



A note on Hopf bifurcations in a delayed diffusive Lotka–Volterra predator–prey system[☆]

Shanshan Chen^a, Junping Shi^b, Junjie Wei^{a,*}

^a Department of Mathematics, Harbin Institute of Technology, Harbin, Heilongjiang, 150001, PR China

^b Department of Mathematics, College of William and Mary, Williamsburg, VA, 23187-8795, USA

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ABSTRACT

The diffusive Lotka–Volterra predator–prey system with two delays is reconsidered here. The stability of the coexistence equilibrium and associated Hopf bifurcation are investigated by analyzing the characteristic equations, and our results complement earlier ones. We also obtain that in a special case, a Hopf bifurcation of spatial inhomogeneous periodic solutions occurs in the system.

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1. Introduction

Partial functional-differential equations have been proposed as mathematical models for biological phenomena by many researchers in recent years. In the last 15 years especially, the stability/instability and bifurcation of equilibrium solutions for reaction–diffusion equations/systems with a delay effect have been considered extensively. The theory of partial functional-differential equations and the related bifurcation theory have been developed for analyzing various mathematical questions that have arisen from models of population biology, biochemical reactions and other applications [1–4].

For the models with a single population, So and Yang [5] investigated the global attractivity of the equilibrium for the diffusive Nicholson's blowflies equation with Dirichlet boundary condition; So, Wu and Yang [6] and Su et al. [7] also studied the Hopf bifurcation on the diffusive Nicholson's blowflies equation with Dirichlet boundary condition; Yi and Zou [8] investigated the global attractivity of the diffusive Nicholson blowflies equation with Neumann boundary condition; Busenberg and Huang [9], and Su, Wei and Shi [10] investigated the Hopf bifurcation of a reaction–diffusion population model with delay and Dirichlet boundary condition, which occurs at the spatially inhomogeneous equilibrium; Davidson and Gourley [11] (and also [10]) studied the dynamics of a diffusive food-limited population model with delay and Dirichlet boundary condition. For multiple-population models, there are many results on predator–prey systems (see e.g. [12–20]).

In this work we consider the following Lotka–Volterra predator–prey system:

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = d_1 \frac{\partial^2 u(t, x)}{\partial x^2} + u(t, x)[r_1 - a_1 u(t, x) - a_2 v(t - \nu, x)], & t > 0, x \in (0, \pi), \\ \frac{\partial v(t, x)}{\partial t} = d_2 \frac{\partial^2 v(t, x)}{\partial x^2} + v(t, x)[-r_2 + a_3 u(t - \tau, x) - a_4 v(t, x)], & t > 0, x \in (0, \pi), \\ \frac{\partial u(t, x)}{\partial x} = \frac{\partial v(t, x)}{\partial x} = 0, & t \geq 0, x = 0, \pi, \end{cases} \quad (1.1)$$

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* Corresponding author.

E-mail address: weijj@hit.edu.cn (J. Wei).

where $u(t, x)$ and $v(t, x)$ are interpreted as the densities of prey and predator populations. Moreover, τ, r_1, r_2, a_2, a_3 are positive constants and ν, a_1, a_4 are non-negative constants. More biological explanation of the above delayed diffusive Lotka–Volterra prey–predator system can be found in [12].

In [12], Faria assumed that

$$a_3r_1 - a_1r_2 > 0, \tag{1.2}$$

and then system (1.1) has a positive equilibrium

$$E_* = (u_*, v_*) = \left(\frac{a_2r_2 + a_4r_1}{a_1a_4 + a_2a_3}, \frac{a_3r_1 - a_1r_2}{a_1a_4 + a_2a_3} \right).$$

Due to the difficulties in the analysis of the characteristic equations, Faria studied the instability of the equilibrium E_* and associated Hopf bifurcations with some assumptions on the coefficients in reaction terms. In [4], Wu studied the Hopf bifurcation of system (1.1) when $\nu = 0, a_4 = 0$, and he obtained that under some assumptions on the coefficients, then the system (1.1) can give rise to a Hopf bifurcation of spatially inhomogeneous periodic solutions.

In this paper we also assume (1.2); hence the system (1.1) possesses a positive equilibrium E_* . In this note, we obtain two new results for (1.1) which complement the ones in [12]. First we show that a similar instability analysis of E_* holds when the two diffusion coefficients are close to each other but without additional conditions on the coefficients in the reaction terms. Secondly we prove that in a special case of $a = b = 0$ and $d_1 = d_2$, a Hopf bifurcation of spatially inhomogeneous periodic solutions occurs and the bifurcating periodic solutions are unstable.

The rest of the paper is organized as follows. In Section 2, we analyze the stability of the positive equilibrium E_* through the study of the characteristic equations. We show some results on the distribution of the roots of the characteristic equations and these results are supplementary to the ones in Faria [12]. We also show that the positive equilibrium E_* can be destabilized through a Hopf bifurcation as τ increases when the two diffusion coefficients are close to each other. In Section 3, we consider a special case when $a = b = 0$ and $d_1 = d_2$.

2. Stability analysis and bifurcation

In this section, we will carry out the analysis of stability and Hopf bifurcation of the system (1.1) and give some results supplementary to those of Faria [12].

In [12], after the time-scaling $t \rightarrow t/\tau$, the change of variables $u \rightarrow a_3u = \bar{u}, v \rightarrow a_2v = \bar{v}$, and dropping the bars for simplification, system (1.1) is transformed into

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = \tau d_1 \frac{\partial^2 u(t, x)}{\partial x^2} + \tau u(t, x)[r_1 - au(t, x) - v(t - r, x)], & t > 0, x \in (0, \pi), \\ \frac{\partial v(t, x)}{\partial t} = \tau d_2 \frac{\partial^2 v(t, x)}{\partial x^2} + \tau v(t, x)[-r_2 + u(t - 1, x) - bv(t, x)], & t > 0, x \in (0, \pi), \\ \frac{\partial u(t, x)}{\partial x} = \frac{\partial v(t, x)}{\partial x} = 0, & t \geq 0, x = 0, \pi, \end{cases} \tag{2.1}$$

where $r = \nu/\tau, a = a_1/a_3, b = a_4/a_2$. The positive equilibrium $E_* = (u_*, v_*)$ is now given by

$$u_* = \frac{r_2 + br_1}{ab + 1}, \quad v_* = \frac{r_1 - ar_2}{ab + 1},$$

with the assumptions (which we will always assume in the rest of this paper)

$$r_1 > 0, \quad r_2 > 0, \quad r \geq 0, \quad a \geq 0, \quad b \geq 0, \quad r_1 - ar_2 > 0. \tag{2.2}$$

From [12] (5.6_k), we know that the characteristic equations for the equilibrium E_* are

$$\Delta_k(\lambda, \tau) = \lambda^2 + A_k\tau\lambda + B_k\tau^2 + C_*\tau^2e^{-\lambda(1+r)}, \quad k = 0, 1, 2, \dots, \tag{2.3_k}$$

where

$$A_k = d_1k^2 + d_2k^2 + au_* + bv_*, \quad B_k = (d_1k^2 + au_*)(d_2k^2 + bv_*), \quad \text{and} \quad C_* = u_*v_*.$$

If $i\sigma_k (\sigma_k > 0)$ is a root of Eq. (2.3_k), then we have

$$\begin{cases} \sigma_k^2 - B_k\tau^2 = C_*\tau^2 \cos \sigma_k(1 + r), \\ \sigma_k A_k = C_*\tau^2 \sin \sigma_k(1 + r), \end{cases}$$

which leads to

$$\rho^4 + (A_k^2 - 2B_k)\rho^2 + B_k^2 - C_*^2 = 0, \tag{2.4}$$

where

$$A_k^2 - 2B_k = (d_1^2 + d_2^2)k^4 + 2(d_1au_* + d_2bv_*)k^2 + (a^2u_*^2 + b^2v_*^2) \geq 0,$$

$$B_k^2 - C_*^2 = (d_1k^2 + au_*)^2(d_2k^2 + bv_*)^2 - u_*^2v_*^2, \quad \text{and} \quad \rho = \frac{\sigma_k}{\tau}.$$

So if

$$ab \geq 1, \tag{2.5}$$

then $B_k^2 - C_*^2 > 0$, and Eqs. (2.3_k), $k \geq 0$, have no imaginary roots, and if

$$ab < 1, \tag{2.6}$$

then there is an integer K_0 such that Eq. (2.4) has a positive real root

$$\rho_k = \frac{1}{\sqrt{2}} \left[2B_k - A_k^2 + \sqrt{(2B_k - A_k^2)^2 - 4(B_k^2 - C_*^2)} \right]^{1/2}$$

if $k \leq K_0$ and has no positive real roots if $k > K_0$. So Eqs. (2.3_k), $k > K_0$, have no imaginary roots and each of Eqs. (2.3_k), $k \leq K_0$, has only a couple of imaginary roots $\pm i\sigma_n^k$ at τ_n^k where

$$\sigma_n^k = \frac{\arccos \frac{\rho_k^2 - B_k}{C_*} + 2n\pi}{1 + r}, \quad n = 0, 1, 2, \dots, \quad k = 0, 1, \dots, K_0,$$

$$\tau_n^k = \frac{\sigma_n^k}{\rho_k}, \quad n = 0, 1, 2, \dots, \quad k = 0, 1, \dots, K_0,$$

if $ab < 1$ and $a^2 + b^2 > 0$.

If $a = b = 0$, then

$$\sigma_n^0 = \frac{2(n + 1)\pi}{1 + r}, \quad n = 0, 1, 2, \dots,$$

$$\tau_n^0 = \frac{\sigma_n^0}{\rho_0}, \quad n = 0, 1, 2, \dots,$$

and σ_n^k, τ_n^k ($k \geq 1$) are the same as those above.

If $d_1 = d_2 = d$, then

$$A_k = 2m_k + p, \quad B_k = m_k^2 + m_kp + q,$$

where

$$m_k = dk^2, \quad p = au_* + bv_*, \quad q = abu_*v_*,$$

and

$$2B_k - A_k^2 = -2m_k^2 - 2m_kp - (a^2u_*^2 + b^2v_*^2),$$

$$B_k^2 - C_*^2 = (m_k^2 + m_kp + q)^2 - C_*^2.$$

Hence we have the following lemma.

Lemma 2.1. Assume that $d_1 = d_2 = d$.

1. If $ab < 1$ and $a^2 + b^2 > 0$ are satisfied, then

$$\tau_n^{k+1} > \tau_n^k, \quad 0 \leq k \leq K_0, \quad n = 0, 1, \dots$$

2. If $a = b = 0$ is satisfied, then

$$\tau_n^{k+1} > \tau_n^k, \quad 1 \leq k \leq K_0, \quad n = 0, 1, \dots$$

Proof. When $d_1 = d_2$, we have

$$\rho_k^2 = \frac{1}{2} \left[\sqrt{(p^2 - 4q)(4m_k^2 + 4m_kp + p^2) + 4C_*^2} - 2m_k^2 - 2m_kp + 2q - p^2 \right],$$

$$\rho_k^2 - B_k = \frac{1}{2} \left[\sqrt{(p^2 - 4q)(4m_k^2 + 4m_kp + p^2) + 4C_*^2} - 4m_k^2 - 4m_kp - p^2 \right].$$

If $p^2 - 4q = 0$, it is obvious that $\tau_n^{k+1} > \tau_n^k$, so we assume that $p^2 - 4q > 0$ since $p^2 - 4q \geq 0$.

Suppose that

$$x = \sqrt{(p^2 - 4q)(4m_k^2 + 4m_k p + p^2) + 4C_*^2};$$

then

$$x \geq \sqrt{(p^2 - 4q)p^2 + 4C_*^2},$$

and

$$\tau_n^k = \frac{\arccos\left(\frac{x - \frac{x^2 - 4C_*^2}{p^2 - 4q}}{2C_*}\right) + 2n\pi}{\frac{1+r}{\sqrt{2}}\left(x - \frac{x^2 - 4C_*^2}{2(p^2 - 4q)} - \frac{1}{2}p^2 + 2q\right)^{\frac{1}{2}}} \stackrel{\text{def}}{=} g(x).$$

It is easy to verify that if $y > z \geq p^2 - 4q$ and y, z are in the domain of g , then $g(y) > g(z)$.

So we can obtain that if $ab < 1$ and $a^2 + b^2 > 0$ are satisfied, then

$$\tau_n^{k+1} > \tau_n^k, \quad 0 \leq k \leq K_0, \quad n = 0, 1, \dots,$$

and if $a = b = 0$ is satisfied, then

$$\tau_n^{k+1} > \tau_n^k, \quad 1 \leq k \leq K_0, \quad n = 0, 1, \dots \quad \square$$

It is obvious that $\tau_{n+1}^k > \tau_n^k$, so we have $\tau_0^0 = \min\{\tau_n^k\}_{0 \leq k \leq K_0, n=0,1,\dots}$ if $d_1 = d_2 = d, ab < 1$, and $a^2 + b^2 > 0$. From Lemma 2.1 and the continuous dependence of τ_n^k on d_1 and d_2 we have the following proposition.

Proposition 2.2. Assume that (2.2) holds, $ab < 1$, and $a^2 + b^2 > 0$; then there exists an $\epsilon \in (d, a, b, r_i, r)$ such that for any $d_1, d_2 \in (d - \epsilon, d + \epsilon)$, $\tau_0^0 = \min\{\tau_n^k\}_{0 \leq k \leq K_0, n=0,1,\dots}$.

Suppose that $\lambda_k(\tau) = \mu_k(\tau) + i\sigma_k(\tau)$ is the root of Eq. (2.3_k) satisfying

$$\mu_k(\tau_n^k) = 0, \quad \sigma_k(\tau_n^k) = \pm\sigma_n^k;$$

then using the same method as in [12, Theorem 3.2] we have the following transversality result.

Lemma 2.3. Assume that (2.2) holds, $ab < 1$, and $a^2 + b^2 > 0$; then $\mu'_k(\tau_n^k) > 0$ for $0 \leq k \leq K_0$ and $n = 0, 1, 2, \dots$

From Lemma 2.3, Proposition 2.2, [12, Theorem 3.3] and [3, Theorem 3.3.2], we have the following conclusions on the distribution of the roots of Eqs. (2.3_k), $k \geq 0$.

Lemma 2.4. Assume that (2.2) holds.

1. When $ab \geq 1$, then all of the roots of Eqs. (2.3_k) ($k \geq 0$) have negative real parts for $\tau \in [0, \infty)$.
2. When $ab < 1$ and $a^2 + b^2 > 0$, then for any $d > 0$ there exists an $\epsilon \in (d, a, b, r_i, r)$ defined in Proposition 2.2 such that for any $d_1, d_2 \in (d - \epsilon, d + \epsilon)$:
 - (i) If $\tau \in [0, \tau_0^0)$, then all of the roots of Eqs. (2.3_k) ($k \geq 0$) have negative real parts.
 - (ii) If $\tau = \tau_0^0$, then all of the roots of Eq. (2.3₀) except $\pm i\sigma_0^0$ and Eq. (2.3_k) ($k \geq 1$) have negative real parts.
 - (iii) If $\tau \in (\tau_0^0, \min(\tau_1^0, \tau_1^1))$, Eq. (2.3₀) has only one pair of roots with positive real parts, and all of the roots of Eqs. (2.3_k) ($k \geq 1$) have negative real parts.
 - (iv) If $\tau > \min(\tau_1^0, \tau_1^1)$, then Eqs. (2.3_k) ($k \geq 0$) have at least two pair of roots with positive real parts.

This lemma gives the spectral properties when d_1 and d_2 are close to each other, which is complementary to Theorem 5.1 of Faria [12]. Remarkably in this theorem τ_0^0 equals τ_0 of [12], and σ_0^0 equals σ_0 of [12]. Here we do not assume $ab(a u_* + b v_*)^2 \leq u_* v_*$ as in [12] but we have the additional assumption on the diffusion coefficients d_1 and d_2 . Spectral properties in Lemma 2.4 immediately lead to the following results on the dynamics of system (1.1) (or equivalently (2.1)).

Theorem 2.5. Consider system (1.1), and assume that (2.2) holds.

1. If $ab \geq 1$, then E_* is locally asymptotically stable.
2. If $ab < 1$ and $a^2 + b^2 > 0$, then for any $d > 0$ there exists an $\epsilon \in (d, a, b, r_i, r)$ defined in Proposition 2.2 such that for any

$$d_1, d_2 \in (d - \epsilon, d + \epsilon),$$

E_* is locally asymptotically stable when $\tau \in [0, \tau_0^0)$, and is unstable when $\tau > \tau_0^0$. Furthermore, the system undergoes a Hopf bifurcation of spatially homogeneous periodic orbits at E_* when $\tau = \tau_0^0$.

From this theorem we know that when the diffusion coefficients for the prey and predator are very close to each other in the delayed diffusive Lotka–Volterra prey–predator system, the diffusion terms have no impact on the local stability of the positive equilibrium E_* . Here we also do not assume $ab(a u_* + b v_*)^2 \leq u_* v_*$ as in [12] but we have an additional assumption on the diffusion coefficients d_1 and d_2 .

3. A special case

In this section we will analyze system (1.1) (or equivalently (2.1)) in the special case when $a = b = 0$ and $d_1 = d_2 = d$. It can be easily verified that

$$\tau_n^k = \frac{\arccos\left(1 - \frac{2d^2k^4}{C_*}\right) + 2n\pi}{(1+r)\sqrt{C_* - d^2k^4}}, \quad 1 \leq k \leq K_0, \quad \text{and} \quad n = 0, 1, 2, \dots,$$

$$\tau_n^0 = \frac{2(n+1)\pi}{(1+r)\sqrt{C_*}}, \quad n = 0, 1, 2, \dots$$

From [12, Theorem 3.4] and Lemma 2.1, we obtain:

Theorem 3.1. Assume that (2.2) holds, $a = b = 0$, and $d_1 = d_2 = d$.

1. When $d^2 - C_* \geq 0$, then all of the roots of Eqs. (2.3_k) ($k \geq 1$) have negative real parts for $\tau \in [0, \infty)$.
2. When $d^2 - C_* < 0$:
 - (i) If

$$\tau_0^1 = \frac{\arccos\left(1 - \frac{2d^2}{C_*}\right)}{(1+r)\sqrt{C_* - d^2}} > \frac{2\pi}{(1+r)\sqrt{C_*}} = \tau_0^0, \tag{3.1}$$

then all of the roots of Eqs. (2.3_k) ($k \geq 1$) have negative real parts for $\tau \in [0, \tau_0^0]$.

- (ii) If

$$\tau_0^1 = \frac{\arccos\left(1 - \frac{2d^2}{C_*}\right)}{(1+r)\sqrt{C_* - d^2}} < \frac{2\pi}{(1+r)\sqrt{C_*}} = \tau_0^0, \tag{3.2}$$

then a Hopf bifurcation of spatially inhomogeneous periodic solutions occurs at E_* for system (1.1) and these spatially inhomogeneous periodic solutions are unstable when τ is near τ_0^1 .

Proof. When $a = b = 0, d_1 = d_2 = d$, the characteristic equations of system (1.1) are

$$\lambda^2 + A_k\tau\lambda + B_k\tau^2 + C_*\tau^2e^{-\lambda(1+r)} = 0, \quad (k = 0, 1, 2, \dots),$$

where

$$A_k = 2d_k^2, \quad B_k = d^2k^4, \quad \text{and} \quad C_* = u_*v_*.$$

Then Eq. (2.4) becomes

$$\rho^4 + 2m_k^2\rho^2 + d^2k^4 - C_*^2 = 0. \tag{3.3}$$

If $d^2 - C_* \geq 0$, then Eq. (3.3) has no positive roots for $k \geq 1$, so all of the roots of Eqs. (2.3_k) ($k \geq 1$) have negative real parts for $\tau \in [0, \infty)$.

If $d^2 - C_* < 0$, then Eq. (3.3) has a positive root for $k = 1$. So if

$$\frac{\arccos\left(1 - \frac{2d^2}{C_*}\right)}{(1+r)\sqrt{C_* - d^2}} > \frac{2\pi}{(1+r)\sqrt{C_*}},$$

we have $\tau_0^0 < \tau_0^1$ and $\tau_0^1 < \tau_0^k, 1 \leq k \leq K_0$, from Lemma 2.1. Then all of the roots of Eqs. (2.3_k) ($k \geq 1$) have negative real parts for $\tau \in [0, \tau_0^1]$. If

$$\frac{\arccos\left(1 - \frac{2d^2}{C_*}\right)}{(1+r)\sqrt{C_* - d^2}} < \frac{2\pi}{(1+r)\sqrt{C_*}},$$

we have $\tau_0^0 > \tau_0^1$, and when $\tau = \tau_0^1$, Eqs. (2.3_k) ($k \geq 0$) have no pure imaginary roots except $k = 1$. From [12, Theorem 3.4], we know that (2.3_k) has at least two roots with positive real parts when $\tau > 0$. So when $\tau = \tau_0^1$, Eqs. (2.3_k) ($k \geq 0$) have only one pair of simple imaginary roots and at least two roots with positive real parts. Then a Hopf bifurcation of spatially inhomogeneous periodic solutions occurs at E_* for system (1.1) when $\tau = \tau_0^1$, and these spatially inhomogeneous periodic solutions are unstable. \square

Remark 3.2. In Theorem 5.2 of [12], Faria gave a sufficient condition for all of the roots of Eqs. (2.3_k) ($k \geq 1$) to have negative real parts for $\tau \in [0, \tau_0^0]$ when $a = b = 0$. In this theorem we give a sufficient and necessary condition for all of the roots of Eqs. (2.3_k) ($k \geq 1$) to have negative real parts for $\tau \in [0, \tau_0^0]$ with the assumption $d_1 = d_2 = d$. We also obtain a sufficient condition for the occurrence of Hopf bifurcation of spatially inhomogeneous periodic solutions.

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