

A New Stochastic Individual-Based Model for Pattern Formation and its Application to Predator–Prey Systems

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Abstract Reaction–diffusion theory has played a very important role in the study of pattern formation in biology. However, a group of individuals is described by a single state variable representing population density in reaction–diffusion models, and interaction between individuals can be included only phenomenologically. In this paper, we propose a new scheme that seamlessly combines individual-based models with elements of reaction–diffusion theory and apply it to predator–prey systems as a test of our scheme. In the model, starvation periods and the time to reproductive maturity are modeled for individual predators. Similarly, the life cycle and time to reproductive maturity of an individual prey are modeled. Furthermore, both predators and prey migrate through a two-dimensional space. To include animal migration in the model, we use a relationship between the diffusion and the random numbers generated according to a two-dimensional bivariate normal distribution. Despite the simplicity of this model, our scheme successfully produces logistic patterns and oscillations in the population size of both predator and prey. The peak for the predator population oscillation lags slightly behind the prey peak. The simplicity of this scheme will aid additional study of spatially distributed negative-feedback systems.

Keywords Pattern formation · Stochastic model · Cellular automata · Reaction–diffusion · Predator–prey

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1 Introduction

Self-organized pattern formation is a fundamental problem in biology [1]. We focus on the formation of ecological patterns, where a web of interacting species and complex communities are constructed. Two-species systems [2, 3] (especially, predator–prey systems) have been extensively investigated, and many models have been proposed [4], such as the Lotka–Volterra type. In these classical models, the population dynamics of various species do not explicitly introduce spatial effects. Migration effects were later added to these models using reaction–diffusion theory on the population dynamics. Reaction–diffusion theory is a powerful computational tool for the production of a variety of spot and stripe patterns, much like those found on many animals [5]. It has successfully reproduced various patterns observed not only in biology, but also in general science. Especially in biology, because a group of individuals is described by a single state variable representing population size in reaction–diffusion models, interaction between individuals can be included phenomenologically [6, 7]. In population-based models, all individuals are assumed to be identical and are lumped together. This makes it difficult to understand the relationship between the proposed models and real systems. For example, spiral patterns and Belousov–Zhabotinskii patterns are successfully reproduced using reaction–diffusion theory. However, in biological cases, the origin of these patterns may not be clearly understood [8]. To interpret these difficult cases, models based on individuals are increasingly applied to biology [9]. Various individual-based schemes have been proposed [10–21]. For simulation studies, lattice models or patch-panel models are often adopted to introduce the migration of animals [10–14].

The pioneering Lotka–Volterra model provided an intuitive understanding of the predator–prey system despite its known deficiencies. Similarly, an influential work by May [22] reveals the transition of population patterns from an extinction mode, a stable mode, or an oscillatory mode to the chaotic mode as the population growth rate increases. May solved the discrete-time analog of the logistic equation for population growth. We propose a new simple scheme for the study of predator–prey systems. We combine an individual-based modeling approach with elements of reaction–diffusion theory. The basis for our model is very different from May’s single-species model, but our model results in similar population transition patterns and produces Belousov–Zhabotinskii patterns in the chaotic state. In this paper, the state is assumed to be a chaotic state when irregular population oscillations are observed. This model may contribute to the fundamental understanding of ecological problems such as locust outbreaks in Africa [24] and other spatially distributed negative-feedback systems [25].

2 Computational Scheme of the Predator–Prey Model

Predation models (including the Lotka–Volterra type) introduce elements such as the growth rate of prey, predation rates, predator mortality, and the rate at which the predator population grows by consuming prey. These are all population parameters and do not describe individual organisms. Our model (see Fig. 1) accounts for individual predators, modeling both starvation and time to reproductive maturity. The life cycle and reproductive maturation of an individual prey are also modeled.

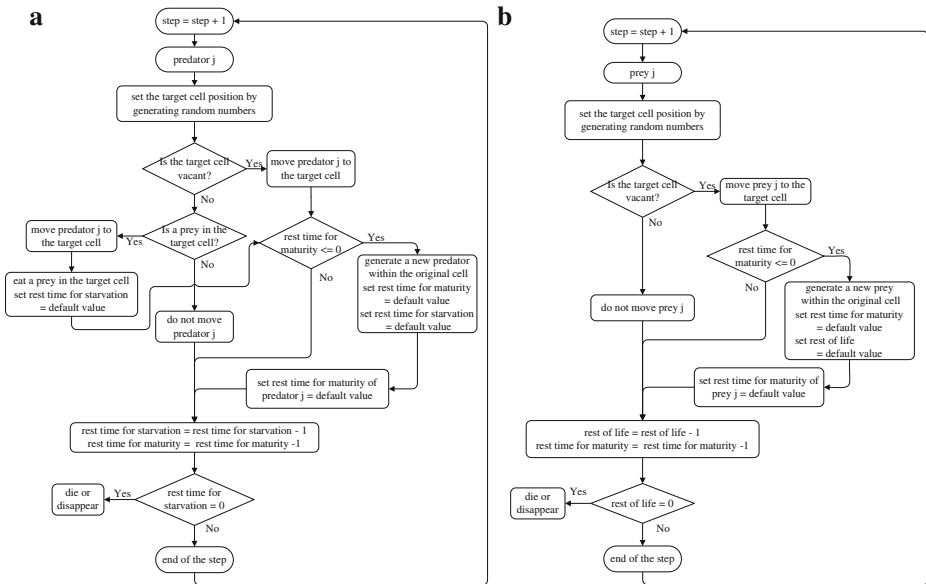


Fig. 1 **a** The migration algorithm of predators. Predators move stochastically, driven by randomly generated numbers with the standard deviation σ_{pred} . Predators starve and proliferate. Unless a predator eats a prey animal before the starvation timer reaches 0, it starves to death. After consuming prey, the starvation timer is reset to $t_{\text{pred}}^{\text{starv}}$. When a predator survives longer than the time to reproductive maturity, a single offspring is produced and remains in the original cell while the parent moves stochastically and its reproductive maturity timer is reset to $t_{\text{pred}}^{\text{reprod}}$. **b** The migration algorithm of prey animals. Prey animals move stochastically, driven by randomly generated numbers with the standard deviation σ_{prey} . Prey animals mature and proliferate. When a prey animal's life timer reaches 0, it dies. If a prey animal reaches reproductive maturity, it produces a single offspring that remains in the original cell while the parent moves stochastically and its reproductive maturity timer is reset to $t_{\text{prey}}^{\text{reprod}}$.

Both predators and prey migrate through a space modeled using a two-dimensional $L_x \times L_y$ array. For simplicity, we have adopted the exclusion principle so that only one animal can occupy a given cell at any one time. To model animal migration, we generate random numbers that exhibit a two-dimensional bivariate normal distribution with variance σ^2 . The macroscopic density of both predators and prey is defined by the number of animals in an area of $2\sigma \times 2\sigma$ because migrating animals are typically in this area after a single time step (see Appendix 1 for details). Variance (σ^2) is proportional to the random walk diffusion constant. Thus, our model seamlessly integrates a scheme that models individuals with reaction–diffusion theory. Mathematically, if the cell size Δ decreases while keeping L and $\Delta \cdot \sigma$ constant (see Appendices 2 and 3), the model provides well-defined number densities of animals. This means that a discrete cell approximation gradually transforms to a continuous variable model. The following simulation study confirms this tendency (see Fig. 5a and b).

Our computational methodology is as follows: First, we distributed N_{pred}^0 predators and N_{prey}^0 prey randomly in the two-dimensional $L_x \times L_y$ array with a periodic boundary condition. Predators and prey then move stochastically, driven by

randomly generated numbers with the standard deviations σ_{pred} and σ_{prey} . Random numbers are generated according to the Box–Muller transformation method [23]. This transforms a two-dimensional continuous uniform distribution into a two-dimensional bivariate normal distribution. Predators starve and proliferate, and prey mature and proliferate. The rest time for starvation and reproduction for a predator are defined as $t_{\text{pred}}^{\text{starv}}$ and $t_{\text{pred}}^{\text{reprod}}$. Similarly, the life expectancy and rest time for the reproduction of each prey animal are defined as $t_{\text{prey}}^{\text{life}}$ and $t_{\text{prey}}^{\text{reprod}}$. Each predator and each prey animal are assumed to have two clocks. Unless a predator eats a prey animal before the starvation timer reaches 0, it starves to death. After consuming prey, the starvation timer is reset to the default value $t_{\text{pred}}^{\text{starv}}$. When a predator survives for the period of $t_{\text{pred}}^{\text{reprod}}$, a single offspring is produced and remains in the original cell while the parent moves stochastically (with standard deviation σ_{pred}) and its reproductive maturity timer is reset to $t_{\text{pred}}^{\text{reprod}}$. Each prey animal has a fixed lifetime $t_{\text{prey}}^{\text{life}}$, and when a prey animal's life timer reaches 0, it dies. Because every animal is born at a different time, the initial clock value for each individual animal must be set randomly. A prey animal reaches reproductive maturity after a period of $t_{\text{prey}}^{\text{reprod}}$. If a prey animal reaches reproductive maturity, it produces a single offspring that remains in the original cell while the parent moves stochastically (with standard deviation σ_{prey}) and its reproductive maturity timer is reset to $t_{\text{prey}}^{\text{reprod}}$. We define the prey density n_{prey} as the number of prey animals in an area of $(2\sigma_{\text{prey}})^2$ and the predator density n_{pred} as the number of predators in an area of $(2\sigma_{\text{pred}})^2$. The density of any animal is better defined as a σ value that is increased, whereas $\Delta \cdot \sigma$ is kept constant. This is so because, as σ values increase, the discrete nature of the population density gradually disappears. See Appendix 2 for details.

3 Results

As our model has six parameters, extensive numerical study is required to clarify the general properties of the system. In Fig. 2, we show a typical example of the phase diagram describing predator populations. In this case, we fix four parameters ($\sigma_{\text{pred}} = 5$, $\sigma_{\text{prey}} = 2$, $t_{\text{prey}}^{\text{reprod}} = 2$, and $t_{\text{prey}}^{\text{life}} = 10$) while changing the values of two parameters ($t_{\text{pred}}^{\text{starv}}$ and $t_{\text{pred}}^{\text{reprod}}$). The array size for this example is $N_x = N_y = 2,000$ ($L_x = N_x \Delta$ and $L_y = N_y \Delta$ in real space), and the total number of animals (predators and prey) must be equal to or less than $N_x \times N_y = 4 \times 10^6$. In this study, the following conditions $\sigma/N_x \ll 1$ and $\sigma/N_y \ll 1$ must be satisfied to avoid the effect from the boundary. We presented only one case herein, but similar population dynamics were observed under different assumptions.

In the upper triangle area in Fig. 2 [domain 0], $t_{\text{pred}}^{\text{starv}} > t_{\text{pred}}^{\text{reprod}}$. It is nonbiological because predators are guaranteed to reproduce even without prey, and over the long-term, predators will hunt all prey to extinction. The lower triangle in Fig. 2 can be divided into following four domains, dubbed (1) the extinction domain, (2) the stable domain, (3) the oscillation domain, and (4) the chaotic domain. As shown in Fig. 3, every predator starves to death in domain (1). In domain (2), both the predator and prey populations approach equilibrium values. This result is consistent

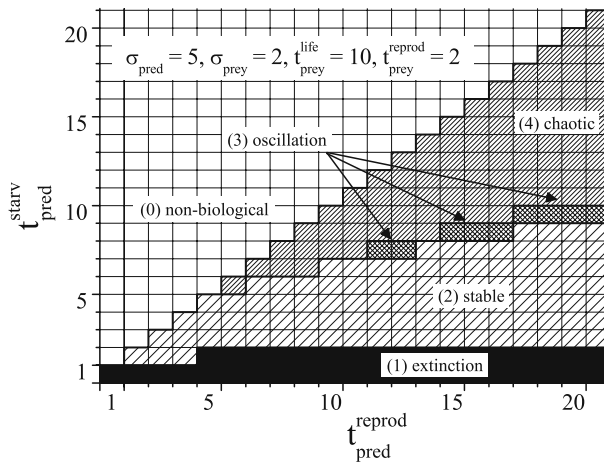


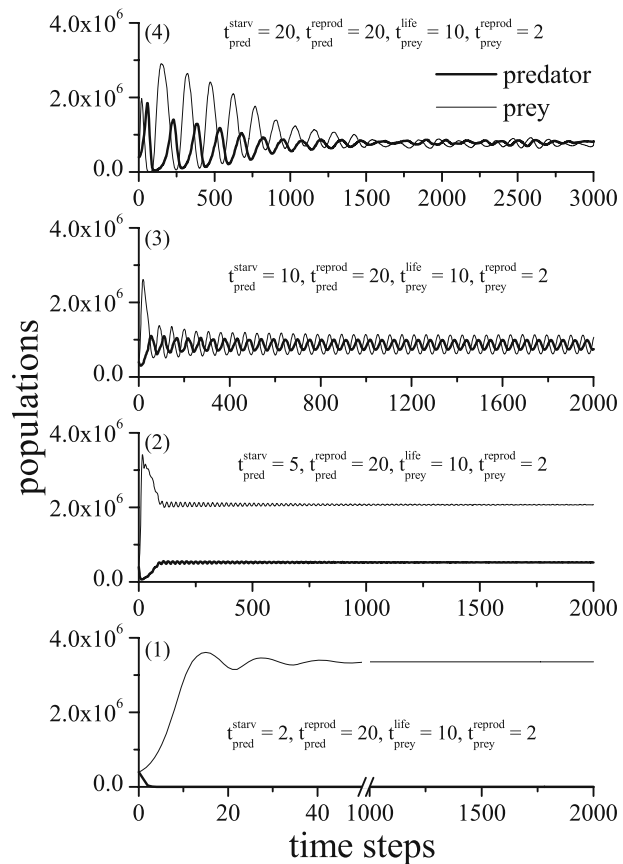
Fig. 2 Phase diagram of predator–prey systems. With an increase of $t_{\text{pred}}^{\text{starv}}$ or a decrease of $t_{\text{pred}}^{\text{reprod}}$, the growth rate of the predator population increases. In this paper, we used $\sigma_{\text{pred}} = 5$, $\sigma_{\text{pre}} = 2$, $t_{\text{pre}}^{\text{reprod}} = 2$, and $t_{\text{pre}}^{\text{life}} = 10$. There are five domains: (0) is the nonbiological domain, where predators can proliferate without prey. (1) is the extinction domain, in which predators die out. (2) is the stable domain, in which there is no variation in predator and prey populations after equilibrium is reached. (3) is the oscillatory domain, in which the populations of both predator and prey oscillate. In this domain, the predators’ oscillation peak lags slightly behind the prey’s oscillation peak. (4) is the chaotic domain, in which spiral patterns of predator and prey densities occur

with the prediction generated by the logistic equation. In domain (3), the populations of both predator and prey oscillate, with the peak of the predators’ oscillation lagging slightly behind the peak of the prey’s oscillation. This is characteristic of predation models such as those of the Lotka–Volterra type. Spatial population density oscillations occurred uniformly (type I) or nonuniformly (type II) over the whole space (see Fig. 4). In type II, the whole space is divided into several clusters. Individual clusters oscillate independently, but the overall population still exhibits a regular oscillation. In domain (4), we have observed Belousov–Zhabotinskii type spiral patterns, as shown in Fig. 5. Figure 6 shows the development of populations over time when different initial conditions are adopted. It shows that the predator and prey equilibrium states do not depend on the initial population values (although, as Fig. 7 illustrates, there exists a critical domain). Obviously, when the initial prey population is much smaller than the initial predator population, predators go extinct. For simplicity, we presented only cases from domain (2) herein. To illustrate the effect of migration, four cases with different σ_{pred} and σ_{pre} values are shown in Figs. 8 and 9. The prey equilibrium population depends little on the value of $t_{\text{pre}}^{\text{life}}$, $t_{\text{pre}}^{\text{reprod}}$, and σ_{pre} . Similarly, the predator equilibrium population depends little on the values of $t_{\text{pre}}^{\text{life}}$ and $t_{\text{pre}}^{\text{reprod}}$.

4 Discussion

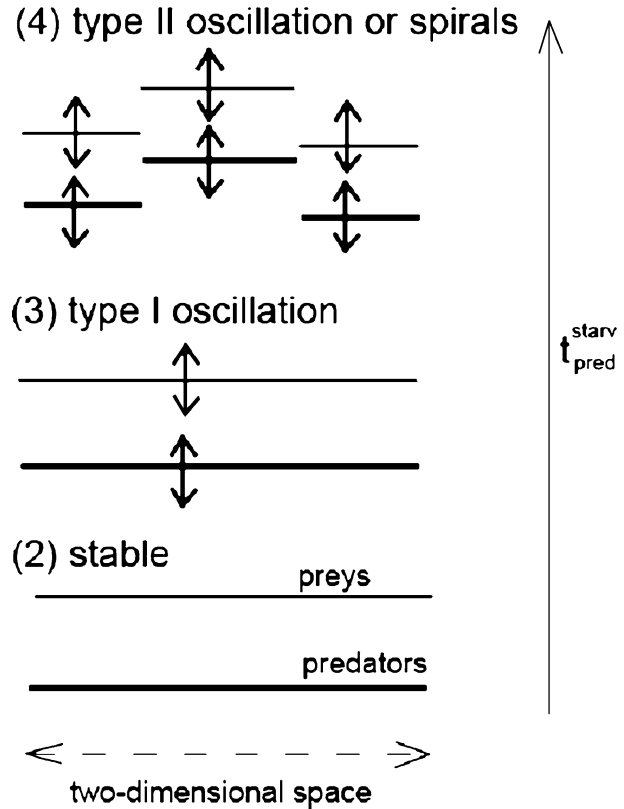
We have proposed a simple ecological model. Nonetheless, results from different approaches have been successfully reproduced by a single scheme. For example,

Fig. 3 The four patterns that were observed in the simulation study shown in Fig. 2 concerning predator and prey populations. With an increase of $t_{\text{pred}}^{\text{starv}}$, (1) the extinction state ($t_{\text{pred}}^{\text{starv}} = 2$), (2) the stable state ($t_{\text{pred}}^{\text{starv}} = 5$), (3) the oscillatory state ($t_{\text{pred}}^{\text{starv}} = 10$), and (4) the chaotic state ($t_{\text{pred}}^{\text{starv}} = 20$) appear in turn from bottom to top



May [22] obtained influential results by studying the discrete logistic nonlinear equation for single-species population growth, $N_{i+1} = rN_i(1 - N_i)$. As the intrinsic growth rate (r) increases, four population dynamics emerge. Type 1: When $r < 1$, the population always goes extinct. Type 2: When $1 < r < 3$, the population grows and reaches a nonzero equilibrium state. Type 3: When $3 < r < 3.57$, the population oscillates around the equilibrium state. Type 4: When $3.57 < r < 4$, bifurcation and chaos emerge. N_i is a dimensionless population measure at the i -th generation. The time step in our simulation is not generational, but a very similar phenomenon was observed in our model. Namely, the pattern of predator population growth moves from Type 1 through Type 4 as $t_{\text{pred}}^{\text{starv}}$ increases, reproducing a Belousov–Zhabotinskii type spiral pattern. As shown in domain (3) of Fig. 2, characteristic predation equations of the Lotka–Volterra type were obtained. Both the predator and prey populations oscillate, with the predators’ oscillation peak lagging slightly behind the prey’s oscillation peak. This result is consistent with that of the predation systems that do not involve the migration of animals. Two distinct spatial types (I and II) were observed in domain (3). In type I, spatial uniformity was observed, but type II is not uniform through space (see Fig. 4). The original Lotka–Volterra model was plagued by a dependence on initial parameter values. Our model does not suffer

Fig. 4 The population density dynamics of the predation system. With an increase of $t_{\text{pred}}^{\text{starv}}$, the growth rate of the predator population increases. Then, type I and type II oscillations appear in turn from the stable state. Although individual animals are always moving randomly, local densities of predator and prey, namely $n_{\text{pred}}(i, j)$ and $n_{\text{prey}}(i, j)$, do not change with time in the stable state. In type I, not only global synchronization of $n_{\text{pred}}(i, j)$, but also that of $n_{\text{prey}}(i, j)$, is achieved, although there is a phase difference between $n_{\text{pred}}(i, j)$ and $n_{\text{prey}}(i, j)$. In type II, global synchronization is broken, but synchronization is still maintained in many local areas. Furthermore, the overall population exhibits a regular oscillation. In the chaotic state, such a regular oscillation of the overall population is broken



from initial population dependence except in a very small domain, with a small initial prey population. This threshold value relating to a low initial prey population has been demonstrated to affect the sustainability of ecological systems (similar figures to Figs. 6 and 7 were obtained in domain (3) of Fig. 3, although these results are not presented herein).

Our study indicates the existence of two types of spatial population density correlations for macroscopic pattern formation, as is shown in Fig. 4. One is the correlation within the predator and prey groups. The other is the correlation between the predator and prey groups. These correlations suggest the following interpretation: When the spatial correlation within a group is sufficiently strong, predator and prey populations develop uniformly through space (type I). However, if the correlation within a group is intermediate, uniformity is not sustained (type II). If the correlation between different groups in the type II domain is still strong, then regular population oscillations still occur. In the chaotic domain, the correlation between groups is also weak. This may be why irregular population oscillations are observed in the chaotic domain. On the other hand, because both spatial correlations are very strong in domain (1), a stable and uniform state occurs. Further study is necessary to confirm the above speculation.

Our stochastic approach successfully combines individual-based modeling and reaction–diffusion theory. Our original objective was to develop a simple scheme

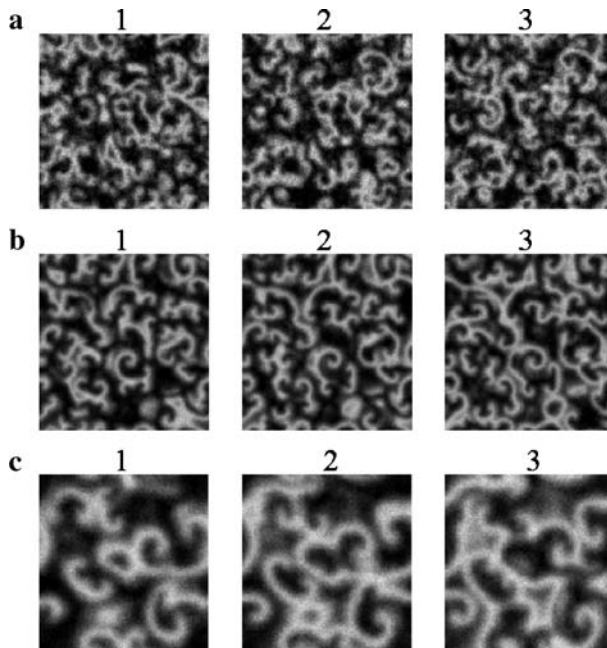


Fig. 5 Belousov–Zhabotinskii type spiral patterns observed in the chaotic domain. The *lighter gray color* corresponds to the higher local density of predator n_{pred} . These pictures were generated in 20 time-step intervals. The images were generated with the variables **a** $\sigma_{\text{pred}} = 5$, $\sigma_{\text{prey}} = 2$, $N_x = N_y = 2,000$, **b** $\sigma_{\text{pred}} = 10$, $\sigma_{\text{prey}} = 4$, $N_x = N_y = 4,000$, and **c** $\sigma_{\text{pred}} = 10$, $\sigma_{\text{prey}} = 4$, $N_x = N_y = 2,000$. The local density of predator $n_{\text{pred}}(i, j)$ is obtained using its definition, namely [the number of predators occupying the (i, j) cell]/ $(2\sigma_{\text{pred}})^2$. Therefore, $0 \leq n_{\text{pred}}(i, j) \leq 1$ ($1 \leq i \leq N_x/2\sigma_{\text{pred}}$, $1 \leq j \leq N_y/2\sigma_{\text{pred}}$), and we have 200×200 cells for cases **a** and **b**, and 100×100 cells for case **c**. As the local density in case **b** has four times higher gradations than that in case **a**, spiral patterns in the case **b** appear more clearly than those of case **a**. See Appendix 2 and Fig. 11 for details. Spiral patterns in case **c** are 2×2 times larger than those in case **a**. The similarity of observed patterns shows scalability of the lattice space discussed in Appendix 2

Fig. 6 The equilibrium state is independent of initial population values. The above graph presents the typical development of predator and prey populations in domain (2) of Fig. 2

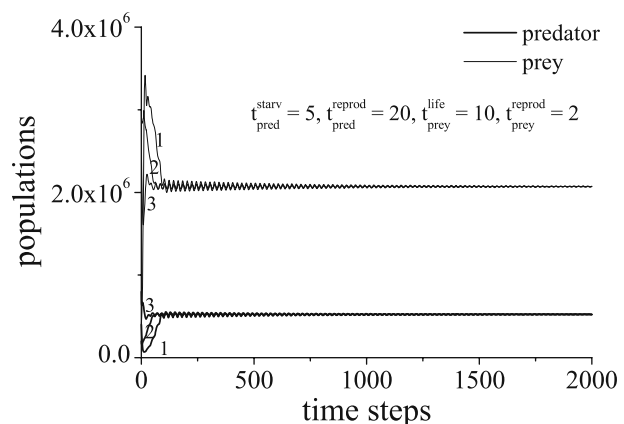
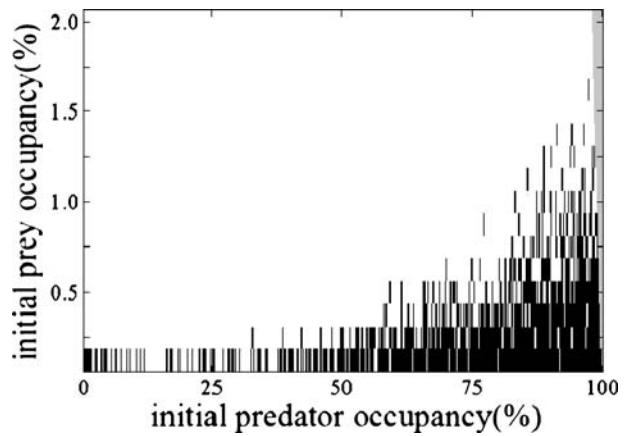


Fig. 7 Ecological sustainability. *Dark areas* indicate initial population values under which predators go extinct. For any predator density, there is a threshold prey density that sustains the equilibrium state from Fig. 2. This chart presents cases from domain (2) of Fig. 2. In our model, the total number of animals (predators and prey) must be equal to or less than $N_x \times N_y = 4,000,000$. In the gray domain, the population exceeds this value, so it is excluded from this study



for studying the general properties of predation systems, so detailed study of the chaotic domain remains for future research. Predation systems include a negative-feedback loop, so we plan to apply our model to other biological negative-feedback systems.

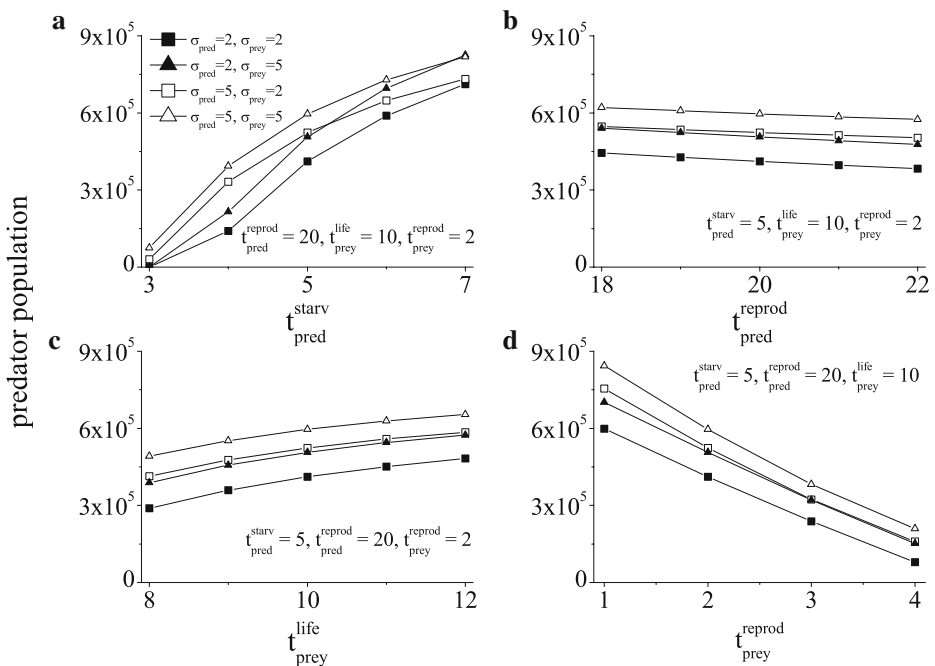


Fig. 8 Equilibrium predator populations for different combinations of σ values

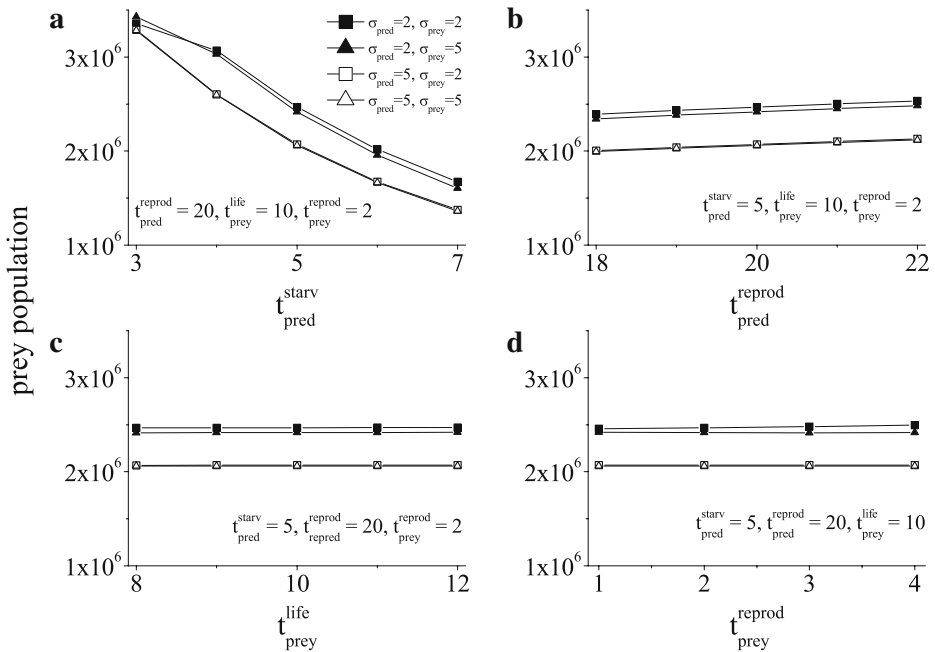


Fig. 9 Equilibrium prey populations for different combinations of σ values

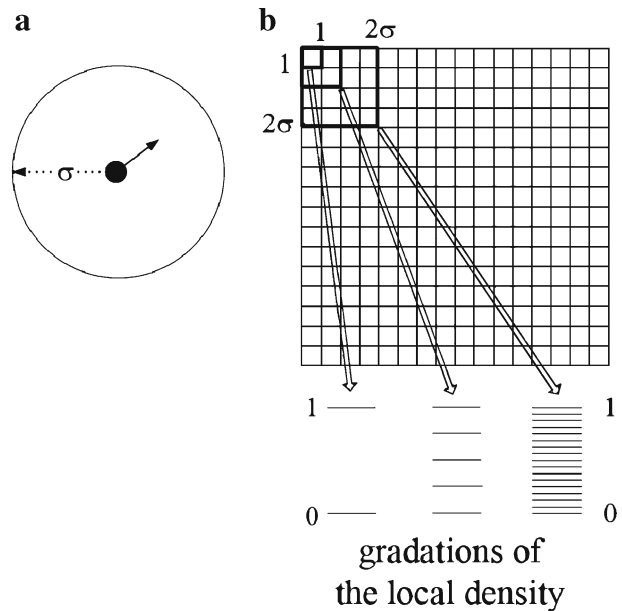
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Appendix

1 The Definition of the Local Densities (Occupancies) of Predator and Prey

To introduce the concept of the local density or occupancy of the predator and prey populations, the number of animals within a unit area should fluctuate little across several time steps. Otherwise, the concept of local density loses its meaning. To model animal migration, we have generated random numbers that exhibit a two-dimensional bivariate normal distribution with a variance of σ^2 . This means that migrating animals are typically in an area of $\pi\sigma^2$ after a single time step. Thus, in an area of $\pi\sigma^2$, the number of animals fluctuates little across several time steps. We adopt an area of $2\sigma \times 2\sigma$ rather than $\pi\sigma^2$ as the computer simulation uses a square lattice. Thus, the local densities of predator and prey (n_{pred} and n_{prey}) are defined as the number of animals occupying an area of $2\sigma \times 2\sigma$. As shown in Fig. 10b, the number of gradations increases as the number of cells in a unit area increases, causing patterns to appear more clearly. Usually, predators and prey have different σ values, in which case, different unit areas are used.

Fig. 10 **a** An animal migration during a unit time step. **b** Local densities (or occupancies) for three different unit areas. A $2\sigma \times 2\sigma$ area is chosen instead of $\pi\sigma^2$ area because the total space in this simulation is square



2 Scalability of the Lattice Space

To see the scalability of the lattice space, we compare two cases in Fig. 11. Because the migration distance of an animal is characterized by σ , similar patterns are produced when the distance in real space remains unchanged. But the gradation for the local density or occupancy of the animal increases with σ . Thus, as σ increases, patterns remain similar but appear more clearly.

3 Relationship between the Lattice Space and Real Space

When we approximate real space with the lattice space, we encounter a problem when animals attempt to move to an already occupied cell. In such a case, we advance the animal's internal clock without moving it. However, such a problem can be solved, as the size of a unit cell Δ becomes smaller. To explain, consider approximating the real space $L_x \times L_y$ with the following two kinds of lattice spaces: (a) $N_x \cdot \Delta_a \times N_y \cdot \Delta_a$ and (b) $(2N_x) \cdot (\Delta_a/2) \times (2N_y) \cdot (\Delta_a/2)$, as shown in Fig. 12, where the unit cell size in lattice (a) is Δ_a and in lattice (b) is $\Delta_b = \Delta_a/2$. In cases (1) and (2), using lattice (a), an animal stays in the same cell or moves to the next cell, respectively. The migration of an animal in real space should be independent of the lattice chosen. However, the probability of finding another animal in the final cell using lattice (b) is one in four, because only one of four cells is the target cell. These cases illustrate that the probability of an animal moving to an occupied cell decreases as Δ decreases. Consequently, our model's deficiencies gradually disappear, as Δ is decreased, and σ is increased, whereas $\Delta \cdot \sigma$ is kept constant.

Fig. 11 A comparison of two cases, **a** $\sigma_1 = 1$ and **b** $\sigma_2 = 2$, to confirm that the lattice space is scalable. Patterns produced in both cases are similar to each other, but the patterns appear more clearly in case **b**

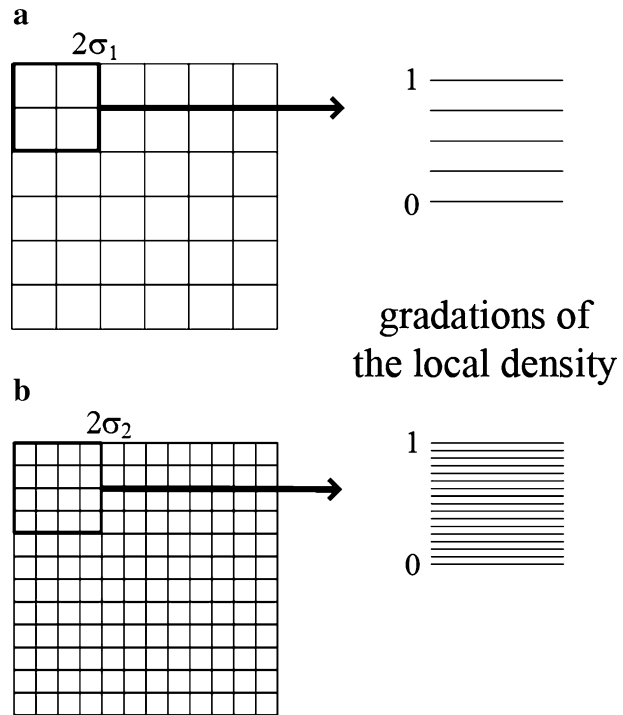
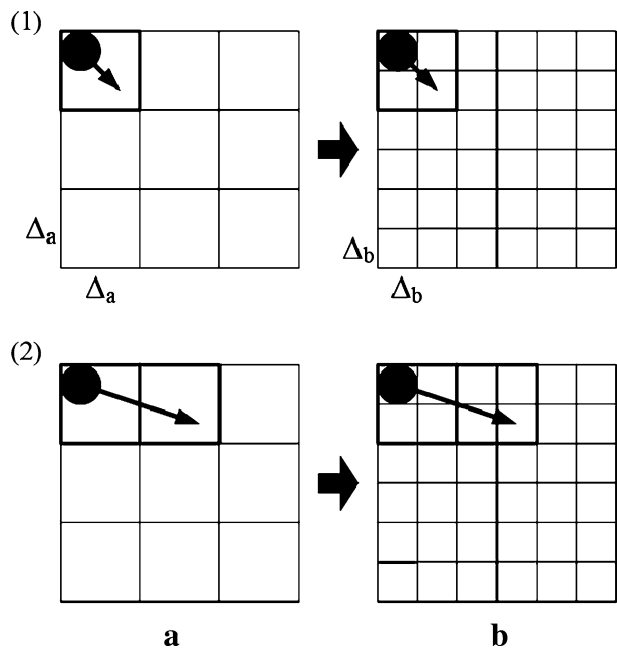


Fig. 12 The relationship between the lattice space and real space. Where $\Delta_a \sigma_a = \Delta_b \sigma_b$, $\Delta_b = \Delta_a/2$, and $\sigma_b = 2\sigma_a$. The approximation produced by the model is improved as the size of a cell is decreased. In this study, animals are assumed to be smaller in size than a single cell



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