



Analysis of a diffusive predator-prey system with anti-predator behaviour and maturation delay

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ABSTRACT

The dynamics of a diffusive predator-prey system with anti-predator behaviour and maturation delay subject to Neumann boundary condition is investigated in this paper. The global stability of boundary equilibrium is studied. For coexisting equilibrium, Turing instability induced by diffusion and Hopf bifurcation induced by time delay are studied. By the theory of normal form and center manifold method, the conditions for determining the bifurcation direction and the stability of the bifurcating periodic solution are derived.

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1. Introduction

Many researchers have studied predator-prey model [1–11], since it exists universally and is important with other biological systems. Among these models, all authors label the animals as predator or prey, and suppose predator feeds on prey. In the real world, anti-predator behaviour of prey population exists and many experiments have shown that this behaviour is achieved in two ways. One way is that morphological changes or through changes in behaviour [12,13]. Another way is that the prey attack their predators [14,15]. For the first way, some authors have studied it and suggest that more efficient anti-predator behaviour is beneficial to the prey population, and can reduce the predator density. For the second way, Tang and Xiao propose a predator-prey model by introducing a parameter as the rate of anti-predator behaviour of prey to the predator population [16]. They suppose that adult prey can attack and even kill the juvenile predators.

In predator-prey models, the functional response of predators to prey density is essential and it can enrich the dynamics of predator-prey systems. In ecology, many factors can affect functional responses, such as prey escape ability, predator hunting ability and structure of the prey habitat [17,18]. Generally, functional responses can be divided into types: prey-dependent (such as Holling I-III [19]) and predator-dependent (such as Beddington-DeAngelis [20], Crowley-Martin [21], Hassel-Varley [22]). In [23], Skalski and Gilliam suggest that three predator-dependent func-

tional responses can provide better description of predator feeding over a range of predator-prey abundances present. In some cases, the Beddington-DeAngelis type performed even better.

In the real world, predators and their preys distribute inhomogeneously in different spatial location at time t , and more and more researchers study diffusive predator-prey model. In addition, diffusion can induce Turing instability, pattern formation, spatially inhomogeneous periodic solutions and exhibit rich dynamical properties [24–28]. In predator-prey models, time delay always occurs in maturation time, capturing time, gestation time or others. Many scholars have studied the delayed predator-prey systems, since it can exhibits rich dynamics [29–32]. Time delay may affect the stable or unstable outcome of prey densities due to predation.

2. Method

2.1. Model formulation

Denote $u(x, t)$ and $v(x, t)$ as prey and predator densities at the location x and time t respectively. We consider the following system

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} = d_1 \Delta u + ru \left(1 - \frac{u}{K}\right) - \frac{Buv}{C+A_1u+A_2v}, & x \in (0, \Omega), t > 0 \\ \frac{\partial v(x,t)}{\partial t} = d_2 \Delta v + v \left[\frac{EBu(t-\tau)}{C+A_1u(t-\tau)+A_2v(t-\tau)} - d - su \right], & x \in (0, \Omega), t > 0 \\ u_x(0, t) = v_x(0, t) = 0, u_x(\Omega, t) = v_x(\Omega, t) = 0, & t > 0 \\ u(x, \theta) = u_0(x, \theta) \geq 0, v(x, \theta) = v_0(x, \theta) \geq 0, & x \in [0, \Omega], \theta \in [-\tau, 0]. \end{cases} \quad (2.1)$$

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All the parameters in the model are positive:
 d_1 and d_2 are diffusion coefficients of prey and predator respectively;

- r is intrinsic growth rate of prey;
- K is the carrying capacity of the prey in ecosystem;
- B is the maximum predator attack rate;
- C is the half-saturation constant;
- A_1 is the effect of handling time for predators;
- A_2 is the magnitude of interference among predators;
- E is the conversion efficiency of prey into the predator;
- d is the death rate of predator;
- s is the rate of anti-predator behaviour of prey to the predator population;

τ is time delay and measures the maturation period of predator.

The prey and predator diffuse within the considered habitat $[0, \Omega]$. The prey follows the logistic growth formulation with no predator. The predation predator on prey is modeled as a Beddington–DeAngelis type functional response $(Bv/(C + A_1u + A_2v))$. The growth rate of predator is formulated to be $EBu(t - \tau)/(C + A_1u(t - \tau) + A_2v(t - \tau))$, depending on the prey and predator densities at time $t - \tau$. Similar to the work in [16], we suppose the prey can attack the predator. In system (2.1), the boundary condition is Neumann boundary condition, based on the hypothesis that the region is closed, with no prey and predator species entering and leaving the region at the boundary.

2.2. Non-dimensionalization

For the convenience to study the model (2.1), we perform non-dimensionalization. Denote $a = \frac{B}{rC}$, $b = \frac{A_1}{C}$, $c = \frac{A_2}{C}$, $e = \frac{EB}{C}$. System (2.1) can be rewritten as:

$$\begin{cases} \frac{\partial u(x,t)}{\partial t} = d_1 \Delta u + ru \left[1 - \frac{u}{K} - \frac{av}{1+bu+cv} \right], & x \in (0, \Omega), t > 0 \\ \frac{\partial v(x,t)}{\partial t} = d_2 \Delta v + v \left[\frac{eu(t-\tau)}{1+bu(t-\tau)+cv(t-\tau)} - d - su \right], & x \in (0, \Omega), t > 0 \\ u_x(0, t) = v_x(0, t) = 0, u_x(\Omega, t) = v_x(\Omega, t) = 0, & t > 0 \\ u(x, \theta) = u_0(x, \theta) \geq 0, v(x, \theta) = v_0(x, \theta) \geq 0, & x \in [0, \Omega], \\ \theta \in [-\tau, 0]. \end{cases} \tag{2.2}$$

For convenience, we assume $\Omega = l\pi$, where $l > 0$ in the rest of this paper.

The rest of this paper is organized as follows. In Section 3, we discuss the existence of coexistent equilibria. In Section 4, we study global stability of the boundary equilibrium. In Section 5, we study the stability of coexistent equilibria and Hopf bifurcation, including Turing instability induced by diffusion, the stability and direction of bifurcating periodic solution. In Section 6, we give some numerical simulations. In Section 7, we give a conclusion.

3. Equilibrium analysis

This manuscript mainly study the stability and Hopf bifurcation of equilibria for the model (2.2). So we first analyze the existence of equilibria including boundary equilibria and coexisting equilibrium. Obviously, system (2.2) has two boundary equilibria $(0, 0)$ and $(K, 0)$. In this paper, we mainly focus on the coexisting equilibrium point of the system (2.2). Now we discuss the existence of coexisting equilibrium point. Suppose (u_*, v_*) is coexisting equilibrium point of the system (2.2). we can easily obtained that $v_* = \frac{eu_*(K-u_*)}{aK(d+su_*)}$. Obviously, $v_* > 0$ implies $u_* < K$. Submitting $v_* = \frac{eu_*(K-u_*)}{aK(d+su_*)}$ into the second equation, yields

$$h(u) = (ce - abKs)u^2 - K(ce + a(bd - e + s))u - adK = 0 \tag{3.1}$$

If $s \neq \frac{ce}{abK}$, Eq. (3.1) has two roots

$$\begin{aligned} u_+ &= \frac{K(ce+a(bd-e+s))+\sqrt{K^2(ce+a(bd-e+s))^2+4adK(ce-abKs)}}{2(ce-abKs)} \\ u_- &= \frac{K(ce+a(bd-e+s))-\sqrt{K^2(ce+a(bd-e+s))^2+4adK(ce-abKs)}}{2(ce-abKs)}. \end{aligned} \tag{3.2}$$

Then system (2.2) has coexisting equilibrium (u_*, v_*) if and only if $h(u) = 0$ has root u_* such that $0 < u_* < K$. Clearly, $h(0) = -adK < 0$ and $h(K) = aK(K(e - s(1 + bK)) - d - bdK)$.

Case I: $s \neq \frac{ce}{abK}$ and $s < e/(1 + bK) - d/K$. In this case, $h(u)$ is a parabola and $h(K) > 0$, system (2.2) has a unique coexisting equilibrium (u_+, v_+) , where $v_+ = \frac{eu_+(K-u_+)}{aK(d+su_+)}$.

Case II: $\max\{\frac{ce}{abK}, e/(1 + bK) - d/K, \frac{e(a+c)-abd}{a+2abK}\} < s < e - bd - ce/a$ and $(K(ce + a(bd - e + s)))^2 + 4adK(ce - abKs) > 0$. In this case, $h(K) < 0$ and $h(u)$ is a parabola going downwards, with the axis of symmetry in the interval $(0, K)$, and has two roots. System (2.2) has two coexisting equilibria (u_+, v_+) and (u_-, v_-) , where $v_- = \frac{eu_-(K-u_-)}{aK(d+su_-)}$.

Case III: $s = \frac{ce}{abK}$. Denote $u_0 = \frac{ad}{a(e-bd-ce/abK)-ce}$. If $0 < u_0 < K$, then system (2.2) has a unique coexisting equilibrium (u_0, v_0) , where $v_0 = \frac{eu_0(K-u_0)}{aK(d+su_0)}$.

4. Global stability of the boundary equilibrium

In this section, we discuss the global stability of the boundary equilibrium $(K, 0)$ by using the similar method in [33]. Consider the case $s > e/(1 + bK)$. Denote

$$\begin{aligned} g_1(\phi, \psi) &= r\phi_1 \left(1 - \frac{\phi_1}{K} \right) - \frac{ar\phi_1\phi_2}{1+b\phi_1+c\phi_2}, \\ g_2(\phi, \psi) &= \frac{e\psi_1\phi_2}{1+b\psi_1+c\psi_2} - d\phi_2 - s\phi_1\phi_2, \end{aligned}$$

where $\phi = (\phi_1, \phi_2)^T$, $\psi = (\psi_1, \psi_2)^T$. It is easy to check that $g = (g_1, g_2)$ is mixed quasi-monotone in $\mathbb{R}_+^2 \times \mathbb{R}_+^2$. Define $(\hat{u}, \hat{v}) = (0, 0)$ and $(\tilde{u}, \tilde{v}) = (M_1, M_2)$, where $M_1 \geq K$ and $M_2 > 0$. Then (\hat{u}, \hat{v}) and (\tilde{u}, \tilde{v}) are coupled upper and lower solutions of the system (2.2), since

$$\begin{aligned} r\hat{u} \left(1 - \frac{\hat{u}}{K} \right) - \frac{ar\hat{u}\hat{v}}{1+b\hat{u}+c\hat{v}} &\leq 0, \quad \frac{e\hat{u}\hat{v}}{1+b\hat{u}+c\hat{v}} - d\hat{v} - s\hat{u}\hat{v} \leq 0, \\ r\tilde{u} \left(1 - \frac{\tilde{u}}{K} \right) - \frac{ar\tilde{u}\tilde{v}}{1+b\tilde{u}+c\tilde{v}} &\geq 0, \quad \frac{e\tilde{u}\tilde{v}}{1+b\tilde{u}+c\tilde{v}} - d\tilde{v} - s\tilde{u}\tilde{v} \geq 0. \end{aligned}$$

Choose M_1 and M_2 as sufficiently large, from Theorem 2.1 in [34], we know that there exists a unique global nonnegative solution (u, v) for system (2.2) with nonnegative initial value

$$u_0(x, \theta), v_0(x, \theta), \quad x \in [0, L\pi], \theta \in [-\tau, 0]$$

and $u_0(x, \theta) \neq 0$ and $v_0(x, \theta) \neq 0$. Using the maximum principle, we can obtain that $u(x, t), v(x, t) > 0$ for $t > 0$.

Let $(\hat{u}, \hat{v}) = (\epsilon, 0)$ and $(\tilde{u}, \tilde{v}) = (K, \delta(\epsilon))$, where ϵ is a small positive number and $\delta(\epsilon) > 0$ such that $\delta(\epsilon)[a - (1 - \epsilon/K)c] \leq (1 - \epsilon/K)(1 + b\epsilon)$. We can verify that $(\epsilon, 0)$ and $(K, \delta(\epsilon))$ are also coupled upper and lower solutions of the system (2.2). When

$$\epsilon < \phi_1, \psi_1 < K, \quad 0 < \phi_2, \psi_2 < \delta(\epsilon)$$

from the boundedness of the partial derivative of g_i ($i = 1, 2$) with respect to ϕ, ψ , we know that g_i satisfy the Lipschitz condition. Denote the Lipschitz constants by K_i ($i = 1, 2$). There exists a unique global solution (u, v) to the system (2.2), and it such that $(\epsilon, 0) \leq (u, v) \leq (K, \delta(\epsilon))$ whenever $(\epsilon, 0) \leq (u_0(x, \theta), v_0(x, \theta)) \leq (K, \delta(\epsilon))$, by the Theorem 2.1 in [34].

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