^{(2)}(0)\right)^2 + a_{26}q^{(2)}(0)q^{(4)}(0) + a_{27}q^{(2)}(0)q^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right) \right) \right.$$
$$\left. + \bar{q}_3^*\left(a_{34}\left(q^{(2)}(-1)\right)^2 + a_{35}q^{(2)}(-1)q^{(4)}(-1) \right) \right],$$

Figure 3 The track of the states x_1, x_2, y_1, and y_2 for $\tau_1 = 1.3865 > 1.3785 = \tau_{10}$.

Figure 4 The phase plot of the states x_2, y_1, and y_2 for $\tau_1 = 1.3865 > 1.3785 = \tau_{10}$.

$$g_{11} = \tau_{20}^* \bar{D} \Bigg[\bar{q}_2^* \bigg(2a_{25} q^{(2)}(0) \bar{q}^{(2)}(0) + a_{26} \big(q^{(2)}(0) \bar{q}^{(4)}(0) + \bar{q}^{(2)}(0) q^{(4)}(0) \big)$$

$$+ a_{27} \bigg(q^{(2)}(0) \bar{q}^{(2)} \Big(-\frac{\tau_{1*}}{\tau_{20}^*} \Big) + \bar{q}^{(2)}(0) q^{(2)} \Big(-\frac{\tau_{1*}}{\tau_{20}^*} \Big) \bigg) \bigg) + \bar{q}_3^* \big(2a_{34} q^{(2)}(-1) \bar{q}^{(2)}(-1)$$

$$+ a_{35} \big(q^{(2)}(-1) \bar{q}^{(4)}(-1) + \bar{q}^{(2)}(-1) q^{(4)}(-1) \big) \big) \Bigg],$$

$$g_{02} = 2\tau_{20}^* \bar{D} \Bigg[\bar{q}_2^* \bigg(a_{25} \big(\bar{q}^{(2)}(0) \big)^2 + a_{26} \bar{q}^{(2)}(0) \bar{q}^{(4)}(0) + a_{27} \bar{q}^{(2)}(0) \bar{q}^{(2)} \Big(-\frac{\tau_{1*}}{\tau_{20}^*} \Big) \bigg)$$

$$+ \bar{q}_3^* \big(a_{34} \big(\bar{q}^{(2)}(-1) \big)^2 + a_{35} \bar{q}^{(2)}(-1) \bar{q}^{(4)}(-1) \big) \Bigg],$$

$$g_{21} = 2\tau_{20}^* \bar{D} \Bigg[\bar{q}_2^* \big(a_{25} \big(2W_{11}^{(2)}(0) + W_{20}^{(2)}(0) \bar{q}^{(2)}(0) \big)$$
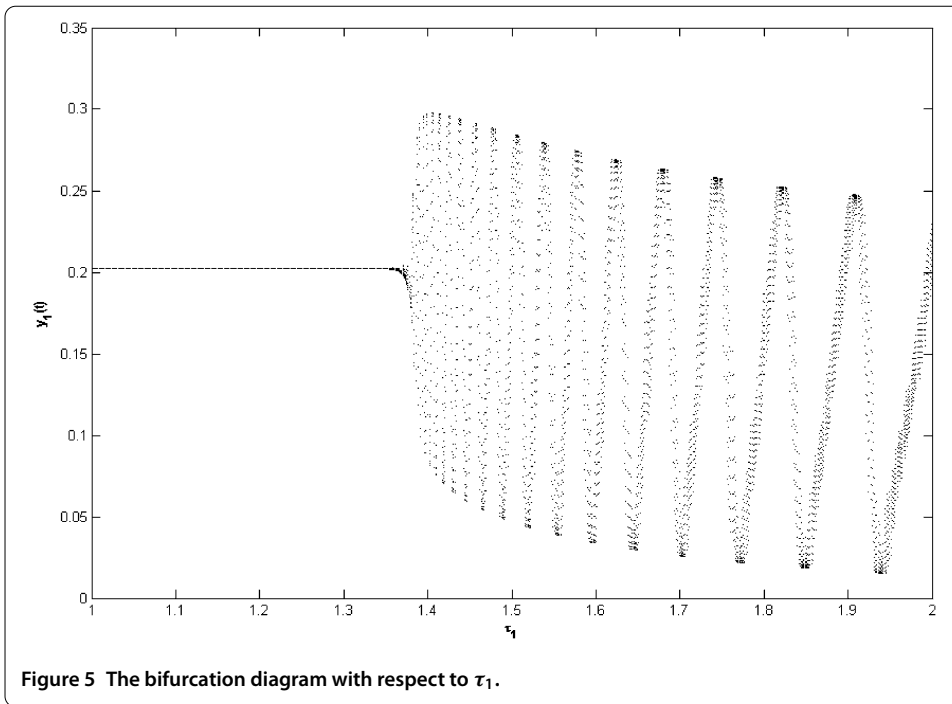
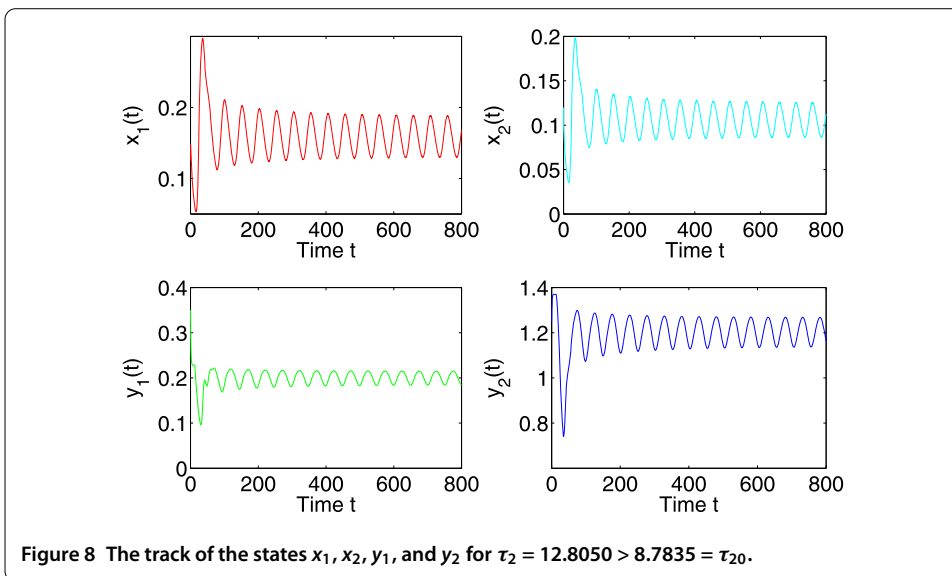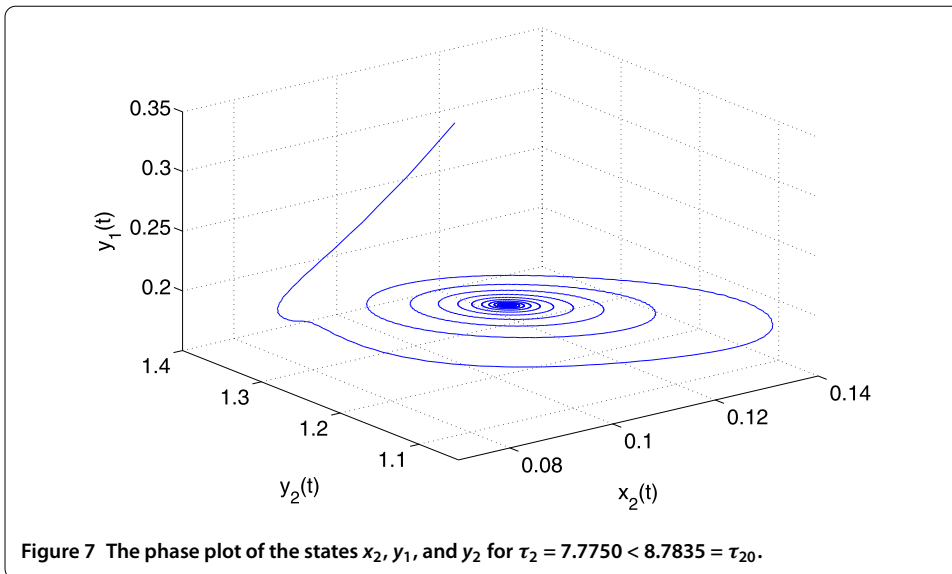**Figure 5 The bifurcation diagram with respect to τ_1.**
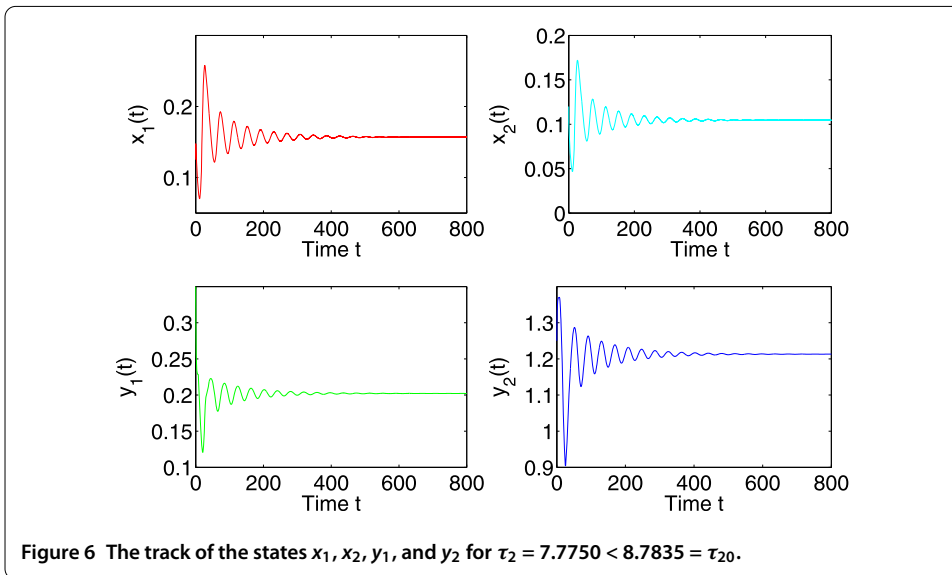
Figure 6 The track of the states x_1, x_2, y_1, and y_2 for $\tau_2 = 7.7750 < 8.7835 = \tau_{20}$.
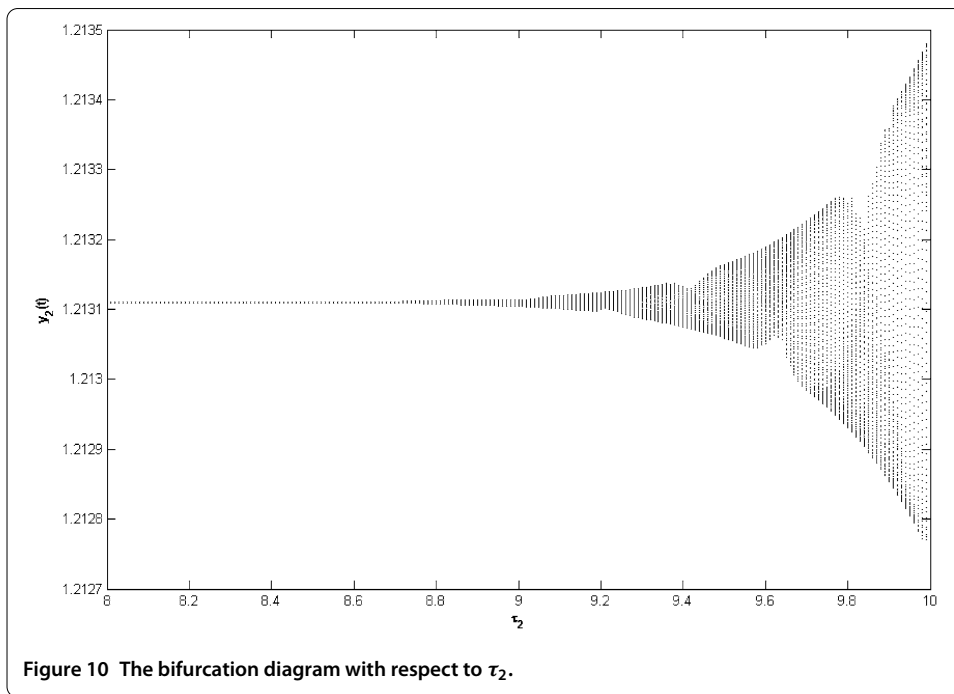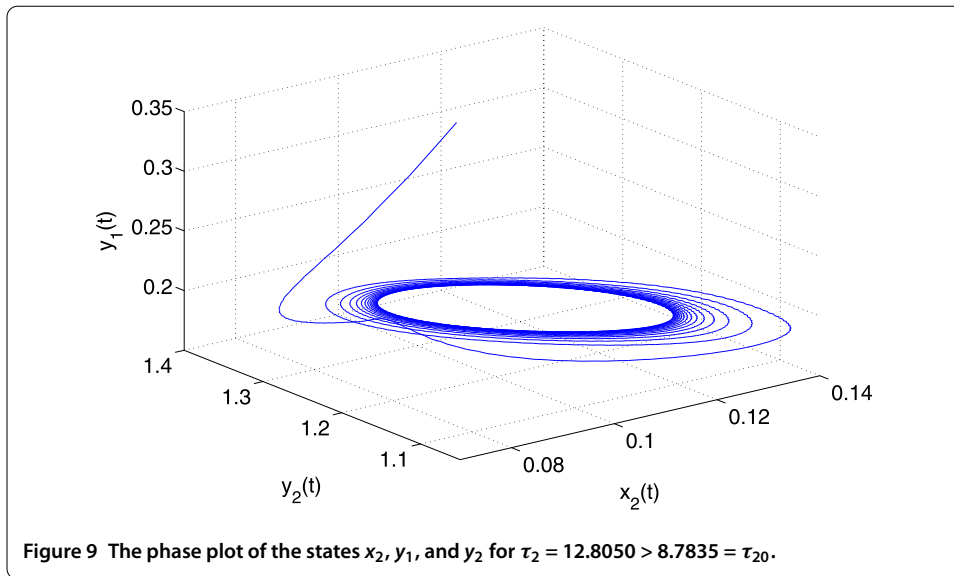
$$
\begin{aligned}
&+ a_{26}\left(W_{11}^{(2)}(0)q^{(4)}(0) + \frac{1}{2}W_{20}^{(2)}(0)\bar{q}^{(4)}(0) + W_{11}^{(4)}(0)q^{(2)}(0) \right. \\
&\left. + \frac{1}{2}W_{20}^{(4)}(0)\bar{q}^{(2)}(0) \right) + a_{27}\left(W_{11}^{(2)}(0)q^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right) + \frac{1}{2}W_{20}^{(2)}(0)\bar{q}^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right) \right. \\
&\left. + W_{11}^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right)q^{(2)}(0) + W_{20}^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right)\bar{q}^{(2)}(0) \right) + a_{28}\left(\left(q^{(2)}(0)\right)^2\bar{q}^{(4)}(0) \right. \\
&\left. + 2q^{(2)}(0)q^{(4)}(0)\bar{q}^{(2)}(0)\right) + 3a_{29}\left(q^{(2)}(0)\right)^2\bar{q}^{(2)}(0)) \\
&+ \bar{q}_3^*\big(a_{34}\big(2W_{11}^{(2)}(-1)q^{(2)}(-1) + W_{20}^{(2)}(-1)\bar{q}^{(2)}(-1)\big)
\end{aligned}
$$

Figure 7 The phase plot of the states x_2, y_1, and y_2 for $\tau_2 = 7.7750 < 8.7835 = \tau_{20}$.

Figure 8 The track of the states x_1, x_2, y_1, and y_2 for $\tau_2 = 12.8050 > 8.7835 = \tau_{20}$.

$$
+ a_{35}\left(W_{11}^{(2)}(-1)q^{(4)}(-1) + \frac{1}{2} W_{20}^{(2)}(-1)\bar{q}^{(4)}(-1) + W_{11}^{(4)}(-1)q^{(2)}(-1)\right.
$$

$$
\left. + \frac{1}{2} W_{20}^{(4)}(-1)\bar{q}^{(2)}(-1)\right) + a_{36}\left(\left(q^{(2)}(-1)\right)^2 \bar{q}^{(4)}(-1)\right.
$$

$$
\left. + 2q^{(2)}(-1)q^{(4)}(-1)\bar{q}^{(2)}(-1)\right) + 3a_{37}\left(q^{(2)}(-1)\right)^2 \bar{q}^{(2)}(-1)\bigg)\bigg],
$$

with

$$
W_{20}(\theta) = \frac{ig_{20}q(0)}{\omega_2^* \tau_{20}^*} e^{i\omega_2^* \tau_{20}^* \theta} + \frac{i\bar{g}_{02}\bar{q}(0)}{3\omega_2^* \tau_{20}^*} e^{-i\omega_2^* \tau_{20}^* \theta} + E_1 e^{2i\omega_2^* \tau_{20}^* \theta},
$$

$$
W_{11}(\theta) = -\frac{ig_{11}q(0)}{\omega_2^* \tau_{20}^*} e^{i\omega_2^* \tau_{20}^* \theta} + \frac{i\bar{g}_{11}\bar{q}(0)}{\omega_2^* \tau_{20}^*} e^{-i\omega_2^* \tau_{20}^* \theta} + E_2,
$$

Figure 9 The phase plot of the states x_2, y_1, and y_2 for $\tau_2 = 12.8050 > 8.7835 = \tau_{20}$.

Figure 10 The bifurcation diagram with respect to τ_2.

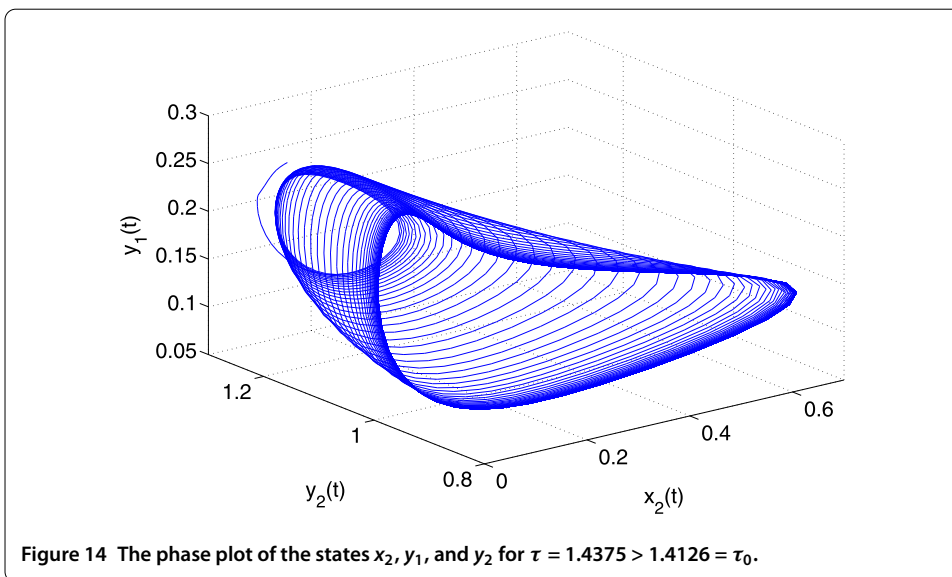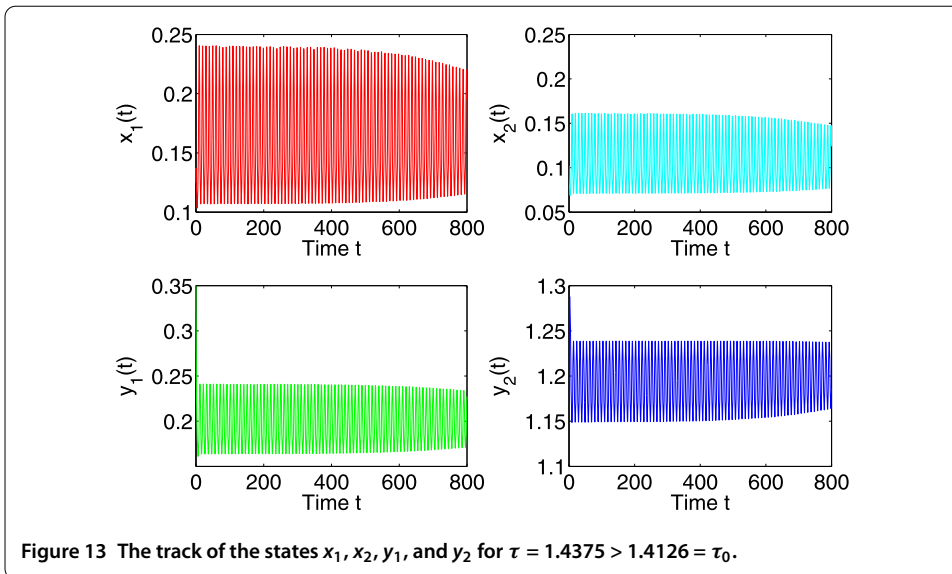where E_1 and E_2 can be computed as the following equations, respectively:

$$
\begin{pmatrix}
2i\omega_2^* - a_{11} & -a_{12} & 0 & 0 \\
-a_{21} & 2i\omega_2^* - a_{22} - b_{22}e^{-2i\omega_2^*\tau_{1*}} & 0 & -a_{24} \\
0 & -c_{32}e^{-i\omega_2^*\tau_{20}^*} & 2i\omega_2^* - a_{33} & -c_{34}e^{-i\omega_2^*\tau_{20}^*} \\
0 & 0 & -a_{43} & 2i\omega_2^* - a_{44}
\end{pmatrix}
E_1 = 2
\begin{pmatrix}
0 \\
E_1^{(2)} \\
E_1^{(3)} \\
0
\end{pmatrix},
$$

$$
\begin{pmatrix}
a_{11} & a_{12} & 0 & 0 \\
a_{21} & a_{22} + b_{22} & 0 & a_{24} \\
0 & c_{32} & a_{33} & c_{34} \\
0 & 0 & a_{43} & a_{44}
\end{pmatrix}
E_2 = -
\begin{pmatrix}
0 \\
E_2^{(2)} \\
E_2^{(3)} \\
0
\end{pmatrix},
$$

Figure 11 The track of the states x_1, x_2, y_1, and y_2 for $\tau = 1.3820 < 1.4126 = \tau_0$.

Figure 12 The phase plot of the states x_2, y_1, and y_2 for $\tau = 1.3820 < 1.4126 = \tau_0$.
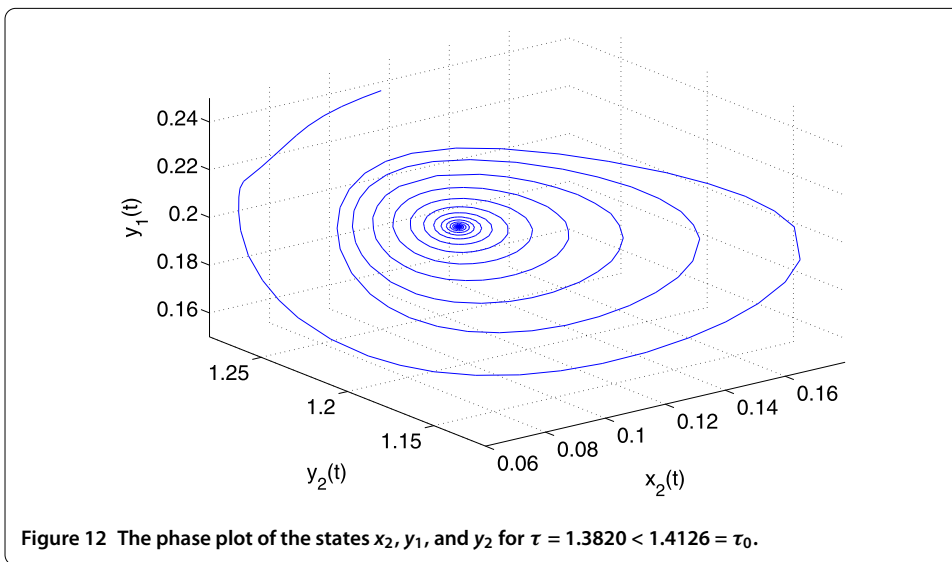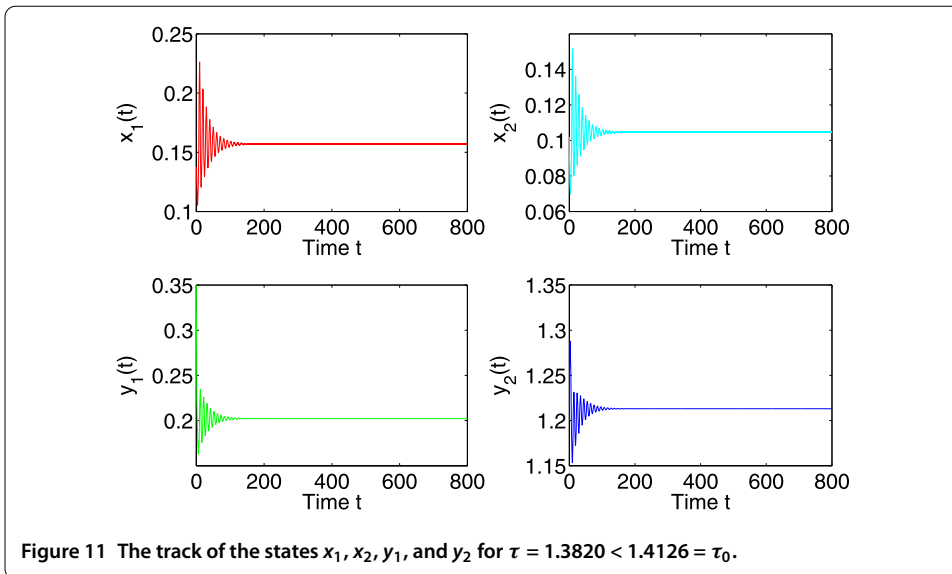
with

$$E_1^{(2)} = a_{25}\big(q^{(2)}(0)\big)^2 + a_{26}q^{(2)}(0)q^{(4)}(0) + a_{27}q^{(2)}(0)q^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right),$$

$$E_1^{(3)} = a_{34}\big(q^{(2)}(-1)\big)^2 + a_{35}q^{(2)}(-1)q^{(4)}(-1),$$

$$E_2^{(2)} = 2a_{25}q^{(2)}(0) + a_{26}\big(q^{(2)}(0)\bar{q}^{(4)}(0) + \bar{q}^{(2)}(0)q^{(4)}(0)\big)$$

$$\qquad + a_{27}\left(q^{(2)}(0)\bar{q}^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right) + \bar{q}^{(2)}(0)q^{(2)}\left(-\frac{\tau_{1*}}{\tau_{20}^*}\right)\right),$$

$$E_2^{(3)} = 2a_{34}q^{(2)}(-1)\bar{q}^{(2)}(-1) + a_{35}\big(q^{(2)}(-1)\bar{q}^{(4)}(-1) + \bar{q}^{(2)}(-1)q^{(4)}(-1)\big).$$

Figure 13 The track of the states x_1, x_2, y_1, and y_2 for $\tau = 1.4375 > 1.4126 = \tau_0$.

Figure 14 The phase plot of the states x_2, y_1, and y_2 for $\tau = 1.4375 > 1.4126 = \tau_0$.

Therefore, we can calculate the following values:

$$C_1(0) = \frac{i}{2\omega_2^* \tau_{20}^*} \left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3} \right) + \frac{g_{21}}{2}, \qquad \mu_2 = -\frac{\mathrm{Re}\{C_1(0)\}}{\mathrm{Re}\{\lambda'(\tau_{20}^*)\}},$$

$$\beta_2 = 2\mathrm{Re}\{C_1(0)\}, \qquad T_2 = -\frac{\mathrm{Im}\{C_1(0)\} + \mu_2 \, \mathrm{Im}\{\lambda'(\tau_{20}^*)\}}{\omega_2^* \tau_{20}^*}. \tag{27}$$

Based on the discussion above, we can obtain the following results.

Theorem 5 *For system* (4), *if $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical (subcritical); if $\beta_2 < 0$ ($\beta_2 > 0$), then the bifurcating periodic solutions are stable (unstable); if $T_2 > 0$ ($T_2 < 0$), then the period of the bifurcating periodic solutions increases (decreases).*
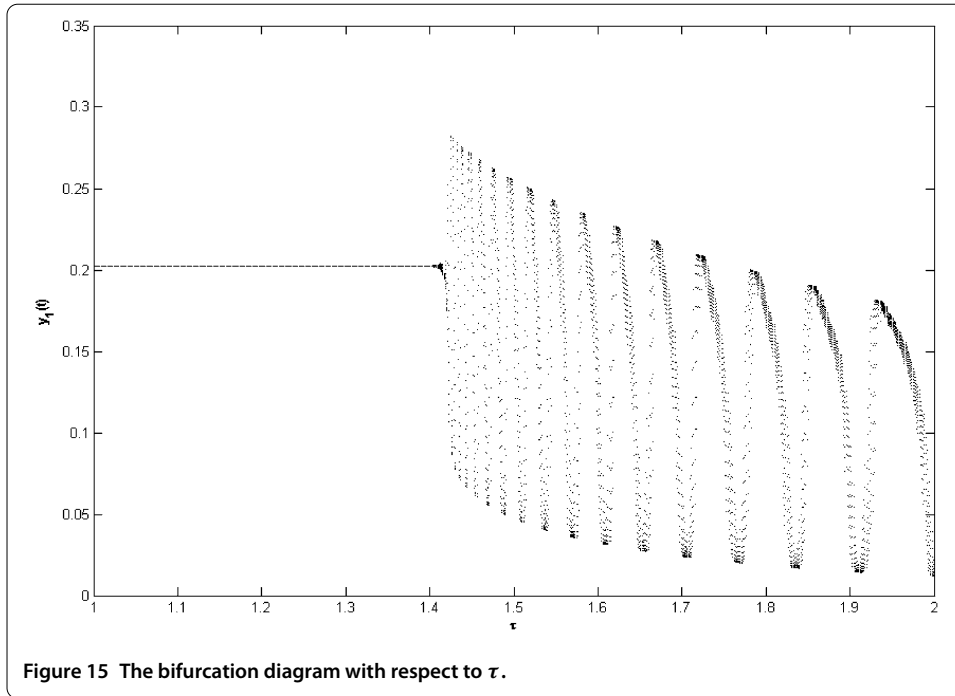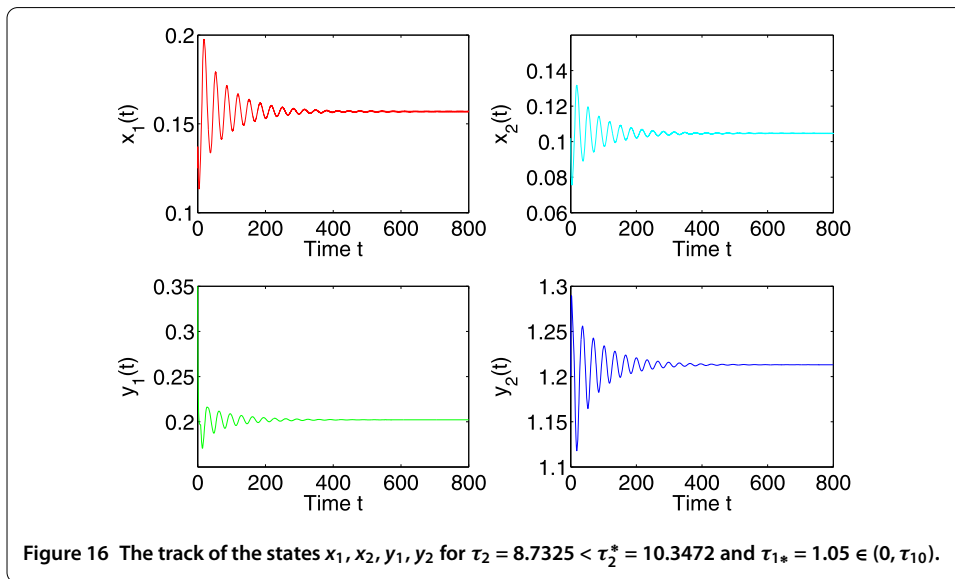
**Figure 15 The bifurcation diagram with respect to τ.**

Figure 16 The track of the states x_1, x_2, y_1, y_2 for $\tau_2 = 8.7325 < \tau_2^* = 10.3472$ and $\tau_{1*} = 1.05 \in (0, \tau_{10})$.
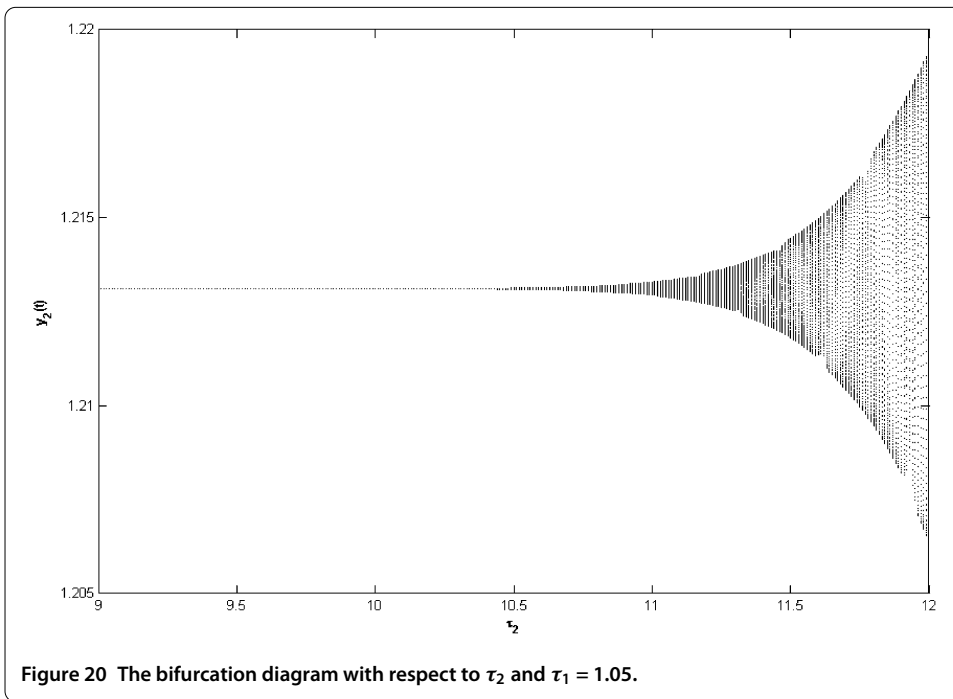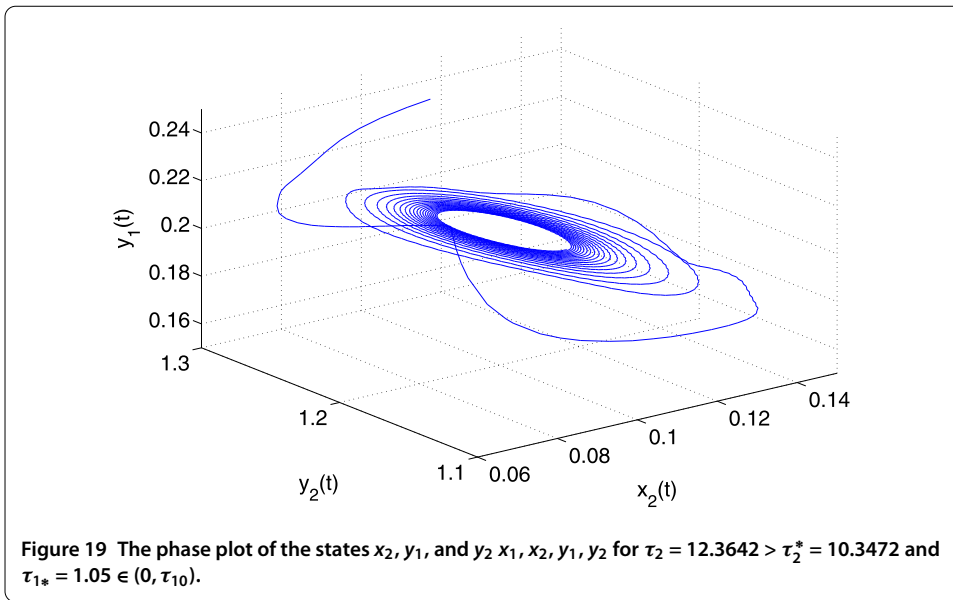
4 Numerical example

In this section, we give a numerical example to support the theoretical results in Section 2 and Section 3. We consider the following system:

$$\begin{cases} \frac{dx_1(t)}{dt} = 6x_2(t) - 3x_1(t) - x_1(t), \\ \frac{dx_2(t)}{dt} = 3x_1(t) - 0.25x_2(t) - 15x_2x_2(t - \tau_1) - \frac{3.25x_2(t)y_2(t)}{1+4.5x_2(t)}, \\ \frac{dy_1(t)}{dt} = \frac{2.05x_2(t-\tau_2)y_2(t-\tau_2)}{1+4.5x_2(t-\tau_2)} - 0.75y_1(t) - 0.125y_1(t), \\ \frac{dy_2(t)}{dt} = 0.75y_1(t) - 0.125y_2(t), \end{cases} \tag{28}$$

Figure 17 The phase plot of the states x_2, y_1, and y_2 x_1, x_2, y_1, y_2 for $\tau_2 = 8.7325 < \tau_2^* = 10.3472$ and $\tau_{1*} = 1.05 \in (0, \tau_{10})$.

Figure 18 The track of the states x_1, x_2, y_1, y_2 for $\tau_2 = 12.3642 > \tau_2^* = 10.3472$ and $\tau_{1*} = 1.05 \in (0, \tau_{10})$.
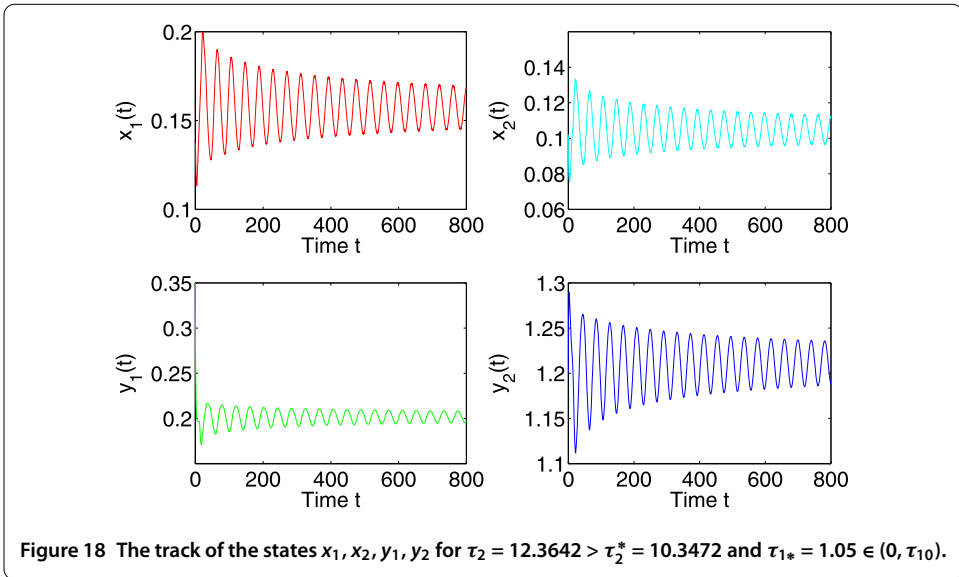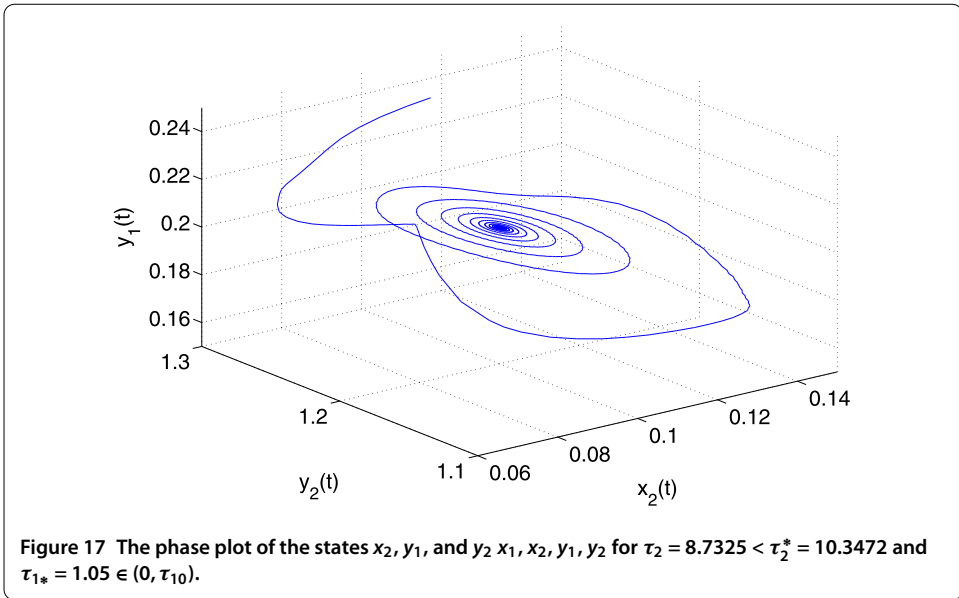
which has a unique positive equilibrium $E^*(0.15695067, 0.10463378, 0.20218508, 1.21311045)$.

We have $\tau_1 > 0$, $\tau_2 = 0$. By some complex computations, we obtain $\omega_{10} = 2.5011$, $\tau_{10} = 1.3785$. Further, we have $f_1'(v_1^*) = 0.0914 > 0$. Thus, the conditions (H$_{21}$) and (H$_{22}$) hold. According to Theorem 1, the positive equilibrium E^* of system (28) is asymptotically stable when $\tau_1 < \tau_{10}$. This property can be illustrated by Figures 1 and 2. However, once τ_1 passes through the critical value τ_{10}, the positive equilibrium E^* of system (28) will lose its stability and a Hopf bifurcation occurs and a family of periodic solutions bifurcate from the positive equilibrium E^* of system (28), which can be shown as in Figures 3 and 4. This property can also be seen from the bifurcation diagram with respect to τ_1 in Figure 5. Similarly, we have $\omega_{20} = 0.7361$, $\tau_{20} = 8.7835$ for $\tau_1 = 0$, $\tau_2 > 0$. The corresponding waveforms, phase plots and bifurcation diagram are shown in Figures 6-10.

Figure 19 The phase plot of the states x_2, y_1, **and** y_2 x_1, x_2, y_1, y_2 **for** $\tau_2 = 12.3642 > \tau_2^* = 10.3472$ **and** $\tau_{1*} = 1.05 \in (0, \tau_{10})$.

Figure 20 The bifurcation diagram with respect to τ_2 **and** $\tau_1 = 1.05$.

We have $\tau_1 = \tau_2 = \tau > 0$. We can obtain $\omega_0 = 2.9285$ and then we get $\tau_0 = 1.4126$. From Theorem 3, we can conclude that when τ increases from zero to τ_0 the positive equilibrium E^* of system (28) is asymptotically stable, then it will lose its stability and a Hopf bifurcation occurs once $\tau > \tau_0$. As can be seen from Figures 11 and 12, when $\tau = 1.3820 \in (0, 1.4126)$, the positive equilibrium E^* of system (28) is asymptotically stable. However, if we let $\tau = 1.4375 > \tau_0 = 1.4126$, the positive equilibrium E^* of system (28) loses its stability and a Hopf bifurcation occurs, which can be shown as in Figures 13, 14 and 15.

We have $\tau_2 > 0$ and $\tau_1 = 1.05 \in (0, \tau_{10})$. We can obtain $\omega_2^* = 0.3795$, $\tau_{20}^* = 10.3472$. By Theorem 4, the positive equilibrium E^* of system (28) is asymptotically stable when $\tau_2 \in [0, \tau_{20}^*)$ and the positive equilibrium E^* of system (28) becomes unstable when $\tau_2 > \tau_{20}^*$ and a family of periodic solutions bifurcate from the positive equilibrium E^*, which can be illustrated by Figures 16-20.

Finally, by complex computations, we obtain $C_1(0) = -14.2305 - 23.6892i$, $\lambda'(\tau_{20}^*) = 12.3301 - 19.7682i$. Further, we can obtain $\mu_2 = 1.1541 > 0$, $\beta_2 = -28.4610 < 0$, $T_2 = 11.8428 > 0$. According to Theorem 5, we know that the Hopf bifurcation of system (28) with respect to τ_2 with $\tau_1 = 1.05 \in (0, \tau_{10})$ is supercritical, the bifurcating periodic solutions are stable and increase.

5 Conclusion

In this paper, by incorporating the feedback delay of the mature prey and the time delay due to the gestation of the mature predator into the system considered in the literature [9], we get a delayed predator-prey system with stage structure for both the predator and the prey, which is an extension of the literature [9]. Compared with the literature [9], we mainly consider the effects of the two delays on the predator-prey system.

By regarding the possible combination of the two delays as the bifurcation parameter, and analyzing the characteristic equation of the linearized system at the positive equilibrium, the sufficient conditions for the local stability of the positive equilibrium and the existence of a Hopf bifurcation are established. It has been shown that when the value of the delay is below the corresponding critical value, the system is asymptotically stable. However, once the value of the delay is greater than the corresponding critical value, there will be a Hopf bifurcation at the positive equilibrium of the system and a family of periodic solutions occur. For the further investigation, formulas are derived to determine direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions by using the normal form theory and center manifold theorem. From the numerical simulations, one can conclude that the species in system (4) could coexist in an oscillatory mode with some available delays of the mature prey and the mature predator under some certain conditions. This is valuable from the point of view of ecology.

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