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Stable territory formation in ecology and its potential generality in pattern formations

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HIGHLIGHTS

- We propose a new stochastic individual-based scheme to predator–prey systems.
- Our scheme can produce stable Turing patterns.
- Our scheme can work as a logical bridge with the reaction–diffusion theory.

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ABSTRACT

Stable territory formation is frequently observed in ecology. Until now, only the reaction–diffusion scheme has successfully produced stable patterns in the predator–prey system. However, it is a density-based scheme and in principle it cannot be used to derive a comprehensive understanding from a mean-field scheme. The application of our new stochastic individual-based scheme to predator–prey systems successfully produced stable patterns such as net, stripe, and lattice patterns for the first time. This study clearly shows that non-interacting time is an important factor in stable pattern formation. Specifically, of high importance is the existence of finite time to build the appetites of predators. In some cases, extreme increases of the appetites of predators lead to chaotic changes of the population, which are similar to the locust outbreak in Africa.

1. Introduction

It is a matter of life and death for any biological organism to construct a stable body and maintain it with only small fluctuations. Since the pioneering study by Turing (1952), his idea has been successfully applied to various systems using the reaction–diffusion scheme, which is a mathematical generalization of Turing's idea by Meinhardt (Koch and Meinhardt, 1994). However, there were two problems in Turing's condition for stable pattern formation. First, it is not a necessary and sufficient condition for the stable pattern formation. Namely, it does not guarantee stable pattern formation completely. Second, the reaction–diffusion scheme is a density-based formalism. Therefore, in principle, the details of individual interactions cannot be derived from any numerical investigation. Thus, various individual-based schemes have been proposed (Grimm and Railsback, 2005; De Angelis and Mooij, 2005). For simulation studies, lattice models or patch-panel models are often adopted to introduce the migration of animals (Taninaka, 1988; Satulovsky and Tome, 1994; Satoh, 1989; Carneiro and Charret, 2007; Wilson et al., 1993; Gurney and Veitch, 2000; Hosseini, 2006).

To clarify the microscopic mechanism of pattern formation, in this letter we will focus on the predator–prey system (Nagano, 2002; Murray, 2001). An advantage of this system is that the interaction between individuals can be defined without any ambiguity. Recently, we succeeded in the construction of phase diagram in the predator–prey system by adopting a combination of the population density dynamics and the reaction–diffusion theory (Nagano and Maeda, 2012). Using this system, any microscopic study can be verified macroscopically.

In attempting to resolve the fundamental problem of the reaction–diffusion scheme, we developed a stochastic individual-based model and applied it to the predator–prey system (Yokoyama et al., 2008); however, we could not reproduce stable patterns. On the other hand, our reaction–diffusion model study confirmed the existence of stable patterns in the predator–prey system. Furthermore, this study highlighted the missing components of our stochastic model. Thus, herein, we revised our previous stochastic model and reproduced stable lattice, stripe, and net patterns.

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We also show that the existence of non-interacting time is a very important factor for stable pattern formation.

2. Stochastic nature of the diffusion constant

When the diffusion constant is provided, one can derive information on density development as a function of time by solving the corresponding diffusion equation. Although this is a well established method, density itself is a macroscopic concept and in principle individual motion is not definitively known. To fill in this fundamental gap, recently we proposed the following stochastic method (Yokoyama et al., 2008). Assuming that variance (σ^2) is proportional to the diffusion constant, we generated random numbers that exhibited a two-dimensional bivariate normal distribution with variance σ^2 using the Box–Muller transformation method (Box and Muller, 1958). Then, the individual movement was determined from the randomly generated numbers. The basis of this scheme is the similarity of the analytic solution of the diffusion equation and the normal distribution function with variance σ^2. Therefore, we can specify stochastic individual movement when the standard deviation σ is given.

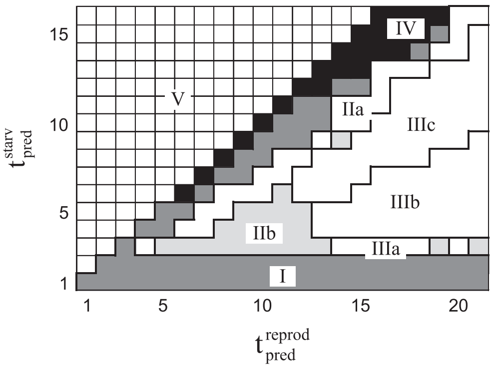

Fig. 1. Phase diagram of the predator prey system when $\sigma_{pred}=5$, $\sigma_{prey}=2$, $t_{prey}^{life}=10$, and $t_{prey}^{reprod}=3$. There are five distinct domains. Domain I is the extinction domain. Domain II is the chaotic domain. This domain is divided further into two subdomains, IIa and IIb, depending on the time development of the total populations. Domain III is the stable domain, which is further divided into three subdomains, IIIa, IIIb, and IIIc, depending on the degree of fluctuations. In Domain IV, both predators and prey die out. Domain V is the nonbiological area.

3. Computational scheme

Our computational methodology is as follows (See ODD; Grimm et al., 2010). First, we distributed N_{pred}^0 predators and N_{prey}^0 prey randomly in the two dimensional $L_x \times L_y$ array with the periodic boundary condition. To model animal migration, we generated random numbers that exhibited a two-dimensional bivariate normal distribution with variance σ^2. Predators and prey then move stochastically, driven by randomly generated numbers with the standard deviations σ_{pred} and σ_{prey}. For simplicity, the exclusion principle was adopted so that only one animal can occupy a given cell at any one time.

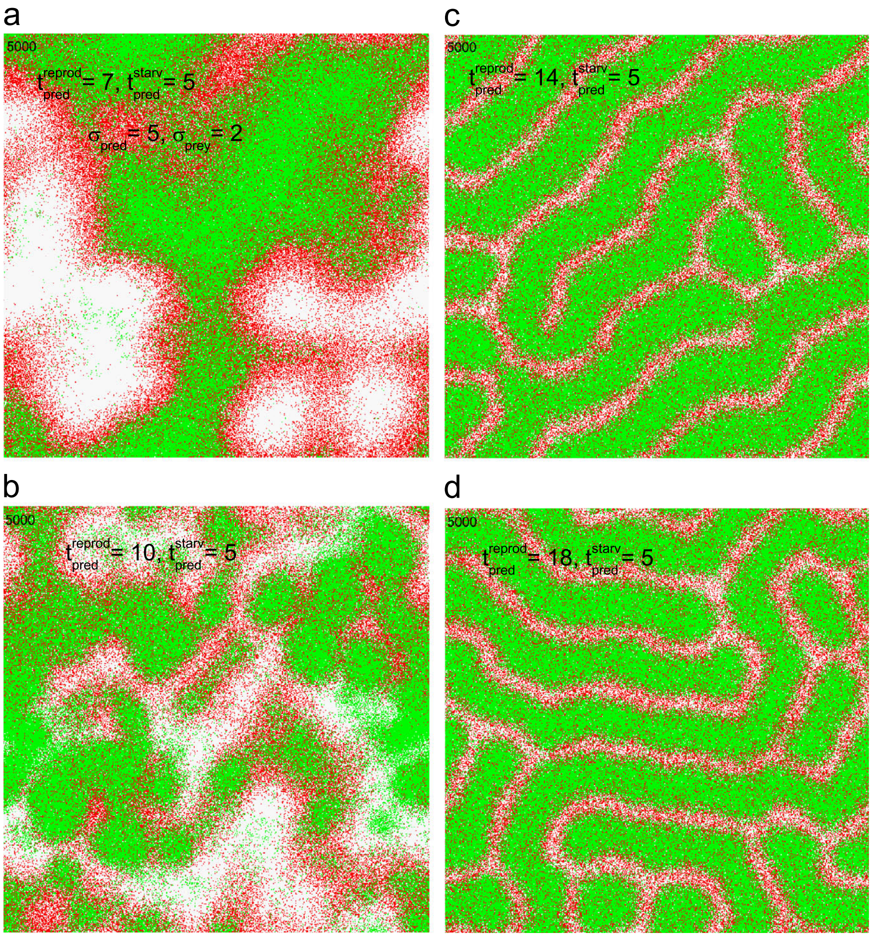

Fig. 2. The effect of t_{pred}^{reprod} in pattern formation (See Supplementary material for Fig. 2c). Two-dimensional predator and prey patterns when the time step = 5000. As in Fig. 1, when $t_{pred}^{starv}=5$ and the value of t_{pred}^{reprod} is increased, we encounter (a) Domain IIa, (b) Domain IIb, and (c) and (d) Domain IIIb. Red points and green points indicate predators and prey, respectively. White points show vacant cells. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)