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Diverse self-organized patterns and complex pattern transitions in a discrete ratio-dependent predator–prey system

Tousheng Huang*, Hongju Yang, Huayong Zhang*, Xuebing Cong, Ge Pan

Research Center for Engineering Ecology and Nonlinear Science, North China Electric Power University, Beijing 102206, PR China

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ABSTRACT

The spatiotemporal complexity of a discrete ratio-dependent predator–prey system is investigated via development of a coupled map lattice model. Through stability analysis and bifurcation analysis, the critical conditions for stable homogeneous stationary and oscillatory states are determined. Meanwhile, pattern formation conditions are derived by Turing instability analysis. Based on the theoretical results, numerical simulations are performed, exhibiting rich patterns of spatiotemporal dynamics of the discrete system. On the route to chaos induced by Neimark–Sacker bifurcation, dynamic variation occurs from invariant cycles, experiencing periodic window and period-doubling process, to chaotic attractors. A variety of patterns are self-organized and demonstrate diverse types in configuration, including cold spots, labyrinth, cold stripes-spots, spirals, hot stripes, circles, arcs, disk, mosaics and fractals. Complex pattern transitions occur among the diverse patterns, suggesting sensitivity of pattern formation to parameter variations. Moreover, spatiotemporal chaos is found in pattern formation process, where tiny variations in initial conditions can result to the self-organization of different patterns. This approach reveals great diversity and complexity of pattern self-organization and pattern transition in predator–prey interactions, promoting comprehending on the spatiotemporal complexity of spatially extended predator–prey system.

1. Introduction

Predation process plays an important role in promoting life evolution and maintaining ecological balance and biodiversity [1,2]. As one of the most important relationships widely existing in natural ecosystems, predation can determine the stability of population, community and ecosystem [3]. From biological point of view, investigations on predator–prey systems provide profound perspective for the basic properties of ecological systems.

The study of predator–prey systems originates from the research of biologist Lotka and mathematician Volterra, who proposed a classical predator–prey model, i.e., Lotka–Volterra model [4,5]. The predation relationship in the Lotka–Volterra model is merely described by a linear production of predator density and prey density. Following the approach of Lotka and Volterra, a variety of predator–prey models have been established, applying different functional responses [6–11]. A functional response describes how predator and prey interact with each other, and exerts a key role in studying the dynamic behaviors of the predator–prey system. In 1959, Canadian scholar Holling proposed three kinds of functional response of

* Corresponding authors.
E-mail addresses: tous_huang@ncepu.edu.cn (T. Huang), rceens@ncepu.edu.cn (H. Zhang).

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predator to prey, Holling type I, II and III, based on numerous experiments for different species [6]. Later, many more types of functional responses were put forward and explored, such as Holling type IV [7], ratio-dependent type [8], Beddington-DeAngelis type [9,10], Leslie-Gower type [11], and so on.

The diversity of functional responses leads to complexity of predator–prey dynamics. Banerjee and Abbas [12] studied temporal dynamics of a ratio-dependent predator–prey model and found that stable and unstable limit cycles coexist and enclose a stable equilibrium when parametric conditions are given in the domain bounded by Hopf bifurcation, homoclinic bifurcation curves and saddle-node bifurcation curve of limit cycles. Lin and Chen [13] determined a unique globally attractive almost periodic solution in a Volterra model with Beddington–DeAngelis functional response and mutual interference. Haque [14] performed a detailed study on Beddington–DeAngelis predator–prey model and found that the system can exhibit saddle-node, transcritical, Hopf-Andronov and Bogdanov-Takens bifurcations under influence of intra-specific competition among predators. Besides the functional responses, many other factors such as Alee effect [15], seasonal perturbations [16], prey refuge [17], etc., were also considered and investigated in predator–prey systems, revealing complexity of predator–prey interactions in various circumstances.

Recently, predator–prey systems have been studied in structured populations in cyclical interactions with alliance-specific heterogeneous invasion rates [36] and noise-guided evolution within cyclical interactions [37]. It was shown that defensive alliances can emerge if the chain length is more than 3. Moreover, predator–prey interactions can emerge spontaneously in evolutionary settings relevant to public goods, as reported in [38–40]. In evolutionary games, the spontaneous emergence of cyclic dominance also acts one of the main driving forces behind complex pattern formation, which, in turn, is responsible for many differences between evolutionary outcomes reported in well-mixed and structured populations [41]. Overall, this subject on structured populations received many attentions and much more has been done.

The predator–prey interactions always take place in space. For studying the spatial predator–prey dynamics, various types of spatiotemporal dynamic models have been established. Among these models, reaction-diffusion models have been applied most widely and extensively [18]. Pattern self-organization via Turing instability mechanism of the reaction-diffusion models is the key for understanding and revealing the spatiotemporal complexity of spatially extended predator–prey systems. Until now, a variety of complex predator–prey patterns have been explained by the reaction-diffusion models, such as patterns of spots, gaps, stripes, hexagons, labyrinth, spirals, circles, and so on [8–10,18]. Moreover, different pattern self-organizations can be found with the variation of prey growth, predator death, functional response, numerical response and diffusion type [9,12,19–22]. Actually, this is a hot topic on which many researchers have been continuously exerting their efforts. For example, Guin introduced replaceable food source for predator and self- and cross-diffusion in a ratio-dependent predator–prey system, determining new spatiotemporal dynamics under Turing instability [35].

Generally, there are two paradigms for developing reaction-diffusion models to investigate spatiotemporal dynamics of the predator–prey systems, i.e., continuous way and discrete way. Via comparison, many scholars have found that the discrete model is more practical than the continuous model for describing the population dynamics of some insects and plants that have a quick generation change [23]. There are many methods to develop discrete models, among which coupled map lattice (CML) models are comparatively mature [23–25]. A coupled map lattice is a dynamic model in which time variable and space variable are discrete and state variables are continuous [24,25]. Unusually, a CML can be developed from discretizing the corresponding continuous reaction-diffusion model [10,21,26]. As so far, the research works on applying CMLs to investigate ecological systems are still few documented, however, many new attractive results are indeed generated by the CMLs [10,21,23,26–28]. Huang et al. [10] developed a CML model for describing a space- and time-discrete Beddington–DeAngelis type predator–prey system, and found new dynamic complexity that former corresponding continuous model does not possess, including a surprising variety of predator–prey patterns and new characteristics for the self-organized patterns. Via the application of discrete reaction-diffusion models, the spatiotemporal complexity of predator–prey systems can be further profoundly understood [23,26,27].

In this research, the coupled map lattice model is applied to study the spatiotemporal dynamics of a spatially extended predator–prey system with replaceable food source for predator and ratio-dependent functional response. As predator has alternate source of food other than the prey available to it, the predator shows a logistic growth in case of extinction of the prey. An investigation on such predator–prey system may enhance our understanding on the spatiotemporal complexity of complicated food webs. In literature, merely continuous reaction-diffusion models have been developed for such predator–prey system. When considering discrete time variable and space variable, new nonlinear characteristics and complex pattern formation may present [10,23,26]. Moreover, due to the similarity of research problems, the potential applicability of the proposed approach in this research can also extend to broader areas of population dynamics and evolution, such as spatiotemporal complexity of competitive systems, and physics of social systems [42,43]. The exploration in this research is arranged as the following. Section 2 develops the CML model for the discrete space-time predator–prey system. Section 3 analyzes the stable homogeneous stationary state, Neimark–Sacker bifurcation and Turing instability and determines the pattern formation conditions. Section 4 demonstrates the bifurcation diagram and various pattern formations via numerical simulation. Section 5 provides discussion and conclusions.

2. Discrete space-time predator–prey system

At the beginning, we introduce the continuous ordinary differential equations describing temporal dynamics of the predator–prey system, which demonstrates two characteristics: (1) ratio-dependent functional response [34], (2) predator