Bifurcation analysis of a diffusive predator–prey system with Crowley–Martin functional response and delay

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ABSTRACT

In this paper, we investigate the dynamics of a diffusive predator–prey system with Crowley–Martin functional response and delay subject to Neumann boundary condition. More precisely, we study the stability and Turing instability of positive equilibrium for non-delay system, instability and Hopf bifurcation induced by time delay for delay system. In addition, by the theory of normal form and center manifold method, we derive conditions for determining the bifurcation direction and the stability of the bifurcating periodic solution.

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1. Introduction

One of the dominant theme in both ecology and mathematical ecology is predator-prey model. It exists universally and is important with other biological systems. Many researchers have studied it and derived some important results [1–6].

In predator-prey models, the functional response of predators to prey density is essential. It represents a predator's per capita feeding rate on prey. Different functional responses enrich the dynamics of predator-prey systems. In ecology, functional responses may affect by prey escape ability, structure of the prey habitat and predator hunting ability [7,8]. Functional responses can be divided into types: prey-dependent (functional response is a function of only prey's density) and prey-predator-dependent (functional response is a function of both prey and predator's density). For example, Holling I–III [9] are prey-dependent functional responses and Beddington–DeAngelis [10], Crowley–Martin [11], Hassel–Varley [12] prey-predator-dependent functional responses.

Some researchers have considered predator-prey models with prey-dependent functional responses, and obtained some useful result [13–16]. In recently, some studies suggest that a more suitable general predator–prey model should be with prey-predator-dependent functional responses [17–21]. Skalski and Gilliam [22] indicted that three prey-predator-dependent functional responses (Beddington–DeAngelis, Crowley–Martin, and Hassell–Varley) can provide better description of predator feeding over a range of predator–prey abundances present. In particular,

Beddington–DeAngelis or Hassell–Varley model is suitable for the case that predator feeding rate becomes independent of predator density at high prey density and Crowley–Martin model suitable for the case that predator feeding rate is decreased by higher predator density even when prey density is high.

In [23], Tripathi et al. studied a predator-prey model with Crowley–Martin functional response and time delay, that is

$$
\begin{cases}
\frac{dU}{dT} = AU - BU^2 - \frac{CUV}{A_1 + B_1 U + C_1 V + B_1 C_1 UV}, \\
\frac{dV}{dT} = \frac{FU(T-\bar{\tau})V(T-\bar{\tau})}{A_1 + B_1 U(T-\bar{\tau}) + C_1 V(T-\bar{\tau}) + B_1 C_1 U(T-\bar{\tau})V(T-\bar{\tau})} - DV - EV^2.
\end{cases}
\tag{1.1}
$$

with the initial conditions $U(0) = U_0 > 0$, $V(0) = V_0 > 0$, which are biologically meaningful. Here U and V represent prey and predator densities at time t respectively. All the parameters in the model are positive. To know the meaning of these parameters, one can refer to [23]. This model considers predator's intra-species competition, that is the death rate of predator $D + EV$ is a function of densities increase. As predator densities increase, the death rate of predator increases. As predator densities approaches to zero, the death rate approaches to D (a constant). In, [23] the authors investigate the permanence, non-permanence, local asymptotic stability and global asymptotic stability of equilibra for system (1.1).

For simplicity, taking $U = Au/B$, $V = v$, $T = t/A$ and $\tau \bar{\tau}/A$, then (1.1) can be rewritten in the following form

$$
\begin{cases}
\frac{du}{dt} = u - u^2 - \frac{\alpha uv}{1 + au + bv + cuv}, \\
\frac{dv}{dt} = s\left(\frac{\beta u(t-\tau)v(t-\tau)}{1 + au(t-\tau) + bv(t-\tau) + cu(t-\tau)v(t-\tau)} - v - ev^2 \right).
\end{cases}
\tag{1.2}
$$

where

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$$a = \frac{AB_1}{A_1B}, \quad b = \frac{C_1}{A_1}, \quad c = \frac{AB_1C_1}{A_1B}, \quad \alpha = \frac{C}{AA_1}, \quad s = \frac{D}{A},$$

$$e = \frac{E}{D}, \quad \beta = \frac{FA}{A_1BD}.$$

In the real world, predators and their preys distribute inhomogeneous in different spatial location at time t. And they will move or diffuse to areas with smaller population concentration. So in more realistic ecological models, the diffusion should be considered. Assume that the region Ω is closed, with no prey and predator species entering and leaving the region at the boundary. We consider spatial changes in both the species, and a spatial model analogue of the model (1.2) presented takes the following form:

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} = d_1 \Delta u + u - u^2 - \frac{\alpha uv}{1+au+bv+cuv}, & x \in (0, \Omega), \quad t > 0 \\ \frac{\partial v(x,t)}{\partial t} = d_2 \Delta v + s\left(\frac{\beta u(t-\tau)v(t-\tau)}{1+au(t-\tau)+bv(t-\tau)+cu(t-\tau)v(t-\tau)} - v - ev^2\right), \\ \qquad x \in (0, \Omega), \quad t > 0 \\ u_x(0,t) = v_x(0,t) = 0, u_x(\Omega,t) = v_x(\Omega,t) = 0, \quad t > 0 \\ u(x,\theta) = u_0(x,\theta) \geq 0, v(x,\theta) = v_0(x,\theta) \geq 0, \quad x \in [0, \Omega], \\ \qquad \theta \in [-\tau, 0], \end{cases}$$

$$(1.3)$$

In the rest of this paper, we will assume $\Omega = l\pi$, where $l > 0$.

The rest of this paper is organized as follows. In Section 2, we study the dynamics of the non-delay system, including stability and Turing instability of positive equilibrium. In Section 3, we study the effect of delay on the model including stability and Hopf bifurcation at positive equilibrium. In Section 4, we give some numerical simulations to illustrate the theoretical results.

2. Stability analysis of the non-delayed system

Without delay, system (1.3) becomes

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \Delta u + u - u^2 - \frac{\alpha uv}{1+au+bv+cuv}, & x \in (0, l\pi), \\ & t > 0, \\ \frac{\partial v}{\partial t} = d_2 \Delta v + s\left(\frac{\beta uv}{1+au+bv+cuv} - v - ev^2\right), & x \in (0, l\pi), \\ & t > 0, \\ u_x(0,t) = v_x(0,t) = 0, u_x(l\pi,t) = v_x(l\pi,t) = 0, & t > 0, \\ u(x,0) = u_0(x,t) \geq 0, v(x,0) = v_0(x,t) \geq 0, & x \in [0, l\pi]. \end{cases}$$

$$(2.1)$$

Obviously, system (2.1) has two boundary equilibria $E_0 = (0,0)$ and $E_1 = (1,0)$. In [23], authors have studied the existence of positive equilibrium by Descartes rule of sign. In the following, we just suppose system (2.1) has a positive equilibrium $E_*(u_*, v_*)$.

2.1. Local stability analysis of the model without diffusion

For system (2.1) without diffusion, the Jacobian matrix at $E_*(u_*, v_*)$ is

$$J = \begin{pmatrix} a_1 & -a_2 \\ sb_1 & -sb_2 \end{pmatrix},$$

where

$$a_1 = \frac{\alpha u_* v_*(a + cv_*)}{(1 + au_* + bv_* + cu_*v_*)^2} - u_*,$$

$$a_2 = \frac{\alpha u_*(1 + au_*)}{(1 + au_* + bv_* + cu_*v_*)^2} > 0,$$

$$b_1 = \frac{v_* \beta(1 + bv_*)}{(1 + au_* + bv_* + cu_*v_*)^2} > 0,$$

$$b_2 = v_*\left(e + \frac{\beta u_*(b + cu_*)}{(1 + au_* + bv_* + cu_*v_*)^2}\right) > 0. \qquad (2.2)$$

The characteristic equation of system (2.1) without diffusion corresponding to $P = (u_*, v_*)$ is

$$\lambda^2 - tr_0 \lambda + \Delta_0 = 0. \qquad (2.3)$$

The roots of Eq. (2.3) are given by $\lambda_{1,2} = \frac{1}{2}[tr_0 \pm \sqrt{\Delta_0}]$. When

$$tr_0 = a_1 - sb_2 < 0 \quad \text{and} \quad \Delta_0 = s(a_2b_1 - a_1b_2) > 0,$$

the roots of Eq. (2.3) have negative real parts. Make the following hypothesis

$(\mathbf{H_1}) \qquad a_2b_1 - a_1b_2 > 0.$

If $(\mathbf{H_1})$ holds, then $E_*(u_*, v_*)$ is locally asymptotically stable if and only if $a_1 - sb_2 < 0$. Meanwhile, if $a_1 > 0$ when s near a_1/b_2, Eq. (2.3) has a pair of complex eigenvalues $\alpha(s) \pm i\omega(s)$, where

$$\alpha(s) = \frac{1}{2}(a_1 - sb_2), \quad \omega(s) = \frac{1}{2}\sqrt{s(a_1b_2 - a_2b_1)}.$$

and

$$\alpha(a_1/b_2) = 0, \quad \alpha'(a_1/b_2) = -b_2/2, \quad \omega(a_1/b_2) > 0.$$

By the Poincare-Andronov-Hopf Bifurcation Theorem [24], we know that system (2.1) without diffusion undergoes Hopf bifurcation at $P(u_0, v_0)$ when $s = a_1/b_2$.

Summarizing the discussion above, we have the following conclusions.

Theorem 2.1. *Suppose* $(\mathbf{H_1})$ *holds, for system (2.1) without diffusion the following statements are true.*

  (i) *If $a_1 - sb_2 < 0$, then the equilibrium $P(u_*, v_*)$ is locally asymptotically stable;*
  (ii) *If $a_1 > 0$, system (2.1) without diffusion undergoes Hopf bifurcation at $P(u_*, v_*)$ when $s = a_1/b_2$.*

2.2. Turing instability and Hopf bifurcation

For system (2.1) with diffusion, we can easily get characteristic equation at $E_*(u_*, v_*)$

$$\lambda^2 - tr_n \lambda + \Delta_n(s) = 0, \quad n = 0, 1, 2, \cdots, \qquad (2.4)$$

where

$$\begin{cases} tr_n = tr_0 - \frac{n^2}{l^2}(d_1 + d_2), \\ \Delta_n = \Delta_0 - \frac{n^2}{l^2}(d_2a_1 - sd_1b_2) + d_1d_2\frac{n^4}{l^4}, \end{cases} \qquad (2.5)$$

and the eigenvalues are given by

$$\lambda_{1,2}^{(n)}(s) = \frac{tr_n \pm \sqrt{tr_n^2 - 4\Delta_n}}{2}, \quad n = 0, 1, 2, \cdots. \qquad (2.6)$$

Obviously, if $a_1 - sb_2 < 0$, then $tr_n \leq tr_0 < 0$ for $n = 0, 1, 2, \cdots$. Suppose $(\mathbf{H_1})$ holds, then $\Delta_0 = s(a_2b_1 - a_1b_2) > 0$, and if $s \geq \frac{d_2a_1}{d_1b_2}$ also holds, then $\Delta_n \geq \Delta_0 > 0$ for $n = 0, 1, 2, \cdots$.

Denote

$$s_{\mp} = \frac{d_2}{b_2^2 d_1}\left[-(a_1b_2 - 2a_2b_1) \mp 2\sqrt{a_2b_1(a_1b_2 - a_2b_1)}\right] \qquad (2.7)$$

$$z_{\mp} = \frac{1}{2d_1d_2}\left[d_2a_1 - sd_1b_2 \right.$$
$$\left. \mp \sqrt{(d_2a_1 - sd_1b_2)^2 - 4d_1d_2s(a_2b_1 - a_1b_2)}\right], \qquad (2.8)$$

and

$$\sigma = \frac{1}{a_1b_2}\left[2a_2b_1 - a_1b_2 - 2\sqrt{a_2b_1(a_2b_1 - a_1b_2)}\right]. \qquad (2.9)$$

Under $(\mathbf{H_1})$, the following relationship about $\frac{a_1}{b_2}$, $\frac{d_2a_1}{d_1b_2}$ and $s_{\pm}$ hold.

$$\begin{cases} \text{if } \frac{d_1}{d_2} < \sigma, & \text{then } 0 < \frac{a_1}{b_2} < s_- < \frac{d_2a_1}{d_1b_2} < s_+, \\ \text{if } \frac{d_1}{d_2} > \sigma, & \text{then } 0 < s_- < \frac{a_1}{b_2} < \frac{d_2a_1}{d_1b_2} < s_+. \end{cases}$$