GLOBAL HOPF BRANCHES AND MULTIPLE LIMIT CYCLES IN A DELAYED LOTKA-VOLTERRA PREDATOR-PREY MODEL

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Abstract. In recent studies, global Hopf branches were investigated for delayed model of HTLV-I infection with delay-independent parameters. It is shown in [8, 9] that when stability switches occur, global Hopf branches tend to be bounded, and different branches can overlap to produce coexistence of stable periodic solutions. In this paper, we investigate global Hopf branches for delayed systems with delay-dependent parameters. Using a delayed predator-prey model as an example, we demonstrate that stability switches caused by varying the time delay are accompanied by bounded global Hopf branches. When multiple Hopf branches exist, they are nested and the overlap produces coexistence of two or possibly more stable limit cycles.

1. **Introduction.** In mathematical models of biological systems with time delays, it is known that varying a time delay can destabilize an otherwise stable equilibrium and result in sustained oscillations through a mechanism called Hopf bifurcation. When using the time delay as a bifurcation parameter, it is known that Hopf bifurcation can occur in a sequence of bifurcation points. These Hopf branches can extend to infinity or they can be bounded and connect different bifurcation points. It is highly nontrivial to determine whether a global Hopf branch will remain bounded. In a well-known study [1], Kuang and Beretta investigated the phenomenon of stability switch: when the time delay is varied across a sequence of Hopf bifurcation points, the equilibrium can switch back and forth between being stable and being unstable. They have developed an systematic way to detect stability switches in when model parameters are delay-dependent. In a recent study, Li and Shu [8] provided a more geometric explanation for the occurrence of stability switch. They have shown, in a delayed model for HTLV-I infection, that when a cubic polynomial associated with the characteristic polynomial has two positive roots, stability switch occurs. Furthermore, they have investigated the global Hopf branches accompanying the stability switch and shown that the global Hopf branches are bounded and will eventually overlap. The overlap of global Hopf branches can produce the coexistence of stable limit cycles. In a subsequent study [9], we extended the results

in [8] to the case when the cubic polynomial has three positive roots and show that coexistence of stable limit cycles are also possible. Other effects on global Hopf branches include [11, 12].

The previous studies [8, 9, 12] considered a delayed model in which parameters are independent of delay. In this paper, we investigate stability switch as a possible mechanism for the coexistence of stable limit cycles in delayed systems when parameters are delay dependent. Using a delayed Lotka-Volterra type predator-prey model with Holling Type I and Type II functional responses, we show that stability switches in this case produce bounded global Hopf branches that are nested. When multiple Hopf branches exist, the overlap can produce coexistence of stable limit cycles. The effects of the delay in Lotka-Volterra type predator-prey models have been extensively studied in the ecological and mathematical literature (e.g. [4, 5, 10, 13]). Our study is the first to investigate global Hopf branches accompanying stability switches, and establish the stability switch as a mechanism for coexistence of stable limit cycles.

2. **Preliminaries.** We consider a delayed Lotka-Volterra type predator-prey model described by the following system:

$$
\begin{aligned}
x'(t) &= rx(t)\left(1 - \frac{x(t)}{K}\right) - \beta f(x(t))y(t), \\
y'(t) &= \gamma \beta\, e^{-d_j \tau} f(x(t-\tau))y(t-\tau) - dy(t),
\end{aligned}
\tag{1}
$$

where the response function $f(x)$ is increasing for all $x > 0$. We are interested in $f(x)$ of Holling types:

$$
f(x) = x \ \text{[Type I]} \quad \text{and} \quad f(x) = \frac{x}{D+x} \ \text{[Type II]},
$$

Nondimensionalizing the system with the following transform and ignoring additional subscripts,

$$
t_1 = rt, \quad x_1 = x/K,
$$

$$
y_1 = \beta y/r \ \text{(Type I)} \quad \text{or} \quad y_1 = \beta y/rK \ \text{(Type II)},
$$

$$
d_1 = d/r, \quad d_{j1} = d_j/r, \quad D_1 = D/K(\text{Type II only}),
$$

$$
\gamma_1 = \gamma \beta K/r \ \text{(Type I)} \quad \text{or} \quad \gamma_1 = \gamma\beta/r \ \text{(Type II)},
$$

we obtain

$$
\begin{aligned}
x'(t) &= x(t)(1 - x(t)) - f(x(t))y(t), \\
y'(t) &= \gamma\, e^{-d_j \tau} f(x(t-\tau))y(t-\tau) - dy(t).
\end{aligned}
\tag{2}
$$

There are three possible equilibria: the extinction equilibrium $P_0 = (0,0)$, predator extinction equilibrium $P_1 = (1,0)$ and the coexistence equilibrium $P_2 = (x^*, y^*)$, where

$$
x^* = f^{-1}\left(\frac{d}{\gamma}e^{d_j \tau}\right) > 0, \quad y^* = \frac{x^*(1-x^*)}{f(x^*)} = \frac{\gamma x^*(1-x^*)}{de^{d_j \tau}} > 0.
\tag{3}
$$

Existence of P_0 and P_1 is unconditional, while P_2 exists if and only if

$$
\frac{d}{\gamma}e^{d_j \tau} < f(1) \quad \Leftrightarrow \quad R(\tau) := \frac{\gamma f(1)}{d}e^{-d_j \tau} > 1,
\tag{4}
$$

or equivalently,

$$\tau < \tau_m := \frac{1}{d_j} \log \frac{\gamma f(1)}{d} \quad \text{and} \quad R_0 := R(0) = \frac{\gamma f(1)}{d} > 1.$$

Parameter $R(\tau)$ is called the basic reproduction number, it is the average number of offspring reaching adulthood from a single adult over its life span.

Theorem 2.1 (Positivity and Boundedness). *Given any positive initial condition $\phi \in \mathcal{C}^+ \times \mathcal{C}^+, \phi(0) > 0$, where $\mathcal{C}^+ := C([-\tau, 0], \mathbb{R}_+)$, a Banach space of continuous non-negative-valued functions on $[-\tau, 0]$ with infinity norm, the solution of system (2) is positive and ultimately bounded in $\mathcal{C}^+ \times \mathcal{C}^+$. Specifically, all trajectories eventually enter and remain in the following bounded invariant region.*

$$\Gamma = \left\{ (x, y) \in \mathcal{C}^+ \times \mathcal{C}^+ : ||x|| \le 1, ||y|| \le \frac{\gamma e^{-d_j \tau}}{\min\{1, d\}} \right\}.$$

Proof. Positivity of solutions follows from standard theory of autonomous DDE with constant delays. From

$$x'(t) \le x(1 - x),$$

we know that $x(t)$ is ultimately bounded by 1,

$$\limsup_{t \to +\infty} x(t) \le 1.$$

Adding the two equations of (2) we obtain

$$\begin{aligned}
\left(\gamma e^{-d_j \tau} x(t) + y(t + \tau) \right)' &= \gamma e^{-d_j \tau} x(t)(1 - x(t)) - dy(t + \tau) \\
&\le \gamma e^{-d_j \tau}(1 - x(t)) - dy(t + \tau) \\
&\le \gamma e^{-d_j \tau} - \min\{1, d\} \left(\gamma e^{-d_j \tau} x(t) + y(t + \tau) \right),
\end{aligned}$$

and thus

$$\limsup_{t \to +\infty} (\gamma e^{-d_j \tau} x(t) + y(t + \tau)) \le \frac{\gamma e^{-d_j \tau}}{\min\{1, d\}}.$$

This implies that

$$\limsup_{t \to +\infty} y(t) \le \frac{\gamma e^{-d_j \tau}}{\min\{1, d\}},$$

and that all solutions in Γ' will eventually enter and remain in Γ. $\square$

3. **Stability of the boundary equilibrium** P_1. Linearizing system (2) at $P_1 = (1, 0)$ and letting $u = x - 1$, $v = y$, we obtain the following linear system

$$\begin{aligned}
u'(t) &= -u(t) - f(1)v(t), \\
v'(t) &= -dv(t) - \gamma e^{-d_j \tau} f(1)v(t - \tau).
\end{aligned} \tag{5}$$

The characteristic equation of system (5) is

$$\begin{aligned}
D_1(\lambda, \tau) &= \lambda^2 + (d + 1)\lambda + d - \gamma f(1)e^{-d_j \tau}(\lambda + 1) e^{-\lambda \tau} \\
&= (\lambda + 1)(\lambda + d - \gamma f(1)e^{-d_j \tau} e^{-\lambda \tau}) = 0.
\end{aligned} \tag{6}$$

Theorem 3.1 (Stability of P_1).

(1) *If $R(\tau) \le 1$, then the interior equilibrium does not exist and $P_1(1, 0)$ is globally asymptotically stable in Γ;*

(2) *If $R(\tau) > 1$, then $P_1(1, 0)$ is unstable.*

Proof. 1) Let $c := \gamma e^{-d_j \tau} f(1) \le d$. Then

$$
\begin{aligned}
\frac{dy}{dt} &= \gamma e^{-d_j \tau} f(x(t)) y(t - \tau) - dy(t) \\
&\le \gamma e^{-d_j \tau} f(1) y(t - \tau) - dy(t) \\
&= cy(t - \tau) - dy(t).
\end{aligned}
\tag{7}
$$

Consider the Lyapunov function

$$
V(y(t)) = \frac{1}{2} y^2(t) + \frac{c}{2} \int_{t-\tau}^{t} y^2(s) \, ds.
$$

We have $V(0) = 0$, $V(y(t)) \ge 0$, and

$$
\begin{aligned}
\frac{dV(y(t))}{dt} &= y(t) \, y'(t) + \frac{c}{2} (y^2(t) - y^2(t - \tau)) \\
&\le cy(t) y(t - \tau) - dy^2(t) + \frac{c}{2} (y^2(t) - y^2(t - \tau)) \\
&\le \frac{c}{2} \left(y^2(t) + y^2(t - \tau) \right) - dy^2(t) + \frac{c}{2} (y^2(t) - y^2(t - \tau)) \\
&= (c - d) \, y^2(t) \le 0.
\end{aligned}
$$

Using (7), the equality is attained only if $x(t) = 1$ and $y(t) = 0$. The maximal invariant set where $V'(y(t)) = 0$ is the singleton $\{P_1(1, 0)\}$, and thus $(1, 0)$ is globally attractive by LaSalle's Invariance Principle [3, 7].

2) If $R(\tau) > 1$, then $\gamma e^{-d_j \tau} f(1) > d$. Let $\alpha(\lambda) = \lambda + d - \gamma f(1) e^{-d_j \tau - \lambda \tau}$. Then

$$
\alpha(0) = d - \gamma f(1) e^{-d_j \tau} < 0, \quad \alpha(+\infty) = +\infty > 0.
$$

So there exists $\lambda_0 > 0$ such that $\alpha(\lambda_0) = 0$, and $\lambda_0 > 0$ is a characteristic root. Therefore P_1 is unstable. $\qquad\square$

In ecological perspective, Theorem 3.1 implies that if the maturation delay of juvenile predators is so large that the recruitment rate to adulthood is smaller than its death rate, predators will go extinct.

4. **Stability and bifurcation of the coexistence equilibrium P_2.** For $P_2 = (x^*, y^*)$ to exists, it is necessary and sufficient that $\gamma f(1) > d$ and

$$
\tau < \tau_m := \frac{1}{d_j} \log \frac{\gamma f(1)}{d}.
$$

Let $x = x^* + u$, $y = y^* + v$ and $|u|, |v| << 1$. The linearized system at P_2 is

$$
\begin{aligned}
u'(t) &= (1 - 2x^* - y^* f'(x^*)) u(t) - f(x^*) v(t), \\
v'(t) &= \gamma e^{-d_j \tau} y^* f'(x^*) u(t - \tau) + \gamma e^{-d_j \tau} f(x^*) v(t - \tau) - dv(t),
\end{aligned}
\tag{8}
$$

whose characteristic equation is

$$
\begin{aligned}
D(\lambda, \tau) &= \lambda^2 + a_1 \lambda + a_0 + (b_1 \lambda + b_0) \, e^{-\lambda \tau} \\
&=: P(\lambda, \tau) + Q(\lambda, \tau) \, e^{-\lambda \tau} = 0,
\end{aligned}
\tag{9}
$$

with

$$
\begin{aligned}
a_1 &= d + y^* f'(x^*) + 2x^* - 1, \\
a_0 &= d(a_1 - d), \\
b_1 &= -d, \\
b_0 &= -d(2x^* - 1).
\end{aligned}
$$

We investigate possible stability switches as τ increases from zero to τ_m. When $\tau = 0$, the characteristic equation can be simplified as

$$\lambda^2 + H(0)\lambda + \gamma\, y^* f(x^*) f'(x^*) = 0, \tag{10}$$

where

$$H(\tau) = 2x^* + y^* f'(x^*) - 1.$$

Here we used that fact that when $\tau = 0$, $\gamma f(x^*) = d$.

Notice that $\gamma\, y^* f(x^*) f'(x^*) > 0$. If $H(0) < 0$, the two solutions of (10) have positive real parts, thus P_2 is unstable; if $H(0) > 0$, the two solutions both have negative real parts, and P_2 is stable.

For $\tau > 0$, suppose $D(\lambda, \tau) = 0$ has purely imaginary solutions of the form $\lambda = i\omega$ ($\omega > 0$). Noticing that $|e^{-i\omega\tau}| = 1$, we have from (9) that $|P(i\omega, \tau)|^2 - |Q(i\omega, \tau)|^2 = 0$, and thus

$$F(\omega, \tau) := \omega^4 + (a_1 - d)^2\omega^2 + d^2 y^* f'(x^*) J(\tau) = 0, \tag{11}$$

where

$$J(\tau) = y^* f'(x^*) + 4x^* - 2.$$

Let

$$I_- = \{\tau \in (0, \tau_m) : J(\tau) < 0\}, \quad I_+ = \{\tau \in (0, \tau_m) : J(\tau) \geq 0\}.$$

If $I_- = \emptyset$, namely, $J(\tau) \geq 0, \forall \tau \in (0, \tau_m)$, then $F(\omega, \tau)$ has no positive root for $0 < \tau < \tau_m$. Therefore, no characteristic root will cross the imaginary axis, and thus no bifurcation or stability switch occurs. Indeed, one can verify that there is no zero characteristic root in (9) as $a_0 + b_0 \neq 0$. Thus even at τ value where $J(\tau) = 0$, there is no bifurcation or stability switch. Since $2H(\tau) = J(\tau) + y^* f'(x^*)$, which implies $H(0) = y^*(0) f'(x^*(0)) > 0$, P_2 is stable when $\tau = 0$, thus stable for $0 \leq \tau < \tau_m$.

If $I_- \neq \emptyset$, then $F(\omega, \tau)$ has a unique positive solution for $\tau \in I_-$. Rewrite the characteristic equation (9) as

$$e^{i\omega(\tau)\tau} = -\frac{Q(i\omega(\tau), \tau)}{P(i\omega(\tau), \tau)}. \tag{12}$$

Define

$$\theta(\tau) = \arg\{-\frac{Q(i\omega(\tau), \tau)}{P(i\omega(\tau), \tau)}\}. \tag{13}$$

Note that $\theta(\tau)$ is not necessarily unique or continuous. On each interval I_-^k of I_-, by restricting $\theta(\tau)$ to the principal branch, there exists a $\tau_0 \in I_-^k$ such that $\theta(\tau_0) > 0$, and $\theta(\tau)$ is unique, continuous and differentiable by the implicit function theorem. Define

$$S_n(\tau) := \tau - \frac{\theta(\tau) + 2n\pi}{\omega(\tau)}, \quad n \in \mathbb{N}_0. \tag{14}$$

Then zeros of $S_n(\tau)$ are solutions of $D(i\omega, \tau) = 0$. Furthermore, according to [1], we have

$$\text{sign}\left\{\frac{d\text{Re}\,\lambda}{d\tau}\bigg|_{\lambda=i\omega(\tau^*)}\right\} = \text{sign}\left\{\frac{dS_n(\tau)}{d\tau}\bigg|_{\tau=\tau^*}\right\}, \tag{15}$$

since ω is the only positive root and $F'_\omega(\omega, \tau) > 0$.

In the remaining part of the paper, we study model (2) with Holling Type I and Type II functional responses mainly for stability switches and Hopf bifurcations about the coexistence equilibrium P_2 with more details.

5. Holling Type I functional response.

5.1. Stability at P_2 and global Hopf bifurcation. Assume that $f(x) = x$. Then the coexistence equilibrium $P_2(x^*, y^*)$ is

$$x^* = \frac{1}{R(\tau)}, \quad y^* = 1 - \frac{1}{R(\tau)},$$

where

$$R_0 = \gamma/d, \quad R(\tau) = R_0 e^{-d_j \tau}.$$

If $R_0 > 1$, $\tau_m = \frac{1}{d_j} \log R_0$. The corresponding characteristic equation is

$$
\begin{aligned}
D(\lambda, \tau) &= P(\lambda, \tau) + Q(\lambda, \tau)e^{-\lambda\tau} \\
&= \lambda^2 + \left(d + \frac{1}{R(\tau)}\right)\lambda + \frac{d}{R(\tau)} + \left(-d\lambda + d - \frac{2d}{R(\tau)}\right)e^{-\lambda\tau}.
\end{aligned}
\tag{16}
$$

$$F(\omega, \tau) = \omega^4 + \frac{1}{R(\tau)^2}\omega^2 - \frac{d^2}{R(\tau)^2}(R(\tau) - 1)(R(\tau) - 3),$$

$$H(0) = \frac{1}{R_0}, \quad J(\tau) = \frac{3}{R(\tau)} - 1.$$

For $\tau = 0$, equilibrium P_2 is locally asymptotically stable whenever it exists since $H(0) > 0$. For $\tau > 0$, similar to the discussion on $J(\tau)$ in the preceding section, we define

$$
\begin{aligned}
I_- &= \{\tau \in (0, \tau_m) : J(\tau) < 0\} = (0, \tau_c), \\
I_+ &= \{\tau \in (0, \tau_m) : J(\tau) \geq 0\} = [\tau_c, \tau_m),
\end{aligned}
\tag{17}
$$

where $\tau_c = \frac{1}{d_j} \log \frac{R_0}{3}$ is the unique root of $J(\tau)$.

Theorem 5.1. *If $R_0 \leq 3$, then P_2 is locally asymptotically stable wherever it exists for $\tau \in [0, \tau_m)$.*

Proof. Since $R(\tau) = R_0 e^{-d_j \tau} < 3$, $\tau > 0$, we have $I_- = \emptyset$, $I_+ = [0, \tau_m)$, and stability does not change in I_+. Notice that P_2 is stable when $\tau = 0$, we know that P_2 is stable for $\tau \in [0, \tau_m)$. $\square$

5.2. Global Hopf branches and multiple stable periodic solutions. From bifurcation theories [1, 3], as τ increases through τ_1^n, a pair of characteristic roots cross the imaginary axis to the right and Hopf bifurcation occurs. When τ further increases through τ_2^n, a pair of characteristic roots cross the imaginary axis to the left and the Hopf bifurcation terminates. We use DDE-BIFTOOL to numerically explore the global Hopf branches at τ_1^n and τ_2^n. The original parameter values used for simulations are

$$r = 1, \quad K = 50, \quad \beta = 0.08, \quad \gamma = 0.2, \quad d = 0.2, \quad d_j = 0.002. \tag{18}$$

The corresponding parameters after nondimensionalization are

$$\gamma = 0.8, \quad d = 0.2, \quad d_j = 0.002. \tag{19}$$

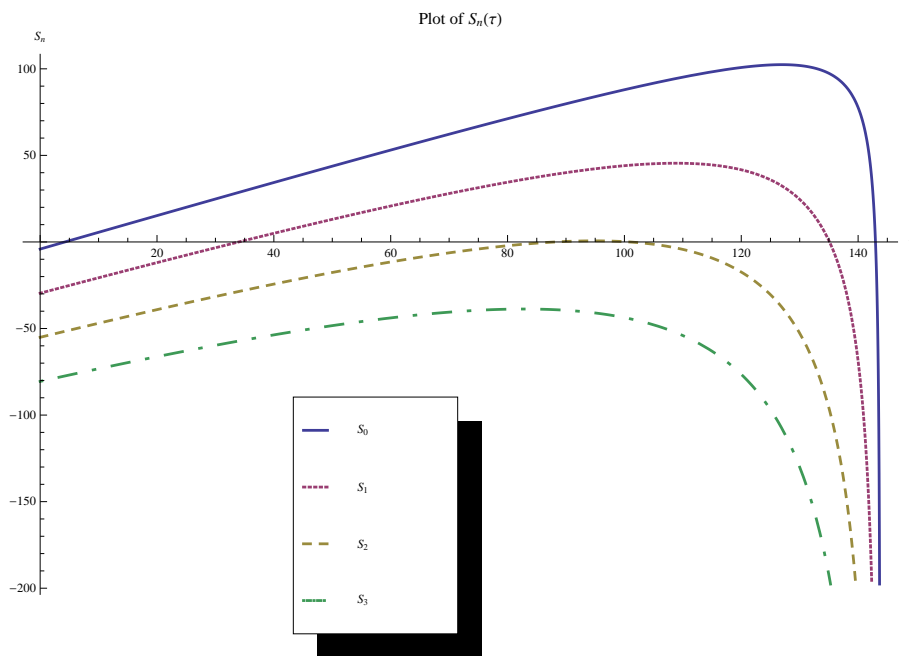Graphs for $S_n(\tau)$ are numerically computed and are shown in Figure 1.

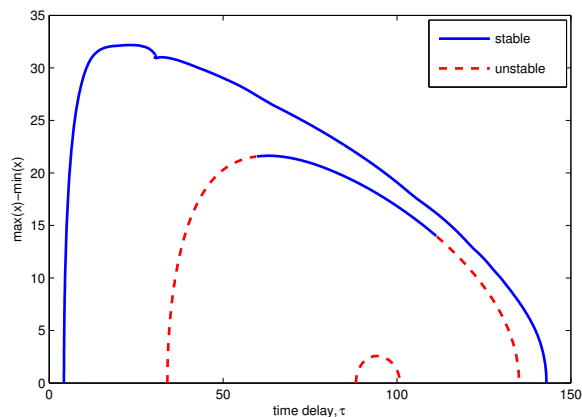FIGURE 1. Graph of $S_n(\tau)$ in the Type I model. We see that only S_0, S_1, S_2 have zeros.

FIGURE 2. Global Hopf branches of the Type I model.

Furthermore, we have

$$
\begin{aligned}
\text{on } S_0: \quad & \tau_1^0 = 4.24465, \quad \tau_2^0 = 142.973; \\
\text{on } S_1: \quad & \tau_1^1 = 33.9897, \quad \tau_2^1 = 135.109; \\
\text{on } S_2: \quad & \tau_1^2 = 88.2029, \quad \tau_2^2 = 100.837.
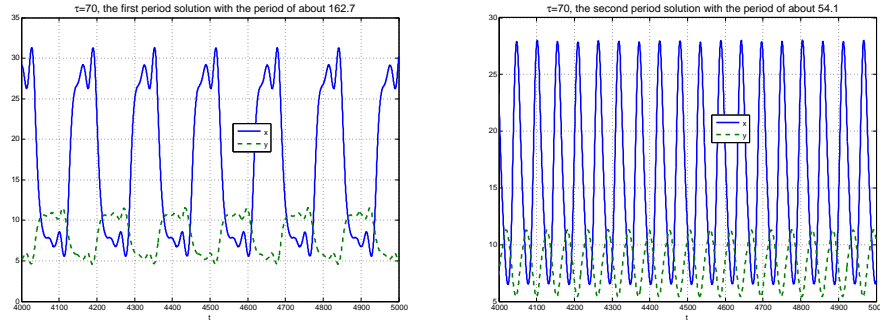\end{aligned}
\tag{20}
$$

FIGURE 3. Two stable periodic solutions for $\tau = 70$, which lies in the overlap of the stable intervals in Figure 2.

Using DDE-BIFTOOL, we computed the global Hopf bifurcation branches as shown in Figure 2.

From Figure 2, we see that global Hopf branches are all bounded and each of them connects a pair of Hopf bifurcation points τ_1^n, τ_2^n. These graphs look similar to those of S_n but they represent different objects. The blue solid curves represent stable Hopf branches, while the red dashed curves represent unstable Hopf branches. We observe that there is an overlap of stable parts on the first two branches, which indicates that two stable limit cycles coexist for the same set of parameters (see an example in Figure 3). In Figure 4, we demonstrate that the largest moduli of the Floquet multipliers for the two periodic solutions in the overlap region are less than one, and the cyclic period of each branch is always an increasing function of the time delay.

6. **Holling Type II functional response.**

6.1. **Stability at P_2 and global Hopf bifurcation.** Assume that $f(x) = \dfrac{x}{D + x}$. Then the coexistence equilibrium $P_2(x^*, y^*)$ is

$$x^* = \frac{D}{S - 1}, \quad y^* = \frac{SD(S - D - 1)}{(S - 1)^2},$$

where

$$S = \frac{\gamma}{d} e^{-d_j \tau},$$

and

$$R_0 = \frac{\gamma}{d} f(1) = \frac{\gamma}{d(1 + D)}, \quad R(\tau) = R_0 e^{-d_j \tau} = \frac{S}{1 + D}.$$
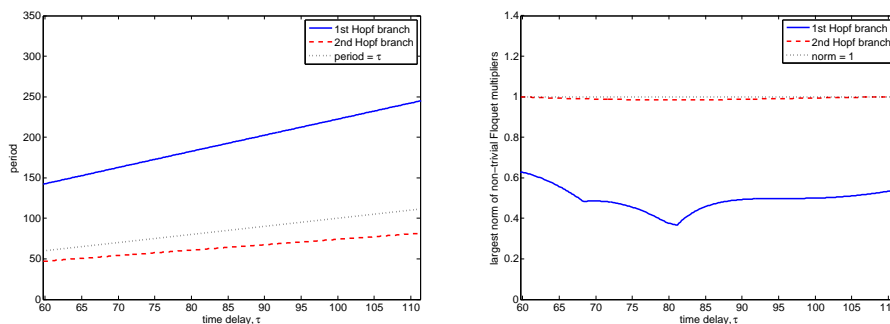
FIGURE 4. Left: periods of periodic solutions on the overlap stable region. Right: norm of the nontrivial Floquet multipliers with largest norm on the overlap stable region.

Equilibrium P_2 exists if $R(\tau) > 1$ or equivalently if $S > 1 + D$. If $R_0 > 1$, $\tau_m = \dfrac{1}{d_j} \log R_0$. We always assume $R_0 > 1$ (which also implies $\gamma > d$) and we will analyze the stability of P_2. Other quantities became

$$H(0) = \frac{d(d(1 + D) + \gamma(D - 1))}{\gamma(\gamma - d)},$$

$$J(\tau) = \frac{d^2 e^{2d_j \tau}(1 + D) + 2\gamma d D e^{d_j \tau} - \gamma^2}{\gamma(\gamma - d e^{d_j \tau})}$$

$$= \frac{\left(\frac{d e^{d_j \tau}}{\gamma}\right)^2 (1 + D) + 3D \left(\frac{d e^{d_j \tau}}{\gamma}\right) - 1}{1 - \left(\frac{d e^{d_j \tau}}{\gamma}\right)}$$

$$= \frac{\left(\frac{1}{S}\right)^2 (1 + D) + 3D \left(\frac{1}{S}\right) - 1}{1 - \left(\frac{1}{S}\right)}.$$

Stability of P_2 when $\tau = 0$ depends on $\text{sgn}\{H(0)\}$. We have

$$H(0) > 0$$
$$\Leftrightarrow d(1 + D) + \gamma(D - 1) > 0$$
$$\Leftrightarrow D > \frac{\gamma - d}{\gamma + d} =: D_0,$$

and

$$H(0) < 0 \Longleftrightarrow D < \frac{\gamma - d}{\gamma + d} = D_0.$$

Therefore, if $D > D_0$, P_2 is locally asymptotically stable when $\tau = 0$, while if $D < D_0$, P_2 is unstable.

For $\tau > 0$, we need to determine $\text{sgn}\{J(\tau)\}$. Using $S = \frac{\gamma}{d}e^{-d_j\tau}$ for $\tau \in (0, \tau_m)$, we get

$$(1 + D) < S < \frac{\gamma}{d} \Longleftrightarrow \frac{d}{\gamma} < \frac{1}{S} < \frac{1}{1+D}.$$

Let

$$h(s) = (1 + D)s^2 + 3Ds - 1.$$

Then $\text{sgn}\{J(\tau)\} = \text{sgn}\{h(1/S)\}$. It can be verified that $h(s)$ has exactly one positive solution, so does $J(\tau)$ since $1/S$ is a monotone function of τ. A sufficient and necessary condition for the positive root to be in $(\frac{d}{\gamma}, \frac{1}{1+D})$ is

$$0 > h(d/\gamma) \Longleftrightarrow D < \frac{\gamma^2 - d^2}{d^2 + 3d\gamma} =: D_1,$$

and

$$0 < h\left(\frac{1}{1+D}\right) \Longleftrightarrow \frac{d}{\gamma} < \frac{1}{1+D}.$$

The second condition is always satisfied since $R_0 = \frac{\gamma}{d(1+D)} > 1$. Hence

$$J(\tau) \text{ has a positive root } \tau_c \text{ in } (0, \tau_m) \quad \Longleftrightarrow \quad D < D_1,$$

where

$$\tau_c = \frac{1}{d_j} \log \frac{\gamma}{d} \frac{-3D + \sqrt{9D^2 + 4(1+D)}}{2(1+D)}.$$

Notice that $D_0 < D_1$ and we have the following theorem.

Theorem 6.1.

(i) *If $D < D_0$, then P_2 is unstable when $\tau = 0$, $I_- = (0, \tau_c) \neq \emptyset$, $\omega(\tau)$ and $S_n(\tau)$ is unique and well defined in I_-.*

(ii) *If $D_0 < D < D_1$, then P_2 is stable when $\tau = 0$, $I_- = (0, \tau_c) \neq \emptyset$, $\omega(\tau)$ and $S_n(\tau)$ is unique and well defined in I_-.*

(iii) *If $D > D_1$, then P_2 is stable when $\tau = 0$ and $I_- = \emptyset$. Thus P_2 is stable for all $\tau \in (0, \tau_m)$.*

6.2. **Global Hopf branches and multiple stable periodic solutions.** Consider the following set of parameter values in original scale:

$$r = 1, \quad K = 50, \quad D = 50, \quad \beta = 4, \quad \gamma = 0.2, \quad d = 0.2, \quad d_j = 0.001. \quad (21)$$

The corresponding parameters after nondimensionalization are

$$D = 1, \quad \gamma = 0.8, \quad d = 0.2, \quad d_j = 0.001. \quad (22)$$

Then we have $\tau_m = 693.15$, $\tau_c = 116.10$, and $H(0) > 0$. This is case (ii) in Theorem 6.1. Graphs of $S_n(\tau)$ are shown in Figure 5.

Then we have

$$\begin{aligned} \text{on } S_0 : \quad \tau_1^0 &= 4.12, \quad \tau_2^0 = 115.08; \\ \text{on } S_1 : \quad \tau_1^1 &= 40.83, \quad \tau_2^1 = 104.37. \end{aligned} \quad (23)$$

Global Hopf branches were computed using DDE-BIFTOOL and are shown in Figure 6. Note that the small piece of red dashed curve attached on the upper branch is real (not a numerical error). Further details need to be examined.
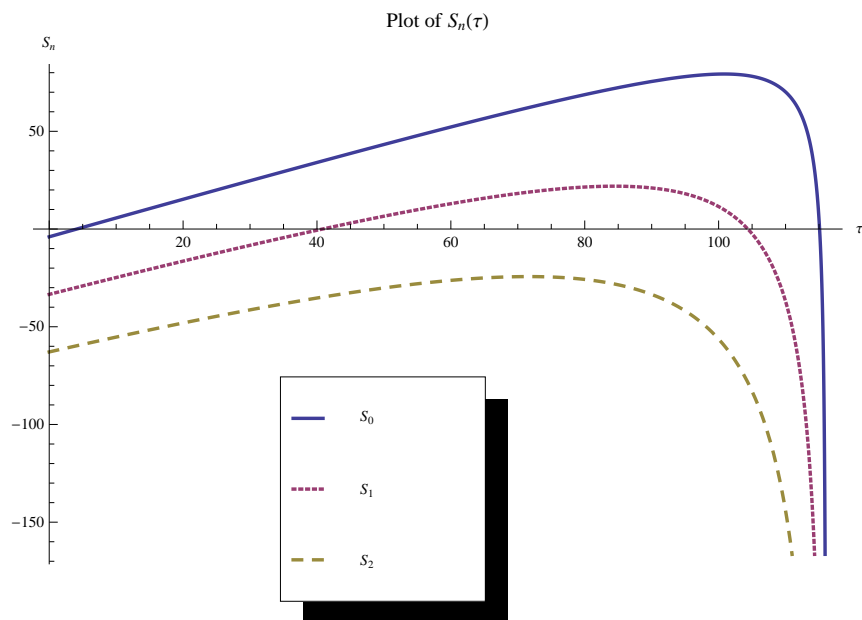
FIGURE 5. Graph of $S_n(\tau)$ in the Type II model. We see that only S_0, S_1 have zeros.
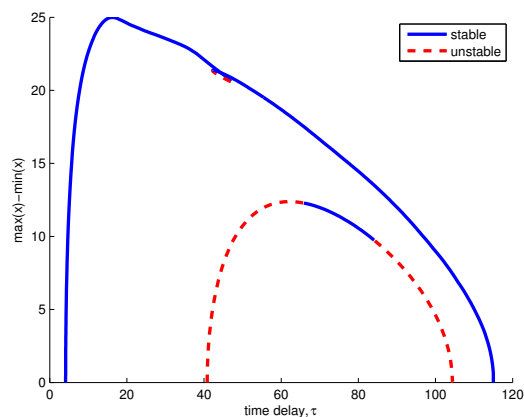

FIGURE 6. Global Hopf branches of the Type II model.

We have observed similar behaviors of the global Hopf branches as in the preceding subsection, when the function response was of Holling Type I. The overlap of stability regions (blue solid portions) shows coexistence of two stable limit cycles in the Holling Type II model (see Figure 7 as an example).

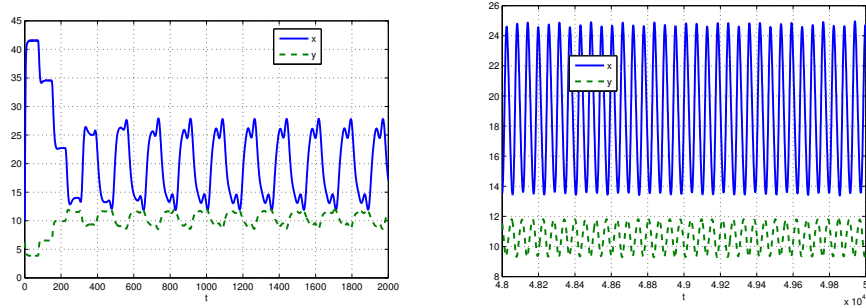In Figure 8, we illustrate existence of torus bifurcations on the lower Hopf branch of Figure 6.

FIGURE 7. Two coexistent stable periodic solutions for $\tau = 73.5$, which lie in the overlap of the stable intervals in Figure 6.
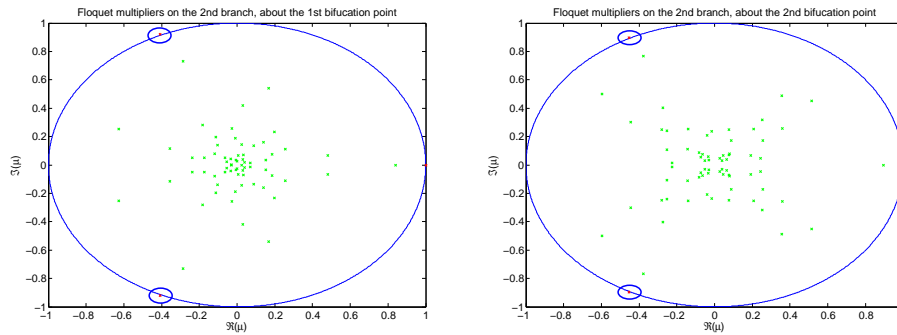

FIGURE 8. Torus bifurcations on the lower branch shown in 6 as a pair of complex Floquet multipliers across the unit circle. Left: A pair of Floquet mutipliers at the first secondary bifurcation point move inside the unit circle; Right: A pair of Floquet mutipliers at the second secondary bifurcation point move outside the unit circle.

On both Hopf branches, the cyclic period is an increasing function of the time delay (see the left panel of Figure 9). The right panel shows that, on the interesting overlap stable region, the largest norm of the nontrivial Floquet multipliers for each branch is less than one.

7. **Discussion.** Our study shows that for a delayed predator-prey model, Hopf bifurcation values of the delay generate global Hopf branches in pairs. When multiple
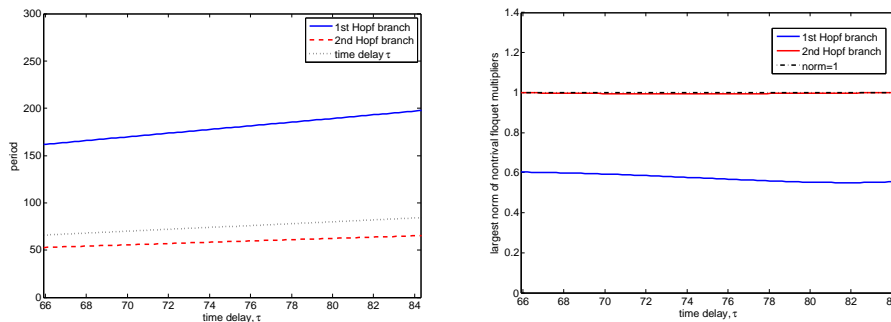
FIGURE 9. Left: periods of periodic solutions on the overlap stable region. Right: the largest norm of the nontrivial Floquet multipliers for the overlap stable region.

Hopf branches exist, the overlap can produce coexistence of two or possibly more stable limit cycles.

Extending periodic solutions around Hopf bifurcation values is a feasible and useful method to find periodic solutions, especially for weakly stable or even instable ones, which are generally hard to observe via DDE23.

Further mathematical theorems need to be developed in depth for the illustration of the relationship between stability switch points and Hopf bifurcations. Stability of global Hopf branches needs to be analytically verified. We propose these intriguing mathematical questions as open problems.

If f is a Holling Type III response function, we can still analyze the model in the same way. The difficulty is that the function $J(\tau)$ may have multiple zeros and thus multiple $S_n(\tau)$ sequences in different τ intervals, which leads to multiple replicates of Figure 5 and Figure 6 on separate τ intervals.

Biologically $d_j < d$ is possible though not general. If predators are on top of a food chain such as human being, juveniles fed and protected by adults are of lower risk, since adults who are out to hunt may be attacked by competing species or may face the risk of being killed by the group defence of their prey. In this case, the juvenile death rate d_j can be much smaller than the adult death rate d.

Numerically it is very easy to encounter the failure of DDE-BIFTOOL when $d_j > d$ and $S_0(\tau)$, $S_1(\tau)$ have intersections with the τ-axis. We do observe multiple $S_n(\tau)$, $n = 0, 1, 2, \cdots$, intersecting with the τ-axis similar to what we see in Figure 1 and Figure 5, for example, when

$$r = 3.92, \quad K = 18, \quad \beta = 850, \quad \gamma = 0.006, \quad d = 0.1, \quad d_j = 0.28,$$

in the model with Type I response function. However, when DDE-BIFTOOL is applied, the first Hopf branch is extended incorrectly. Periodic solutions on the branch given by DDE-BIFTOOL are not really periodic solutions for our model, which can be checked by the Floquet multipliers or DDE23 in MATLAB. As for the second Hopf branches, DDE-BIFTOOL even fails to find periodic solutions around where Hopf bifurcation occurs, whose existence is theoretically proven. Such a failure also happens even for some $d_j < d$. Although no evidence could be found, we believe that similar phenomena observed in Figure 2 and Figure 6 preserve even for $d_j > d$.

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