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STABILITY AND BIFURCATION IN A DELAYED PREDATOR-PREY MODEL WITH HOLLING-TYPE IV RESPONSE FUNCTION AND AGE STRUCTURE

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Abstract. In this article, we study a predator-prey model with age structure, Holling-type IV response, and two time delays. By an algebraic method, we determine all the critical values for these two delays, such that the characteristic equation has purely imaginary roots. This provides a sharp stability region on the parameter plane of the positive equilibrium. Applying integrated semigroup theory and Hopf bifurcation theorem for abstract Cauchy problems with non-dense domain, we can show the occurrence of Hopf bifurcation as the time delays pass through these critical values. In particular, the phenomenon of stability switches can also be observed as the time delays vary. Numerical simulations are carried out to illustrate the theoretical results.

1. Introduction

There is a long history of studies on the interaction between predator and prey in ecology [4, 10, 22, 25]. A typical mathematical model for describing this interaction is

$$\begin{aligned} \dot{x} &= p(x) - yq(x), \\ \dot{y} &= cyq(x) - dy, \end{aligned} \tag{1.1}$$

where $x(t)$ and $y(t)$ are the population densities of the prey and predator, respectively; $p(x)$ is the birth function of prey; $q(x)$ is the intake rate of predator as a function of prey; c is the assimilation efficiency of predator; and d represents predator's death rate. Equation (1.1) has been extensively studied for various choices of $p(x)$ and $q(x)$. The logistic growth is frequently assumed for the increment of prey, that is, $p(x) = rx(1 - x/K)$, where r denotes intrinsic growth rate of prey, and K is the carrying capacity of the prey. Holling type functional responses are probably the most commonly used functions for $q(x)$, and various dynamics, such as global attractivity of equilibrium and existence of limit cycle, can be observed for (1.1) with those functional responses, see [8, 9, 12]. To study the phenomenon of group defense, non-monotonic functional responses are also proposed. A typical choice of non-monotonic functional response is the so-called Holling type IV functional response, i.e. $q(x) = \frac{mx}{x^2+b_1x+a}$, and we refer the readers to [5, 14] for more details.

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If a time delay τ is incorporated in the model (1.1), then it turns into

$$\begin{aligned} \frac{\mathrm{d}x(t)}{\mathrm{d}t} &= p(x) - yq(x(t-\tau)), \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} &= cyq(x(t-\tau)) - dy. \end{aligned} \tag{1.2}$$

Here, the delay τ takes into account the transformation time from prey quantities into predator populations. The dynamical behaviors of (1.2) are shown to be much more complicated than (1.1), see [6, 11, 21, 24] and references therein. In particular, the authors also consider (1.2) for logistic growth $p(x)$ and Holling type IV $q(x)$ with $b_1 = 0$ [18, 28]. However, not much attention has been paid in the case of $b_1 \neq 0$ [**?**].

In this article, we consider a more generalized version of (1.2), namely

$$\begin{gathered} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu u(t,a), \\ \frac{\mathrm{d}V(t)}{\mathrm{d}t} = rV(t)\Big(1 - \frac{V(t)}{K}\Big) - \frac{V(t-\tau_1)\int_0^{+\infty}\beta(a)u(t,a)da}{V^2(t-\tau_1) + b_1V(t-\tau_1) + 1}, \\ u(t,0) = \frac{V(t-\tau_1)\int_0^{+\infty}\beta(a)u(t,a)da}{V^2(t-\tau_1) + b_1V(t-\tau_1) + 1}, \\ u(0,\cdot) = u_0 \in L^1((0,+\infty),\mathbb{R}), V_0 = \phi \in C([-\tau_1,0],\mathbb{R}), \end{gathered} \tag{1.3}$$

where $u(t,a)$ is the density of predator of age a at time t; $V(t)$ is the population of prey; $\beta(a)$ is the maturation function which describes the effects of age on fecundity. If $\beta(a) = 1_{[0,+\infty)}(a)$ and $U(t) = \int_0^{+\infty} u(t,a)da$, then (1.3) will degenerate to (1.2). Throughout this paper, the kernel $\beta(a)$ is assumed to take the form

$$\beta(a) := \begin{cases} \beta^*, & a \geq \tau_2, \\ 0, & a \in [0,\tau_2), \end{cases}$$

such that $\int_0^{+\infty}\beta(a)e^{-\mu a}da = M < +\infty$, where $\tau_2 > 0$ is the maturation period of predator. For age-structure model like (1.3), it is conjectured in [2] that the maturation period τ_2 could induce periodic oscillation. However, this is not rigorously proved until the development of Hopf bifurcation theory for an abstract non-densely defined Cauchy problem in [16]. This theory is established on the basis of centre manifold theorem [19] and normal form reduction [17], under the framework of integrated semigroups [26], and has been successfully applied to many age structured models [27, 15, 29]. Recall that the delay τ may also destablize the positive equilibrium of (1.2), generating periodic solutions. Therefore, it is our interest to investigate the interactive impact of τ_1 and τ_2 on the dynamics of (1.3). By analyzing the characteristic equation of (1.3) at the positive equilibrium, we determine all the values of (τ_1,τ_2) such that the characteristic equation has roots with zero real parts. This will give the sharp region on (τ_1,τ_2)-plane, where (1.3) has locally stable positive equilibrium. Furthermore, as (τ_1,τ_2) passes through the boundary of this region, we can show the existence of periodic solution with different period by Hopf bifurcation theorem.

It should be mentioned that the characteristic equation of (1.3) takes the form

$$P_0(\lambda) + P_1(\lambda)e^{-\lambda\tau_1} + P_2(\lambda)e^{-\lambda\tau_2} + P_3(\lambda)e^{-\lambda(\tau_1+\tau_2)} = 0, \tag{1.4}$$

where $P_k(\lambda)$, $k = 1, 2, 3$ are polynomials of λ. In [13], the authors present a systematic analytic method for finding the crossing curves (on which (1.4) has purely imaginary roots) of (1.4) on (τ_1, τ_2)-plane, which will be employed here to study the characteristic equation of (1.3). When $P_3(\lambda) = 0$, the authors in [7] propose a geometric method for detecting the crossing curves, and list all the possibility of their shapes. As a special case, equation (1.4) with $\tau_1 = \tau_2$ is also studied in [1], presenting the explicit formula for the critical values of Hopf bifurcation.

This article is organized as follows: In Section 2, we formulate the initial age-structured model (1.3) as an abstract Cauchy problem. In Section 3, we show the existence of the positive steady state of system (1.3), and then derive its the characteristic equation. In Section 4, we analyze the distribution of the roots for characteristic equation, and obtain the the crossing curves on (τ_1, τ_2)-plane and crossing directions. These curves will not only determine the stability region for the positive steady state, but also tell where Hopf bifurcation could take place. In particular, for $\tau_1 = \tau_2 = \tau$, we derive the explicit formula for Hopf bifurcation values of τ. In Section 5, we conduct some numerical simulations to verify the results.

2. Transformation to Cauchy problem

Let $\widehat{a} = \frac{a}{\tau_2}, \widehat{t} = \frac{t}{\tau_2}$ and $\widehat{V}(\widehat{t}) = V(\tau_2 \widehat{t}), \widehat{u}(\widehat{t}, \widehat{a}) = \tau_2 u(\tau_2 \widehat{t}, \tau_2 \widehat{a})$. Then, system (1.3) becomes, after dropping the hat,

$$
\begin{gathered}
\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu\tau_2 u(t,a),\\
\frac{\mathrm{d}V(t)}{\mathrm{d}t} = \tau_2\Big[rV(t)\big(1 - \frac{V(t)}{K}\big) - \frac{V(t-\frac{\tau_1}{\tau_2})\int_0^{+\infty}\beta(a)u(t,a)\,\mathrm{d}a}{V^2(t-\frac{\tau_1}{\tau_2}) + b_1 V(t-\frac{\tau_1}{\tau_2}) + 1}\Big],\\
u(t,0) = \frac{\tau_2 V(t-\frac{\tau_1}{\tau_2})\int_0^{+\infty}\beta(a)u(t,a)\,\mathrm{d}a}{V^2(t-\frac{\tau_1}{\tau_2}) + b_1 V(t-\frac{\tau_1}{\tau_2}) + 1},\\
u(0,\cdot) = u_0 \in L^1((0,+\infty),\mathbb{R}), \quad V_0 = \phi \in C([-\frac{\tau_1}{\tau_2}, 0], \mathbb{R}),
\end{gathered}
\tag{2.1}
$$

where the function $\beta(a)$ is now defined by

$$
\beta(a) = \begin{cases} \beta^*, & a \ge 1,\\ 0, & 0 \le a < 1,\end{cases}
$$

with $\beta^* = \delta\mu M e^{\delta\mu\tau_2}$.

To derive the positive equilibrium and its characteristic equation, we need to formulate it into as an abstract non-densely defined Cauchy problem. This can be accomplished by the following steps:

Step 1: Rewrite (2.1) as a system of first order partial differential equations. We denote by $\rho(t,a)$ the density of prey of age a at time t. Let

$$
V(t) := \int_0^{+\infty} \rho(t,a)\,\mathrm{d}a.
$$

Then, from the second equation in system (2.1), we have

$$
\begin{gathered}
\frac{\partial \rho(t,a)}{\partial t} + \frac{\partial \rho(t,a)}{\partial a} = -\tau_2 d\rho(t,a),\\
\rho(t,0) = G(u(t,a), \rho(t,a)),
\end{gathered}
$$

$$\rho(0,a)=\rho_0\in L^1((0,+\infty),\mathbb{R}).$$

Here

$$\begin{aligned}G(u(t,a),\rho(t,a)) =&\tau_2\Big[b\int_0^{+\infty}\rho(t,a)\,\mathrm{d}a\Big(1-\frac{\int_0^{+\infty}\rho(t,a)\,\mathrm{d}a}{K}\Big)+\frac{d(\int_0^{+\infty}\rho(t,a)\,\mathrm{d}a)^2}{K}\\ &-\frac{\int_0^{+\infty}\rho(t-\frac{\tau_1}{\tau_2},a)\,\mathrm{d}a\int_0^{+\infty}\beta(a)u(t,a)\,\mathrm{d}a}{[\int_0^{+\infty}\rho(t-\frac{\tau_1}{\tau_2},a)\,\mathrm{d}a]^2+b_1\int_0^{+\infty}\rho(t-\frac{\tau_1}{\tau_2},a)\,\mathrm{d}a+1}\Big],\end{aligned}$$

and b,d represent the birth and death rate of prey respectively, such that $r=b-d$. Set $w(t,a)=\begin{pmatrix}u(t,a)\\ \rho(t,a)\end{pmatrix}$. We can rewrite (2.1) as

$$\begin{gathered}\frac{\partial w(t,a)}{\partial t}+\frac{\partial w(t,a)}{\partial a}=-Dw(t,a),\\ w(t,0)=\begin{pmatrix}\frac{\tau_2\int_0^{+\infty}\rho(t-\frac{\tau_1}{\tau_2},a)\,\mathrm{d}a\int_0^{+\infty}\beta(a)u(t,a)\,\mathrm{d}a}{(\int_0^{+\infty}\rho(t-\frac{\tau_1}{\tau_2},a)\,\mathrm{d}a)^2+b_1\int_0^{+\infty}\rho(t-\frac{\tau_1}{\tau_2},a)\,\mathrm{d}a+1}\\ G\left(u(t,a),\rho(t,a)\right)\end{pmatrix},\\ w(0,a)=w_0=\begin{pmatrix}u_0\\ \rho_0\end{pmatrix}\in L^1((0,+\infty),\mathbb{R}^2),\end{gathered}\tag{2.2}$$

where

$$D=\begin{pmatrix}\tau_2\mu & 0\\ 0 & \tau_2 d\end{pmatrix}.$$

Step 2: Write (2.2) as an abstract delay equations. Consider the Banach space $X:=\mathbb{R}^2\times L^1\big((0,+\infty),\mathbb{R}^2\big)$, with the usual product norm $\|\begin{pmatrix}\zeta\\ \varphi\end{pmatrix}\|_X=\|\zeta\|_{\mathbb{R}^2}+\|\varphi\|_{L^1}$, for $\begin{pmatrix}\zeta\\ \varphi\end{pmatrix}\in X$, and the space

$$C_A=\Big\{\begin{pmatrix}\zeta(\cdot)\\ \phi(\cdot)\end{pmatrix}\in C\big(\big[-\frac{\tau_1}{\tau_2},0\big],X\big):\zeta(0)=0\Big\}.$$

Define the linear operator $L:D(L)\subset X\to X$ by

$$L\begin{pmatrix}0\\ \varphi\end{pmatrix}=\begin{pmatrix}-\varphi(0)\\ -\varphi'-D\varphi\end{pmatrix}$$

with $D(L)=\{0\}\times W^{1,1}\big((0,+\infty),\mathbb{R}^2\big)$, and the operator $F:C_A\to X$ by

$$F\left(\begin{pmatrix}\zeta(\cdot)\\ \phi(\cdot)\end{pmatrix}\right)=\begin{pmatrix}B\left(\phi(\cdot)\right)\\ 0_{L^1}\end{pmatrix},$$

where

$$B(\phi(\cdot))=\begin{pmatrix}\frac{\tau_2\int_0^{+\infty}\phi_2(-\frac{\tau_1}{\tau_2})(a)\,\mathrm{d}a\int_0^{+\infty}\beta(a)\phi_1(0)(a)\,\mathrm{d}a}{(\int_0^{+\infty}\phi_2(-\frac{\tau_1}{\tau_2})(a)\,\mathrm{d}a)^2+b_1\int_0^{+\infty}\phi_2(-\frac{\tau_1}{\tau_2})(a)\,\mathrm{d}a+1}\\ G\left(\phi_1(0)(\cdot),\phi_2(0)(\cdot)\right)\end{pmatrix}.$$

Then, by setting $y(t)=\begin{pmatrix}0\\ w(t,a)\end{pmatrix}$, we can rewrite (2.2) as the Cauchy problem

$$\begin{gathered}\frac{\mathrm{dy(t)}}{\mathrm{d}t}=Ly(t)+F(y_t),\quad t\geq 0,\\ y(0)=\begin{pmatrix}0\\ w_0\end{pmatrix}\in C_A.\end{gathered}\tag{2.3}$$

Note that L is non-densely defined, since

$$X_0 := \overline{D(L)} = \{0\} \times L^1\left((0,+\infty), \mathbb{R}^2\right).$$

Step 3: Transform (2.3) into an abstract ordinary differential equation. We define $x \in C\big([0,+\infty) \times [-\frac{\tau_1}{\tau_2}, 0]; X\big)$ by $x(t,\theta) = y(t+\theta)$, for $t \geq 0$ and $\theta \in [-\frac{\tau_1}{\tau_2}, 0]$. Therefore, $x(t,\theta)$ satisfies the equation

$$\begin{aligned} \frac{\partial x(t,\theta)}{\partial t} - \frac{\partial x(t,\theta)}{\partial \theta} &= 0, \quad \theta \in [-\frac{\tau_1}{\tau_2}, 0), \\ \frac{\partial x(t,0)}{\partial \theta} &= Lx(t,0) + F(x(t,\cdot)), \quad \theta = 0, \\ x(0,\cdot) &= y_0 \in C_A. \end{aligned} \tag{2.4}$$

Let $Z = X \times C$, $C := C([-\frac{\tau_1}{\tau_2}, 0], X)$ with $\left\|\begin{pmatrix} f \\ \phi \end{pmatrix}\right\| = \|f\|_X + \|\phi\|_C$. If we set $z(t) := \begin{pmatrix} 0 \\ x(t) \end{pmatrix}$, then z satisfies

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} z(t) &= Az(t) + H(z(t)), \quad t > 0, \\ z(0) &= \begin{pmatrix} 0_X \\ y_0 \end{pmatrix} \in Z_0, \end{aligned} \tag{2.5}$$

where $A : D(A) \subset Z \to Z$ and $H : Z_0 \to Z$ with $Z_0 = \{0_X\} \times C_A$ are given by

$$A\begin{pmatrix} 0_X \\ \phi \end{pmatrix} = \begin{pmatrix} -\phi'(0) + L\phi(0) \\ \phi' \end{pmatrix}, \quad H\begin{pmatrix} 0_X \\ \phi \end{pmatrix} = \begin{pmatrix} F(\phi) \\ 0_{C_A} \end{pmatrix}.$$

It is straightforward to show that (2.5) is an abstract non-densely defined Cauchy problem, because $D(A) = \{0_X\} \times \{\phi \in C^1([-\frac{\tau_1}{\tau_2}, 0], X),\ \phi(0) \in D(L)\}$ and $\overline{D(A)} = Z_0 \neq Z$.

The existence and uniqueness of a global and positive solution for system (2.5) follow directly from the results in [20].

3. Equilibria and characteristic equation

3.1. **Equilibria.** Suppose that $\overline{z} = \begin{pmatrix} 0_X \\ \overline{\psi} \end{pmatrix} \in D(A)$ is an equilibrium of (2.1), where

$$\overline{\psi} = \begin{pmatrix} \overline{\zeta}(\cdot) \\ \overline{\phi}(\cdot) \end{pmatrix} \in C^1\left([-\frac{\tau_1}{\tau_2}, 0]; X\right), \overline{\psi}(0) \in D(L), \quad \overline{\phi}(\cdot) = \begin{pmatrix} \overline{\phi_1}(\cdot) \\ \overline{\phi_2}(\cdot) \end{pmatrix}.$$

Then, solving the system

$$\begin{aligned} -\overline{\psi}'(0) + L\overline{\psi}(0) + F(\overline{\psi}) &= 0, \\ \overline{\psi}' &= 0, \end{aligned} \tag{3.1}$$

we arrive at the following conclusion on the existence of a positive equilibrium.

Lemma 3.1. *System* (2.5) *always has the boundary equilibria*

$$\overline{z}_1=\begin{pmatrix}0_X\\ \begin{pmatrix}\overline{\zeta}_1(\cdot)\\ \begin{pmatrix}\overline{\phi}_{11}(\cdot)\\ \overline{\phi}_{12}(\cdot)\end{pmatrix}\end{pmatrix}\end{pmatrix}\quad \text{and}\quad \overline{z}_2=\begin{pmatrix}0_X\\ \begin{pmatrix}\overline{\zeta}_2(\cdot)\\ \begin{pmatrix}\overline{\phi}_{21}(\cdot)\\ \overline{\phi}_{22}(\cdot)\end{pmatrix}\end{pmatrix}\end{pmatrix}$$

with $\overline{\zeta}_1(\theta)=\overline{\zeta}_2(\theta)=0_{\mathbb{R}^2}$,

$$\begin{pmatrix}\overline{\phi}_{11}(\theta)(a)\\ \overline{\phi}_{12}(\theta)(a)\end{pmatrix}=\begin{pmatrix}0\\0\end{pmatrix},\quad \begin{pmatrix}\overline{\phi}_{21}(\theta)(a)\\ \overline{\phi}_{22}(\theta)(a)\end{pmatrix}=\begin{pmatrix}0\\ \tau_2 dKe^{-\tau_2 da}\end{pmatrix}.$$

Furthermore, if

(H1) $K>1$ *and* $b-M=-2$

hold, then there exists a unique positive equilibrium of system (2.5), *given by*

$$\overline{z}=\begin{pmatrix}0_X\\ \begin{pmatrix}\overline{\zeta}(\cdot)\\ \begin{pmatrix}\overline{\phi}_1(\cdot)\\ \overline{\phi}_2(\cdot)\end{pmatrix}\end{pmatrix}\end{pmatrix},\quad \overline{\zeta}(\theta)=0_{\mathbb{R}^2},\quad \begin{pmatrix}\overline{\phi}_1(\theta)(a)\\ \overline{\phi}_2(\theta)(a)\end{pmatrix}=\begin{pmatrix}C_1e^{-\tau_2\mu a}\\ C_2e^{-\tau_2 da}\end{pmatrix},$$

where

$$C_1=\frac{\tau_2\mu Mr(K-1)}{K},\quad C_2=\tau_2 d.$$

The linearized equation of (2.5) around the equilibrium $\bar{z}$ is

$$\frac{\mathrm{d}z(t)}{\mathrm{d}t}=Az(t)+DH(\overline{z})z(t),$$

where

$$DH(\overline{z})\begin{pmatrix}0_X\\ \psi\end{pmatrix}=\begin{pmatrix}DF(\overline{\psi})(\psi)\\ 0_{C_A}\end{pmatrix},\quad \forall\begin{pmatrix}0_X\\ \psi\end{pmatrix}\in D(A),\ \psi=\begin{pmatrix}\zeta(\cdot)\\ \phi(\cdot)\end{pmatrix}$$

with

$$DF(\overline{\psi})(\psi)=\begin{pmatrix}DB(\overline{\phi})(\phi)\\ 0_{L_1}\end{pmatrix}$$

and

$$\begin{aligned}DB(\overline{\phi})(\phi)=&\begin{pmatrix}\frac{\tau_2^2dC_2}{C_2^2+b_1d\tau_2C_2+\tau_2^2d^2} & 0\\ 0 & 0\end{pmatrix}\int_0^{+\infty}\beta(a)\phi(0)(a)\,\mathrm{d}a\\ &+\begin{pmatrix}0 & \frac{C_1M\tau_2^2d^2(\tau_2^2d^2-C_2^2)}{(C_2^2+b_1d\tau_2C_2+\tau_2^2d^2)^2}\\ 0 & -\frac{C_1\tau_2^2d^2(\tau_2^2d^2-C_2^2)}{\mu(C_2^2+b_1d\tau_2C_2+\tau_2^2d^2)^2}\end{pmatrix}\int_0^{+\infty}\phi\Big(-\frac{\tau_1}{\tau_2}\Big)(a)\,\mathrm{d}a\\ &+\begin{pmatrix}0 & 0\\ -\frac{C_2\tau_2^2d}{C_2^2+b_1d\tau_2C_2+\tau_2^2d^2} & \frac{\tau_2bdK-2rC_2}{dK}\end{pmatrix}\int_0^{+\infty}\phi(0)(a)\,\mathrm{d}a.\end{aligned}$$

3.2. **Characteristic equation.** Now, we derive the characteristic equation, that determines the distribution of spectrum of $A+DH(\overline{z})$, to study the local dynamical behavior of $\bar{z}$. Denote $\vartheta:=\min\{\tau_2d,\tau_2\mu\}$, and $\Omega:=\{\lambda\in\mathbb{C}:\mathrm{Re}(\lambda)>-\vartheta\}$. The next lemma from [3] will be used.

Lemma 3.2. *The operators* L *and* A *defined above satisfy the following statements:*

(i) *If* $\lambda \in \Omega$, *then* $\lambda \in \rho(L)$, *and*

$$(\lambda I - L)^{-1}\begin{pmatrix}\delta\\ \psi\end{pmatrix} = \begin{pmatrix}0\\ \varphi\end{pmatrix} \Leftrightarrow \varphi(a) = e^{-\int_0^a(\lambda I + D)\mathrm{d}l}\delta + \int_0^a e^{-\int_s^a(\lambda I+D)\mathrm{d}l}\psi(s)\mathrm{d}s$$

with $\begin{pmatrix}\delta\\ \psi\end{pmatrix} \in X$ *and* $\begin{pmatrix}0\\ \varphi\end{pmatrix} \in D(L)$.

(ii) $\rho(L) = \rho(A)$. *Moreover, for each* $\lambda \in \rho(A)$, *we also have the following explicit formula for the resolvent of* A,

$$(\lambda I - A)^{-1}\begin{pmatrix}f\\ \phi\end{pmatrix} = \begin{pmatrix}0_X\\ \phi\end{pmatrix} \Leftrightarrow \phi(\theta) = e^{\lambda\theta}(\lambda I - L)^{-1}[\psi(0) + f] + \int_\theta^0 e^{\lambda(\theta - s)}\psi(s)\,\mathrm{d}s.$$

Denote $\mathcal{G} := DH(\overline{z})$. By Lemma 3.2, we know $(\lambda I - A)$ is invertible for any $\lambda \in \Omega$. It follows from the identity

$$[I - \mathcal{G}(\lambda I - A)^{-1}] = (\lambda I - A)^{-1}[\lambda I - (A + \mathcal{G})],$$

that $\lambda I - (A + \mathcal{G})$ is invertible if and only if $I - \mathcal{G}(\lambda I - A)^{-1}$ is invertible. Now, we consider

$$[I - \mathcal{G}(\lambda I - A)^{-1}]\begin{pmatrix}\delta_X\\ \varphi_{C_A}\end{pmatrix} = \begin{pmatrix}\gamma_X\\ \psi_{C_A}\end{pmatrix}, \tag{3.2}$$

where

$$\delta_X = \begin{pmatrix}\delta_1\\ \delta_2\end{pmatrix}, \quad \gamma_X = \begin{pmatrix}\gamma_1\\ \gamma_2\end{pmatrix}, \quad \psi_{C_A} = \begin{pmatrix}\psi^1(\cdot)\\ \psi^2(\cdot)\end{pmatrix} \in C^1\left([-\frac{\tau_1}{\tau_2}, 0];\, X\right).$$

Equation (3.2) is equivalent to the equation

$$\begin{gathered}\delta_X - DF(\overline{\psi})\Big[e^{\lambda\theta}(\lambda I - L)^{-1}\left(\varphi_{C_A}(0) + \delta_X\right) + \int_\theta^0 e^{\lambda(\theta - s)}\varphi_{C_A}(s)\,\mathrm{d}s\Big] = \gamma_X,\\ \varphi_{C_A} = \psi_{C_A}.\end{gathered} \tag{3.3}$$

From the first equation of (3.3), we obtain

$$\begin{gathered}\Big(I - DB(\overline{\phi})\big(e^{\lambda\theta}e^{-\int_0^a(\lambda I + D)\,\mathrm{d}l}\big)\Big)\delta_1 = \overline{\delta}_1 + DB(\overline{\phi})\Big[e^{\lambda\theta}\int_0^a e^{-\int_s^a(\lambda I+D)\,\mathrm{d}l}\delta_2(s)\,\mathrm{d}s\Big],\\ \delta_2 = \overline{\delta}_2\,,\end{gathered}$$

which has a unique solution δ_1 for any right hand side term if and only if $\Delta(\lambda)$ is invertible, where

$$\Delta(\lambda) = I - DB(\overline{\phi})\Big(e^{\lambda\theta}e^{-\int_0^a(\lambda I + D)\,\mathrm{d}l}\Big). \tag{3.4}$$

Theorem 3.3. *For the spectrum of* $A + \mathcal{G}$, *we have*

$$\sigma(A + \mathcal{G}) \cap \Omega = \sigma_p(A + \mathcal{G}) \cap \Omega = \{\lambda \in \Omega : \det(\Delta(\lambda)) = 0\}.$$

Proof. Let $\lambda \in \Omega$ and $\det(\Delta(\lambda)) \neq 0$. It then follows from (3.3) that $(I - DF(\overline{\psi})(e^{\lambda\theta}(\lambda I - L)^{-1}))$ is invertible, and

$$(I - DF(\overline{\psi})(e^{\lambda\theta}(\lambda I - L)^{-1}))^{-1}\begin{pmatrix}\overline{\delta}_1\\ \overline{\delta}_2\end{pmatrix} = \delta_X,$$

where

$$\delta_X = \begin{pmatrix}(\Delta(\lambda))^{-1}(\overline{\delta}_1) + DB(\overline{\phi})\big[e^{\lambda\theta}\int_0^a e^{-\int_s^a(\lambda I + D)\,\mathrm{d}l}\overline{\delta}_2(s)\,\mathrm{d}s\big]\\ \overline{\delta}_2\end{pmatrix}.$$

Thus, $(I-\mathcal{G}(\lambda I-A)^{-1})$ is invertible, and

$$(I-\mathcal{G}(\lambda I-A)^{-1})^{-1}\begin{pmatrix}\gamma_X\\ \psi_{C_A}\end{pmatrix}=\begin{pmatrix}\delta_X\\ \psi_{C_A}\end{pmatrix}.$$

Hence, we have $\{\lambda\in\Omega:\det(\Delta(\lambda))\neq 0\}\subset\rho(A+\mathcal{G})\cap\Omega$, which implies $\sigma(A+\mathcal{G})\cap\Omega\subset\{\lambda\in\Omega:\det(\Delta(\lambda))=0\}$.

Suppose that $\lambda\in\Omega$ and $\det(\Delta(\lambda))=0$. We are going to find $\begin{pmatrix}0\\ \psi\end{pmatrix}\in D(A)\backslash\{0\}$ such that

$$(A+\mathcal{G})\begin{pmatrix}0\\ \psi\end{pmatrix}=\lambda\begin{pmatrix}0\\ \psi\end{pmatrix}.$$

From the above argument, it suffices to find $\begin{pmatrix}\alpha\\ \varphi\end{pmatrix}\in Z\backslash\{0\}$ satisfying $[I-\mathcal{G}(\lambda I-A)^{-1}]\begin{pmatrix}\alpha\\ \varphi\end{pmatrix}=0$, or equivalently to find $\begin{pmatrix}\alpha\\ \varphi\end{pmatrix}\neq 0$ such that

$$\begin{gathered}\Delta(\lambda)\alpha=0,\\ \varphi=0.\end{gathered}$$

Since $\det(\Delta(\lambda))=0$, there always exists $\alpha\neq 0$ such that $\Delta(\lambda)\alpha=0$. Thus, $\lambda\in\sigma_P(A+\mathcal{G})$. This proves $\{\lambda\in\Omega:\det(\Delta(\lambda))=0\}\subset\sigma_P(A+\mathcal{G})$. $\square$

After some symbolic manipulation, we obtain the characteristic equation of (2.1),

$$\begin{aligned}&\det(\Delta(\lambda))\\ &=\frac{\lambda^2+\tau_2P\lambda+\tau_2^2Q+(\tau_2S\lambda+\tau_2^2R)e^{-\lambda}+(\tau_2N\lambda+\tau_2^2Y)e^{-\frac{\tau_1}{\tau_2}\lambda}+\tau_2^2He^{-\frac{\tau_1}{\tau_2}\lambda}\cdot e^{-\lambda}}{(\lambda+\tau_2d)(\lambda+\tau_2\mu)}\\ &=:\frac{f_1(\lambda)}{f_2(\lambda)}=0,\end{aligned}\tag{3.5}$$

where

$$\begin{gathered}P=\mu-r+\frac{2rF}{K},\quad Q=\mu(-r+\frac{2rF}{K}),\quad S=-\frac{FM\mu}{G},\\ R=rFM\mu(\frac{K-2F}{GK}),\quad Y=\frac{E(1-F^2)}{G^2}+\frac{EFM(1-F^2)}{G^3},\\ N=\frac{E(1-F^2)}{\mu G},\quad H=-\frac{EFM(1-F^2)}{G^3},\\ E=\frac{C_1}{\tau_2},\quad F=\frac{C_2}{\tau_2 d},\quad G=\frac{C_2^2+bdC_2\tau_2+\tau_2^2d^2}{\tau_2^2d^2}.\end{gathered}$$

Let $\lambda=\tau_2\zeta$. Then

$$f_1(\lambda)=f_1(\tau_2\zeta)=\tau_2^2g(\zeta),$$

where

$$g(\zeta)=\zeta^2+P\zeta+Q+(S\zeta+R)e^{-\tau_2\zeta}+(N\zeta+Y)e^{-\tau_1\zeta}+He^{-(\tau_1+\tau_2)\zeta}.\tag{3.6}$$

4. Hopf bifurcation

In this section, we analyze the distribution of purely imaginary roots of $g(\zeta) = 0$. Specifically, the crossing curves of $g(\zeta) = 0$ will be determined in the case of $\tau_1 \neq \tau_2$, and as a special case of $\tau_1 = \tau_2 = \tau$, we will derive the explicit formula for the critical Hopf bifurcation values.

4.1. The case $\tau_1 \neq \tau_2$.

We use the method in [13] to study $g(\zeta) = 0$. Substituting $\zeta = i\omega$, $\omega > 0$ into $g(\zeta) = 0$, we have

$$(-\omega^2 + Pi\omega + Q + (Ni\omega + Y)e^{-i\omega\tau_1}) + (Si\omega + R + He^{-i\omega\tau_1})e^{-i\omega\tau_2} = 0. \quad (4.1)$$

It then follows from $|e^{-i\omega\tau_2}| = 1$ that

$$|-\omega^2 + Pi\omega + Q + (Ni\omega + Y)e^{-i\omega\tau_1}| = |Si\omega + R + He^{-i\omega\tau_1}|,$$

which implies

$$\begin{aligned}&\omega^4 - (2Q - P^2 - N^2 + S^2)\omega^2 + (Q^2 + Y^2 - R^2 - H^2)\\ &= 2A_1(\omega)\cos(\omega\tau_1) - 2B_1(\omega)\sin(\omega\tau_1),\end{aligned} \quad (4.2)$$

where

$$\begin{aligned}A_1(\omega) &= (Y - PN)\omega^2 + (RH - YQ),\\ B_1(\omega) &= (SH - PY + QN)\omega - N\omega^3.\end{aligned}$$

Let

$$\phi_1(\omega) = arg\{(Y - PN)\omega^2 + RH - YQ + (-N\omega^2 + SH - PY + QN)i\omega\}.$$

Then $A_1(\omega)$ and $A_2(\omega)$ can be written as

$$\begin{aligned}A_1(\omega) &= \sqrt{((Y - PN)\omega^2 + (RH - YQ))^2 + ((SH - PY + QN)\omega - N\omega^3)^2}\\ &\quad \times \cos(\phi_1(\omega)),\\ B_1(\omega) &= \sqrt{((Y - PN)\omega^2 + (RH - YQ))^2 + ((SH - PY + QN)\omega - N\omega^3)^2}\\ &\quad \times \sin(\phi_1(\omega)).\end{aligned} \quad (4.3)$$

Substituting (4.3) into (4.2), we obtain

$$\begin{aligned}&\omega^4 - (2Q - P^2 - N^2 + S^2)\omega^2 + (Q^2 + Y^2 - R^2 - H^2)\\ &= 2\sqrt{((Y - PN)\omega^2 + (RH - YQ))^2 + ((SH - PY + QN)\omega - N\omega^3)^2}\\ &\quad \times \cos(\phi_1(\omega) + \omega\tau_1).\end{aligned} \quad (4.4)$$

For (4.4) to have positive root ω, it is necessary that

$$\begin{aligned}F(\omega) &= [\omega^4 - (2Q - P^2 - N^2 + S^2)\omega^2 + (Q^2 + Y^2 - R^2 - H^2)]^2\\ &\quad - 4[((Y - PN)\omega^2 + (RH - YQ))^2 + ((SH - PY + QN)\omega - N\omega^3)^2]\\ &\quad < 0.\end{aligned} \quad (4.5)$$

On the other hand, if $\omega > 0$ satisfies (4.5), then we can always find τ_1 such that (ω, τ_1) is the root of (4.4). The set of all possible values of $\omega > 0$ satisfying (4.5) is denoted by Ω. From [13, Lemma 3.2], it follows that Ω consists of a finite number of intervals of finite length Ω_k; that is, $\Omega = \bigcup_{k=1}^{N} \Omega_k$ with $|\Omega_k| < \infty$. Let

$$\psi_1(\omega) = \phi_1(\omega) + \omega\tau_1 \in [0, \pi].$$

Then

$$\cos(\psi_1(\omega)) = \frac{\omega^4 - (2Q - P^2 - N^2 + S^2)\omega^2 + (Q^2 + Y^2 - R^2 - H^2)}{2\sqrt{((Y-PN)\omega^2 + (RH - YQ))^2 + ((SH - PY + QN)\omega - N\omega^3)^2}},$$

and therefore,

$$\tau^{\pm}_{1,n_1}(\omega) = \frac{\pm\psi_1(\omega) - \phi_1(\omega) + 2n_1\pi}{\omega}, n_1 \in \mathbb{Z}. \tag{4.6}$$

By an argument as above, if we define

$$A_2(\omega = (YH - RQ) + (R - PS)\omega^2 = \sqrt{A_2(\omega)^2 + B_2(\omega)^2}\cos(\phi_2(\omega)),$$
$$B_2(\omega) = (NH - PR)\omega + S(Q - \omega^2)\omega = \sqrt{A_2(\omega)^2 + B_2(\omega)^2}\sin(\phi_2(\omega)),$$

for $\phi_2(\omega) = arg\{A_2(\omega) + iB_2(\omega)\}$, and

$$\psi_2(\omega) = \phi_2(\omega) + \omega\tau_2 \in [0, \pi],$$

then

$$\tau^{\pm}_{2,n_2}(\omega) = \frac{\pm\psi_2(\omega) - \phi_2(\omega) + 2n_2\pi}{\omega}, \quad n_2 \in \mathbb{Z}. \tag{4.7}$$

According to [13, p.525], the crossing curves of $g(\zeta) = 0$ are given in the following theorem.

Theorem 4.1. *The crossing curves of $g(\zeta) = 0$ are given by*

$$\Gamma = \Big(\cup_{k=1,2,\dots,N} \Gamma^{\pm k}_{n_1,n_2} \Big) \cap \mathbb{R}^2_+, \tag{4.8}$$

where

$$\Gamma^{\pm k}_{n_1,n_2} = \big\{ (\frac{\pm\psi_1(\omega) - \phi_1(\omega) + 2n_1\pi}{\omega}, \frac{\mp\psi_2(\omega) - \phi_2(\omega) + 2n_2\pi}{\omega}) : \omega \in \Omega_k \big\}. \tag{4.9}$$

Note that these crossing curves may intersect τ_1 or τ_2 axis. One can easily identify these intersections along the following lines. For example, if $\tau_1 = 0$ and $\tau_2 > 0$, then $g(\zeta) = 0$ turns into

$$\zeta^2 + (P + N)\zeta + Q + Y + (S\zeta + R + H)e^{-\tau_2\zeta} = 0. \tag{4.10}$$

Assume that

(H2) $P + S + N > 0$, $Q + H + R + Y > 0$, and $Q + H - R - Y < 0$.

Then, all the roots of (4.10) with $\tau_2 = 0$ have strictly negative real parts. Let $i\omega_{20}, \omega_{20} > 0$ be the root of (4.10). Then, we can obtain

$$-\omega_{20}^2 + (P + N)i\omega_{20} + Y + Q + (Si\omega_{20} + R + H)e^{-i\tau_2\omega_{20}} = 0.$$

Separating real and imaginary parts, we obtain

$$\omega_{20}^2 + Y + Q = -(R + H)\cos\omega_{20}\tau_2 - S\omega_{20}\sin\omega_{20}\tau_2,$$
$$(P + N)\omega_{20} = (R + H)\sin\omega_{20}\tau_2 - S\omega_{20}\cos\omega_{20}\tau_2,$$

from which it follows that

$$f_2(\omega_{20}) := \omega_{20}^4 + [(P+N)^2 - S^2 - 2(Y+Q)]\omega_{20}^2 + (Y+Q)^2 - (R+H)^2 = 0. \tag{4.11}$$

Equation (4.11) will have a unique positive root ω_{20}^*, as long as

(H3) $Y + Q - R - H < 0$

holds. Moreover, the associated critical values for τ_2 are

$$\tau_{2n} = \frac{1}{\omega_{20}^*} \arccos[\frac{(R+H)(\omega_{20}^{*2} - Y - Q) + S(P+N)\omega_{20}^{*2}}{(R+H)^2 + S^2\omega_{20}^{*2}}] + \frac{2n\pi}{\omega_{20}^*}, \tag{4.12}$$

for $n = 0, 1, 2 \dots$. Applying the implicit function theorem to (4.10), one has

$$(\frac{d\zeta}{d\tau_2})^{-1} = -\frac{\tau_2}{\zeta} + \frac{S}{\zeta(R+H+S\zeta)} - \frac{2\zeta + (P+N)}{\zeta(\zeta^2 + (P+N)\zeta + Y + Q)}.$$

Since

$$\begin{aligned}
&\operatorname{sign}\{\frac{d(\operatorname{Re}\zeta)}{d\tau_2}\}^{-1}_{\tau_2=\tau_{2n}} \\
&= \operatorname{sign}\{\operatorname{Re}\frac{S}{\zeta(R+H+S\zeta)} + Re\frac{2\zeta + (P+N)}{\zeta(\zeta^2 + (P+N)\zeta + Y + Q)}\}_{\tau_2=\tau_{2n}} \\
&= \operatorname{sign}[\frac{2\omega_{20}^2 + S^2 + (P+N)^2 - 2(Y+Q)}{(R+H)^2 + S^2\omega_{20}^2}].
\end{aligned}$$

To make $\operatorname{sign}\{\frac{d(Re\zeta)}{d\tau_2}\}_{\tau_2=\tau_{2n}} > 0$, we assume that

(H4) $S^2 + (P+N)^2 - 2(Y+Q) > 0$,

so that we have the following conclusions.

Corollary 4.2. *Assume that* $\tau_1 = 0$ *and* (H1)–(H4) *hold. Then the interior equilibrium* $\bar{z}$ *is locally asymptotically stable for* $0 < \tau_2 < \tau_{20}$*, and* (2.1) *undergoes a Hopf bifurcation at* $\tau_2 = \tau_{20}$*, where* τ_{20} *is defined by* (4.12).

Along the same lines as above, we have the following bifurcation results for the case $\tau_2 = 0$ and $\tau_1 > 0$.

Corollary 4.3. *Assume that* $\tau_2 = 0$ *and* (H1), (H2), (H5) *hold. Then, the interior equilibrium* $\bar{z}$ *is locally asymptotically stable for* $0 < \tau_1 < \tau_{10}$*, and* (2.1) *undergoes a Hopf bifurcation at* $\tau_1 = \tau_{10}$*, where*

$$\tau_{10} = \frac{1}{\omega_{10}^*} \arccos[\frac{(Y+H)(\omega_{10}^{*2} - Y - Q) + N(P+S)\omega_{10}^{*2}}{(Y+H)^2 + N^2\omega_{10}^{*2}}],$$

and ω_{10}^* *is the unique positive root of*

$$f_1(\omega_{10}) := \omega_{10}^4 + [(P+S)^2 - N^2 - 2(R+Q)]\omega_{20}^2 + (R+Q)^2 - (Y+H)^2 = 0 \tag{4.13}$$

if and only if

(H5) $R + Q - Y - H < 0$.

Next, we discuss the direction in which the roots of $g(\zeta) = 0$ cross the imaginary axis, as (τ_1, τ_2) deviates from the curve in Γ. As in [7], we call the direction of the curve corresponding to increasing $\omega \in \Omega_k$ the *positive direction*, and the region on the left-hand (right-hand) side as we head in the positive direction of the curve *the region on the left (right)*. As a direct consequence of [7, Proposition 6.1], we have the following conclusions.

Theorem 4.4. *Let* $\omega \in \Omega_k$ *and* $(\tau_1, \tau_2) \in \Gamma^{\pm k}_{n_1,n_2}$ *such that* $i\omega$ *is a simple solution of* $g(\zeta) = 0$*. Then, as* (τ_1, τ_2) *moves from the region on the right to the region on the left of the crossing curve, a pair of complex roots of* $g(\zeta) = 0$ *cross the imaginary axis to the right if*

$$R_2 I_1 - R_1 I_2 > 0, \tag{4.14}$$

where

$$\begin{aligned}
R_1 &= Re\{\frac{\partial g(\zeta,\tau_1,\tau_2)}{\partial \tau_1}\} = N\omega^2\cos\omega\tau_1 - Y\omega\sin\omega\tau_1 - \omega H\sin\omega(\tau_1+\tau_2),\\
I_1 &= Im\{\frac{\partial g(\zeta,\tau_1,\tau_2)}{\partial \tau_1}\} = -N\omega^2\sin\omega\tau_1 - Y\omega\cos\omega\tau_1 - \omega H\cos\omega(\tau_1+\tau_2),\\
R_2 &= Re\{\frac{\partial g(\zeta,\tau_1,\tau_2)}{\partial \tau_2}\} = S\omega^2\cos\omega\tau_2 - R\omega\sin\omega\tau_2 - \omega H\sin\omega(\tau_1+\tau_2),\\
I_2 &= Im\{\frac{\partial g(\zeta,\tau_1,\tau_2)}{\partial \tau_2}\} = -S\omega^2\sin\omega\tau_2 - R\omega\cos\omega\tau_2 - \omega H\cos\omega(\tau_1+\tau_2).
\end{aligned}$$

The crossing is in the opposite direction if the (4.14) *is reversed.*

4.2. **The case $\tau_1 = \tau_2$.** When $\tau_1 = \tau_2$, $g(\zeta) = 0$ becomes

$$h(\zeta) = \zeta^2 + P\zeta + Q + ((S+N)\zeta + (R+Y))e^{-\tau\zeta} + He^{-2\tau\zeta}. \tag{4.15}$$

Suppose that $i\omega(\omega > 0)$ is a root of (4.15), that is,

$$-\omega^2 + Pi\omega + Q + (S_1 i\omega + R_1)e^{-\tau i\omega} + He^{-2\tau i\omega} = 0, \tag{4.16}$$

where $R_1 = R + Y$ and $S_1 = S + N$. Applying equation (2.5) of page 6 in [1], one can conclude that ω must satisfy the polynomial equation

$$\omega^8 + s_1\omega^6 + s_2\omega^4 + s_3\omega^2 + s_4 = 0, \tag{4.17}$$

which has at least one positive solution for ω, by the third inequality of (H2). Here,

$$\begin{gathered}
s_1 = 2P^2 - 4Q - S_1^2,\\
s_2 = 6Q^2 - 2H^2 - 4QP^2 - R_1^2 + P^4 - P^2S_1^2 + 2S_1^2Q + 2HS_1^2,\\
\begin{aligned}
s_3 =& 2R_1^2Q - P^2R_1^2 - 4Q^3 + 2Q^2P^2 - S_1^2Q^2 - 2QS_1^2H\\
&+ 4PS_1R_1H - 2R_1^2H + 4QH^2 - 2H^2P^2 - S_1^2H^2,
\end{aligned}\\
s_4 = \left[-R_1^2 + (Q+H)^2\right](Q-H)^2.
\end{gathered}$$

To present the explicit formula of the critical bifurcation values for τ as in [1], we also define

$$\theta = \frac{F(\omega)}{D(\omega)}, \tag{4.18}$$

where

$$\begin{gathered}
D(\omega) = 2\left[-\omega^4 + (2Q - R_1 + P(-P + S_1))\omega^2 + (-Q + R_1 - H)(Q - H)\right],\\
F(\omega) = 2\omega\left[-R_1P - S_1\omega^2 + (Q+H)S\right].
\end{gathered}$$

Theorem 4.5. *Assume that $\tau_1 = \tau_2 = \tau$, (H1) and* (H2) *holds. Then, equation* (4.17) *has a finite number of positive roots, denoted by ω_N, and* (1.3) *undergoes Hopf bifurcation when $\tau = \tau_N^j$, where*

$$\tau_N^j = \frac{2\arctan\theta + 2j\pi}{\omega_N}, \quad j \in \mathbb{Z},$$

and θ is defined in (4.18).

Suppose that $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ is the root of (4.17) such that $\alpha(\tau_N^j) = 0$ and $\omega(\tau_N^j) = \omega_N$. Denote

$$\begin{aligned}\mathcal{G}(\omega, \theta) &= [R_1(1+\theta^2) + 2H(1-\theta^2)]\,[2\omega(1-\theta^2) + 2P\theta] \\ &\quad - [S_1\omega(1+\theta^2) - 4H\theta]\,[P(1-\theta^2) - 4\omega\theta + S_1(1+\theta^2)].\end{aligned} \tag{4.19}$$

Therefore from [1, Lemma 2.10], we have the following result.

Theorem 4.6. *If $\mathcal{G}(\omega_N, \theta) \neq 0$, then $i\omega_N$ is a simple root of (4.15) for $\tau = \tau_N^j$, and*

$$\begin{aligned}&\frac{d\,\mathrm{Re}\,\lambda(\tau)}{d\tau}\Big|_{\tau=\tau_N^j} = \frac{d\alpha(\tau)}{d\tau}\Big|_{\tau=\tau_N^j} > 0, j \in \mathbb{Z}, \quad \text{if } \mathcal{G}(\omega_N, \theta) > 0, \\ &\frac{d\,\mathrm{Re}\,\lambda(\tau)}{d\tau}\Big|_{\tau=\tau_N^j} = \frac{d\alpha(\tau)}{d\tau}\Big|_{\tau=\tau_N^j} < 0, j \in \mathbb{Z}, \quad \text{if } \mathcal{G}(\omega_N, \theta) < 0.\end{aligned} \tag{4.20}$$

5. Numerical simulations and Summary

We illustrate the occurrence of Hopf bifurcation for system (2.1) by numerical simulations. Choose the following set of parameters:

$$\begin{gathered}\mu = 0.8, \quad r = 1.5, \quad K = 1.6, \quad b_1 = 0.5, \quad M = 2.5, \\ \beta(a) := \begin{cases} 2e^{0.8\tau}, & a \geq \tau, \\ 0, & a \in (0, \tau). \end{cases}\end{gathered} \tag{5.1}$$

Then, one can compute $P = 0.9667$, $Q = 0.1333$, $N = 0$, $Y = -0.5435$, $S = -0.8000$, $R = 1.2000$, $H = 0$. By plotting the graph of $F(\omega)$ (see Figure (1) (left)), we have $\Omega = [0.7134, 1.3606]$, and thus, the crossing curves of $g(\zeta) = 0$ can be obtained, according to (4.6) and (4.7). Moreover, the quantity $R_2I_1 - R_1I_2$, that determines the crossing directions, can be also calculated by Theorem 4.4, see Figure (1) (right). These curve will determine the stable region of the positive steady state of (1.3), i.e., the bottom-left region in (τ_1, τ_2)-plane, where the point B locates at. In addition, when the parameters (τ_1, τ_2) passing through the crossing curves, a periodic solution will be bifurcated from the positive steady state through Hopf bifurcation. It is also observed from Figure (1) (right) that the phenomenon of stability switches takes place, as the parameters (τ_1, τ_2) moves from the point A (periodic solution) to B (stable steady state) and then to C (periodic solution again). The phase portraits of (1.3), with (τ_1, τ_2) determined by A, B and C, are shown in Figure 2.

When $\tau_1 = \tau_2$, solving (4.17), we obtain the unique solution $\omega_1 \approx 1.0857$, and therefore, owing to Theorem 4.5, we further obtain the first Hopf bifurcation value $\tau_1^0 \approx 0.1481$. Using (1.4), one has $\mathcal{G}(\omega_1, \theta_1) \approx 2.6257 > 0$. Hence, the solution will approach the positive equilibrium as $t \to \infty$ for $\tau < \tau_1^0$, and increasing τ destabilizes the equilibrium and a periodic solution is bifurcated, see Figure (3).

This paper mainly investigates the dynamics of a delayed predator-prey model with the Holling-type IV response and age structure, from the Hopf bifurcation point of view. By converting the model (1.3) into an abstract non-densely defined Cauchy problem, we derive the characteristic equation at the positive steady state, which is a transcendental equation involving two time delays. The crossing curves in (τ_1, τ_2)-plane, on which the characteristic equation has purely imaginary roots, are obtained. From these curves, we show that the model could exhibit rich dynamics including Hopf bifurcation and stability switches. It also should be mentioned

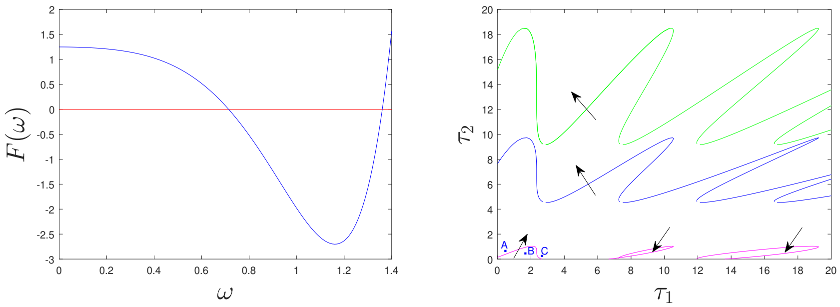
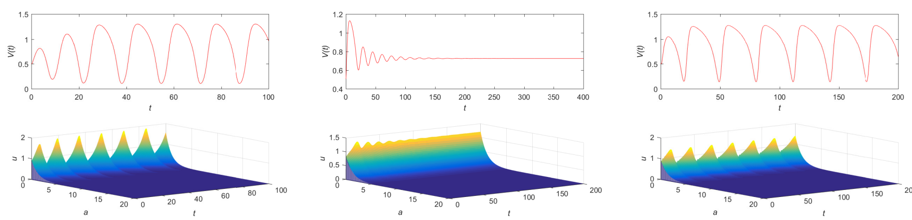


FIGURE 1. Left: the graph of $F(\omega)$. Right: the crossing curves of $g(\zeta) = 0$. Arrows represent the crossing directions, that is, the region on the end of an arrow has two more characteristic roots with positive real parts. Here, the parameter values are given by (5.1), and the functions $V(0) = 1$ and $u(0, a) = 1.3333e^{-0.8a}$ are assigned to the initial values.



$\tau_1 = 0.3$, $\tau_2 = 0.7$ $\tau_1 = 1.5$, $\tau_2 = 1$ $\tau_1 = 2.5$, $\tau_2 = 0.8$

FIGURE 2. A solution of (1.3) with different choice of time delays.

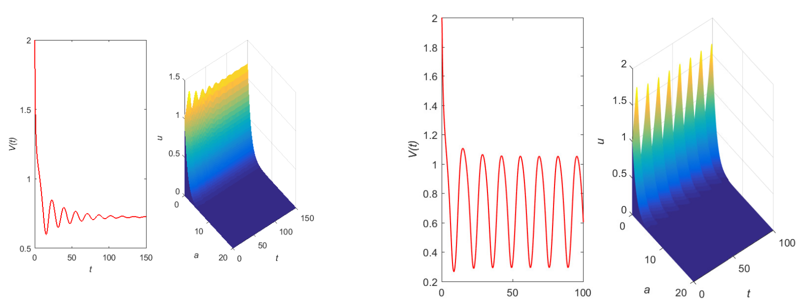


FIGURE 3. Positive equilibrium of (1.3) is stable for $\tau = 0.1 < \tau_1^0$ (left), and (1.3) has periodic solutions for $\tau = 0.5 > \tau_1^0$ (right). The other parameters are the same as Figure 1.

that double Hopf bifurcation may occur if the crossing curve intersects with itself or another crossing curve, since the characteristic equation will have two pairs of roots on the imaginary axis.

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