



A new finding on pattern self-organization along the route to chaos



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ABSTRACT

This research investigates pattern self-organization along the route to chaos in a space- and time-discrete predator–prey system, where the prey shows convection movement in space. Through analysis on Turing instability of the system, pattern self-organization conditions are determined. Based on the conditions, simulations are performed under two initial conditions, demonstrating two pattern transitions along the route to chaos. In the first pattern transition, the patterns start from regular stripes, experiencing twisted stripes, then return to regular stripes again. The second pattern transition is much more complex and shows three stages. Especially, an alternation between ordered patterns and disordered chaos is found, contributing greatly to the spatiotemporal complexity of the system. When the system stays at the homogeneous chaotic states, Turing instability driven by convection and diffusion can still force the self-organization of regular striped patterns. The finding in this research provides a new comprehending for pattern self-organization and transition in spatially extended predator–prey systems.

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1. Introduction

In ecological systems, interactions between species and induced evolution of species are important features. From biological and ecological point of view, predator–prey relationship is one of the most basic and widely existing interactions. Studies in mathematical models are informative in understanding the dynamic relationship between predator and prey and their complex properties [1] and [2]. Since the pioneering works of Lotka and Volterra, a variety of predator–prey models have been developed, revealing and mimicking nonlinear dynamical behaviors of predator–prey interactions in various circumstances, such as periodic oscillations, quasiperiodic motions, chaotic attractors, and so on [2,3,4,5,6] and [7].

Biologically speaking, the predator–prey interactions occur in a spatial world and investigation on the predator–prey interactions over a range of spatial and temporal scales, which comes as a challenge, is necessary and of great ecological significance [7]. Naturally, nonlinear interactions and spatial heterogeneity in predator–prey systems can often lead to spontaneous formation of patterns, which are heterogeneous macrostructure with certain temporal or spatial orderliness [1]. Spatial pattern formation in spatiotemporal predator–prey systems has received significant attention from many researchers during last three decades [1,8,9,10,11] and [12].

Intense research works have been initiated based upon the classical works of Segel and Jackson [13] and Levin and Segel [14], which first explained the self-organization of plankton patchiness due to diffusive instability.

As so far, various types of mathematical models have been developed for studying the pattern formation of predator–prey systems, including cellular automata, evolutionary games, reaction-diffusion models, coupled map lattices (CMLs), etc. Many interesting theoretical results have been obtained recently. For example, Perc and his coworkers found that defensive alliances and spatiotemporal self-organization can emerge spontaneously if the chain length of a predator–prey system is more than three [15] and [16], and that the spontaneous emergence of cyclic dominance acts one of the main driving forces behind complex pattern formation [17]. Killingback et al. proposed a novel competitively coupled map lattice and found that the competitive coupling can result in spontaneous symmetry breaking of a homogeneous initial configuration and the formation of stable spatial patterns [32]. Doebeli and Killingback found that with the assumption of quasi-local competition, the metapopulation can reach a new stable state and result in an irregular spatial pattern of local population abundance [33]. With the application of evolutionary games in space, a few peculiar spatial structures such as spirals and heteroclinic cycles were also discovered [34] and [35]. As recorded in literature, many complex spatial patterns have been revealed for predator–prey systems ranging from plant distributions to plankton aggre-

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gation, such as patterns of spots, stripes, labyrinth, spirals, gaps, and so on [9,18] and [19].

Among the existed spatiotemporal predator–prey models, reaction-diffusion models are the mostly widely used theoretical models for studying spatial pattern formation of predator–prey systems [9,18] and [19]. The nonlinear mechanism for pattern formation of reaction-diffusion models is diffusive instability (or Turing instability), which was introduced by Alan Turing in his seminal work [20] to explain the chemical basis of morphogenesis. With the application of Turing instability, many researchers successfully explained the formation of stationary and non-stationary patchy patterns, driven by the spatial movement of individuals of prey and predator populations. In literature, the development of reaction-diffusion predator–prey models mainly focuses on two aspects. First, diverse reaction functions are proposed to describe the dynamics of predator and prey. These reaction functions may incorporate particular growth functions, functional responses or predator numerical responses [21] and [22]. Second, dispersal of predator and prey populations in space can be described by different diffusion types, such as self-diffusion, convection-diffusion, cross-diffusion [21], etc.

Recently, a few researchers further considered the spatially and temporally discrete forms of reaction-diffusion model and developed a new type of predator–prey model which is given by coupled map lattice (CML) [4,7,8,10,11] and [12]. In comparing with the continuous reaction-diffusion models, the CMLs often show advantages in describing nonlinear characteristics and spatiotemporal complexity of predator–prey systems. For example, Rodrigues et al. [12] revealed a rich variety of pattern formation scenarios in a space- and time-discrete predator–prey system with a strong Allee effect and found spatiotemporal multistability under the effects of different initial conditions. In the research of Huang et al. [8] and [10], they compared the spatial pattern formation between a reaction-diffusion model and its CML version and demonstrated that the nonlinear mechanisms of the CML better capture the complexity of pattern formation of predator–prey systems. Moreover, the CMLs show special capability of describing discontinuous properties (e.g. patchy environment or fragmented habitat) of predator–prey systems [7].

Although lots of theoretical models have been established for predator–prey systems, still few studies focus on applying the CMLs to investigate the spatiotemporal predator–prey dynamics. As described in previous research works, the CMLs can play a key role in fostering the understanding on the pattern formation of space- and time-discrete predator–prey systems [4,7,8,10,11] and [12]. In a new research on space- and time-discrete predator–prey system, Huang and Zhang found the pattern formation is closely related to bifurcation and chaos [4]. First, the cross effects of Turing bifurcation, flip bifurcation and Hopf bifurcation can lead to three nonlinear mechanisms of pattern formation, i.e., pure Turing instability, flip-Turing instability and Hopf–Turing instability. Second, flip bifurcation and Hopf bifurcation start the routes to the homogeneous chaotic oscillating states, at which the spatial symmetry breaking occurring can still lead to the self-organization of ordered predator–prey patterns. Third, along the routes to chaos, ordered patterns may gradually transit to spatiotemporal chaos with complete disorder.

However, the study on pattern formation along the route to chaos is seldom documented in literature. As an important aspect of spatiotemporal complexity, this topic still needs to be explored in the field of ecology and nonlinear dynamics. In this research, we extend the previous research of Huang and Zhang [4], further investigating the pattern formation along the routes to chaos in a reaction-convection-diffusion predator–prey system. The convection in predator–prey systems often results from purely environmental factors which lead to the individuals exhibiting a correlated

motion towards certain direction [23]. Under the effects of convection, the pattern formation of predator–prey systems may present particular nonlinear characteristics.

This work is organized as follows. In Section 2, we propose a CML model to describe the reaction-convection-diffusion predator–prey system, based on the research of Huang and Zhang [4]. In Section 3, the results of stability analysis and bifurcation analysis are provided to determine the pattern formation conditions. In Section 4, numerical simulations are performed to show the pattern formation of the studied predator–prey system. In Section 5, discussion and conclusion are given.

2. The CML model

Based on the research of Cai et al. [18], Huang and Zhang developed a CML model to investigate the bifurcation, chaos and pattern formation of a space- and time-discrete reaction-diffusion predator–prey system [4]. At the beginning, we introduce the Cai’s model, which is given by the following partial differential equations:

$$\frac{\partial U}{\partial T} = r_1 U \left(1 - \frac{U}{K} - \frac{m_1}{U + b_1} \right) - \frac{c_1 UV}{U + K_1} + D_1 \nabla^2 U, \tag{1a}$$

$$\frac{\partial V}{\partial T} = r_2 V \left(1 - \frac{c_2 V}{U + K_2} \right) + D_2 \nabla^2 V, \tag{1b}$$

in which r_1 is the intrinsic growth rate of the prey; K is the prey carrying capacity; $m_1/(U + b_1)$ is the term of additive Allee effect, m_1 and b_1 are the Allee effect constants; $c_1 U/(U + K_1)$ describes the Holling type-II functional response, in which c_1 is the maximum predation rate and K_1 measures the extent to which environment provides protection to U ; $(r_2 - c_2 V/(U + K_2))$ describes a modified Leslie–Gower type numerical response, in which r_2 is the growth rate of the predator, and K_2/c_2 measures the predator carrying capacity in the absence of the prey U , and in such case, the predator v is actually generalist; ∇^2 is the Laplacian operator describing the spatial dispersal of populations, and D_1 and D_2 are the diffusion coefficients corresponding to U and V ; $\nabla^2 = \partial^2/\partial x^2 + \partial^2/\partial y^2$, in which x and y are spatial coordinates in two-dimensional space describing the position of U and V .

In above model, the spatial motions of both predator and prey populations are described by diffusion term, which means the spatial motion of both populations is random, and isotropic, i.e., without any preferred direction. In nature, however, the individuals often exhibit a correlated motion towards certain direction, causing another type of spatiotemporal dynamics occurring in the predator–prey systems. The origin of such directional motion may have different mechanisms. One of the most typical motions is convection, which may be corresponding to the case that the correlated motion caused by purely environmental factors such as wind in case of seeds or pollen spreading or water current in case of plankton communities [24]. In this research, we consider the convection for prey population, and therefore the model (1) is changed to be

$$\frac{\partial U}{\partial T} = r_1 U \left(1 - \frac{U}{K} - \frac{m_1}{U + b_1} \right) - \frac{c_1 UV}{U + K_1} + D_1 \nabla U, \tag{2a}$$

$$\frac{\partial V}{\partial T} = r_2 V \left(1 - \frac{c_2 V}{U + K_2} \right) + D_2 \nabla^2 V, \tag{2b}$$

where $\nabla = \partial/\partial x$ describes the convection operator and D_1 here means the speed of convection for the prey.

For reducing the number of parameters in system (2), change of variables is made. Via the following expressions,

$$u = U/K, v = V/K_2, t = r_1 T, m = m_1/K, b = b_1/K, \\ c = c_1 K_2/r_1 K, k_1 = K_1/K, r = r_2/r_1,$$

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