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Hopf bifurcation of a predator-prey model with time delay and habitat complexity

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Abstract—In this paper, a predator-prey model with time delay and habitat complexity is investigated. By analyzing the characteristic equations, the local stability of each feasible equilibria of the system is discussed and the existence of a Hopf bifurcation at the coexistence equilibrium is established. By choosing the sum of two delays as a bifurcation parameter, we show that Hopf bifurcations can occur as τ crosses some critical values. By deriving the equation describing the flow on the center manifold, we can determine the direction of the Hopf bifurcations and the stability of the bifurcating periodic solutions. Numerical simulations are carried out to illustrate the main theoretical results.

Keywords—Predator-prey system; Delay; Habitat complexity; Hopf bifurcation;

I. Introduction

It is well-known that delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and cause the population to fluctuate. Time delays have been considered in mathematical models of population dynamics and predator-prey systems by many researchers, see [1], [2], [3], [4], [5], [6].

The most commonly used functional response in a predator-prey interaction is Holling Type III [10]. This Type III response function is represented mathematically by

$$g(x) = \frac{ax^2}{1+ahx^2}$$

where a is the attack coefficient and h is the handling time. In his experiment, Holling did not consider the existence of habitat complexity that can reduce the probability of capturing a prey by reducing the searching efficiency of predator. So the formula cannot be used directly in presence of habitat complexity, and thus require modification. Since habitat complexity is more likely to affect the attack coefficient than the handling time for search [11], so the attack coefficient a has to be replaced by $a(1-c)$, where $0 < c < 1$ is a dimension less parameter that measures the degree or strength of habitat complexity. Assume that the complexity is homogeneous throughout the habitat. Then the total number of prey caught, following Kot [12], is given by

$$V = a(1-c)T_s x,$$

where $T_s = T - hV$. Here T is the total time, T_s is the available search time and h is the handling time required per prey. Solving for V, we get the modified Holling type III predation formula that incorporates the effect of habitat complexity as

$$V = \frac{Ta(1-c)x^2}{1+a(1-c)hx^2}.$$

Since predator′s functional response is defined as the amount of prey catch per predator per unit of time, so the functional response in presence of habitat complexity will be represented by

$$g(x) = \frac{a(1-c)x^2}{1+a(1-c)hx^2}.$$

It is to be noted, when $c = 0$, i.e., when there is no complexity, we get back the original Holling Type III response function. Therefore, this modified functional response would be suitable for predator-prey interaction with habitat complexity. In particular, it would be more appropriate for laboratory, for example, in case of Luckinbill experiment[15]. Assume that prey population follows density-dependent logistic growth with intrinsic growth rate r and carrying capacity k. If predation process obeys the modified Type III response function, then the general predator-prey model would be transformed to the following system:

$$\begin{aligned} \frac{dx}{dt} &= rx(1-\frac{x}{k}) - \frac{a(1-c)xy}{1+a(1-c)hx^2}, \\ \frac{dy}{dt} &= \frac{ba(1-c)x(t-\tau)y(t-\tau)}{1+a(1-c)hx^2(t-\tau)} - dy. \end{aligned} \tag{1}$$

In system (1.1), $x(t)$ and $y(t)$ represent the densities of prey and predator at time t respectively.

The initial conditions for system (1.1) take the form

$$\begin{aligned} &x(t) = \phi_1(t),\ y(t) = \psi_2(t), \\ &\phi_1(t) \ge 0,\ \phi_2(t) \ge 0,\ t \in [-\tau, 0), \\ &\phi_1(0) > 0,\ \phi_2(0) > 0, \end{aligned} \tag{2}$$

where $(\phi_1(t),\ \phi_2(t)) \in ([-\tau, 0], R^2_{+0})$.

It is well-known by the fundamental theory of functional differential equations [8], that system (1.1) has a unique solution $(x(t), y(t))$ satisfying initial conditions (1.2). It is easy to show that all solutions of system (1.1) corresponding to initial conditions (1.2) are defined on $[0, +\infty)$ and remain positive for all $t \ge 0$. The organization of this paper is as follows. In the next section, by analyzing the corresponding characteristic equations, the local stability of each of the feasible equilibria of system (1.1) is discussed and the existence of a Hopf bifurcation at the coexistence equilibrium is established. In Section 3, the stability and direction of periodic solutions bifurcating from Hopf bifurcations are investigated by using the normal form theory and the center manifold theorem due

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to Hassard. Finally, in Section 4, numerical simulations are carried out to support the theoretical analysis of the research.

II. LOCAL STABILITY AND HOPF BIFURCATION

In ecology, stress is given on the stability of the coexisting equilibrium. We are, therefore, interested to investigate the local stability of the interior equilibrium of the system (1.1) which is given by $E(x_0, y_0)$, where $x_0 = \sqrt{\frac{d}{a(1-c)(b-hd)}}$ and $y_0 = \frac{br}{dk}x_0(k-x_0)$. Note that x_0 and y_0 will be biologically meaningful if $c < 1 - \frac{d}{ak^2(b-dh)}, hd + \frac{d}{ak^2} < b < 1$.

Let $X(t) = x(t) - x_0, Y(t) = y(t) - y_0$ are the perturbed variables. The system (1.1) can be expressed in the matrix form after linearization as follows:

$$\frac{d}{dt}\begin{pmatrix} X(t) \\ Y(t) \end{pmatrix} = A_1 \begin{pmatrix} X(t) \\ Y(t) \end{pmatrix} + A_2 \begin{pmatrix} X(t-\tau) \\ Y(t-\tau) \end{pmatrix}, \quad (3)$$

where

$$A_1 = \begin{pmatrix} r - \frac{2r}{k}x_0 + \frac{2r(dh-b)(k-x_0)}{kb} & -\frac{d}{b} \\ 0 & -d \end{pmatrix},$$

and

$$A_2 = \begin{pmatrix} 0 & 0 \\ -\frac{2d(hd-b)(k-x_0)}{k} & d \end{pmatrix}.$$

The characteristic equation of system (2.1) is given by

$$|A_1 + A_2 e^{-\xi\tau} - \xi I| = 0$$

namely

$$\Phi(\xi, \tau) = \xi^2 - (A + Be^{-\xi\tau})\xi + (C + De^{-\xi\tau}) = 0, \quad (4)$$

where

$$A = r - \frac{2r}{k}x_0 - \frac{2a(1-c)x_0y_0}{(1 + a(1-c)hx_0^2)^2} - d, \; B = d,$$

$$C = -d(r - \frac{2r}{k}x_0 - \frac{2a(1-c)x_0y_0}{(1 + a(1-c)hx_0^2)^2}),$$

$$D = d(r - \frac{2r}{k}x_0).$$

When there is no delay (i.e., $\tau = 0$), the corresponding characteristic equation is given by

$$\xi^2 - (A + B)\xi + (C + D) = 0$$

and the corresponding eigenvalues are $\xi_{1,2} = \frac{(A+B)\pm\sqrt{(A+B)^2 - 4(C+D)}}{2}$. For the stability of the equilibrium, real parts of the above two roots must be negative. Since $C + D > 0$, so ξ_1 and ξ_2 will have negative real parts if $A + B < 0$. After some algebraic manipulation and considering the existence condition, one can show that the non-delayed system will be stable if the conditions of the following theorem are hold.

Theorem 2.1: The system (1.1) is locally asymptotically stable without delay around the coexisting equilibrium point E if

(I) $hd + \frac{d}{ak^2} < b < 1$,

(II) $1 - \frac{4d^3h^2}{a(2hd-b)^2k^2(b-hd)}c < 1 - \frac{d}{ak^2(b-dh)}$.

For the delay-induced system (1.1), the interior equilibrium E will be asymptotically stable if all the roots of the corresponding characteristic have negative real parts. To determine the nature of the stability, we require the sign of the real parts of the roots of the (2.2). We start with the assumption that E is asymptotically stable in case of non-delayed system and then find conditions for which E is still stable for all delays [13]. By Rouche′s Theorem [14] and the continuity in τ, the transcendental (2.2) has roots with positive real parts if and only if it has purely imaginary roots. From this, we shall be able to find conditions for all eigenvalues to have negative real parts.

Let

$$\xi(\tau) = \eta(\tau) + i\omega(\tau),$$

where η and ω are real. As the interior equilibrium E of the non-delayed system is stable, we have $\eta(0) < 0$. By continuity, if $\tau(> 0)$ is sufficiently small, we still have $\eta(\tau) < 0$ and E is still stable. The change of stability will occur at some values of s for which $\eta(\tau) = 0, \omega(\tau) \neq 0$, that is n will be purely imaginary. Let $\bar{\tau}$ be such that $\eta(\bar{\tau}) = 0$ and $\omega(\bar{\tau}) = \bar{\omega} \neq 0$,so that $\xi = i\omega(\bar{\tau}) = i\bar{\omega}$. In this case, the steady state loses stability and eventually becomes unstable when $\eta(\tau)$ becomes positive. In other words, if such an $\omega(\bar{\tau})$ does not exist, i.e., if ξ be not purely imaginary for any $\tau = \bar{\tau}$, then the steady state E will always be stable.

Now, $i\omega$ is a root of (2.2) if and only if

$$-\bar{\omega}^2 - (A + Be^{-i\bar{\omega}\bar{\tau}})i\bar{\omega} + (C + De^{-\bar{\omega}\bar{\tau}}) = 0.$$

According to the real and imaginary parts of both sides, we get

$$-\bar{\omega}^2 + C = B\bar{\omega}\sin\bar{\omega}\bar{\tau} - D\cos\bar{\omega}\bar{\tau},$$

$$A\bar{\omega} = -(B\bar{\omega}\cos\bar{\omega}\bar{\tau} + D\sin\bar{\omega}\bar{\tau}).$$

From the above two equations, we obtain

$$f(\bar{\omega}) = \bar{\omega}^4 + (A^2 - B^2 - 2C) + (C^2 - D^2) = 0. \quad (5)$$

If we assume $\bar{\omega}^2 = Y, M = A^2 - B^2 - 2C, N = C^2 - D^2$, $f(\bar{\omega})$ could be reduced to

$$\Phi(Y) = Y^2 + MY + N = 0. \quad (6)$$

Note that

$$M = A^2 - B^2 - 2C = (-r + \frac{2rhd}{b} - \frac{2rhd}{bk}x_0)^2$$

is always positive. If $N > 0$ then all roots of the (2.4) have negative real parts for all delay and the equilibrium E is locally asymptotically stable. If $N < 0$, then the (2.4) has one positive root. It follows that the (2.4) will have a positive root $\bar{\omega}$. This implies that the characteristic (2.2) will have a pair of purely imaginary roots $\pm i\bar{\omega}$ such that $\eta(\bar{\tau}) = 0$ and $\omega(\bar{\tau}) = \bar{\omega}$. Solving for $\bar{\tau}$, we have

$$\bar{\tau}_j = \frac{1}{\bar{\omega}}\cos^{-1}(\frac{\bar{\omega}^2(D - AB) - CD}{B^2\bar{\omega}^2 + D^2}) + \frac{2j\pi}{\bar{\omega}}, \; j = 0, 1, 2, 3, \cdots$$

Also we can verify the following transversally condition:

$$\frac{d}{d\tau}Re(\xi) > 0$$

and $\tau = \bar{\tau}$, where $\bar{\tau}$ is the value of $\bar{\tau}_j$ for $j = 0$.

Differentiating (2.2) with respect to τ, we obtain

$$\begin{aligned} &2\xi\tfrac{d\xi}{d\tau} - (A + Be^{-\xi\tau})\tfrac{d\xi}{d\tau} - \xi Be^{-\xi\tau}(-\tau\tfrac{d\xi}{d\tau} - \xi) \\ &+De^{-\xi\tau}(-\tau\tfrac{d\xi}{d\tau} - \xi) = 0 \end{aligned}$$

This gives

$$\begin{aligned} (\tfrac{d\xi}{d\tau})^{-1} &= \tfrac{2\xi - A}{(D\xi - B\xi^2)e^{-\xi\tau}} + \tfrac{B\xi\tau - D\tau - B}{D\xi - B\xi^2} \\ &= \tfrac{2\xi - A}{A\xi^2 - C\xi - \xi^3} - \tfrac{B}{D\xi - B\xi^2} - \tfrac{\tau}{\xi} \end{aligned}$$

At $\tau = \bar{\tau}, \xi = i\bar{\omega}$, since $M > 0$, then

$$\begin{aligned} [\tfrac{d(Re\xi(\tau))}{d\tau}]^{-1}_{\tau=\bar{\tau}} &= \tfrac{(A^2 - B^2 - 2C)\bar{\omega}^2 + 2\bar{\omega}^4}{B^2\bar{\omega}^2 + D^2} \\ &= \tfrac{M\bar{\omega}^2 + 2\bar{\omega}^4}{B^2\bar{\omega}^2 + D^2} > 0, \end{aligned}$$

By continuity, the real part of $\eta(\tau)$ becomes positive when $\tau > \bar{\tau}$ and the steady state becomes unstable. Moreover, a Hopf bifurcation occurs when τ passes through the critical value $\bar{\tau}$. Now we can state the following theorem:

Theorem 2.2: Suppose conditions of the Theorem 2.1 hold. Then the following results are true. (i) If $N \leq 0$, then the equilibrium E of the system (1.1) is locally asymptotically stable for $\tau < \bar{\tau}$ and unstable when $\tau > \bar{\tau}$ where

$$\bar{\tau} = \frac{1}{\bar{\omega}}\cos^{-1}[\frac{\bar{\omega}^2(D - AB) - CD}{B^2\bar{\omega}^2 + D^2}] \qquad (7)$$

when $\tau = \bar{\tau}$, a Hopf-bifurcation occurs as τ passes through the critical value $\bar{\tau}$ [9].
(ii) If $N > 0$, then the equilibrium E of the system (1.1) is locally asymptotically stable for all $\tau \geq 0$.

III. Stability of bifurcated periodic solutions

In the previous section, we have obtained the conditions under which a family of periodic solutions bifurcate from the positive equilibrium of system (1.1) when the delay crosses through the critical value τ_j . In this section, we shall study the direction of these Hopf bifurcations and stability of bifurcated periodic solutions arising through Hopf bifurcations by applying the normal form theory and center manifold theorem introduced by Hassard et al. [9].

Let $\bar{x}(t) = x(t) - x_1^*, \bar{y}(t) = y(t) - y^*$, then system (1.1) can be transformed into

$$\begin{aligned} \tfrac{d\bar{x}(t)}{dt} &= (-r + \tfrac{2rhd}{bk}(k - x_0))\bar{x}(t) - \tfrac{d}{b}\bar{y}(t) - \tfrac{r}{k}\bar{x}(t)^2 \\ &\quad - a(1-c)f(\bar{x}(t), \bar{y}(t)), \\ \tfrac{d\bar{y}}{dt} &= -d\bar{y}(t) + \tfrac{2r(b-dh)(k-x_0)}{bk}\bar{x}(t-\tau) + d\bar{y}(t-\tau) \\ &\quad + ab(1-c)f(\bar{x}(t-\tau), \bar{y}(t-\tau)), \end{aligned} \qquad (8)$$

where

$$f(x, y) = \frac{c_2xy(x + 2x_0) + x^2(c_3 - 2a(1-c)hx_0y_0x)}{c_2^2(c_2 + a(1-c)h(x^2 + 2x_0x))},$$

$$c_2 = 1 + a(1-c)h(x_0)^2, c_3 = y^*(1 - 3a(1-c)h(x_0)^2).$$

Let $t = s\tau, \bar{x}(s\tau) = \hat{x}(s), \bar{y}(s\tau) = \hat{y}(s), \tau = \tau_0 + \mu, \mu \in R, \tau_0$ is defined by (2.5), then system (3.1) can be transformed as an FDE in $C = C([-1, 0], R^2)$, we still denote $x = \hat{x}, y = \hat{y}$,

$$\begin{aligned} \tfrac{dx}{dt} &= (\tau_0 + \mu)((-r + \tfrac{2rhd}{bk}(k - x_0))x(t) - \tfrac{d}{b}y(t) \\ &\quad - \tfrac{r}{k}\bar{x}(t)^2 - a(1-c)f(x(t), y(t))), \\ \tfrac{dy}{dt} &= (\tau_0 + \mu)(-dy(t) + \tfrac{2r(b-dh)(k-x_0)}{bk}x(t-1) \\ &\quad + dy(t-1) + ab(1-c)f(x(t-1), y(t-1))). \end{aligned} \qquad (9)$$

For $\phi = (\phi_1, \phi_2)^T \in C([-1, 0], R^2)$, we define

$$L_\mu\phi = B\phi(0) + C\phi(-1),$$

where

$$B = (\tau_0 + \mu)\begin{pmatrix} -r + \frac{2rhd}{bk}(k - x_0) & -\frac{d}{b} \\ 0 & -d \end{pmatrix},$$

$$C = (\tau_0 + \mu)\begin{pmatrix} 0 & 0 \\ \frac{2r(b-dh)(k-x_0)}{k} & d \end{pmatrix}.$$

and

$$F(\mu, \phi) = (\tau_0 + \mu)\begin{pmatrix} -\frac{r}{k}\phi_1(0)^2 - a(1-c)f(\phi_1(0), \phi_2(0)) \\ ab(1-c)f(\phi_1(-1), \phi_2(-1)). \end{pmatrix}$$

By the Riesz representation theorem, there exists a 2×2 matrix function $\eta(\theta, \mu) : [-1, 0] \longrightarrow R^2$ whose elements are of bounded variation such that

$$L_\mu\phi = \int_{-1}^0[d\eta(\theta, \mu)]\phi(\theta) \quad for\ \phi \in C([-1, 0], R^2). \qquad (10)$$

In fact, we choose

$$\eta(\theta, \mu) = B\delta(\theta) + C\delta(\theta + 1)$$

Then (3.3) is satisfied.

For $\phi \in C([-1, 0], R^2)$, define

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

and

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

Then system (3.1) is equivalent to the following operator equation

$$\dot{U}(t) = A(\mu)U_t + R(\mu)U_t,$$

where $U = (x, y)^T, U_t = U(t + \theta)\ for\ \theta \in [-1, 0]$.

For $\psi \in C([-1, 0], (R^2)^*)$, define

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

For $\phi \in C([-1, 0], R^2)$ and $\psi \in C([-1, 0], (R^2)^*)$, define a bilinear form

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

where $\eta(\theta) = \eta(\theta, 0)$. Then $A(0)$ and A^* are adjoint operators.

From the discussion in Section 2, we know that $\pm i\tau_0\omega_0$ are eigenvalues of $A(0)$ and therefore they are also eigenvalues of A^*. It is not difficult to verify that

Lemma 3.1: $q(\theta) = (1,\rho)^T e^{i\omega_0\tau_0\theta}$ and $q^*(s) = D(1,\rho^*)^T e^{i\omega_0\tau_0 s}$ are the eigenvectors of $A(0)$ and A^* corresponding to the eigenvalue $i\tau_0\omega_0$ and $-i\tau_0\omega_0$ respectively, and $\langle q^*(s), q(\theta)\rangle = 1,\ \langle q^*(s), \bar{q}(\theta)\rangle = 0$, where

$$\rho = -\frac{2r(b-hd)(k-x_0)e^{-i\bar{\omega}\tau_0}}{k(i\bar{\omega}+d-de^{-i\bar{\omega}\tau_0})},$$

$$\rho^* = \frac{d}{b(i\bar{\omega}-d+de^{-i\bar{\omega}\tau_0})},$$

$$\bar{D} = \frac{1}{1+\rho\bar{\rho}^*+\bar{\rho}^*\tau_0 e^{-i\bar{\omega}\tau_0}(d\bar{\rho}+\frac{2r(b-dh)(k-x_0)}{bk})}.$$

Following the algorithms given in Hassard et al[9] and using a computation process similar to that of Wei and Ruan [7] with the help of Mathematic 8.0, we can obtain the coefficients which will be used for determining the important qualities:

$$\begin{aligned}
g_{20} &= 2\tau_0\bar{D}(-\tfrac{r}{k}-\tfrac{a(1-c)c_3}{c_2^3}-\tfrac{2a(1-c)x_0}{c_2^2}\rho \\
&\quad +\tfrac{ab(1-c)}{c_2^3}\bar{\rho}^* e^{-2i\bar{\omega}\tau_0}(c_3+2c_2x_0\rho)),\\
g_{11} &= 2\tau_0\bar{D}(-\tfrac{r}{k}-\tfrac{a(1-c)c_3}{c_2^3}-\tfrac{2a(1-c)x_0}{c_2^2}Re(\rho) \\
&\quad +\tfrac{ab(1-c)}{c_2^3}\bar{\rho}^*(c_3+2c_2x_0Re(\rho))),\\
g_{02} &= 2\tau_0\bar{D}(-\tfrac{r}{k}-\tfrac{a(1-c)c_3}{c_2^3}-\tfrac{2a(1-c)x_0}{c_2^2}\bar{\rho} \\
&\quad +\tfrac{ab(1-c)}{c_2^3}\bar{\rho}^* e^{2i\bar{\omega}\tau_0}(c_3+2c_2x_0\bar{\rho}))\\
g_{21} &= 2\tau_0\bar{D}[(-\tfrac{r}{k}-\tfrac{a(1-c)c_3}{c_2^3})(W_{20}^{(1)}(0)+2W_{11}^{(1)}(0) \\
&\quad +\tfrac{12a^2(1-c)^2hx_0(c_3+c_2y_0)}{c_2^4}-\tfrac{a(1-c)x_0}{c_2^2}(W_{20}^{(1)}(0)\bar{\rho} \\
&\quad +W_{20}^{(2)}(0)+2W_{11}^{(1)}(0)\rho+W_{11}^{(2)}(0)) \\
&\quad -\tfrac{a(1-c)(c_2-4a(1-c)hx_0^2)}{c_2^3}\bar{\rho}] \\
&\quad +\tfrac{ab(1-c)}{c_2^4}\bar{\rho}^* e^{-i\bar{\omega}\tau_0}(c_2c_3(W_{20}^{(1)}(-1) \\
&\quad +2W_{11}^{(1)}(-1))-12a(1-c)hx_0(c_3+c_2y_0) \\
&\quad +c_2^2x_0(W_{20}^{(1)}(-1)+W_{20}^{(2)}(-1))\bar{\rho}e^{2i\bar{\omega}\tau_0} \\
&\quad +c_2(c_2-4a(1-c)hx_0^2)\bar{\rho}))
\end{aligned} \tag{11}$$

where

$$W_{20}(\theta) = \frac{ig_{20}}{w_0\tau_0}q(0)e^{i\omega_0\tau_0\theta}+\frac{i\bar{g}_{20}}{3w_0\tau_0}\bar{q}(0)e^{-i\omega_0\tau_0\theta}+E_1e^{2i\omega_0\tau_0\theta},$$

and

$$W_{11}(\theta) = -\frac{ig_{11}}{w_0\tau_0}q(0)e^{i\omega_0\tau_0\theta}+\frac{i\bar{g}_{11}}{w_0\tau_0}\bar{q}(0)e^{-i\omega_0\tau_0\theta}+E_2.$$

Moreover E_1, E_2 satisfy the following equations, respectively,

$$\begin{pmatrix} r-\frac{2rhd}{bk}(k-x_0)+2i\bar{\omega} & \frac{d}{b} \\ \frac{2r(b-dh)(k-x_0)}{bk}e^{-2i\bar{\omega}\bar{\tau}} & 2i\bar{\omega}+d-de^{-2i\bar{\omega}\tau_0} \end{pmatrix} E_1 = \begin{pmatrix} -\frac{r}{k}-\frac{a(1-c)c_3}{c_2^3}-\frac{2a(1-c)x_0}{c_2^2}\rho \\ \frac{ab(1-c)}{c_2^3}e^{-2i\bar{\omega}\tau_0}(c_3+2c_2x_0\rho) \end{pmatrix},$$

$$\begin{pmatrix} r-\frac{2rhd}{bk}(k-x_0) & \frac{d}{b} \\ \frac{2r(b-dh)(k-x_0)}{bk} & 0 \end{pmatrix} E_2 = \begin{pmatrix} -\frac{r}{k}-\frac{a(1-c)c_3}{c_2^3}-\frac{2a(1-c)x_0}{c_2^2}\rho \\ \frac{ab(1-c)}{c_2^3}(c_3+2c_2x_0\rho) \end{pmatrix},$$

Because each g_{ij} is expressed by the parameters and delay in (1.1), we can compute the following quantities:

$$\begin{aligned}
C_1(0) &= \tfrac{i}{2\omega_0\tau_0}(g_{11}g_{20}-2|g_{11}|^2-\tfrac{1}{3}|g_{02}|^2)+\tfrac{g_{21}}{2},\\
\mu_2 &= -\tfrac{ReC_1(0)}{Re\lambda'(\tau_0)},\\
\beta_2 &= 2Re\{C_1(0)\},\\
T_2 &= \tfrac{ImC_1(0)+\mu_2 Im\lambda'(\tau_0)}{\omega_0\tau_0}.
\end{aligned} \tag{12}$$

It is known that 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 bifurcating periodic solutions exist for $\tau > \tau_0$ ($\tau < \tau_0$). β_2 determines the stability of the bifurcating periodic solutions: the bifurcating periodic solutions on the center manifold are stable (unstable) if $\beta_2 < 0$ ($\beta_2 > 0$); and T_2 determines the period of the bifurcating periodic solutions: the period increases (decreases) if $T_2 > 0 (T_2 < 0)$.

From the discussion in Section 2, we know that $Re(\lambda'(\tau_0)) > 0$, therefore we have the following result,

Theorem 3.1: The direction of the Hopf bifurcation of system (1.1) at the origin when $\tau = \tau_j (j = 0,1,2,\cdots)$ is supercritical (subcritical) and the bifurcating periodic solutions on the center manifold are stable (unstable) if $Re\{C_1(0)\} < 0 (> 0)$; particularly, when $\tau = \tau_0$, the stability of the bifurcating periodic solutions is the same as that on the center manifold.

IV. Computer simulations

To demonstrate the algorithm for determining the properties of Hopf bifurcation in Section 3 and the Hopf bifurcation results in Section 4, we carry out numerical simulations on a particular case of (1.1) in the following form.

In (1.1), let $a = 0.045, b = 0.215, d = 1, h = 0.05, c = 0.5, k = 898; r = 2.5$. It is easy to show that system (1.1) has a unique coexistence equilibrium

$$E^*(16.4122, 8.66033).$$

By calculation, we have

$$C - D = -1.05016 < 0, \bar{\omega} \approx 0.39336,$$

$$\tau_0 \approx 0.853, C_1(0) \approx 0.0915442 - 0.776854i,$$

$$\mu_2 \approx -0.0720903, \beta_2 \approx 0.183088, T_2 \approx -0.665963.$$

By Theorem 2.1, E^* is locally asymptotically stable if $0 < \tau < \tau_0$ and is unstable if $\tau > \tau_0$, and system (1.1) undergoes a Hopf bifurcation at E^* when $\tau = \tau_0$, we know that the bifurcation is supercritical and the bifurcating periodic solution is asymptotically stable(see Fig. 1). With the increasing of the delays, System (1.1) will show the complicated dynamical behaviors. A numerical simulation illustrates this fact (see Fig. 2).

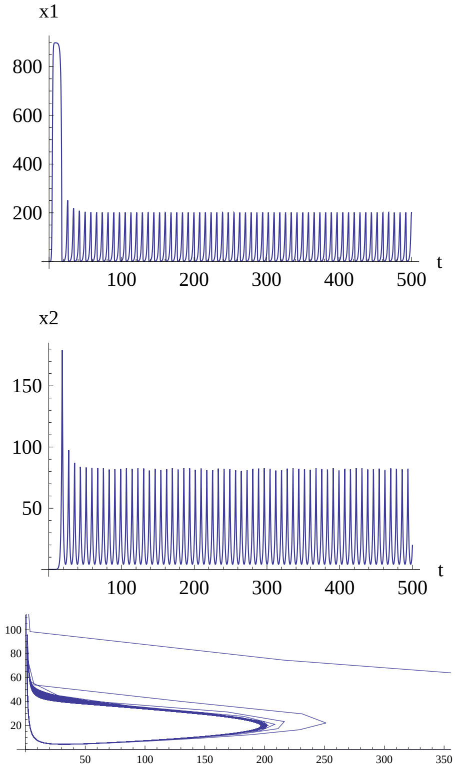

Fig1: $\tau = 0.9 > 0.853, E^*$ is unstable.

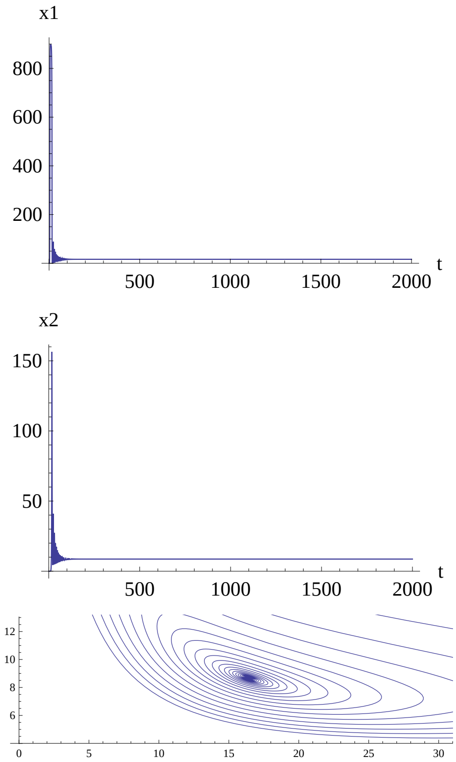

Fig2: $\tau = 0.8 < 0.853, E^*$ is locally asymptotically stable.

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References

[1] J.M. Cushing, Integro-differential equations and delay models in population dynamics, in: Lecture Notes in Biomathematics 20, Springer-Verlag, Berlin, Heidelberg, New York, 1977.
[2] K. Gopalsamy, Stability and Oscillations in Delay Differential Equations of Population Dynamics, Kluwer Academic, Dordrecht, Norwell, MA 1992.
[3] Y. Kuang, Delay Differential Equations with Applications in Population Dynamics, Academic Press, New York, 1993.
[4] M.S. Bartlett, On theoretical models for competitive and predatory biological systems, Biometrika 44 (1957) 27-42.
[5] E. Beretta, Y. Kuang, Global analyses in some delayed ratio-dependent predator-prey systems, Nonlinear Anal. TMA 32 (1998) 381-408.
[6] P.J. Wangersky, W.J. Cunningham, Time lag in prey-predator population models, Ecology 38 (1957) 136-139.
[7] J.Wei, S. Ruan, Stability and bifurcation in a neural network model with two delays, Physica D 130 (1999) 255-272.
[8] J.K. Hale, Theory of Functional Differential Equations, Springer, New York, 1976.
[9] B. Hassard, N. Kazarinoff, Y. Wan, Theory and Applications of Hopf Bifurcation, Cambridge University Press, Cambridge, 1981.
[10] C.S. Holling, Some characteristics of simple types of predation and parasitism, Can. Entomologist 91 (1959) 385-398.
[11] I.J. Winfield, The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, Rutilus rutilus, rudd, Scardinius erythrophthalmus, and perch, Perca fluviatilis, J. Fish Biol. 29 (1986) 37-48.
[12] M. Kot, Elements of Mathematical Ecology, Cambridge Univ. Press, Cambridge, 2001.
[13] R.V. Culshaw, S. Ruan, A Delay-differential equation model of HIV infection of CD4+ T-cells, Math. Biosci. 165 (2000) 27-39.
[14] J. Dieudonne, Foundations of Modern Analysis, Academic Press, New York, 1960.
[15] L. Luckinbill, Coexistence in laboratory populations of Paramecium aurelia and its predator Didinium nasutum, Ecology 54 (1973) 1320-1327.