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Multiple Bifurcations in a Delayed Predator–Prey System with Nonmonotonic Functional Response

Dongmei Xiao[1]

Department of Mathematics, Central China Normal University, Wuhan, Hubei 430079, China

and

Shigui Ruan[2]

Department of Mathematics and Statistics, Dalhousie University, Halifax, Nova Scotia, Canada B3H 3J5

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A delayed predator–prey system with nonmonotonic functional response is studied by using the normal form theory of retarded functional differential equations developed by Faria and Magalhães. The bifurcation analysis of the model indicates that there is a Bogdanov–Takens singularity for any time delay value. A versal unfolding of the model at the Bogdanov–Takens singularity is obtained. On the other hand, it is shown that small delay changes the stability of the equilibrium of the model for some parameters and the system can exhibit Hopf bifurcation as the time delay passes through some critical values.

1. INTRODUCTION

In microbial dynamics or chemical kinetics, the functional response describes the uptake of substrate by the microorganisms. In general the response function $p(x)$ is monotone. However, there are experiments that indicate that nonmonotonic responses occur at the microbial level: when the nutrient concentration reaches a high level an inhibitory effect on the specific growth rate may occur. This is often seen when micro-organisms are used for waste decomposition or for water purification (cf. Bush and Cook [2]). The so-called Monod–Haldane function

$$p(x) = \frac{mx}{a + bx + x^2}$$

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has been proposed and used to model the inhibitory effect at high concentrations (Andrews [1]). In experiments on the uptake of phenol by pure culture of *Pseudomonas putida* growing on phenol in continuous culture, Sokol and Howell [11] proposed a simplified Monod–Haldane function of the form

$$p(x) = \frac{mx}{a+x^2}$$

and found that it fits their experimental data significantly better than the Monod–Haldane function and is simpler since it involves only two parameters. Let $x(t)$ and $y(t)$ denote the population densities of the prey and predator, respectively. Recently, we (see [14]) have studied a predator–prey system with nonmonotonic functional response

$$\begin{aligned} \dot{x}(t) &= rx(t)\left(1-\frac{x(t)}{K}\right)-\frac{x(t)\,y(t)}{a+x^2(t)}, \\ \dot{y}(t) &= y(t)\left[\frac{\mu x(t)}{a+x^2(t)}-D\right] \end{aligned} \tag{1.1}$$

and found that the model undergoes a series of bifurcations including saddle-node bifurcation, Hopf bifurcation, and homoclinic bifurcation.

Based on some experimental data, Caperon [3] observed that there is a time delay between the changes in substrate concentration and the corresponding changes in the bacterial growth rate. Following Caperon's observation, Bush and Cook [2] modified system (1.1) to allow the growth rate of microorganism to depend on the substrate concentrations τ units of time earlier. Their model is a system of two delay differential equations of the form

$$\begin{aligned} \dot{x}(t) &= rx(t)\left(1-\frac{x(t)}{K}\right)-\frac{x(t)\,y(t)}{a+x^2(t)}, \\ \dot{y}(t) &= y(t)\left[\frac{\mu x(t-\tau)}{a+x^2(t-\tau)}-D\right], \end{aligned} \tag{1.2}$$

where r, K, a, μ, D, and τ are positive constants.

In this paper, we consider system (1.2) in the closed first quadrant of the (x, y) plane. We will investigate the effect of the time delay on bifurcations of the system. It is well known that the time delay cannot change the number and location of equilibria of system (1.2). When $\tau = 0$, there are some parameter values of $r, K, a, \mu,$ and D such that system (1.2) exhibits Bogdanov–Takens bifurcation (see [14]). We will show that the delayed system (1.2) still has a Bogdanov–Takens singularity for any $\tau > 0$. Therefore, the time delay does not affect the occurrence of Bogdanov–Takens bifurcation. On the other hand, it is known that a small time delay usually does not change the stability of the equilibria. We will see that for system (1.2), when $\tau = 0$ there exist some parameter values such that system (1.2) has a positive equilibrium which is a stable multiple focus in the interior of the first quadrant. When $\tau > 0$ this equilibrium becomes unstable and Hopf bifurcation always occurs for some $\tau_k > 0$.

We would like to mention that though Faria and Magalhães [5] gave an example on Bogdanov–Takens bifurcation in a scalar delay differential equation, to the best of our knowledge, this paper is the first dealing with Bogdanov–Takens bifurcation in a predator-prey system with delay. The Hopf bifurcation analysis of a planar system with delay involves studying the distribution of the roots to a second degree transcendental equation. Such transcendental equations have been investigated by many researchers, see, for example, Freedman and Rao [7], Kuang [10], Táboas [15], Ruan [12], Ruan and Wei [13], Zhao *et al.* [16], etc. However, the direction and stability of the non-trivial periodic orbits bifurcated from the equilibrium have rarely studied. Especially, for the case when $\tau = 0$ the equilibrium is a multiple focus of multiplicity one and is stable for some parameter values. We shall use the normal form theory for Hopf bifurcations in RFDE due to Faria and Magalhães [4] and [6] to analyze the direction and stability of the non-trivial periodic orbits of system (1.2) in this case.

This paper is organized as follows. In Section 2, following the technique of Faria and Magalhães [5] we compute the normal form of system (1.2) at the degenerate equilibrium and show this equilibrium is in fact a Bogdanov–Takens singularity. We also discuss the versal unfolding of system (1.2) at this Bogdanov–Takens singularity depending on the original parameters. In section 3, for a set of parameter values of $r, K, a, \mu,$ and D, we study the effect of the time delay τ on the stability of the equilibrium. By choosing τ as a bifurcation parameter and following the procedure of Faria and Magalhães [6] we compute the normal form for the Hopf bifurcation of system (1.2).

2. BOGDANOV–TAKENS BIFURCATION

As it is typical for predator-prey systems, the x-axis, y-axis and the interior of the first quadrant are all invariant under system (1.2). Also, there are a hyperbolic saddle point at the origin and an equilibrium $(K, 0)$ for all permissible parameters. It is easy to check that system (1.1) has a unique interior equilibrium (x_0, y_0) if and only if $\mu^2 - 4aD^2 = 0$ and $\mu < 2KD$. Furthermore, when $\mu = KD$ the equilibrium (x_0, y_0) is a cusp of codimension 2 (i.e., a Bogdanov–Takens singularity) as shown in [14], where $x_0 = \mu/2D$, $y_0 = ra$. Since time delay does not affect the number and location of equilibria, (x_0, y_0) is still a unique interior equilibrium for the delayed system (1.2) when $\mu^2 - 4aD^2 = 0$ and $\mu = KD$. We will discuss if the interior equilibrium (x_0, y_0) is also a Bogdanov–Takens singularity for system (1.2). Denote by μ_0, a_0, D_0, and K_0 if they satisfy $\mu^2 - 4aD^2 = 0$ and $\mu = KD$.

Consider the following retarded functional differential equations (RFDE)

$$
\begin{aligned}
\dot{x}(t) &= rx(t)\left(1 - \frac{x(t)}{K_0}\right) - \frac{x(t)\,y(t)}{a_0 + x^2(t)}, \\
\dot{y}(t) &= y(t)\left(\frac{\mu_0 x(t-\tau)}{a_0 + x^2(t-\tau)} - D_0\right)
\end{aligned}
\tag{2.1}
$$

in the phase space $C := C([-\tau, 0]; R^2)$, here $\tau > 0$ is a constant. It is convenient to reparametrize system (2.1) so that it becomes

$$
\begin{aligned}
\dot{x}(t) &= \tau\left[rx(t)\left(1 - \frac{x(t)}{K_0}\right) - \frac{x(t)\,y(t)}{a_0 + x^2(t)}\right], \\
\dot{y}(t) &= \tau\left[y(t)\left(\frac{\mu_0 x(t-1)}{a_0 + x^2(t-1)} - D_0\right)\right].
\end{aligned}
\tag{2.2}
$$

The advantage is that we can work in a fixed phase space $C_1 := C([-1, 0]; R^2)$ when τ varies.

First of all, we translate the equilibrium (x_0, y_0) of system (2.2) to the origin. Let $x_1 = x - x_0$, $x_2 = y - y_0$. Then system (2.2) becomes

$$
\begin{aligned}
\dot{x}_1(t) &= \tau\left[-\frac{x_0}{a_0 + x_0^2}\, x_2(t) + \sum_{i+j\geqslant 2} \frac{1}{i!\,j!}\, f_{ij}^{(1)} x_1^i(t)\, x_2^j(t)\right], \\
\dot{x}_2(t) &= \tau\left[\sum_{i+j\geqslant 2} \frac{1}{i!\,j!}\, f_{ij}^{(2)} x_1^i(t-1)\, x_2^j(t)\right],
\end{aligned}
\tag{2.3}
$$

where $i, j \geqslant 0$,

$$f_{ij}^{(1)} = \left.\frac{\partial^{i+j} f^{(1)}}{\partial^i x \, \partial^j y}\right|_{(x_0,\, y_0)}, \qquad f_{ij}^{(2)} = \left.\frac{\partial^{i+j} f^{(2)}}{\partial^i x \, \partial^j y}\right|_{(x_0,\, y_0)},$$

$$f^{(1)} = rx\left(1 - \frac{x}{K_0}\right) - \frac{xy}{a_0 + x^2}, \qquad f^{(2)} = y\left(\frac{\mu_0 x}{a_0 + x^2} - D_0\right).$$

Linearization at the zero equilibrium yields

$$\begin{aligned} \dot{x}_1(t) &= -\frac{\tau x_0}{a_0 + x_0^2}\, x_2(t), \\ \dot{x}_2(t) &= 0. \end{aligned} \tag{2.4}$$

The linear system (2.4) has $\lambda = 0$ as a double characteristic value and no other characteristic values.

Now we consider the normal form of system (2.3) at the singularity (0, 0). For simplicity, we rewrite system (2.4) as

$$\dot{X}(t) = L(X_t),$$

here $X(t) = (x_1(t), x_2(t))$, $L(\phi) = L\binom{\phi_1(-1)}{\phi_2(0)}$, and $\phi = (\phi_1, \phi_2)$. According to the normal form theory developed by Faria and Magalhães [5] we know that the center manifold of system (2.4) at the origin is two dimensional and system (2.3) can be reduced to an ODE in the plane.

Let A_0 be the infinitesimal generator of system (2.4). Consider $\Lambda = \{0\}$ and denote by P the invariant space of A_0 associated with the eigenvalue $\lambda = 0$. Using the formal adjoint theory of RFDE in [5], we know that the phase space C_1 can be decomposed by Λ as $C_1 = P \oplus Q$. Let Φ and Ψ be the bases for P and P^*, the space associated with the eigenvalue $\lambda = 0$ of the adjoint equation, respectively, and be normalized so that $(\Phi, \Psi) = I$, where $(\cdot, \cdot)$ is the bilinear form defined in section 2 of [5]. We refer to [5] for the unexplained notations and definitions. Φ and Ψ are 2×2 matrices of the form

$$\Phi(\theta) = \begin{pmatrix} 1 & \theta \\ 0 & -\dfrac{a_0 + x_0^2}{\tau x_0} \end{pmatrix} = \begin{pmatrix} 1 & \theta \\ 0 & -\dfrac{\mu_0}{\tau D_0} \end{pmatrix}, \qquad -1 \leqslant \theta \leqslant 0,$$

$$\Psi(s) = \begin{pmatrix} 1 & \dfrac{\tau D_0}{\mu_0} s \\ 0 & -\dfrac{\tau D_0}{\mu_0} \end{pmatrix}, \qquad 0 \leqslant s \leqslant 1.$$

The matrix B satisfying $\dot{\Phi} = \Phi B$ is given by

$$B = \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}.$$

Enlarging the phase space C_1 by considering the space $BC = \{\phi : [-1, 0] \to R^2;\ \phi$ is continuous on $[-1, 0)$ with a jump discontinuity at $0\}$, we can see that the projection of C_1 upon P, associated with the decomposition $C_1 = P \oplus Q$, is now replaced by π: $BC \to P$, which leads to the decomposition

$$BC = P \oplus \operatorname{Ker} \pi$$

following [5]. Now decompose x in system (2.3) according to the preceding decomposition of BC, in the form $x = \Phi z + y$, with $z \in R^2$ and $y \in \operatorname{Ker} \pi \cap D(A_0) = Q'$. Hence, system (2.3) in the center manifold is equivalent to the system

$$\dot{z} = Bz + \Psi(0)\, F(\Phi z), \tag{2.5}$$

where

$$F(\phi) = \begin{pmatrix} \tau \sum\limits_{i+j \geqslant 2} \dfrac{1}{i!\, j!}\, f_{ij}^{(1)} [\phi_1(0)]^i\, [\phi_2(0)]^j \\ \tau \sum\limits_{i+j \geqslant 2} \dfrac{1}{i!\, j!}\, f_{ij}^{(2)} [\phi_1(-1)]^i\, [\phi_2(0)]^j \end{pmatrix},$$

where $\phi = (\phi_1, \phi_2)$. Writing F in its Taylor expansion up to the second order terms in the form $F(z) = \frac{1}{2!} F_2(z) + O(|z|^3)$, we have

$$\begin{aligned} \dot{z}_1 &= z_2 + \frac{1}{2!} \tau f_{20}^{(1)} z_1^2 + \tau P_1(z_1, z_2), \\ \dot{z}_2 &= -\frac{1}{2!} \frac{\tau^2 D_0}{\mu_0} f_{20}^{(2)} (z_1 - z_2)^2 + \tau P_2(z_1, z_2), \end{aligned} \tag{2.6}$$

where $f_{20}^{(1)} = -rD_0/\mu_0$, $f_{20}^{(2)} = -rD_0$, P_1 and P_2 are C^∞ functions in (z_1, z_2) at least of the third order.

In the neighborhood of the origin, we make the inverse transformation

$$\bar{z}_1 = z_1, \qquad \bar{z}_2 = z_2 + \frac{\tau}{2} f_{20}^{(1)} z_1^2 + \tau P_1(z_1, z_2).$$

After dropping the bars, system (2.6) becomes

$$
\begin{aligned}
\dot{z}_1 &= z_2, \\
\dot{z}_2 &= \alpha z_1^2 + \beta z_1 z_2 + \gamma z_2^2 + P_3(z_1, z_2),
\end{aligned}
\tag{2.7}
$$

here

$$
\alpha = \frac{r\tau^2 D_0^2}{2\mu_0}, \qquad \beta = -\frac{r\tau D_0 + r\tau^2 D_0^2}{\mu_0}, \qquad \gamma = \frac{r\tau^2 D_0^2}{2\mu_0},
$$

and P_3 is a C^∞ function in (z_1, z_2) at least of the third order whose coefficients are functions of $\tau, r, D_0, \mu_0, a_0,$ and K_0. By the nonresonance conditions among the set Λ, we can eliminate the z_2^2 term in the second equation of system (2.7) and obtain

$$
\begin{aligned}
\dot{z}_1 &= z_2, \\
\dot{z}_2 &= \alpha z_1^2 + \beta z_1 z_2 + P_4(z_1, z_2),
\end{aligned}
\tag{2.8}
$$

where P_4 is a C^∞ function in (z_1, z_2) at least of the third order. The above arguments imply that

THEOREM 2.1. *For any $\tau > 0$, the equilibrium (x_0, y_0) of system* (2.1) *is a Bogdanov–Takens singularity, the dynamics in a neighborhood of (x_0, y_0) is generically determined by the quadratic terms of system* (2.1).

It is more interesting to determine a versal unfolding for the original system (2.1) or system (2.2) with a Bogdanov–Takens singularity, i.e., to determine which of the parameters $r, K, D, a, \mu,$ and τ can be chosen as bifurcation parameters such that system (2.1) exhibits Bogdanov–Takens bifurcation. We cannot get any versal unfoldings of this Bogdanov–Takens singularity if we require that system (2.2) always has an equilibrium (x_0, y_0), as stated in [5], for all bifurcation parameters. However, if we give up this restraint and assume the following condition instead

(H) System (2.2) has a Bogdanov–Takens singularity (x_0, y_0) when all bifurcation parameters equal to zero,

then we can obtain a versal unfolding of this Bogdanov–Takens singularity depending on all parameters of the original system. For this, choose K and D in system (2.2) as the bifurcation parameters, i.e. consider $1/K_0 + \lambda_1$ and $D_0 + \lambda_2$, where λ_1 and λ_2 vary in a small neighborhood of $(0, 0)$. Adding these perturbations to system (2.2), we obtain

$$\dot{x}(t) = \tau\left[rx(t)\left(1 - \frac{x(t)}{K_0}\right) - \frac{x(t)\,y(t)}{a_0 + x^2(t)} - r\lambda_1 x^2(t) \right], \tag{2.9}$$
$$\dot{y}(t) = \tau y(t)\left(\frac{\mu_0 x(t-1)}{a_0 + x^2(t-1)} - D_0 - \lambda_2 \right).$$

When $\lambda_1 = \lambda_2 = 0$, system (2.9) has a Bogdanov–Takens singularity (x_0, y_0) and there exists a two-dimensional center manifold.

Let $y_1 = x - x_0$, $y_2 = y - y_0$. Then system (2.9) becomes

$$\dot{y}_1(t) = -r\tau x_0^2 \lambda_1 - 2r\tau x_0 \lambda_1 y_1(t) - \frac{\tau x_0}{a_0 + x_0^2}\, y_2(t) + \sum_{i+j\geqslant 2} \frac{1}{i!\,j!}\, \tau g_{ij}^{(1)} y_1^i(t)\, y_2^j(t), \tag{2.10}$$
$$\dot{y}_2(t) = -\tau y_0 \lambda_2 - \tau\lambda_2 y_2(t) + \sum_{i+j\geqslant 2} \frac{1}{i!\,j!}\, \tau g_{ij}^{(2)} y_1^i(t-1)\, y_2^j(t),$$

where $i, j \geqslant 0$,

$$g_{ij}^{(1)} = \left.\frac{\partial^{i+j} g^{(1)}}{\partial^i x\, \partial^j y}\right|_{(x_0,\, y_0,\, \lambda_1)}, \qquad g_{ij}^{(2)} = \left.\frac{\partial^{i+j} g^{(2)}}{\partial^i x\, \partial^j y}\right|_{(x_0,\, y_0,\, \lambda_2)},$$
$$g^{(1)} = rx\left(1 - \frac{x}{K_0}\right) - \frac{xy}{a_0 + x^2} - r\lambda_1 x^2, \qquad g^{(2)} = y\left(\frac{\mu_0 x}{a_0 + x^2} - D_0 - \lambda_2 \right).$$

We decompose the enlarged phase space BC of system (2.10) as $BC = P \oplus \operatorname{Ker} \pi$. Then y in system (2.10) can be decomposed as $y = \Phi z + u$ with $z \in R^2$ and $u \in Q'$. Hence, system (2.10) is decomposed as

$$\dot{z} = B_1 + B_2 z + \Psi(0)\, G(\Phi z + u), \tag{2.11}$$
$$\dot{u} = A_{Q'} u + (I - \pi)\, X_0[B_0 + B_2(\Phi(0)\, z + u(0)) + G(\Phi z + u)],$$

where

$$X_0(\theta) = \begin{cases} I, & \theta = 0 \\ 0, & -1 \leqslant \theta < 0, \end{cases}$$

$$B_0 = \begin{pmatrix} -r x_0^2 \tau \lambda_1 \\ -\tau y_0 \lambda_2 \end{pmatrix}, \qquad B_1 = \Psi(0)\, B_0, \qquad B_2 = \begin{pmatrix} -2r\tau x_0 \lambda_1 & 1 \\ 0 & -\tau\lambda_2 \end{pmatrix},$$

and

$$G(\phi)=\begin{pmatrix} \sum_{i+j\geqslant 2} \frac{1}{i!\,j!}\tau g_{ij}^{(1)}[\phi_1(0)]^i\,[\phi_2(0)]^j \\ \sum_{i+j\geqslant 2} \frac{1}{i!\,j!}\tau g_{ij}^{(2)}[\phi_1(-1)]^i\,[\phi_2(0)]^j \end{pmatrix},$$

here $\phi=(\phi_1, \phi_2)$.

To compute the normal form of system (2.10) at (x_0, y_0), consider

$$\dot{z}=B_1+B_2 z+\Psi(0)\,G(\Phi z),$$

that is,

$$\begin{aligned} \dot{z}_1 &= -r\tau a_0\lambda_1-2r\tau x_0\lambda_1 z_1+z_2-\left(r\tau\lambda_1+\frac{r\tau D_0}{2\mu_0}\right)z_1^2+\tau R_1(z_1, z_2), \\ \dot{z}_2 &= \frac{1}{2}r\tau^2 x_0\lambda_2-\tau\lambda_2 z_2+\frac{1}{2}\frac{r\tau^2 D_0^2}{\mu_0}(z_1-z_2)^2+\tau R_2(z_1, z_2), \end{aligned} \tag{2.12}$$

where R_1 and R_2 are C^∞ functions in (z_1, z_2) at least of the third order. Following the procedure of deriving normal form in Kuznetsov [10], system (2.12) can be reduced to

$$\begin{aligned} \dot{z}_1 &= z_2, \\ \dot{z}_2 &= \gamma_1+\gamma_2 z_2+\alpha z_1^2+\beta z_1 z_2+R(z_1, z_2, \gamma_1, \gamma_2), \end{aligned} \tag{2.13}$$

here $\gamma_1=(1/2)\,r\tau^2 x_0\lambda_2$, $\gamma_2=-\tau\lambda_2+(r\tau x_0/2)(r\tau^2 D_0-4)\,\lambda_1$, and $R=O(|\gamma|^2)+O(|\gamma z|^3)$.

Hence, when $\tau^2 r D_0\neq 4$, system (2.9) exhibits Bogdanov–Takens bifurcation.

THEOREM 2.2. *When $\tau^2 r D_0\neq 4$, there exists a unique smooth curve HL corresponding to homoclinic bifurcation and a unique smooth curve H corresponding to Hopf bifurcation, such that system (2.9) has a unique and hyperbolic stable cycle for parameter values inside the region bounded by H and HL in the lower half plane $\lambda_2<0$ and no cycles outside this region. The local representations of these bifurcations curves are given by*

$$HL=\left\{(\lambda_1, \lambda_2);\ \gamma_2-\frac{5}{7}\beta\sqrt{-\frac{\gamma_1}{\alpha}}=0,\ \gamma_1<0\right\}$$

and

$$H = \left\{ (\lambda_1, \lambda_2);\ \gamma_2 - \beta \sqrt{-\frac{\gamma_1}{\alpha}} = 0,\ \gamma_1 < 0 \right\}.$$

3. HOPF BIFURCATION

It has been shown in [14] that for the ODE model (1.1), when $\mu^2 > 4aD^2$ and $K > (\mu + \sqrt{\mu^2 - 4aD^2})/2D$, there are two positive equilibria: a focus (x_1, y_1) and a hyperbolic saddle (x_2, y_2). Moreover, when $K = (2\mu - \sqrt{\mu^2 - 4aD^2})/2D$ the focus (x_1, y_1) is a multiple focus. The third focal value (i.e. the Liapunov number) at (x_1, y_1) is $\alpha_3 = 0$ when $\mu = [(18 + 2\sqrt{6})/3]\, aD^2$. This means that (x_1, y_1) could be a multiple focus of multiplicity at least two for some parameter values, but when $4aD^2 < \mu < [(18 + 2\sqrt{6})/3]\, aD^2$ and $K = (2\mu - \sqrt{\mu^2 - 4aD^2})/2D$, (x_1, y_1) is a multiple focus of multiplicity one, which is stable. In this section, we are interested in studying the effect of the delay on the stability of (x_1, y_1) when (x_1, y_1) is a stable multiple focus of multiplicity one.

It is well-known that a small delay does not change the stability of the equilibrium in many biological systems, i.e., if the system has a stable equilibrium when the time delay $\tau = 0$, then this equilibrium is still stable when τ varies in a small neighborhood of zero. We will show that for system (1.2) a small delay can change the stability of the equilibrium. By choosing τ as the bifurcation parameter, we will discuss the Hopf bifurcation of system (1.2) for a class of parameters a, μ, K, and D by using the normal form theory developed by Faria and Magalhães [4] and [6].

We first need conditions to ensure that (x_1, y_1) is a stable focus of multiplicity one and no any nontrival closed orbits (periodic orbits or homoclinic orbits) for the ODE system (1.1), which can be stated as in the following lemma. For more details we refer to [14].

LEMMA 3.1. *If* $4aD^2 < \mu^2 \leqslant \frac{16}{3}\, aD^2$ *and* $K = (2\mu - \sqrt{\mu^2 - 4aD^2})/2D$, *then system* (1.1) *has an interior equilibrium* (x_1, y_1), *which is stable, and there is no nontrival closed orbit (neither periodic orbit nor homoclinic orbit) in the interior of the first quadrant, where*

$$x_1 = \frac{\mu - \sqrt{\mu^2 - 4aD^2}}{2D}, \qquad y_1 = r\left(1 - \frac{x_1}{K}\right)(a + x_1^2).$$

In fact, the equilibrium (x_1, y_1) is a multiple focus of multiplicity one, which is stable.

THEOREM 3.2. *Suppose that* $4aD^2 < \mu^2 \leqslant (16/3)\, aD^2$ *and* $K = (2\mu - \sqrt{\mu^2 - 4aD^2})/2D$. *Then system* (1.2) *has an interior equilibrium* (x_1, y_1), *which is unstable for* $0 < \tau \ll 1$.

Proof. Let $X_1 = x - x_1$, $X_2 = y - y_1$. Then system (1.2) becomes

$$\begin{aligned}
\dot{X}_1(t) &= -\frac{x_1}{a + x_1^2} X_2(t) + \sum_{i+j \geqslant 2} \frac{1}{i!\, j!} h_{ij}^{(1)} X_1^i(t)\, X_2^j(t), \\
\dot{X}_2(t) &= \frac{\mu y_1(a - x_1^2)}{(a + x_1^2)^2} X_1(t-\tau) + \sum_{i+j \geqslant 2} \frac{1}{i!\, j!} h_{ij}^{(2)} X_1^i(t-\tau)\, X_2^j(t),
\end{aligned} \tag{3.1}$$

where $i, j \geqslant 0$,

$$h_{ij}^{(1)} = \left.\frac{\partial^{i+j} h^{(1)}}{\partial^i x\, \partial^j y}\right|_{(x_1, y_1)}, \qquad h_{ij}^{(2)} = \left.\frac{\partial^{i+j} h^{(2)}}{\partial^i x\, \partial^j y}\right|_{(x_1, y_1)},$$

$$h^{(1)} = rx\left(1 - \frac{x}{K}\right) - \frac{xy}{a + x^2}, \qquad h^{(2)} = y\left(\frac{\mu x}{a + x^2} - D\right).$$

To study the stability of the origin, consider the linearized system at (0, 0)

$$\begin{aligned}
\dot{X}_1(t) &= -\frac{x_1}{a + x_1^2} X_2(t), \\
\dot{X}_2(t) &= \frac{\mu y_1(a - x_1^2)}{(a + x_1^2)^2} X_1(t-\tau).
\end{aligned} \tag{3.2}$$

System (3.2) has the characteristic equation

$$\Delta(\lambda, \tau) = \lambda^2 + q e^{-\lambda\tau} = 0, \tag{3.3}$$

where

$$q = \frac{\mu x_1 y_1 (a - x_1^2)}{(a + x_1^2)^3} > 0.$$

It is clear that the characteristic equation (3.3) has no real roots and $\Delta(\lambda, 0) = 0$ has only a pair of conjugate purely imaginary roots $\pm i\sqrt{q}$.

Assume that $\lambda = u + iv$ is a root of (3.3) for $\tau > 0$. Then we have

$$H_1(u, v, \tau) = u^2 - v^2 + qe^{-u\tau}\cos v\tau = 0,$$
$$H_2(u, v, \tau) = 2uv - qe^{-u\tau}\sin v\tau = 0.$$

Using the Implicit Function Theorem, we can see that $(H_1(u, v, \tau), H_2(u, v, \tau)) = (0, 0)$ defines u, v as functions of τ, i.e., $u = u(\tau)$ and $v = v(\tau)$ in a neighborhood of $\tau = 0$ such that

$$u(0) = 0, \qquad v(0) = \sqrt{q}, \qquad \frac{d}{d\tau}u(\tau)\bigg|_{\tau=0} > 0.$$

Therefore, $u(\tau) > 0$ as $\tau > 0$. This completes the proof of the theorem. ∎

It follows from the above discussion that there exist

$$\tau_k = \frac{2k\pi}{\sqrt{q}}, \qquad k = 0, 1, 2, \ldots$$

such that the characteristic equation (3.3) has two simple complex roots $u(\tau) \pm iv(\tau)$ that cross the imaginary axis transversely at $\tau = \tau_k$:

$$u(\tau_k) = 0, \qquad v(\tau_k) = \sqrt{q} > 0, \qquad u'(\tau_k) > 0.$$

And (3.3) has no other roots when $\tau = \tau_k$ in the imaginary axis which are multiples of $i\sqrt{q}$. Hence, Hopf bifurcation may occur at $\tau = \tau_k$.

Next, choosing τ as a bifurcation parameter and following the normal form theory developed by Faria and Magalhães [6], we discuss the explicit expressions of the normal form of system (3.1) in terms of the original parameters in the small neighborhood of τ_k. For $\tau > 0$, rewrite system (3.1) as

$$\begin{aligned}\dot{X}_1(t) &= \tau\left[-\frac{x_1}{a+x_1^2}X_2(t) + \sum_{i+j\geqslant 2}\frac{1}{i!\,j!}h_{ij}^{(1)}X_1^i(t)\,X_2^j(t)\right],\\ \dot{X}_2(t) &= \tau\left[\frac{\mu y_1(a-x_1^2)}{(a+x_1^2)^2}X_1(t-1) + \sum_{i+j\geqslant 2}\frac{1}{i!\,j!}h_{ij}^{(2)}X_1^i(t-1)\,X_2^j(t)\right],\end{aligned} \tag{3.4}$$

and the linearized system is

$$\begin{aligned}\dot{X}_1(t) &= -\frac{\tau x_1}{a+x_1^2}X_2(t),\\ \dot{X}_2(t) &= \frac{\tau\mu y_1(a-x_1^2)}{(a+x_1^2)^2}X_1(t-1).\end{aligned} \tag{3.5}$$

Let A be the generator of the linear semigroup corresponding to (3.5). When $\tau = \tau_k$, A has a pair of purely imaginary characteristic roots $\pm i2k\pi$, which are simple, and no other characteristic roots with zero real part. Introduce a new parameter $\nu = \tau - \tau_k$, system (3.4) can be written as

(3.6)

$$\dot{X}_1(t) = -\frac{\tau_k x_1}{a + x_1^2} X_2(t) - \frac{\nu x_1}{a + x_1^2} X_2(t) + (\tau_k + \nu) \sum_{i+j \geqslant 2} \frac{1}{i!\, j!} h_{ij}^{(1)} X_1^i(t) X_2^j(t),$$

$$\dot{X}_2(t) = \frac{\tau_k \mu y_1 (a - x_1^2)}{(a + x_1^2)^2} X_1(t-1) + \frac{\nu \mu y_1 (a - x_1^2)}{(a + x_1^2)^2} X_1(t-1)$$

$$+ (\tau_k + \nu) \sum_{i+j \geqslant 2} \frac{1}{i!\, j!} h_{ij}^{(2)} X_1^i(t-1) X_2^j(t).$$

We simply denote it by

$$\dot{X}(t) = \begin{pmatrix} 0 & -\dfrac{\tau_k x_1}{a + x_1^2} \\ \dfrac{\tau_k \mu y_1 (a - x_1^2)}{(a + x_1^2)^2} & 0 \end{pmatrix} \begin{pmatrix} X_1(t-1) \\ X_2(t) \end{pmatrix} + H_0(X_t, \nu).$$

For any ν, system (3.6) has an equilibrium at $(0, 0)$. The phase space is $C_1 = C([-1, 0]; R^2)$. Fix a $k \in N = \{1, 2, ...\}$, define $\Lambda = \{-i2k\pi, i2k\pi\}$. We will apply the normal form theory in [6] to system (3.6).

Let the phase space C_1 be decomposed by Λ as $C_1 = P \oplus Q$, where P is the generalized eigenspace associated with Λ. Consider the bilinear form $(\cdot, \cdot)$ associated with the linear system

$$\dot{X}_1(t) = -\frac{\tau_k x_1}{a + x_1^2} X_2(t),$$

(3.7)

$$\dot{X}_2(t) = \frac{\tau_k \mu y_1 (a - x_1^2)}{(a + x_1^2)^2} X_1(t-1).$$

Let Φ and Ψ be bases for P and P^* associated with the eigenvalues $\pm i2k\pi$ of the adjoint equations, respectively, and let them be normalized so that $(\Phi, \Psi) = I$. Here, it is convenient to combine one complex coordinate and two complex conjugate basis vectors to describe a two-dimensional real subspace P. Consider system (3.6) in $C([-1, 0]; \mathbb{C})$, still denoted by C_1.

Note that $\dot{\Phi} = \Phi B$, where B is a diagonal matrix of the form $B = \operatorname{diag}(i2k\pi, -i2k\pi)$. Therefore, Φ and Ψ are 2×2 matrices of the form

$$\Phi(\theta) = [\phi_1(\theta), \phi_2(\theta)], \quad \phi_1(\theta) = e^{i2k\pi\theta} v, \quad \phi_2(\theta) = \overline{\phi_1(\theta)}, \quad -1 \leqslant \theta \leqslant 0,$$

$$\Psi(s) = \begin{pmatrix} \psi_1(s) \\ \psi_2(s) \end{pmatrix}, \quad \psi_1(s) = e^{-i2k\pi s} u^T, \quad \psi_2(s) = \overline{\psi_1(s)}, \quad 0 \leqslant s \leqslant 1,$$

where the bar means complex conjugation, u^T is the transpose of u, and u, v are vectors in $\mathbb{C}^2$,

$$u = \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} \dfrac{1}{2+i2k\pi} \\[2ex] \dfrac{ix_1}{\sqrt{q}\,(a+x_1^2)(2+i2k\pi)} \end{pmatrix},$$

$$v = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} 1 \\[1ex] \dfrac{-i\sqrt{q}\,(a+x_1^2)}{x_1} \end{pmatrix}.$$

Enlarging the phase space C_1 by considering the space BC and using the decomposition $X_t = \Phi z(t) + y_t$, $z \in \mathbb{C}^2$, $y_t \in Q'$, we decompose system (3.6) as

$$\begin{aligned} \dot{z} &= Bz + \Psi(0)\, H_0(\Phi z + y, \nu), \\ \dot{y} &= A_{Q'} y + (I - \pi)\, X_0 H_0(\Phi z + y, \nu). \end{aligned} \tag{3.8}$$

Following the procedure of reducing normal form in [6], we consider

$$\Psi(0)\, H_0(\Phi z + y, \nu) = \frac{1}{2} h_2(z, y, \nu) + \frac{1}{3!} h_3(z, y, \nu) + h.o.t.,$$

where $h_j(z, y, \nu)(j = 1, 2)$ are homogeneous polynomials in (z, y, ν) of degree j with coefficients in $\mathbb{C}^2$ and $h.o.t.$ stands for higher order terms. Thus, in a finite dimensional locally invariant manifold tangent to the invariant subspace P of (3.7) at $x = 0$, $\nu = 0$, the normal form of (3.8) is given by

$$\dot{z} = Bz + \frac{1}{2} \bar{h}_2(z, 0, \nu) + \frac{1}{3!} \bar{h}_3(z, 0, \nu) + h.o.t., \tag{3.9}$$

where $\bar{h}_2, \bar{h}_3$ are the second and third order terms in (z, v), respectively. Using the notations in [6], we have

$$\bar{h}_2(z, 0, v) = \mathrm{Proj}_{\mathrm{Ker}(M_2{}')}\, h_2(z, 0, v),$$

where

$$\mathrm{Ker}(M_2') = \mathrm{span}\left\{ \begin{pmatrix} z_1 v \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ z_2 v \end{pmatrix} \right\},$$

$$h_2(z, 0, v) = \begin{pmatrix} 2i\sqrt{q}\, u^T v z_1 v + a_{20} z_1^2 + a_{11} z_1 z_2 + a_{02} z_2^2 \\ -2i\sqrt{q}\, \bar{u}^T \bar{v} z_2 v + \bar{a}_{20} z_1^2 + \bar{a}_{11} z_1 z_2 + \bar{a}_{02} z_2^2 \end{pmatrix},$$

in which

$$\begin{aligned} a_{20} &= \tau_k (h_{20}^{(1)} u_1 + h_{11}^{(1)} v_2 u_1 + h_{20}^{(2)} e^{-4ik\pi} u_2 + h_{11}^{(2)} e^{-2ik\pi} v_2 u_2), \\ a_{11} &= \tau_k (2h_{20}^{(1)} u_1 + 2h_{20}^{(2)} u_2 + h_{11}^{(2)} (e^{-2ik\pi} \bar{v}_2 + e^{2ik\pi} v_2)\, u_2), \\ a_{02} &= \tau_k (h_{20}^{(1)} u_1 + h_{11}^{(1)} \bar{v}_2 u_1 + h_{20}^{(2)} e^{4ik\pi} u_2 + h_{11}^{(2)} e^{2ik\pi} \bar{v}_2 u_2). \end{aligned}$$

Therefore,

$$\frac{1}{2}\bar{h}_2(z, 0, v) = \begin{pmatrix} i\sqrt{q}\, u^T v z_1 v \\ -i\sqrt{q}\, \bar{u}^T \bar{v} z_2 v \end{pmatrix}.$$

To eliminate these nonresonant terms in the quadratic terms $h_2(z, 0, v)$, we have to make a series of transformations of variables, which can change the coefficients of the cubic terms of $h_3(z, 0, v)$. Notice that

$$\mathrm{Ker}(M_3') = \mathrm{span}\left\{ \begin{pmatrix} z_1^2 z_2 \\ 0 \end{pmatrix}, \begin{pmatrix} z_1 v \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ z_1 z_2^2 \end{pmatrix}, \begin{pmatrix} 0 \\ z_2 v^2 \end{pmatrix} \right\}.$$

However, the terms $O(|z|\, v^2)$ are irrelevant to determine the generic Hopf bifurcation. Hence, we only need to compute the coefficient of $z_1^2 z_2$. After some computations we find that the coefficient of $z_1^2 z_2$ is

$$c = \frac{i}{4k\pi}\left(a_{20} a_{11} - 2\,|a_{11}|^2 - \frac{1}{3}\,|a_{02}|^2 \right) + \frac{1}{2}\, a_{21},$$

where

$$a_{21} = \tau_k [3h_{30}^{(1)} u_1 + h_{21}^{(1)} v_2 u_1 + 3h_{30}^{(2)} e^{-2ik\pi} u_2 + h_{21}^{(2)} (e^{-4ik\pi} \bar{v}_2 + 2v_2)\, u_2].$$

Thus,

$$\frac{1}{3!}\bar{h}_3(z, 0, v) = \begin{pmatrix} c z_1^2 z_2 \\ \bar{c} z_1 z_2^2 \end{pmatrix} + O(|z|\, v^2).$$

The normal form (3.9) relative to P can be written in real coordinates (x, y), through the change of variables $z_1 = x - iy$, $z_2 = x + iy$. Followed by the use of polar coordinates (r, θ), $x = r\cos\theta$, $y = r\sin\theta$, this normal form becomes

$$\begin{aligned} \dot{r} &= c_1 \nu r + c_2 r^3 + O(\nu^2 r + |(r,\nu)|^4), \\ \dot{\theta} &= -2k\pi + O(|(r,\nu)|), \end{aligned} \tag{3.10}$$

where $c_1 = k\pi\sqrt{q}/(1+k^2\pi^2)$, $c_2 = \operatorname{Re} c$.

We have the following theorem.

THEOREM 3.3. *If* $c_2 \neq 0$ *and* $\tau_k > 0$, *then system* (3.6) *exhibits a generic Hopf bifurcation. The periodic orbits of system* (3.6) *bifurcating from the origin and* $\nu = 0$ *satisfy*

$$r(t,\nu) = \sqrt{-\frac{c_1\nu}{c_2}} + O(\nu), \qquad \theta(t,\nu) = -2k\pi t + O(|\nu|^{1/2})$$

so that

(i) *if* $c_1c_2 < 0$ ($c_1c_2 > 0$ *respectively*), *there exists a unique nontrivial periodic orbit in the neighborhood of* $r = 0$ *for* $\nu > 0$ ($\nu < 0$ *respectively*) *and no nontrivial periodic orbit for* $\nu < 0$ ($\nu > 0$ *respectively*);

(ii) *the nontrivial periodic solutions in the center manifold are stable if* $c_2 < 0$ *and unstable if* $c_2 > 0$. *They are always unstable in the whole phase space* C_1 *since on the center manifold they are unstable for* $\tau_k > 0$.

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