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Competitive exclusion and coexistence of a delayed reaction–diffusion system modeling two predators competing for one prey

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ABSTRACT

In this work, we study a time delayed reaction–diffusion system with homogeneous Neumann boundary conditions. This system describes two predators competing for the same prey. By the method of upper and lower solutions, we obtain sufficient conditions for the competitive exclusion principle to hold and sufficient conditions of the global asymptotic stability of positive constant solution. By taking time delay as the bifurcation parameter, spatially homogeneous and inhomogeneous Hopf bifurcation at the positive constant solution are proved to occur for a sequence of critical values of the delay parameter. It is shown that there are three coexistence forms for the three species: steady states, spatial homogeneous and inhomogeneous periodic oscillations.

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1. Introduction

It is well known that resource competition is common in nature and society. Competitive exclusion or competitive coexistence is important mechanism of natural selection in the resource competition model. The competitive exclusion principle asserts that no two populations competing for a common resource can live indefinitely in the same ecological niche. The earliest statements of the competitive exclusion principle can be tracked back to Darwin [1]. The simplest mathematical formulations of this principle describe competition for a static limiting resource. This case was already modeled by Volterra [2]. He concluded that one of the two competitors drives the other to extinction, under all reasonable biological assumptions. His analysis was later improved by Lotka [3]. Utida [4] tried to construct a laboratory system showing violations of the competitive exclusion of any form. The author pointed out that nothing, excludes "experimental oscillatory coexistence" of two parasitoids competing for the same host.

Since then, competitive exclusion or coexistence in many resource competition models have become a central object of research (such as predator–prey models [5–11], chemostat models [12–15], multi-strain epidemic models [16–19]). Hsu et al. [5] introduced and studied the following competitive problem of the two predators for a prey model with Holling-II

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functional response:

$$\begin{cases} \dfrac{dx}{dt} = r\left(x - \dfrac{x}{k}\right) - \dfrac{c_1 x y_1}{a_1 + x} - \dfrac{c_2 x y_2}{a_2 + x}, \\ \dfrac{dy_1}{dt} = \left(\dfrac{m_1 c_1 x}{a_1 + x} - d_1\right) y_1, \\ \dfrac{dy_2}{dt} = \left(\dfrac{m_2 c_2 x}{a_2 + x} - d_2\right) y_2. \end{cases} \tag{1.1}$$

Here $x(t)$ is the prey, $y_1(t)$ and $y_2(t)$ are predators competing for the same prey. In the absence of predation, the prey grows logistically with intrinsic growth rate r and carrying capacity k. The ith $(i = 1, 2)$ predator consumers the prey according to the Holling-II functional response $\frac{c_i x y_i}{a_i + x}$ and its growth rate is $\frac{m_i c_i x y_i}{a_i + x}$, where m_i is the conversion efficiency coefficient; c_i is the search rate; a_i is the handling times. d_i is the death rate. The authors gave some analytic results about the competitive exclusion of the two competitors. In [6] they did extensive numerical simulations to indicate the possibility of coexistence of two competing predators. Following the numerical observations, there have been several theoretical results. Butler and Waltman [7] proved a coexistence by using the bifurcation technique from a limit cycle in the (x, y_1) plane. However, their result is only local and the system is not uniformly persistence. Muratori and Rinaldi [8] and Liu et al. [9] considered the case where the intrinsic growth rate of the prey is large and used geometric singular perturbation method to establish the coexistence of two predators in the form of stable relaxation oscillations. Hsu et al. [10] investigated model (1.1) with functional response of Beddington–DeAngelis type (i.e., $\frac{c_i x y_i}{a_i + x}$ is replaced by $\frac{c_i x y_i}{a_i + x + b_i y_i}$). They obtained the parameter range of the validity of the competitive exclusion principle and showed that there are two coexistence states for the three species: periodic oscillations and steady states. The authors explored some differences in comparison with model (1.1). Recently, Llibre and Xiao [11] considered model (1.1) with linear functional response (i.e., $\frac{c_i x y_i}{a_i + x}$ is replaced by $c_i y_i$). Therein, the authors obtained sufficient and necessary conditions for the competitive exclusion principle to hold. When the competitive exclusion principle does not hold, if carrying capacity parameter k is bounded, then either the three species coexist at a positive equilibrium or both competing predators go to extinction and the prey exists. On the other hand, if parameter k is unlimited, then the three species coexist in the form of periodic oscillations.

In the aforementioned work, the resource competition models are described by a system of ordinary differential equations. Considerably less effort has been devoted to the study of resource competition models with time delays and diffusion effects due to its complexity. The dynamical models in the form reaction–diffusion equations have been extensively investigated in various natural sciences. In order to reflect the real dynamical behaviors of models that depend on the past history of systems, it is reasonable to incorporate time delays into the systems. Especially in mathematical biology, physics and chemistry, many models of population dynamics can be described by the delayed reaction–diffusion equations [20–22]. In this paper we study the following resource competition model of two predators competing for one prey with time delays and spatial diffusion:

$$\begin{cases} u_{1t} = d_1 \Delta u_1 + u_1 \left[a_1 - b_{11} u_1 - b_{12} u_2(x, t - \tau_2) - b_{13} u_3(x, t - \tau_3)\right], \\ u_{2t} = d_2 \Delta u_2 + u_2 \left[-a_2 + b_{21} u_1(x, t - \tau_1) - b_{22} u_2\right], \\ u_{3t} = d_3 \Delta u_3 + u_3 \left[-a_3 + b_{31} u_1(x, t - \tau_1) - b_{33} u_3\right], \quad (x, t) \in \Omega \times (0, \infty), \\ \dfrac{\partial u_1}{\partial \nu} = \dfrac{\partial u_2}{\partial \nu} = \dfrac{\partial u_3}{\partial \nu} = 0, \quad (x, t) \in \partial\Omega \times (0, \infty), \\ u_j(x, t) = \eta_j(x, t) \geq 0, \quad (x, t) \in \overline{\Omega} \times \left[-\tau_j, 0\right], \ (j = 1, 2, 3), \end{cases} \tag{1.2}$$

where Δ is the Laplace operator, $\Omega \subset \mathbb{R}^N$ is a bounded domain with smooth boundary $\partial\Omega$ and ν is the outward unit normal on $\partial\Omega \cdot d_j,\ a_j,\ b_{jj},\ j = 1, 2, 3,\ b_{12},\ b_{21},\ b_{13},\ b_{31}$ are all positive constants and τ_j is nonnegative constant. d_j is the diffusion rate of jth species, b_{jj} measure the intra-specific competition of the prey, the first predator and the second predator, respectively; b_{12} and b_{13} denote the predation rate of per capita of the first predator and the second predator, respectively; b_{21} and b_{31} represent conversion rates of the prey to the first predator and the second predator, respectively. τ_1 is the delay in the predator maturation, τ_2 and τ_3 are called the hunting delay [23]. The initial function $\eta_j(x, t)$ is Hölder continuous on $\overline{\Omega} \times \left[-\tau_j, 0\right]$. The purpose of this paper is to determine the outcome of competition for system (1.2), namely, under what conditions the competitive exclusion principle holds and under what conditions coexistence of two competing predators occurs.

The structure of this paper is arranged as follows. In Section 2, we give some known results which are required later. In Section 3, we study the global asymptotic stability of all forms of nonnegative constant solutions. In Section 4, we consider the existence of Hopf bifurcation at the positive constant solution. Several numerical simulations are presented in Section 5 to illustrate the obtained results. We end with a brief conclusion in Section 6.

2. Preliminaries

In this section we present some preliminary results. These results will be useful for us to prove the results in next section.

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