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Effect of directional migration on Lotka-Volterra system with desert

Takashi Nagatani[a], Kei-ichi Tainaka[b], Genki Ichinose[c,*]

[a] Department of Mechanical Engineering, Shizuoka University, Hamamatsu 432-8561, Japan
[b] Graduate School of Science and Technology, Shizuoka University, Hamamatsu 432-8561, Japan
[c] Department of Mathematical and Systems Engineering, Shizuoka University, Hamamatsu, 432-8561, Japan

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ABSTRACT

Migration is observed across many species. Several authors have studied ecological migration by applying cellular automaton (CA). In this paper, we present a directional migration model with desert on a one-dimensional lattice where a traffic CA model and a lattice Lotka-Volterra system are connected. Here predators correspond to locomotive animals while prey is immobile plants. Predators migrate between deserts and fertile lands repeatedly. Computer simulations reveal the two types of phase transition: coexistence of both species and prey dominance, which is caused by both benefit and cost of migration. In the coexistence phase, the steady-state density of predators usually increases by migration as long as the desert size is small and their mortality rate is low. In contrast, the prey density increases, even if the desert size becomes large. Such a paradox comes from the indirect effect: predators go extinct by the increase of desert size, so that the plant density can increase. Moreover, we find several self-organized spatial patterns: 1) predators form a stripe pattern; namely swarms. 2) The velocity of predators is high on deserts, but very low on fertile land. 3) Predators give birth only on fertile lands.

1. Introduction

Migration is an essential behavioral trait observed in many animals (Aidley, 1981; Riede, 2004; Silva et al., 2013). Potential for migration is considered even in the studies of artificial organisms (Ito et al., 2016; Olson and Knoester, 2016; Sayama, 2008). For migrating animals, the change of habitat is necessary for various reasons (Dingle and Drake, 2007; McLaren, 1974; Shaw, 2016). So far, many migration models have been studied including microbes, insects, and animals (Guerra et al., 2014; Potts et al., 2016; Ravichandar et al., 2017; Tilman et al., 1997). We focus on cellular automaton (CA) models. Most previous studies have realized migration as random walk (Hernandez-Suarez, 2016; Kitamura et al., 2006; Sasmal and Ghosh, 2017; Sato et al., 2015). In the random walk, however, the area of activity is very small. On the contrary, many animals show long-distance migrations. For example, carnivores have large activity areas (Schwartz et al., 2002). Few models have considered such a long-distance migration (Alerstam et al., 2003; Barbaro et al., 2009). In the present article, we integrate long-distance migration and birth-death processes. We assume plants locate in patchy environments and animals move from one fertile land (patch) to another as illustrated in Fig. 1 (a), where circles denote the fertile lands. Hereafter we refer to "desert" as the region outside the patches. It is advantageous for predators to find a new fertile land by migration. However, if there exist deserts between the current and new fertile lands, predators must migrate due to the costs caused by their mortality. Then, the population dynamics significantly change due to the balance between migration advantage and mortality cost.

Moreover, we change the size of deserts to explore the influence of habitat destruction. Habitat destruction is one of the primary causes of species extinction in recent history (Alwan and El-Gohary, 2011; Bascompte and Solé, 1998; Coudrain et al., 2013; Tilman and Downing, 1994). Desertification affects the survival of animals that migrate across deserts. Even if the destruction is restricted to a local area, its accumulation increases the risk of extinction. In the present paper, by simply changing the desert size, we find a paradox: when the desert size becomes large, the prey population increases in the stationary state.

For the aspect of population dynamics of animals, Lattice Lotka-Volterra models have been studied by many authors. We use the following model (Satulovsky and Tomé, 1994; Sutherland, 1994; Tainaka, 1994; Tainaka and Fukazawa, 1992):

$$X + Y \rightarrow 2Y \tag{1a}$$

* Corresponding author.
E-mail addresses: nagatani.takashi@shizuoka.ac.jp (T. Nagatani), tainaka.keiichi@shizuoka.ac.jp (K.-i. Tainaka), ichinose.genki@shizuoka.ac.jp, igenki@gmail.com (G. Ichinose).

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(a)

(b)

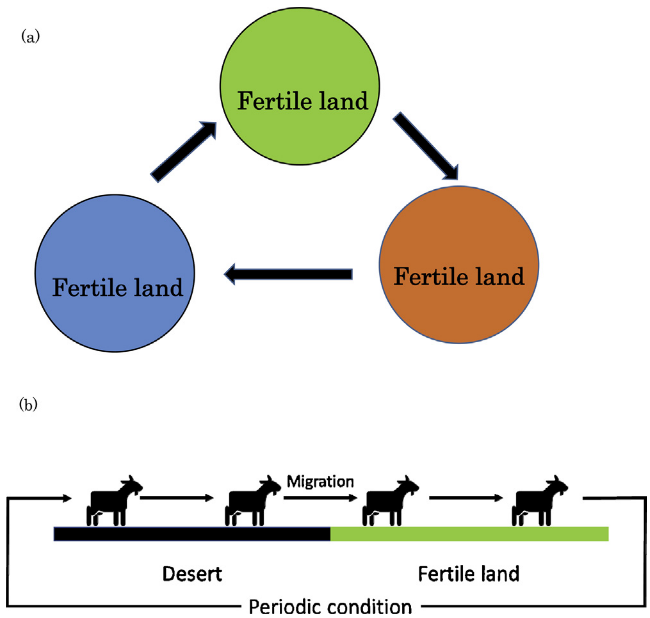

Fig. 1. Schematic illustration of migration. (a) The migration model. The circles mean fertile land with rich food, but the land outside the circles is poor. We refer to this land as desert. (b) Illustration of migration between desert and fertile land. Predators (migrants) go forward (rightward) on a one-dimensional lattice.

$$X + O \rightarrow 2X \quad (1b)$$

$$Y \rightarrow O \quad (1c)$$

where X and Y denote prey and predator, respectively, and the symbol O denotes empty. Here, predators correspond to animals that can migrate while prey is plants (fruit or vegetables). Thus, the locations of prey are fixed. The processes (1a), (1b) and (1c) indicate the predation of Y, the reproduction of X and the death of Y, respectively. It is known that both species X and Y cannot coexist on a one-dimensional (1-d) lattice, but they can coexist on a 2-d lattice (Tainaka, 1989, 1988). In the present paper, we show both species can coexist, by using an ecological migration model based on a cellular automaton (CA) on a 1-d lattice, when the multiple layers for the lattice are considered

2. Model and simulation

Since we consider a long-distance movement over a year for animals, one way (rightward) movement is taken into account. In the case of a short time (a few days), predators (animals) move in various directions. However, when the duration is over a year, animals may move toward a certain direction in the long-distance migration across the desert. Therefore, we consider the unidirectional movement.

Migration means the unidirectional movement of predators. In the case of non-migration, predators stop (do not move in any direction). When one defines the position of predator k at time t as $P_k(t)$, migration and non-migration are represented by $P_k(t+1) > P_k(t)$ and $P_k(t+1) = P_k(t)$, respectively, in terms of mathematical formulation.

We consider a two-layer one-dimensional lattice with periodic boundary conditions. Fig. 1(b) shows the schematic illustration of the animals' migration between desert and fertile land. As we consider the periodic boundary conditions, a fertile land followed by a desert is repeated. Animals move uni-directionally (rightward) on both desert and fertile land. Prey exist only on the first layer (lane) and do not move. Prey can be considered as plants. Animals (predators) exist only on the second layer. Fig. 2 shows the labelling

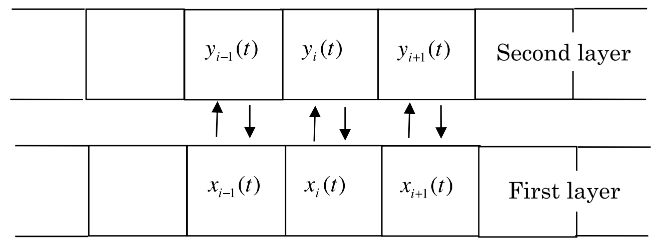

Fig. 2. Predator-prey system on a one-dimensional lattice with two layers. There exist prey (immobile food) only on the first layer and predators (locomotive animals) only on the second layer. Predators on the second layer can eat prey on the first layer. The states of prey and predators at time t are represented by $x_i(t)$and $y_i(t)$ [see Eq. (2)]. Each lattice site takes X (prey) or O (empty) on the first layer, and Y (predator) or O (empty) on the second layer. More than one individual is not allowed in the same site on the same layer.

of each site on the two layers, where $x_i(t)$ and $y_i(t)$ mean the state of prey and predators at time t (at the position i) respectively:

$$x_i(t) = \begin{bmatrix} 1(X) \\ 0(O) \end{bmatrix}, \quad y_i(\mathrm{t}) = \begin{bmatrix} 1(Y) \\ 0(O) \end{bmatrix}. \quad (2)$$

The predation (1a) is redefined in accordance with our traffic model. If both prey and predator occupy the same position, predation occurs: the predator eats the prey. Reactions take place stochastically. Then, the predation (1a) is defined by

$$X \rightarrow O(\mathrm{on\,1st\,layer}), \quad (3a)$$

$$Y + O \rightarrow 2Y(\mathrm{on\,2nd\,layer}), \quad (3b)$$

These reactions occur with the same probability r_Y (reproduction probability of Y). The reactions (1b) and (1c) can be represented by

$$X + O \rightarrow 2X(\mathrm{rate}\,r_X)\mathrm{on\,1st\,layer}, \quad (3c)$$

$$Y \rightarrow O(\mathrm{rate}\,m_Y)\mathrm{on\,2nd\,layer}, \quad (3d)$$

where r_X (m_Y) is the reproduction probability of X (the mortality probability of Y). Thus, the model is non-deterministic.

Simulations of the CA model on a one-dimensional lattice with two layers are carried out by local interaction. Desert is set in the region of $0 \le i < l$ and fertile land lies in the region of $l \le i < L$, where l is the size of the desert and L the total size of the lattice. The simulation procedure is as follows.

1) Initially, prey (X) are distributed randomly in the region of $l \le i < L$ on the 1st layer of the lattice with probability x_0. Cells in region of $0 \le i < l$ on the 1st layer are empty. Predators (Y) are distributed randomly on the 2nd layer with probability y_0.
2) All sites are updated simultaneously.

Reaction processes are performed in the following steps:

i) Reaction (3c). If a site is X on the 1st layer, it reproduces offspring at one of its nearest-neighbor sites by probability r_X at random. If both neighboring sites are occupied by X, then we skip this reaction.
ii) Reaction (3d). If a site on the 2nd layer is Y, then it becomes O by probability m_Y.
iii) Reactions (3a) and (3b). When X and Y occupy the same position, then X becomes O by the probability r_Y on the 1st layer, and Y reproduces offspring at one of its two nearest-neighbor sites at random. If both neighboring sites are occupied by Y, then we skip both reactions (3a) and (3b).

After the above reaction processes, the predators move on to the 2nd layer. The movement is carried out by using the deterministic