Journal of Dynamics and Differential Equations
https://doi.org/10.1007/s10884-022-10176-9

Complex Dynamics in a General Diffusive Predator–Prey Model with Predator Maturation Delay

Wanxiao Xu[1] · Hongying Shu[2] · Zheng Tang[1] · Hao Wang[3]

Received: 10 February 2022 / Revised: 29 April 2022 / Accepted: 10 May 2022

Abstract
We formulate and analyze a general diffusive predator–prey system with predator maturation delay. Global asymptotic stability of the predator-free equilibrium and uniform persistence results are obtained under different conditions on model parameters. We then use Leray–Schauder degree theory to establish the existence of the spatial heterogeneous steady state. Moreover, we prove the global existence of nonconstant positive steady states bifurcated from the positive constant steady state. Taking the time delay as the bifurcation parameter, we conduct local and global Hopf bifurcation analysis and prove the boundedness of global Hopf branches. Rigorous analyses for global Hopf bifurcation and branches are challenging but important in understanding global transitions of dynamics.

Keywords Predator-prey · Reaction-diffusion equations · Maturation delay · Positive steady states · Periodic orbits · Global bifurcation

Mathematics Subject Classification 35K57 · 37L10 · 92D25

1 Introduction

The predator–prey system has been intensively studied since the work of Lotka [10] and Volterra [29]. The nonlinear interaction between predators and prey can induce rich dynamics. Most predator–prey systems possess a stable limit cycle which explains the sustained periodic oscillations in observed population data of animal communities [11]. Reaction-diffusion equations can be used to model aquatic ecosystems and to investigate spatiotemporal plankton dynamics [13]. One of the widely used models was proposed by Rosenzweig and MacArthur

✉ Hongying Shu
hshu@snnu.edu.cn

1 School of Mathematical Sciences, Tongji University, Shanghai 200092, People's Republic of China

2 School of Mathematics and Statistics, Shaanxi Normal University, Xi'an 710062, People's Republic of China

3 Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton AB T6G 2G1, Canada

[17, 18]. A more general model was investigated in [27], where global bifurcation and spatial pattern formation were studied.

Even for a spatial homogeneous predator–prey system without diffusion, the predator maturation delay may induce rich dynamics [6, 12, 26]. In [8], bounded global Hopf branches were investigated for delay differential equations with delay-dependent parameters. One of the main tools was the geometric stability switch criteria introduced in [1, 2]. This technique has been recently applied in the Hopf bifurcation analysis of delayed differential systems [9, 19, 21, 24].

In this paper, we will incorporate predator maturation delay into the general diffusive Rosenzweig-MacArthur model [18, 27]. Let $u(x,t)$ and $v(x,t)$ be the densities of the prey and the adult predator, respectively. We use τ to denote a cutoff age for the maturation delay of the predator. We further assume that juvenile predators cannot catch prey [28]. Then we obtain the following diffusive predator–prey model with predator maturation delay:

$$\begin{aligned}
\frac{\partial u(x,t)}{\partial t} &= d_1\Delta u(x,t) + b(u(x,t)) - \beta g(u(x,t))v(x,t), \quad x\in\Omega, t>0,\\
\frac{\partial v(x,t)}{\partial t} &= d_2\Delta v(x,t) + \gamma\beta e^{-s\tau}\int_\Omega K(x,y)g(u(y,t-\tau))v(y,t-\tau)dy\\
&\quad - \mu v(x,t), \quad x\in\Omega, t>0,
\end{aligned} \tag{1.1}$$

where Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary $\partial\Omega$, $b(u)$ is the growth rate of the prey in the absence of adult predators, $g(u)$ is the predator functional response. The parameters d_1 and d_2 represent the diffusion coefficients of prey and adult predators, respectively. $K(x,y)$ is a general nonnegative kernel function, which is continuous and $\int_\Omega K(x,y)dy = 1$ for any $x\in\Omega$. β is the catch rate of the adult predators, γ is the energy transform rate for adult predators, s is the death rate of juvenile predators, and μ is the nature death rate of adult predators. The term $e^{-s\tau}$ is the survival probability of a juvenile predator from birth to mature. Here all parameters are positive, and we consider a closed environment in the sense that Neumann boundary conditions are assumed.

In this paper, we consider the case that $K(x,y) = \delta(x-y)$. Note that the Dirac delta function can be regarded as the limit of the heat kernel when the diffusion rate approaches zero. The biological explanation of our assumption is that the spatial diffusion of immature predators (such as birds) is much smaller than that of mature predators. Rescaling the model (1.1) by $\widetilde{u} = u/\beta$, $\widetilde{v} = v/(\gamma\beta)$, $\widetilde{b}(\widetilde{u}) = b(\beta\widetilde{u})/\beta$, $\widetilde{g}(\widetilde{u}) = \gamma\beta g(\beta\widetilde{u})$ and dropping $\widetilde{\cdot}$ for convenience, model (1.1) with Dirac delta kernel function can be rewritten as

$$\begin{aligned}
&\frac{\partial u(x,t)}{\partial t} = d_1\Delta u(x,t) + b(u(x,t)) - g(u(x,t))v(x,t), \quad x\in\Omega, t>0,\\
&\frac{\partial v(x,t)}{\partial t} = d_2\Delta v(x,t) + e^{-s\tau}g(u(x,t-\tau))v(x,t-\tau) - \mu v(x,t), \quad x\in\Omega, t>0,\\
&\frac{\partial u(x,t)}{\partial \nu} = \frac{\partial v(x,t)}{\partial \nu} = 0, \quad x\in\partial\Omega, t>0,\\
&u(x,\theta) = u_0(x,\theta)\ge 0, v(x,\theta) = v_0(x,\theta)\ge 0, \quad x\in\Omega, \theta\in[-\tau,0].
\end{aligned} \tag{1.2}$$

Throughout this paper, we make the following assumptions:

($\mathbf{H}_1$) $b\in C^1(\mathbb{R}^+)$, $\exists\, K>0$ such that $b(0)=b(K)=0$ and $b(u)(u-K)<0$ for $u\neq K$.
($\mathbf{H}_2$) $g\in C^1(\mathbb{R}^+)$, $g(0)=0$, $g'(u)>0$ for any $u\ge 0$.

Typical functions satisfying the above assumptions are $b(u) = ru(1-\frac{u}{K})$ (logistic growth) or $b(u) = ru(1-\frac{u}{K})(u+a)$ (weak Allee effect), where $r>0$ and $K>a>0$, and

$g(u) = cu$ (Holling type I), $g(u) = \frac{cu}{u+a}$ (Holling type II), $g(u) = \frac{cu^k}{u^k+a}$ (Holling type III), $g(u) = c(1 - e^{-au})$ (Ivlev type), where $c, a > 0$ and $k > 1$.

The rest of this paper is organized as follows. In Sect. 2, we present some preliminary results on positiveness, boundedness, and uniform persistence of solutions. We also investigate the global stability of the predator-free steady state and local stability of the positive constant steady state. In Sect. 3, we establish the existence of the positive heterogeneous steady state via Leray–Schauder degree theory [7], and analyze the steady state bifurcation from the positive constant steady state. In Sect. 4, we use the delay $\tau > 0$ as the bifurcation parameter and study the Hopf bifurcation with periodic orbits bifurcated from the positive constant steady state. In Sect. 5, we conduct numerical simulations to illustrate our analytical results, and compare dynamics of local and nonlocal models. Finally we summarize this paper in Sect. 6.

2 Preliminary Results and Basic Dynamics

Denote by $X = L^2(\Omega)$ the Hilbert space of integrable functions with usual inner product, $\mathcal{C} := C([-\tau, 0], X^2)$ the Banach space of continuous map from $[-\tau, 0]$ to X^2 with the sup norm, and $\mathcal{C}^+$ the nonnegative cone of $\mathcal{C}$. Given a continuous function $(u(x,t), v(x,t))$ on $\Omega \times [-\tau, \infty)$, we define $(u_t, v_t) \in \mathcal{C}$ as $(u_t(\theta), v_t(\theta)) = (u(\cdot, t+\theta), v(\cdot, t+\theta))$ for $\theta \in [-\tau, 0]$. Let $\Theta(t) : \mathcal{C}^+ \to \mathcal{C}^+$ with $t \geq 0$ be the solution semiflow associated with (1.2). Our next results establish the existence, uniqueness, and boundedness of the solution to (1.2).

Proposition 2.1 *For each initial condition $u_0(x,\theta), v_0(x,\theta) \geq 0 (\not\equiv 0)$, system (1.2) admits a unique solution $(u(x,t), v(x,t))$ such that $u(x,t), v(x,t) > 0$ for all $(x,t) \in \overline{\Omega} \times (0,\infty)$, and $\limsup_{t\to\infty} u(x,t) \leq K$, $\limsup_{t\to\infty} v(x,t) \leq K + \max_{[0,K]} b(u)/\mu$. Moreover, the solution semiflow $\Theta(t)$ admits a global compact attractor in $\mathcal{C}^+$.*

Proof Let $(u_1(t), v_1(t))$ be the unique solution to

$$\begin{aligned} &u'(t) = b(u(t)) - g(u(t))v(t), \quad v'(t) = e^{-s\tau} g(u(t-\tau))v(t-\tau) - \mu v(t), \\ &u(\theta) = \sup_{\overline{\Omega}} u_0(x,\theta), \quad v(\theta) = \sup_{\overline{\Omega}} v_0(x,\theta) \text{ for } \theta \in [-\tau, 0]. \end{aligned} \tag{2.1}$$

It is readily seen that $\limsup_{t\to\infty} u_1(t) \leq K$. Especially, for any $\epsilon > 0$, there exists $t_1 > 0$ such that $u_1(t) \leq K + \epsilon$ for $t > t_1$. Then, from system (2.1) we get

$$u_1'(t-\tau) + v_1'(t) \leq b(u_1(t-\tau)) - \mu v_1(t) \leq \max_{[0,K]} b(u) + \mu(K+\epsilon) - \mu(u_1(t-\tau) + v_1(t))$$

for $t > t_1$, and thus $\limsup_{t\to\infty} v_1(t) \leq K + \max_{[0,K]} b(u)/\mu$. Note that (1.2) is a mixed quasi-monotone system [15,Definition 2.1]. It then follows from the definition of lower/upper-solution in Definition 2.2 in [15] that $(\overline{u}(x,t), \overline{v}(x,t)) = (u_1(t), v_1(t))$ and $(\underline{u}(x,t), \underline{v}(x,t)) = (0,0)$ are a pair of upper-solution and lower-solution to (1.2), respectively. Thus, Theorem 3.1 in [15] implies that (1.2) has a unique global solution $(u(x,t), v(x,t))$ which satisfies $0 \leq u(x,t) \leq u_1(t)$, $0 \leq v(x,t) \leq v_1(t)$ for all $(x,t) \in \overline{\Omega} \times [0,\infty)$. Consequently, $\limsup_{t\to\infty} u(x,t) \leq \limsup_{t\to\infty} u_1(t) \leq K$ and $\limsup_{t\to\infty} v(x,t) \leq \limsup_{t\to\infty} v_1(t) \leq K + \max_{[0,K]} b(u)/\mu$. The strong maximum principle implies that $u(x,t), v(x,t) > 0$ for all $(x,t) \in \overline{\Omega} \times (0,\infty)$. Especially, the semiflow $\Theta(t)$ is point dissipative. It follows from [30] that $\Theta(t)$ is compact for all $t > \tau$. Hence, by [4,Theorem 3.4.8], $\Theta(t)$ admits a nonempty global attractor in $\mathcal{C}^+$. This completes the proof. □

We now carry out the stability analysis of constant steady states of (1.2). Clearly, system (1.2) always has two constant steady states $(0,0)$ and $(K,0)$, and a positive constant steady state (u^*, v^*) exists if $g(K) > \mu$ and $0 \le \tau < \widehat{\tau} := \frac{ln(g(K)/\mu)}{s}$, where

$$u^* = g^{-1}(\mu e^{s\tau}) < K, \quad v^* = \frac{b(u^*)}{\mu} e^{-s\tau}. \tag{2.2}$$

Linearizing (1.2) at a constant steady state $(\hat{u}, \hat{v})$, we obtain

$$\frac{\partial U}{\partial t} = d\Delta U + L(U_t) \tag{2.3}$$

with domain $Y := \{(u,v)^T : u, v \in C^2(\Omega) \cap C^1(\overline{\Omega}), u_\nu = v_\nu = 0 \text{ on } \partial\Omega\}$, where $U(x,t) = (u(x,t), v(x,t))^T$, $d = \mathrm{diag}(d_1, d_2)$, and $L : \mathcal{C} \to X^2$ be a bounded linear operator given by $L(\phi) = J\phi(0) + J_\tau \phi(-\tau)$ for $\phi = (\phi_1, \phi_2)^T \in \mathcal{C}$ with

$$J = \begin{pmatrix} b'(\hat{u}) - g'(\hat{u})\hat{v} & -g(\hat{u}) \\ 0 & -\mu \end{pmatrix}, \quad J_\tau = \begin{pmatrix} 0 & 0 \\ e^{-s\tau} g'(\hat{u})\hat{v} & e^{-s\tau} g(\hat{u}) \end{pmatrix}.$$

Then the characteristic equation for linear system (2.3) is

$$\lambda z - d\Delta z - L(e^{\lambda \cdot} z) = 0, \ \text{for } z \in Y \backslash \{0\},$$

which is equivalent to $\det(\lambda I + \delta_n d - J - e^{-\lambda\tau} J_\tau) = 0$ for integer $n \ge 0$, where

$$0 = \delta_0 < \delta_1 \le \cdots \le \delta_n \le \delta_{n+1} \le \cdots \text{ and } \lim_{n \to \infty} \delta_n = \infty \tag{2.4}$$

are the eigenvalues of $-\Delta$ in Ω with Neumann boundary condition [3]. Then the stability of constant boundary steady states can be analyzed as follows.

Theorem 2.2 (i) *The trivial steady state* $(0,0)$ *of* (1.2) *is unstable for all* $\tau \ge 0$.

(ii) *If either* $g(K) < \mu$ *or* $g(K) > \mu, \tau > \widehat{\tau}$ *holds, then* $(K,0)$ *of* (1.2) *is globally asymptotically stable.*

(iii) *If* $g(K) > \mu$ *and* $\tau \in [0, \widehat{\tau})$ *hold, then* $(K,0)$ *is unstable, and system* (1.2) *has a positive constant steady state* (u^*, v^*).

Proof (i) The characteristic equation at $(0,0)$ is $(\lambda + \delta_n d_1 - b'(0))(\lambda + \delta_n d_2 + \mu) = 0$ for integer $n \ge 0$. One eigenvalue is $b'(0) > 0$, thus $(0,0)$ is unstable for all $\tau \ge 0$.
(ii) The characteristic equation at $(K,0)$ is given by $(\lambda + \delta_n d_1 - b'(K))(\lambda + \delta_n d_2 + \mu - g(K)e^{-s\tau}e^{-\lambda\tau}) = 0$ for integer $n \ge 0$. Since $-\delta_n d_1 + b'(K) < 0$ for all integer $n \ge 0$, then the local stability of $(K,0)$ is determined by the eigenvalues to

$$\lambda + \delta_n d_2 + \mu - g(K)e^{-s\tau}e^{-\lambda\tau} = 0, \ n = 0, 1, 2 \cdots. \tag{2.5}$$

Note that either $g(K) < \mu$ or $g(K) > \mu, \tau > \widehat{\tau}$ implies that $\delta_n d_2 + \mu > g(K)e^{-s\tau}$ for all integer $n \ge 0$. It then follows from [22,Lemma 6] that all eigenvalues of (2.5) have negative real parts. Thus, $(K,0)$ is locally asymptotically stable if either $g(K) < \mu$ or $g(K) > \mu, \tau > \widehat{\tau}$ holds. We next show that $(K,0)$ is globally attractive in $\mathcal{C}^+$. Define a Lyapunov functional $\mathbb{L}_1 : \mathcal{C}^+ \to \mathbb{R}$,

$$\mathbb{L}_1(\phi) = \int_\Omega \phi_2(0)^2 dx + g(K)e^{-s\tau} \int_\Omega \int_{-\tau}^0 \phi_2(\theta)^2 d\theta dx, \ \text{for } \phi = (\phi_1, \phi_2) \in \mathcal{C}^+.$$

Calculating the time derivative of $\mathbb{L}_1(\phi)$ along the solution of (1.2) yields

$$\begin{aligned}\frac{d\mathbb{L}_1}{dt} &\le -2d_2\int_\Omega |\nabla v|^2 dx + \int_\Omega \big(2g(K)e^{-s\tau}v(x,t)v(x,t-\tau)\\ &\quad -2\mu v(x,t)^2 + g(K)e^{-s\tau}(v(x,t)^2 - v(x,t-\tau)^2)\big)\, dx\\ &= 2(g(K)e^{-s\tau}-\mu)\int_\Omega v(x,t)^2 dx \le 0.\end{aligned}$$

The maximal invariant subset of $d\mathbb{L}_1/dt = 0$ is the singleton $\{(K,0)\}$. By LaSalle-Lyapunov invariance principle [5], $(K,0)$ is globally attractive in $\mathcal{C}^+$. We thus conclude the global stability of $(K,0)$.
(iii) If $g(K) > \mu$ and $\tau \in [0,\widehat{\tau})$ hold, then $\mu < g(K)e^{-s\tau}$, that is, $\delta_0 d_2 + \mu < g(K)e^{-s\tau}$. This, together with [22,Lemma 6], implies that there exists one positive eigenvalue of (2.5). We thus obtain $(K,0)$ is unstable if $g(K) > \mu$ and $\tau \in [0,\widehat{\tau})$ hold. □

Theorem 2.3 *If $g(K) > \mu$ and $\tau = \widehat{\tau}$, then $(K,0)$ of system (1.2) is globally asymptotically stable.*

Proof Let $\bar{\Lambda} = \{\lambda \in \mathbb{C}, \lambda$ is an eigenvalue of (2.5) with $\mathrm{Re}\lambda = 0\}$. When $g(K) > \mu$ and $\tau = \widehat{\tau}$, then the characteristic equation (2.5) at $(K,0)$ has an eigenvalue 0, and all other eigenvalues have negative real parts, that is, $\bar{\Lambda} = \{0\}$. Thus, (1.2) satisfies the nonresonance condition relative to $\bar{\Lambda}$. We now explore the local stability of $(K,0)$ by calculating the normal forms. Let $w = (w_1, w_2)^T = (K-u, v)^T$. We obtain

$$\begin{aligned}\partial_t w_1(x,t) &= d_1\Delta w_1(x,t) + b'(K)w_1(x,t) + g(K)w_2(x,t)\\ &\quad + [-b(K-w_1(x,t)) - b'(K)w_1(x,t)\\ &\quad + g(K-w_1(x,t))w_2(x,t) - g(K)w_2(x,t)],\\ \partial_t w_2(x,t) &= d_2\Delta w_1(x,t) + e^{-s\tau}g(K)w_2(x,t-\tau) - \mu w_2(x,t)\\ &\quad + [e^{-s\tau}g(K-w_1(x,t-\tau))w_2(x,t-\tau) - e^{-s\tau}g(K)w_2(x,t-\tau)].\end{aligned}$$

Note that $e^{-s\tau}g(K) = \mu$. By using the standard notation in delay differential equations $w_t(\theta) = w(t+\theta)$, the above system can be written as an abstract equation $\dot{w}_t = \bar{A}w_t + \bar{F}(w_t)$ on $\mathcal{C} = C([-\tau,0], X^2)$, $\bar{A}$ is a linear operator defined as $(\bar{A}\phi)(\theta) = \phi'(\theta)$ for $\theta \in [-\tau, 0)$,

$$(\bar{A}\phi)(0) = \begin{pmatrix} d_1\Delta & 0\\ 0 & d_2\Delta\end{pmatrix}\phi(0) + \begin{pmatrix} b'(K) & g(K)\\ 0 & -\mu\end{pmatrix}\phi(0) + \begin{pmatrix} 0 & 0\\ 0 & \mu\end{pmatrix}\phi(-\tau),$$

and $\bar{F}$ is a nonlinear operator defined as $[\bar{F}(\phi)](\theta) = 0$ for $\theta \in [-\tau, 0)$ and

$$[\bar{F}(\phi)](0) = \begin{pmatrix} -b(K-\phi_1(0)) - b'(K)\phi_1(0) + g(K-\phi_1(0))\phi_2(0) - g(K)\phi_2(0)\\ e^{-s\tau}g(K-\phi_1(-\tau))\phi_2(-\tau) - e^{-s\tau}g(K)\phi_2(-\tau)\end{pmatrix}.$$

For $\psi \in C([0,\tau], X^2)$ and $\phi \in C([-\tau,0], X^2)$, we introduce a bilinear form

$$\begin{aligned}\langle\psi,\phi\rangle &= \int_\Omega \left[\psi(0)^T\phi(0) + \int_{-\tau}^0 \psi(\theta+\tau)^T \begin{pmatrix} 0 & 0\\ 0 & \mu\end{pmatrix}\phi(\theta)d\theta\right]dx\\ &= \int_\Omega \left[\psi_1(0)\phi_1(0) + \psi_2(0)\phi_2(0) + \mu\int_{-\tau}^0 \psi_2(\theta+\tau)\phi_2(\theta)d\theta\right]dx.\end{aligned}$$

Now, we choose $\psi = (0,1)^T$ and $\phi = (-g(K)/b'(K), 1)$ to be the left and right eigenfunctions, respectively, of the linear operator $\bar{A}$ with respect to the eigenvalue 0. We have the decomposition $w_t = z\phi + y$ with $\langle \psi, y\rangle = 0$. Hence,

$$\langle \psi, \dot{w}_t\rangle = \dot{z}\langle \psi, \phi\rangle + \langle \psi, \dot{y}\rangle = \dot{z}\langle \psi, \phi\rangle.$$

Moreover, since $\bar{A}\phi = 0$ and $\langle \psi, \bar{A}y\rangle = 0$, we have

$$\langle \psi, \dot{w}_t\rangle = \langle \psi, \bar{A}w_t\rangle + \langle \psi, \bar{F}(w_t)\rangle = \langle \psi, \bar{F}(w_t)\rangle.$$

Coupling the above two equations gives

$$\dot{z}\langle \psi, \phi\rangle = \langle \psi, \bar{F}(z\phi + y)\rangle = \int_\Omega \psi^T[\bar{F}(z\phi + y)](0)dx = \int_\Omega [\bar{F}(z\phi + y)]_2(0)dx.$$

If the initial value is a small perturbation of the equilibrium $(K, 0)$, then z is also small with positive initial value $z(0)$ and $y = O(z^2)$. By Taylor expansion, we obtain

$$\begin{aligned}[\bar{F}(z\phi + y)]_2(0) &= e^{-s\tau}[g(K - z\phi_1(-\tau) - y_1(-\tau)) - g(K)][z\phi_2(-\tau) + y_2(-\tau)] \\ &= e^{-s\tau} z^2 g'(K)g(K)/b'(K) + O(z^3).\end{aligned}$$

On the other hand, it is easy to calculate that $\langle \psi, \phi\rangle = \int_\Omega (1 + \mu\tau)dx$. Finally, we derive the following normal form

$$\dot{z} = \frac{e^{-s\tau} g'(K)g(K)}{b'(K)(1 + \mu\tau)} z^2 + O(z^3).$$

Since $g(K) > 0$, $g'(K) > 0$ and $b'(K) < 0$, the zero solution of the above equation with positive initial value is locally asymptotically stable. This proves the local asymptotic stability of $(K, 0)$ for the original system (1.2) on $\mathcal{C}^+$. On account of the global attractivity of $(K, 0)$ in $\mathcal{C}^+$ proved in Theorem 2.2(ii), this equilibrium is globally asymptotically stable in $\mathcal{C}^+$ when $g(K) > \mu$ and $\tau = \widehat{\tau}$. □

Denote $\mathbb{X}_0 := \{(\phi_1, \phi_2) \in \mathcal{C}^+ : \phi_1 \not\equiv 0 \text{ and } \phi_2 \not\equiv 0\}$ and $\partial\mathbb{X}_0 := \mathcal{C}^+ \backslash \mathbb{X}_0 = \{(\phi_1, \phi_2) \in \mathcal{C}^+ : \phi_1 \equiv 0 \text{ or } \phi_2 \equiv 0\}$. Let M_∂ be the largest positively invariant set in $\partial\mathbb{X}_0$, and $\omega(\phi)$ be the omega limit set of the orbit $\gamma^+(\phi) := \bigcup_{t\geq 0}\{\Theta(t)\phi\}$. Then $M_\partial = \{(\phi_1, \phi_2) \in \mathcal{C}^+ : \phi_2 \equiv 0\}$, and $\omega(\phi) = \{(0, 0), (K, 0)\}$ for all $\phi \in M_\partial$. Introduce a generalized distance function $p : \mathcal{C}^+ \to \mathbb{R}_+$ as

$$p(\phi) = \min_{x\in\bar{\Omega}, i=1,2} \phi_i(x, 0) \text{ for all } \phi = (\phi_1, \phi_2) \in \mathcal{C}^+.$$

Recall that $\Theta(t)$ denotes the solution semiflow of (1.2) on $\mathcal{C}^+$. By strong maximum principle [30,Theorem 2.5], $p(\Theta(t)\phi) > 0$ for all $\phi \in \mathbb{X}_0$. Since $p^{-1}(0, \infty) \subset \mathbb{X}_0$, the condition (P) in [25,Section 3] is satisfied. We have the following uniform persistence result.

Theorem 2.4 *Assume that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$, then there exists an $\eta > 0$ such that for any $\phi \in \mathbb{X}_0$ and $(u(\cdot, t + \cdot), v(\cdot, t + \cdot)) = \Theta(t)\phi$, we have $\liminf_{t\to\infty} u(x, t) \geq \eta$ and $\liminf_{t\to\infty} v(x, t) \geq \eta$ for any $x \in \bar{\Omega}$.*

Proof Denote $W^s((\hat{u}, \hat{v}))$ as the stable manifold of a constant steady state $(\hat{u}, \hat{v})$. We claim that $W^s((0, 0)) \cap p^{-1}(0, \infty) = \emptyset$. Assume to the contrary that there exists $\phi \in \mathcal{C}^+$ with $p(\phi) > 0$ such that $(u(x, t), v(x, t)) \to (0, 0)$ as $t \to \infty$. Hence, for any small $\epsilon_1 > 0$, there exists $t_1 > 0$ such that $0 < u(x, t), v(x, t) < \epsilon_1$ for all $x \in \Omega$ and $t > t_1$. Then the first equation in (1.2) and Proposition 2.1 lead to there exists a constant $c_g > 0$ such that

$$\frac{\partial u(x, t)}{\partial t} > d_1\Delta u(x, t) + b(u(x, t)) - \epsilon_1 c_g u(x, t), \quad x \in \Omega, t > t_1.$$

Note that $b(u) - \epsilon_1 c_g u$ exists a unique positive zero, denoted by $u_* > 0$. Thus, from Lemma 2.2 in [23], the reaction-diffusion equation

$$\frac{\partial w_1(x,t)}{\partial t} = d_1 \Delta w_1(x,t) + b(w_1(x,t)) - \epsilon_1 c_g w_1(x,t), \quad x \in \Omega, t > t_1$$

with Neumann boundary condition admits a unique positive steady state u_*, which is globally asymptotically stable in $C(\bar{\Omega}, \mathbb{R}_+)$. Then the comparison principle implies that $\lim_{t\to\infty} u(x,t) \geq u_* > 0$. This is a contradiction. Thus, $W^s((0,0)) \cap p^{-1}(0,\infty) = \emptyset$.

We now verify $W^s((K,0)) \cap p^{-1}(0,\infty) = \emptyset$. Assume to the contrary that there exists $\phi \in \mathcal{C}^+$ with $p(\phi) > 0$ such that $\lim_{t\to\infty}(u(x,t), v(x,t)) = (K,0)$. Note that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$ imply that we choose a small $\epsilon_2 > 0$ such that $\mu < g(K - \epsilon_2)e^{-s\tau}$. And there exists $t_2 > 0$ such that $u(x,t) > K - \epsilon_2$ for all $x \in \Omega$ and $t > t_2 - \tau$. Then the second equation in (1.2) implies that

$$\frac{\partial v(x,t)}{\partial t} > d_2 \Delta v(x,t) + e^{-s\tau} g(K - \epsilon_2) v(x, t-\tau) - \mu v(x,t), \quad x \in \Omega, t > t_2.$$

Similarly, the comparison principle, $\mu < g(K - \epsilon_2)e^{-s\tau}$, and the above inequality lead to $\lim_{t\to\infty} v(x,t) > 0$. This contradicts to the fact $\lim_{t\to\infty}(u(x,t), v(x,t)) = (K,0)$. Therefore, we have $W^s((\hat{u}, \hat{v})) \cap p^{-1}(0,\infty) = \emptyset$ with $(\hat{u}, \hat{v}) = (0,0)$ or $(K,0)$. By [25,Theorem 3], there exists an $\eta > 0$ such that $\liminf_{t\to\infty} p(\Theta(t)\phi) \geq \eta$ for any $\phi \in \mathcal{C}^+$. □

We now analyze the stability of the positive constant steady state (u^*, v^*). The corresponding characteristic equation is

$$\triangle_n(\lambda, \tau) := \lambda^2 + p_{n,1}\lambda + p_{n,0} + (q_{n,1}\lambda + q_{n,0})e^{-\lambda\tau}, \; n = 0, 1, 2\cdots, \tag{2.6}$$

where

$$\begin{aligned} p_{n,1} &= \delta_n(d_1 + d_2) - b'(u^*) + g'(u^*)v^* + \mu, \quad q_{n,1} = -\mu, \\ p_{n,0} &= (\delta_n d_1 - b'(u^*) + g'(u^*)v^*)(\delta_n d_2 + \mu), \, q_{n,0} = \mu(b'(u^*) - \delta_n d_1). \end{aligned} \tag{2.7}$$

Let $\alpha = g'(u^*)v^* - b'(u^*)$. When $\tau = 0$, the characteristic Eq. (2.6) becomes $\lambda^2 + (p_{n,1} + q_{n,1})\lambda + (p_{n,0} + q_{n,0}) = 0$ for integer $n \geq 0$, where $p_{n,1} + q_{n,1} = \delta_n(d_1 + d_2) + \alpha$ and $p_{n,0} + q_{n,0} = \delta_n^2 d_1 d_2 + \alpha\delta_n d_2 + \mu g'(u^*)v^*$. We obtain the following results on the stability of (u^*, v^*) when $\tau = 0$.

Lemma 2.5 *Assume that $g(K) > \mu$, consider system (1.2) when $\tau = 0$. Then (u^*, v^*) is locally asymptotically stable if $(\mathbf{A}_1)$: $(\frac{b(u)}{g(u)})' \mid_{u^*} < 0$ holds, unstable if $(\mathbf{A}_2)$: $(\frac{b(u)}{g(u)})' \mid_{u^*} > 0$ holds.*

Remark 2.6 If there exists $\widehat{\sigma} \in (0, K)$ such that $(\frac{b(u)}{g(u)})'(u - \widehat{\sigma}) < 0$ for $u \in [0, \widehat{\sigma}) \cup (\widehat{\sigma}, K]$, then $(\mathbf{A}_1)$ holds if and only if $\widehat{\sigma} < u^* < K$, and $(\mathbf{A}_2)$ holds if and only if $0 < u^* < \widehat{\sigma}$.

In the sequel, we assume that $(\mathbf{A}_1)$ holds. Thus a stability change at (u^*, v^*) can only happen when one or more eigenvalues cross the imaginary axis to the right. $(\mathbf{A}_1)$ ensures $\alpha > 0$, which yields $p_{n,0} + q_{n,0} > 0$ for all n, then 0 cannot be an eigenvalue. Therefore, we only need to look for a pair of purely imaginary eigenvalues for some $\tau > 0$. Substituting $\lambda = i\omega$ ($\omega > 0$) into (2.6) and separating the real and imaginary part, we have

$$q_{n,1}\omega \sin\omega\tau + q_{n,0}\cos\omega\tau = \omega^2 - p_{n,0}, \quad q_{n,1}\omega\cos\omega\tau - q_{n,0}\sin\omega\tau = -p_{n,1}\omega, \tag{2.8}$$

for $n = 0, 1, 2 \cdots$. Squaring and adding both equations of (2.8) lead to

$$F_n(\omega, \tau) := \omega^4 + (p_{n,1}^2 - 2p_{n,0} - q_{n,1}^2)\omega^2 + (p_{n,0}^2 - q_{n,0}^2) = 0, \ n = 0, 1, 2 \cdots, \tag{2.9}$$

where

$$p_{n,1}^2 - 2p_{n,0} - q_{n,1}^2 = (d_1^2 + d_2^2)\delta_n^2 + 2\alpha(d_1 + d_2)\delta_n + \alpha^2 > 0,$$
$$p_{n,0} + q_{n,0} > 0, \ p_{n,0} - q_{n,0} = d_1 d_2 \delta_n^2 + 2d_1\mu\delta_n + \alpha d_2 \delta_n + (\alpha - b'(u^*))\mu.$$

Clearly, $p_{n,0} - q_{n,0} > 0$ for all nonnegative integer n if and only if

$$(\mathbf{B}_0) : g'(u^*)/g(u^*) \geq 2b'(u^*)/b(u^*).$$

If $(\mathbf{B}_0)$ is satisfied, then $F_n(\omega, \tau)$ has no positive zeros, and $(\mathbf{A}_1)$ holds. Thus, all eigenvalues stay in the open left-half complex plane. Consequently, we have the following result on the stability of (u^*, v^*)

Theorem 2.7 *Assume that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$. Then (u^*, v^*) of (1.2) is locally asymptotically stable if $(\boldsymbol{B}_0)$ holds.*

3 Heterogeneous Steady States and Steady State Bifurcations

In this section, we will establish the existence of positive heterogeneous steady state via Leray–Schauder degree theory [7], and investigate the steady state bifurcation of (1.2) bifurcating from the positive constant steady state (u^*, v^*). Note that the steady state of (1.2) satisfies the following elliptic equations:

$$\begin{aligned} &-d_1\Delta u(x) = b(u(x)) - g(u(x))v(x), \quad x \in \Omega, \\ &-d_2\Delta v(x) = e^{-s\tau}g(u(x))v(x) - \mu v(x), \quad x \in \Omega, \\ &u_\nu = v_\nu = 0, \quad x \in \partial\Omega. \end{aligned} \tag{3.1}$$

On account of Theorem 2.2(ii), a positive heterogeneous steady state exists only if $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$. Throughout this section, we assume these necessary conditions hold. We claim that any nonnegative steady state (u, v) other than $(K, 0)$ and $(0, 0)$ should be positive; namely, $u(x) > 0$ and $v(x) > 0$ for all $x \in \overline{\Omega}$. Assume $v(x_0) = 0$ for some $x_0 \in \overline{\Omega}$. The strong maximum principle implies that $v(x) \equiv 0$, and hence

$$0 \geq \int_\Omega (u - K)b(u)dx = \int_\Omega -(u - K)d_1\Delta u dx = d_1 \int_\Omega |\nabla(u - K)|^2 dx \geq 0.$$

Consequently, $u(x) \equiv 0$ or $u(x) \equiv K$. Now, we assume $v(x) > 0$ for all $x \in \overline{\Omega}$. It follows from strong maximum principle that $u(x) > 0$ for all $x \in \overline{\Omega}$. In particular, all nonnegative heterogeneous steady states are positive.

We next show that all positive steady states are bounded from above and below by some positive constants independent of steady states.

Theorem 3.1 *Assume that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$. There exist two positive constants $\underline{M}$ and $\overline{M}$, depending on $d_1, d_2, \mu, K, b, g, \Omega$, such that $\underline{M} \leq u(x), v(x) \leq \overline{M}$ for all $x \in \overline{\Omega}$, where $(u(x), v(x))$ is any positive solution of (3.1).*

Proof Since $-d_1\Delta u \leq b(u)$, we obtain from [16,Lemma 2.3] that $u(x) \leq K$ for all $x \in \overline{\Omega}$. Adding the two equations in (3.1) gives $-\Delta(d_1 u + d_2 v) \leq C - (\mu/d_2)(d_1 u + d_2 v)$, where

$C = \max_{[0,K]} b(u) + d_1 K\mu/d_2 > 0$ is a constant depending only on model parameters. It then follows from [16,Lemma 2.3] that u and v are bounded above by a positive constant $\overline{M} = C/\mu + K$.

Next, we want to show that $\|u\|_\infty$ and $\|v\|_\infty$ are bounded below by a positive constant independent of the solution. Assume to the contrary that there exist a sequence of positive steady states (u_n, v_n) such that either $\|u_n\|_\infty \to 0$ or $\|v_n\|_\infty \to 0$ as $n \to \infty$. An integration of the second equation in (3.1) yields

$$\int_\Omega v_n(x)(e^{-s\tau} g(u_n(x)) - \mu)dx = 0. \tag{3.2}$$

If $\|u_n\|_\infty \to 0$ as $n \to \infty$, then there exists a large n such that $e^{-s\tau} g(u_n(x)) - \mu < -\mu/2$, and the integral on the left-hand side of the above equation is negative, a contradiction. Thus, we have $\|v_n\|_\infty \to 0$ as $n \to \infty$. Upon extracting a subsequence, we may assume without loss of generality that (u_n, v_n) converges to a nonnegative steady state $(u_\infty, 0)$ as $n \to \infty$. According to the argument at the beginning of this section, we have either $u_\infty \equiv 0$ or $u_\infty \equiv K$. Since $\|u_n\|_\infty \to 0$ would lead to a contradiction, we obtain $u_\infty \equiv K$ and hence $\lim_{n\to\infty} e^{-s\tau} g(u_n(x)) - \mu = e^{-s\tau} g(K) - \mu > 0$, which again contradicts to the equation (3.2). Therefore, we have proved that $\|u\|_\infty$ and $\|v\|_\infty$ are bounded below by a positive constant independent of the solution. Finally, we obtain from Harnack's inequality (c.f. [16,Lemma 2.2] or [3,Corollary 3.11]) that both $u(x)$ and $v(x)$ are uniformly bounded below by a positive constant $\underline{M}$ independent of the steady state. □

3.1 Nonexistence of Positive Heterogeneous Steady States

In this subsection, we prove nonexistence of positive heterogeneous steady states of system (1.2) when the diffusion rates d_1 and d_2 are sufficiently large.

Theorem 3.2 *Assume that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$. There exists a positive constant d^* that depends on μ, K, b, g, Ω and δ_1, such that if* $\min\{d_1, d_2\} > d^*$, *then system* (1.2) *has no positive heterogeneous steady states.*

Proof Let (u, v) be a positive solution of system (3.1). Denote the averages of the solution on Ω by

$$\overline{u} = \frac{1}{|\Omega|}\int_\Omega u dx, \quad \overline{v} = \frac{1}{|\Omega|}\int_\Omega v dx.$$

Recall from the proof of Theorem 2.7 that $u(x) \le K$. Integrating the equations in (3.1) gives

$$\overline{v} = \frac{e^{-s\tau}}{\mu|\Omega|}\int_\Omega b(u(x))dx \le \frac{e^{-s\tau}}{\mu} \max_{0\le u\le K} b(u) := M_v.$$

We then obtain from (3.1) and $\int_\Omega [u(x)-\overline{u}]dx = \int_\Omega [v(x)-\overline{v}]dx = 0$ that allowdisplaybreaks

$$\begin{aligned} d_1 \int_\Omega |\nabla(u-\overline{u})|^2 dx &= \int_\Omega (u-\overline{u})(b(u)-g(u)v)dx \\ &= \int_\Omega (b(u)-b(\overline{u}))(u-\overline{u})dx + \int_\Omega (g(\overline{u})\overline{v}-g(u)v)(u-\overline{u})dx \\ &\le \left(\max_{[0,K]} b'(u) + \frac{g(K)^2}{2}\right)\int_\Omega (u-\overline{u})^2 dx + \frac{1}{2}\int_\Omega (v-\overline{v})^2 dx, \\ d_2 \int_\Omega |\nabla(v-\overline{v})|^2 dx &= \int_\Omega (v-\overline{v})\left(e^{-s\tau} g(u)v - \mu v\right) dx \\ &= \int_\Omega e^{-s\tau}(v-\overline{v})\left(g(u)v - g(\overline{u})\overline{v}\right) dx - \int_\Omega (\mu v - \mu\overline{v})(v-\overline{v})dx \\ &\le \frac{(\max_{[0,K]} g'(u))^2}{2}\int_\Omega (u-\overline{u})^2 dx + \left(g(K)+\frac{M_v^2}{2}\right)\int_\Omega (v-\overline{v})^2 dx. \end{aligned}$$

Let $M_1 = \max_{[0,K]} b'(u) + (g(K)^2 + (\max_{[0,K]} g'(u))^2)/2$, and $M_2 = g(K) + (M_v^2+1)/2$. By Poincaré's inequality, we have

$$d_1 \int_\Omega |\nabla(u-\overline{u})|^2 dx + d_2 \int_\Omega |\nabla(v-\overline{v})|^2 dx \le d^* \int_\Omega [|\nabla(u-\overline{u})|^2 + |\nabla(v-\overline{v})|^2] dx,$$

where $d^* = \max\{M_1/\delta_1, M_2/\delta_1\}$ is a positive constant depending on μ, K, b, g, Ω and δ_1. If (u, v) is a positive heterogeneous steady state, then $\min\{d_1, d_2\} \le d^*$. This completes the proof. □

3.2 Existence of Positive Heterogeneous Steady States

In this subsection, we will use Leray–Schauder degree theory to find sufficient conditions for the existence of positive heterogeneous solutions of system (3.1). Let $d^* > 0$ be given as in Theorem 3.2. For each homotopy parameter $r \in [0, 1]$, we consider the elliptic equations

$$\begin{aligned} &-[(1-r)d_1 + 2rd^*]\Delta u(x) = b(u(x)) - g(u(x))v(x), \quad x \in \Omega, \\ &-[(1-r)d_2 + 2rd^*]\Delta v(x) = e^{-s\tau} g(u(x))v(x) - \mu v(x), \quad x \in \Omega, \\ &u_\nu = v_\nu = 0, \quad x \in \partial\Omega. \end{aligned} \tag{3.3}$$

Using a similar argument as in the proof of Theorem 3.1, we can find two positive constants, still denoted by $\underline{M}$ and $\overline{M}$, which depend on d^*, d_1, d_2, μ, K, b, g, Ω, such that any positive solution of the above equations is bounded by these two constants: $\underline{M} \le u(x), v(x) \le \overline{M}$ for all $x \in \overline{\Omega}$. It is noted that $\underline{M}$ and $\overline{M}$ are independent of the homotopy parameter $r \in [0, 1]$. Now, we can regard the solution of (3.3) as a fixed point of the map

$$\mathcal{F}(r): \begin{pmatrix} u \\ v \end{pmatrix} \mapsto \begin{pmatrix} (I-\Delta)^{-1}\{u + [b(u) - g(u)v]/[(1-r)d_1 + 2rd^*]\} \\ (I-\Delta)^{-1}\{v + [e^{-s\tau} g(u)v - \mu v]/[(1-r)d_2 + 2rd^*]\} \end{pmatrix},$$

which is compact on the function space $\mathbf{X} = \{(u, v) : u, v \in C^1(\overline{\Omega}), u_\nu = v_\nu = 0 \text{ on } \partial\Omega\}$. Let U be an open subset of $\mathbf{X}$ defined as

$$U = \{(u, v) \in \mathbf{X} : \underline{M}/2 < u(x), v(x) < 2\overline{M} \text{ for } x \in \overline{\Omega}\},$$

such that, for each $r \in [0, 1]$, the map $\mathcal{F}(r)$ does not possess any fixed point on the boundary ∂U. In view of Theorem 3.2, the positive constant steady state (u^*, v^*) defined in (2.2) is the unique fixed point of the map $\mathcal{F}(1)$ in U. It then follows from the homotopy invariance of Leray–Schauder degree that

$$\deg(I - \mathcal{F}(0), U, 0) = \deg(I - \mathcal{F}(1), U, 0) = 1. \tag{3.4}$$

If $\mathcal{F}(0)$ does not possess any heterogeneous fixed point in U, then (u^*, v^*) is the unique fixed point of $\mathcal{F}(0)$ in U. Linearizing $\mathcal{F}(0)$ about the fixed point (u^*, v^*) gives

$$\mathcal{L} = \begin{pmatrix} (I-\Delta)^{-1} & 0 \\ 0 & (I-\Delta)^{-1} \end{pmatrix} \begin{pmatrix} 1 + [b'(u^*) - g'(u^*)v^*]/d_1 & -g(u^*)/d_1 \\ e^{-s\tau} g'(u^*)v^*/d_2 & 1 \end{pmatrix}.$$

Recall from (2.4) that $0 = \delta_0 < \delta_1 < \cdots$ are the eigenvalues of $-\Delta$ in Ω with Neumann boundary condition. For each $j \in \mathbb{N}$, we let m_j be the multiplicity of δ_j, and $\lambda_j^\pm$ be the eigenvalues of the matrix

$$M_j = \begin{pmatrix} [b'(u^*) - g'(u^*)v^*]/d_1 - \delta_j & -g(u^*)/d_1 \\ e^{-s\tau} g'(u^*)v^*/d_2 & -\delta_j \end{pmatrix}. \tag{3.5}$$

Introduce a quadratic function

$$h(\delta) = \delta^2 - \frac{b'(u^*) - g'(u^*)v^*}{d_1}\delta + \frac{e^{-s\tau} g(u^*)g'(u^*)v^*}{d_1 d_2}. \tag{3.6}$$

It is readily seen that the determinant of M_j is $h(\delta_j)$. By a simple calculation, we find that the eigenvalues of $\mathcal{L} - I$ are $\lambda_j^\pm/(1 + \delta_j)$ with $j = 0, 1, \cdots$. According to [14,Theorem 2.8.1], the Leray–Schauder degree for an isolated fixed point has the following expression

$$\deg(I - \mathcal{F}(0), U, 0) = (-1)^\gamma = (-1)^{\sum_{j \in J} m_j}, \tag{3.7}$$

where γ is the number of positive eigenvalues (counting multiplicities) of $\mathcal{L} - I$, and J is collection of indices $j \in \mathbb{N}$ when the matrix M_j has exactly one simple positive eigenvalue; or equivalently, either (i) $h(\delta_j) < 0$ or (ii) $h(\delta_j) = 0$ and $2\delta_j < [b'(u^*) - g'(u^*)v^*]/d_1$. Since $g'(u) > 0$ for all $u \geq 0$ by ($\mathbf{H}_2$), we have $h(0) > 0$. If $h(\delta)$ does not possess two distinct positive roots, then J is empty and $\deg(I - \mathcal{F}(0), U, 0) = 1$. Now, we assume that

$$\frac{b'(u^*) - g'(u^*)v^*}{2d_1} > \sqrt{\frac{e^{-s\tau} g(u^*)g'(u^*)v^*}{d_1 d_2}}; \tag{3.8}$$

namely, the quadratic equation $h(\delta) = 0$ has two distinct positive roots, denoted by $\delta^- < \delta^+$. We have the following result on the existence of positive heterogeneous steady state.

Theorem 3.3 *Assume that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$. Let (u^*, v^*) be the positive constant steady state defined in (2.2). Assume the inequality (3.8) holds, and denote by $\delta^- < \delta^+$ the two distinct positive roots of the quadratic function $h(\delta)$ defined in (3.6). Let $0 = \delta_0 < \delta_1 < \cdots$ be the eigenvalues of $-\Delta$ in Ω with Neumann boundary condition given in (2.4). The multiplicities of these eigenvalues are denoted by $m_1, m_2, \cdots$. There exist $j, k \in \mathbb{N}$ such that $\delta_j < \delta^- \leq \delta_{j+1} \leq \delta_k < \delta^+ \leq \delta_{k+1}$. If $\sum_{l=j+1}^{k} m_l$ is odd, then system (1.2) possesses at least one positive heterogeneous solution.*

Proof Note that $h(\delta_l) < 0$ if $j+1 < l \leq k$ and $h(\delta_l) > 0$ if $l \leq j$ or $l > k+1$. For $l = k+1$, either (i) $h(\delta_l) > 0$ or (ii) $h(\delta_l) = 0$ and $2\delta_l > [b'(u^*) - g'(u^*)v^*]/d_1$. For $l = j+1$, either (i) $h(\delta_l) < 0$ or (ii) $h(\delta_l) = 0$ and $2\delta_l < [b'(u^*) - g'(u^*)v^*]/d_1$. Hence, the matrix M_j

defined in (3.5) has exactly one simple positive eigenvalue if and only if $j+1 \le l \le k$; namely, the set $J = \{j+1, \cdots, k\}$.

Now we assume to the contrary that system (3.1) has no positive heterogeneous solution. We obtain from (3.4) and (3.7) that

$$1 = \deg(I - \mathcal{F}(0), U, 0) = (-1)^{\sum_{l=j+1}^{k} m_l} = -1,$$

a contradiction. This completes the proof. □

To conclude this subsection, we present the following corollary with intervals of d_2 on which the positive heterogeneous solutions exist.

Corollary 3.4 *Assume that $g(K) > \mu$, $\tau \in [0, \widehat{\tau})$, and $[b'(u^*) - g'(u^*)v^*]/d_1 \in (\delta_l, \delta_{l+1})$ for some $l \ge 2$. Assume further that the multiplicity m_j is odd for all $j \le l$. We rearrange the finite set*

$$\left\{ \frac{e^{-s\tau} g(u^*) g'(u^*) v^*}{[b'(u^*) - g'(u^*)v^*]\delta_j - d_1 \delta_j^2} \right\}_{j=1}^{l}$$

in increasing order and denote the elements as $d_{2,1} < \cdots < d_{2,l}$. Then system (3.1) possesses at least one positive heterogeneous solution if $d_2 \in \bigcup_{1 \le k \le l/2} (d_{2,2k-1}, d_{2,2k})$.

3.3 Steady State Bifurcations

In this subsection, we choose $u^* := \sigma$ to be the bifurcation parameter and investigate the nonconstant positive steady state bifurcating from (u^*, v^*) via the method developed in [20]. In addition to $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$, we shall make the following assumptions:

($\mathbf{S}_0$) There exists $\widehat{\sigma} \in (0, K)$ such that $(\frac{b(u)}{g(u)})'(u - \widehat{\sigma}) < 0$ for $u \in [0, \widehat{\sigma}) \cup (\widehat{\sigma}, K]$.
($\mathbf{S}_1$) All eigenvalues δ_i in (2.4) are simple for $i \ge 0$.

Let $(\hat{u}, \hat{v})^T = (u - u^*, v - v^*)^T$, and dropping $\hat{\cdot}$, system (3.1) can be rewritten in the abstract form

$$\mathcal{F}(\sigma, u, v) := \begin{pmatrix} d_1 \Delta u + b(u+\sigma) - g(u+\sigma)(v + \frac{b(\sigma)}{g(\sigma)}) \\ d_2 \Delta v + (\frac{\mu g(u+\sigma)}{g(\sigma)} - \mu)(v + \frac{b(\sigma)}{g(\sigma)}) \end{pmatrix} = 0, \ \ (\sigma, u, v) \in \mathbb{R}^+ \times \mathcal{X},$$

where $\mathcal{X} = \{(u, v) : u, v \in H^2(\Omega), u_\nu = v_\nu = 0 \text{ on } \partial\Omega\}$. The Fréchet derivative of $\mathcal{F}$ is

$$D_{(u,v)}\mathcal{F}(\sigma, 0, 0) = \mathrm{L}(\sigma) = \begin{pmatrix} d_1 \Delta - \alpha(\sigma), & -g(\sigma) \\ \mu b(\sigma) \frac{g'(\sigma)}{g^2(\sigma)}, & d_2 \Delta \end{pmatrix},$$

where L is the linearization operator at (u^*, v^*) for (1.2) and

$$\alpha(\sigma) = \frac{b(\sigma) g'(\sigma)}{g(\sigma)} - b'(\sigma) = -g(\sigma) \left(\frac{b(\sigma)}{g(\sigma)} \right)'.$$

It follows from ($\mathbf{S}_0$) and ($\mathbf{H}_2$) that $\alpha(0) = \alpha(\widehat{\sigma}) = 0$; $\alpha(\sigma) < 0$ for $\sigma \in (0, \widehat{\sigma})$, $\alpha(\sigma) > 0$ for $\sigma > \widehat{\sigma}$; $\alpha'(0) = -g'(0)(\frac{b}{g})'(0) < 0$ and $\alpha'(\widehat{\sigma}) = -g(\widehat{\sigma})(\frac{b}{g})''(\widehat{\sigma}) > 0$. The characteristic equation of L is

$$\lambda^2 + T_i(\sigma)\lambda + D_i(\sigma) = 0, \ \ i = 0, 1, 2, \cdots, \text{ with}$$
$$T_i(\sigma) = (d_1 + d_2)\delta_i + \alpha(\sigma), \ \ D_i(\sigma) = d_1 d_2 \delta_i^2 + d_2 \alpha(\sigma) \delta_i + \mu \frac{b(\sigma) g'(\sigma)}{g(\sigma)}.$$

Similar to [20, 32], we define steady state bifurcation values σ_0 by the condition.

(**H**) there exists integer $i \geq 0$ such that $D_i(\sigma_0) = 0$, $T_i(\sigma_0) \neq 0$, $\frac{dD_i(\sigma_0)}{d\sigma} \neq 0$, and $D_j(\sigma_0) \neq 0$, $T_j(\sigma_0) \neq 0$ for $j \neq i$.

The steady state bifurcation curve is defined by the following equation:

$$\{(\sigma, p) \in \mathbb{R}_+^2 : D(\sigma, p) := d_1 d_2 p^2 + d_2 \alpha(\sigma) p + \mu \frac{b(\sigma) g'(\sigma)}{g(\sigma)} = 0\};$$

or equivalently,

$$p = p_\pm(\sigma) := \frac{-d_2\alpha(\sigma) \pm \sqrt{d_2(q(\sigma)d_2 - 4d_1\mu)\frac{b(\sigma)g'(\sigma)}{g(\sigma)}}}{2d_1 d_2}, \; q(\sigma) = \frac{\alpha^2(\sigma) g(\sigma)}{b(\sigma) g'(\sigma)}. \tag{3.9}$$

Note that $D(\sigma, p)$ has no critical points in $\mathbb{R}_+^2$. Thus, the steady state bifurcation curve is a bounded connected smooth curve. Since $\frac{b(0)}{g(0)} = \lim\limits_{u \to 0} \frac{b(u)}{g(u)} = \frac{b'(0)}{g'(0)} > 0$, it follows from the profile of $\alpha(\sigma)$ that

$$q(0) = q(\widehat{\sigma}) = 0, q(\sigma) > 0 \text{ in } (0, \widehat{\sigma}), q'(0) > 0, q'(\widehat{\sigma}) < 0, \exists\, \widetilde{\sigma} \in (0, \widehat{\sigma}) \text{ s.t. } q(\widetilde{\sigma}) = \max_{[0,\widehat{\sigma}]} q(\sigma).$$

Thus, the equation $q(\sigma)d_2 - 4d_1\mu = 0$ has at least two different roots, denoted by $\sigma^- < \sigma^+$ in $(0, \widehat{\sigma})$. Hence, $p_\pm(\sigma) > 0$ only for $\sigma \in \Sigma_0 := \{\sigma \in [\sigma^-, \sigma^+] : q(\sigma) \geq 4d_1\mu/d_2\}$. We summarize the result on $p_\pm(\sigma)$ in the following lemma.

Lemma 3.5 *Assume that $g(K) > \mu$, $\tau \in [0, \widehat{\tau})$ and $(\boldsymbol{S}_0)$ hold. Denote $M_* := \min\limits_{\Sigma_0} p_-(\sigma)$, $M^* := \min\limits_{\Sigma_0} p_+(\sigma)$. Let $p_\pm(\sigma)$ and $q(\sigma)$ be defined as in (3.9).*

(i) *There exist $0 < \sigma^- < \sigma^+ < \widehat{\sigma}$ such that $p_+(\sigma) \geq p_-(\sigma) > 0$ for $\sigma \in \Sigma_0$, and $\lim\limits_{\sigma \to \sigma^-} p_\pm(\sigma) = -\frac{\alpha(\sigma^-)}{2d_1}$, $\lim\limits_{\sigma \to \sigma^+} p_\pm(\sigma) = -\frac{\alpha(\sigma^+)}{2d_1}$. Moreover, the steady state bifurcation occurs only for $p \in [M_*, M^*]$.*

(ii) *If we further assume that $q''(\sigma) \leq 0$ in $(0, \widehat{\sigma})$, then $\Sigma_0 = [\sigma^-, \sigma^+]$, and the steady state bifurcation curve $\{(\sigma, p) \in \mathbb{R}_+^2 : D(\sigma, p) = 0\}$ is a smooth closed loop connecting $(\sigma^-, -\frac{\alpha(\sigma^-)}{2d_1})$ and $(\sigma^+, -\frac{\alpha(\sigma^+)}{2d_1})$.*

Since $\delta_0 = 0$, we have $D_0(\sigma) > 0$ and $T_0(\sigma) = \alpha(\sigma) < 0$ for $\sigma \in (0, \widehat{\sigma})$. Thus we only need to find the integer $i \geq 1$ such that (**H**) is satisfied for $\sigma \in [\sigma^-, \sigma^+]$. Lemma 3.5 implies that $D_i(\sigma) \neq 0$ in $[\sigma^-, \sigma^+]$ if $\delta_i \in (-\infty, M_*) \cup (M^*, \infty)$; for any $\delta_i \in [M_*, M^*]$, there exists at least two $\sigma_{i,1}^S, \sigma_{i,2}^S$ such that $D(\sigma_{i,k}^S, \delta_i) = D_i(\sigma_{i,k}^S) = 0$ with $k = 1, 2$, and these $\sigma_{i,k}^S$ are possible steady state bifurcation points.

Next, we verify the transversality condition. Substituting $p_\pm(\sigma)$ into $D(\sigma, p) = 0$ and taking the derivative with respect to σ, we obtain

$$p'_\pm(\sigma_i^S) = -\frac{\partial D(\sigma_i^S, p_\pm(\sigma_i^S))/\partial\sigma}{d_2(2d_1 p_\pm(\sigma_i^S) + \alpha(\sigma_i^S))} = -\frac{dD_i(\sigma_i^S)/d\sigma}{d_2(2d_1 p_\pm(\sigma_i^S) + \alpha(\sigma_i^S))}.$$

If we further assume that $q''(\sigma) \leq 0$ in $(0, \widehat{\sigma})$, then $p_\pm(\sigma_i^S) \neq \frac{-\alpha(\sigma_i^S)}{2d_1}$ for $\sigma_i^S \in (\sigma^-, \sigma^+)$. Therefore, if $p'_\pm(\sigma_i^S) \neq 0$, then $\frac{dD_i(\sigma_i^S)}{d\sigma} \neq 0$ for $\sigma_i^S \in (\sigma^-, \sigma^+)$.

Summarizing the above analysis and using local steady state bifurcation results in [32,Theorem 3.2], we obtain the existence of the local bifurcation of steady state solutions. For the global steady state bifurcation, we apply Theorem 4.3 in [20] and further use a similar argument as in the proof of Theorem 4.4 in [27] to obtain the global existence of steady state solutions.

Theorem 3.6 *Assume that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$, $q''(\sigma) \leq 0$ in $(0, \widehat{\sigma})$, $(\boldsymbol{S}_0)$-$(\boldsymbol{S}_1)$ and*

($\boldsymbol{S}_2$) *There exist integers $k > l \geq 1$ such that $\delta_{l-1} < M_* \leq \delta_l < \cdots < \delta_k \leq M^* < \delta_{k+1}$, where M_* and M^* are defined in Lemma 3.5.*

Define $\{\sigma \in (\sigma^-, \sigma^+) : p_\pm(\sigma) = \delta_\iota$ for integer $l \leq \iota \leq k\} := \{\sigma_i^S : 1 \leq i \leq 2(k-l+1)\}$ with decreasing order: $\sigma^- < \sigma^S_{2(k-l+1)} \leq \cdots \leq \sigma_2^S \leq \sigma_1^S < \sigma^+$. We suppose that $\sigma_i^S \neq \sigma_j^S$, $p'_\pm(\sigma_i^S) \neq 0$, $\delta_n \neq -\frac{\alpha(\sigma_i^S)}{d_1+d_2}$ for any integers $i, j \in [1, 2(k-l+1)]$ and $n \geq 1$. Then for integer $i \in [1, 2(k-l+1)]$,

- (i) *there is a smooth curve Γ_i of positive solutions of (3.1) bifurcating from $(\sigma, u, v) = (\sigma_i^S, \sigma_i^S, v(\sigma_i^S))$ with $\Gamma_i \subseteq \mathbf{Q}_i$, where $\mathbf{Q}_i$ is a global branch of positive solutions of (3.1), and $v(\sigma) = \frac{b(\sigma)}{g(\sigma)}$;*
- (ii) *near $(\sigma, u, v) = (\sigma_i^S, \sigma_i^S, v(\sigma_i^S))$, $\Gamma_i = \{(\sigma_i(w), u_i(w), v_i(w)) : w \in (-\epsilon, \epsilon)\}$, where $u_i(w) = \sigma_i^S + w a_i \phi_i(x) + w\psi_{1,i}(w)$, $v_i(w) = \sigma_i^S + w b_i \phi_i(x) + \theta\psi_{2,i}(w)$ for some smooth functions $\sigma_i, \psi_{1,i}, \psi_{2,i}$ such that $\sigma_i(0) = \sigma_i^S$, $\psi_{1,i}(0) = \psi_{2,i}(0) = 0$ and (a_i, b_i) satisfies $\mathrm{L}(\sigma_i^S)[(a_i, b_i)^T\phi_i(x)] = (0, 0)^T$;*
- (iii) *either $\mathbf{Q}_i$ contains another $(\sigma_j^S, \sigma_j^S, v(\sigma_j^S))$ for integer $j \in [1, 2(k-l+1)]$ and $j \neq i$, or $\mathbf{Q}_i$ is not compact.*

4 Hopf Bifurcation Analysis

In this section, using the delay $\tau > 0$ as the bifurcation parameter, we analyze patterned solutions of (1.2) bifurcating from the positive constant steady state (u^*, v^*), which include spatially homogeneous and nonhomogeneous periodic orbits. In the sequel, we assume that $g(K) > \mu$, $\tau \in [0, \widehat{\tau})$, $(\mathbf{A}_1)$ and $(\mathbf{S}_1)$ hold, which implies that the local stability of (u^*, v^*) for system (1.2) without delay.

4.1 Existence of Hopf Bifurcations

To identify Hopf bifurcation value τ^*, we study the existence of a pair of purely imaginary eigenvalues of (2.6) for some $\tau^* > 0$. Recall from Sect. 2, a pair of purely imaginary eigenvalues exist only if $F_n(\omega, \tau)$ in (2.9) has positive zeros for some integer $n \geq 0$. We know that $F_n(\omega, \tau) = 0$ has a unique positive root if and only if $p_{n,0} < q_{n,0}$ for integer $n \geq 0$. Clearly, $F_0(\omega, \tau)$ has exactly one positive root ω_0 if and only if

$$(\mathbf{B}_1) : g'(u^*)/g(u^*) < 2b'(u^*)/b(u^*).$$

To ensure the existence of positive zeros of $F_n(\omega, \tau)$ for some integer $n \geq 0$, we assume that $(\mathbf{B}_1)$ is satisfied in this section.

If $p_{n,0} < q_{n,0}$ for some integer $n \geq 0$, the implicit function theorem implies that there exists a unique C^1 function

$$\omega_n(\tau) = \left(\left[q_{n,1}^2 + 2p_{n,0} - p_{n,1}^2 + \sqrt{(p_{n,1}^2 - 2p_{n,0} - q_{n,1}^2)^2 - 4(p_{n,0}^2 - q_{n,0}^2)}\right]/2\right)^{1/2}$$

such that $F_n(\omega_n(\tau), \tau) = 0$ for $\tau \in [0, \widehat{\tau})$. Set

$$I_n = \{\tau : 0 \leq \tau < \widehat{\tau} \text{ satisfies } p_{n,0} < q_{n,0}\}. \tag{4.1}$$

It follows from ($\mathbf{B}_1$)-($\mathbf{S}_1$) that there exists a integer $N_1 \geq 0$, such that $I_{N_1} \neq \emptyset$, $I_n = \emptyset$ for $n \geq N_1 + 1$, and $I_{N_1} \subset I_{N_1-1} \subset \cdots \subset I_1 \subset I_0$. For $i\omega_n(\tau)$ to be a purely imaginary eigenvalue of (2.6), $\omega_n(\tau)$ needs to satisfy the system

$$\begin{aligned} \sin(\omega_n(\tau)\tau) &= \frac{\omega_n(-\mu\omega_n^2 + p_{n,1}q_{n,0} + \mu p_{n,0})}{\mu^2\omega_n^2 + q_{n,0}^2} := g_{n,1}(\tau), \\ \cos(\omega_n(\tau)\tau) &= \frac{(q_{n,0} + \mu p_{n,1})\omega_n^2 - p_{n,0}q_{n,0}}{\mu^2\omega_n^2 + q_{n,0}^2} := g_{n,2}(\tau), \end{aligned} \tag{4.2}$$

for integer $n \geq 0$. For $\tau \in I_n$, let $\theta_n(\tau)$ be the unique solution of $\sin\theta_n(\tau) = g_{n,1}(\tau)$ and $\cos\theta_n(\tau) = g_{n,2}(\tau)$ in $(0, 2\pi]$, that is,

$$\theta_n(\tau) = \begin{cases} \arccos g_{n,2}(\tau), & \text{if } \omega_n^2(\tau) < p_{n,0} + p_{n,1}q_{n,0}/\mu, \\ 2\pi - \arccos g_{n,2}(\tau), & \text{if } \omega_n^2(\tau) \geq p_{n,0} + p_{n,1}q_{n,0}/\mu. \end{cases}$$

According to Beretta and Kuang [2], we define

$$S_n^k(\tau) = \tau\omega_n(\tau) - (\theta_n(\tau) + 2k\pi) \text{ for } \tau \in I_n \text{ with integer } k \geq 0. \tag{4.3}$$

One can check that, for integer $0 \leq n \leq N_1$, $\pm i\omega_n(\tau_n^*)$ are a pair of purely imaginary eigenvalues of $\triangle_n(\lambda, \tau) = 0$ if and only if τ_n^* is the zero of $S_n^k(\tau)$ for some integer $k \geq 0$. Obviously, for integer $0 \leq n \leq N_1$, we have $S_n^k(\tau) > S_n^{k+1}(\tau)$ for $\tau \in I_n$ and integer $k \geq 0$; when $\tau = 0$, the asymptotic stability of (u^*, v^*) implies that $S_0^0(0) < 0$. Denote

$$\widehat{\tau}_n = \sup I_n := \sup\{\tau : 0 \leq \tau < \widehat{\tau} \text{ satisfies } p_{n,0} < q_{n,0}\} \text{ for integer } 0 \leq n \leq N_1. \tag{4.4}$$

Note that $\lim\limits_{\tau \to \widehat{\tau}^-} (p_{0,0}(\tau) - q_{0,0}(\tau)) > 0$, and $p_{n,0} - q_{n,0}$ is increasing w.r.t n, which implies that $\widehat{\tau}_n < \widehat{\tau}$, $\widehat{\tau}_n$ is decreasing w.r.t n, and $p_{0,0}(\widehat{\tau}_n) - q_{0,0}(\widehat{\tau}_n) = 0$. Hence, $\omega_n(\tau) \to 0$ as $\tau \to \widehat{\tau}_n^-$. This, together with (4.2), yields $\lim\limits_{\tau \to \widehat{\tau}_n^-} \sin\theta_n(\tau) = 0$ and $\lim\limits_{\tau \to \widehat{\tau}_n^-} \cos\theta_n(\tau) = -1$. Thus we have $\lim\limits_{\tau \to \widehat{\tau}_n^-} \theta_n(\tau) = \pi$, and $\lim\limits_{\tau \to \widehat{\tau}_n^-} S_n^k(\tau) = -(2k+1)\pi < 0$.

Note from (2.9) that F_n is an increasing function of ω and δ_n. Consider ω_n as a function of δ_n. It follows from implicit differentiation that $\omega_n' < 0$. In particular, $\omega_j(\tau) > \omega_{j+1}(\tau)$ for any $0 \leq j \leq N_1 - 1$ and $\tau \in I_{j+1}$. Next, we observe from (4.2) that

$$q_{n,0}g_{n,2} - \mu\omega_n g_{n,1} = w_n^2 - p_{n,0}, \quad q_{n,0}g_{n,1} + \mu\omega_n g_{n,2} = \omega_n p_{n,1},$$

where $g_{n,1} = \sin\theta_n$ and $g_{n,2} = \cos\theta_n$. We regard $p_{n,0}, q_{n,0}, w_n, \theta_n$ as functions of δ_n and take derivative on both sides of the first equation. It follows the second equation that

$$\theta_n' = \frac{-2w_n w_n' + p_{n,0}' + q_{n,0}'\cos\theta_n - \mu\omega_n'\sin\theta_n}{q_{n,0}\sin\theta_n + \mu\omega_n\cos\theta_n} = \frac{-2w_n w_n' + p_{n,0}' + q_{n,0}'\cos\theta_n - \mu\omega_n'\sin\theta_n}{\omega_n p_{n,1}}.$$

Recall that the assumption ($\mathbf{A}_1$) implies $p_{n,1} > \mu$ and the assumption ($\mathbf{B}_1$) implies $q_{n,0} > p_{n,0} > 0$. Hence, we have $q_{n,0}\sin\theta_n = \omega_n(p_{n,1} - \mu\cos\theta_n) > 0$ and $\sin\theta_n > 0$. Moreover, we obtain from (2.7) and ($\mathbf{A}_1$) that $p'_{n,0} > |q'_{n,0}| > -q_{n,0}\cos\theta_n$. Combining these results gives $\theta'_n > 0$. In particular, $\theta_j(\tau) < \theta_{j+1}(\tau)$ for $\tau \in I_{j+1}$. Finally, it follows from the definition of $S_n^k(\tau)$ in (4.3) that $S_{n+1}^k < S_n^k$ for $\tau \in I_{n+1}$.

From [2,Theorem 2.2], we obtain

$$\mathrm{Sign}\left(\frac{dRe\lambda(\tau)}{d\tau}|_{\tau=\tau_n^*}\right) = \mathrm{Sign}\left(\frac{\partial F_n}{\partial\omega}(\omega_n(\tau_n^*), \tau_n^*)\right)\mathrm{Sign}\left(\frac{dS_n^k(\tau_n^*)}{d\tau}\right).$$

Note that $\frac{\partial F_n}{\partial\omega} > 0$ for any integer $n \geq 0$. To summarize, we have the following lemma about the property of $S_n^k(\tau)$ and the transversality condition.

Lemma 4.1 *Assume that $g(K) > \mu$, $\tau \in [0, \widehat{\tau})$, ($\boldsymbol{A}_1$), ($\boldsymbol{B}_1$) and ($\boldsymbol{S}_1$) hold, let $S_n^k(\tau)$, $\widehat{\tau}_n$ and $\triangle_n(\lambda, \tau)$ defined in (4.3), (4.4) and (2.6), respectively.*

(i) *For integers $0 \leq n \leq N_1$ and $k \geq 0$, $S_n^0(0) < 0$, $\lim\limits_{\tau\to\widehat{\tau}_n^-} S_n^k(\tau) < 0$, $S_n^k(\tau) > S_n^{k+1}(\tau)$ for any $\tau \in I_n$, and $S_{n+1}^k < S_n^k$ for $\tau \in I_{n+1}$.*

(ii) *Suppose that for some integers $0 \leq n \leq N_1$ and $k \geq 0$, $S_n^k(\tau)$ has a positive root $\tau_n^* \in I_n$, then a pair of simple purely imaginary roots $\pm i\omega_n(\tau_n^*)$ of $\triangle_n(\lambda, \tau) = 0$ exist at $\tau = \tau_n^*$ and*

$$Sign\left(Re\lambda'(\tau_n^*)\right) = Sign\left(dS_n^k(\tau_n^*)/d\tau\right).$$

Moreover, this pair of purely imaginary roots $\pm i\omega_n(\tau_n^*)$ cross the imaginary axis from left to right at $\tau = \tau_n^*$ if $(S_n^k)'(\tau_n^*) > 0$, and from right to left if $(S_n^k)'(\tau_n^*) < 0$.

If $\sup\limits_{\tau\in I_0} S_0^0(\tau) < 0$, $S_n^k(\tau)$ has no zeros in I_n for all integers $n \in [0, N_1]$ and $k \geq 0$. This precludes the existence of purely imaginary eigenvalues and thus yields that (u^*, v^*) is locally asymptotically stable for all $\tau \in [0, \widehat{\tau})$.

If $\sup\limits_{\tau\in I_0} S_0^0(\tau) = 0$, $S_0^0(\tau)$ has a zero of even multiplicity in I_0, denote by τ^*, such that $dS_0^0(\tau^*)/d\tau = 0$. This, together with Lemma 4.1(ii) implies that the transversality condition at τ^* is not satisfied and all eigenvalues remain to the left of the pure imaginary axis. Hence, (u^*, v^*) is still locally asymptotically stable for $\tau \in [0, \widehat{\tau})$.

If $\sup\limits_{\tau\in I_0} S_0^0(\tau) > 0$, it follows from Lemma 4.1(i) that $S_0^0(\tau)$ has at least two zeros in I_0. For simplicity, we assume that

($\mathbf{B}_2$) $\sup\limits_{\tau\in I_0} S_0^0(\tau) > 0$ and $S_n^k(\tau)$ has at most two zeros (counting multiplicity) for some integers $n \in [0, N_1]$ and $k \geq 0$.

Assumption ($\mathbf{B}_2$) ensures that there exists a integer $N_2 \in [0, N_1]$ such that, for any integer $n \in [0, N_2]$, there exists a integer $K_n \geq 1$ such that each $S_n^i(\tau)$ has two simple zeros (denoted by τ_n^i and $\tau_n^{2K_n-i-1}$) for integer $0 \leq i \leq K_n - 1$, and has no zeros for $i \geq K_n$. Hence, Lemma 4.1(i) implies that, for integer $n \in [0, N_2]$, there are $2K_n$ simple zeros τ_n^j of $S_n^k(\tau)$ for all integer $k \geq 0$ and $0 < \tau_n^0 < \tau_n^1 < \tau_n^2 < \cdots < \tau_n^{2K_n-1} < \widehat{\tau}_n$. Moreover, Lemma 4.1(ii) leads to $dS_n^i(\tau_n^i)/d\tau > 0$ and $dS_n^{2K_n-i-1}(\tau_n^i)/d\tau < 0$ for each $0 \leq i \leq K_n-1$. If we further have $\tau_n^i \neq \tau_m^j$ and $\tau_n^{2K_n-i-1} \neq \tau_m^j$ for all integers $m \in [0, N_2], m \neq n$, $j \in [0, 2K_m - 1]$, then a pair of simple conjugate purely imaginary eigenvalues $\pm i\omega_n(\tau_n^i)$ cross the imaginary axis from left to right, and a pair of simple conjugate purely imaginary eigenvalues $\pm i\omega_n(\tau_n^{2K_n-i-1})$ cross the imaginary axis from right to left. Now, we consider the collection of all τ_n^i with integers $(n, i) \in [0, N_2] \times [0, K_n]$. If a value appears more than once in the collection, then there are at least two pairs of purely imaginary roots and thus the condition of Hopf bifurcation is violated. For this reason, we only keep the values which appear exactly once in the collection and rearrange them in increasing order. Denote the new set by

$$\Sigma_H = \{\tau_i^H : 0 \leq i \leq 2K - 1\} \text{ with a integer } 0 < K \leq \sum_{j=0}^{N_2} K_j. \tag{4.5}$$

Obviously, τ_0^H and τ_{2K-1}^H are the two simple zeros of $S_0^0(\tau)$, system (1.2) undergoes a Hopf bifurcation at (u^*, v^*) when $\tau = \tau_i^H$ for each $0 \leq i \leq 2K - 1$. Furthermore, (u^*, v^*) is locally asymptotically stable for $\tau \in [0, \tau_0^H) \cup (\tau_{2K-1}^H, \widehat{\tau})$, and unstable for $\tau \in (\tau_0^H, \tau_{2K-1}^H)$. To summarize, we have the following results on the stability of (u^*, v^*) and the existence of Hopf bifurcation.

Theorem 4.2 *Assume that $g(K) > \mu$, $\tau \in [0, \widehat{\tau})$, $(\boldsymbol{A}_1)$-$(\boldsymbol{S}_1)$ hold, let I_n, $S_n^k(\tau)$ and τ_H^i defined in (4.1), (4.3) and (4.5), respectively. Denote $\Sigma_0^H = \{\tau \in \Sigma_H : S_0^k(\tau) = 0$ for some integer $k \geq 0\}$.*

- (i) *If either $I_0 = \varnothing$ or $\sup_{\tau \in I_0} S_0^0(\tau) \leq 0$, then (u^*, v^*) is locally asymptotically stable for $\tau \in [0, \widehat{\tau})$.*
- (ii) *If $(\boldsymbol{B}_1)$-$(\boldsymbol{B}_2)$ hold, then there exist exactly $2K$ local Hopf bifurcation values, namely, $0 < \tau_0^H < \tau_1^H < \cdots < \tau_{2K-1}^H < \widehat{\tau}$. (u^*, v^*) is locally asymptotically stable for $\tau \in [0, \tau_0^H) \cup (\tau_{2K-1}^H, \widehat{\tau})$, and unstable for $\tau \in (\tau_0^H, \tau_{2K-1}^H)$. Moreover, the bifurcating periodic solutions from $\tau \in \Sigma_0^H$ are spatially homogeneous, which coincides with the periodic orbits of the corresponding ODE system; and the bifurcating periodic solutions from $\tau \in \Sigma_H \backslash \Sigma_0^H$ are spatially nonhomogeneous.*

4.2 Global Hopf Bifurcation Analysis

Theorem 4.2 states that periodic solutions can bifurcate from $e^* = (u^*, v^*)$ when τ is near the local Hopf bifurcation values $\tau_i^H \in \Sigma_H$. In this subsection, we study the global continuation of these local bifurcating periodic solutions via the global Hopf bifurcation theorem [31]. Let $z(t) = (z_1(t), z_2(t))^T = (u(\cdot, \tau t) - u^*, v(\cdot, \tau t) - v^*)^T$. System (1.2) can be rewritten as a semilinear functional differential equation

$$z'(t) = \widetilde{A}z(t) + \widetilde{F}(z_t, \tau, T), \ (t, \tau, T) \in \mathbb{R}_+ \times [0, \widehat{\tau}) \times \mathbb{R}_+, \tag{4.6}$$

where $z_t \in \widetilde{Y} := C([-1, 0], X^2)$ with $z_t(\theta) = z(t + \theta)$ for $\theta \in [-1, 0]$, $\widetilde{A} = \mathrm{diag}(\tau d_1 \Delta - \tau\mu, \tau d_2 \Delta - \tau\mu)$, and

$$\widetilde{F}(z_t) = \begin{pmatrix} \tau b(z_{1t}(0) + u^*) - \tau g(z_{1t}(0) + u^*)(z_{2t}(0) + v^*) + \tau\mu z_{1t}(0) \\ \tau e^{-s\tau} g(z_{1t}(-1) + u^*)(z_{2t}(-1) + v^*) - \tau\mu v^* \end{pmatrix}.$$

Let $\{\widetilde{T}(t)\}_{t \geq 0}$ be the semigroup generated by the operator $\widetilde{A}$ with Neumann boundary condition on Ω. Then, we have $\widetilde{T}(t) \to 0$ as $t \to \infty$. Furthermore, the solution of (4.6) satisfies the integral equation

$$z(t) = \widetilde{T}(t)z(0) + \int_0^t \widetilde{T}(t - s)\widetilde{F}(z_s)ds. \tag{4.7}$$

Denote $z(t)$ as a periodic solution of (4.7) with period γ, we obtain

$$z(t) = z(t+\gamma) = \widetilde{T}(t+\gamma)z(0) + \int_0^{t+\gamma} \widetilde{T}(t+\gamma-s)\widetilde{F}(z_s)ds$$
$$= \widetilde{T}(t+\gamma)z(0) + \int_{-\gamma}^{t} \widetilde{T}(t-s)\widetilde{F}(z_s)ds.$$

By using the above equation repeatedly, we have

$$z(t) = \widetilde{T}(t+n\gamma)z(0) + \int_{-n\gamma}^{t} \widetilde{T}(t-s)\widetilde{F}(z_s)ds.$$

Letting $n \to \infty$, note that $\widetilde{T}(t+n\gamma)z(0) \to 0$ as $n \to \infty$, then the above equation is equivalent to

$$z(t) = \int_{-\infty}^{t} \widetilde{T}(t-s)\widetilde{F}(z_s)ds. \tag{4.8}$$

Thus, a periodic solution of (4.8) is also a periodic solution of (4.7). It follows from [30,Chapter 6.5] that the integral operator on the right-hand side of (4.8) is differentiable, completely continuous, and G-equivariant. Theorem 3.2 implies that e^* is the unique positive steady state solution of (1.2) when $\min\{d_1, d_2\} > d^*$. The condition($\mathbf{A}_1$) ensures that 0 cannot be an eigenvalue of (2.6) for any $\tau \geq 0$, which implies that the assumption (H1) in [30,Chapter 6.5] holds. It follows from Theorem 4.2 that, when $\tau = \tau_i^H$ for some integer $i \in [0, 2K-1]$, the characteristic equation (2.6) has exactly one pair of purely imaginary eigenvalues $\pm i\omega_n(\tau_i^H)$ for some integer $n \in [0, N_2]$. Hence, the assumption (H2) in [30,Chapter 6.5] holds. It can be checked easily from (2.6) and (4.6) that the smoothness condition (H3) in [30,Chapter 6.5] is also satisfied. According to the definitions in [30], we define the local steady state manifold

$$\mathbb{M} = \{(e^*, \tau, T) : |\tau - \tau_i^H| < \epsilon_1, |T - 2\pi/(\omega_n(\tau_i^H)\tau_i^H)| < \epsilon_2\} \subset X^2 \times \mathbb{R}_+^2,$$

for sufficiently small $\epsilon_1, \epsilon_2 > 0$. For $(\tau, \omega) \in [\tau_i^H - \epsilon_1, \tau_i^H + \epsilon_1] \times [\omega_n(\tau_i^H) - \epsilon_2, \omega_n(\tau_i^H) + \epsilon_2]$, $\pm i\omega_n(\tau_i^H)$ is an eigenvalue of (2.6) if and only if $\tau = \tau_i^H$ and $\omega = \omega_n(\tau_i^H)$. Thus, we conclude that $(e^*, \tau_i^H, 2\pi/(\omega_n(\tau_i^H)\tau_i^H))$ is an isolated singular point in $\mathbb{M}$. Furthermore, it follows from Lemma 4.1(ii) that the crossing number $\zeta(e^*, \tau_i^H, 2\pi/(\omega_n(\tau_i^H)\tau_i^H))$ at each of these centers is

$$\zeta(e^*, \tau_i^H, 2\pi/(\omega_n(\tau_i^H)\tau_i^H)) = -\mathrm{Sign}\left(\mathrm{Re}\lambda'(\tau_i^H)\right) = \begin{cases} -1, \ 0 \leq i \leq K-1, \\ 1, \ K \leq i \leq 2K-1. \end{cases}$$

Thus the condition (H4) in [30] holds. Next, we define a closed subset Γ of $X^2 \times \mathbb{R}_+^2$ by

$$\widetilde{\Gamma} = Cl\{(z, \tau, T) \in X^2 \times \mathbb{R}_+^2 : z \text{ is a nontrivial } T\text{-periodic solution of (4.6)}\}.$$

For each integer $0 \leq i \leq 2K-1$, let $\mathbf{P}(e^*, \tau_i^H, T_i)$ be the connected component of (e^*, τ_i^H, T_i) in $\widetilde{\Gamma}$. Theorem 4.2(ii) gives the sufficient conditions to ensure that $\mathbf{P}(e^*, \tau_i^H, T_i)$ is nonempty subset of $\widetilde{\Gamma}$.

Before we state our results on global Hopf bifurcation branches, we shall further investigate the properties of periodic solutions of (4.6).

Lemma 4.3 *Assume that $g(K) > \mu$ and $\tau \in [0, \widehat{\tau})$, then all nonnegative periodic solutions $(u(x,t), v(x,t))$ of (4.6) are uniformly bounded, namely, $\eta \leq u(x,t) \leq K$ and*

$\eta \le v(x,t) \le K + \max\limits_{[0,K]} b(u)/\mu$ *for all* $(x,t) \in \bar{\Omega} \times \mathbb{R}_+$*, where* η *is defined in Theorem* 2.4.

Proof We claim $u(x,t) \le K$ for all $(x,t) \in \bar{\Omega} \times \mathbb{R}_+$. Otherwise, if there exists $(x_1,t_1) \in \bar{\Omega} \times \mathbb{R}_+$, such that $u(x_1,t_1) > K$, then $\lim\limits_{n\to\infty} u(x_1, t_1+nT) = u(x_1,t_1) > K$, where T is the period of the periodic solution $(u(x,t), v(x,t))$. This contradicts the fact that $\limsup\limits_{t\to\infty} u(x,t) \le K$ for all $x \in \bar{\Omega}$ in Proposition 2.1. Hence, K is a uniform upper bound of $u(x,t)$. Similarly, we can prove $v(x,t)$ has a uniform upper bound $K + \max\limits_{[0,K]} b(u)/\mu$ from Proposition 2.1, and $u(x,t)$, $v(x,t)$ have a uniform lower bound η from Theorem 2.4. This ends the proof. □

Lemma 4.4 *Assume that* $g(K) > \mu$, $\tau \in [0, \widehat{\tau})$*, and*

($\boldsymbol{B}_3$) $\sigma_0 < u^* < K$*, where* $\sigma_0 \in (\widehat{\sigma}, K)$ *is the unique positive root of* $b(u)/g(u) = b'(0)/g'(0)$, $\widehat{\sigma} \in [0,K]$ *such that* $\left(\frac{b(u)}{g(u)}\right)'(u-\widehat{\sigma}) < 0$ *for* $u \in [0,K]$ *and* $u \ne \widehat{\sigma}$.

Then system (1.2) *has no nontrivial periodic solution of period* τ*. Moreover,* (u^*, v^*) *is globally asymptotically stable of system* (1.2) *when* $\tau = 0$.

Proof Assume to the contrary, $(u(x,t), v(x,t))$ is a nontrivial periodic solution of (1.2) with period τ, that is, $(u(x,t-\tau), v(x,t-\tau)) = (u(x,t), v(x,t))$. Then it satisfies the following system

$$\begin{aligned}
&\partial u/\partial t = d_1 \Delta u + b(u) - g(u)v, \quad x \in \Omega, t > 0,\\
&\partial v/\partial t = d_2 \Delta v + e^{-s\tau} g(u)v - \mu v, \quad x \in \Omega, t > 0,\\
&u_\nu = v_\nu = 0, \quad x \in \partial\Omega, t \ge 0,\\
&u(x,0) = u_0(x,0) \ge (\not\equiv)0, v(x,0) = v_0(x,0) \ge (\not\equiv)0, \quad x \in \Omega.
\end{aligned} \tag{4.9}$$

For $\phi = (\phi_1, \phi_2) \in C(\bar{\Omega}, \mathbb{R}^2_+)$, we define a Lyapunov functional $\mathbb{L}_2 : C(\bar{\Omega}, \mathbb{R}^2_+) \to \mathbb{R}$,

$$\mathbb{L}_2(\phi) = \int_\Omega \left(e^{-s\tau} \int_{u^*}^{\phi_1} \frac{g(\theta) - g(u^*)}{g(\theta)} d\theta + (\phi_2 - v^* \ln \phi_2) \right) dx.$$

Calculating the time derivative of $\mathbb{L}_2(\phi)$ along the solution of (4.9) leads to

$$\frac{d\mathbb{L}_2}{dt} = \int_\Omega \left(e^{-s\tau}(g(u) - g(u^*)) \left(\frac{b(u)}{g(u)} - \frac{b(u^*)}{g(u^*)} \right) - d_1\mu \frac{g'(u)}{g^2(u)} |\nabla u|^2 - d_2 v^* \frac{|\nabla v|^2}{v^2} \right) dx.$$

Note that ($\mathbf{B}_3$) implies that $\left(\frac{b(u)}{g(u)} - \frac{b(u^*)}{g(u^*)}\right)(u - u^*) < 0$ for $u \ne u^*$. This, together with $g'(u) > 0$ for $u \ge 0$, yields that

$$(g(u) - g(u^*)) \left(\frac{b(u)}{g(u)} - \frac{b(u^*)}{g(u^*)} \right) < 0 \text{ for } u \ne u^*.$$

Thus, $d\mathbb{L}_2/dt \le 0$ for all $(u(x,t), v(x,t)) \in C(\bar{\Omega}, \mathbb{R}^2_+)$. The maximal invariant subset of $d\mathbb{L}_2/dt = 0$ is the singleton $\{(u^*, v^*)\}$. By LaSalle-Lyapunov invariance principle, (u^*, v^*) attracts every positive solution of (4.9). This precludes the existence of nontrivial nonnegative periodic solution of system (1.2) with period τ. □

Remark 4.5 The assumption ($\mathbf{B}_3$) is satisfied for many commonly used functions $b(u)$ and $g(u)$, for instance, when $b(u) = ru(1-u/K)$ is the logistic growth and $g(u) = \beta u$ is a linear function. A sufficient condition for ($\mathbf{B}_3$) to hold is that the ratio $b(u)/g(u)$ is non-increasing in $[0, K]$.

Theorem 4.6 *Consider model (4.6) with $g(K) > \mu$, $\tau \in [0, \widehat{\tau})$, and $\min\{d_1, d_2\} > d^*$. Assume that ($\boldsymbol{S}_1$) and ($\boldsymbol{B}_1$)-($\boldsymbol{B}_3$) hold. For each $0 \le i \le 2K-1$, we define $\tau_i^H \in \Sigma_H$ and d^* as in (4.5) and Theorem 3.2, respectively. Denote $\Sigma_H^0 := \{\tau \in \Sigma_H : S_n^0(\tau) = 0$ for integer $n \in [0, N_2]\}$. Then we have the following results:*

(i) *For each $\tau_j^H \in \Sigma_H \backslash \Sigma_H^0$, there exist integers $k_j \in [1, K_j]$ and $n_j \in [0, N_2]$ such that $S_{n_j}^{k_j}(\tau_j^H) = 0$. Moreover, the global Hopf branch $\mathbf{P}(e^*, \tau_j^H, T_j)$ is bounded. If $m \in [0, 2K-1]$ is another integer with $k_m \neq k_j$, then $\mathbf{P}(e^*, \tau_j^H, T_j) \cap \mathbf{P}(e^*, \tau_m^H, T_m) = \emptyset$.*

(ii) *For each $\tau_j^H \in \Sigma_H \backslash \Sigma_H^0$ with $1 \le j \le K-1$, there exists an integer $l \in [K, 2K-2]$ such that $S_{n_j}^{k_j}(\tau)$ has exactly two distinct zeros τ_j^H and τ_l^H. Moreover, the two global Hopf branches $\mathbf{P}(e^*, \tau_j^H, T_j)$ and $\mathbf{P}(e^*, \tau_l^H, T_l)$ are identical and connected by a pair of Hopf bifurcation values τ_j^H and τ_l^H. For each $\tau \in (\tau_j^H, \tau_l^H)$, model (4.6) has at least one periodic solution with period in $(\frac{1}{k_j+1}, \frac{1}{k_j})$.*

Proof Lemma 4.4 implies that system (4.6) does not have nontrivial nonnegative periodic solutions of period 1, nor does it have nontrivial nonnegative periodic solutions of period $1/n$ for any integer $n \ge 1$. If τ is sufficiently close to the bifurcation point τ_j^H, we obtain from local Hopf bifurcation theorem that $\omega_{n_j}\tau \in (2k_j\pi, 2k_j\pi + 2\pi)$. Note that the period $T_j = 2\pi/(\omega_{n_j}\tau)$. Thus, we have $1/(k_j+1) < T_j < 1/k_j$ for $k_j \ge 1$ and $T_j > 1$ for $k_j = 0$. If $k_j \ge 1$, since system (4.6) has no nontrivial periodic solution of period $1/k_j$ nor $1/(k_j + 1)$, by continuity of Hopf bifurcation branch, the periods on $\mathbf{P}(e^*, \tau_j^H, T_j)$ are bounded in $(\frac{1}{k_j+1}, \frac{1}{k_j})$. Lemma 4.3 implies that the global Hopf branch $\mathbf{P}(e^*, \tau_j^H, T_j)$ has bounded τ-components and bounded solutions. Thus, the global Hopf branch $\mathbf{P}(e^*, \tau_j^H, T_j)$ is bounded when $k_j \ge 1$. If $k_j = 0$, a similar argument shows that the periods on $\mathbf{P}(e^*, \tau_j^H, T_j)$ are always greater than 1. Therefore, any two global Hopf branches $\mathbf{P}(e^*, \tau_j^H, T_j)$ and $\mathbf{P}(e^*, \tau_l^H, T_l)$ with $k_j \neq k_l$ do not intersect. This proves (i).

Lemma 4.3 gives the uniform lower positive bound of the nontrivial periodic solution of (4.6). Theorem 3.2 precludes the existence of nonnegative heterogeneous steady states of (4.6) when $\min\{d_1, d_2\} > d^*$. Thus, we do not need to consider the boundary equilibrium. An application of the global Hopf bifurcation theorem in [30,Chapter 6.5] together with an argument similar to that in the proof of [21,Theorem 2] gives (ii). □

Note that if the periods of any nontrivial periodic solutions of system (4.6) are bounded, then the global Hopf branch $\mathbf{P}(e^*, \tau_j^H, T_j)$ is bounded for each $\tau_j^H \in \Sigma_H^0$. We leave the proof of upper boundedness of the periods of any nontrivial periodic solutions of (4.6) as an open problem.

5 Numerical Exploration

In this section, we use numerical exploration to illustrate our theoretical results on the model dynamics. Following an earlier work in [8], we choose the growth function of the prey as $b(u) = ru(1 - u/K)$ and the predator functional response as $g(u) = cu/(1+u)$. According to Theorems 2.2, 2.3 and 4.2, the stability region of system (1.2) in the $c - \tau$ space can be plotted in Fig. 1. We choose the domain $\Omega = (0, 2\pi)$ and the parameter values as follows. $d_1 = 1, d_2 = 1, r = 0.8, K = 3, c = 1, s = 0.6, \mu = 0.2$. A simple calculation gives $\widehat{\tau} = 2.2029$, $\sup I_0 = 1.7418$ and $\sup I_1 = 0.4576$. We further obtain that $\sup_{I_0} S_0^0(\tau) > 0$,

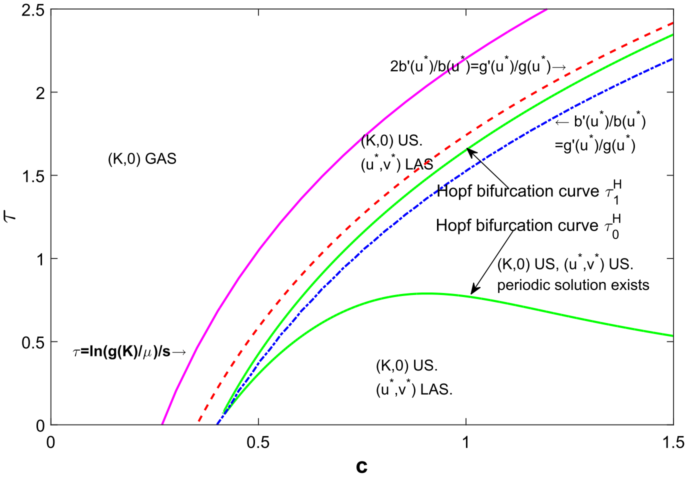


Fig. 1 The stability region of (1.2) in the $c-\tau$ space

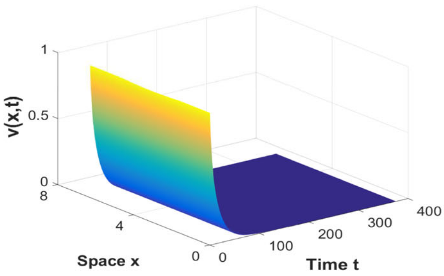
$\sup_{I_0} S_0^1(\tau) < 0$, $\sup_{I_0} S_1^0(\tau) < 0$, and $S_0^0(\tau)$ has exactly two zeros in I_0: $\tau_0^H = 0.7725$ and $\tau_1^H = 1.6522$. The dynamics of system (1.2) are summarized as follows:

(i) If $\tau \in [\widehat{\tau}, \infty)$, then $(K, 0)$ is globally asymptotically stable; see Fig. 2(a).
(ii) If $\tau \in (0, \tau_0^H) \cup (\tau_1^H, \widehat{\tau})$, then $(K, 0)$ is unstable, and (u^*, v^*) is locally asymptotically stable; see Fig. 2(b).
(iii) If $\tau \in (\tau_0^H, \tau_1^H)$, then $(K, 0)$ and $(u^*, v^*) = (1.9764, 0.8124)$ are unstable. Moreover, there exists a periodic solution bifurcation from (u^*, v^*); see Fig. 2(c). System (1.2) undergoes a Hopf bifurcation at (u^*, v^*) when $\tau = \tau_i^H$ for $i = 0, 1$.

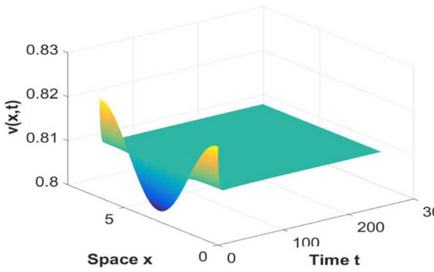
Theorem 3.3 gives sufficient conditions for the existence of positive heterogeneous steady states. Set the parameter values in Fig. 3, we calculate $\delta^- \approx 0.031$, $\delta^+ \approx 1.06$, and $\delta_i = i^2/36 \in (\delta^-, \delta^+)$ for integer $i \in [2, 6]$. Thus, there exists five simple eigenvalues of $-\Delta$ in Ω with Neumann boundary condition in the interval (δ^-, δ^+). It then follows from Theorem 3.3 that system (1.2) has at least one positive heterogeneous solution $(u(x), v(x))$, as shown in Fig. 3. To illustrate the steady state bifurcation at (u^*, v^*), we set the domain $\Omega = (0, 2\pi)$ and the parameter values: $d_1 = 1, d_2 = 3, r = 1, K = 11.9, c = 2, \mu = 0.3$. We choose $\sigma := \frac{0.3e^{s\tau}}{2-0.3e^{s\tau}}$ as the bifurcation parameter by varying parameters s and τ. Then $\delta_i = i^2/4$ for integer $i \geq 0$ and

$$T(\sigma, p) = 4p + \frac{\sigma(0.168\sigma - 0.916)}{1+\sigma},$$
$$D(\sigma, p) = 3p^2 + \frac{3\sigma(0.168\sigma - 0.916)}{1+\sigma}p + \frac{0.3(1-\sigma/11.9)}{1+\sigma}.$$

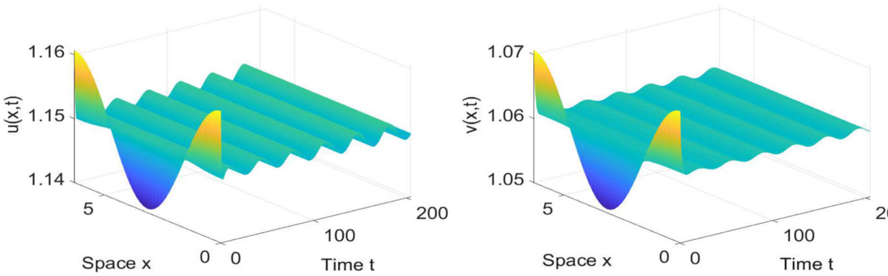
As shown in Fig. 4, the equation $D(\sigma, \delta_1) = 0$ has two different roots: $\sigma_1^S = 1.4$ and $\sigma_2^S = 2.763$, and the equation $D(\sigma, \delta_j) = 0$ has no real roots for $j \neq 1$ and $j \geq 0$. We further compute $p'_+(\sigma_1^S) = 0.2317 > 0$ and $p'_-(\sigma_2^S) = -0.09037 < 0$. According to Theorem 3.6, there are two steady state bifurcations, corresponding to the steady state bifurcation values σ_1^S, σ_2^S, respectively.



(a) $\tau = 3 > \hat{\tau}$, $(3, 0)$ is globally asymptotically stable.



(b) $\tau = 2 \in (\tau_1^H, \hat{\tau})$, (u^*, v^*) is locally asymptotically stable.



(c) A periodic solution bifurcated from (u^*, v^*) for $\tau = 1.64 \in (\tau_0^H, \tau_1^H)$.

Fig. 2 The dynamics of system (1.2) for different delay. Initial conditions for (a) are $u_0(x, \theta) = v_0(x, \theta) = 1 + 0.01 \cos x$, for (b) and (c) are $u_0(x, \theta) = u^* + 0.01 \cos x$, $v_0(x, \theta) = v^* + 0.01 \cos x$ for $\theta \in [-\tau, 0]$

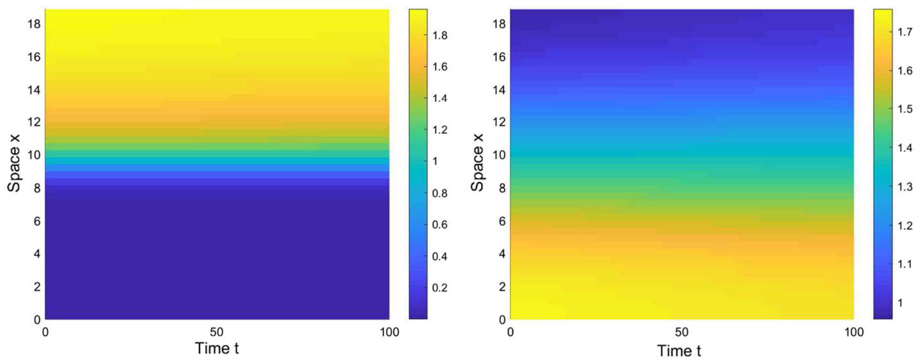


Fig. 3 Projection of the heterogeneous positive steady state $(u(x), v(x))$ on $x - t$ plane. Parameter values are $d_1 = 0.5$, $d_2 = 0.02$, $r = 6.5$, $K = 2.8$, $c = 6$, $s = 10$, $\mu = 10^{-4}$, $\tau = 1$ and $\Omega = (0, 6\pi)$

To demonstrate the coexistence of multiple global Hopf branches, we choose the domain $\Omega = (0, 2\pi)$ and a different set of parameter values:

$$d_1 = 1, d_2 = 2, r = 10, K = 3, c = 15, s = 0.05, \mu = 6.75. \tag{5.1}$$

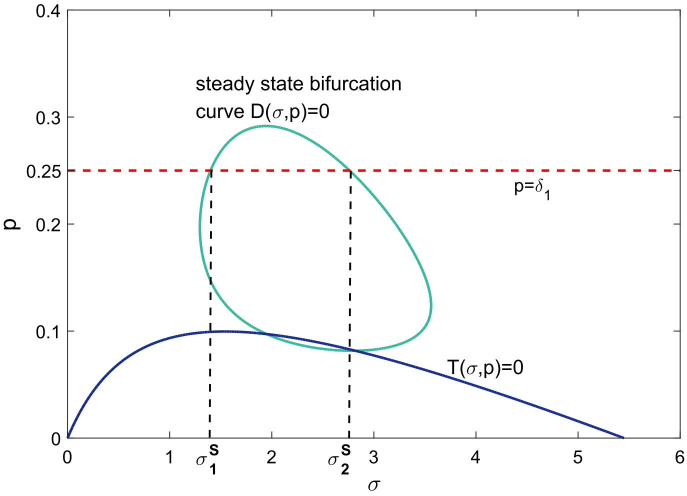


Fig. 4 Graph of $D(\sigma, p) = 0$, $T(\sigma, p) = 0$, and $p = n^2/4$ for integer $n \geq 1$. This gives steady state bifurcation values σ_1^S and σ_2^S

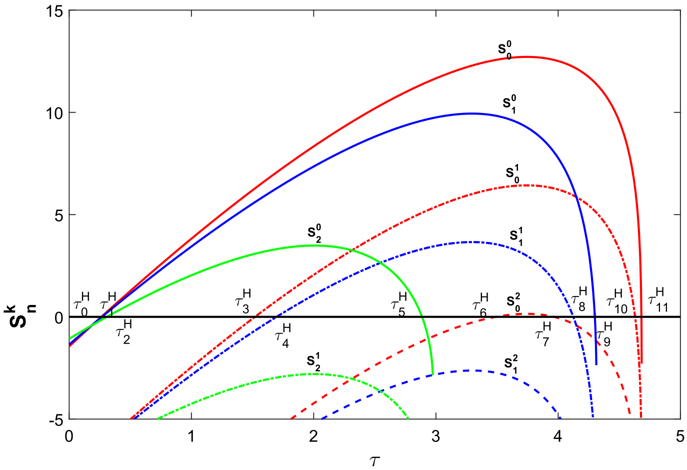


Fig. 5 The graphs of S_n^k for integers $0 \leq n, k \leq 2$. This gives the Hopf bifurcation values τ_j^H for integer $0 \leq j \leq 11$

It follows from Sect. 4 that $\sup I_0 \approx 4.68$, $\sup I_1 \approx 4.31$, $\sup I_2 \approx 2.98$, and $I_n = \emptyset$ for $n \geq 3$. By Theorem 4.2, there are exactly 12 Hopf bifurcation values, namely,

$$\begin{aligned}&\tau_0^H \approx 0.26 < \tau_1^H \approx 0.27 < \tau_2^H \approx 0.31 < \tau_3^H \approx 1.52 < \tau_4^H \approx 1.70 < \tau_5^H \approx 2.89\\ &< \tau_6^H \approx 3.49 < \tau_7^H \approx 3.97 < \tau_8^H \approx 4.12 < \tau_9^H \approx 4.30 < \tau_{10}^H \approx 4.63 < \tau_{11}^H \approx 4.68,\end{aligned}$$

as shown in Fig. 5. Theorems 4.2 and 4.6 imply that (u^*, v^*) is locally asymptotically stable for $\tau \in [0, \tau_0^H) \cup (\tau_{11}^H, \widehat{\tau})$, and unstable for $\tau \in (\tau_0^H, \tau_{11}^H)$; and model (1.2) has at least one periodic solution for $\tau \in (\tau_0^H, \tau_{11}^H)$. Moreover, the bifurcating periodic solutions from $\tau \in \{\tau_0^H, \tau_3^H, \tau_6^H, \tau_7^H, \tau_{10}^H, \tau_{11}^H\}$ are spatially homogeneous, and the bifurcating periodic solutions from $\tau \in \{\tau_1^H, \tau_2^H, \tau_4^H, \tau_5^H, \tau_8^H, \tau_9^H\}$ are spatially nonhomogeneous, see Fig. 6. It

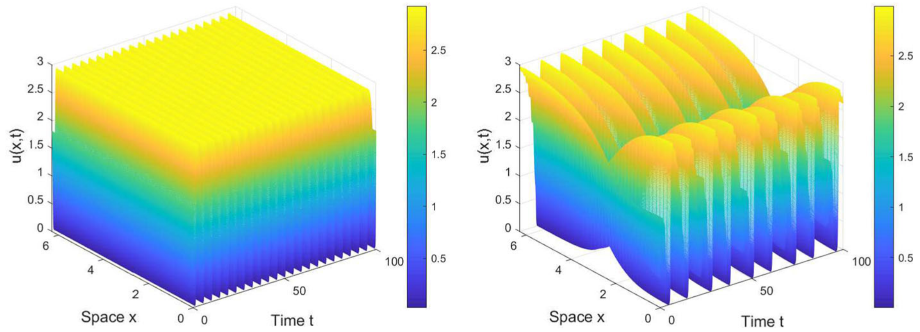
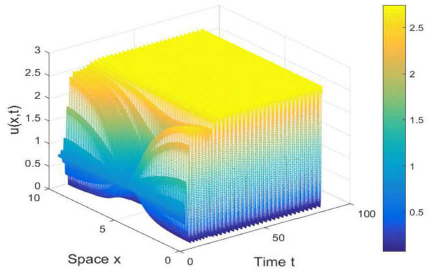
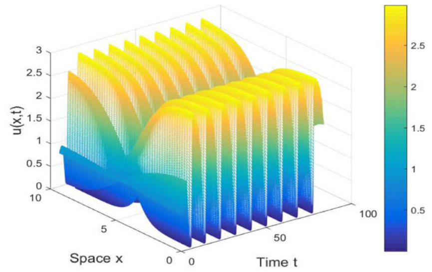


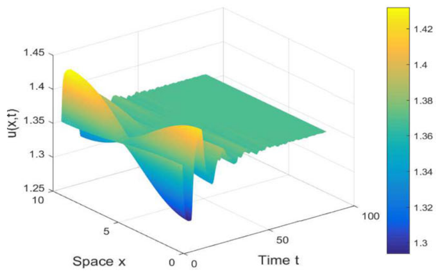
Fig. 6 Left: $\tau = 0.264 \in (\tau_0^H, \tau_1^H)$, a bifurcating spatially homogeneous periodic solution exists. Right: $\tau = 1.36 \in (\tau_1^H, \tau_3^H)$, a bifurcating spatially non-homogeneous periodic solution exists



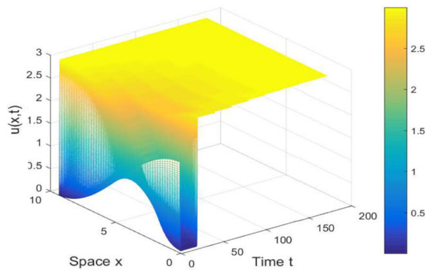
(a) A stable spatially homogeneous periodic solution exists with a small delay $\tau = 0.1$.



(b) A stable spatially heterogeneous periodic solution exists with a mediate delay $\tau = 1$.



(c) The positive constant steady state is stable with a large delay $\tau = 5$.



(d) $(3, 0)$ is stable if the delay is too large $\tau = 20$.

Fig. 7 Time delay induces different dynamical behaviors for the nonlocal model (1.1) with the truncated normal density function $K(x, y)$

is also verified by numerical simulations that the periods of the periodic solutions for (1.2) are bounded. It then follows from Theorem 4.6 that all global Hopf branches are bounded and connected by a pair of Hopf bifurcation values.

To consider the combination impacts of nonlocal interaction and time delay on the model dynamics, we choose the nonlocal kernel function as the density function of the truncated normal distribution:

$$K(x, y) = \frac{e^{-2|x-y|^2}}{\int_\Omega e^{-2|x-y|^2} dy}.$$

It is clear that $\int_\Omega K(x, y)dy = 1$ and for each x, $K(x, y)$ achieves its maximum at $y = x$. The other parameter values are chosen as in (5.1) and the domain $\Omega = (0, 3\pi)$. Numerical simulation suggests that the spatially homogeneous time periodic solution is stable for small delay $\tau = 0.1$ (Fig. 7(a)), the spatially heterogeneous time periodic solution exists and is stable for mediate delay $\tau = 1$ (Fig. 7(b)), while the positive constant steady state is stable for large delay $\tau = 5$ (Fig. 7(c)). However, if the time delay exceeds the critical value $\ln(g(K)/\mu)/s$, then the solution converges to the predator-free steady state; see Fig. 7(d). It seems that the nonlocal interaction in the delayed term can induce more interesting dynamics than the local model. Due to the lack of available analytical techniques, we leave the theoretical analysis of the nonlocal model with time delay as future work.

6 Concluding Remarks

We investigated a general diffusive predator–prey system with predator maturation delay in this paper. This model generalized many models studied in the literature and our theoretical results extended the global dynamic results obtained for the models without delay. Under certain conditions on model parameters, we obtained global asymptotic stability of the predator-free equilibrium and uniform persistence of solutions. With the aid of Leray–Schauder degree theory, we proved the existence of a spatial heterogeneous steady state. We also analyzed steady state bifurcation and Hopf bifurcation. Global Hopf bifurcation analysis was further conducted to show that global Hopf branches are bounded and connected by a pair of bifurcation points. There is an open problem in global Hopf bifurcation analysis: to prove that the periods of any nontrivial periodic solutions of system (4.6) are bounded.

Our theoretical results are illustrated by numerical simulations. We compared the dynamics of the local model to those of the nonlocal model. Clearly the nonlocal interaction in the delayed term leads to more exciting dynamics. However, rigorous analysis is not feasible yet, and we leave this as an open problem for future development of new mathematical techniques.

Acknowledgements H. Shu was partially supported by the National Natural Science Foundation of China (11971285) and the Fundamental Research Funds for the Central Universities (GK201902005). H. Wang was partially supported by the Natural Sciences and Engineering Research Council of Canada (Discovery Grant RGPIN-2020-03911 and Accelerator Grant RGPAS-2020-00090).

Data Availability Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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