Stability and Hopf bifurcation analysis in a stage-structured predator-prey system with two time delays

Yongkun Li and Meng Hu

Abstract—A stage-structured predator-prey system with two time delays is considered. By analyzing the corresponding characteristic equation, the local stability of a positive equilibrium is investigated and the existence of Hopf bifurcations is established. Formulae are derived to determine the direction of bifurcations and the stability of bifurcating periodic solutions by using the normal form theory and center manifold theorem. Numerical simulations are carried out to illustrate the theoretical results. Based on the global Hopf bifurcation theorem for general functional differential equations, the global existence of periodic solutions is established.

Keywords—Predator-prey system; Stage structure; Time delay; Hopf bifurcation; Periodic solution; Stability.

I. INTRODUCTION

THE predator-prey system is very important in population modeling and has been studied by many authors (see,[1-7]). The effect of the past history on the stability of system is also an important problem in population biology. It is generally recognized that some kinds of time delays are inevitable in population interactions and tend to be destabilizing in the sense that longer delays may destroy the stability of positive equilibria. Time delay due to the gestation is a common example, because generally the consumption of prey by the predator throughout its past history governs the present birth rate of the predator. Predator-prey systems with time delays have received much attention in the past few years (see, [1-4,6,7,10]).

In pioneering work [2], the author considered the periodic solutions of a predator-prey system of Lotka-Volterra type with a finite number of discrete delays. The model takes the following form:

$$\begin{cases} \dot{x}(t) = x(t) \left[r_1 - \sum_{j=1}^m a_{1j} x(t - \tau_{1j}) - \sum_{j=1}^m b_{1j} y(t - \rho_{1j}) \right], \\ \dot{y}_1(t) = y(t) \left[r_2 - \sum_{j=1}^m a_{2j} x(t - \tau_{2j}) - \sum_{j=1}^m b_{2j} y(t - \rho_{2j}) \right], \end{cases}$$

$$(1)$$

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where r_1, r_2 are real constants with $r_i > 0$, $a_{ij}, b_{ij}, \tau_{ij}, \rho_{ij}$ (i = 1, 2, j = 1, 2, ..., m) are nonnegative constants. Not all of a_{1j} and not all of b_{2j} (j = 1, 2, ..., m) are zeros.

But, the author[2] ignored the stage structure of species. In the natural world, almost all animals have the stage structure of immature and mature. Specialized stages may exist for dispersal or for dormancy. The vital rates (rates of survival, development and reproduction) almost always depend on age, size, or development stage. Stage-structured models have received great attention in recent years.

Very recently, Gao[3] reduced system (1) to a stage structure of immature and mature of species, and the system described by the following form:

$$\begin{cases} \dot{u}(t) = u(t)[r_1 - a_{11}u(t) - a_{12}v_1(t - \tau_1)], \\ \dot{v}_1(t) = v_1(t)[-r_2 + a_{21}u(t - \tau_2) \\ -a_{22}v_1(t)] + \theta v_2(t), \\ \dot{v}_2(t) = bv_1(t) - (\theta + \delta)v_2(t), \end{cases}$$
(2)

where v_1 and v_2 denote the population of mature and immature predator, respectively. Suppose that the rate of transition from immature individuals to mature individuals is proportional to the existing immature population with proportional constant $\theta > 0$, and the death rate of mature and immature population are proportional to the existing mature and immature population with proportional constants $r_2 > 0$ and $\delta > 0$, respectively. Moreover, we then assume that the birth rate of immature population is proportional to the existing mature population with proportional constant b > 0. The predation decreases the average growth rate of prey linearly with a certain time delay τ_1 , this assumption corresponds to the fact that predators cannot hunt prey when the predators are infant; predators have to mature for a duration of τ_1 units of time before they are capable of decreasing the average growth rate of the prey species; τ_2 is the time delay due to gestation, the delay in time for prey biomass to increase predator number. System (2) is more reasonable in the natural world. For example, frog feeds on pest, but tadpole is not able to feed on pest.

The initial conditions for system (2) take the form

$$(\phi(s), \psi_1(s), \psi_2(s)) \in C_+ = C[(-\tau, 0), R_+^3],$$

$$\phi(0) > 0, \psi_1(0) > 0, \psi_2(0) > 0,$$

where $\tau = \max\{\tau_1, \tau_2\}, R_+^3 = \{(u, v_1, v_2) \in R^3 | u \ge 0, v_1 \ge 0, v_2 \ge 0\}.$

In [3], the authors obtained the time delay is harmless for permanence of the stage-structured system. If $\frac{a_{12}}{a_{22}} \frac{a_{21}}{a_{11}} < 1$,

sufficient conditions which guarantee the global stability of positive equilibrium are given. If $\frac{a_{12}}{a_{22}}\frac{a_{21}}{a_{11}} > 1$, showed that the unique positive equilibrium is locally asymptotically stable when time delay is sufficiently small. But neither the direction and stability of the local Hopf bifurcation nor the global continuation of the local Hopf bifurcation are considered in their paper.

Recently, great attention has been received and a large body of work has been carried out on the existence of Hopf bifurcations in delayed population models or in models of epidemic and viral dynamics(see, for example, [1], [4], [5], [8] and references cited therein). The stability of positive equilibria and the existence and the direction of Hopf bifurcations were discussed respectively in the references mentioned above.

However, the existence of these periodic solutions remain valid only in a small neighborhood of the critical value, and the investigated models include only one time delay. It is natural to ask if these non-constant periodic solutions which are obtained through local Hopf bifurcation can still exist for large values of the parameters τ and how about if the system with two time delays.

To this aim, motivated by the above discussion, in this paper, we will consider the system (2) to discuss these problems.

The organization of this paper is as follows. In the next section, by choosing the time delay τ (= $\tau_1 + \tau_2$) as a parameter and analyzing the associated characteristic equation of a linearized system, we investigate the linear stability of the positive equilibrium for system (2). In addition, we get sufficient conditions for the existence of Hopf bifurcations. In Section 3, we derive formulae to determine the direction of bifurcations and the stability of bifurcating periodic solutions by using the normal form theory and center manifold theorem. In Section 4, numerical simulations are carried out to illustrate the theoretical results. In Section 5, based on the global Hopf bifurcation theorem for general functional differential equations, we investigate the global existence of periodic solutions by using degree theory methods.

II. LOCAL STABILITY AND HOPF BIFURCATIONS

In this section, we discuss the stability of a positive equilibrium and the existence of Hopf bifurcations for system (2).

Let

$$\tilde{u} = a_{11}u, \quad \tilde{v}_1 = a_{22}v_1, \quad \tilde{v}_2 = \frac{a_{22}}{b}v_2,$$

then system (2) becomes

$$\begin{cases} \dot{\tilde{u}}_{1}(t) = \tilde{u}(t)[r_{1} - \tilde{u}(t) - \alpha \tilde{v}_{1}(t - \tau_{1})], \\ \dot{\tilde{v}}_{1}(t) = \tilde{v}_{1}(t)[-r_{2} + \beta \tilde{u}(t - \tau_{2}) - \tilde{v}_{1}(t)] + \gamma \tilde{v}_{2}(t), \\ \dot{\tilde{v}}_{2}(t) = \tilde{v}_{1}(t) - \eta \tilde{v}_{2}(t), \end{cases}$$
(3)

where

$$\alpha = \frac{a_{12}}{a_{22}}, \ \beta = \frac{a_{21}}{a_{11}}, \ \gamma = b\theta, \ \eta = \theta + \delta.$$

If the following holds:

$$(\mathbf{H}_1) \qquad (r_2 - r_1 \beta) \eta < \gamma < (\frac{r_1}{\alpha} + r_2) \eta,$$

then system (3) has a unique positive equilibrium $z^* = (u^*, v_1^*, v_2^*)$, where

$$u^* = r_1 - \alpha v_1^*, \ v_1^* = \eta v_2^*, \ v_2^* = \frac{\gamma + r_1 \beta \eta - r_2 \eta}{\eta^2 (1 + \alpha \beta)}.$$

Let $\bar{u} = \tilde{u} - u^*$, $\bar{v}_1^* = \tilde{v}_1 - v_1^*$, $\bar{v}_2 = \tilde{v}_2 - v_2^*$. Dropping the bars, system (3) becomes

$$\begin{cases} \dot{u}(t) = (r_1 - 2u^* - \alpha y_1^*)u(t) - \alpha u^*v_1(t - \tau_1) \\ -u^2(t) - \alpha u(t)v_1(t - \tau_1), \\ \dot{v}_1(t) = \beta v_1^*u(t - \tau_2) + (-r_2 + \beta u^* - 2v_1^*)v_1(t) \\ + \gamma v_2(t) - v_1^2(t) + \beta v_1(t)u(t - \tau_2), \\ \dot{v}_2(t) = v_1(t) - \eta v_2(t), \end{cases}$$
(4)

Let $x(t)=u(t-\tau_2),y_1(t)=v_1(t),y_2(t)=v_2(t),$ then system (4) becomes

$$\begin{cases} \dot{x}(t) = (r_1 - 2x^* - \alpha y_1^*)x(t) - \alpha x^* y_1(t - \tau) \\ -x^2(t) - \alpha x(t)y_1(t - \tau), \\ \dot{y}_1(t) = \beta y_1^* x(t) + (-r_2 + \beta x^* - 2y_1^*)y_1(t) \\ +\gamma y_2(t) - y_1^2(t) + \beta y_1(t)x(t), \\ \dot{y}_2(t) = y_1(t) - \eta y_2(t), \end{cases}$$
 (5)

where $\tau = \tau_1 + \tau_2$.

The characteristic equation of system (5) at the origin is of the form

$$\lambda^{3} + p_{2}\lambda^{2} + p_{1}\lambda + p_{0} + (q_{1}\lambda + q_{0})e^{-\lambda\tau} = 0,$$
 (6)

where

$$\begin{array}{ll} p_0 = \eta x^* y_1^*, & p_1 = x^* y_1^* + \frac{\gamma x^*}{\eta} + \eta x^* + \eta y_1^*, \\ p_2 = x^* + y_1^* + \frac{\gamma}{\eta} + \eta, & q_0 = \eta \alpha \beta x^* y_1^*, & q_1 = \alpha \beta x^* y_1^*. \end{array}$$

When $\tau = 0$, equation (6) becomes

$$\lambda^3 + p_2 \lambda^2 + (p_1 + q_1)\lambda + p_0 + q_0 = 0, \tag{7}$$

in which

$$p_2 = x^* + y_1^* + \frac{\gamma}{\eta} + \eta > 0, p_0 + q_0 = \eta x^* y_1^* + \eta \alpha \beta x^* y_1^* > 0,$$

$$p_{2}(p_{1} + q_{1}) - (p_{0} + q_{0})$$

$$= \left(x^{*} + y_{1}^{*} + \frac{\gamma}{\eta} + \eta\right) \left(x^{*}y_{1}^{*} + \frac{\gamma x^{*}}{\eta} + \eta x^{*} + \eta y_{1}^{*} + \alpha \beta x^{*}y_{1}^{*}\right)$$

$$-(\eta x^{*}y_{1}^{*} + \eta \alpha \beta x^{*}y_{1}^{*}) > 0.$$

By Hurwitz criterion, we know that all roots of equation (7) have negative real parts.

When $\tau>0$, noting that $i\omega(\omega>0)$ is a root of (6) if and only if ω satisfies

$$\begin{cases} q_1 \omega \cos 2\omega \tau - q_0 \sin 2\omega \tau = \omega^3 - p_1 \omega, \\ q_1 \omega \sin 2\omega \tau + q_0 \cos 2\omega \tau = p_2 \omega^2 - p_0. \end{cases}$$
 (8)

In view of (8), by a direct calculation, we have

$$\omega^6 + h_2 \omega^4 + h_1 \omega^2 + h_0 = 0, \tag{9}$$

where

$$h_0 = p_0^2 - q_0^2$$
, $h_1 = p_1^2 - q_1^2 - 2p_0p_2$, $h_2 = p_2^2 - 2p_1$.

For equation (9), assume

$$(H_2)$$
 $\alpha\beta > 1$

holds, we have

$$h_0 = (\eta x^* y_1^*)^2 - (\eta \alpha \beta x^* y_1^*)^2 < 0,$$

$$h_1 = (x^* y_1^* + \frac{\gamma x^*}{\eta} + \eta x^* + \eta y_1^*)^2 - (\alpha \beta x^* y_1^*)^2$$

Hence, equation (9) has only one positive real root
$$\omega_0$$
. Let

$$\tau_j = \frac{1}{\omega_0} \arcsin \frac{p_2 q_1 - q_0) \omega_0^3 + (p_1 q_0 - p_0 q_1) \omega_0}{q_1^2 \omega_0^2 + q_0^2} + \frac{2\pi j}{\omega_0},$$

where $j = 0, 1, 2, \ldots$, then equation (6) has a pair of purely imaginary roots $\pm i\omega_0$ with $\tau = \tau_i$.

Lemma 1. For equation (6), if (H_1) and (H_2) hold, then we have the following transversal condition

$$\operatorname{Re}\left(\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right|_{\lambda=i\omega_0}\right) > 0.$$

Proof: Differentiating both sides of (6) with respect to τ

$$[3\lambda^2 + 2p_2\lambda + p_1 + (q_1 - \tau(q_1\lambda + q_0))e^{-\lambda\tau}]\frac{\mathrm{d}\lambda}{\mathrm{d}\tau} = \lambda(q_1\lambda + q_0)e^{-\lambda\tau}.$$

For convenience, we study $(d\lambda/d\tau)^{-1}$ instead of $d\lambda/d\tau$. We

$$\begin{split} \left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} &= \frac{3\lambda^2 + 2p_2\lambda + p_1 + q_1e^{-\lambda\tau}}{\lambda(q_1\lambda + q_0)e^{-\lambda\tau}} - \frac{\tau}{\lambda} \\ &= -\frac{3\lambda^2 + 2p_2\lambda + p_1}{\lambda(\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} + \frac{q_1}{\lambda(q_1\lambda + q_0)} - \frac{\tau}{\lambda} \end{split}$$

Hence.

$$\operatorname{Re} \left(\frac{\mathrm{d} \lambda}{\mathrm{d} \tau} \right)^{-1} \Big|_{\lambda = i \omega_0} = \frac{3 \omega_0^4 + 2 h_2 \omega_0^2 + h_1}{q_1^2 \omega_0^2 + q_0^2} > 0.$$

Therefore.

$$\operatorname{sign} \left\{ \operatorname{Re} \left(\frac{\mathrm{d} \lambda}{\mathrm{d} \tau} \right) \big|_{\lambda = i \omega_0} \right\} = \operatorname{sign} \left\{ \operatorname{Re} \left(\frac{\mathrm{d} \lambda}{\mathrm{d} \tau} \right)^{-1} \big|_{\lambda = i \omega_0} \right\} > 0.$$

This completes the proof of Lemma 1.

Lemma 2. ([9]) Assume (H_1) and (H_2) hold, then

- (i) when $\tau \in [0, \tau_0)$, all roots of equation (6) have strictly negative real parts.
- (ii) when $\tau = \tau_0$, equation (6) has a pair of conjugate purely imaginary roots $\pm i\omega_0$, and all other roots have strictly negative real parts.
- (iii) when $\tau > \tau_0$, equation (6) has at least one root with positive real part.

Applying Lemma 2, we have the following result.

Theorem 1. For system (5), if (H_1) and (H_2) are satisfied, then

- (i) when $\tau \in [0, \tau_0)$, the zero solution is asymptotically
- (ii) when $\tau > \tau_0$, the zero solution is unstable;
- (iii) $\tau = \tau_j$, (j = 0, 1, 2, ...) are the values of Hopf bifurcations, where τ_i are defined by (10).

III. DIRECTION AND STABILITY OF HOPF BIFURCATIONS

In the previous section, we obtained conditions under which a family of periodic solutions bifurcate from the positive equilibrium at the critical values $\tau_j (j = 0, 1, 2, ...)$. In this section, we study the direction of bifurcations and the stability of bifurcating periodic solutions. The method we used here is based on the normal form theory and center manifold theory introduced by Hassard et al. in [13].

Now, we re-scale the time by $t = s\tau$, $\hat{x}_1(s) = x_1(s\tau)$, $\hat{x}_2(s) = x_2(s\tau), \ \hat{y}(s) = y(s\tau), \ \tau = \tau_0 + \mu, \ \mu \in R, \ \text{and still}$ denote by $x_1(t) = \hat{x}_1(s), x_2(t) = \hat{x}_2(s), y(t) = \hat{y}(s)$, then system (5) can be written as

$$\begin{cases} \dot{x}(t) = (\tau_0 + \mu)[(r_1 - 2x^* - \alpha y_1^*)x(t) - \alpha x^* y_1(t-1) \\ -x^2(t) - \alpha x(t)y_1(t-1)], \\ \dot{y}_1(t) = (\tau_0 + \mu)[\beta y_1^*x(t) + (-r_2 + \beta x^* - 2y_1^*)y_1(t) \\ +\gamma y_2(t) - y_1^2(t) + \beta y_1(t)x(t)], \\ \dot{y}_2(t) = (\tau_0 + \mu)[y_1(t) - \eta y_2(t)]. \end{cases}$$

For $\varphi=(\varphi_0,\varphi_1,\varphi_2)^T\in C[-1,0]=C([-1,0],R^3)$, define a family of operators

$$L_{\mu}\varphi = B_1\varphi(0) + B_2\varphi(-1), \tag{12}$$

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$$f(\mu,\varphi) = (\tau_0 + \mu) \begin{bmatrix} -\varphi_1^2(0) - \alpha \varphi_1(0) \varphi_2(-1) \\ -\varphi_2^2(0) + \beta \varphi_2(0) \varphi_1(0) \\ 0 \end{bmatrix}.$$

By the Riesz representation theorem, there exists a matrix whose components are bounded variation functions $\eta(\theta, \mu)$: $[-1,0] \to R^3$, such that $L_\mu \varphi = \int_{-1}^0 d\eta(\theta,\mu) \varphi(\theta)$, for $\varphi \in C$. In fact, we can choose

$$\eta(\theta, \mu) = (\tau_0 + \mu) B_1(\varphi_1(0), \varphi_2(0), \varphi_3(0))^T \delta(\theta) -(\tau_0 + \mu) B_2 \delta(\theta + 1),$$
(13)

where δ is the Dirac delta function.

For $\varphi = (\varphi_0, \varphi_1, \varphi_2)^T \in C^1[-1, 0]$, define

$$\begin{split} A(\mu)\varphi &= \left\{ \begin{array}{l} \dot{\varphi}(\theta)\;,\quad \theta \in [-1,0),\\ \int_{-1}^{0} \mathrm{d}\eta(s,\mu)\varphi(s)\;,\quad \theta = 0, \end{array} \right.\\ R(\mu)\varphi &= \left\{ \begin{array}{l} 0\;,\quad \theta \in [-1,0),\\ f(\mu,\varphi)\;,\quad \theta = 0. \end{array} \right. \end{split}$$

Hence, equation (11) can be rewritten as

$$\dot{U}_t = A(\mu)U_t + R(\mu)U_t,\tag{14}$$

where $U = (x_1, x_2, y)^T$. For $\psi \in C^1[0, 1]$, define

$$A^*\psi(s) = \begin{cases} -\dot{\psi}(s), & s \in [-1,0), \\ \int_{-1}^0 d\eta^T(t,0)\psi(-t), & s = 0. \end{cases}$$
(15)

For $\varphi \in C([-1,0]\,,C^3)$ and $\psi \in C([0,1]\,,(C^3)^*),$ define a bilinear inner product

$$\langle \psi, \varphi \rangle = \bar{\psi}^{\mathsf{T}}(0)\varphi(0) - \int_{\theta=-1}^{0} \int_{\xi=0}^{\theta} \bar{\psi}^{\mathsf{T}}(\xi-\theta) \mathrm{d}\eta(\theta)\varphi(\xi) d\xi,$$
(16)

where $\eta(\theta)=\eta(\theta,0)$. Then, A=A(0) and A^* are adjoint operators. By the discussion in Section 2 and transformation $t=s\tau$, we know that $\pm i\tau_0\omega_0$ are eigenvalues of A. Thus, they are also eigenvalues of A^* . We first need to calculate the eigenvector of A(0) and A^* corresponding to $i\omega_0\tau_0$ and $-i\omega_0\tau_0$, respectively.

Suppose that $q(\theta)=(1,q_2,q_3)^{\mathrm{T}}e^{i\tau_0\omega_0\theta}$ and $q^*(s)=D(1,q_2^*,q_3^*)^{\mathrm{T}}e^{i\tau_0\omega_0s}$ are eigenvectors of A and A^* corresponding to $i\tau_0\omega_0$ and $-i\tau_0\omega_0$, respectively. By the definition of A(0) and A^* and (12-13), we can obtain

$$\begin{split} q_2 &= \frac{r_1 - 2x^* - \alpha y_1^* - i\omega_0}{\alpha x^* e^{-i\tau_0\omega_0}}, \\ q_3 &= \frac{r_1 - 2x^* - \alpha y_1^* - i\omega_0}{(\eta + i\omega_0)\alpha x^* e^{-i\tau_0\omega_0}}, \\ q_2^* &= \frac{2x^* - r_1 + \alpha y_1^* - i\omega_0}{\beta y_1^*}, \\ q_3^* &= \frac{\gamma(2x^* - r_1 + \alpha y_1^* - i\omega_0)}{(\eta - i\omega_0)\beta y_1^*}. \end{split}$$

In order to assure $\langle q^*(\theta), q(\theta) \rangle = 1$, we need to determine the value of D. From (16), we have

Thus, we can choose D as

$$D = \left[1 + \bar{q}_2 q_2^* + \bar{q}_3 q_3^* + \tau_0 \alpha \bar{q}_2 x^* e^{i\tau_0 \omega_0}\right]^{-1}.$$

Now we calculate the coordinates to describe the center manifold C_0 at $\mu=0$. Let U_t be the solution of equation (14) when $\mu=0$, and define

$$z(t) = \langle q^*, U_t \rangle, \quad W(t, \theta) = U_t(\theta) - 2Re\{z(t)q(\theta)\}.$$
 (17)

On the center manifold C_0 , we have $W(t, \theta) = W(z(t), \bar{z}(t), \theta)$, where

$$W(z, \overline{z}, \theta) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z \overline{z} + W_{02}(\theta) \frac{\overline{z}^2}{2} + \dots, (18)$$

z and \bar{z} are local coordinates for center manifold C_0 in the direction of q^* and \bar{q}^* . Note that W is real if U_t is real, we consider only real solutions. For the solution $U_t \in C_0$, since $\mu = 0$, then

$$\dot{z}(t) = i\tau_0 \omega_0 z(t) + \overline{q}^*(0) f_0(z, \overline{z}). \tag{19}$$

We rewrite this equation as $\dot{z}(t) = i\tau_0\omega_0z(t) + g(z,\overline{z})$ with

$$g(z,\overline{z}) = g_{20}\frac{z^2}{2} + g_{11}z\overline{z} + g_{02}\frac{\overline{z}^2}{2} + g_{21}\frac{z^2\overline{z}}{2} + \dots$$
 (20)

Hence,

$$g(z,\bar{z}) = \bar{q}^*(0)f_0(z,\bar{z}) = \bar{q}^*(0)f(0,U_t).$$

Substitute $U_t(\theta)$ into above and comparing the coefficients with (20), we get

$$\begin{cases} g_{20} = 2\tau_0 \bar{D}[\bar{q}_2^*(\beta q_2 q_3 - q_3^2) - (q_2^2 + \alpha q_2 q_3 e^{-i\tau_0\omega_0})], \\ g_{11} = \tau_0 \bar{D}[\bar{q}_2^*(\beta \bar{q}_2 q_3 + \beta q_2 \bar{q}_3 - 2q_3 \bar{q}_3) \\ - (2q_2 \bar{q}_2 + \alpha \bar{q}_2 q_3 e^{-i\tau_0\omega_0} + \alpha q_2 \bar{q}_3 e^{i\tau_0\omega_0})], \\ g_{02} = 2\tau_0 \bar{D}[\bar{q}_2^*(\beta \bar{q}_2 q_3 - \bar{q}_3^2) - (\bar{q}_2^2 + \alpha \bar{q}_2 \bar{q}_3 e^{i\tau_0\omega_0})], \\ g_{21} = \tau_0 \bar{D}[\bar{q}_2^*[\beta(\bar{q}_2 W_{20}^{(2)}(0) + 2q_2 W_{11}^{(2)}(0) \\ + 2q_3 W_{11}^{(1)}(0) + \bar{q}_3 W_{20}^{(1)}(0)) \\ - (2W_{20}^{(2)}(0)\bar{q}_3 + 4q_3 W_{11}^{(2)}(0))] - [2W_{20}^{(1)}(0)\bar{q}_2 \\ + 4q_2 W_{11}^{(1)}(0) + \alpha(W_{20}^{(1)}(0)\bar{q}_3 e^{i\tau_0\omega_0} \\ + 2q_3 W_{11}^{(1)}(0) e^{-i\tau_0\omega_0} + 2q_2 W_{11}^{(2)}(-1) \\ + \bar{q}_2 W_{20}^{(2)}(-1))]]. \end{cases}$$

Now we calculate $W_{20}(\theta)$ and $W_{11}(\theta)$. From (14) and (17), we have

$$\dot{W} = \dot{U}_t - \dot{z}q - \dot{\overline{z}}\overline{q}
= \begin{cases}
AW - 2Re\{\overline{q}^*(0)F_0q(\theta)\}, & \theta \in [-1,0) \\
AW - 2Re\{\overline{q}^*(0)F_0q(\theta)\} + F_0, & \theta = 0
\end{cases}$$

$$\stackrel{\text{def}}{=} AW + H(z, \overline{z}, \theta).$$

where

$$H(z, \overline{z}, \theta) = h_{20}(\theta) \frac{z^2}{2} + h_{11}(\theta) z \overline{z} + h_{02}(\theta) \frac{\overline{z}^2}{2} + \dots$$
 (22)

For $\theta \in [-1, 0)$, we can get

$$(A-2i\tau_0\omega_0)W_{20}(\theta) = -h_{20}(\theta), AW_{11}(\theta) = -h_{11}(\theta).$$
 (23)

From (22), we know that for $\theta \in [-1, 0)$,

$$\begin{split} H(z,\bar{z},\theta) &= -2Re\{\bar{q}^*(0)F_0q(\theta)\} \\ &= -g(z,\bar{z})q(\theta) - \bar{g}(z,\bar{z})\bar{q}(\theta) \\ &= -(g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + \ldots)q(\theta) \\ &- (\bar{g}_{20}\frac{\bar{z}^2}{2} + \bar{g}_{11}z\bar{z} + \bar{g}_{02}\frac{z^2}{2} + \ldots)\bar{q}(\theta). \end{split}$$

Comparing the coefficients with (22), we can obtain

$$h_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), \quad h_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta).$$

$$W_{20}(\theta) = \frac{ig_{20}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta} + \frac{i\bar{g}_{02}}{3\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta} + Ee^{2i\tau_0\omega_0\theta}.$$
(24)

$$W_{11}(\theta) = -\frac{ig_{11}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta} + \frac{\bar{g}_{11}}{i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta} + F.$$
 (25)

In what follows, we seek appropriate E and F. The definition of A and (23) imply that

$$\int_{-1}^{0} d\eta(\theta) W_{20}(\theta) = 2i\tau_0 \omega_0 W_{20}(0) - h_{20}(0)$$
 (26)

and

$$\int_{-1}^{0} d\eta(\theta) W_{11}(\theta) = -h_{11}(0). \tag{27}$$

By the definition of $H(z, \bar{z}, \theta)$ in (22), we have

$$h_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + \tau_0 H_1, \tag{28}$$

$$h_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + \tau_0 H_2, \tag{29}$$

where

$$H_1 = \begin{bmatrix} -2(q_2^2 + \alpha q_2 q_3 e^{-i\tau_0 \omega_0}) \\ 2(\beta q_2 q_3 - q_3^2) \\ 0 \end{bmatrix},$$

$$H_2 = \begin{bmatrix} -2q_2 \bar{q}_2 - \alpha(\bar{q}_2 q_3 e^{-i\tau_0 \omega_0} + q_2 \bar{q}_3 e^{i\tau_0 \omega_0}) \\ \beta(\bar{q}_2 q_3 + q_2 \bar{q}_3) - 2q_3 \bar{q}_3 \\ 0 \end{bmatrix}.$$

Substituting (24) into (28), we obtain

$$\begin{bmatrix} r_1 - 2x^* - \alpha y_1^* - 2\mathrm{i}\omega_0 & -\alpha x^* e^{-2\mathrm{i}\omega_0 \tau_0} \\ -\beta y_1^* & -r_2 + \beta x^* - 2y_1^* - 2\mathrm{i}\omega_0 \\ 0 & 1 \end{bmatrix}$$

$$\begin{bmatrix} 0 \\ \gamma \\ -\eta - 2\mathrm{i}\omega_0 \end{bmatrix} E = H_1.$$

Hence, we have $E = \frac{1}{\Delta_1} (E_1^1, E_1^2, E_1^3)^T$, where

Hence, we have
$$E=\frac{1}{\Delta_1}\left(E_1^1,E_1^2,E_1^3\right)^{\mathrm{T}}$$
, where
$$\Delta_1=\begin{vmatrix}r_1-2x^*-\alpha y_1^*-2\mathrm{i}\omega_0&-\alpha x^*e^{-2\mathrm{i}\omega_0\tau_0}\\-\beta y_1^*&-r_2+\beta x^*-2y_1^*-2\mathrm{i}\omega_0\\0&1\end{vmatrix}$$

$$E_1^1=\begin{vmatrix}r_1-2x^*-\alpha y_1^*-2\mathrm{i}\omega_0\\-\beta y_1^*&-r_2+\beta x^*-2y_1^*-2\mathrm{i}\omega_0\\0&1\end{vmatrix}$$

$$E_1^1=\begin{vmatrix}r_1-2x^*-\alpha y_1^*-2\mathrm{i}\omega_0\\0&1\end{vmatrix}$$

$$C_1(0)=\frac{\mathrm{i}}{2\tau_0\omega_0}(g_{20}g_{11}-2|g_{11}|^2-\frac{1}{3}|g_{02}|^2)+\frac{g_{21}}{2}},$$

$$\mu_2=-\frac{\mathrm{Re}C_1(0)}{\mathrm{Re}\lambda'(\tau_0)},$$

$$T_2=-\frac{\mathrm{Im}C_1(0)+\mu_2\mathrm{Im}\lambda'(\tau_0)}{\tau_0\omega_0},$$

$$\beta_2=2\mathrm{Re}C_1(0).$$
From the expression of $C_1(0)$ in (30), it is easy to ge values of μ_2 , $\mu_2=1$ and $\mu_2=1$ and the direction of the Hopf bifurcation: if $\mu_2=1$ determines the direction of the Hopf bifurcation: if $\mu_2=1$ determines the stability of the bifurcating periodic solutions: if $\mu_2=1$ determines the stability of the bifurcating periodic solutions: if $\mu_2=1$ determines the period of bifurcating periodic solutions: the period increase (decrease $T_2>0$) bifurcating periodic solutions: the period increase (decrease $T_2>0$).

On the other hand, by (23), we get
$$\dot{W}_{20}(\theta)=2\mathrm{i}\tau_0\omega_0W_{20}(\theta)-\frac{1}{2}\psi_{20}(\theta)$$
. Solving it, we have
$$W_{20}(\theta)=\frac{ig_{20}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta}+\frac{i\bar{g}_{02}}{3\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta}+Ee^{2i\tau_0\omega_0\theta}.$$
 Similarly, we can get
$$W_{11}(\theta)=-\frac{ig_{11}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta}+\frac{\bar{g}_{11}}{i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta}+F. \tag{25}$$

$$U_{11}(\theta)=-\frac{ig_{11}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta}+\frac{\bar{g}_{11}}{i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta}+F. \tag{25}$$

$$U_{11}(\theta)=-\frac{ig_{11}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta}+\frac{\bar{g}_{11}}{i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta}+F. \tag{25}$$

Similarly, substituting (25) into (29), we can get F = $\frac{1}{\Lambda_2} \left(F_2^1, F_2^2, F_2^3 \right)^{\text{T}}$, where

$$\Delta_{2} = \begin{vmatrix} r_{1} - 2x^{*} - \alpha y_{1}^{*} & -\alpha x^{*} & 0 \\ -\beta y_{1}^{*} & -r_{2} + \beta x^{*} - 2y_{1}^{*} & \gamma \\ 0 & 1 & -\eta \end{vmatrix},$$

$$F_{2}^{1} = \begin{vmatrix} -2q_{2}\bar{q}_{2} - \alpha(\bar{q}_{2}q_{3}e^{-i\tau_{0}\omega_{0}} + q_{2}\bar{q}_{3}e^{i\tau_{0}\omega_{0}}) \\ \beta(\bar{q}_{2}q_{3} + q_{2}\bar{q}_{3}) - 2q_{3}\bar{q}_{3} \\ 0 \\ -\alpha x^{*} & 0 \\ -r_{2} + \beta x^{*} - 2y_{1}^{*} & \gamma \\ 1 & -\eta \end{vmatrix},$$

$$F_{2}^{2} = \begin{vmatrix} r_{1} - 2x^{*} - \alpha y_{1}^{*} \\ -\beta y_{1}^{*} \\ 0 \\ -2q_{2}\bar{q}_{2} - \alpha(\bar{q}_{2}q_{3}e^{-i\tau_{0}\omega_{0}} + q_{2}\bar{q}_{3}e^{i\tau_{0}\omega_{0}}) & 0 \\ \beta(\bar{q}_{2}q_{3} + q_{2}\bar{q}_{3}) - 2q_{3}\bar{q}_{3} & \gamma \\ 0 & -\eta \end{vmatrix},$$

$$F_{2}^{3} = \begin{vmatrix} r_{1} - 2x^{*} - \alpha y_{1}^{*} & -\alpha x^{*} \\ -\beta y_{1}^{*} & -r_{2} + \beta x^{*} - 2y_{1}^{*} \\ 0 & 1 \\ -2q_{2}\bar{q}_{2} - \alpha(\bar{q}_{2}q_{3}e^{-i\tau_{0}\omega_{0}} + q_{2}\bar{q}_{3}e^{i\tau_{0}\omega_{0}}) \\ \beta(\bar{q}_{2}q_{3} + q_{2}\bar{q}_{3}) - 2q_{3}\bar{q}_{3} \\ 0 \end{vmatrix}.$$

Based on the analysis above, we see that g_{ij} in (21) is determined by the parameters and the time delay in (4). Thus, we can calculate the following values

$$\begin{cases}
C_{1}(0) = \frac{1}{2\tau_{0}\omega_{0}}(g_{20}g_{11} - 2|g_{11}|^{2} - \frac{1}{3}|g_{02}|^{2}) + \frac{g_{21}}{2}, \\
\mu_{2} = -\frac{\operatorname{Re}C_{1}(0)}{\operatorname{Re}\lambda'(\tau_{0})}, \\
T_{2} = -\frac{\operatorname{Im}C_{1}(0) + \mu_{2}\operatorname{Im}\lambda'(\tau_{0})}{\tau_{0}\omega_{0}}, \\
\beta_{2} = 2\operatorname{Re}C_{1}(0).
\end{cases} (30)$$

From the expression of $C_1(0)$ in (30), it is easy to get the values of μ_2 , β_2 and t_2 . On the other hand, we know that μ_2 determines the direction of the Hopf bifurcation: if μ_2 > 0(<0), then the Hopf bifurcation is supercritical(subcritical) and the bifurcating periodic solutions exist for $\tau > \tau_0(<\tau_0)$; β_2 determines the stability of the bifurcating periodic solutions: if $\beta_2 < 0 (> 0)$ the bifurcating periodic solutions are stable(unstable); and T_2 determines the period of the bifurcating periodic solutions: the period increase(decrease) if $T_2 > 0 (< 0).$

IV. NUMERICAL SIMULATIONS

As an example, we present some numerical results of system (4) at different values. We consider the following system

$$\begin{cases} \dot{u}(t) = -0.1308u(t) - 0.7846v_1(t - \tau_1) \\ -u^2(t) - 6.0000u(t)v_1(t - \tau_1), \\ \dot{v}_1(t) = 0.1231u(t - \tau_2) - 0.5615v_1(t) + 0.9000v_2(t) \\ -v_1^2(t) + 2.0000v_1(t)u(t - \tau_2), \\ \dot{v}_2(t) = v_1(t) - 1.8000v_2(t), \end{cases}$$
(31)

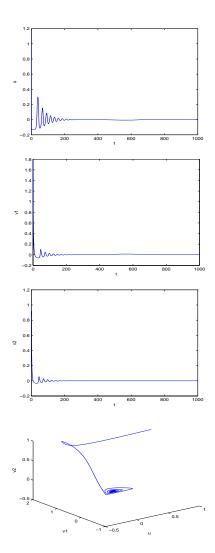


Fig.1 Behavior and phase portrait of system 31 with $\tau_1=\tau_2=1,\ (\tau_1+\tau_2<\tau_0)$. The positive equilibrium $z^*(0.1308,0.0615,0.0342)$ is asymptotically stable.

which has only one positive equilibrium $z^*(0.1308, 0.0615, 0.0342)$, when $\tau_1 = \tau_2 = 0$, the positive equilibrium $z^*(0.1308, 0.0615, 0.0342)$ is asymptotically stable. If follows from the discussion in Section 2 that $\omega_0 = 0.2571, \tau_0 = 2.6679, \frac{d\lambda(\tau_0)}{d\tau} = 0.0247 - 0.0181i$, and the conditions indicated in Theorem 1 is satisfied. Hence, we can say that as τ increase, stability switch may occur, the value of τ where stability switch occurs is $\tau_0 = 2.6679, (\tau_0 = \tau_1 + \tau_2)$. Thus, the positive equilibrium

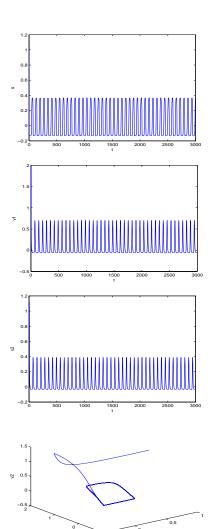


Fig.2 Behavior and phase portrait of system (31) with $\tau_1=6, \tau_2=8, \ (\tau_1+\tau_2>\tau_0)$. The bifurcating periodic solutions from $z^*(0.1308,0.0615,0.0342)$ occur.

 $z^*(0.1308, 0.0615, 0.0342)$ is asymptotically stable when $0 \le \tau < \tau_0$ as is illustrated by the computer simulations (see Fig.1).

When τ passes through the critical value τ_0 , z^* loses its stability and a Hopf bifurcation occurs, that is, a family of periodic solutions bifurcate from z^* , as is illustrated by the computer simulations (see Fig.2). From the formulae (30) in Section 3, it follows that $C_1(0) = -7.4847 - 1.4530i$, $\mu_2 = 303.0243$, $\beta_2 = -14.9694$, $T_2 = 10.1154$. Since $\mu_2 > 0$ and $\beta_2 < 0$, the Hopf bifurcation is supercritical and the direction of the bifurcation is $\tau > \tau_0$ and these bifurcating periodic solutions from z^* at τ_0 are stable.

Remark 1. If we take $\tau_1 = \tau_2$ in system (1), by similar calculating, the critical value of Hopf bifurcation occurs when $\tau^* = 1.3340$. So, when $\tau_1 = \tau_2 < 1.3340$, the positive equilibrium $z^*(0.1308, 0.0615, 0.0342)$ is asymptotically stable, when $\tau_1 = \tau_2 > 1.3340$, a Hopf bifurcation occurs. In this paper, the positive equilibrium $z^*(0.1308, 0.0615, 0.0342)$

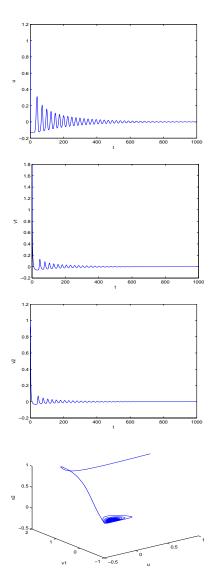


Fig.3 Behavior and phase portrait of system (31) with $\tau_1=1,\ \tau_2=1.5,\ (\tau_1<\tau^*,\ \tau_2>\tau^*,\ \tau_1+\tau_2<\tau_0).$ The positive equilibrium $z^*(0.1308,0.0615,0.0342)$ is asymptotically stable.

is asymptotically stable, we only need $\tau_1 + \tau_2 < 2.6679$, and when $\tau_1 + \tau_2 > 2.6679$, a Hopf bifurcation occurs(See Fig.3, Fig.4).

V. GLOBAL HOPF BIFURCATION

In this section, we study the existence of global Hopf bifurcations. The method we used here is based on the global Hopf bifurcating theorem for general functional differential equations introduced by Wu in [15]. For convenience, we write system (5) as the following form:

$$\dot{z} = F(z_t, \tau),\tag{32}$$

where $z = (x, y_1, y_2)^{\mathrm{T}}, \ z_t(\theta) = z(t + \theta) \in C([-1, 0], R^3).$ Define

$$X = C([-\tau, 0], R^3),$$

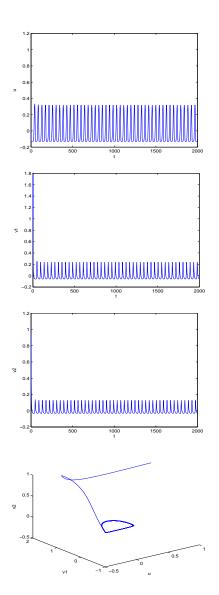


Fig.4 Behavior and phase portrait of system (31) with $\tau_1=1<\tau_0,\ \tau_2=3>\tau_0,\ (\tau_1<\tau^*,\ \tau_2>\tau^*,\ \tau_1+\tau_2>\tau_0).$ The bifurcating periodic solutions from $z^*(0.1308,0.0615,0.0342)$ occur.

$$\begin{split} \Sigma &= Cl\{(z(t),\tau,T) \in X \times R \times R^+, z(t) \text{ is a} \\ &\quad T - \text{periodic solution of (3)}\}, \\ N &= \{(\bar{z},\bar{\tau},\bar{T}), F(\bar{z},\bar{\tau},\bar{T}) = 0\}. \end{split}$$

Let $l_{(z^*,\tau_j,\frac{2\pi}{\omega_0})}$ be the connected component of $(z^*,\tau_j,\frac{2\pi}{\omega_0})$ in Σ , where τ_j and ω_0 are defined in (10).

Applying Theorem 2.1 in [3], we can obtain the following lemma directly.

Lemma 3. All solutions of system (5) are uniformly bounded.

Lemma 4. If (H_1) holds, then system (5) has no nontrivial periodic solutions of period τ .

Proof: Assume system (5) has a nontrivial periodic solu-

tion of period τ , then the following system

$$\begin{cases}
\dot{x}(t) = (r_1 - 2x^* - \alpha y_1^*)x(t) - \alpha x^* y_1(t) \\
-x^2(t) - \alpha x(t)y_1(t), \\
\dot{y}_1(t) = \beta y_1^* x(t) + (-r_2 + \beta x^* - 2y_1^*)y_1(t) \\
+\gamma y_2(t) - y_1^2(t) + \beta y_1(t)x(t), \\
\dot{y}_2(t) = y_1(t) - \eta y_2(t)
\end{cases} (33)$$

has periodic solutions. System (33) can be rewritten as

$$\begin{cases} \dot{x}_{1}(t) = -x(t)[(x(t) - x^{*}) + (y_{1}(t) - y_{1}^{*})], \\ \dot{x}_{2}(t) = \frac{r_{2}}{y_{2}^{*}}[y_{1}(t)(y_{2}(t) - y_{2}^{*}) - y_{2}(t)(y_{1}(t) - y_{1}^{*})] \\ -y_{1}(t)[(y_{1}(t) - y_{1}^{*}) - \beta(x(t) - x^{*})], \\ \dot{y}(t) = \frac{1}{y_{2}^{*}}[y_{2}(t)(y_{1}(t) - y_{1}^{*}) - y_{1}(y_{2}(t) - y_{2}^{*})]. \end{cases}$$
(34)

$$V(t) = \sum_{i=1}^{2} c_i \Big(y_i(t) - y_i^* - y_i^* \ln \frac{y_i(t)}{y_i^*} \Big) + x(t) - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) \\ = \deg_B \bigg(H^-(z^*, \tau_j, \frac{2\pi}{\omega_0}), \Omega_{\epsilon, \frac{2\pi}{\omega_0}} \bigg) + x(t) - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) \\ = \deg_B \bigg(H^-(z^*, \tau_j, \frac{2\pi}{\omega_0}), \Omega_{\epsilon, \frac{2\pi}{\omega_0}} \bigg) + x(t) - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) \\ = \deg_B \bigg(H^-(z^*, \tau_j, \frac{2\pi}{\omega_0}), \Omega_{\epsilon, \frac{2\pi}{\omega_0}} \bigg) + x(t) - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) \\ = \deg_B \bigg(H^-(z^*, \tau_j, \frac{2\pi}{\omega_0}), \Omega_{\epsilon, \frac{2\pi}{\omega_0}} \bigg) + x(t) - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) \\ = \deg_B \bigg(H^-(z^*, \tau_j, \frac{2\pi}{\omega_0}), \Omega_{\epsilon, \frac{2\pi}{\omega_0}} \bigg) + x(t) - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) \\ = 2\pi - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) + x(t) - x^* - x^* \ln \frac{x(t)}{x^*}, \quad \gamma \bigg(z^*, \tau_j, \frac{2\pi}{\omega_0} \bigg) \\ = 2\pi - x^* - x$$

where c_1 and c_2 are positive constants to be determined.

Calculating the derivative of V(t) along positive solutions to system (34), it follows that

$$\dot{V}(t) = \sum_{i=1}^{2} c_{i}(y_{i}(t) - y_{i}^{*}) \frac{\dot{y}_{i}(t)}{y_{i}(t)} + (x(t) - x^{*}) \frac{\dot{x}(t)}{x(t)}
= \frac{c_{2}(y_{2}(t) - y_{2}^{*})}{y_{2}^{*}y_{2}(t)} [y_{2}(t)(y_{1}(t) - y_{1}^{*})
-y_{1}(t)(y_{2}(t) - y_{2}^{*})]
+ \frac{c_{1}(y_{1}(t) - y_{1}^{*})}{y_{2}^{*}y_{1}(t)} [y_{1}(t)(y_{2}(t) - y_{2}^{*})
-y_{2}(t)(y_{1}(t) - y_{1}^{*})] - c_{1}(y_{1}(t) - y_{1}^{*})
[(y_{1}(t) - y_{1}^{*}) - \beta(x(t) - x^{*})]
-(x(t) - x^{*})[(x(t) - x^{*}) + \alpha(y_{1}(t) - y_{1}^{*})].$$
(35)

Setting $c_1 = c_2 = \frac{\alpha}{\beta}$, then it follows from (35) that

$$\dot{V}(t) = -\frac{\alpha}{\beta y_2^*} \left(\sqrt{\frac{y_1(t)}{y_2(t)}} (y_2(t) - y_2^*) - \sqrt{\frac{y_2(t)}{y_1(t)}} (y_1(t) - y_1^*) \right)^2 - \frac{\alpha}{\beta} (y_1(t) - y_1^*)^2 - (x(t) - x^*)^2 < 0.$$

Applying Barbalat's lemma [11], we conclude that

$$\lim_{t \to \infty} (x(t), y_1(t), y_2(t)) = (x^*, y_1^*, y_2^*),$$

which contradicts the fact that system (33) has periodic

Theorem 2. Suppose that (H_1) (H_2) and (H_3) hold, then for each $\tau > \tau_i(j = 0, 1, 2...)$, system (5) has at least j + 1periodic solutions, where τ_j is defined in (10).

Proof: The characteristic matrix of system (5) at the positive equilibrium z^* is of the form

$$\Delta(z^*, \tau, p)(\lambda) = \begin{bmatrix} r_1 - 2x^* - \alpha y_1^* - \lambda \\ \beta y_1^* \\ 0 \\ -\alpha x^* e^{-\lambda \tau} & 0 \\ -r_2 + \beta x^* - 2y_1^* - \lambda & \gamma \\ 1 & -\eta - \lambda \end{bmatrix}. (36)$$

By Lemma 1, it can be verified that $(z^*, \tau_j, \frac{2\pi}{\omega_0})$ are isolated centers.

Let

$$\Omega_{\epsilon,\frac{2\pi}{\omega_0}} = \bigg\{ (\eta,p) : 0 < \eta < \epsilon, \Big| p - \frac{2\pi}{\omega_0} \Big| < \epsilon \bigg\}.$$

Clearly, if $|\tau - \tau_j| \leq \delta$ and $(\eta, p) \in \partial \Omega_{\epsilon}$, then

$$\det(\Delta(z^*, \tau, p)\left(\eta + i\frac{2\pi}{p})\right) = 0,$$

if and only if $\eta = 0, \tau = \tau_j, p = \frac{2\pi}{\omega_0}$. Define

$$H^{\pm}(z^*, \tau_j, \frac{2\pi}{\omega_0})(\eta, p) = \Delta(z^*, \tau_j \pm \delta, p)(\eta + i\frac{2\pi}{n}),$$

then we have the crossing number of isolated center $(z^*, \tau_j, \frac{2\pi}{\omega_0})$ as follows

$$\gamma\left(z^*, \tau_j, \frac{2\pi}{\omega_0}\right) = \deg_B\left(H^-(z^*, \tau_j, \frac{2\pi}{\omega_0}), \Omega_{\epsilon, \frac{2\pi}{\omega_0}}\right) \\
-\deg_B\left(H^+(z^*, \tau_j, \frac{2\pi}{\omega_0}), \Omega_{\epsilon, \frac{2\pi}{\omega_0}}\right) = -1.$$

By Theorem 3.3 of Wu [15], we conclude that the connected component $l_{(z^*,\tau_j,\frac{2\pi}{\omega_0})}$ through $(z^*,\tau_j,\frac{2\pi}{\omega_0})$ in Σ is nonempty. Meanwhile, we have

$$\sum_{(z,\tau,p)\in l_{(z^*,\tau_j,\frac{2\pi}{20D})}}\gamma(z,\tau,p)<0,$$

and hence $l_{(z^*,\tau_j,\frac{2\pi}{\omega_0})}$ is unbounded. Lemma 3 implies that the projection of $l_{(z^*,\tau_j,\frac{2\pi}{\omega_0})}$ onto the z-space is bounded. From the definition of τ_i in (10), we have $\frac{2\pi}{\omega_0} < \tau_j$ for $j \geq 1$. Lemma 4 implies that the projection of $l_{(z^*,\tau_j,\frac{2\pi}{\omega_0})}$ onto the τ -space is bounded. Assume the projection of $l_{(z^*,\tau_j,\frac{2\pi}{\omega_0})}$ onto the τ -space is $(0,\tau^*)$ and $\tau^* > \tau_j$. Applying Lemma 4, we know $(z, \tau, p) \in l_{(z^*, \tau_i, \frac{2\pi}{2})}$ implies $p < \tau_j$. This shows that in order for $l_{(z^*,\tau_j,\frac{2\pi}{2dq})}$ to be unbounded, its projection onto the τ -space must be unbounded. Consequently, the projection of $l_{(z^*, au_j, \frac{2\pi}{d\omega})}$ onto the τ -space includes $[\tau_j, \infty)$. This shows that, for each τ_j , system (3) has j+1 nonconstant periodic solutions. The proof is complete.

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