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Dynamics in a diffusive predator–prey system with ratio-dependent predator influence^{*}

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ABSTRACT

A diffusive predator-prey system with predator functional response subject to Neumann boundary conditions is considered. Existence, nonexistence, and boundedness of positive steady state solutions are shown to identify the ranges of parameters of spatial pattern formation. Hopf and steady-state bifurcation analyses are carried out in detail. These results provide theoretical evidences to the complex spatio-temporal dynamics found by numerical simulation.

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1. Introduction

The dynamic relationship between predators and their preys has long been and will continue to be one of the dominant topics in mathematical ecology due to its universal existence and importance. Since the classical Lotka–Volterra models have the unavoidable limitation to precisely describe many realistic phenomena in biology, in some cases, they should make way to more sophisticated models from both mathematical and biological points of view. Leslie [1] and Leslie and Gower [2] considered a classical Leslie type predator–prey system. The new predator–prey system takes the following form (Freedman and Mathsen [3], Hsu and Huang [4]):

$$\begin{cases} \dot{u}_1 = u_1 g(u_1) - u_2 p(u_1), \\ \dot{u}_2 = u_2 q\left(\frac{u_2}{u_1}\right), \end{cases}$$
(1.1)

where $u_1(t)$ and $u_2(t)$ represent the densities of prey and predators at time t, respectively; g(u), p(u), and q(u) are smooth functions with respect to u. More precisely, g(u) represents the natural per capita growth function and describes the specific growth rate of the prey in the absence of predators, while p(u) represents the functional response of predators to the prey and describes the change in the density of the prey attacked per unit time per predator as the prey density changes. Throughout this paper, we always assume that g(0) > 0, p(0) = 0, q(0) > 0, q'(0) < 0, and there exists K > 0 such that g(K) = 0 and g'(K) < 0 for some K > 0, $g'(u) \le 0$, p(u) > 0, and $q'(u) \le 0$ for any u > 0.

Obviously, g(u) = a - bu and q(u) = s - hu with positive constants a, b, s and h satisfy all assumptions, where a and b are the intrinsic growth rate and the environment carrying capacity of prey, respectively; the parameter s stands for an intrinsic growth rate of predator and h is a measure of the food quality that the prey provides for conversion into predator birth. In the case, the system (1.1) can be classified into five types depending on functional response p(u). The simplest

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model is type I functional response of the form p(u) = mu with a positive constant m, it becomes the so-called Leslie–Gower model. The function response is obtained by assuming that in the time available for searching, the total change in the prey density/substrate concentration is proportional to the prey density/substrate concentration. Thus, more reasonable response functions should be nonlinear and bounded. The saturating functional response $\frac{mu}{c+u}$ was proposed by Michaelis and Menten in studying enzymatic reactions, where the parameter *m* denotes the maximum growth rate of product species, *u* is the substrate concentration, and c is the substrate concentration at which the rate of product formation is half maximal. Later, Holling [5] also used the function as one of the predator functional responses. It is now referred to as a Michaelis-Menten function or a Holling type-II function. When the functional responses p(u) takes the form $p(u) = \frac{mu^2}{(c+u)(d+u)}$ with positive constants m, c and d, it is called a sigmoidal response function, while simplification $p(u) = \frac{mu^2}{c+u^2}$ is know as a Holling type-III function. Colling [6] also used the response function $p(u) = \frac{mu^2}{(c+u)(d+u)}$ in a mite predator–prev interaction model and called it a Holling type-IV function (see Taylor [7]).

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So far, model (1.1) has been investigated by many authors in either qualitative or numerical analysis, and lots of interesting phenomena, such as stable limit cycles, semi-stable limits cycles, bifurcation, global stability of the unique constant positive steady-state periodic solutions, have been uncovered (we refer interested readers to [8-11]). If taking into account the effect of diffusion, instead of the ordinary differential system (1,1), we need to consider the following reaction-diffusion system

$$\begin{cases}
\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + u_1 g(u_1) - u_2 p(u_1) & \text{in } \Omega \times (0, \infty), \\
\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + u_2 q\left(\frac{u_2}{u_1}\right) & \text{in } \Omega \times (0, \infty), \\
\frac{\partial u_1}{\partial \mathbf{n}} = \frac{\partial u_2}{\partial \mathbf{n}} = 0 & \text{on } \partial \Omega \times (0, \infty), \\
u_1(x, 0) = \varphi(x) > 0, \quad u_2(x, 0) = \psi(x) \ge 0, & \text{in } \Omega,
\end{cases}$$
(1.2)

where $d_1 > 0$, $d_2 > 0$, Δ denotes the Laplacian operator on \mathbb{R}^N , **n** is the outward unit normal vector on $\partial \Omega$. The homogeneous Neumann boundary condition means that the two species have zero flux across the boundary $\partial \Omega$.

Compared with system (1.1), system (1.2) has more complicated and more abundant dynamical behavior. Some complicated spatiotemporal patterns emerge in a large part due to the effect of the diffusion. A complete and rigorous analysis of the dynamics of system (1.2) has not been achieved. Some researchers just studied the dynamical behaviors of some specific models of (1.2). For example, Du and Hsu [12] considered the following diffusive predator-prey model with Leslie-Gower functional response (type I):

$$\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + u_1 (a - bu_1) - c u_1 u_2 \qquad \text{in } \Omega \times (0, \infty),
\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + s u_2 \left(1 - \frac{u_2}{u_1} \right) \qquad \text{in } \Omega \times (0, \infty),
\frac{\partial u_1}{\partial \mathbf{n}} = \frac{\partial u_2}{\partial \mathbf{n}} = 0 \qquad \text{on } \partial \Omega \times (0, \infty).$$
(1.3)

Du and Hsu [12] showed that (1,3) has no non-constant positive steady-state solutions when the a, b, s and h are all constants and satisfy suitable conditions, while a non-constant positive steady-state solution can be created when the species concentrate on some region of spatial habitat Ω . In particular, by choosing a suitable coefficient function which vanishes in a subdomain of Ω , Du and Hsu [12] showed that certain patterned solutions can be obtained in a heterogeneous environment.

Chen and Shi [13], Peng and Wang [14,15] considered the following diffusive system with Holling–Tanner functional response (type II):

$$\begin{cases} \frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + u_1 (a - u_1) - \frac{u_1 u_2}{m + u_1} & \text{in } \Omega \times (0, \infty), \\ \frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + u_2 \left(b - \frac{u_2}{\gamma u_1} \right) & \text{in } \Omega \times (0, \infty), \\ \frac{\partial u_1}{\partial \mathbf{n}} = \frac{\partial u_2}{\partial \mathbf{n}} = 0 & \text{on } \partial \Omega \times (0, \infty), \\ u_1(x, 0) = \varphi(x) > 0, \quad u_2(x, 0) = \psi(x) \ge 0, & \text{in } \Omega. \end{cases}$$
(1.4)

Peng and Wang [14] investigated the existence/non-existence of non-constant steady-state solutions of (1.4) by means of Leray-Schauder degree theory. Peng and Wang [15] studied the local and global stability of the unique positive equilibrium of (1.4). Chen and Shi [13] investigated the global stability of the constant steady-state solution of (1.4) by using a comparison method. For a model more general than (1.4), Ryu [16] investigated the existence/non-existence of nonconstant steady-state solutions as well as the local and global stability of the constant steady-state solution. Li, Jiang, and Shi [17] discussed the asymptotical behavior and the diffusive-driven instability of the constant steady-state solution of (1.4) and also investigated the stability of the Hopf bifurcating spatially homogeneous periodic solution. The study of equation (1.2) is very few,

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