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Persistence, Stability and Hopf Bifurcation in a Diffusive Ratio-Dependent Predator–Prey Model with Delay

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In this paper, we study the persistence, stability and Hopf bifurcation in a ratio-dependent predator–prey model with diffusion and delay. Sufficient conditions independent of diffusion and delay are obtained for the persistence of the system and global stability of the boundary equilibrium. The local stability of the positive constant equilibrium and delay-induced Hopf bifurcation are investigated by analyzing the corresponding characteristic equation. We show that delay can destabilize the positive equilibrium and induce spatially homogeneous and inhomogeneous periodic solutions. By calculating the normal form on the center manifold, the formulae determining the direction and the stability of Hopf bifurcations are explicitly derived. The numerical simulations are carried out to illustrate and extend our theoretical results.

Keywords: Predator–prey model; delay; stability; Hopf bifurcation; periodic solution.

1. Introduction

Based on different biological assumptions, several predator–prey models are proposed. There is evidence that when resources are scarce relative to predator density and predators have to search for food, the predator's per-capita growth rate should decline with its density [Akcakaya *et al.*, 1995; Arditi *et al.*, 1991; Berryman, 1992; Cosner *et al.*, 1999]. However, in those traditional prey-dependent predator–prey models, where the predation rate (hence the per capita growth rate of the predator) is a function of the prey population only and is independent of the density of predators, such models cannot reflect this feature. To accommodate this feature, Arditi and Ginzburg [Akcakaya *et al.*, 1995; Arditi & Ginzburg, 1989] suggested that a more

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suitable predator–prey theory should be based on the so-called ratio-dependent theory, which assumes that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. In this context, the following ratio-dependent type predator–prey model with Michaelis–Menten type functional response have received great attention among theoretical and mathematical biologists

$$\begin{cases} \dfrac{dN}{dt} = rN\left(1 - \dfrac{N}{K}\right) - \dfrac{\alpha NP}{\alpha\beta N + P}, \\ \dfrac{dP}{dt} = \dfrac{\eta\alpha NP}{\alpha\beta N + P} - \gamma P, \end{cases} \tag{1}$$

where N, P stand for prey and predator densities, respectively. $r, K, \alpha, \beta, \eta, \gamma$ are positive constants that represent prey intrinsic growth rate, environmental carrying capacity, total attack rate for predator, handing time, conversion rate and predator death rate, respectively. System (1) and its more general version have been widely studied by many authors and these studies have shown that such models exhibit much richer dynamics than the traditional ones (see, for example, [Fan *et al.*, 2003; Kuang & Beretta, 1998; Kuang, 1999; Hsu *et al.*, 2001; Ruan *et al.*, 2010; Xiao & Ruan, 2001] and references therein). The effects of discrete and distributed delays on dynamics of the system have been investigated in [Xu *et al.*, 2002; Beretta & Kuang, 1998; Xiao & Li, 2003; Xu *et al.*, 2009].

In reality, the species are distributed over space and interact with each other within their spatial domain. The importance of spatial models has been recognized by biologists for a long time and these models have been one of the dominant themes in both ecology and mathematical ecology due to their universal existence and importance [Gause, 1935; Okubo & Levin, 2001; Murray, 2002]. On the other hand, biological species often do not respond to the variation of the environment instantaneously, instead they generally respond to the variations in the past. Incorporating time delay into a population model would more realistically reflect such a fact. Moreover, as far as prey–predator interaction is concerned, typically there is also a delay in conveying the biomass of the prey to that of the predator (often referred to as the gestation time). Recently, there has been an extensive literature and increasing interest in the studies of the joint effect of delay and diffusion on predator–prey models (see, for example, [Chen *et al.*, 2013; Faria, 2001; Hu & Li, 2010; Liu & Yuan, 2004; Yan, 2007; Zuo & Wei, 2011; Zuo, 2013] and references cited therein). Recently, [Aly *et al.*, 2011; Song & Zou, 2014a, 2014b] explored the dynamics of a diffusive ratio-dependent predator–prey model that results from adding a random diffusion term to each equation in (1). Nevertheless, to the best of our knowledge, there is no work yet investigating the dynamics of the diffusive *ratio-dependent* predator–prey model *with delay*. Considering that the reproduction of predator after consuming the prey is not instantaneous, but is mediated by some time lag required for gestation, we study the following ratio-dependent predator–prey model with diffusion and delay

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d_u \triangle u(x,t) + ru(x,t)\left(1 - \dfrac{u(x,t)}{K}\right) - \dfrac{\alpha u(x,t)v(x,t)}{\alpha\beta u(x,t) + v(x,t)}, \\ \dfrac{\partial v(x,t)}{\partial t} = d_v \triangle v(x,t) + \left(\dfrac{\eta\alpha u(x,t-\tau)}{\alpha\beta u(x,t-\tau) + v(x,t-\tau)} - \gamma\right) v(x,t), \end{cases} \tag{2}$$

where d_u and d_v are the diffusion coefficients for the prey and predator, respectively, and $\tau \geq 0$ is the delay required for gestation which vastly differs from species to species. To make our model general so that it can be applied to as many species as possible, we do not specify the delay to any particular value.

In order to reduce the number of parameters, we rescale (2). Setting

$$\tilde{u} = \frac{\alpha\beta}{\eta K}u, \quad \tilde{v} = \frac{\alpha\beta}{\eta^2 K}v, \quad \tilde{t} = \frac{\eta t}{\beta}$$

and then dropping the tilde for simplicity of notations, system (1) with the spatial interval $x \in [0, \pi]$ and Neumann boundary condition takes the form

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d_1 \triangle u(x,t) + au(x,t)\left(1 - \dfrac{u(x,t)}{b}\right) - \dfrac{bu(x,t)v(x,t)}{bu(x,t)+v(x,t)}, \\ \dfrac{\partial v(x,t)}{\partial t} = d_2 \triangle v(x,t) + \left(\dfrac{bu(x,t-\tau)}{bu(x,t-\tau)+v(x,t-\tau)} - c\right)v(x,t), \\ u_x(0,t) = u_x(\pi,t) = v_x(0,t) = v_x(\pi,t) = 0, \quad t \geq 0, \\ u(x,t) = \phi(x,t) \geq 0 \ (\not\equiv 0), \quad v(x,t) = \psi(x,t) \geq 0 \ (\not\equiv 0), \quad (x,t) \in [0,\pi] \times [-\tau, 0], \end{cases} \tag{3}$$

where

$$d_1 = \frac{d_u \beta}{\eta}, \quad d_2 = \frac{d_v \beta}{\eta},$$

$$a = \frac{r\beta}{\eta}, \quad b = \frac{\alpha\beta}{\eta}, \quad c = \frac{\gamma\beta}{\eta},$$

and d_i $(i = 1,2), a, b, c$ can be interpreted as normalized diffusion coefficient, intrinsic growth rate for the prey, environmental carrying capacity, and death rate for the predator, respectively. In the following, for simplification of notations, we always use $u(t)$ for $u(x,t)$, $v(t)$ for $v(x,t)$, $u(t-\tau)$ for $u(x, t-\tau)$ and $v(t-\tau)$ for $v(x, t-\tau)$ if no confusion is caused. We would like to mention that for system (3) or similar systems without delay, the local and global stabilities of the unique positive constant equilibrium, dissipation, persistence as well as the existence of nonconstant positive steady states, Turing instability and Hopf–Turing bifurcation, spatiotemporal complexity, self-organized spatial patterns and chaos have been studied by many authors (see, for example, [Aly *et al.*, 2011; Banerjee, 2010; Banerjee & Petrovskii, 2011; Bartumeus *et al.*, 2001; Fan & Li, 2006; Pang & Wang, 2003; Song & Zou, 2014a, 2014b; Wang *et al.*, 2007] and references therein). The main object of this paper is to investigate the effect of the delay and diffusion on the dynamics of system (3). The persistence, stability and delay-induced Hopf bifurcations are studied. We will show that the delay will destabilize the stable positive constant equilibrium to become unstable and there exist infinite critical values of delay such that the spatially homogenous and inhomogenous periodic orbits bifurcate from the positive constant equilibrium.

The rest of the paper is organized as follows. In Sec. 2, persistence and the global stability of the boundary equilibrium are studied. In Sec. 3, the local stability of the positive constant equilibrium, the existence of delay-induced Hopf bifurcations will be investigated. In Sec. 4, the formulas for determining the direction and stability of Hopf bifurcations are derived by using the normal form theory for partial functional differential equations. In Sec. 5, some numerical simulations are presented to illustrate and extend the theoretical results. The paper ends with a conclusion.

2. Persistence and Global Stability of the Boundary Equilibrium

Simple mathematical arguments show that system (3) has three constant equilibria: the zero equilibrium $E_0 = (0,0)$ (total extinct); the boundary equilibrium $E_1 = (b, 0)$ (extinction of predator); and the positive equilibrium $E^* = (u^*, v^*)$ (coexistence of prey and predator) with

$$u^* = \frac{b(a + (c-1)b)}{a} > 0,$$

$$v^* = \frac{b(1-c)u^*}{c} = \frac{b^2(1-c)(a+(c-1)b)}{ac} > 0,$$

which exists if and only if the following condition holds:

$$(H_1) \qquad 0 < c < 1, \quad a > b(1-c).$$

First, we can deduce the following persistence properties.

Theorem 1. *If $0 < c < 1$ and $0 < b < 1$, then system (3) has the persistence properties for all $\tau \geq 0$, that is, for any initial values $\phi(x,t) > 0$ $(\not\equiv 0), \psi(x,t) \geq 0$ $(\not\equiv 0), t \in [-\tau, 0]$, there exists a positive constant ε_0 such that*

$$\liminf_{t\to+\infty} \min_{x\in[0,\pi]} u(x,t) \geq \varepsilon_0,$$

$$\liminf_{t\to+\infty} \min_{x\in[0,\pi]} v(x,t) \geq \varepsilon_0.$$

Proof. By the maximum principle, for the initial value $\phi(x,t) \geq 0$, $\psi(x,t) \geq 0$, $t \in [-\tau, 0]$, the solutions $(u(x,t), v(x,t))$ of system (3) satisfy $u(x,t) \geq 0$ and $v(x,t) \geq 0$. In terms of the first equation of system (3), we have

$$\frac{\partial u(t)}{\partial t} - d_1 \triangle u(t) \geq au(t)\left(1 - b - \frac{u(t)}{b}\right).$$

Let $z(t)$ be the solution of the ODE

$$\dot{z}(t) = az(t)\left(1 - b - \frac{z(t)}{b}\right),$$

$$z(0) = \max_{x\in[0,\pi]} u(x,t), \quad t \geq 0.$$

Then $\lim_{t\to\infty} z(t) = b(1-b)$. It follows from the comparison principle of parabolic equations that for $b < 1$,

$$\liminf_{t\to+\infty} \min_{x\in[0,\pi]} u(x,t) \geq b(1-b) > 0. \tag{4}$$

So, there exists a positive number $T_1 > 0$ such that

$$u(x,t) \geq \frac{b(1-b)}{2} = \varsigma > 0, \quad x\in[0,\pi], \ t \geq T_1. \tag{5}$$

From the second equation of system (3), we have

$$\frac{\partial v(t)}{\partial t} - d_2 \triangle v(t) \leq (1-c)v(t). \tag{6}$$

Let $z(t)$ be the solution of the ODE

$$\dot{z}(t) = (1-c)z(t), \quad z(0) = \max_{x\in[0,\pi]} v(x,t),$$

then we get

$$z(t-\tau) = e^{(c-1)\tau} z(t). \tag{7}$$

From (6), (7) and the comparison principle, we have $v(x,t) \leq z(t)$ for $x \in [0,\pi], t \geq 0$ and then

$$v(x,t-\tau) \leq z(t-\tau) = e^{(c-1)\tau} z(t), \quad x\in[0,\pi], \ t \geq \tau.$$

By the second equation of systems (3), (5) and (7), we obtain

$$\frac{\partial v(t)}{\partial t} - d_2\triangle v(t) \geq v(t)\left(-c + \frac{b\varsigma}{b\varsigma + v(t)e^{(c-1)\tau}}\right) = v(t)\frac{b(1-c)\varsigma - ce^{(c-1)\tau}v(t)}{b\varsigma + ce^{(c-1)\tau}v(t)}, \quad t \geq T_2 = \max\{T_1, \tau\}. \tag{8}$$

Let $z(t)$ be the solution of the ODE

$$\dot{z}(t) = z(t)\frac{b(1-c)\varsigma - ce^{(c-1)\tau}z(t)}{b\varsigma + ce^{(c-1)\tau}z(t)},$$

$$z(T_2) = \min_{z\in[0,\pi]} v(x,t), \quad t \geq T_2.$$

Then,

$$\lim_{t\to\infty} z(t) = \frac{b(1-c)\varsigma e^{(1-c)\tau}}{c}.$$

Again by the comparison principle, we obtain that for $0 < c < 1$,

$$\liminf_{t\to+\infty} \min_{x\in[0,\pi]} v(x,t) \geq \frac{b(1-c)\varsigma e^{(1-c)\tau}}{c} > 0. \tag{9}$$

Therefore, for $0 < c < 1$ and $0 < b < 1$, letting $\varepsilon_0 = \min\{b(1-b), \frac{b(1-c)\varsigma e^{(1-c)\tau}}{c}\}$, by (4) and (9) the proof is complete. ■

For the boundary equilibrium $E_1(1,0)$, we have the following results on the local and global stabilities.

Theorem 2

(i) *If $c > 1$, then for any initial values $\phi(x,t) \geq 0$ ($\not\equiv 0$), $\psi(x,t) \geq 0$ ($\not\equiv 0$), $t \in [-\tau, 0]$, the boundary equilibrium E_1 of system (3) is globally asymptotically stable for all $\tau \geq 0$;*

(ii) *If $0 < c < 1$, the boundary equilibrium E_1 of system (3) is unstable for all $\tau \geq 0$.*

Proof

(i) The inequality (6), together with the comparison principle of parabolic equations, implies that when $c > 1$,

$$\limsup_{t\to+\infty} \max_{x\in[0,\pi]} v(x,t) \leq 0.$$

In addition, note that $v(x,t) \geq 0$. So, for $c > 1$,

$$\lim_{t\to+\infty} v(x,t) = 0, \quad \text{for } x\in[0,\pi]. \tag{10}$$

From the first equation of system (3), we have

$$\frac{\partial u(t)}{\partial t} - d_1\triangle u(t) \leq au(t)\left(1 - \frac{u(t)}{b}\right).$$

By the comparison principle, we can obtain that

$$\limsup_{t\to+\infty} \max_{x\in[0,\pi]} u(x,t) \leq b. \tag{11}$$

Therefore, for any sufficiently small ε_1, there exists a sufficiently large positive number T_3 such that

$u(x,t) \leq b + \varepsilon_1$ for $t > T_3, x \in [0,\pi]$. In addition, note that $u \geq 0$ and $\lim_{(u,v)\to(0^+,0^+)} buv/(bu+v) = 0$. This, together with (10), implies that

$$\lim_{t\to+\infty} \frac{bu(x,t)v(x,t)}{bu(x,t)+v(x,t)} = 0, \quad \text{for } x \in [0,\pi]. \tag{12}$$

By (12), $\forall\, \epsilon \in (0,1)$, there exists $T(\epsilon) > T_3 > 0$ such that

$$\frac{bu(x,t)v(x,t)}{bu(x,t)+v(x,t)} < \epsilon, \quad \text{for } t > T(\epsilon),\ \ x \in [0,\pi]. \tag{13}$$

It follows from (13) and the first equation of system (3) that for $t > T(\varepsilon)$,

$$\frac{\partial u(t)}{\partial t} - d_1 \triangle u(t) > a(1-\varepsilon)u(t)\left(1 - \frac{u(t)}{b(1-\varepsilon)}\right),$$

which leads to

$$\liminf_{t\to+\infty} \min_{x\in[0,\pi]} u(x,t) \geq b(1-\varepsilon).$$

Since ϵ is a sufficiently small positive number, we have

$$\liminf_{t\to+\infty} \min_{x\in[0,\pi]} u(x,t) \geq b. \tag{14}$$

In terms of (11) and (14), we have

$$\lim_{t\to+\infty} u(x,t) = b, \quad \text{for } x \in [0,\pi]. \tag{15}$$

By (10) and (15), the conclusion (i) of Theorem 2 is verified.

(ii) The linearization of system (3) at $E_1(b,0)$ is

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \triangle u - au - v, \\[2ex] \dfrac{\partial v}{\partial t} = d_2 \triangle v + (1-c)v. \end{cases} \tag{16}$$

It is easy to verify that under the Neumann boundary condition, the characteristic equations of the linearized equations (16) are given by

$$(\lambda + d_1k^2 + a)(\lambda + d_2k^2 + c - 1) = 0, \qquad k = 0,1,2,\ldots. \tag{17}$$

Clearly, when $c < 1$ and $k = 0$, (17) has a positive real root $\lambda = 1 - c > 0$. Thus, when $c < 1$, the boundary equilibrium $E_1(b,0)$ of system (3) is unstable. This completes the proof. ■

3. Stability of the Positive Equilibrium and Hopf Bifurcation Induced by Delay

In this section, we study the influence of the delay on the stability of the positive equilibrium E^* of system (3) and delay-induced bifurcation scenario.

Let

$$\begin{aligned} f^{(1)}(u,v) &= au\Big(1 - \frac{u}{b}\Big) - \frac{buv}{bu+v}, \\ f^{(2)}(u,v,w) &= \frac{buv}{bu+w} - cv. \end{aligned} \tag{18}$$

Then linearization of (3) at the equilibrium E^* is

$$\begin{pmatrix} \dfrac{\partial u(t)}{\partial t} \\[2ex] \dfrac{\partial v(t)}{\partial t} \end{pmatrix} = d\Delta \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} + A_0 \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} + A_1 \begin{pmatrix} u(t-\tau) \\ v(t-\tau) \end{pmatrix}, \tag{19}$$

with

$$d\Delta = \begin{pmatrix} d_1\Delta & 0 \\ 0 & d_2\Delta \end{pmatrix}, \quad A_0 = \begin{pmatrix} a_{11} & a_{12} \\ 0 & 0 \end{pmatrix},$$

$$A_1 = \begin{pmatrix} 0 & 0 \\ a_{21} & a_{22} \end{pmatrix},$$

where

$$\begin{aligned} a_{11} &= \frac{\partial f^{(1)}}{\partial u}(u^*,v^*) = b - a - bc^2, \\ a_{12} &= \frac{\partial f^{(1)}}{\partial v}(u^*,v^*) = -c^2 < 0, \\ a_{21} &= \frac{\partial f^{(2)}}{\partial u}(u^*,v^*,v^*) = b(1-c)^2 > 0, \\ a_{22} &= \frac{\partial f^{(2)}}{\partial w}(u^*,v^*,v^*) = c(c-1) < 0. \end{aligned} \tag{20}$$

The characteristic equation of (19) is

$$\det(\lambda I - M_k - A_0 - A_1 e^{-\lambda\tau}) = 0, \tag{21}$$

where I is the 2×2 identity matrix and $M_k = -k^2\,\mathrm{diag}(d_1,d_2), k \in \mathbb{N}_0 = \{0,1,2,\ldots\}$. It follows from (21) that the characteristic equations for the positive constant equilibrium E^* are the following sequence of quadratic transcendental equations

$$\begin{aligned}\Delta_k(\lambda,\tau) &= \lambda^2 + ((d_1+d_2)k^2 - a_{11})\lambda \\ &\quad + d_1 d_2 k^4 - d_2 a_{11} k^2 \\ &\quad + (J_0 - d_1 a_{22} k^2 - a_{22}\lambda)e^{-\lambda\tau} \\ &= 0, \end{aligned} \tag{22}$$

where $k \in \mathbb{N}_0$, and

$$\begin{aligned}J_0 &= a_{11}a_{22} - a_{12}a_{21} \\ &= c(1-c)(a+bc-b) > 0.\end{aligned}$$

When $\tau = 0$, the characteristic equation (22) becomes the following sequence of quadratic polynomial equations

$$\lambda^2 + T_k\lambda + J_k = 0, \tag{23}$$

where

$$\begin{aligned}T_k &= (d_1+d_2)k^2 - (a_{11}+a_{22}), \\ J_k &= d_1 d_2 k^4 - (d_1 a_{22} + d_2 a_{11})k^2 + J_0.\end{aligned} \tag{24}$$

Equation (24) has been studied in detail in [Song & Zou, 2014a] and the related Turing instability, Hopf bifurcation and their interactions for system (3) without delay have been studied in [Song & Zou, 2014a, 2014b]. Here, we are interested in how the delay affects the stability of the positive equilibrium E^* of system (3) and delay-induced periodic oscillations. So, in the following, we always assume that the positive equilibrium E^* of system (3) without delay is asymptotically stable, which is equivalent to the condition $T_k > 0, J_k > 0$ for any $k \in \mathbb{N}_0$.

Assume that $i\omega$ $(\omega > 0)$ is a root of Eq. (22). Then we have

$$\begin{aligned}&-\omega^2 + ((d_1+d_2)k^2 - a_{11})i\omega + d_1 d_2 k^4 - d_2 a_{11} k^2 \\ &\quad + (J_0 - d_1 a_{22} k^2 - a_{22}\omega i)e^{-i\omega\tau} = 0.\end{aligned} \tag{25}$$

Separating the real and imaginary parts of Eq. (25) leads to

$$\begin{cases} -\omega^2 + d_1 d_2 k^4 - d_2 a_{11} k^2 \\ \qquad + (J_0 - d_1 a_{22} k^2)\cos\omega\tau - a_{22}\omega\sin\omega\tau = 0, \\ ((d_1+d_2)k^2 - a_{11})\omega - a_{22}\omega\cos\omega\tau \\ \qquad - (J_0 - d_1 a_{22} k^2)\sin\omega\tau = 0, \end{cases} \tag{26}$$

which implies that

$$\omega^4 + P_k\omega^2 + Q_k = 0, \quad k = 0,1,2,\ldots, \tag{27}$$

where

$$\begin{aligned}P_k &= (d_1^2 + d_2^2)k^4 - 2d_1 a_{11} k^2 + a_{11}^2 - a_{22}^2 \\ &= (d_1 k^2 - a_{11})^2 + (d_2 k^2 + a_{22})(d_2 k^2 - a_{22}), \\ Q_k &= J_k(d_1 d_2 k^4 + (d_1 a_{22} - d_2 a_{11})k^2 - J_0).\end{aligned} \tag{28}$$

Setting

$$\begin{aligned}\tilde{Q}_k &= (d_1 d_2 k^4 + (d_1 a_{22} - d_2 a_{11})k^2 - J_0) \\ &= (d_1 k^2 - a_{11})(d_2 k^2 + a_{22}) + a_{12}a_{21},\end{aligned} \tag{29}$$

then the sign of Q_k coincides with that of $\tilde{Q}_k$ since $J_k > 0$.

Notice that $\tilde{Q}_k$ is a quadratic polynomial with respect to k^2 and $-J_0 < 0$. Thus, by (29) we can conclude that there exists $k_1 \in \mathbb{N}_0$, such that

$$\begin{aligned}&\tilde{Q}_k < 0 \quad \text{for } 0 \le k \le k_1 \quad \text{and} \\ &\tilde{Q}_k > 0 \quad \text{for } k \ge k_1 + 1, \ k \in \mathbb{N}_0.\end{aligned} \tag{30}$$

Denote the positive real root of the equation $\tilde{Q}_k = 0$ by k_0. Then $k_1 < k_0 < k_1 + 1$ since $J_k > 0$ and Eq. (22) has zero root for $k \in \mathbb{N}_0$. It follows from (29) that

$$k_0^2 = \frac{d_2 a_{11} - d_1 a_{22} + \sqrt{(d_2 a_{11} - d_1 a_{22})^2 + 4 d_1 d_2 J_0}}{2 d_1 d_2} \tag{31}$$

and

$$(d_1 k_0^2 - a_{11})(d_2 k_0^2 + a_{22}) = -a_{12}a_{21} = bc^2(1-c)^2 > 0. \tag{32}$$

By (31), we have

$$d_1 k_0^2 - a_{11} = \frac{-(d_1 a_{22} + d_2 a_{11}) + \sqrt{(d_2 a_{22} - d_2 a_{11})^2 - 4 d_1 d_2 a_{12} a_{21}}}{2 d_2} > 0 \tag{33}$$

since $a_{12}a_{21} < 0$. It follows from (32) and (33) that

$$d_2 k_0^2 + a_{22} > 0. \tag{34}$$

By (28), we have

$$\begin{aligned}P_{k_0} &= (d_1k_0^2 - a_{11})^2 \\ &\quad + (d_2k_0^2 + a_{22})(d_2k_0^2 - a_{22}) \\ &> 0, \end{aligned} \tag{35}$$

where we have used (34) and $a_{22} < 0$.

Notice that $k_1+1 > k_0$. Thus, by (30) and (35), we get

$$P_k > 0, \quad \text{for } k \geq k_1 + 1, \;\; k_1 \in \mathbb{N}_0. \tag{36}$$

From (30) and (36), we can conclude that for each $k \in \{0, 1, \ldots, k_1\}$, Eq. (27) has only one positive real root ω_k^+, where

$$\omega_k = \frac{\sqrt{2}}{2}\sqrt{-P_k + \sqrt{P_k^2 - 4Q_k}}, \tag{37}$$

but for $k \in \mathbb{N}_0$ and $k \geq k_1 + 1$, Eq. (27) has no positive real roots.

According to the above discussions, the following results on Eq. (22) follow immediately.

Lemma 1. *Assume that* (H_1) *holds,* $J_k, T_k > 0$ *for all* $k \in \mathbb{N}_0$*, and* k_1 *and* ω_k *are defined by (30) and (37), respectively. Then Eq. (22) has a pair of purely imaginary roots* $\pm i\omega_k$ *for each* $k \in \{0, 1, \ldots, k_1\}$ *and has no purely imaginary roots for* $k \geq k_1 + 1$.

By (26), we have

$$\begin{aligned}\sin\omega\tau &= \frac{a_{22}\omega(d_1d_2k^4 - d_2a_{11}k^2 - \omega^2) + ((d_1+d_2)k^2 - a_{11})(J_0 - d_1a_{22}k^2)\omega}{(J_0 - d_1a_{22}k^2)^2 + a_{22}^2\omega^2} \triangleq F_{ks}(\omega), \\ \cos\omega\tau &= \frac{(\omega^2 - d_1d_2k^4 + d_2a_{11}k^2)(J_0 - d_1a_{22}k^2) + ((d_1+d_2)k^2 - a_{11})a_{22}\omega^2}{(J_0 - d_1a_{22}k^2)^2 + a_{22}^2\omega^2} \triangleq F_{kc}(\omega).\end{aligned} \tag{38}$$

For $k \in \{0, 1, \ldots, k_1\}$, define

$$\tau_{kj} = \begin{cases} \dfrac{1}{\omega_k}(\arccos F_{kc}(\omega_k) + 2j\pi), & \text{if } F_{ks} \geq 0, \\[2ex] \dfrac{1}{\omega_k}(2\pi - \arccos F_{kc}(\omega_k) + 2j\pi), & \text{if } F_{ks} < 0. \end{cases} \tag{39}$$

Clearly, $\tau_{k0} = \min_{j\in\mathbb{N}_0}\{\tau_{kj}\}$. Let $\lambda(\tau) = \alpha(\tau) + i\beta(\tau)$ be the roots of Eq. (25) near $\tau = \tau_{kj}$ satisfying $\alpha(\tau_{kj}) = 0, \beta(\tau_{kj}) = \omega_k$. Then, we have the following transversality condition.

Lemma 2. *For* $k \in \{0, 1, \ldots, k_1\}$ *and* $j \in \mathbb{N}_0$, $\frac{d\,\mathrm{Re}(\lambda)}{d\tau}|_{\tau=\tau_{kj}} > 0$.

Proof. Differentiating the two sides of Eq. (22) with respect to τ, we obtain

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda + (d_1+d_2)k^2 - a_{11})e^{\lambda\tau} - a_{22}}{\lambda(J_0 - d_1a_{22}k^2 - a_{22}\lambda)} - \frac{\tau}{\lambda}.$$

By (26), (28) and (37), we have

$$\begin{aligned}\mathrm{Re}\left(\frac{d\lambda}{d\tau}\bigg|_{\tau=\tau_{kj}}\right)^{-1} &= \mathrm{Re}\left(\frac{(2i\omega_k + (d_1+d_2)k^2 - a_{11})e^{i\omega_k\tau_{kj}} - a_{22}}{i\omega_k(J_0 - d_1a_{22}k^2 - a_{22}\omega_k i)}\right) \\ &= \frac{((d_1+d_2)k^2 - a_{11})(a_{22}\omega_k\cos\omega_k\tau_{kj} + (J_0 - d_1a_{22}k^2)\sin\omega_k\tau_{kj})}{(a_{22}^2(\omega_k)^2 + (J_0 - d_1a_{22}k^2)^2)\omega_k} \\ &\quad + \frac{2((J_0 - d_1a_{22}k^2)\cos\omega_k\tau_{kj} - a_{22}\omega_k\sin\omega_k\tau_{kj}) - a_{22}^2}{a_{22}^2(\omega_k)^2 + (J_0 - d_1a_{22}k^2)^2}\end{aligned}$$

$$= \frac{2(\omega_k)^2 + ((d_1^2 + d_2^2)k^4 - 2d_1 a_{11} k^2 + a_{11}^2 - a_{22}^2)}{a_{22}^2(\omega_k)^2 + (J_0 - d_1 a_{22} k^2)^2}$$

$$= \frac{2(\omega_k)^2 + P_k}{a_{22}^2(\omega_k)^2 + (J_0 - d_1 a_{22} k^2)^2} = \frac{\sqrt{P_k^2 - 4Q_k}}{a_{22}^2(\omega_k)^2 + (J_0 - d_1 a_{22} k^2)^2} > 0.$$

This completes the proof. ■

By Lemmas 1 and 2 and the qualitative theory of partial functional differential equations [Wu, 1996], we arrive at the following results on the stability and Hopf bifurcation.

Theorem 3. *Assume that* (H_1) *holds,* $T_k, J_k > 0$ *for all* $k \in \mathbb{N}_0$*, and* ω_k *and* τ_{kj} *are defined by (37) and (39), respectively. Denote the minimum of the critical values of delay by* $\tau_* = \min_{k\in\{0,1,\ldots,k_1\}}\{\tau_{k0}\}$.

(i) *The positive equilibrium* E^* *of system (3) is asymptotically stable for* $\tau \in [0, \tau_*)$ *and unstable for* $\tau \in (\tau_*, +\infty)$;
(ii) *System (3) undergoes Hopf bifurcations near the positive equilibrium* E^* *at* $\tau = \tau_{kj}$ *for* $k \in \{0, 1, \ldots, k_1\}$ *and* $j \in \mathbb{N}_0$.

4. Direction and Stability of Spatially Hopf Bifurcation

From Theorem 3, we know that system (3) undergoes Hopf bifurcations near the equilibrium E^* at $\tau = \tau_{kj}$, i.e. a family of spatially homogeneous and inhomogeneous periodic solutions bifurcate from the positive constant steady state E^* of (3). In this section, we investigate the direction and stability of these Hopf bifurcations by using the normal formal theory of partial functional differential equation due to [Faria, 2000]. Without loss of generality, denote any one of these critical values by τ_* at which the characteristic equation (22) has a pair of simply purely imaginary roots $\pm i\omega_*$.

Let

$$X = \left\{(u, v) \in W^{2,2}(0, \pi),\ \frac{\partial u}{\partial x} = \frac{\partial v}{\partial x} = 0 \text{ at } x = 0, \pi\right\}.$$

Setting $\tilde{u}(\cdot, t) = u(\cdot, \tau t) - u^*, \tilde{v}(\cdot, t) = v(\cdot, \tau t) - v^*$, $\tilde{U}(t) = (\tilde{u}(\cdot, t), \tilde{v}(\cdot, t))$ and then dropping the tildes for simplification of notation, system (3) can be written as the equation in the space $\mathcal{C} = C([-1, 0], X)$

$$\frac{dU(t)}{dt} = \tau d\Delta U(t) + L(\tau)(U_t) + f(U_t, \tau), \tag{40}$$

where for $\varphi = (\varphi_1, \varphi_2)^T \in \mathcal{C}$, $L(\mu)(\cdot) : \mathcal{C} \to X$ and $f : \mathcal{C} \times R \to X$ are given, respectively, by

$$L(\tau)(\varphi) = \tau \begin{pmatrix} a_{11}\varphi_1(0) + a_{12}\varphi_2(0) \\ a_{21}\varphi_1(-1) + a_{22}\varphi_2(-1) \end{pmatrix},$$

$$f(\varphi, \tau) = \tau \begin{pmatrix} \displaystyle\sum_{i+j\geq 2} \frac{1}{i!j!} f_{ij}^{(1)} \varphi_1^i(0)\varphi_2^j(0) \\ \displaystyle\sum_{i+j+l\geq 2} \frac{1}{i!j!l!} f_{ijl}^{(2)} \varphi_1^i(-1)\varphi_2^j(0)\varphi_2^l(-1) \end{pmatrix}, \tag{41}$$

where $f^{(1)}, f^{(2)}$ are defined by (18) and

$$f_{ij}^{(1)} = \frac{\partial^{i+j} f^{(1)}}{\partial u^i \partial v^j}(u^*, v^*),$$

$$f_{ijl}^{(2)} = \frac{\partial^{i+j+l} f^{(2)}}{\partial u^i \partial v^j \partial w^l}(u^*, v^*, v^*).$$

Note that in the following, for $\varphi = (\varphi_1, \varphi_2)^T \in C = C([-1, 0], \mathbb{R}^2)$, we also use the same formulae $L(\tau)(\varphi)$ as in (41).

Letting $\tau = \tau_* + \alpha, \alpha \in \mathbb{R}$, and then Eq. (40) is written as

$$\frac{\partial U(t)}{dt} = \tau_* d\Delta U(t) + L(\tau_*)(U_t) + F(U_t, \alpha), \tag{42}$$

where

$$F(\varphi, \alpha) = \alpha d\Delta\varphi(0) + L(\alpha)(\varphi) + f(\varphi, \tau_* + \alpha), \quad \text{for } \varphi \in \mathcal{C}.$$

So, $\alpha = 0$ is the Hopf bifurcation value for Eq. (42) and $\Lambda_0 = \{-i\tau_*\omega_*, i\tau_*\omega_*\}$ is the set of eigenvalues on the imaginary axis of the infinitesimal generator associated with the flow of the following linearized system of Eq. (42) at the origin

$$\frac{\partial U(t)}{dt} = \tau_* d\Delta U(t) + L(\tau_*)(U_t). \tag{43}$$

The eigenvalues of $\tau_* d\Delta$ on X are $\mu_k^i = -d_i\tau_* k^2$, $i = 1, 2, k \in \mathbb{N}_0$, with corresponding normalized eigenfunctions β_k^i, where

$$\beta_k^1(x) = \begin{pmatrix} \gamma_k(x) \\ 0 \end{pmatrix}, \quad \beta_k^2(x) = \begin{pmatrix} 0 \\ \gamma_k(x) \end{pmatrix},$$

$$\gamma_k(x) = \frac{\cos(kx)}{\|\cos(kx)\|_{2,2}}, \quad k \in \mathbb{N}_0.$$

Let $\mathcal{B}_k = \text{span}\{[v(\cdot), \beta_k^i]\beta_k^i \,|\, v \in \mathcal{C}, i = 1, 2\}$, where the inner product $[\cdot,\cdot]$ is defined by

$$[u, v] = \int_0^{\ell\pi} u^T v dx, \quad \text{for } u^T = (u_1, u_2)^T, \quad v = (v_1, v_2)^T \in X.$$

Then it is easy to verify that $L(\tau^*)(\mathcal{B}_k) \subset \text{span}\{\beta_k^1, \beta_k^2\}, k \in \mathbb{N}_0$. Assume that $z_t(\theta) \in C = C([-1, 0], \mathbb{R}^2)$ and

$$z_t^T(\theta)\begin{pmatrix} \beta_k^1 \\ \beta_k^2 \end{pmatrix} \in \mathcal{B}_k.$$

Then, on $\mathcal{B}_k$, the linear equation (43) is equivalent to the ODE on $\mathbb{R}^2$

$$\dot{z}(t) = \begin{pmatrix} \mu_k^1 & 0 \\ 0 & \mu_k^2 \end{pmatrix} z(t) + L(\tau_*)(z_t) \tag{44}$$

with the characteristic equation given by (22). Suppose that there exists $k \in \mathbb{N}_0$ such that when $\tau = \tau_*$, Eq. (22) for fixed k has a pair of purely imaginary roots $\pm i\omega_*$ and all other roots of Eq. (22) have negative real parts. Define the adjoint bilinear form on $C^* \times C$, $C^* = C([0, 1], \mathbb{R}^{2*})$, as follows

$$\langle \psi(s), \phi(\theta)\rangle = \psi(0)\phi(0) - \int_{-1}^0 \int_0^\theta \psi(\xi - \theta) d\eta(\theta)\phi(\xi)d\xi, \quad \text{for } \psi \in C^*, \ \phi \in C.$$

Then, for Eq. (44) with fixed k, the dual bases Φ_k and Ψ_k for its eigenspace P and its dual space P^* are, respectively, given by

$$\Phi_k = (pe^{i\omega_*\tau_*\theta}, \bar{p}e^{-i\omega_*\tau_*\theta}) \quad \text{and}$$
$$\Psi_k = \text{col}(q^T e^{-i\omega_*\tau_* s}, \bar{q}^T e^{i\omega_*\tau_* s})$$

such that $\langle \Phi_k, \Psi_k\rangle = I_2$, where I_2 is a 2×2 identity matrix and

$$p = \begin{pmatrix} p_1 \\ p_2 \end{pmatrix} = \begin{pmatrix} 1 \\ \dfrac{i\omega_* + d_1k^2 - a_{11}}{a_{12}} \end{pmatrix},$$

$$q = \begin{pmatrix} q_1 \\ q_2 \end{pmatrix} = q_1 \begin{pmatrix} 1 \\ \dfrac{i\omega_* + d_1k^2 - a_{11}}{a_{21}} e^{i\omega_*\tau_*} \end{pmatrix},$$

with

$$q_1 = \left(1 + \tau_*(i\omega_* + d_1k^2 - a_{11}) + \frac{(\tau_* a_{22} + e^{i\omega_*\tau_*})(i\omega_* + d_1k^2 - a_{11})^2}{a_{12}a_{21}}\right)^{-1}.$$

Following the procedure of [Faria, 2000] closely, we can obtain the following normal form on the center manifold

$$\dot{z} = Bz + \begin{pmatrix} A_{k1}z_1\alpha \\ \overline{A}_{k1}z_2\mu \end{pmatrix} + \begin{pmatrix} A_{k2}z_1^2z_2 \\ \overline{A}_{k2}z_1z_2^2 \end{pmatrix} + O(|z|\mu^2 + |z^4|). \tag{45}$$

The coefficient A_{k1} of the normal form (45) is easily calculated by

$$A_{k1} = -k^2(d_1q_1p_1 + d_2q_2p_2) + i\omega_* q^T p. \tag{46}$$

The coefficient A_{k2} of the normal form (45) is defined by

$$A_{k2} = \frac{i}{2\omega_*\tau_*}\left(a_{k20}a_{k11} - 2|a_{k11}|^2 - \frac{1}{3}|a_{k02}|^2\right) + \frac{1}{2}(a_{k21} + b_{k21}). \tag{47}$$

a_{k20}, a_{k11}, a_{k02} and a_{k21} can be calculated as follow:

$$a_{k20} = \begin{cases} \dfrac{\tau_*}{\sqrt{\pi}}(b_1q_1 + b_2q_2), & k = 0, \\ 0, & k \neq 0, \end{cases} \quad a_{k11} = \begin{cases} \dfrac{\tau_*}{\sqrt{\pi}}(b_3q_1 + b_4q_2), & k = 0, \\ 0, & k \neq 0, \end{cases}$$

$$a_{k02} = \begin{cases} \frac{\tau_*}{\sqrt{\pi}}(\bar{b}_1 q_1 + \bar{b}_2 q_2), & k = 0, \\ 0, & k \neq 0, \end{cases} \quad a_{k21} = \begin{cases} \frac{\tau_*}{\pi} b_4, & k = 0, \\ \frac{3\tau_*}{2\pi} b_4, & k \neq 0, \end{cases}$$

with

$$b_1 = f_{20}^{(1)} p_1^2 + 2f_{11}^{(1)} p_1 p_2 + f_{02}^{(1)} p_2^2,$$

$$b_2 = f_{200}^{(2)} p_1^2 e^{-2i\omega_*\tau_*} + f_{002}^{(2)} p_2^2 e^{-2i\omega_*\tau_*} + 2f_{110}^{(2)} p_1 p_2 e^{-i\omega_*\tau_*} + 2f_{101}^{(2)} p_1 p_2 e^{-2i\omega_*\tau_*} + 2f_{011}^{(2)} p_2^2 e^{-i\omega_*\tau_*},$$

$$b_3 = f_{20}^{(1)} |p_1|^2 + 2f_{11}^{(1)} \mathrm{Re}\{p_1 \bar{p}_2\} + f_{02}^{(1)} |p_2|^2,$$

$$b_4 = f_{200}^{(2)} |p_1|^2 + f_{002}^{(2)} |p_2|^2 + 2f_{110}^{(2)} \mathrm{Re}\{p_1 \bar{p}_2 e^{-i\omega_*\tau_*}\} + 2f_{101}^{(2)} \mathrm{Re}\{p_1 \bar{p}_2\} + 2f_{011}^{(2)} \mathrm{Re}\{|p_2|^2 e^{i\omega_*\tau_*}\},$$

$$\begin{aligned} b_5 = {} & q_1(f_{30}^{(1)} p_1 |p_1|^2 + f_{03}^{(1)} p_2 |p_2|^2 + f_{21}^{(1)} (p_1^2 \bar{p}_2 + 2|p_1|^2 p_2) + f_{12}^{(1)} (p_2^2 \bar{p}_1 + 2|p_2|^2 p_1)) \\ & + q_2((f_{300}^{(2)} p_1 |p_1|^2 + f_{003}^{(2)} p_2 |p_2|^2 + f_{201}^{(2)} (p_1^2 \bar{p}_2 + 2p_2 |p_1|^2) + f_{102}^{(2)} (p_2^2 \bar{p}_1 + 2p_1 |p_2|^2)) e^{-i\omega_*\tau_*} \\ & + f_{210}^{(2)} (p_1^2 \bar{p}_2 e^{-2i\omega_*\tau_*} + 2p_2 |p_1|^2) + f_{012}^{(2)} p_2 |p_2|^2 (2 + e^{-2i\omega_*\tau_*})). \end{aligned}$$

The calculation of b_{k21} is somewhat tedious. We first calculate $h_{k20}(\theta)$ and $h_{k11}(\theta)$ as follows:

$$h_{k20}(\theta) = -\frac{1}{i\omega_*\tau_*}\left(a_{k20} e^{i\omega_*\tau_*\theta} p + \frac{1}{3}\bar{a}_{k02} e^{-i\omega_*\tau_*\theta} \bar{p}\right) + e^{2i\omega_*\tau_*\theta} W_{k1},$$

$$h_{k11}(\theta) = \frac{2}{i\omega_*\tau_*}(a_{k11} e^{i\omega_*\tau_*\theta} p - \bar{a}_{k11} e^{-i\omega_*\tau_*\theta} \bar{p}) + W_{k2},$$

where $W_{k1} = \left(W_{k1}^{(1)}, W_{k1}^{(2)}\right)^T, W_2 = \left(W_{k2}^{(1)}, W_{k2}^{(2)}\right)^T$ with

$$W_{k1}^{(1)} = \frac{c_{kj}(b_1(2i\omega_* - a_{22} e^{-2i\omega_*\tau_*}) + b_2 a_{12})}{(2i\omega_* - a_{11})(2i\omega_* - a_{22} e^{-2i\omega_*\tau_*}) - a_{12} a_{21} e^{-2i\omega_*\tau_*}},$$

$$W_{k1}^{(2)} = \frac{c_{kj}(b_1 a_{21} e^{-2i\omega_*\tau_*} + b_2(2i\omega_* - a_{11}))}{(2i\omega_* - a_{11})(2i\omega_* - a_{22} e^{-2i\omega_*\tau_*}) - a_{12} a_{21} e^{-2i\omega_*\tau_*}},$$

$$W_{k2}^{(1)} = \frac{2c_{kj}(b_4 a_{12} - b_3 a_{22})}{a_{11} a_{22} - a_{12} a_{21}}, \quad W_{k2}^{(2)} = \frac{2c_{kj}(b_3 a_{21} - b_4 a_{11})}{a_{11} a_{22} - a_{12} a_{21}}$$

and

$$c_{kj} = \begin{cases} \frac{1}{\sqrt{\pi}}, & j = k = 0, \\ \frac{1}{\sqrt{\pi}}, & j = 0, \ k \neq 0, \\ \frac{1}{\sqrt{2\pi}}, & j = 2k \neq 0, \\ 0, & \text{otherwise}. \end{cases} \tag{48}$$

And then we have

$$b_{k21} = \begin{cases} M_0, & k = 0, \\ M_0 + \dfrac{\sqrt{2}}{2} M_{2k}, & k \neq 0, \end{cases}$$

where for $j = 0, 2k$,

$$M_j = \frac{2\tau_*}{\sqrt{\pi}} q^T \begin{pmatrix} c_1 h_{j11}^{(1)}(0) + c_2 h_{j11}^{(2)}(0) + \bar{c}_1 h_{j20}^{(1)}(0) + \bar{c}_2 h_{j20}^{(2)}(0) \\ c_3 h_{j11}^{(1)}(-1) + c_4 h_{j11}^{(2)}(-1) + \bar{c}_3 h_{j20}^{(1)}(-1) + \bar{c}_4 h_{j20}^{(2)}(-1) \\ + c_5 h_{j11}^{(2)}(0) + \bar{c}_5 h_{j20}^{(2)}(0) \end{pmatrix}$$

with

$$c_1 = f_{20}^{(1)} p_1 + f_{11}^{(1)} p_2,$$

$$c_2 = f_{11}^{(1)} p_1 + f_{02}^{(1)} p_2,$$

$$c_3 = f_{200}^{(2)} p_1 e^{-i\omega_*\tau_*} + f_{110}^{(2)} p_2 + f_{101}^{(2)} p_2 e^{-i\omega_*\tau_*},$$

$$c_4 = f_{002}^{(2)} p_2 e^{-i\omega_*\tau_*} + f_{101}^{(2)} p_1 e^{-i\omega_*\tau_*} + f_{011}^{(2)} p_2,$$

$$c_5 = f_{110}^{(2)} p_1 e^{-i\omega_*\tau_*} + f_{011}^{(2)} p_2 e^{-i\omega_*\tau_*}.$$

So, the coefficients A_{k1} and A_{k2} of the normal form (45) are completely determined. Through the change of variables $z_1 = w_1 - iw_2$, $z_2 = w_1 + iw_2$ and $w_1 = \rho\cos\xi$, $w_2 = \rho\sin\xi$, the normal form (45) becomes the following polar coordinate system

$$\dot{\rho} = \iota_{k1}\alpha\rho + \iota_{k2}\rho^3 + O(\alpha^2\rho + |(\rho,\alpha)|^4),$$

$$\dot{\xi} = -\omega_*\tau_* + O(|(\rho,\alpha)|)$$

with $\iota_{k1} = \mathrm{Re}\,A_{k1}$, $\iota_{k2} = \mathrm{Re}\,A_{k2}$.

It is well known from [Chow & Hale, 1982] that the sign of $\iota_{k1}\iota_{k2}$ determines the direction of the bifurcation (supercritical if $\iota_{k1}\iota_{k2} < 0$, subcritical if $\iota_{k1}\iota_{k2} > 0$), and the sign of ι_{k2} determines the stability of the nontrivial periodic orbits (stable if $\iota_{k2} < 0$, unstable if $\iota_{k2} > 0$). Thus, if system (3) is given, then the direction and stability of the Hopf bifurcation at $\tau = \tau_*$ can be determined by the parameters of the system. For the Hopf bifurcation corresponding to $k = 0$, the normal form is the same as for the system without diffusion.

5. Numerical Simulations

In this section, we perform some numerical simulations to confirm and extend our analytical results. Since the true values of the model parameters are very difficult and costly, if not impossible, here we can only choose some artificial values to test our theoretical results. Taking $d_1 = 0.02, d_2 = 0.2, c = 0.6$, Fig. 1 shows the bifurcation diagram in the $b-a$ plane for system (3) without delay (see [Song & Zou, 2014a] for details). The critical curves in Fig. 1 are defined by the following

$$H_0: \ a = \frac{16}{25}b - \frac{6}{25}, \quad b > 1;$$

$$\ell_1: \ a = \frac{28}{55}b - \frac{1}{50}, \quad \frac{11}{60} < b \leq \frac{143}{180};$$

$$\ell_2: \ a = \frac{38}{65}b - \frac{2}{25}, \quad \frac{143}{180} < b \leq \frac{221}{60};$$

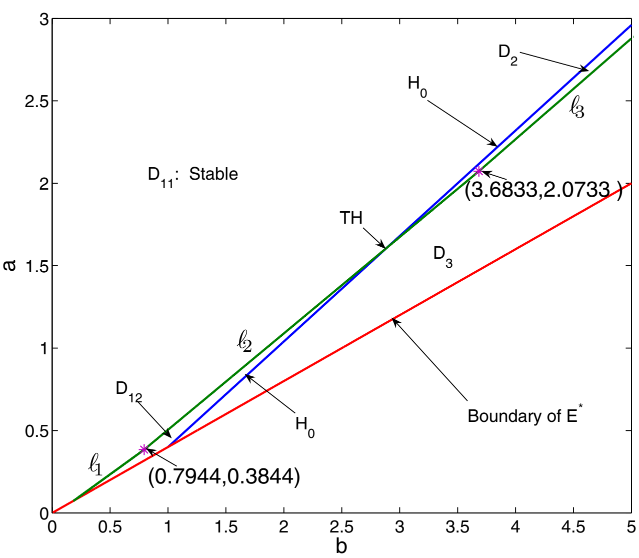

Fig. 1. Bifurcation diagram for system (3) with $d_1 = 0.02, d_2 = 0.2, c = 0.6$, in the b–a plane. The positive equilibrium E^* is asymptotically stable in D_{11} and unstable otherwise. In D_{12}, Turing instability occurs. In D_2, only Hopf bifurcations occur. In D_3, there exist Hopf and steady state bifurcations.

$$\ell_3: \ a = \frac{52}{85}b - \frac{9}{50}, \quad \frac{221}{60} < b \leq \frac{731}{60}.$$

When $(b, a) \in D_{11}$, $D_k > 0, J_k > 0$ for all $k \in \mathbb{N}_0$ then the positive equilibrium E^* of system (3) without delay is asymptotically stable. Theorem 3 shows that when $(b, a) \in D_{11}$, there exists a critical value of delay, say τ_*, such that the positive equilibrium E^* of system (3) is asymptotically stable for $\tau \in [0, \tau_*)$ and unstable for $\tau \in (\tau_*, +\infty)$.

Taking $a = 0.5, b = 0.4$ such that $(a, b) \in D_{11}$, then the positive equilibrium is $E^* \doteq (0.2720, 0.0725)$, which is asymptotically stable for $\tau = 0$. From (28), we have

$$P_k = \frac{101}{2500}k^4 + \frac{61}{6250}k^2 + \frac{121}{62500} > 0, \quad \text{for all } k \in \mathbb{N}_0$$

and

$$Q_k = \left(\frac{1}{250}k^4 + \frac{67}{1250}k^2 + \frac{51}{625}\right)\left(\frac{1}{250}k^4 + \frac{11}{250}k^2 - \frac{51}{625}\right) \begin{cases} < 0, & k = 0, 1, \\ > 0, & k \geq 2. \end{cases}$$

So, Hopf bifurcations induced by delay occur for $k = 0$ and $k = 1$. From (39), we obtain the critical values of delay as follows

$$\tau_{00} \doteq 4.9501, \quad \tau_{01} \doteq 27.0765, \ldots;$$
$$\tau_{10} \doteq 9.9936, \quad \tau_{11} \doteq 38.9345, \ldots.$$

By Theorem 3, the positive equilibrium $E^*(0.2720, 0.0725)$ is asymptotically stable for $\tau < \tau_{00}$. Figure 2 is the numerical simulation of system (3) for $\tau = 4.5$. When the delay increasingly crosses through the critical value $\tau_{00} \doteq 4.9501$, the positive equilibrium E^* loses its stability and the Hopf bifurcation occurs. The direction and stability of the Hopf bifurcation can be determined by the signs of ι_{k1} and ι_{k2}. By the procedure in Sec. 4, $\iota_{01} \doteq 0.0514, \iota_{02} \doteq -0.5371$. So, the Hopf bifurcation occurring at τ_{00} is supercritical and the corresponding Hopf bifurcating periodic orbits are stable. Taking $\tau = 5.2 > \tau_{00}$, the numerical simulation results of system (3) are shown in Fig. 3, which is in agreement with the theoretical results. In the numerical simulations for Figs. 2 and 3, the initial conditions are $u(x, t) = 0.2 + 0.1\cos x; v(x, t) = 0.1 - 0.01\cos x, (x, t) \in [0, \pi] \times [-\tau, 0]$. If τ is increasing across the critical value $\tau_{10} \doteq 9.9936$, a spatially inhomogenous periodic solution like $\cos(x)$ shape occurs near the positive equilibrium E^*. For this Hopf bifurcation, we have $\iota_{11} \doteq 0.6784, \iota_{12} \doteq -0.9256$, which means that the Hopf bifurcation is supercritical and the bifurcating periodic solution is stable on the center manifold. However, the bifurcating periodic solution bifurcating from the critical value τ_{10} must be unstable on the whole phase space since the characteristic equation always has roots with positive real parts for $\tau > \tau_{00} \doteq 4.9501$. Taking the initial values as $u(x, t) = 0.2720 - 0.002\cos x; v(x, t) = 0.0725 + 0.0025\cos x$, $(x, t) \in [0, \pi] \times [-\tau, 0]$, close to the center subspace, Fig. 4 shows the numerical simulation result for $\tau = 10 > \tau_{10}$. Figures 4(a) and 4(c) also show that the spatially inhomogenous periodic solution bifurcating from the critical value τ_{10} is unstable.

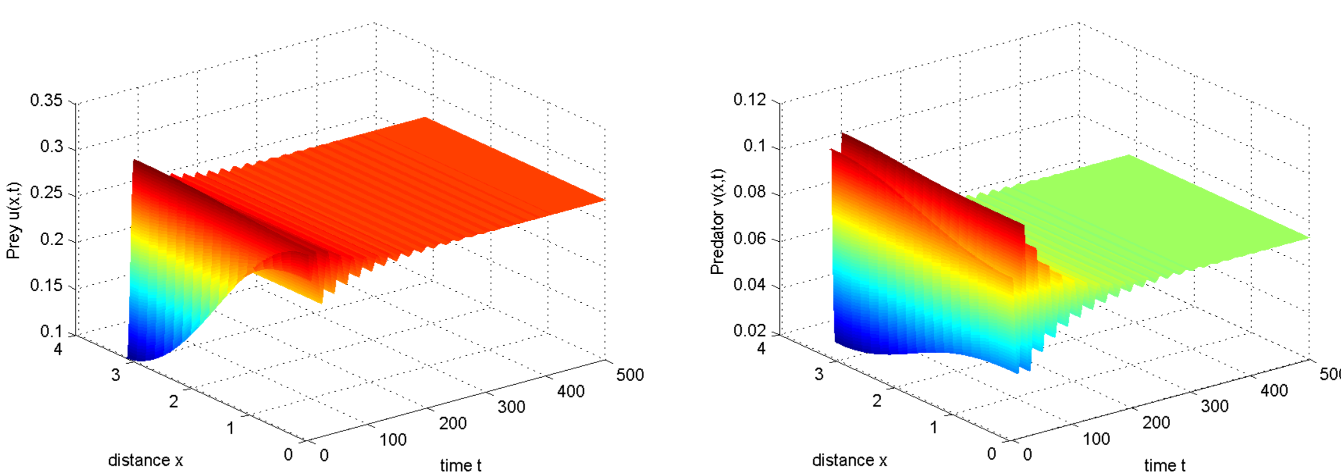

Fig. 2. Numerical simulations of system (3) for $d_1 = 0.02, d_2 = 0.2, c = 0.6$, $(b, a) = (0.4, 0.5) \in D_{11}$ and $\tau = 4.5 < \tau_{00}$. The positive equilibrium $E^*(0.2720, 0.0725)$ of system (3) is asymptotically stable for $\tau \in [0, \tau_{00})$.

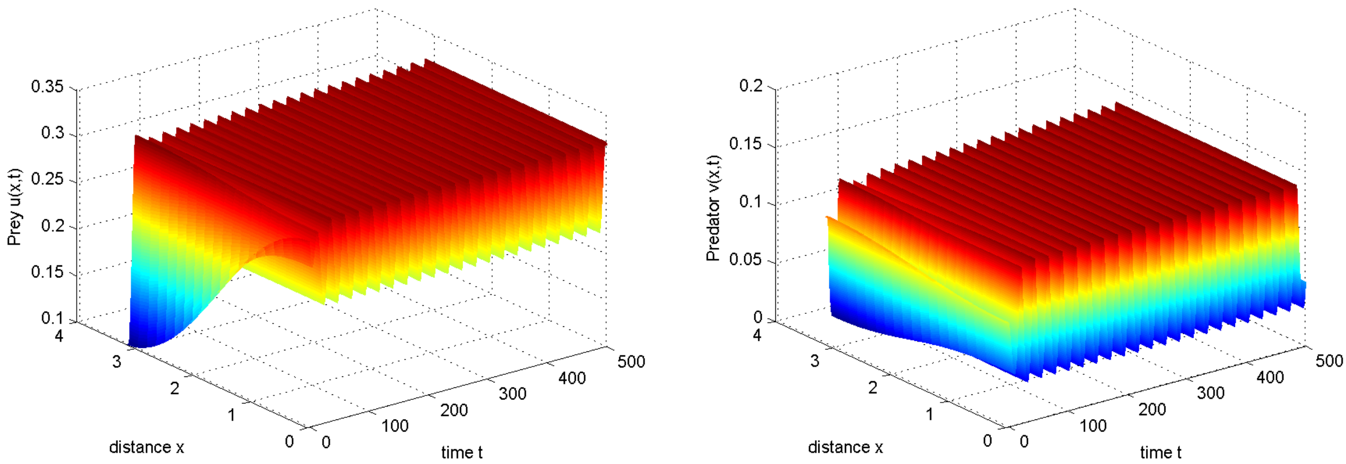

Fig. 3. Numerical simulations of system (3) for $d_1 = 0.02, d_2 = 0.2, c = 0.6$, $(b, a) = (0.4, 0.5) \in D_{11}$ and $\tau = 5.2 > \tau_{00}$. When $\tau > \tau_{00}$, the positive equilibrium $E^*(0.2720, 0.0725)$ becomes unstable and there exist stable spatially homogeneous periodic solutions.

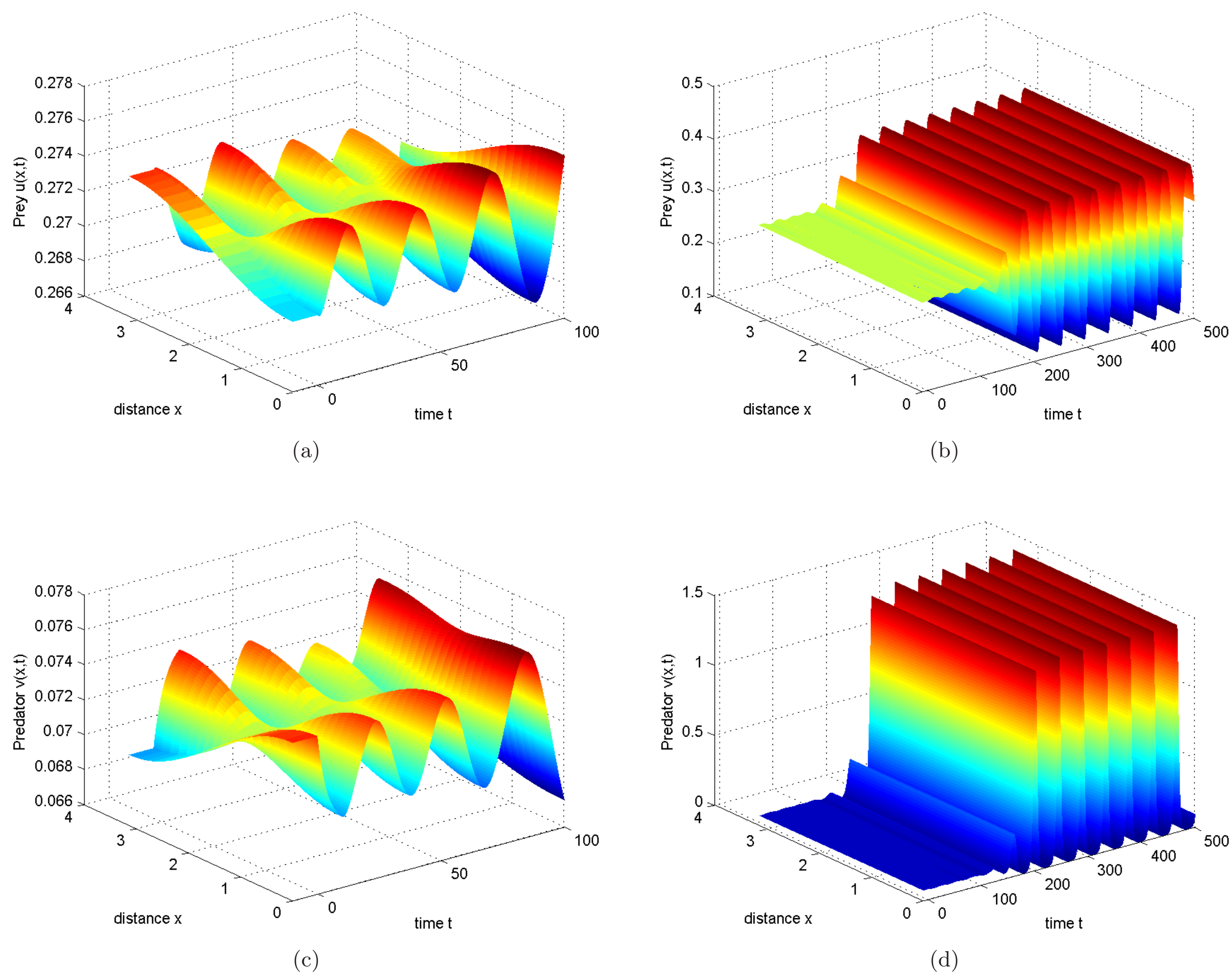

Fig. 4. Numerical simulations of system (3) for $d_1 = 0.02, d_2 = 0.2, c = 0.6$, $(b, a) = (0.4, 0.5) \in D_{11}$ and $\tau = 10 > \tau_{10}$. There exist unstable spatially inhomogeneous periodic solutions. Numerical simulation also show that there exists solutions connecting the unstable spatially inhomogenous periodic solution to spatially homogenous periodic solution.

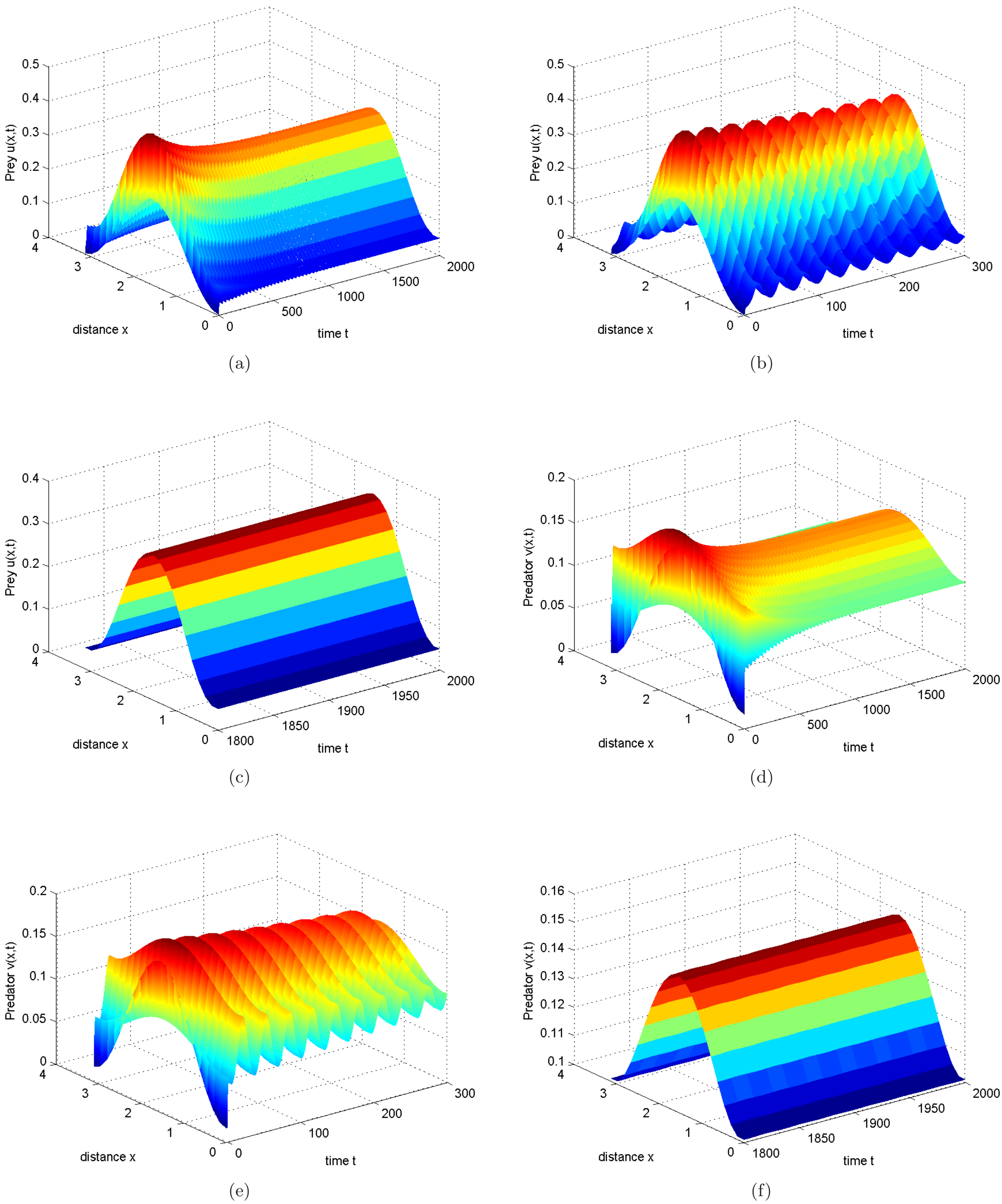

Fig. 5. Numerical simulation of system (3) for $d_1 = 0.02, d_2 = 0.2, c = 0.5$, $(b, a) = (1.1, 0.5) \in D_{12}$, and $\tau = 1.8 < \tau_{00}$. The steady state is stable for $\tau < \tau_{00}$.

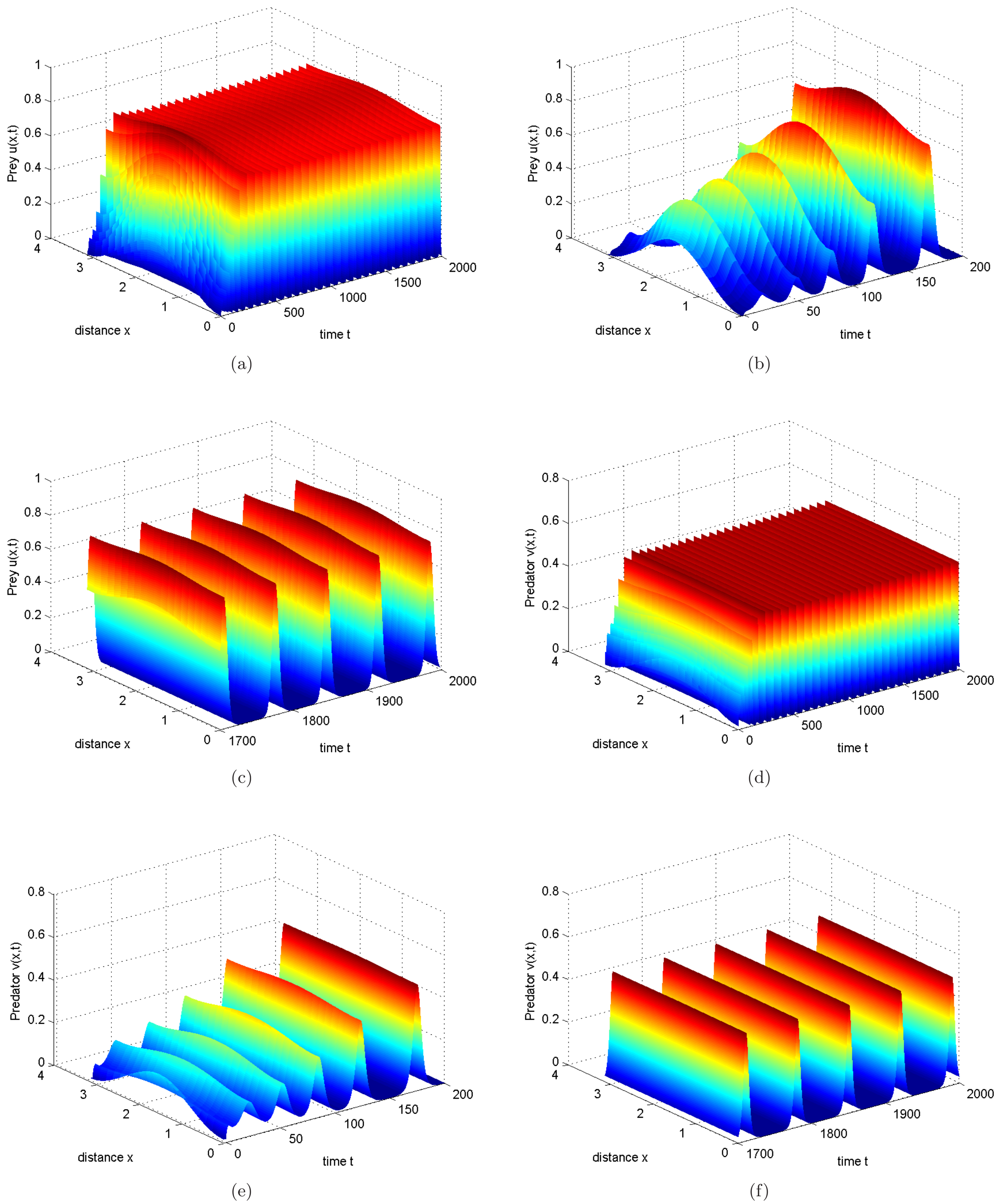

Fig. 6. Numerical simulation of system (3) for $d_1 = 0.02, d_2 = 0.2, c = 0.5$, $(b, a) = (1.1, 0.5) \in D_{12}$, and $\tau = 2.4 > \tau_{00}$. The steady state is unstable for $\tau > \tau_{00}$ and there exists a stable spatially homogeneous periodic solution.

However, the long-term behavior [see Figs. 4(b) and 4(d)] is stable homogenous periodic solution similar to Fig. 3. So, there exists solutions connecting the unstable spatially inhomogenous periodic solution to stable spatially homogenous periodic solution, as shown in Figs. 4(b) and 4(d).

Taking $a = 0.5, b = 1.1$ such that $(a, b) \in D_{12}$, the positive constant equilibrium of system (3) is $E^* \doteq (0.1320, 0.0968)$. This positive constant equilibrium is unstable and a supercritical pitchfork bifurcation occurs, which implies that system (3) has two stable steady states like $\cos 2x$ shape. In the following, we numerically investigate the influence of delay on the dynamics of the system. From (28), we have

$$P_k = \frac{101}{2500}k^4 - \frac{51}{6250}k^2 - \frac{999}{62500} = \begin{cases} < 0, & k = 0, \\ > 0, & k \geq 1 \end{cases}$$

and

$$Q_k = \left(\frac{1}{250}k^4 - \frac{9}{250}k^2 + \frac{9}{625}\right)\left(\frac{1}{250}k^4 - \frac{57}{1250}k^2 - \frac{9}{625}\right) \begin{cases} < 0, & k = 0, 3 \\ > 0, & \text{otherwise.} \end{cases}$$

Thus, Eq. (27) has positive real roots only for $k = 0, 3$. From (39), we have

$$\tau_{00}^+ \doteq 1.8399 < \tau_{30}^+ \doteq 37.6515.$$

The positive constant equilibrium $E^*(0.1320, 0.0968)$ is unstable for all $\tau \geq 0$. The first critical value of τ for Hopf bifurcation is $\tau_{00} \doteq 1.8399$. In the following numerical simulations, we choose $u(x, t) = 0.1320 - 0.13 \cos x; v(x, t) = 0.0968 - 0.08 \cos x,\ (x, t) \in [0, \pi] \times [-\tau, 0]$, as the initial values. When $\tau < \tau_{00}$, the numerical simulation shows that the steady state is still stable (see Fig. 5). Although the short-term behavior is oscillating [see Figs. 5(b) and 5(e)], the long-term behavior is a stable steady state [see Figs. 5(c) and 5(f)]. When $\tau > \tau_{00}$, the steady state becomes unstable and there exists a periodic solution as shown in Fig. 6. At first, the solution oscillates near the steady state [see Figs. 6(b) and 6(e)], but finally converges to a stable spatially homogeneous periodic solution [see Figs. 6(c) and 6(f)]. Figures 6(a) and 6(b) also show the existence of the heteroclinic orbit connecting the steady state to periodic solution.

6. Conclusion

A ratio-dependent predator–prey model with diffusion and delay is investigated. The sufficient conditions independent of diffusion and delay for the persistence, global stability of the boundary equilibrium are given. If the normalized intrinsic growth for the prey and death rate for the predator are small ($0 < b, c < 1$), then the system has the persistence properties regardless of the quantities of diffusion and delay. If the positive constant equilibrium does not exist and the normalized death rate for the predator then is large ($c \leq 1$), then the boundary equilibrium is global stability. For the positive constant equilibrium, we found that the time delay due to the gestation plays an important role. It was shown that the asymptotic stability or instability of positive equilibrium depends upon the magnitude of delay. We also found that delay can drive a stable constant equilibrium to an unstable one, i.e. there is a critical value τ_* such that for $\tau < \tau_*$, the positive equilibrium is stable and it reduces as delay passes through this critical magnitude from lower to higher values. Also, there exists a sequence of critical values of delay such that spatially homogeneous and inhomogeneous periodic solutions can arise through Hopf bifurcations.

We have derived the analytical expressions that determine the properties of bifurcating periodic solutions by using the normal form theory. These analytical results are supported with numerical examples. Our analytical results are based on the basic assumption that the positive constant equilibrium of the system without delay is stable. But numerical examples, also extend the analytical results. If the positive constant equilibrium of the system without delay is unstable, numerical results show that delay has an important effect on the spatiotemporal dynamics of the system. The heteroclinic orbit connecting the spatially inhomogeneous steady state to spatially homogeneous periodic solution has been found in the numerical simulations.

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References

Akcakaya, H. R., Arditi, R. & Ginzburg, L. R. [1995] "Ratio-dependent prediction: An abstraction that works," *Ecology* **76**, 995–1004.

Aly, S., Kim, I. & Sheen, D. [2011] "Turing instability for a ratio-dependent predator–prey model with diffusion," *Appl. Math. Comput.* **217**, 7265–7281.

Arditi, R. & Ginzburg, L. R. [1989] "Coupling in predator–prey dynamics: Ratio-dependence," *J. Theoret. Biol.* **139**, 311–326.

Arditi, R., Ginzburg, L. R. & Akcakaya, H. R. [1991] "Variation in plankton densities among lakes: A case for ratio-dependent models," *Amer. Natural.* **138**, 1287–1296.

Aronson, D. G. & Weinberger, H. F. [1975] "Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation," *Partial Differential Equations and Related Topics*, Lecture Notes in Math., Vol. 446 (Springer, Berlin), pp. 5–49.

Banerjee, M. [2010] "Self-replication of spatial patterns in a ratio-dependent predator–prey model," *Math. Comput. Model.* **51**, 44–52.

Banerjee, M. & Petrovskii, S. [2011] "Self-organised spatial patterns and chaos in a ratio-dependent predator–prey system," *Theor. Ecol.* **4**, 37–53.

Bartumeus, F., Alonso, D. & Catalan, J. [2001] "Self-organized spatial structures in a ratio-dependent predator–prey model," *Physica A* **295**, 53–57.

Beretta, E. & Kuang, Y. [1998] "Global analyses in some delayed ratio-dependent predator–prey systems," *Nonlin. Anal.* **32**, 381–408.

Berryman, A. A. [1992] "The origin and evolution of predator–prey theory," *Ecology* **73**, 1530–1535.

Chen, S., Shi, J. & Wei, J. [2013] "Time delay-induced instabilities and Hopf bifurcations in general reaction–diffusion systems," *J. Nonlin. Sci.* **23**, 1–38.

Chow, S. N. & Hale, J. K. [1982] *Methods of Bifurcation Theory* (Springer-Verlag, NY).

Cosner, C., DeAngelis, D. L., Ault, J. S. & Olson, D. B. [1999] "Effects of spatial grouping on the functional response of predators," *Theoret. Pop. Biol.* **56**, 65–75.

Fan, M., Wang, Q. & Zou, X. [2003] "Dynamics of a nonautonomous ratio-dependent predator–prey system," *Proc. Roy. Soc. Edin. A* **133**, 97–118.

Fan, Y. & Li, W. [2006] "Global asymptotic stability of a ratio-dependent predator–prey system with diffusion," *J. Comput. Appl. Math.* **188**, 205–227.

Faria, T. [2000] "Normal forms and Hopf bifurcation for partial differential equations with delay," *Trans. Amer. Math. Soc.* **352**, 2217–2238.

Faria, T. [2001] "Stability and bifurcation for a delayed predator–prey model and the effect of diffusion," *J. Math. Anal. Appl.* **254**, 433–463.

Gause, G. F. [1935] *The Struggle for Existence* (Williams and Wilkins, Baltimore).

Hsu, S., Hwang, T. & Kuang, Y. [2001] "Global analysis of the Michaelis–Menten type ratio-dependent predator–prey system," *J. Math. Biol.* **42**, 489–506.

Hu, G. & Li, W. [2010] "Hopf bifurcation analysis for a delayed predator–prey system with diffusion effects," *Nonlin. Anal.: Real World Appl.* **11**, 819–826.

Kuang, Y. & Beretta, E. [1998] "Global qualitative analysis of a ratio-dependent predator–prey system," *J. Math. Biol.* **36**, 389–406.

Kuang, Y. [1999] "Rich dynamics of Gause-type ratio-dependent predator–prey systems," *Fields Instit. Comm.* **21**, 325–337.

Liu, Z. & Yuan, R. [2004] "The effect of diffusion for a predator–prey system with nonmonotonic functional response," *Int. J. Bifurcation and Chaos* **14**, 4309–4316.

Murray, J. D. [2002] *Mathematical Biology II* (Springer-Verlag, Heidelberg).

Okubo, A. & Levin, S. [2001] *Diffusion and Ecological Problems: Modern Perspectives* (Springer, Berlin).

Pang, P. & Wang, M. [2003] "Qualitative analysis of a ratio-dependent predator–prey system with diffusion," *Proc. Roy. Soc. Edin. A* **133**, 919–942.

Ruan, S., Tang, Y. & Zhang, W. [2010] "Versal unfoldings of predator–prey systems with ratio-dependent functional response," *J. Diff. Eqs.* **249**, 1410–1435.

Song, Y. & Zou, X. [2014a] "Bifurcation analysis of a diffusive ratio-dependent predator–prey model," *Nonlin. Dyn.*, to appear.

Song, Y. & Zou, X. [2014b] "Spatiotemporal dynamics in a diffusive ratio-dependent predator–prey model near a Hopf–Turing bifurcation point," *Comput. Math. Appl.* **67**, 1978–1997.

Turing, A. M. [1952] "The chemical basis of morphogenesis," *Philos. Trans. Roy. Soc. Lond. B* **237**, 37–72.

Wang, W., Liu, Q. & Jin, Z. [2007] "Spatiotemporal complexity of a ratio-dependent predator–prey system," *Phys. Rev. E* **75**, 051913–051921.

Wu, J. [1996] *Theory and Applications of Partial Functional Differential Equations* (Springer-Verlag, NY).

Xiao, D. & Ruan, S. [2001] "Global dynamics of a ratio-dependent predator–prey system," *J. Math. Biol.* **43**, 221–290.

Xiao, D. & Li, W. [2003] "Stability and bifurcation in a delayed ratio-dependent predator–prey system," *Proc. Edin. Math. Soc.* **45**, 205–220.

Xu, R., Davidson, F. A. & Chaplain, M. A. J. [2002] "Persistence and stability for a two-species ratio-dependent predator–prey system with distributed time delay," *J. Math. Anal. Appl.* **269**, 256–277.

Xu, R., Gan, Q. & Ma, Z. [2009] "Stability and bifurcation analysis on a ratio-dependent predator–prey model with time delay," *J. Comput. Appl. Math.* **230**, 187–203.

Yan, X. [2007] "Stability and Hopf bifurcation for a delayed prey–predator system with diffusion effects," *Appl. Math. Comput.* **192**, 552–566.

Zuo, W. & Wei, J. [2011] "Stability and Hopf bifurcation in a diffusive predatory–prey system with delay effect," *Nonlin. Anal.: Real World Appl.* **12**, 1998–2011.

Zuo, W. [2013] "Global stability and Hopf bifurcations of a Beddington–DeAngelis type predator–prey system with diffusion and delays," *Appl. Math. Comput.* **223**, 423–435.