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GLOBAL STABILITY AND HOPF BIFURCATION IN A DELAYED DIFFUSIVE LESLIE–GOWER PREDATOR–PREY SYSTEM*

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In this paper, we consider a delayed diffusive Leslie–Gower predator–prey system with homogeneous Neumann boundary conditions. The stability/instability of the coexistence equilibrium and associated Hopf bifurcation are investigated by analyzing the characteristic equations. Furthermore, using the upper and lower solutions method, we give a sufficient condition on parameters so that the coexistence equilibrium is globally asymptotically stable.

Keywords: Predator–prey; delay; reaction–diffusion; Hopf bifurcation; global stability.

1. Introduction

Predator–prey systems (or consumer–resource systems) are basic differential equation models for describing the interactions between two species with a pair of positive–negative feedbacks. While the predator–prey model of systems of two ordinary differential equations has relatively simple dynamics due to the powerful Poincaré–Bendixon theory, the models of more species, or the models with spatial structure, delay effect, nonlocal effect are mathematically much more challenging.

In this article, we revisit a classical predator–prey model due to Leslie and Gower [Leslie, 1948; Leslie & Gower, 1960]:

$$\begin{cases} \dfrac{du}{dt} = u(p - \alpha u - \beta v), \\ \dfrac{dv}{dt} = \mu v\left(1 - \dfrac{v}{u}\right), \end{cases} \tag{1}$$

where p, α are positive, and the prey is assumed to grow in logistic patterns; parameters μ, β are positive. Several ecological treatises are regarded (1) as a prototypical predator–prey system (see [May, 1973] and [Pielou, 1977]). It is known that system (1) has a globally asymptotically stable equilibrium (see [Korobeinikov, 2001]).

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When the spatial dispersal is also considered, system (1) becomes

$$\begin{cases} \dfrac{\partial u}{\partial t} - d_1\Delta u = u(p - \alpha u - \beta v), & x \in \Omega, \quad t > 0, \\ \dfrac{\partial v}{\partial t} - d_2\Delta v = \mu v\left(1 - \dfrac{v}{u}\right), & x \in \Omega, \quad t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \end{cases} \tag{2}$$

where the habitat Ω is a bounded domain in $\mathbf{R}^n$, $n \geq 1$; ν is the outer normal direction for $x \in \partial\Omega$; and the imposed no-flux boundary condition means that the system is a closed one. Du and Hsu [2004] studied the dynamics of system (2). They proved that when $\alpha/\beta > s_0$, where s_0 is the unique positive root of the equation $32s^3 + 16s^2 - s - 1 = 0$ which is located in $(1/5, 1/4)$, the positive constant equilibrium $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ attracts every positive solution of system (2). Some results in [Du & Hsu, 2004] were generalized in [Ko & Ryu, 2007].

For some predator–prey systems, the growth rate per capita of the predator and prey depend on the past time. In a survey, Ruan [2009] showed that delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and induce bifurcations. He considered the dynamics of predator–prey models with discrete delay without diffusion in [Ruan, 2009].

In this paper, we consider the delay effect on the diffusion–reaction system (2). We assume that the predation of the predator in the earlier times will decrease the rate of the prey population in later times, and the consumption of preys in earlier times will increase the predator population in a later time. Then the system (2) becomes the following delayed diffusive predator–prey system with homogeneous Neumann boundary conditions

$$\begin{cases} \dfrac{\partial u(t,x)}{\partial t} - d_1\Delta u(t,x) = u(t,x)(p - \alpha u(t,x) - \beta v(t-\tau_1, x)), & x \in \Omega, \quad t > 0, \\ \dfrac{\partial v(t,x)}{\partial t} - d_2\Delta v(t,x) = \mu v(t,x)\left(1 - \dfrac{v(t,x)}{u(t-\tau_2, x)}\right), & x \in \Omega, \quad t > 0, \\ \dfrac{\partial u(t,x)}{\partial \nu} = \dfrac{\partial v(t,x)}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ u(x,t) = u_0(x,t) > 0, & x \in \Omega, \quad t \in [-\tau_2, 0], \\ v(x,t) = v_0(x,t) > 0, & x \in \Omega, \quad t \in [-\tau_1, 0], \end{cases} \tag{3}$$

where Ω is bounded smooth domain in $\mathbf{R}^n, u(t,x)$ and $v(t,x)$ are the population densities of prey and predator respectively, the Laplacian operator $\Delta w(t,x) = \sum_{i=1}^n \frac{\partial^2 w(t,x)}{\partial x_i^2}$ for $w = u, v$ shows the diffusion effect, the boundary condition is assumed to be a no-flux one so that the system is closed, and $d_1, d_2, p, \alpha, \beta, \mu$ are all positive constants. We assume τ_1 and τ_2 are all non-negative, which represent the delay effects.

Our main result is that, with the addition of the delays, if $\alpha > \beta$, then the positive constant equilibrium is globally asymptotically stable for any $\tau_1 \geq 0, \tau_2 \geq 0$. Notice that in [Du & Hsu, 2004], the global stability is proved without delays but for $\alpha > s_0\beta$, for some $s_0 \in (1/5, 1/4)$, their method is to construct a Lyapunov functional. We use the upper-lower solutions method introduced by Pao [1996, 1997, 2002]). On the other hand, if $\alpha < \beta$, then there exists $\tau_* > 0$ such that the positive constant equilibrium is stable for $\tau_1 + \tau_2 < \tau_*$, and it is unstable for $\tau_1 + \tau_2 > \tau_*$. At the threshold value $\tau_1 + \tau_2 = \tau_*$, a Hopf bifurcation occurs and spatially homogeneous periodic orbits emerge from the coexistence equilibrium as it changes the stability. Our first result on global stability when $\alpha > \beta$ regardless of delays shows that the delays for this case do not change the qualitative behavior of the system, but when $\alpha < \beta$, a large delay could destabilize the equilibrium state and oscillatory patterns dominate the dynamics. We comment that the corresponding ODE model (1) does not possess any closed cycle, thus the oscillatory patterns are induced by delay effect. In some other predator–prey models, oscillatory patterns can be induced by either delay or a system parameter in ODE model.

It is interesting to note that a similar threshold phenomenon occurs for the logistic equation with a discrete delay of the form:

$$\frac{\partial u(x,t)}{\partial t} = d\Delta u(x,t) + ru(x,t)[1 - \alpha u(x,t) - \beta u(x, t-\tau)], \quad x \in \Omega, \ t > 0. \qquad (4)$$

It is known that for the ODE case [Ruan, 2006] and PDE case [Pao, 1996], if $\alpha > \beta$, that is, if the instantaneous term is dominant, then the unique positive steady state is globally asymptotically stable. But when $\alpha < \beta$, then a Hopf bifurcation occurs when τ increases, see [Ruan, 2006] for the ODE case, and [Su *et al.*, 2011] for PDE case with Dirichlet boundary conditions.

Leslie–Gower model with delays have been considered recently by Yuan and Song [2009a, 2009b], and they conducted the stability analysis and analyzed the associated Hopf bifurcations. But their delays were different from ours and they considered neither the effect of diffusion nor the global stability. On the other hand, system (2) is a special case ($r = 0$) of diffusive predator–prey system of Holling–Tanner type:

$$\begin{cases} \dfrac{\partial u}{\partial t} - d_1\Delta u = u\left(p - \alpha u - \dfrac{\beta v}{1 + rv}\right), \\ \qquad\qquad x \in \Omega, \ t > 0, \\ \dfrac{\partial v}{\partial t} - d_2\Delta v = \mu v\left(1 - \dfrac{v}{u}\right), \quad x \in \Omega, \ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega, \ t > 0. \end{cases} \qquad (5)$$

The corresponding ODE system of (5) was proposed by Tanner [1975]. Hsu and Hwang [1995, 1998] and Hainzl [1992] have given a detailed description of qualitative behavior of the ODE system of (5). Peng and Wang [2005, 2007] considered the existence/nonexisentence of nonconstant steady state solutions of (5) as well as the global stability of constant steady state solution. We comment that stability/instability and Hopf bifurcations of delayed reaction–diffusion predator–prey systems have also been considered in [Ge & He, 2008; Faria, 2001; Feng & Lu, 1997; Hu & Li, 2010; Li & Wu, 2009; Thieme & Zhao, 2001; Wang, 2007; Xu & Ma, 2009; Yan, 2007, 2010].

The rest of this paper is organized as follows. In Sec. 2, we analyze the local stability/instability of the constant coexistence equilibrium of system (3) through the study of associated characteristic equations, and we also consider the occurrence of the Hopf bifurcation at the positive equilibrium when $\alpha < \beta$ as the sum of the delays $\tau_1 + \tau_2$ crosses a critical value τ_*. In Sec. 3, we prove the global asymptotical stability of the constant coexistence equilibrium when $\alpha > \beta$ for any $\tau_1, \tau_2 \geq 0$, by using the method of upper/lower solutions. We make some concluding remarks in Sec. 4.

2. Local Stability and Hopf Bifurcation

In this section, we analyze the local stability of coexistence equilibrium of system (3). Denote

$$X = \{(u, v)^T : u, v \in L^2(\Omega)\},$$

$$\langle u, v\rangle = \langle u_1, v_1\rangle_{L^2} + \langle u_2, v_2\rangle_{L^2}, \quad \tau = \tau_1 + \tau_2,$$

for $u = (u_1, u_2), v = (v_1, v_2) \in X$, then $(X, \langle\cdot,\cdot\rangle)$ is a Hilbert space. In the function space $C([-\tau, 0], X)$, system (3) can be regarded as an abstract functional differential equation.

It is easy to see that system (3) has two nonnegative equilibria $(\frac{p}{\alpha}, 0)$ and $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$. From the analysis of the characteristic equation of $(\frac{p}{\alpha}, 0)$, one can show that $(\frac{p}{\alpha}, 0)$ is always a saddle point, as is in the case of the corresponding ordinary differential equations. Thus in the following, we only analyze the stability/instablity of the coexistence equilibrium $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$. Linearizing system (3) at this coexistence equilibrium, we obtain that

$$\frac{dU(t)}{dt} = d\Delta U(t) + L(U_t), \qquad (6)$$

where $d\Delta = (d_1\Delta, d_2\Delta)$,

$$\mathrm{dom}(d\Delta) = \left\{(u, v)^T : u, v \in W^{2,2}(\Omega), \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0\right\},$$

and $L : C([-\tau, 0], X) \to X$ is given by

$$L(\phi) = \begin{pmatrix} -\dfrac{\alpha}{\alpha+\beta}p\phi_1(0) - \dfrac{\beta}{\alpha+\beta}p\phi_2(-\tau_1) \\ -\mu\phi_2(0) + \mu\phi_1(-\tau_2) \end{pmatrix},$$

for $\phi = (\phi_1, \phi_2)^T \in C([-\tau, 0], X)$. From [Wu, 1996], we obtain that the characteristic equation for the liner system (6) is

$$\lambda y - d\Delta y - L(e^{\lambda \cdot} y) = 0, \quad y \in \mathrm{dom}(d\Delta), \ \ y \neq 0. \tag{7}$$

It is well known that the eigenvalue problem

$$\begin{cases} -\Delta\psi = \lambda\psi, & x \in \Omega, \\ \dfrac{\partial\psi}{\partial\nu} = 0, & x \in \partial\Omega, \end{cases}$$

has eigenvalues $0 = \lambda_0 < \lambda_1 \leq \lambda_2 \leq \cdots \leq \lambda_n \leq \lambda_{n+1} \leq \ldots$, with the corresponding eigenfunctions $\psi_n(x)$. Substituting

$$y = \sum_{n=0}^{\infty} \psi_n(x) \begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix}$$

into the characteristic Eq. (7), we obtain

$$\begin{pmatrix} -\dfrac{\alpha}{\alpha+\beta}p - \lambda_n d_1 & -\dfrac{\beta}{\alpha+\beta}pe^{-\lambda\tau_1} \\ \mu e^{-\lambda\tau_2} & -\mu - \lambda_n d_2 \end{pmatrix} \begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix} = \lambda \begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix}, \quad n = 0, 1, 2, \ldots.$$

Therefore, the characteristic Eq. (7) is equivalent to

$$\Delta_n(\lambda, \tau) = \lambda^2 + A_n\lambda + B_n + Ce^{-\lambda\tau} = 0, \quad n = 0, 1, 2, \ldots, \tag{8_n}$$

where

$$A_n = \frac{\alpha}{\alpha+\beta}p + \mu + (d_1 + d_2)\lambda_n,$$

$$B_n = \left(\lambda_n d_1 + \frac{\alpha}{\alpha+\beta}p\right)(\lambda_n d_2 + \mu),$$

$$C = \mu\frac{\beta}{\alpha+\beta}p, \quad \text{and} \quad \tau = \tau_1 + \tau_2.$$

The stability/instability of constant coexistence equilibrium $(u, v) = (\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ can be determined by the distribution of the roots of Eqs. (8_n), $n = 0, 1, 2, \ldots$. The equilibrium $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ is locally asymptotically stable if all the roots of Eqs. (8_n), $n = 0, 1, 2, \ldots$ have negative real parts. From the result of [Ruan & Wei, 2007], the sum of the multiplicities of the roots of Eq. (8_n) in the open right half plane changes only if a root appears on or crosses the imaginary axis. It can be easily verified that 0 is not a root of Eqs. (8_n) for $n = 0, 1, 2, \ldots$, and all the roots of Eqs. (8_n), ($n = 0, 1, 2, \ldots$) have negative real parts when $\tau_1 = \tau_2 = 0$.

If $\pm i\sigma(\sigma > 0)$ is a pair of roots of Eq. (8_n), then we have

$$\begin{cases} \sigma^2 - B_n = C\cos\sigma\tau, \\ \sigma A_n = C\sin\sigma\tau, \end{cases} \quad n = 0, 1, 2, \ldots,$$

which lead to

$$\sigma^4 + (A_n^2 - 2B_n)\sigma^2 + B_n^2 - C^2 = 0, \quad n = 0, 1, 2, \ldots, \tag{9_n}$$

where

$$A_n^2 - 2B_n = \left(d_1\lambda_n + \frac{\alpha}{\alpha+\beta}p\right)^2 + (d_2\lambda_n + \mu)^2,$$

$$B_n^2 - C^2 = \left(\lambda_n d_1 + \frac{\alpha}{\alpha+\beta}p\right)^2 (\lambda_n d_2 + \mu)^2 - \left(\mu\frac{\beta}{\alpha+\beta}p\right)^2. \tag{10}$$

Then we know that if $\alpha \geq \beta$, $B_n^2 - C^2 \geq 0$ and Eqs. (9_n) has no positive roots for $n = 0, 1, 2, \ldots$. So all the roots of Eqs. (8_n) for $n = 0, 1, 2, \ldots$ have negative real parts. Then we arrive at the following result.

Proposition 1. *Suppose that $d_1, d_2, \mu, p > 0$, and $\alpha \geq \beta > 0$, then the constant coexistence equilibrium $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ of system (3) is locally asymptotically stable for any $\tau_1, \tau_2 \geq 0$.*

Proof. In the case of $\tau_1 = \tau_2 = 0$, we use the method in [Kim & Lin, 2008] to prove the local stability. Substituting $\lambda = \lambda_n\xi$ into Eq. (8_n), we have

$$\lambda_n^2\xi^2 + A_n\lambda_n\xi + B_n + C = 0.$$

Then denote

$$\phi_n(\xi) = \lambda_n^2\xi^2 + A_n\lambda_n\xi + B_n + C.$$

Since $\lambda_n \to \infty$ as $n \to \infty$, then we have that

$$\lim_{n\to\infty} \frac{\phi_n(\xi)}{\lambda_n^2} = \xi^2 + (d_1 + d_2)\lambda + d_1 d_2 \triangleq \tilde{\phi}(\xi).$$

Hence $\tilde{\phi}(\xi) = 0$ has two roots ξ_1, ξ_2 with negative real parts and there exists a negative constant

ϵ such that

$$\mathcal{R}e(\xi_1), \quad \mathcal{R}e(\xi_2) \le \epsilon.$$

Hence there exists $n_0 > 0$ such that for any $n > n_0$, the two roots $\xi_{n,1}, \xi_{n,2}$ of $\phi_n(\xi) = 0$ satisfy

$$\mathcal{R}e(\xi_{n,1}), \quad \mathcal{R}e(\xi_{n,2}) \le \epsilon/2.$$

Hence the real parts of all the roots of Eq. (8_n) are less than $\lambda_n\epsilon/2$ for any $n > n_0$. So we can choose $\tilde{\gamma} < 0$ such that all the roots λ of Eq. (8_n), ($n \ge 0$) satisfy $\mathcal{R}e(\lambda) \le \tilde{\gamma} < 0$, and consequently, we have the local stability of the positive equilibrium.

In the case of $\tau_1, \tau_2 > 0$, from [Wu, 1996, Chapter 3, Theorem 1.10], we have that for any given $\gamma < 0$, there exist only finite number of roots λ of Eq. (8_n), ($n \ge 0$) that satisfy $\mathcal{R}e(\lambda) \ge \gamma$. Since all the roots of Eq. (8_n), ($n \ge 0$) have negative real parts, we can choose $\tilde{\gamma} < 0$ such that all the roots λ of Eq. (8_n), ($n \ge 0$) satisfy $\mathcal{R}e(\lambda) \le \tilde{\gamma} < 0$, and consequently, we have the local stability of the positive equilibrium. ■

In Sec. 4, we will prove that when $\alpha > \beta$, then the constant coexistence equilibrium is indeed globally asymptotically stable for any τ_1, $\tau_2 \ge 0$.

If $\alpha < \beta$, then there exists $N_0 \ge 0$ such that for $0 \le n \le N_0$, Eq. (9_n) has a unique positive real root

$$\sigma_n = \left(\frac{-(A_n^2 - 2B_n) + \sqrt{(A_n^2 - 2B_n)^2 - 4(B_n^2 - C^2)}}{2}\right)^{\frac{1}{2}},$$

and Eq. (8_n) has a pair of pure imaginary roots $\pm i\sigma_n$ when

$$\tau = \tau_n^j = \tau_n^0 + \frac{2j\pi}{\sigma_n}, \quad j = 0, 1, 2, \ldots,$$
$$\text{and} \quad \tau_n^0 = \frac{\arccos \dfrac{\sigma_n^2 - B_n}{C}}{\sigma_n}. \tag{11}$$

The result of the distribution of the roots of single Eq. (8_n) can be found in [Ruan, 2009] a general form for DDEs modeling predator–prey systems. In this paper, the diffusion is considered, so the characteristic equations are not always single second degree transcendental polynomial equation. So we need to investigate them further in the following.

A more detailed description of $\tau = \tau_n^j$, for $j = 0, 1, 2, \ldots$ and $0 \le n \le N_0$ can be obtained. It is clear from (11) that $\tau_n^{j+1} > \tau_n^j$. The following lemma shows that

$$\tau_{N_0}^j \ge \tau_{n+1}^j \ge \tau_n^j \ge \cdots \ge \tau_1^j > \tau_0^j,$$

and hence we have a complete ordering of the bifurcation values τ_n^j.

Lemma 1. *Suppose that* $\alpha < \beta$, *then*

$$\tau_{N_0}^j \ge \tau_{n+1}^j \ge \tau_n^j \ge \cdots \ge \tau_1^j > \tau_0^j,$$

for $j = 0, 1, 2, \ldots$.

Proof. From the above analysis, we know

$$\sigma_n^2 = \frac{-(A_n^2 - 2B_n) + \sqrt{(A_n^2 - 2B_n)^2 - 4(B_n^2 - C^2)}}{2}$$
$$= \frac{2}{\sqrt{\dfrac{(A_n^2 - 2B_n)^2}{(C^2 - B_n^2)^2} + \dfrac{4}{C^2 - B_n^2}} + \dfrac{A_n^2 - 2B_n}{C^2 - B_n^2}},$$

where $A_n^2 - 2B_n$ and $B_n^2 - C^2$ are given in (10). Since $C^2 - B_n^2$ is decreasing in n and $A_n^2 - 2B_n$ is increasing in n and

$$0 = \lambda_0 < \lambda_1 \le \lambda_2 \le \cdots \le \lambda_n \le \lambda_{n+1} \le \cdots,$$

we obtain

$$\sigma_{N_0}^2 \le \cdots \le \sigma_{n+1}^2 \le \sigma_n^2 \le \cdots \le \sigma_1^2 < \sigma_0^2.$$

Also $\tau_n^j = \frac{\arccos \frac{\sigma_n^2 - B_n}{C} + 2j\pi}{\sigma_n}$, where $B_n = (\lambda_n d_1 + \frac{\alpha}{\alpha+\beta}p)(\lambda_n d_2 + \mu)$, thus we obtain that

$$\tau_{N_0}^j \ge \tau_{n+1}^j \ge \tau_n^j \ge \cdots \ge \tau_1^j > \tau_0^j,$$

for $j = 0, 1, 2, \ldots$. ■

Let $\kappa_n(\tau) = \gamma_n(\tau) + i\sigma_n(\tau)$ be the pair of roots of Eq. (8_n) satisfying $\gamma_n(\tau_n^j) = 0$ and $\sigma_n(\tau_n^j) = \sigma_n$ when τ is close to τ_n^j. Then we have the following transversality condition.

Lemma 2. *Suppose that* $\alpha < \beta$, *then* $\gamma_n'(\tau_n^j) > 0$ *for* $j = 0, 1, 2, \ldots,$ *and* $0 \le n \le N_0$.

Proof. Substituting $\lambda_n(\tau)$ into Eq. (8_n) and taking the derivatives with respect to τ yields

$$\left[\left.\frac{d\gamma_n}{d\tau}\right|_{\tau=\tau_n^j}\right]^{-1} = Re\left[\left.\left(\frac{2e^{\lambda\tau}}{C} + \frac{A_n e^{\lambda\tau}}{C\lambda} - \frac{\tau}{\lambda}\right)\right|_{\tau=\tau_n^j}\right] = \frac{2\cos\sigma_n\tau_n^j}{C} + \frac{A_n\sin\sigma_n\tau_n^j}{C\sigma_n}.$$

Since σ_n and τ_n^j satisfy $\sigma_n^2 - B_n = C\cos\sigma_n\tau_n^j$ and $\sigma_n A_n = C\sin\sigma_n\tau_n^j$, and from the expression of σ_n^2, then we have

$$\left[\left.\frac{d\gamma_n}{d\tau}\right|_{\tau=\tau_n^j}\right]^{-1} = \frac{2\sigma_n^2 - 2B_n}{C^2} + \frac{A_n^2}{C^2} = \frac{\sqrt{(A_n^2 - 2B_n)^2 - 4B_n^2 + 4C^2}}{C^2}.$$

Therefore $\gamma_n'(\tau_n^j) > 0$. ■

From this transversality condition, we know that when τ passes through these critical values τ_n^j, the sum of the multiplicities of the roots of Eq. (8_n) in the open right half plane will increase by at least two.

From Lemma 1 we know that $\tau_0^0 = \min\{\tau_n^j : 0 \le n \le N_0, j = 0, 1, 2, \ldots\}$. Denote $\tau_* = \tau_0^0$. Fix d_1, d_2, p, α, and choose β as a bifurcation parameter, then $\tau_*(\beta)$ can be regarded as a function of the bifurcation parameter β. It is clear that

$$\tau_*(\beta) = \frac{\arccos\dfrac{\sigma_0^2 - B_0}{C}}{\sigma_0}, \tag{12}$$

where

$$\sigma_0 = \left(\frac{-(A_0^2 - 2B_0) + \sqrt{(A_0^2 - 2B_0)^2 - 4(B_0^2 - C^2)}}{2}\right)^{\frac{1}{2}},$$

$$A_0 = \frac{\alpha}{\alpha+\beta}p + \mu, \quad B_0 = \mu\frac{\alpha}{\alpha+\beta}p, \quad \text{and} \quad C = \mu\frac{\beta}{\alpha+\beta}p.$$

Here we give a qualitative description of the function $\tau = \tau_*(\beta)$.

Theorem 1. *Suppose that $\alpha < \beta$, then the domain of the function $\tau = \tau_*(\beta)$ is (α, ∞),*

$$\lim_{\beta\to\alpha^+} \tau_*(\beta) = \infty, \quad \lim_{\beta\to+\infty} \tau_*(\beta) > 0,$$

and $\tau_*(\beta)$ is a strictly decreasing function of β.

Proof. Since $\tau^*(\beta)$ is well-defined for any $\beta > \alpha$, then the domain of $\tau = \tau_*(\beta)$ is (α, ∞). From the expression of $\tau_*(\beta)$ and $\lim_{\beta\to\alpha^+}\sigma_0(\beta) = 0$, we can easily obtain that $\lim_{\beta\to\alpha^+}\tau_*(\beta) = \infty$, and $\lim_{\beta\to\infty}\tau_*(\beta) > 0$.

To prove that $\tau_*(\beta)$ is a strictly decreasing function of β, we observe that

$$\sigma_0^2 = \frac{-(A_0^2 - 2B_0) + \sqrt{(A_0^2 - 2B_0)^2 - 4(B_0^2 - C^2)}}{2} = \frac{2}{\sqrt{\dfrac{(A_0^2 - 2B_0)^2}{(C^2 - B_0^2)^2} + \dfrac{4}{C^2 - B_0^2}} + \dfrac{A_0^2 - 2B_0}{C^2 - B_0^2}},$$

and

$$\frac{\sigma_0^2}{C} = \frac{-(A_0^2 - 2B_0) + \sqrt{(A_0^2 - 2B_0)^2 - 4(B_0^2 - C^2)}}{2C} = \frac{2}{\sqrt{\dfrac{(A_0^2 - 2B_0)^2C^2}{(C^2 - B_0^2)^2} + \dfrac{4C^2}{C^2 - B_0^2}} + \dfrac{C(A_0^2 - 2B_0)}{C^2 - B_0^2}}.$$

Since $C^2 - B_0^2$ is strictly increasing in β, $\frac{C^2 - B_0^2}{C}$ is strictly increasing in β, $\frac{B_0}{C}$ is strictly decreasing in β, and $A_0^2 - 2B_0$ is strictly decreasing in β, we can obtain that σ_0 and $\frac{\sigma_0^2}{C}$ are strictly increasing in β. Now from

$$\tau_*(\beta) = \frac{\arccos\dfrac{\sigma_0^2 - B_0}{C}}{\sigma_0},$$

and $\frac{B_0}{C}$ is strictly decreasing in β, we obtain that $\tau_*(\beta)$ is a strictly decreasing function of β. ■

From Lemmas 1 and 2, we obtain the following theorem.

Theorem 2. *Suppose that $d_1, d_2, \mu, p > 0$, and $\alpha < \beta$. Let τ_* be defined as in (12).*

(1) *If* $0 \le \tau_1 + \tau_2 < \tau_*$, *then the coexistence equilibrium* $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ *of system (3) is locally asymptotically stable*;
(2) *If* $\tau_1 + \tau_2 > \tau_*$, *then the coexistence equilibrium* $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ *of system (3) is unstable*;
(3) *The system (3) undergoes a Hopf bifurcation of homogeneous periodic orbits at* $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ *when* $\tau_1 + \tau_2 = \tau_*$, *that is, system (3) has a periodic orbit homogenous in space when* $\tau_1+\tau_2$ *is in* $(\tau_*, \tau_* + \epsilon)$ *or* $(\tau_* - \epsilon, \tau_*)$ *for sufficiently small* ϵ.

Proof. When $\tau_1 = \tau_2 = 0$, all the roots of Eq. (8_n), $n = 0, 1, 2, \ldots$ have negative real parts. Recall that $\tau_* = \min\{\tau_n^j : 0 \le n \le N_0, j = 0, 1, 2, \ldots\}$. From Lemma 2 and Corollary 2.4 of [Ruan & Wei, 2007], we obtain that if $0 \le \tau_1 + \tau_2 < \tau_*$, all the roots of Eq. (8_n), $n = 0, 1, 2, \ldots$ have negative real parts, and if $\tau_1 + \tau_2 > \tau_*$, Eq. (8_n), $n = 0, 1, 2, \ldots$ have at least a pair of roots with positive real parts. So when $0 \le \tau_1 + \tau_2 < \tau_*$, then $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ of system (3) is locally asymptotically stable, and when $\tau_1+\tau_2 > \tau_*$, then $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ of system (3) is unstable. When $\tau_1 + \tau_2 = \tau_*$, Eq. (8_n), $n = 0, 1, 2, \ldots$, have a pair of purely imaginary roots. From Lemma 2 we know that the roots satisfy the transversality condition. So system (3) undergoes a Hopf bifurcation at $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ when $\tau_1 + \tau_2 = \tau_*$. Since $\tau_* = \tau_0^0$, these bifurcating periodic orbits are spatially homogeneous ones. ■

Theorem 2 shows that if $\alpha < \beta$, the coexistence equilibrium of the delayed diffusive predator–prey system (3) loses its stability through a Hopf bifurcation, and the bifurcating spatially homogeneous periodic orbits are in fact the periodic orbits of the corresponding delayed predator–prey system without diffusion.

3. Global Stability

In this section, we prove that when $\alpha > \beta$, the constant coexistence equilibrium is indeed globally asymptotically stable. To achieve that we utilize upper-lower solution method in [Pao, 1996, 2002]. In the following theorem we use the same notation as that in [Pao, 2002], that is, $(u_1(t,x), v_1(t,x)) > (u_2(t,x), v_2(t,x))$ denote $u_1(t,x) > u_2(t,x)$, and $v_1(t,x) > v_2(t,x)$.

Theorem 3. *Suppose that* $d_1, d_2, \mu, p > 0, \alpha > \beta > 0$ *and* $\tau_1, \tau_2 \ge 0$. *Then for any initial value* $(u_0(x,t), v_0(x,t)) > (0,0)$, *the corresponding positive solution* $(u(x,t), v(x,t))$ *of system (3) converges uniformly to* $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ *as* $t \to +\infty$.

Proof. From the maximum principle of parabolic equations, we obtain that for any initial value $(u_0(x,t), v_0(x,t)) > (0,0)$, the corresponding nonnegative solution $(u(x,t), v(x,t))$ are strictly positive for $t > 0$. We choose ϵ so that

$$0 < \epsilon < \frac{p}{\beta} - \frac{p}{\alpha}.$$

It is well-known that if $w(t,x)$ satisfies a diffusive logistic equation

$$\begin{cases} \dfrac{\partial w}{\partial t} - d\Delta w = w(a - bw), & x \in \Omega, \quad t > 0, \\ \dfrac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ w(0,x) = w_0(x) \ge (\not\equiv) 0, & x \in \Omega, \end{cases}$$

where $d, a, b > 0$, then $w(t,x) \to a/b$ uniformly for $x \in \overline{\Omega}$ as $t \to \infty$.

Because u satisfies

$$\begin{aligned} \frac{\partial u(t,x)}{\partial t} - d_1\Delta u &= u(p - \alpha u - \beta v(t - \tau_1)) \\ &\le u(p - \alpha u), \end{aligned}$$

then from comparison principle of parabolic equations and the convergence for diffusive logistic equation, there exists $t_1 > 0$ such that $u(t,x) < \frac{p}{\alpha} + \epsilon$ for $t \ge t_1$, and consequently

$$\begin{aligned} \frac{\partial v(t,x)}{\partial t} - d_2\Delta v &= \mu v\left(1 - \frac{v}{u(t - \tau_2)}\right) \\ &< \mu v\left(1 - \frac{v}{(p/\alpha) + \epsilon}\right), \end{aligned}$$

for $t \ge t_1 + \tau_2$. Again from the comparison principle and the result for diffusive logistic equation, there exists $t_2 > t_1$ satisfying $u(t,x) < \frac{p}{\alpha} + \epsilon$ and $v(t,x) < \frac{p}{\alpha} + \epsilon$ for any $t \ge t_2$. Since $(u, v) > (0,0)$ for $t > 0$ and $x \in \Omega$, then for sufficiently small $0 < \delta < 1$, there exists $t_* > t_2 + \tau$ such that $(u(t,x), v(t,x)) > (\frac{\delta}{\alpha}(p - \beta(\frac{p}{\alpha} + \epsilon)), \frac{\delta}{\alpha}(p - \beta(\frac{p}{\alpha} + \epsilon))) > (0,0)$ for any $t \in [t_* - \tau, t_*]$. In summary, for any initial value $(u_0(x,t), v_0(x,t)) > (0,0)$, there exists $t_*(u_0, v_0)$ such that the corresponding positive solution $(u(x,t), v(x,t))$

satisfying

$$\left(\frac{\delta}{\alpha}\Big(p-\beta\Big(\frac{p}{\alpha}+\epsilon\Big)\Big), \frac{\delta}{\alpha}\Big(p-\beta\Big(\frac{p}{\alpha}+\epsilon\Big)\Big)\right) < (u(x,t),v(x,t)) \le \left(\frac{p}{\alpha}+\epsilon, \frac{p}{\alpha}+\epsilon\right)$$

for any $t \in [t_* - \tau, t_*]$.

Denote $(\tilde{c}_1, \tilde{c}_2) = (\frac{p}{\alpha}+\epsilon, \frac{p}{\alpha}+\epsilon)$ and $(\hat{c}_1,\hat{c}_2) = (\frac{\delta}{\alpha}(p-\beta(\frac{p}{\alpha}+\epsilon)), \frac{\delta}{\alpha}(p-\beta(\frac{p}{\alpha}+\epsilon)))$, then $(0,0) < (\hat{c}_1,\hat{c}_2) < (\tilde{c}_1,\tilde{c}_2)$ and

$$0 \ge \tilde{c}_1(p-\alpha\tilde{c}_1-\beta\hat{c}_2), \quad 0 \ge \mu\tilde{c}_2\left(1-\frac{\tilde{c}_2}{\tilde{c}_1}\right),$$

$$0 \le \hat{c}_1(p-\alpha\hat{c}_1-\beta\tilde{c}_2), \quad 0 \le \mu\hat{c}_2\left(1-\frac{\hat{c}_2}{\hat{c}_1}\right).$$

It is clear that there exists $K>0$ such that for any $(\hat{c}_1,\hat{c}_2) \le (u_1,v_1),(u_2,v_2) \le (\tilde{c}_1,\tilde{c}_2)$,

$$|u_1(p-\alpha u_1-\beta v_1) - u_2(p-\alpha u_2-\beta v_2)| \le K(|u_1-u_2|+|v_1-v_2|),$$

$$\left|\mu v_1\left(1-\frac{v_1}{u_1}\right) - \mu v_2\left(1-\frac{v_2}{u_2}\right)\right| \le K(|u_1-u_2|+|v_1-v_2|).$$

We define two iterate sequences $(\tilde{c}_1^m, \tilde{c}_2^m)$ and $(\hat{c}_1^m,\hat{c}_2^m)$ as follows: for $m \ge 1$,

$$\tilde{c}_1^m = \tilde{c}_1^{m-1} + \frac{1}{K}\tilde{c}_1^{m-1}(p-\alpha\tilde{c}_1^{m-1}-\beta\hat{c}_2^{m-1}),$$

$$\tilde{c}_2^m = \tilde{c}_2^{m-1} + \frac{1}{K}\tilde{\mu}c_2^{m-1}\left(1-\frac{\tilde{c}_2^{m-1}}{\tilde{c}_1^{m-1}}\right),$$

$$\hat{c}_1^m = \hat{c}_1^{m-1} + \frac{1}{K}\hat{c}_1^{m-1}(p-\alpha\hat{c}_1^{m-1}-\beta\tilde{c}_2^{m-1}),$$

$$\hat{c}_2^m = \hat{c}_2^{m-1} + \frac{1}{K}\mu\hat{c}_2^{m-1}\left(1-\frac{\hat{c}_2^{m-1}}{\hat{c}_1^{m-1}}\right),$$

where $(\tilde{c}_1^0,\tilde{c}_2^0) = (\tilde{c}_1,\tilde{c}_2)$ and $(\hat{c}_1^0,\hat{c}_2^0) = (\hat{c}_1,\hat{c}_2)$.

Then for $m \ge 1, (\hat{c}_1,\hat{c}_2) \le (\hat{c}_1^m,\hat{c}_2^m) \le (\hat{c}_1^{m+1},\hat{c}_2^{m+1}) \le (\tilde{c}_1^{m+1},\tilde{c}_2^{m+1}) \le (\tilde{c}_1^m,\tilde{c}_2^m) \le (\tilde{c}_1, \tilde{c}_2)$, there exist $(\bar{c}_1,\bar{c}_2) > (0,0)$ and $(\check{c}_1,\check{c}_2) > (0,0)$ satisfying $\lim_{m\to\infty}\tilde{c}_1^m = \bar{c}_1, \lim_{m\to\infty}\tilde{c}_2^m = \bar{c}_2, \lim_{m\to\infty}\hat{c}_1^m = \check{c}_1, \lim_{m\to\infty}\hat{c}_2^m = \check{c}_2$ and

$$0 = \bar{c}_1(p-\alpha\bar{c}_1-\beta\check{c}_2), \quad 0 = \mu\bar{c}_2\left(1-\frac{\bar{c}_2}{\bar{c}_1}\right),$$

$$0 = \check{c}_1(p-\alpha\check{c}_1-\beta\bar{c}_2), \quad 0 = \mu\check{c}_2\left(1-\frac{\check{c}_2}{\check{c}_1}\right).$$

Since $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ is the unique positive constant equilibrium of (3), then we must have $(\bar{c}_1,\bar{c}_2) = (\check{c}_1,\check{c}_2) = (\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$. Then from Theorem 2.2 of [Pao, 2002], we obtain that for any non-negative initial value $(u_0(x,t),v_0(x,t))$ satisfying $(\hat{c}_1,\hat{c}_2) < (u_0(x,t),v_0(x,t)) < (\tilde{c}_1,\tilde{c}_2)$, the corresponding non-negative solution $(u(x,t),v(x,t))$ of (3) converges uniformly to $(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta})$ as $t\to\infty$. Since for any initial value $(u_0(x,t),v_0(x,t)) > (0,0)$, there exists $t_*(u_0,v_0)$ such that the corresponding positive solution $(u(x,t),v(x,t))$ satisfying

$$(\hat{c}_1,\hat{c}_2) < (u,v) < (\tilde{c}_1,\tilde{c}_2)$$

for $t \in [t_*-\tau, t_*]$, then we obtain the desired conclusion. ■

4. Conclusions

From Theorems 1–3, we obtain a rather complete picture of the dynamics of system (3). When $\beta < \alpha$, then the positive constant equilibrium attracts all the solutions with positive initial values for all delays $\tau_1, \tau_2 \ge 0$. However when $\beta > \alpha$, the delays affect the stability of the constant existence equilibrium, that is, the coexistence equilibrium loses its stability through a Hopf bifurcation when $\tau_1+\tau_2$ increases. Hence, $\beta = \alpha$ can be regarded as a threshold parameter value for different qualitative behavior. Note that $\tau_*(\beta)$ is a strictly decreasing function of β (Theorem 1), hence we can illustrate our results in a bifurcation diagram as in Fig. 1.

Finally we use some numerical simulations to end our discussions. We fix $d_1 = 0.1, d_2 = 0.2$,

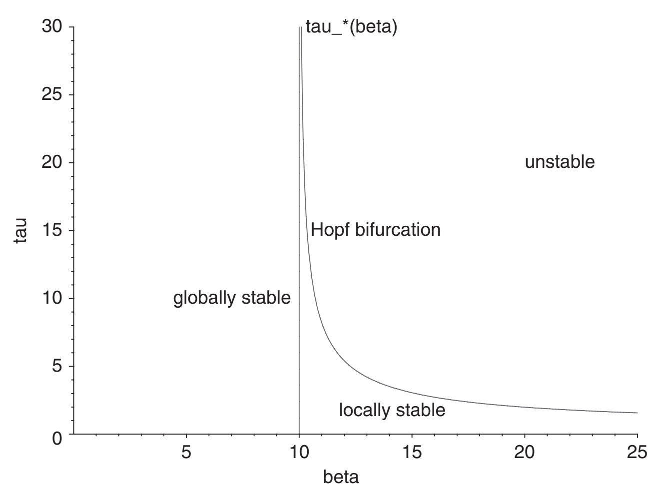

Fig. 1. Bifurcation diagram with parameters β and $\tau = \tau_1+\tau_2$. Here $d_1 = 0.1, d_2 = 0.2, \alpha = 10, \mu = 1, p = 2$.

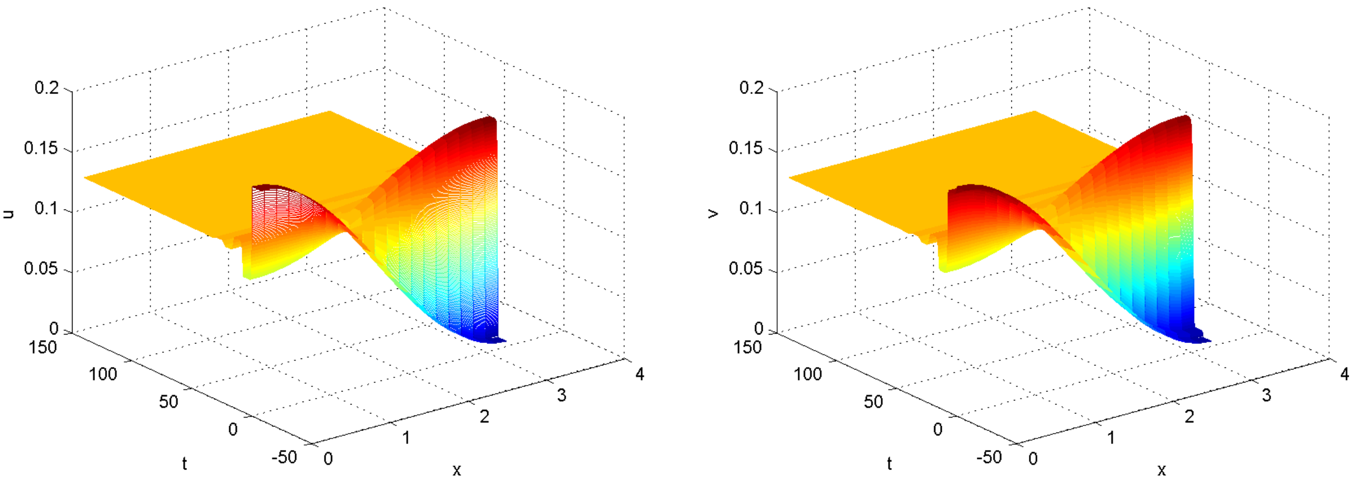

Fig. 2. Convergence to constant equilibrium in the global stability region. Here $\beta = 5, \tau_1 = 0, \tau_2 = 7$, and initial values: $u(x,0) = 0.1 + 0.09\cos x, x \in [0,\pi], v(x,t) = 0.1 + 0.09\cos x, x \in [0,\pi], t \in [-7,0]$.

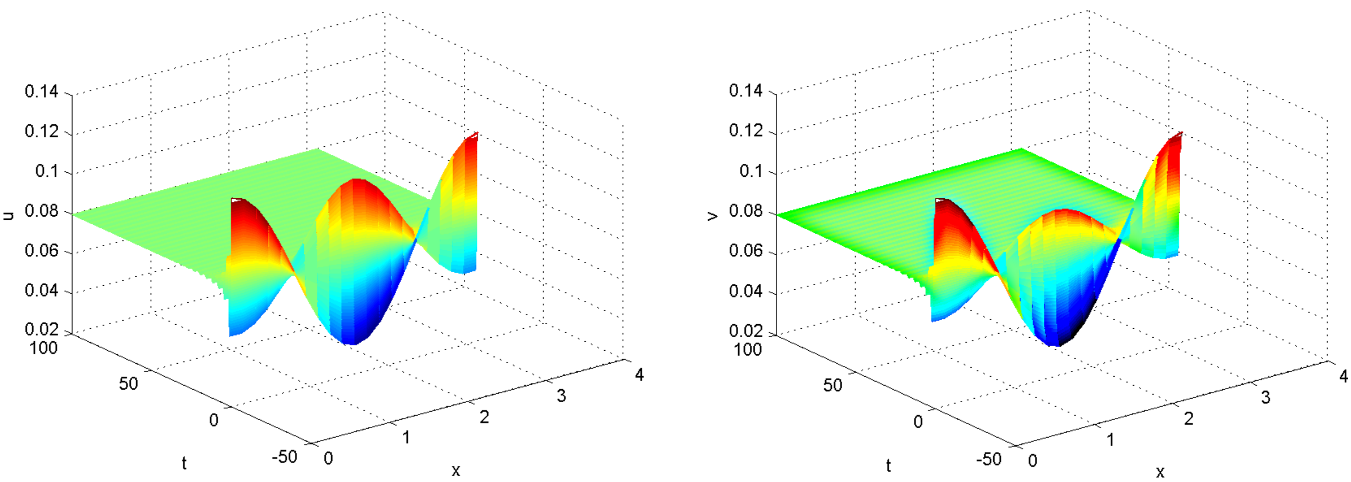

Fig. 3. Convergence to constant equilibrium in the local stability region. Here $\beta = 15$, $\tau_1 = 0$, $\tau_2 = 1$, and initial values: $u(x,0) = 0.08 + 0.45\cos 2x, x \in [0,\pi], v(x,t) = 0.08 + 0.45\cos x, x \in [0,\pi], t \in [-1,0]$. In this case, the Hopf bifurcation value $\tau_* = 3.06$.

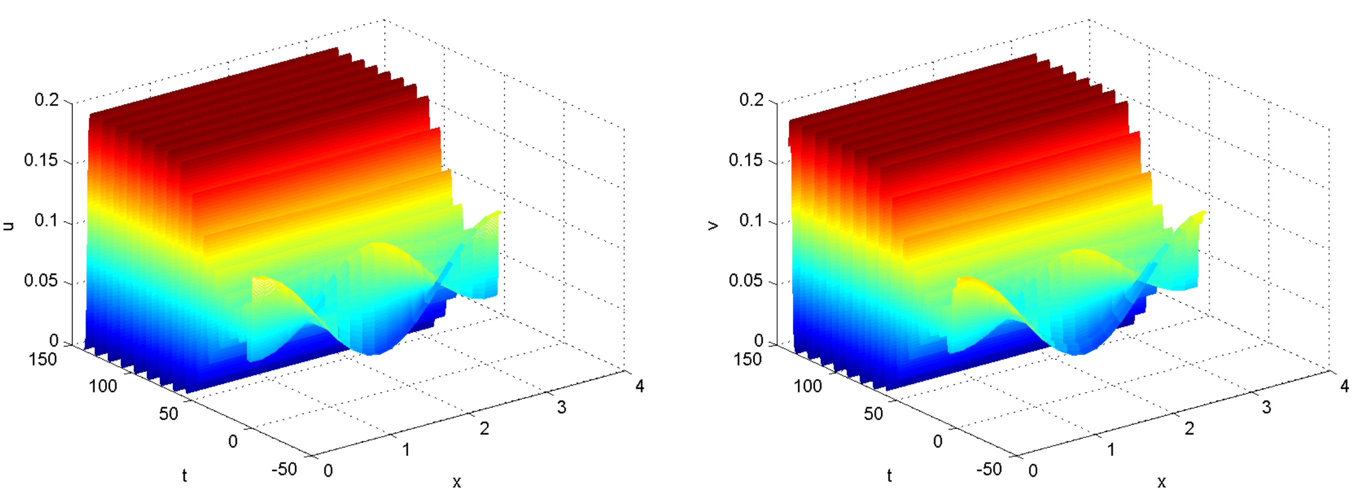

Fig. 4. Convergence to spatially homogeneous periodic orbit in the unstable region. Here $\beta = 15$, $\tau_1 = 0$, $\tau_2 = 3.5$, and initial values: $u(x,0) = 0.08 + 0.45\cos 2x, x \in [0,\pi], v(x,t) = 0.08 + 0.45\cos x, x \in [0,\pi], t \in [-3.5,0]$. In this case, the Hopf bifurcation value $\tau_* = 3.06$.

$\alpha = 10, \mu = 1, p = 2$ and let $\Omega = (0, \pi)$ in the following. In all figures, the left panel shows the graph of $u(x,t)$ and the right panel shows the one of $v(x,t)$.

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