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Complex dynamics in a delay differential equation with two delays in tick growth with diapause

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Abstract

We consider a delay differential equation for tick population with diapause, derived from an age-structured population model, with two time lags due to normal and diapause mediated development. We derive threshold conditions for the global asymptotic stability of biologically important equilibria, and give a general geometric criterion for the appearance of Hopf bifurcations in the delay differential system with delay-dependent parameters. By choosing the normal development time delay as a bifurcation parameter, we analyze the stability switches of the positive equilibrium, and examine the onset and termination of Hopf bifurcations of periodic solutions from the positive equilibrium. Under some technical conditions, we show that global Hopf branches are bounded and connected by a pair of Hopf bifurcation values. This allows us to show that diapause can lead to the occurrence of multiple stability switches, coexistence of two stable limit cycles, among other rich dynamical behaviours.

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1. Introduction

Ticks, as vectors, are responsible for the transmission of Lyme borreliosis, tick-borne encephalitis, human granulocytic anaplasmosis and human babesiosis [11]. They are the second, next to mosquitoes, vector of vector-borne diseases with substantial impact on human health [19]. We refer to [10] and [9] for discussions on the tick lifecycle and tick ecology.

Our focus here is diapause, a physiological phenomenon which was investigated mainly by entomologists in the past but now received much attention in the study of tick population dynamics and tick-borne disease transmission dynamics [4]. The first instance of tick diapause was described more than one century ago [3]. Alfeev [1,2] categorized diapause characteristics for the ticks. The diapause behaviour is controlled by many factors such as photoperiod [18] and temperature [17]. Some tick population dynamics models were proposed in [7,17] to study the environmental impact on diapause. On the other hand, it was demonstrated that diapause plays an important role on seasonal patterns of tick activity [13]. However, the impact of diapause on the complex life cycle of ticks remains unclear [11].

To the best of our knowledge, there have been very few tick diapause models developed to incorporate both diapause delay and normal development delay. In [28], Zhang and Wu considered the following model with development delay and diapause delay:

$$x'(t) = -\mu x(t) + f((1-\alpha)\theta x(t-\tau) + \alpha\theta x(t-2\tau)), \tag{1.1}$$

and calculated the first Hopf bifurcation value by introducing and analyzing the so-called parametric trigonometric functions. Global continuation of the Hopf branch was also investigated in [27], and it was shown that all global Hopf branches of periodic solutions, with periods within $[3\tau, 6\tau]$, are unbounded, and hence periodic solutions exist for all large delay.

In this paper, we consider a different delay differential equation derived from the following age-structured model

$$\partial_t u_i(t,a) + \partial_a u_i(t,a) = -d_i(a)u_i(t,a), \quad i = 1, 2,$$

where $u_1(t,a)$ and $u_2(t,a)$ are the densities of ticks with a normal development delay τ_1 and a diapause mediated delay $\tau_2 = \tau_d + \tau_2$ respectively at time t and age a, where τ_d is the duration of diapause. The population of matured ticks at time t is then given by

$$x(t) = \int_{\tau_1}^{\infty} u_1(t,a)da + \int_{\tau_2}^{\infty} u_2(t,a)da.$$

Assuming that the mortality rates of matured and immatured ticks are μ and δ, respectively; namely,

$$d_i(a) = \begin{cases} \mu, & a > \tau_i, \\ \delta, & a < \tau_i, \end{cases}$$

one can obtain that

$$
\begin{aligned}
x'(t) &= \int_{\tau_1}^{\infty} \partial_t u_1(t,a)da + \int_{\tau_2}^{\infty} \partial_t u_2(t,a)da \\
&= -\mu x(t) - \int_{\tau_1}^{\infty} \partial_a u_1(t,a)da - \int_{\tau_2}^{\infty} \partial_a u_2(t,a)da \\
&= -\mu x(t) + u_1(t,\tau_1) + u_2(t,\tau_2),
\end{aligned}
$$

under the assumption that $u_1(t,\infty) = u_2(t,\infty) = 0$. Choosing the birth rate as the Ricker function $f(x) = rxe^{-sx}$ and letting p_1 and p_2 be the portions of new ticks in the two groups with normal development and diapause delays:

$$u_i(t,0) = p_i f(x(t)), \quad i = 1,2,$$

we obtain, from the integration of the age-structured equation along the characteristic line that

$$u_i(t,\tau_i) = u_i(t-\tau_i,0)e^{-\delta\tau_i} = p_i e^{-\delta\tau_i} f(x(t-\tau_i)).$$

Substituting this into the equation for $x'(t)$ gives

$$x'(t) = -\mu x(t) + p_1 e^{-\delta\tau_1} f(x(t-\tau_1)) + p_2 e^{-\delta\tau_2} f(x(t-\tau_2)). \tag{1.2}$$

In what follows, without loss of generality, we assume $r = s = 1$, for otherwise, we can scale x by a factor s and redefine p_i as $p_i r$. Before scaling, we have $p_1 + p_2 = 1$ and $f'(0) = r$. After scaling, the equalities become $p_1 + p_2 = r$ and $f'(0) = 1$. The parameters p_1 and p_2 are no longer probability constants. Instead, they are the two proportions of r divided in the ticks with development delays τ_1 and τ_2, respectively. Note that our model differs from (1.1) in two manners: (1) the growth term in our model is a linear combination of Ricker's reproduction functions of $x(t-\tau_i)$, while the growth term in (1.1) is the Ricker's reproduction function of a linear combination of $x(t-\tau_i)$; and (2) our coefficients in the linear combination (i.e., $p_i e^{-\delta\tau_i}$) are delay dependent while the coefficients in (1.1) are delay independent based on the assumption that the mortality of immature ticks is negligible.

In our study here, we will investigate the impact of diapause on the dynamical behaviours of our model. We will also give a general approach for the bifurcation analysis of delay differential systems with two delays and delay dependent parameters. We organize this paper as follows. In Section 2, we state some preliminary results on the positiveness and boundedness of the solutions and the stability of the trivial equilibrium. In Section 3, we derive a geometric criterion for a general delay differential system with two delays and delay dependent parameters. In Section 4, we investigate stability and Hopf bifurcation of the positive equilibrium. In Section 5, we conduct a global Hopf bifurcation analysis for periodic solutions with periods not equal to 4τ. In Section 6, we plot some illustrations from our numerical explorations. In Section 7, we give a brief summary and discuss on future open problems.

2. Preliminaries

We choose the phase space of model (1.2) as the Banach space $\mathcal{C} := C([-\tau_2, 0], \mathbb{R})$ equipped with the supremum norm. If $x(t)$ is continuous for all $t \geq -\tau_2$, we denote $x_t \in \mathcal{C}$ as $x_t(\theta) = x(t+\theta)$ for $\theta \in [-\tau_2, 0]$ and $t \geq 0$. For biological applications, the initial condition of (1.2) is given as

$$x_0 = \phi \in \mathcal{C}^+ \text{ and } \phi(0) > 0, \tag{2.1}$$

where $\mathcal{C}^+$ is the nonnegative cone of $\mathcal{C}$. The existence and uniqueness of the solution of model (1.2) with initial condition (2.1) follow from the theory of functional differential equations [12]. Furthermore, we can prove by contradition that $x(t)$ is nonnegative for all $t > 0$. Consequently, $x'(t) \geq -\mu x(t)$, which implies that $x(t) \geq \phi(0)e^{-\mu t} > 0$ for $t > 0$. Note that $f(x) \leq f(1) = 1/e$. We have $x'(t) \leq p_1 e^{-\delta\tau_1 - 1} + p_2 e^{-\delta\tau_2 - 1} - \mu x(t)$, which implies that

$$\limsup_{t\to\infty} x(t) \leq \frac{p_1 e^{-\delta\tau_1} + p_2 e^{-\delta\tau_2}}{\mu e}. \tag{2.2}$$

Note that model (1.2) has a trivial equilibrium 0. Based on the linearized model about the trivial equilibrium, we define the basic reproduction ratio as

$$R_0 = \frac{p_1 e^{-\delta\tau_1} + p_2 e^{-\delta\tau_2}}{\mu}. \tag{2.3}$$

It is easily seen that the model admits a unique positive equilibrium $x^* = \ln R_0$ if $R_0 > 1$, and no positive equilibrium if $R_0 \leq 1$. To analyze the stability of the equilibria, we need the following lemma which characterizes the root distribution of a general exponential transcendental polynomial.

Lemma 2.1. *Let $a_0 > 0$, $\tau_i \geq 0$ and $b_i \geq 0$ with $i = 1, 2$ such that $b_1 b_2 \neq 0$. Then the transcendental polynomial*

$$\varphi(\lambda) = \lambda + a_0 - b_1 e^{-\lambda\tau_1} - b_2 e^{-\lambda\tau_2}$$

has a unique real root whose sign is the same as the sign of $-\varphi(0) = b_1 + b_2 - a_0$. Furthermore, if $a_0 \geq b_1 + b_2$, then all non-real roots of $\varphi(\lambda)$ have negative real parts.

Proof. Since $\varphi'(\lambda) = 1 + b_1\tau_1 e^{-\lambda\tau_1} + b_2\tau_2 e^{-\lambda\tau_2} > 0$ and $\varphi(\pm\infty) = \pm\infty$, $\varphi(\lambda)$ has a unique real root λ_0. If $\varphi(0) > 0$ then $\lambda_0 < 0$. If $\varphi(0) < 0$ then $\lambda_0 > 0$. Consequently, the sign of this unique real root λ_0 is the same as the sign of $-\varphi(0) = b_1 + b_2 - a_0$. If $\varphi(\xi + i\eta) = 0$ for some $\xi \geq 0$ and $\eta \in \mathbb{R}$, then we have from $\mathrm{Re}\varphi(\xi + i\eta) = 0$ that

$$a_0 \leq \xi + a_0 = b_1 e^{-\xi\tau_1}\cos(\eta\tau_1) + b_2 e^{-\xi\tau_2}\cos(\eta\tau_2) \leq b_1 + b_2.$$

The equality $a_0 = b_1 + b_2$ holds if and only if $\xi = 0$, $b_1\cos(\eta\tau_1) = b_1$ and $b_2\cos(\eta\tau_2) = b_2$, which together with $\mathrm{Im}\varphi(\xi + i\eta) = 0$ imply that

$$\eta = -b_1 e^{-\xi\tau_1}\sin(\eta\tau_1) - b_2 e^{-\xi\tau_2}\sin(\eta\tau_2) = 0.$$

Hence, all non-real roots of $\varphi(\lambda)$ have negative real parts. This completes the proof. □

Theorem 2.2. *If $R_0 \le 1$, then the trivial equilibrium 0 of (1.2) is globally asymptotically stable in $\mathcal{C}^+$; whereas if $R_0 > 1$, then the trivial equilibrium 0 is unstable, and there exists a unique positive equilibrium $x^* = \ln R_0$.*

Proof. The characteristic equation associated with the linearization of model (1.2) at 0 is

$$\lambda + \mu - p_1 e^{-\delta\tau_1} e^{-\lambda\tau_1} - p_2 e^{-\delta\tau_2} e^{-\lambda\tau_2} = 0.$$

It follows from Lemma 2.1 that all eigenvalues have negative real parts if and only if $R_0 < 1$, and there exists at least one positive eigenvalue if $R_0 > 1$. Thus, the trivial equilibrium is locally asymptotically stable provided that $R_0 < 1$, and is unstable if $R_0 > 1$. This result could also be obtained from the observation that the linearized delay differential equation about the trivial equilibrium is actually monotone and that the local asymptotic stability of the trivial equilibrium for the delay differential equation is the same as that for the corresponding ordinary differential equation: $x'(t) = -\mu x(t) + (p_1 e^{-\delta\tau_1} + p_2 e^{-\delta\tau_2})x(t)$; see [25, Corollary 5.2]. For the critical case $R_0 = 1$, 0 is the only real eigenvalue and all other eigenvalues have negative real parts, we can further obtain the local stability of the trivial equilibrium by using the normal form theory. To see this, we first rewrite the delay differential equation (1.2) as an abstract equation on $\mathcal{C}$: $\dot{x}_t = Ax_t + F(x_t)$, where A and F are the linear and nonlinear operators defined as

$$(A\phi)(\theta) = \begin{cases} -\mu\phi(0) + p_1 e^{-\delta\tau_1}\phi(-\tau_1) + p_2 e^{-\delta\tau_2}\phi(-\tau_2), & \theta = 0, \\ \phi'(\theta), & \theta \in [-\tau_2, 0), \end{cases}$$

and

$$[F(\phi)](\theta) = \begin{cases} p_1 e^{-\delta\tau_1} g(\phi(-\tau_1)) + p_2 e^{-\delta\tau_2} g(\phi(-\tau_2)), & \theta = 0, \\ 0, & \theta \in [-\tau_2, 0), \end{cases}$$

for $\phi \in \mathcal{C}$. Here, for simplicity, we define $g(x) = f(x) - x = x(e^{-x} - 1)$. It is noted that $g(x) = -x^2 + O(x^3)$ as $x \to 0$. Next, we introduce a bilinear form

$$\langle \psi, \varphi \rangle = \psi(0)\varphi(0) + p_1 e^{-\delta\tau_1} \int_{-\tau_1}^{0} \psi(\theta + \tau_1)\varphi(\theta)d\theta + p_2 e^{-\delta\tau_2} \int_{-\tau_2}^{0} \psi(\theta + \tau_2)\varphi(\theta)d\theta$$

for $\psi \in C[0, \tau_2]$ and $\varphi \in C[-\tau_2, 0]$. It is readily seen from $R_0 = 1$ that $\varphi \equiv 1$ is the eigenfunction of A with respect to the eigenvalue 0. We set $\psi \equiv 1$ and project x_t on the eigenspace spanned by φ: $x_t = z\varphi + y$ such that $\langle \psi, y \rangle = 0$. Consequently, $\dot{x}_t = \dot{z}\varphi + \dot{y}$ and $\langle \psi, \dot{y} \rangle = 0$. It then follows from $\dot{x}_t = Ax_t + F(x_t)$ and $A\varphi = 0$ that

$$\dot{z}\langle \psi, \varphi \rangle = \langle \psi, \dot{x}_t \rangle = \langle \psi, Ay + F(z\varphi + y) \rangle.$$

A simple calculation gives $\langle\psi,\varphi\rangle = 1 + \tau_1 p_1 e^{-\delta\tau_1} + \tau_2 p_2 e^{-\delta\tau_2}$, $\langle\psi, Ay\rangle = 0$, and $\langle\psi, F(z\varphi + y)\rangle = p_1 e^{-\delta\tau_1} g(z + y(-\tau_1)) + p_2 e^{-\delta\tau_2} g(z + y(-\tau_2))$. Recall that $g(\varepsilon) = -\varepsilon^2 + O(\varepsilon^3)$ as $\varepsilon \to 0$. If $x_0 \in \mathcal{C}^+$ is a small perturbation of the trivial equilibrium, then z is also small and $y = O(z^2)$. We finally obtain the normal form for the delay differential equation (1.2) on the eigenspace spanned by φ:

$$(1 + \tau_1 p_1 e^{-\delta\tau_1} + \tau_2 p_2 e^{-\delta\tau_2})\dot{z} = -(p_1 e^{-\delta\tau_1} + p_2 e^{-\delta\tau_2}) z^2 + O(z^3).$$

Since $x_0 \in \mathcal{C}^+$, we have $z(0) \geq 0$. The trivial equilibrium 0 of the above equation is locally asymptotically stable on $\mathbb{R}^+$, which implies that the trivial equilibrium 0 of the original model (1.2) is also locally asymptotically stable on $\mathcal{C}^+$.

When $R_0 \leq 1$, we construct the following Lyapunov functional $L : \mathcal{C}^+ \mapsto \mathbb{R}$ to show the global attractivity of the trivial equilibrium.

$$L(x_t) = x_t(0) + p_1 e^{-\delta\tau_1} \int_{-\tau_1}^{0} x_t(s) e^{-x_t(s)} ds + p_2 e^{-\delta\tau_2} \int_{-\tau_2}^{0} x_t(s) e^{-x_t(s)} ds.$$

Calculating the derivative of L with respect to t along solutions of (1.2), we obtain

$$\frac{dL}{dt} = (p_1 e^{-\delta\tau_1} + p_2 e^{-\delta\tau_2}) x(t) e^{-x(t)} - \mu x(t) \leq \mu(R_0 - 1) x(t) \leq 0.$$

Note that $dL/dt = 0$ if and only if $x(t) = 0$. By the Lyapunov-LaSalle Invariance Principle [12,20], we obtain the global attractiveness of the trivial equilibrium, which together with the local asymptotic result implies the global asymptotic stability of the trivial equilibrium if $R_0 \leq 1$. □

3. A geometric criterion for Hopf bifurcation values in delay differential systems

In this section, we consider the case that $\tau_d = \tau_1 =: \tau$ (namely, $\tau_2 = 2\tau_1$) and study the occurrence of possible Hopf bifurcation values when the time lag is increased. The characteristic equation for a general model with two delays (τ and 2τ) and delay dependent parameters can be written as

$$\Delta(\lambda, \tau) := P_n(\lambda, \tau) + Q_m(\lambda, \tau) e^{-\lambda\tau} + S_l(\lambda, \tau) e^{-2\lambda\tau} = 0, \tag{3.1}$$

where

$$P_n(\lambda, \tau) = \sum_{k=0}^{n} p_k(\tau)\lambda^k, \quad Q_m(\lambda, \tau) = \sum_{k=0}^{m} q_k(\tau)\lambda^k, \text{ and } S_l(\lambda, \tau) = \sum_{k=0}^{l} s_k(\tau)\lambda^k.$$

Here, $n, m, l \in \mathbb{N}_0, n > \max\{m, l\}, \tau \geq 0$, and $p_k(\tau), q_k(\tau), s_k(\tau)$ are continuous and differentiable functions of τ. $P_n(\lambda, \tau)$, $Q_m(\lambda, \tau)$ and $S_l(\lambda, \tau)$ are analytic in λ and differentiable in τ. Denote

$$A(\lambda,\tau) = \mathrm{Re}\left(-\frac{Q_m(\lambda,\tau)+S_l(\lambda,\tau)e^{-\lambda\tau}}{P_n(\lambda,\tau)}\right),$$

$$B(\lambda,\tau) = \mathrm{Im}\left(-\frac{Q_m(\lambda,\tau)+S_l(\lambda,\tau)e^{-\lambda\tau}}{P_n(\lambda,\tau)}\right).$$

Then, the characteristic equation (3.1) is equivalent to

$$D(\lambda,\tau) := A(\lambda,\tau) + iB(\lambda,\tau) - e^{\lambda\tau} = 0, \tag{3.2}$$

where $A(\lambda,\tau)$ and $B(\lambda,\tau)$ are analytic in λ and differentiable in τ. We assume that

(i) $(A(0,\tau)-1)^2 + B(0,\tau)^2 \neq 0$ for any $\tau \geq 0$.
(ii) If $\lambda = i\omega$, $\omega \in \mathbb{R}$, then $(A(i\omega,\tau)-1)^2 + B(i\omega,\tau)^2 \neq 0$ for any $\tau \geq 0$.
(iii) $\limsup_{|\lambda|\to\infty,\ \mathrm{Re}\lambda\geq 0} A(\lambda,\tau)^2 + B(\lambda,\tau)^2 < 1$ for any $\tau \geq 0$.
(iv) $\widetilde{G}(\omega,\tau) = A(i\omega,\tau)^2 + B(i\omega,\tau)^2 - 1$ for each $\tau \geq 0$ has at most a finite number of real zeros, and each positive zero $\omega(\tau)$ of $\widetilde{G}(\omega,\tau)$ is continuous and differentiable in τ whenever it exists.

Assumption (i) implies that 0 is not a characteristic root of (3.2); (ii) ensures that the functions $S_n(\tau)$ with $n \in \mathbb{N}_0$ (to be defined below) are differentiable; (iii) ensures that there is no root entering the right (left) half of the complex plane from the left (right) half through infinities; (iv) ensures that there are only finite critical values for roots to cross the imaginary axis. This assumption is needed to compute the derivative of the imaginary roots with respect to τ.

If $\lambda = \pm i\omega(\tau)$ with $\omega(\tau) > 0$ are a pair of imaginary roots of the characteristic equation (3.2), then $\sin(\omega\tau) = B(i\omega,\tau)$, $\cos(\omega\tau) = A(i\omega,\tau)$. Consequently,

$$\widetilde{G}(\omega,\tau) = A(i\omega,\tau)^2 + B(i\omega,\tau)^2 - 1 = 0. \tag{3.3}$$

Let I be the interval of τ on which the above equation has at least one positive root $\omega(\tau)$. If I is empty, then there does not exist any Hopf bifurcation value. To study the geometric criterion of Hopf bifurcation values, we shall assume in the remaining of this section that I is nonempty. For any $\tau \in I$, we define $\theta(\tau) \in [0, 2\pi)$ as the solution of

$$\sin\theta(\tau) = B(i\omega,\tau), \quad \cos\theta(\tau) = A(i\omega,\tau).$$

Thus, for any $\tau \in I$, we have $\omega(\tau)\tau = \theta(\tau) + 2n\pi$ for some $n \in \mathbb{N}_0$. Define

$$S_n(\tau) = \omega(\tau)\tau - \theta(\tau) - 2n\pi, \text{ for } \tau \in I,\ n \in \mathbb{N}_0.$$

We have the following geometric criterion for the verification of transversality condition for a general model with multiple delays.

Theorem 3.1. *Assume that I is non-empty and that $S_n(\tau)$ has a positive root $\tau^* \in I$ for some $n \in \mathbb{N}_0$, then (3.2) has a pair of simple purely imaginary roots $\pm i\omega(\tau^*)$. Moreover, we have the following transversality condition:*

$$Sign\left(Re\lambda'(\tau^*)\right) = Sign\left(-\frac{\partial \widetilde{G}}{\partial \omega}(\omega(\tau^*), \tau^*)\right) Sign\ S_n'(\tau^*).$$

Proof. Substituting $\lambda(\tau)$ into the characteristic equation (3.2) and taking the derivative with respective to τ, we obtain

$$\mathrm{Re}\lambda'(\tau^*) = Re\left(-\frac{A_\tau + iB_\tau - \lambda e^{\lambda\tau}}{A_\lambda + iB_\lambda - \tau e^{\lambda\tau}}\right).$$

Note that $iA_\lambda = A_\omega$, $iB_\lambda = B_\omega$, $e^{\lambda\tau} = A + iB$, and at $\tau = \tau^*$, $\lambda = i\omega$. We obtain

$$\begin{aligned}\mathrm{Re}\lambda'(\tau^*) &= Re\left(-\frac{A_\tau + iB_\tau - i\omega(A+iB)}{-iA_\omega + B_\omega - \tau(A+iB)}\right)\\ &= Re\left(-\frac{(A_\tau + \omega B) + i(B_\tau - \omega A)}{(B_\omega - \tau A) - i(A_\omega + \tau B)}\right),\end{aligned}$$

which implies that

$$\mathrm{Sign}\left(\mathrm{Re}\lambda'(\tau^*)\right) = -\mathrm{Sign}\left(A_\tau B_\omega - A_\omega B_\tau + \omega(BB_\omega + AA_\omega) - \tau(AA_\tau + BB_\tau)\right).$$

Since $\widetilde{G}_\omega = 2(AA_\omega + BB_\omega)$, $\widetilde{G}_\tau = 2(AA_\tau + BB_\tau)$ and $\widetilde{G}_\omega\omega' + \widetilde{G}_\tau = 0$, we have

$$\mathrm{Sign}\left(\mathrm{Re}\lambda'(\tau^*)\right) = -\mathrm{Sign}\left(A_\tau B_\omega - A_\omega B_\tau + \frac{1}{2}\omega\widetilde{G}_\omega + \frac{1}{2}\tau\omega'\widetilde{G}_\omega\right). \tag{3.4}$$

Differentiating $\sin\theta(\tau) = B(i\omega, \tau)$ with respect to τ gives $\theta' = (B_\omega\omega' + B_\tau)/A$. Consequently,

$$\begin{aligned}G_\omega A\theta' &= G_\omega(B_\omega\omega' + B_\tau) = -G_\tau B_\omega + G_\omega B_\tau\\ &= -2(AA_\tau + BB_\tau)B_\omega + 2(AA_\omega + BB_\omega)B_\tau = 2A(A_\omega B_\tau - A_\tau B_\omega).\end{aligned}$$

In view of (3.4) and $S_n' = \omega'\tau + \omega - \theta'$, we obtain

$$\begin{aligned}\mathrm{Sign}\left(\mathrm{Re}\lambda'(\tau^*)\right) &= -\mathrm{Sign}\left(\tau\omega'\widetilde{G}_\omega + \omega\widetilde{G}_\omega - \theta'\widetilde{G}_\omega\right)\\ &= \mathrm{Sign}\left(-\frac{\partial \widetilde{G}}{\partial \omega}(\omega(\tau^*), \tau^*)\right) \mathrm{Sign}\ S_n'(\tau^*).\end{aligned}$$

This ends the proof. □

Remark 3.2. If $S_l(\lambda, \tau) = 0$, then the characteristic equation (3.1) reduces to the characteristic equation considered in [5]. Theorem 3.1 generalizes [5, Theorem 2.2] to delay differential systems with multiple delays and delay dependent parameters.

4. Stability and Hopf bifurcation of the positive equilibrium

In this section, we always assume that $R_0 > 1$, which ensures the instability of trivial equilibrium 0 and the existence of the unique positive equilibrium $x^* = \ln R_0$. In the sequel, we consider a special case of (1.2) with $\tau_2 = 2\tau_1$, and we refer to the papers [28] for the justification of this constraint. For simplicity, we drop the subscript 1 in the following arguments, and rewrite the model (1.2) as

$$x'(t) = p_1 e^{-\delta\tau} f(x(t-\tau)) + p_2 e^{-2\delta\tau} f(x(t-2\tau)) - \mu x(t). \tag{4.1}$$

4.1. Stability of the positive equilibrium

We will investigate the stability of x^* and identify the parameter range in which the time delay can destabilize x^* and lead to Hopf bifurcations. Denote

$$\tau_{max} = \frac{1}{\delta} \ln \frac{\sqrt{p_1^2 + 4p_2\mu} + p_1}{2\mu}.$$

It is obvious that $R_0 > 1$ if and only if $\frac{p_1+p_2}{\mu} > 1$ and $\tau \in [0, \tau_{max})$. The characteristic equation associated with the linearization of (4.1) around x^* is

$$\lambda + \mu - a(\tau)e^{-\lambda\tau} - b(\tau)e^{-2\lambda\tau} = 0, \tag{4.2}$$

where

$$a(\tau) = p_1 e^{-\delta\tau} e^{-x^*}(1 - x^*), \quad b(\tau) = p_2 e^{-2\delta\tau} e^{-x^*}(1 - x^*). \tag{4.3}$$

Note that when $\tau = 0$, the characteristic root of (4.2) is $\lambda(0) = a(0) + b(0) - \mu = -\mu \ln \frac{p_1+p_2}{\mu} < 0$, which implies that x^* is locally asymptotically stable. As τ increases, x^* may lose its stability if and only if when some eigenvalues cross the imaginary axis to the right. In view of $a(\tau) + b(\tau) - \mu = -\mu x^* < 0$, 0 is not an eigenvalue of the characteristic equation (4.2) for any $\tau \in [0, \tau_{max})$. We thus consider the possibility of purely imaginary roots $\lambda = \pm i\omega$ with $\omega > 0$ for $\tau > 0$. Substituting $\lambda = i\omega$ into (4.2) gives

$$e^{i\omega\tau}(i\omega + \mu) - a(\tau) - b(\tau)e^{-i\omega\tau} = 0.$$

Separating the real and imaginary parts, we obtain

$$\sin(\omega\tau) = \frac{-\omega\, a(\tau)}{\omega^2 + \mu^2 - b^2(\tau)}, \quad \cos(\omega\tau) = \frac{a(\tau)\,(\mu + b(\tau))}{\omega^2 + \mu^2 - b^2(\tau)}. \tag{4.4}$$

Squaring and adding the above two equations lead to

$$G(\omega) := \omega^4 + (2\mu^2 - 2b^2 - a^2)\omega^2 + (\mu + b)^2(\mu - b - a)(\mu - b + a) = 0. \tag{4.5}$$

Thus, $\pm i\omega$ are a pair of pure imaginary eigenvalues of (4.2) only if $G(\omega)=0$. In view of $\mu-b-a=\mu x^*>0$, one can easily obtain the following lemma counting the number of simple positive roots of G.

Lemma 4.1. *(i) $G(\omega)$ does not have any positive root if and only if*

$$(\boldsymbol{H}_0):\ \ \textit{either}\ \ a^2<-8b(\mu+b)\ \ \textit{or}\ \ -a\le\mu-b\le 2(\mu+b)\ \ \textit{holds}.$$

(ii) $G(\omega)$ has exactly one simple positive root if and only if

$$(\boldsymbol{H}_1):\ \ \textit{either}\ \ -a>\mu-b\ \ \textit{or}\ \ -a=\mu-b<-4b\ \ \textit{holds}.$$

(iii) $G(\omega)$ has two simple positive roots if and only if

$$(\boldsymbol{H}_2):\ -a<\mu-b<-4b\ \ \textit{and}\ \ a^2>-8b(b+\mu)\ \ \textit{hold}.$$

Denote

$$\overline{\tau}=\frac{1}{\delta}\ln\frac{\sqrt{p_1^2+4p_2e\mu}+p_1}{2e\mu}<\tau_{max}.$$

We obtain the global stability result of x^* by constructing a suitable Lyapunov functional.

Proposition 4.2. *All solutions of model* (4.1) *with nontrivial initial conditions converge to x^* if either*

$$1<\frac{p_1+p_2}{\mu}\le e\ \textit{and}\ \tau\in[0,\tau_{max}), \tag{4.6}$$

or

$$\frac{p_1+p_2}{\mu}>e\ \textit{and}\ \tau\in[\overline{\tau},\tau_{max}). \tag{4.7}$$

Proof. If either (4.6) or (4.7) holds, then $0<x^*\le 1$, which implies that $a(\tau)\ge 0$ and $b(\tau)\ge 0$. Since $\mu-a-b=\mu x^*>0$, it is easily seen that $-a\le\mu-b\le 2(\mu+b)$. Hence, $(\mathbf{H}_0)$ is satisfied. It follows from Lemma 4.1 that $G(z)$ does not have any positive root. Therefore, for any $\tau\in[0,\tau_{max})$, the eigenvalues of (4.2) have negative real parts, which implies that x^* is locally asymptotically stable. Recall from (2.2) that

$$\limsup_{t\to\infty}x(t)\le\frac{p_1e^{-\delta\tau}+p_2e^{-2\delta\tau}}{\mu e}=\frac{e^{x^*}}{e}\le 1.$$

Let $\Gamma:=\{\phi\in\mathcal{C}^+:\|\phi\|\le 1,\phi(0)>0\}$. By an argument similar to the proof of [24, Lemma 3.1], we can prove that the region Γ is positively invariant and absorbing in $\mathcal{C}^+$ with respect to model (4.1). To establish the global stability of x^*, it suffices to show that x^* is globally attractive in Γ. Define a Lyapunov functional $V:\Gamma\to\mathbb{R}$,

$$V(x_t) = x_t(0) - x^* \ln x_t(0) + p_1 e^{-\delta\tau} \int_{-\tau}^{0} \big(f(x_t(s)) - f(x^*) \ln f(x_t(s))\big)\, ds$$

$$+ p_2 e^{-2\delta\tau} \int_{-2\tau}^{0} \big(f(x_t(s)) - f(x^*) \ln f(x_t(s))\big)\, ds,$$

where $f(x) = xe^{-x}$. Calculating the time derivative of V along the solution of (4.1) yields

$$\begin{aligned}\frac{dV}{dt} =& - \mu x(t) + \left(p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}\right) f(x(t)) + \mu x^* \\ &- \frac{p_1 e^{-\delta\tau} x^* f(x(t-\tau))}{x(t)} - \frac{p_2 e^{-2\delta\tau} x^* f(x(t-2\tau))}{x(t)} \\ &+ f(x^*)\left(p_1 e^{-\delta\tau} \ln \frac{f(x(t-\tau))}{f(x(t))} + p_2 e^{-2\delta\tau} \ln \frac{f(x(t-2\tau))}{f(x(t))}\right).\end{aligned}$$

Denote $h(\theta) = \theta - 1 - \ln\theta$ for $\theta > 0$. By using $\mu x^* = (p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}) f(x^*)$, we obtain

$$\begin{aligned}\frac{dV}{dt} =& \mu x(t)(\frac{f(x(t))}{f(x^*)} - 1)(\frac{x^*}{x(t)} - \frac{f(x^*)}{f(x(t))}) - \mu x^* h\left(\frac{x(t) f(x^*)}{x^* f(x(t))}\right) \\ &- p_1 e^{-\delta\tau} f(x^*) h\left(\frac{x^* f(x(t-\tau))}{x(t) f(x^*)}\right) - p_2 e^{-2\delta\tau} f(x^*) h\left(\frac{x^* f(x(t-2\tau))}{x(t) f(x^*)}\right).\end{aligned}$$

Since $f(x)$ is strictly increasing and concave down on $[0, 1]$, we have $f(x)/x > f'(x)$ for all $x \in (0, 1]$. Hence, the function $f(x)/x$ is strictly decreasing on $(0, 1]$. If $x(t) \in (0, x^*)$, then $f(x(t)) < f(x^*)$ and $f(x(t))/x(t) > f(x^*)/x^*$. If $x(t) \in (x^*, 1]$, then $f(x(t)) > f(x^*)$ and $f(x(t))/x(t) < f(x^*)/x^*$. Consequently, we obtain

$$(\frac{f(x(t))}{f(x^*)} - 1)(\frac{x^*}{x(t)} - \frac{f(x^*)}{f(x(t))}) \le 0 \;\text{ for all }\; x(t) \in (0, 1],$$

and the equalities hold only if $x(t) \equiv x^*$. Note that $h(\theta) \ge 0$ for all $\theta > 0$ and $h(\theta) = 0$ if and only if $\theta = 1$. Therefore, $dV/dt \le 0$ for all $x_t \in \Gamma$, and $dV/dt = 0$ if and only if $x(t) \equiv x^*$. Thus the maximal compact invariant set in $\{dV/dt = 0\}$ is the singleton $\{x^*\}$. By the LaSalle Invariance Principle [12], x^* is globally attractive in Γ. Since Γ is absorbing in $\mathcal{C}^+$, the omega limit set $\omega(\phi) \subset \Gamma$ for any initial value $\phi \in \mathcal{C}^+$ with $\phi(0) > 0$. Moreover, $\omega(\phi)$ is internally chain transitive by [30, Lemma 1.2.1]. In view of [30, Theorem 1.2.1], x^* is actually globally attractive in $\{\phi \in \mathcal{C}^+ : \phi(0) > 0\}$. Since x^* is also locally asymptotically stable, we conclude that x^* is globally asymptotically stable in $\{\phi \in \mathcal{C}^+ : \phi(0) > 0\}$ provided that either (4.6) or (4.7) holds. □

Proposition 4.3. *The positive equilibrium x^* is locally asymptotically stable, if either*

$$(i)\;\; \frac{p_1 + p_2}{\mu} \le e^2, \tau \in [0, \tau_{max}); \;\; or \;\; (ii)\;\; \frac{p_1 + p_2}{\mu} > e^2, \tau \in [\widehat{\tau}, \overline{\tau})$$

holds, where $\widehat{\tau} = \frac{1}{\delta}\ln\frac{\sqrt{p_1^2+4p_2e^2\mu}+p_1}{2e^2\mu} < \overline{\tau}$.

Proof. From Theorem 4.2, we obtain that x^* is globally asymptotically stable if $\frac{p_1+p_2}{\mu} \le e$ and $\tau \in [0, \tau_{max})$. It suffices to prove that x^* is locally asymptotically stable if either (i') $e < \frac{p_1+p_2}{\mu} \le e^2$, $\tau \in [0, \tau_{max})$ or (ii) holds. Either (i') or (ii) implies $1 < x^* \le 2$, which implies that $a(\tau) < 0$ and $b(\tau) < 0$. Denote $\alpha = 1/(1-x^*) \le -1$. It is readily seen that $\mu = \alpha a(\tau) + \alpha b(\tau) \ge -a(\tau) - b(\tau)$. We claim that $(\mathbf{H}_0)$ holds. If $a(\tau)^2 < -8b(\tau)[\mu + b(\tau)]$, then $(\mathbf{H}_0)$ holds. If $a(\tau)^2 \ge -8b(\tau)[\mu + b(\tau)]$, since $\mu + b(\tau) \ge -a(\tau)$, we have $-a(\tau) \ge -8b(\tau)$. Consequently, $\mu \ge -9b(\tau) \ge -3b(\tau)$, which is the same as $2[\mu + b(\tau)] \ge \mu - b(\tau)$. Moreover, we obtain $\mu - b(\tau) \ge \mu \ge -a(\tau) - b(\tau) \ge -a(\tau)$. Thus, $(\mathbf{H}_0)$ still holds, which implies that x^* is locally asymptotically stable if either (i) or (ii) holds by Lemma 4.1. □

Summarizing the above analysis, we obtain the following results on the stability of x^*.

Theorem 4.4.

(i) *If* $1 < \frac{p_1+p_2}{\mu} \le e$*, then* x^* *is globally asymptotically stable in* $X := \{\phi \in \mathcal{C}^+ : \phi(0) > 0\}$ *for all* $\tau \in [0, \tau_{max})$.

(ii) *If* $e < \frac{p_1+p_2}{\mu} \le e^2$*, then* x^* *is locally asymptotically stable for* $\tau \in [0, \overline{\tau})$ *and globally asymptotically stable in* X *for* $\tau \in [\overline{\tau}, \tau_{max})$.

(iii) *If* $\frac{p_1+p_2}{\mu} > e^2$*, then* x^* *is locally asymptotically stable for* $\tau \in [\widehat{\tau}, \overline{\tau})$ *and globally asymptotically stable in* X *for* $\tau \in [\overline{\tau}, \tau_{max})$.

4.2. Hopf bifurcation analyses

A necessary condition for the existence of Hopf bifurcation is that $\frac{p_1+p_2}{\mu} > e^2$ and $\tau \in (0, \widehat{\tau})$. Throughout this subsection, we will conduct Hopf bifurcation analysis under this condition. It is readily seen that $x^* > 2$, $a(\tau) < 0$ and $b(\tau) < 0$. If $(\mathbf{H}_1)$ holds, then implicit function theorem implies the existence of a unique C^1 function $\omega = \omega_+(\tau)$ such that $G(\omega_+(\tau)) = 0$ for $0 < \tau < \widehat{\tau}$; if $(\mathbf{H}_2)$ holds, there exist two C^1 functions $\omega_\pm(\tau)$ such that $G(\omega_\pm(\tau)) = 0$ for $0 < \tau < \widehat{\tau}$, where

$$\omega_\pm(\tau) = \sqrt{\frac{a^2 - 2\mu^2 + 2b^2 \mp a\sqrt{a^2 + 8b(b+\mu)}}{2}}. \tag{4.8}$$

If $\pm i\omega_+(\tau)$ (resp., $\pm i\omega_-(\tau)$) is a pair of purely imaginary roots of (4.2), then $\omega_+(\tau)$ (resp., $\omega_-(\tau)$) is a solution to (4.4). For convenience, we denote by I_1 (resp., I_2) the subset of $[0, \widehat{\tau}]$ such that $(\mathbf{H}_1)$ (reps., $(\mathbf{H}_2)$) holds. Set $I = I_1 \cup I_2$. For $\tau \in I$, let $\theta_\pm(\tau) \in [0, 2\pi)$ be the unique solution of

$$\sin\theta_\pm = \frac{-a(\tau)\omega_\pm}{\omega_\pm^2 + \mu^2 - b^2(\tau)}, \quad \cos\theta_\pm = \frac{a(\tau)\,(\mu + b(\tau))}{\omega_\pm^2 + \mu^2 - b^2(\tau)}. \tag{4.9}$$

Note that $\omega_+^2 + \mu^2 - b^2(\tau) > 0$ for all $\tau \in I$, which implies $\sin\theta_+(\tau) > 0$. Since $G(b^2(\tau) - \mu^2) = -2a^2(\tau)b(\tau)(\mu + b(\tau))$ and $\frac{G(b^2(\tau)-\mu^2)}{\omega_-^2+\mu^2-b^2(\tau)} > 0$, we have $\cos\theta_-(\tau) < 0$. Thus,

$$\theta_+(\tau) = \arccos\left(\frac{a(\tau)(\mu + b(\tau))}{\omega_+^2 + \mu^2 - b^2(\tau)}\right), \quad \theta_-(\tau) = \pi - \arcsin\frac{-a(\tau)\omega_-}{\omega_-^2 + \mu^2 - b^2(\tau)}.$$

Now, we define

$$S_n^{\pm}(\tau) = \tau\omega_{\pm}(\tau) - \theta_{\pm}(\tau) - 2n\pi \tag{4.10}$$

for $\tau \in I$ and $n \in \mathbb{N}_0$. One can check that $\pm i\omega_{\pm}(\tau^*)$ are a pair of purely imaginary eigenvalues of (4.2) if and only if $S_n^{\pm}(\tau^*) = 0$ for some $n \in \mathbb{N}_0$.

Lemma 4.5. *For any $n \in \mathbb{N}_0$, $S_n^+(\tau) > S_{n+1}^+(\tau)$ for $\tau \in I$, $S_n^-(\tau) > S_{n+1}^-(\tau)$ and $S_n^+(\tau) > S_n^-(\tau)$ for $\tau \in I_2$. Moreover, $S_0^+(0) < 0$.*

Proof. For any $n \in \mathbb{N}_0$, it is easily seen that $S_n^+(\tau) > S_{n+1}^+(\tau)$ for $\tau \in I$ and $S_n^-(\tau) > S_{n+1}^-(\tau)$ for $\tau \in I_2$. We claim that $\theta_+(\tau) < \theta_-(\tau)$ for all $\tau \in I_2$. Assume to the contrary that $\theta_+(\tau_c) \geq \theta_-(\tau_c)$ for some $\tau_c \in I_2$. Note that $\theta_+(\tau) \in (0, \pi)$ and $\theta_-(\tau) \in (\pi/2, 3\pi/2)$ by (4.9). It follows that $\pi/2 < \theta_-(\tau_c) \leq \theta_+(\tau_c) < \pi$; namely, $\cos\theta_+(\tau_c) < 0$ and $\sin\theta_-(\tau_c) > 0$. On account of $\omega_+ > \omega_-$ and (4.9), we obtain $\mu + b(\tau_c) > 0$ and $\omega_+^2 + \mu^2 - b^2(\tau_c) > \omega_-^2 + \mu^2 - b^2(\tau_c) > 0$. It then follows from $a(\tau_c) < 0$ that

$$\cos\theta_+(\tau_c) = \frac{a(\tau_c)\,(\mu + b(\tau_c))}{\omega_+^2 + \mu^2 - b^2(\tau_c)} > \frac{a(\tau_c)\,(\mu + b(\tau_c))}{\omega_-^2 + \mu^2 - b^2(\tau_c)} = \cos\theta_-(\tau_c),$$

which implies $\theta_+(\tau_c) < \theta_-(\tau_c)$, a contradiction. Thus, we conclude that $\theta_+(\tau) < \theta_-(\tau)$ for all $\tau \in I_2$. By the definition of $S_0^{\pm}(\tau)$ and $\omega_+ > \omega_-$, we have

$$\frac{\theta_+}{\omega_+} < \frac{\theta_-}{\omega_-} \quad \text{and} \quad S_0^+(\tau) > S_0^-(\tau) \quad \text{for} \quad \tau \in I_2.$$

Therefore, $S_n^+(\tau) > S_n^-(\tau)$ for all $\tau \in I_2$ and $n \in \mathbb{N}_0$. When $\tau = 0$, the asymptotic stability of x^* implies that $S_0^+(0) < 0$. This ends the proof. □

As we will see later, the signs of the following functions play an important role in bifurcation analysis.

$$\mathrm{Sign}(\mu + b) = \mathrm{Sign}(\omega_-^2 + \mu^2 - b^2) = \mathrm{Sign}(\sin\theta_-) = -\mathrm{Sign}(\cos\theta_+). \tag{4.11}$$

In the following lemma, we investigate the sign of $\mu + b(\tau)$.

Lemma 4.6. *If $\frac{p_1+p_2}{\mu} > e^{2+p_1/p_2}$, then $\mu + b(\tau)$ has a unique zero on $(0, \widehat{\tau})$, denoted by $\check{\tau}$. Moreover, $\mu + b(\tau) < 0$ for $\tau \in (0, \check{\tau})$ and $\mu + b(\tau) > 0$ for $\tau \in (\check{\tau}, \widehat{\tau})$. On the other hand, if $\frac{p_1+p_2}{\mu} \leq e^{2+p_1/p_2}$, then $\mu + b(\tau) > 0$ for all $\tau \in (0, \widehat{\tau})$.*

Proof. By using $\mu = p_1 e^{-\delta\tau} e^{-x^*} + p_2 e^{-2\delta\tau} e^{-x^*}$ and the definition of $b(\tau)$ in (4.3), we obtain

$$\mu + b(\tau) = -e^{-\delta\tau} e^{-x^*}\left((\ln\frac{p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}}{\mu} - 2)p_2 e^{-\delta\tau} - p_1\right).$$

Set $g(\tau) = (\ln \frac{p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}}{\mu} - 2)p_2 e^{-\delta\tau} - p_1$. It is readily seen that $g'(\tau) \leq 0$, $g(0) = (\ln \frac{p_1+p_2}{\mu} - 2)p_2 - p_1$, and $g(\widehat{\tau}) = -p_1 < 0$. If $\frac{p_1+p_2}{\mu} \leq e^{2+p_1/p_2}$, then $g(0) \leq 0$, which implies that $g(\tau) < 0$ and $\mu + b(\tau) > 0$ for all $\tau \in (0, \widehat{\tau})$.

On the other hand, if $\frac{p_1+p_2}{\mu} > e^{2+p_1/p_2}$, then $g(0) > 0$. It follows from the intermediate value theorem that there exists a unique $\breve{\tau} \in (0, \widehat{\tau})$ such that $g(\breve{\tau}) = 0$. Moreover, $g(\tau) > 0$ for $\tau \in (0, \breve{\tau})$ and $g(\tau) < 0$ for $\tau \in (\breve{\tau}, \widehat{\tau})$. This completes the proof. □

Let $\lambda(\tau) = \xi(\tau) + i\omega(\tau)$ be a root of the characteristic equation (4.2) near $\tau = \tau^*$ satisfying $\xi(\tau^*) = 0$ and $\omega^* = \omega(\tau^*) > 0$. It can be calculated that

$$A(i\omega, \tau) = \frac{(a(\tau) + b(\tau)\cos(\omega\tau))\mu - b(\tau)\omega\sin(\omega\tau)}{\mu^2 + \omega^2}$$

and

$$B(i\omega, \tau) = \frac{-\omega(a(\tau) + b(\tau)\cos(\omega\tau)) - b(\tau)\mu\sin(\omega\tau)}{\mu^2 + \omega^2}.$$

Consequently,

$$\begin{aligned}\widetilde{G}(\omega, \tau) &= \frac{a(\tau)^2 + b(\tau)^2 + 2a(\tau)b(\tau)\cos(\omega\tau) - \omega^2 - \mu^2}{\mu^2 + \omega^2} \\ &= -\frac{G}{(\omega^2 + \mu^2 - b^2)(\mu^2 + \omega^2)}.\end{aligned}$$

By using Theorem 3.1, we have the following transversality condition

$$\begin{aligned}\text{Sign}\left(\text{Re}\lambda'(\tau^*)\right) &= \text{Sign}\left(-\frac{\partial \widetilde{G}}{\partial \omega}(\omega(\tau^*), \tau^*)\right) \text{Sign } S_n'(\tau^*) \\ &= \text{Sign}(\omega(\tau^*)^2 + \mu^2 - b(\tau^*)^2) \text{ Sign}\left(\frac{\partial G}{\partial \omega}(\omega(\tau^*), \tau^*)\right) \text{Sign } S_n'(\tau^*),\end{aligned}$$

where $S_n(\tau^*) = \omega(\tau^*)\tau^* - \theta(\tau^*) - 2n\pi = 0$ for some $n \in \mathbb{N}_0$. It is easily seen that

$$\omega_+(\tau^*)^2 + \mu^2 - b(\tau^*)^2 > 0, \quad \frac{\partial G}{\partial \omega}(\omega_+(\tau^*), \tau^*) > 0 \text{ and } \frac{\partial G}{\partial \omega}(\omega_-(\tau^*), \tau^*) < 0.$$

Now, we are ready to provide a simple geometric method in the examination of the transversality condition.

Theorem 4.7. *Assume that for some $n \in \mathbb{N}_0$ the function $S_n^+(\tau)$ (resp., $S_n^-(\tau)$) has a positive root $\tau^* \in I$, then a pair of simple purely imaginary roots $\pm i\omega_+(\tau^*)$ (resp., $\pm i\omega_-(\tau^*)$) of (4.2) exist at $\tau = \tau^*$, and*

$$Sign\left(Re\lambda'(\tau^*)\right) = Sign\,\frac{dS_n^+(\tau^*)}{d\tau},$$
$$\left(resp.,\ Sign\left(Re\lambda'(\tau^*)\right) = -\,Sign\,(\omega_-(\tau^*)^2+\mu^2-b(\tau^*)^2)\ Sign\,\frac{dS_n^-(\tau^*)}{d\tau}\right).$$

Moreover, this pair of simple purely imaginary roots $\pm i\omega_+(\tau^*)$ (resp., $\pm i\omega_-(\tau^*)$) crosses the imaginary axis from left to right at $\tau=\tau^*$ if $Re\lambda'(\tau^*)>0$, and from right to left if $Re\lambda'(\tau^*)<0$.

If $\sup_{\tau\in I} S_0^+(\tau)\le 0$, then $S_0^+(\tau)$ has either a zero of even multiplicity or no zero in I. Moreover, $S_0^-(\tau)$ and $S_n^\pm(\tau)$ for all $n\in\mathbb{N}$ have no zero in I. Therefore, all eigenvalues remain to the left of the pure imaginary axis as τ increases from 0 to $\widehat{\tau}$; namely, x^* is locally asymptotically stable for all $\tau\in[0,\widehat{\tau}]$.

If $\sup_{\tau\in I} S_0^+(\tau)>0$, it then follows from $S_0(0)<0$ that $S_0^+(\tau)$ has at least one zero of odd multiplicity. In the remaining part of this subsection, we assume that $\frac{p_1+p_2}{\mu}>e^2\ge\frac{\sqrt{p_1^2+p_2^2}}{\mu}$, which guarantees that

$$\begin{aligned}2\mu^2-2b(\tau)^2-a(\tau)^2 &> 2(\mu^2-b(\tau)^2-a(\tau)^2)\\ &> 2\left(\mu^2-(p_1^2+p_2^2)e^{-2x^*}(1-x^*)^2\right)\ge 2\left(\mu^2-\frac{p_1^2+p_2^2}{e^4}\right)\ge 0,\end{aligned}$$

for $\tau\in(0,\widehat{\tau})$. Therefore, $(\mathbf{H}_2)$ cannot be satisfied; namely, $I_2=\emptyset$. Moreover, $(\mathbf{H}_1)$ is satisfied if and only if $\mu-b(\tau)<-a(\tau)$. Consequently,

$$I=I_1=\{\tau\in[0,\widehat{\tau}]:\mu-b(\tau)<-a(\tau)\}.$$

Note that $(\mu-b(\tau)+a(\tau))e^{\delta\tau+x^*}=p_1(2-x^*)+p_2e^{-\delta\tau}x^*<2p_1+(p_2-p_1)x^*$. If $p_1>p_2$, then $[0,\tau_b]\subset I_1$,

$$\tau_b=\frac{1}{\delta}\ln\frac{\sqrt{p_1^2+4p_2\mu\beta}+p_1}{\mu\beta}<\widehat{\tau},\quad \beta=e^{\frac{2p_1}{p_1-p_2}}.$$

If I_1 is nonempty, we denote $\tau_H=\sup_{\tau\in I_1}\tau$. Since $\mu-b(\widehat{\tau})+a(\widehat{\tau})=p_2e^{-2\delta\widehat{\tau}}e^{-x^*}x^*>0$, we have $0<\tau_H<\widehat{\tau}$. As $\tau\to\tau_H$, we have $\omega_+(\tau)\to 0$. This, together with (4.9), implies that $\lim_{\tau\to\tau_H^-}\sin\theta_+(\tau)=0$ and $\lim_{\tau\to\tau_H^-}\cos\theta_+(\tau)=-1$. Therefore, $\lim_{\tau\to\tau_H^-}\theta_+(\tau)=\pi$, $\lim_{\tau\to\tau_H^-}S_n^+(\tau)=-\pi$ for $n\in\mathbb{N}_0$. In view of $S_0^+(0)<0$, the function $S_0^+(\tau)$ has at least two zeros in I provided that $\sup_{\tau\in I}S_0^+(\tau)>0$. For simplicity, we assume that

(B$_1$) $\frac{p_1+p_2}{\mu}>e^2\ge\frac{\sqrt{p_1^2+p_2^2}}{\mu}$, $\sup_{\tau\in I}S_0^+(\tau)>0$, and $S_n^+(\tau)$ has at most two zeros (counting multiplicity).

Under the assumption ($\mathbf{B}_1$), for any $n \in \mathbb{N}_0$, $S_n^+(\tau)$ has either zero or two simple zeros. Now, we collect all simple zeros of $S_n^+(\tau)$ with $n \in \mathbb{N}_0$ and list them in increasing order: $0 < \tau_0 < \tau_1 < \cdots < \tau_{2K-1} < \widehat{\tau}$ ($K \in \mathbb{N}$). It is easily seen that for each integer $0 \le i \le K-1$, we have $dS_m^+(\tau_i)/d\tau > 0$ and $dS_m^+(\tau_{2K-i-1})/d\tau < 0$ for some $m \in \mathbb{N}_0$. Therefore, the pair of simple conjugate purely imaginary eigenvalues $\pm i\omega_+(\tau_i)$ crosses the imaginary axis from left to right, and the pair of simple conjugate purely imaginary eigenvalues $\pm i\omega_+(\tau_{2K-i-1})$ crosses the imaginary axis from right to left. This implies that system (4.1) undergoes a Hopf bifurcation at x^* when $\tau = \tau_j$ $(0 \le j \le 2K-1)$. Moreover, x^* is locally asymptotically stable for $\tau \in [0, \tau_0) \cup (\tau_{2K-1}, \tau_{max})$, and unstable for $\tau \in (\tau_0, \tau_{2K-1})$.

For each $n = 0, \cdots, K$, $S_n^+(\tau)$ has two simple zeros τ_n and τ_{2K-n-1}. Let T_n be the period of the periodic solution bifurcated at τ_n. Applying the Hopf bifurcation theorem for delay differential equations [15,12], we have

$$\mathrm{T}_n = \frac{2\pi}{\omega_+(\tau_n)} = \frac{2\pi\tau_k}{\theta_+(\tau_n) + 2n\pi},$$
$$\mathrm{T}_{2K-n-1} = \frac{2\pi}{\omega_+(\tau_{2K-n-1})} = \frac{2\pi\tau_{2K-n-1}}{\theta_+(\tau_{2K-n-1}) + 2n\pi}.$$

If $\frac{p_1+p_2}{\mu} \le e^{2+p_1/p_2}$, it follows from Lemma 4.6 and (4.11) that $\cos\theta_+(\tau_j) < 0$. Since $\sin\theta_+(\tau_j) > 0$, we obtain $\theta_+(\tau_j) \in (\pi/2, \pi)$. Hence, $\frac{2\tau_n}{2n+1} < \mathrm{T}_n < \frac{4\tau_n}{4n+1}$ and $\frac{2\tau_{2K-n-1}}{2n+1} < \mathrm{T}_{2K-n-1} < \frac{4\tau_{2K-n-1}}{4n+1}$. To summarize, we have the following results on stability of x^* and Hopf bifurcation.

Theorem 4.8. *Consider model (4.1) with $\frac{p_1+p_2}{\mu} > e^2$.*

(i) *If either $I = \emptyset$ or $\sup_{\tau \in I} S_0^+(\tau) \le 0$, then x^* is locally asymptotically stable for all $\tau \in [0, \tau_{max})$.*

(ii) *If ($\mathbf{B}_1$) holds, then there exist exactly $2K$ local Hopf bifurcation values, namely, $0 < \tau_0 < \tau_1 < \cdots < \tau_{2K-1} < \widehat{\tau}$ such that model (4.1) undergoes a Hopf bifurcation at x^* when $\tau = \tau_j$ for $0 \le j \le 2K-1$. x^* is locally asymptotically stable for $\tau \in [0, \tau_0) \cup (\tau_{2K-1}, \tau_{max})$, and unstable for $\tau \in (\tau_0, \tau_{2K-1})$. Moreover, if $\frac{p_1+p_2}{\mu} \le e^{2+p_1/p_2}$, then for any $n = 0, 1, \cdots, K-1$, when τ is sufficiently close to τ_n (resp., τ_{2K-n-1}), the period T_n (resp., T_{2K-n-1}) of periodic solution bifurcated at τ_n (resp., τ_{2K-n-1}) satisfies $\mathrm{T}_n \in (\frac{2\tau_n}{2n+1}, \frac{4\tau_n}{4n+1})$ (resp., $\mathrm{T}_{2K-n-1} \in (\frac{2\tau_{2K-n-1}}{2n+1}, \frac{4\tau_{2K-n-1}}{4n+1})$).*

4.3. Stability switches of the positive equilibrium

In this subsection, we investigate the stability switches of x^* based on the characteristic equation (4.2). Throughout this subsection, we assume that $\frac{p_1+p_2}{\mu} > e^2 \ge \frac{2p_1^2}{\mu p_2}$, which implies that $p_1 \le p_2 e^{-\delta\widehat{\tau}}$. For $\tau \in (0, \widehat{\tau})$, we have

$$(\mu - b(\tau) + a(\tau))e^{\delta\tau + x^*} = p_1(2 - x^*) + p_2 e^{-\delta\tau} x^* > 2p_1 + (p_2 e^{-\delta\widehat{\tau}} - p_1)x^* > 0.$$

Hence, ($\mathbf{H}_1$) cannot be satisfied and $I_1 = \emptyset$. Note that $(\mu + 3b(\tau))e^{\delta\tau + x^*} < p_1 - 2p_2 e^{-\delta\widehat{\tau}} < 0$. The condition ($\mathbf{H}_2$) is satisfied if and only if $a(\tau)^2 > -8b(\tau)(b(\tau) + \mu)$. Consequently,

$$I = I_2 = \{\tau \in [0, \widehat{\tau}] : a(\tau)^2 > -8b(\tau)(b(\tau) + \mu)\}.$$

If I_2 is nonempty, we denote $\tau_S = \sup_{\tau \in I_2} \tau$. Since $a(\widehat{\tau})^2 + 8b(\widehat{\tau})(b(\widehat{\tau}) + \mu) = e^{-2\delta\widehat{\tau}} e^{-4} p_1(p_1 - 8p_2 e^{-\delta\widehat{\tau}}) < 0$, we have $0 < \tau_S < \widehat{\tau}$. For simplicity, we assume that

(B$_2$) $\frac{p_1+p_2}{\mu} > e^2 \geq \frac{2p_1^2}{\mu p_2}$, $\sup_{\tau \in I} S_0^+(\tau) > 0$, $S_0^+(\tau_S) < 0$, and $S_n^{\pm}(\tau)$ has at most two zeros (counting multiplicity).

Assumption (**B**$_2$) implies that for each $n \in \mathbb{N}_0$ the function $S_n^{\pm}(\tau)$ has either zero or two simple zeros. Now, we collect all simple zeros of $S_n^+(\tau)$ with $n \in \mathbb{N}_0$ and list them in increasing order: $0 < \tau_0^1 < \tau_1^1 < \cdots < \tau_{2K_1-1}^1 < \widehat{\tau}$ ($K_1 \in \mathbb{N}$). We also collect all simple zeros of $S_n^-(\tau)$ with $n \in \mathbb{N}_0$ and list them in increasing order: $0 < \tau_0^2 < \tau_1^2 < \cdots < \tau_{2K_2-1}^2 < \widehat{\tau}$ ($K_2 \in \mathbb{N}$). Clearly, for each integers $0 \leq i \leq K_1 - 1$ and $0 \leq j \leq K_2 - 1$, we have $dS_m^+(\tau_i^1)/d\tau > 0$, $dS_m^-(\tau_j^2)/d\tau > 0$ and $dS_m^+(\tau_{2K-i-1}^1)/d\tau < 0$, $dS_m^-(\tau_{2K_2-j-1}^2)/d\tau < 0$ for some $m \in \mathbb{N}_0$. From Lemma 4.5, we have $S_0^+(\tau) > S_0^-(\tau)$, which implies that $\tau_0^1 < \tau_0^2$ and $\tau_{2K_1-1}^1 > \tau_{2K_2-1}^2$, that is

$$\tau_0^1 = \min_{\tau \in J} \tau,\ \ \tau_{2K_1-1}^1 = \max_{\tau \in J} \tau,\ \ J = \{\tau_0^1, \tau_1^1, \cdots, \tau_{2K_1-1}^1, \tau_0^2, \tau_1^2, \cdots, \tau_{2K_2-1}^2\}.$$

If $S_0^- < S_1^+$, then $S_m^- = S_0^- - 2m\pi < S_1^+ - 2m\pi = S_{m+1}^+$ for any $m \in \mathbb{N}_0$. Thus, system (4.1) undergoes a Hopf bifurcation at x^* when $\tau \in J$, and x^* is locally asymptotically stable for $\tau \in [0, \tau_0^1) \cup (\tau_{2K_1-1}^1, \tau_{max})$, and unstable for $\tau \in (\tau_0^1, \tau_{2K_1-1}^1)$.

If $S_0^- = S_1^+$, then $S_m^- = S_{m+1}^+$ for any $m \in \mathbb{N}_0$, which implies that Hopf bifurcation occurs only when $\tau = \tau_0^1$ or $\tau = \tau_{2K_1-1}^1$. For $\tau \in J - \{\tau_0^1, \tau_{2K_1-1}^1\}$, there exist two pairs of conjugate purely imaginary eigenvalues, then system (4.1) undergoes a double Hopf bifurcation. Moreover, x^* is locally asymptotically stable for $\tau \in [0, \tau_0^1) \cup (\tau_{2K_1-1}^1, \tau_{max})$, and unstable for $\tau \in (\tau_0^1, \tau_{2K_1-1}^1)$.

If $S_0^- > S_1^+$, then $S_m^- > S_{m+1}^+$ for any $m \in \mathbb{N}_0$. This yields

$$\begin{aligned}\tau_0^1 < \tau_0^2 < \tau_1^1 < \tau_1^2 < \cdots < \tau_m^2 < \tau_{m+1}^1 < \tau_{m+1}^2 < \tau_{m+2}^1 \\ < \cdots < \tau_{2K_1-2}^2 < \tau_{2K_1-2}^1 < \tau_{2K_2-1}^2 < \tau_{2K_1-1}^1.\end{aligned}$$

Thus, system (4.1) undergoes a Hopf bifurcation at x^* when $\tau \in J$. If further, either $(p_1 + p_2)/\mu < e^{2+p_1/p_2}$ or $\breve{\tau} < \tau_0^1$, then $\mu + b(\tau) > 0$ for $\tau \in [\tau_0^1, \widehat{\tau}]$. By (4.11) and Theorem 4.7, we have $Re\lambda'(\tau_j^2) < 0$ and $Re\lambda'(\tau_{2k_2-j-1}^2) > 0$ for $0 \leq j \leq k_2 - 1$. Hence, all bifurcation values $\tau \in J$ are stability switches, that is, x^* is locally asymptotically stable for $\tau \in [0, \tau_0^1) \cup (\tau_0^2, \tau_1^1) \cup \cdots \cup (\tau_{2K_1-2}^1, \tau_{2K_2-1}^2) \cup (\tau_{2K_1-1}^1, \tau_{max})$, and unstable for $\tau \in (\tau_0^1, \tau_0^2) \cup (\tau_1^1, \tau_1^2) \cup \cdots \cup (\tau_{2K_2-2}^2, \tau_{2K_1-2}^1) \cup (\tau_{2K_2-1}^2, \tau_{2K_1-1}^1)$. On the other hand, if $\breve{\tau} > \tau_0^1$, then $\mu + b(\tau) < 0$ for $\tau \in [\tau_0^1, \widehat{\tau}]$. By (4.11) and Theorem 4.7, we have $Re\lambda'(\tau_j^2) > 0$ and $Re\lambda'(\tau_{2k_2-j-1}^2) < 0$ for $0 \leq j \leq k_2 - 1$. This implies that x^* is locally asymptotically stable for $\tau \in [0, \tau_0^1) \cup (\tau_{2K_1-1}^1, \tau_{max})$, and unstable for $\tau \in (\tau_0^1, \tau_{2K_1-1}^1)$. To summarize, we have the following results on stability switches of x^* and Hopf bifurcation.

Theorem 4.9. *Consider model* (4.1) *with (**B**$_2$). Let $\breve{\tau}$ be defined as in Lemma 4.6.*

(i) *If* $S_0^- < S_1^+$*, then system* (4.1) *undergoes a Hopf bifurcation at* x^* *when* $\tau \in J$*. Moreover,* x^* *is locally asymptotically stable for* $\tau \in [0, \tau_0^1) \cup (\tau_{2K_1-1}^1, \tau_{max})$*, and unstable for* $\tau \in (\tau_0^1, \tau_{2K_1-1}^1)$.

(ii) *If* $S_0^- = S_1^+$*, then system* (4.1) *undergoes a Hopf bifurcation at* x^* *when* $\tau = \tau_0^1$ *or* $\tau = \tau_{2K_1-1}^1$*, double Hopf bifurcation occurs at* $\tau \in J - \{\tau_0^1, \tau_{2K_1-1}^1\}$*. Moreover,* x^* *is locally asymptotically stable for* $\tau \in [0, \tau_0^1) \cup (\tau_{2K_1-1}^1, \tau_{max})$*, and unstable for* $\tau \in (\tau_0^1, \tau_{2K_1-1}^1)$.

(iii) *If* $S_0^- > S_1^+$*, then system* (4.1) *undergoes a Hopf bifurcation at* x^* *when* $\tau \in J$*. If further, either* $(p_1 + p_2)/\mu < e^{2+p_1/p_2}$ *or* $\breve{\tau} < \tau_0^1$*, then all bifurcation values are stability switches,* x^* *is locally asymptotically stable for* $\tau \in [0, \tau_0^1) \cup (\tau_0^2, \tau_1^1) \cup \cdots \cup (\tau_{2K_1-2}^1, \tau_{2K_2-1}^2) \cup (\tau_{2K_1-1}^1, \tau_{max})$*, and unstable for* $\tau \in (\tau_0^1, \tau_0^2) \cup (\tau_1^1, \tau_1^2) \cup \cdots \cup (\tau_{2K_2-2}^2, \tau_{2K_1-2}^1) \cup (\tau_{2K_2-1}^2, \tau_{2K_1-1}^1)$*. On the other hand, if* $\breve{\tau} > \tau_0^1$*, then* x^* *is locally asymptotically stable for* $\tau \in [0, \tau_0^1) \cup (\tau_{2K_1-1}^1, \tau_{max})$*, and unstable for* $\tau \in (\tau_0^1, \tau_{2K_1-1}^1)$.

Remark 4.10. When $p_2 = 0$ (no diapause), our model reduces to the Nicholson blowfly equation considered in [23], and Theorems 2.2 and 4.4 generalize the results in [23, Theorem 2.2] and [23, Theorem 3.8], respectively. In [23], it was proven that there is at most one pair of stability switches of the positive equilibrium if $p_2 = 0$. However, this is no longer valid when $p_2 > 0$. Theorem 4.9 indicates that diapause may induce multiple stability switches of the positive equilibrium.

5. Global Hopf bifurcation analyses

Theorems 4.8 and 4.9 give us sufficient conditions for the existence of periodic solutions bifurcated from x^* when τ is near the local Hopf bifurcation values. In this section, we will discuss the global continuation of periodic solutions bifurcated from the bifurcation point as the bifurcation parameter τ varies. We shall use the global Hopf bifurcation theorem for delay differential equations [26] to show that model (4.1) admits periodic solutions globally for τ in a finite interval including the values that are not necessarily near the Hopf bifurcation values. Let $z(t) = x(\tau t)$. Model (4.1) can be rewritten as a general functional differential equation

$$z'(t) = F(z_t, \tau, T), \quad (t, \tau, T) \in \mathbb{R} \times \widehat{I} \times \mathbb{R}_+, \tag{5.1}$$

where $\widehat{I} = [0, \widehat{\tau})$, $z_t(s) = z(t+s)$ for $s \in [-2, 0]$, and $z_t \in Y := C([-2, 0], \mathbb{R}_+)$, and

$$F(z_t, \tau, T) = p_1 e^{-\delta\tau} \tau z(t-1) e^{-z(t-1)} + p_2 e^{-2\delta\tau} \tau z(t-2) e^{-z(t-2)} - \mu\tau z(t). \tag{5.2}$$

Restricting F on the subspace of Y which consists of all nonnegative constant functions, we obtain

$$F\,|_{\mathbb{R}_+ \times \widehat{I} \times \mathbb{R}_+} = (p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}) \tau z e^{-z} - \mu\tau z,$$

which is clearly twice continuously differentiable. Thus, the condition (**A1**) in [26] holds. By Theorem 2.2, the set of stationary solutions of model (5.1) is given by

$$\mathbf{E}(F) = \{(0, \tau, T) : \tau \in \widehat{I}, T \in \mathbb{R}_+\} \cup \{(x^*, \tau, T) : \tau \in \widehat{I}, T \in \mathbb{R}_+\}.$$

For any stationary solution $(\widetilde{z}, \tau, T) \in \mathbf{E}(F)$, the characteristic function is

$$\begin{aligned}\Delta_{(\widetilde{z},\tau,T)}(\lambda) &= \lambda - DF(\widetilde{z}, \tau, T)(e^{\lambda \cdot}) \\ &= \lambda + \mu\tau - p_1 \tau e^{-\delta\tau}(1-\widetilde{z})e^{-\widetilde{z}}e^{-\lambda} - p_2 \tau e^{-2\delta\tau}(1-\widetilde{z})e^{-\widetilde{z}}e^{-2\lambda}.\end{aligned}$$

If $R_0 > 1$, then $DF(\widetilde{z}, \tau, T) \neq 0$ for any $(\widetilde{z}, \tau, T) \in \mathbf{E}(F)$, which implies that 0 cannot be an eigenvalue of any stationary solution of (5.1). Hence, the condition (**A**2) in [26] holds. Moreover, it follows from (5.2) that the smoothness condition (**A**3) in [26] is satisfied. Theorem 4.8 implies that if $\frac{p_1+p_2}{\mu} > e^2$ and either $(\mathbf{B}_1)$ or $(\mathbf{B}_2)$ holds, then for each integer $0 \leq j \leq 2K-1$ the stationary solution $(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ is an isolated centre of (5.1), where $\omega_j = \omega_+(\tau_j)$ is defined in (4.8). Furthermore, the set of all positive integers m such that $im(2\pi/\widetilde{T})$ with $\widetilde{T} = 2\pi/(\omega_j\tau_j)$ is a purely imaginary characteristic value contains only one element $\{1\}$. By Lemma 4.7, the crossing number $\gamma_1(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ at each isolated centre is

$$\gamma_1(x^*, \tau_j, \frac{2\pi}{\omega_j\tau_j}) = -\text{Sign}\left(\text{Re}\lambda'(\tau_j)\right) = \begin{cases} -1, & 0 \leq j \leq K-1, \\ 1, & K \leq j \leq 2K-1. \end{cases} \tag{5.3}$$

Thus, the condition (**A**4) in [26] holds. We define a closed subset $\Sigma(F)$ of $Y \times \widehat{I} \times \mathbb{R}_+$ by

$$\Sigma(F) = \mathcal{C}l\{(z, \tau, T) \in Y \times \widehat{I} \times \mathbb{R}_+ : z \text{ is a nontrivial T-periodic solution}\}.$$

For each integer $0 \leq j \leq 2K-1$, we denote by $\mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ the connected component of $(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ in $\Sigma(F)$. Theorem 4.8 guarantees that $\mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ is a nonempty subset of $\Sigma(F)$.

To find the interval of τ in which periodic solutions exist, we shall further investigate the properties of periodic solutions of (5.1).

Lemma 5.1. *Let $z(t)$ be a nonconstant and nonnegative periodic solution of* (5.1)*. There exist constants $\epsilon > 0$ and $M = \frac{p_1+p_2}{\mu e}$ such that for any $t \in \mathbb{R}$, $\epsilon \leq z(t) \leq M$.*

Proof. It follows from the proof of (2.2) that $\limsup_{t\to\infty} z(t) \leq \frac{p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}}{\mu e} \leq M$. Since $z(t)$ is periodic, we have $z(t) \leq M$ for all $t \geq 0$. Let $z_{min} := \min_{t\in\mathbb{R}} z(t) = z(t_2) > 0$ for some $t_2 > 0$. It follows from $z'(t_2) = 0$ that

$$\mu z(t_2) = p_1 e^{-\delta\tau} z(t_2-1)e^{-z(t_2-1)} + p_2 e^{-2\delta\tau} z(t_2-2)e^{-z(t_2-2)}. \tag{5.4}$$

We claim that either $z(t_2-1) \geq x^*$ or $z(t_2-2) \geq x^*$. Otherwise,

$$\mu z(t_2) > p_1 e^{-\delta\tau} z(t_2)e^{-x^*} + p_2 e^{-2\delta\tau} z(t_2)e^{-x^*} = \mu z(t_2),$$

a contradiction. Let $\epsilon = \min\{p_1 e^{-\delta\tau}, p_2 e^{-2\delta\tau}\}x^* e^{-M}/\mu > 0$. It then follows from (5.4), $\max\{z(t_2-1), z(t_2-2)\} \geq x^*$ and $z(t) \leq M$ that

$$\mu z(t_2) \geq \min\{p_1 e^{-\delta\tau}, p_2 e^{-2\delta\tau}\}e^{-M}[z(t_2-1) + z(t_2-2)] \geq \mu\epsilon.$$

Therefore, $z(t_2) \geq \epsilon > 0$. This ends the proof. □

Lemma 5.2. *If $\frac{p_1+p_2}{\mu} > e^2$, then (5.1) has no nonconstant and nonnegative periodic solution of period 2.*

Proof. Assume to the contrary that $z(t)$ is a nonconstant and nonnegative periodic solution of (5.1) with period 2. Define $u_1(t) = z(t)$ and $u_2(t) = z(t-1)$. Then $(u_1(t), u_2(t))$ is a nonconstant and nonnegative periodic solution of the following plane system

$$\begin{aligned} u_1'(t) &= p_1 e^{-\delta\tau}\tau u_2 e^{-u_2} + p_2 e^{-2\delta\tau}\tau u_1 e^{-u_1} - \mu\tau u_1(t) := P(u_1, u_2), \\ u_2'(t) &= p_1 e^{-\delta\tau}\tau u_1 e^{-u_1} + p_2 e^{-2\delta\tau}\tau u_2 e^{-u_2} - \mu\tau u_2(t) := Q(u_1, u_2). \end{aligned} \tag{5.5}$$

Set $H = \frac{1}{u_1 u_2}$, $\alpha_1 = p_1 e^{-\delta\tau}$ and $\alpha_2 = p_2 e^{-2\delta\tau}$, then we have

$$\frac{\partial(HP)}{\partial u_1} + \frac{\partial(HQ)}{\partial u_2} = -\tau H\left(\alpha_1\left(\frac{u_2 e^{-u_2}}{u_1} + \frac{u_1 e^{-u_1}}{u_2}\right) + \alpha_2(u_1 e^{-u_1} + u_2 e^{-u_2})\right) < 0.$$

Dulac-Bendixson's criterion [20] indicates that system (5.5) has no periodic solutions. This is a contradiction and the proof is complete. □

Our next lemma excludes the existence of periodic solutions of (5.1) of period 4 by using the general Bendixson's criterion developed by Li and Muldowney [16].

Lemma 5.3. *Assume that $\frac{p_1+p_2}{\mu} > e^2$, $\frac{p_1}{\mu} < \frac{2}{3}\sigma e^2$ and $\frac{p_2}{\mu} < \frac{1}{3}\sigma e^2$, where $\sigma > 1$ is the largest root of $ye^{3-ye} = 1$. Then model (5.1) has no nonconstant and nonnegative periodic solutions of period 4.*

Proof. First, we list some facts which will be used frequently throughout the proof. Note that $\sigma > 1$ and $f(\sigma e) = \sigma e^{1-\sigma e} = e^{-2}$. It is easy to verify that $\sigma < 1.5$ and $f(1 - 2\sigma/3) > e^{-2}$. For $\tau \in [0, \widehat{\tau}]$, we have

$$\frac{p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}}{\mu} \geq \frac{p_1 e^{-\delta\widehat{\tau}} + p_2 e^{-2\delta\widehat{\tau}}}{\mu} = e^2,$$

and

$$\frac{p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}}{\mu} \leq \frac{p_1 e^{-\delta\tau}}{\mu} + \frac{p_2}{\mu} \leq \frac{p_1 e^{-\delta\tau}}{\mu} + \frac{1}{3}\sigma e^2.$$

Thus, $p_1 e^{-\delta\tau}/\mu > (1 - \sigma/3)e^2$. A similar argument shows that $p_2 e^{-2\delta\tau}/\mu > (1 - 2\sigma/3)e^2$.

Next, we prove the nonexistence of 4-periodic solution by contradiction. Suppose that $z(t)$ is a nonconstant and nonnegative 4-periodic solution of (5.1). It is readily seen from Lemma 5.1 that $z(t) \leq (p_1 + p_2)/(\mu e) \leq \sigma e$. Denote $m = \min_{t\in\mathbb{R}} z(t) = z(t_2)$ for some $t_2 > 0$. We have

$$m = \frac{p_1 e^{-\delta\tau}}{\mu} z(t_2 - 1)e^{-z(t_2-1)} + \frac{p_2 e^{-2\delta\tau}}{\mu} z(t_2 - 2)e^{-z(t_2-2)}.$$

Similar as in the proof of Lemma 5.1, we have either $z(t_2-1) \geq x^*$ or $z(t_2-2) \geq x^*$. If $z(t_2-1) \geq x^*$, then $f(z(t_2-1)) > f(\sigma e) = e^{-2}$ and

$$m > \frac{p_1 e^{-\delta\tau}}{\mu} f(z(t_2-1)) > \frac{p_1 e^{-\delta\tau}}{\mu} e^{-2} > 1-\sigma/3.$$

If $z(t_2-2) \geq x^*$, then $f(z(t_2-2)) > f(\sigma e) = e^{-2}$ and

$$m > \frac{p_2 e^{-2\delta\tau}}{\mu} f(z(t_2-2)) > \frac{p_2 e^{-2\delta\tau}}{\mu} e^{-2} > 1-2\sigma/3.$$

In either case, we have $f(m) \geq f(1-2\sigma/3) > e^{-2}$, which implies $f(z(t)) > e^{-2}$ for all $t \geq 0$. Consequently,

$$m > \frac{p_1 e^{-\delta\tau} + p_2 e^{-2\delta\tau}}{\mu} e^{-2} \geq 1.$$

Now, we let $u_i(t) = z(t+1-i)$ with $i = 1, 2, 3, 4$. Then $(u_1(t), u_2(t), u_3(t), u_4(t))$ is a nonconstant and nonnegative periodic solution of the following system:

$$\begin{aligned}
u_1'(t) &= p_1 e^{-\delta\tau} \tau u_2 e^{-u_2} + p_2 e^{-2\delta\tau} \tau u_3 e^{-u_3} - \mu\tau u_1(t), \\
u_2'(t) &= p_1 e^{-\delta\tau} \tau u_3 e^{-u_3} + p_2 e^{-2\delta\tau} \tau u_4 e^{-u_4} - \mu\tau u_2(t), \\
u_3'(t) &= p_1 e^{-\delta\tau} \tau u_4 e^{-u_4} + p_2 e^{-2\delta\tau} \tau u_1 e^{-u_1} - \mu\tau u_3(t), \\
u_4'(t) &= p_1 e^{-\delta\tau} \tau u_1 e^{-u_1} + p_2 e^{-2\delta\tau} \tau u_2 e^{-u_2} - \mu\tau u_4(t).
\end{aligned} \tag{5.6}$$

Denote $\Omega = \{u \in \mathbb{R}^4 : 1 \leq u_i \leq \sigma e, i = 1, 2, 3, 4\}$. It suffices to establish the nonexistence of nonconstant and nonnegative periodic solutions of (5.6) in Ω. The Jacobian matrix $J(u)$ of (5.6) is given by

$$J(u) = -\mu\tau \begin{pmatrix} 1 & \beta_1 g(u_2) & \beta_2 g(u_3) & 0 \\ 0 & 1 & \beta_1 g(u_3) & \beta_2 g(u_4) \\ \beta_2 g(u_1) & 0 & 1 & \beta_1 g(u_4) \\ \beta_1 g(u_1) & \beta_2 g(u_2) & 0 & 1 \end{pmatrix},$$

where $\beta_1 = p_1 e^{-\delta\tau}/\mu$, $\beta_2 = p_2 e^{-2\delta\tau}/\mu$ and $g(x) = (x-1)e^{-x}$. The second additive compound matrix [16] of $J(u)$, denoted by $J^{[2]}(u)$, is given as

$$\mu\tau \begin{pmatrix} -2 & -\beta_1 g(u_3) & -\beta_2 g(u_4) & \beta_2 g(u_3) & 0 & 0 \\ 0 & -2 & -\beta_1 g(u_4) & -\beta_1 g(u_2) & 0 & 0 \\ -\beta_2 g(u_2) & 0 & -2 & 0 & -\beta_1 g(u_2) & -\beta_2 g(u_3) \\ \beta_2 g(u_1) & 0 & 0 & -2 & -\beta_1 g(u_4) & \beta_2 g(u_4) \\ \beta_1 g(u_1) & 0 & 0 & 0 & -2 & -\beta_1 g(u_3) \\ 0 & \beta_1 g(u_1) & -\beta_2 g(u_1) & \beta_2 g(u_2) & 0 & -2 \end{pmatrix}.$$

The Lozinskiĭ measure [6] with respect to the l^∞ norm in $\mathbb{R}^6$, denoted by $\zeta(J^{[2]}(u))$, is

$$\max\{-2+\beta_1|g(u_3)|+\beta_2(|g(u_4)|+|g(u_3)|),\ -2+\beta_1(|g(u_4)|+|g(u_2)|),$$
$$-2+(\beta_1+\beta_2)|g(u_2)|+\beta_2|g(u_3)|,\ -2+\beta_2|g(u_1)|+(\beta_1+\beta_2)|g(u_4)|,$$
$$-2+\beta_1(|g(u_1)|+|g(u_3)|),\ -2+(\beta_1+\beta_2)|g(u_1)|+\beta_2|g(u_2)|\}\mu\tau.$$

For any $u \in [1, \sigma e]$, $|g(u)| = g(u) \le g(2) = e^{-2}$. This together with $\beta_1 < p_1/\mu < 2\sigma e^2/3 < e^2$ and $\beta_2 < p_2/\mu < \sigma e^2/3 < e^2/2$ implies that the Lozinskiǐ measure $\zeta(J^{[2]}(u)) < 0$. By [16, Corollary 3.5], system (5.6) has no nonconstant and nonnegative periodic solution in Ω, which leads to a contradiction. This completes the proof. □

Note that the technical conditions $p_1/\mu < 2\sigma e^2/3$ and $p_2/\mu < \sigma e^2/3$ are used to prove nonexistence of 4-periodic solution. As we see later in the numerical exploration, the result of Lemma 5.3 seems to be true when these conditions are violated. We thus conjecture that 4-periodic solution does not exist if $p_1 + p_2 > \mu e^2$.

For any integer $0 \le j \le 2K-1$, Lemma 5.1 implies the projection of $\mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ onto Y is bounded. Lemmas 5.2 and 5.3 show that model (5.1) has no periodic solution with period 2 or 4, and thus has no periodic solution with period $2/(2n+1)$ or $4/(4n+1)$ for any $n \in \mathbb{N}_0$. It follows from Theorem 4.8(ii) that the period T_n of a periodic solution located on the connected component $\mathbf{C}(x^*, \tau_n, 2\pi/(\omega_n\tau_n))$ satisfies

$$\frac{2}{2n+1} < T_n < \frac{4}{4n+1} \tag{5.7}$$

for any integer $0 \le n \le K-1$. Similarly, $\frac{2}{2n+1} < T_{2K-n-1} < \frac{4}{4n+1}$. Hence, the projection of $\mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ onto the T-space is bounded. Note that $\tau \in [0, \widehat{\tau})$, which is a bounded interval. Therefore, $\mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ is bounded in $Y \times \widehat{I} \times \mathbb{R}_+$.

The periodic solutions are all bounded away from zero by Lemma 5.1. Thus there is no need to consider the boundary equilibrium. We define $\mathbf{E}_1(F) = \{(x^*, \tau, T),\ (\tau, T) \in \widehat{I} \times \mathbb{R}_+\}$. It then follows from the global bifurcation theorem ([26, Theorem 3.3]) that $\mathcal{E} := \mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j)) \cap \mathbf{E}_1(F)$ is finite and $\sum_{(\widetilde{z},\tau,T)\in\mathcal{E}} \gamma_1(\widetilde{z}, \tau, T) = 0$.

Summarizing the discussion above, and further using an argument similar to [23, Theorem 4.6], we arrive at our conclusion concerning the global existence of periodic solutions and the properties of the global Hopf branches.

Theorem 5.4. *Assume that $e^{2+p_1/p_2} \ge \frac{p_1+p_2}{\mu} > e^2$, $\frac{p_1}{\mu} < \frac{2}{3}\sigma e^2$, $\frac{p_2}{\mu} < \frac{1}{3}\sigma e^2$ and either ($\boldsymbol{B}_1$) or ($\boldsymbol{B}_2$) holds, for $j = 0, 1, \ldots, 2K-1$, denote τ_j as a simple zero of $S^+_{n_j}(\tau)$ or $S^-_{n_j}(\tau)$ for some $n_j \in \mathbb{N}_0$. Then we have the following results on model (5.1).*

(i) *All global Hopf branches $\mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j))$ are bounded.*
(ii) *For each $n \le K-1$, the two global Hopf branches $\mathbf{C}(x^*, \tau_n, 2\pi/(\omega_n\tau_n))$ and $\mathbf{C}(x^*, \tau_{2K-n-1}, 2\pi/(\omega_{2K-n-1}\tau_{2K-n-1}))$ coincide with each other, and thus connect a pair of Hopf bifurcation values τ_n and τ_{2K-n-1}. Moreover, for each $\tau \in (\tau_n, \tau_{2K-n-1})$, model (5.1) has at least one periodic solution with period in $(2/(2n+1), 4/(4n+1))$.*
(iii) *$\mathbf{C}(x^*, \tau_j, 2\pi/(\omega_j\tau_j)) \cap \mathbf{C}(x^*, \tau_r, 2\pi/(\omega_r\tau_r)) = \emptyset$ when $r \ne 2K-j-1$.*

Remark 5.5. In this section, we have always assumed that $\mu + b(\tau) > 0$ for all $\tau \in (0, \widehat{\tau})$, which, according to (4.11), guarantees that $\theta_\pm(\tau)$ lie in $(\pi/2, \pi)$. This condition is essential in finding a uniform upper bound for the periods of periodic solutions in a global Hopf branch. If $\mu + b(\tau) < 0$ for some τ, then $\theta_{\pm}(\tau)$ may lie in $(0, \pi/2)$, and we will not be able to find an upper bound for the periods of periodic solutions. However, as we see later in the numerical exploration, we still observe and thus conjecture that the global Hopf branches are bounded.

The global bifurcation result of our model is quite different from that for (1.1). It was proven in [27] that all global Hopf branches in (1.1) are unbounded. Since the coefficients in our model are delay dependent, and the trivial equilibrium 0 is globally asymptotically stable for large τ, the periodic solutions may only exist for τ in a bounded domain. The biological interpretation is that the mortality during development or diapause will inhibit the reproduction of tick population if the delay is too large.

It was proven in [27] that (1.1) does not have 3τ-periodic solutions. For our model (1.2), we have to prove that 4τ-periodic solutions (and consequently, 2τ-periodic solutions) do not exist, which together with (5.7) implies that the periods of all periodic solutions are uniformly bounded from below and above.

6. Numerical exploration

In this section, we conduct some numerical simulations by using the following parameter values elaborated from the literature [14,21,22,29]: $\delta = 0.7$ per year, $p_2 = 400$ per year, $p_1 = 30$ per year, and $\mu = 20$ per year. The delay τ has the unit in years. It is easy to calculate $\breve{\tau} \approx 0.71 < \widehat{\tau} \approx 0.81 < \overline{\tau} \approx 1.59 < \tau_{max} \approx 2.40$. Clearly, there exists a unique positive equilibrium x^* if and only if $\tau \le \tau_{max}$. By Theorem 4.9, there are six bifurcation values:

$$\tau_0^1 \approx 0.03 < \tau_0^2 \approx 0.16 < \tau_1^1 \approx 0.30 < \tau_2^1 \approx 0.60 < \tau_1^2 \approx 0.65 < \tau_3^1 \approx 0.71,$$

as shown in Fig. 1. Correspondingly, $\omega_+(\tau_0^1) \approx 1.09$, $\omega_-(\tau_0^2) \approx 4.22$, $\omega_+(\tau_1^1) \approx 7.45$, $\omega_+(\tau_2^1) \approx 7.62$, $\omega_-(\tau_1^2) \approx 4.49$, and $\omega_+(\tau_3^1) \approx 1.58$. Note that $\breve{\tau} > \tau_0^1$. Theorem 4.9 implies that x^* is locally asymptotically stable for $\tau \in [0, \tau_0^1) \cup (\tau_3^1, \tau_{max})$, and unstable for $\tau \in (\tau_0^1, \tau_3^1)$. This is also confirmed in the bifurcation diagram in Fig. 2. As τ increases and crosses the first bifurcation point τ_0^1, the positive equilibrium x^* becomes unstable, and a stable periodic solution bifurcates from τ_0^1. When τ crosses the last bifurcation point τ_3^1, there exists no more periodic solutions and the positive equilibrium x^* regains its stability. If τ keeps increasing and approaches τ_{max}, then the positive equilibrium vanishes to the trivial equilibrium; see Fig. 2.

Fig. 3 plots the three global Hopf branches $\mathbf{C}(x^*, \tau_k^1, 2\pi/(\omega_+(\tau_k^1)\tau_k^1))$ and $\mathbf{C}(x^*, \tau_0^2, 2\pi/(\omega_-(\tau_0^2)\tau_0^2))$ with $k = 0, 1$, by using the Matlab package DDE-BIFTOOL developed by Engelborghs et al. [8]. We observe that all branches are bounded and connect a pair of Hopf bifurcation values. Note that we have proved boundedness of global Hopf branches under the condition $\mu + b(\tau) > 0$ for all $\tau \in [0, \widehat{\tau}]$. For the parameter values chosen in our simulation, we observe that $\mu + b(\tau)$ is not always positive. Our simulation results suggest that the global Hopf branches should still be bounded even if $\mu + b(\tau)$ is negative for some τ.

It is noted that periodic solutions exist for $\tau \in (\tau_0^1, \tau_3^1)$. When $\tau \in (\tau_0^2, \tau_1^2)$, there are more than two periodic solutions. By calculating the Floquet multipliers (see Fig. 4(a)), we observe that the periodic solutions on the first global Hopf branch is always stable (i.e., Floquet multiplier is equal to one), the periodic solutions on the third global Hopf branch is always unstable (i.e., Floquet multiplier is greater than one). Recall that in Fig. 2, we also observe that there exists a stable periodic solution when $\tau \in (\tau_0^1, \tau_3^1)$, which coincides with the blue curve in Fig. 4(a). On the

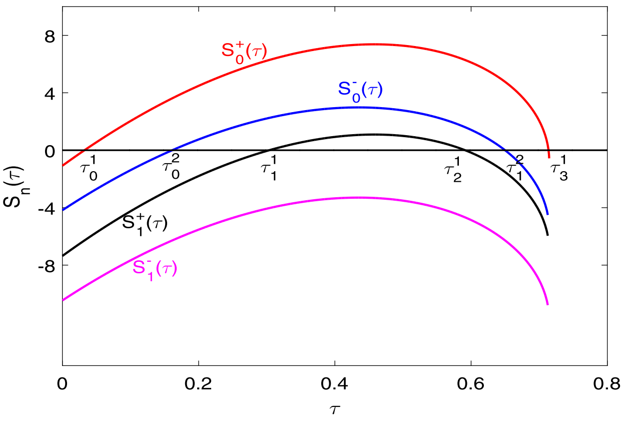

Fig. 1. The graphs of $S_n^{\pm}(\tau)$ $(n = 0, 1)$, which give bifurcation values.

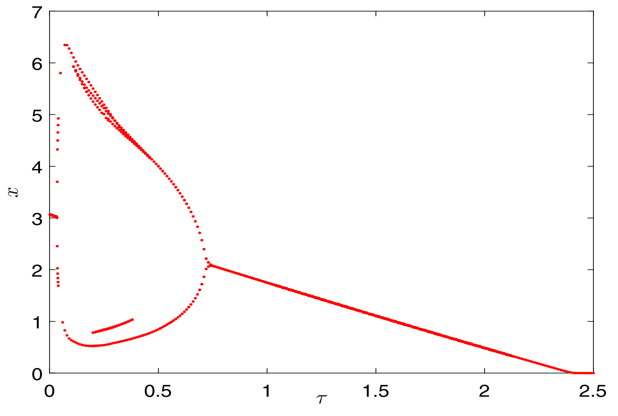

Fig. 2. Bifurcation diagram of (4.1) with τ as the bifurcation parameter.

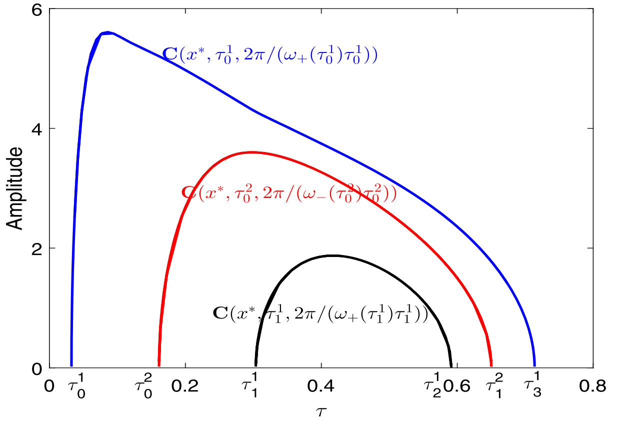

Fig. 3. All global Hopf branches of model (4.1).

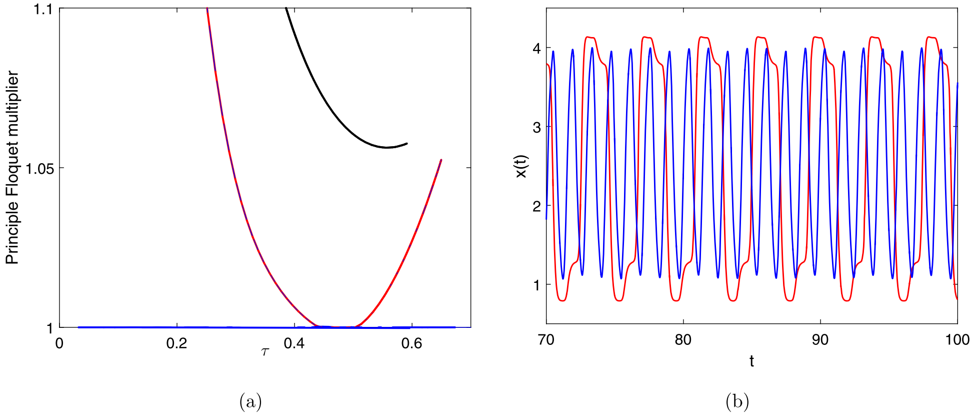

Fig. 4. (a) The principal Floquet multipliers of periodic solutions on all Hopf branches; (b) two coexisting stable periodic solutions for $\tau = 0.47$. (For interpretation of the colours in the figure(s), the reader is referred to the web version of this article.)

second global Hopf branch, the periodic solutions switch stability twice as τ increases from τ_0^2 to τ_1^2; namely, they are unstable for small or large τ, but stable for τ near 0.47; see Fig. 4(a).

It is interesting to note that there are two stable periodic solutions when τ is near 0.47. In Fig. 4(b), we fix $\tau = 0.47$ and solve the delay differential equation with two different initial conditions. After sufficient long time, the solutions are close to two different periodic orbits.

7. Summary and discussion

In this paper, we proposed a tick diapause model with two delays and delay dependent parameters. Global stability analysis of equilibria and global Hopf bifurcation analysis on periodic solutions were conducted for the proposed delay differential equation. We constructed suitable Lyapunov functionals to obtain global asymptotic stability of equilibria under certain conditions. We provided a simple proof of the geometric criterion for a general delay differential system with two delays and delay dependent parameters. This criterion generalizes the classical result for the single delay case in [5]. We also used the generalized Bendixson's criterion in [16] to prove nonexistence of 4-periodic solution for the scaled delay differential equation. We apply the global Hopf bifurcation theory in [26] to prove that the global Hopf branches are bounded and connected by two bifurcation values. Our theoretical analysis demonstrated that diapause may induce multiple stability switches of the positive equilibrium. This phenomenon was not observed in the single delay case, say, in the Nicholson's blowflies model [23] or stage-structured differential equations with unimodal feedback [24]. Numerical exploration suggests another phenomenon that a periodic solution is stable whenever the positive equilibrium is unstable, and two stable periodic solutions may coexist.

There are some interesting problems worth further investigations. For instance, it is possible that the two delays are not proportional, but differ by a constant. In this case, one should set $\tau_2 = \tau_1 + c$, where c is a constant, and treat τ_1 as the bifurcation parameter. A more general case is when these two delays are not related and a more complicated Hopf bifurcation analysis with two bifurcation parameters is required. In the proof of boundedness for global Hopf branches, we had to exclude the existence of 4-periodic solutions for the scaled delay differential equation. To prove this, we imposed a technical condition that both $p_1/(2\mu)$ and p_2/μ are bounded by $\sigma e^2/3$, where $\sigma > 1$ is the largest positive root of $f(\sigma e) = e^{-2}$. From numerical exploration, it is conjectured that this technical condition should be released; namely, 4-periodic solution does not exist as long as $(p_1 + p_2)/\mu > e^2$.

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