

Spatial and temporal dynamics in mate-choice systems

Nitta, T.¹, Y. Sakisaka², T. Hashimoto³, B. Saito⁴, J. Yoshimura⁴, K. Tainaka⁴

¹ *Department of Nautical Engineering, Tokai University, Shimizu, Shizuoka 424-8610, Japan*

Email: tokiya@scc.u-tokai.ac.jp

² *Center for Humanities and Sciences, Ibaraki Prefectural University of Health Sciences. 300-0394, Japan*

³ *School of Information Science, Japan Advanced Institute of Science and Technology, 923-1292, Japan*

⁴ *Department of Systems Engineering, Shizuoka University, Hamamatsu 432-8561, Japan*

Abstract: Some species have dimorphism in male; two types of males are distinguishable by their appearance. One is usually large called a dominant male, and the other is small called a subordinate male. The latter male often takes a strategy as sneaker that is usually not very conspicuous, but lives around the edges of dominant males. It sneaks fertilizations behind the dominant male. In most cases, females more prefer the dominant males than sneakers. A concrete example is orangutans. There are two types of adult male. The matured adult male (MA) has wide cheek pads and the average weight of MA is more than twice that of adult females. In contrast, the arrested adult male (AA) remains comparable in size to an adult female. The AA males are sneakers and forcibly copulate with females.

Heretofore, many authors have studied male dimorphism. They usually applied the theory of evolutionarily stable strategy (ESS), and explained the evolution of alternative male tactics, especially the evolution of sneaker. Another theory to explain the sneaker is “best of bad job” (BOBJ). Though both ESS and BOBJ have accounted for the origin of alternative male tactics, these theories never take into account the sustainability of individuals.

The present paper deals with such a mate-choice system on a square lattice, and focuses on the sustainability. Each lattice site is assumed to take one of four states: large or dominant male (X), small subordinate male (Y), female (Z) and empty (O). Females are assumed to prefer X compared to Y. Birth processes are carried out by two methods: local and global interactions. In the former, interaction occurs between adjacent sites, whereas in the latter it occurs between any pair of lattice sites.

We first report the simulation results by global interaction. The results completely agree with the predictions of mean-field theory. Depending on parameter values, the population dynamics can be classified into two phases: unconditional extinction (UE) and survival/extinction (SE). In the UE phase, the species always goes extinct; the population cannot survive for any initial conditions. On the other hand, in the SE phase, the Allee effect can be observed. The SE phase has three equilibria; two are stable (extinction and survival), while one is unstable. When both male and female have high densities at the initial state, the system reaches the survival equilibrium. Otherwise, the system goes to the extinction. The Allee effect thus represents the threshold between survival and extinction.

In real ecosystems, the interaction occurs locally. In the case of local interaction, the population dynamics qualitatively explained by the mean-field theory. Both UE and SE phases are confirmed, and in the latter phase the Allee effect is also observed. To explore the population sustainability, we obtain the equilibrium densities in stable states. It is found that the results for local simulations essentially differ from those for global simulations. Namely, in the case of local interaction, sustainable region is very narrow in parameter space, compared to the global interaction (mean-field theory). The survival equilibrium in local interaction is always situated near the extinction; it is not so easy to find mating partners in the neighborhood.

In both local and global simulations, we find that the survival density of the overall population increases with an increase in reproductive rate of small males (Y). Under local simulations, the average density of the overall population is close to zero. When the reproductive rate of small male (Y) increases, it acts as the avoidance of population extinction. This implies that sneaker is adaptive for the sustainability of all individuals.

Keywords: *lattice model, mate-choice systems, mean-field theory, Allee effect, male dimorphism*

1. INTRODUCTION

Some species have two types of males (dimorphism). One is called a dominant male, and the other is called a subordinate or satellite male. Good examples are salmon and orangutan. The salmon male phenotypes occur in two distinct morphs: the large ‘hooknose’ and the small ‘jack’ (e.g. Tanaka *et al.*, 2009). Females more prefer the large hooknose (dominant male), and they spawn around the dominant males. Jacks occupy refuges near spawning beds to sneak fertilizations. Orangutans (*Pongo pygmaeus*) also have two forms of males: the matured adult male (MA) is called a dominant male. The average weight of MA is more than twice that of adult females. In contrast, the arrested adult male (AA) remains comparable in size to an adult female. The AA males are sneakers and forcibly copulate with females. Many authors have studied male dimorphism to explain the evolution of sneakers. One of main theories is evolutionarily stable strategy (ESS) (e.g. Gross, 1985; Imhof *et al.*, 2005; Iqbal and Toor, 2001; Nowak and Sigmund, 2004). Recently, the male dimorphisms in salmon and orangutan have been explained by our coauthors; Tanaka *et al.* (2009a) applied ESS for salmon and Tainaka *et al.* (2007) applied it for orangutan. Another theory to explain the sneaker is “best of bad job” (BOBJ) (e.g. Lee and Hays, 2004). However, both ESS and BOBJ never take into account the sustainability of individuals.

In the field of ecology, lattice models have a growing interest (e.g. Tainaka *et al.*, 2006; Nitta *et al.*, 2008). Recently, our coauthors have presented a lattice model of mating population to explain the optimality of a strategy (e.g., sex ratio) not by ESS but by the sustainability (e.g. Tainaka *et al.*, 2006). The present paper extends this model to deal with such a mate-choice system. In the section 2, we explain our model. It contains two important parameters α and β , where α denotes the sex ratio (male ratio per total population), and β is the ratio of large males per total males. The values of these parameters are determined by genetic or non-genetic factors. Monte Carlo simulations are carried out by two methods: local and global interactions. In the former, interaction occurs between neighboring sites, whereas in the latter it occurs between any pair of lattice sites. In the section 3, the mean-field theory is presented to predict the simulation results of global interaction. The section 4 is devoted to report the simulation results for both local and global interactions. Simulation results of global interaction completely agree with the predictions of mean-field theory. We find for local simulations that the population dynamics qualitatively explained by the mean-field theory, but sustainable region is very narrow in parameter space, compared to the global interaction (mean-field theory). In the final section we discuss the sustainability and the evolution of sneakers.

2. MODEL AND METHODS

2.1. Model

Consider a mating population on a two-dimensional lattice (see Fig. 1). Our model is an extension of the mating population introduced by Tainaka *et al.* (2006). The population on a square lattice is composed from large males (X), small males (Y) and females (Z). Each lattice site takes one of four states: X, Y, Z or empty (O). Females are assumed to prefer X compared Y. Birth and death processes update the lattice. The death process is defined by

$$j \longrightarrow O \quad (\text{rate: } m_j), \quad (1a)$$

where $j = X, Y, Z$, and m_j is the mortality rate of j .

On the other hand, birth process is expressed by

$$O \longrightarrow X \quad (\text{rate: } B\alpha\beta), \quad (1b)$$

$$O \longrightarrow Y \quad (\text{rate: } B\alpha(1-\beta)), \quad (1c)$$

$$O \longrightarrow Z \quad (\text{rate: } B(1-\alpha)), \quad (1d)$$

where the parameter B is the birth rate. In the case of global interaction, birth rate B is defined by

$$B = r_X xz + r_Y yz.$$

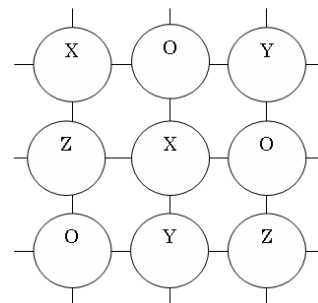


Figure 1. Stochastic cellular automaton on a two-dimensional lattice. Each lattice site takes one of three states: large male (X), small male (Y) and female (Z). The site O means the empty.

Here r_j is reproductive rate of male j ($=X, Y$), and x, y and z are overall densities of X, Y and Z , respectively. In the birth rate of local interaction, the overall densities should be replaced by local densities.

2. 2. Simulation Methods

Simulations are carried out by two methods; local and global interactions. In the former, interaction occurs between adjacent sites, whereas in the latter interaction occurs between any pair of lattice sites. Both methods merely differ the birth rate B . The lattice site is updated as follows:

- 1) Initially, we distribute X, Y and Z , where each lattice point is one of four sites; X, Y, Z and O .
- 2) To update, we choose a target site randomly.
 - i) If the site is occupied by j ($j = X, Y, Z$), then the death process (1a) is performed. Namely, the site j is changed into O with the rate m_j .
 - ii) If the site is empty (O), we perform the birth processes. The site O becomes X, Y or Z by the rate $B\alpha\beta$, $B\alpha(1-\beta)$ or $B(1-\alpha)$, respectively.

We repeat step 2) by L^2 times, where L^2 is the total number of lattice sites. In this paper, we put $L = 100$. This step is called a Monte Carlo step. We further continue the updates, until the system reaches stationary state.

3. MEAN-FIELD THEORY

When the lattice size is infinite, the population dynamics for global interaction can be represented by the mean-field theory:

$$\frac{dx}{dt} = -m_x x + (r_x xz + r_y yz)(1-x-y-z)\alpha\beta, \quad (2a)$$

$$\frac{dy}{dt} = -m_y y + (r_x xz + r_y yz)(1-x-y-z)\alpha(1-\beta), \quad (2b)$$

$$\frac{dz}{dt} = -m_z z + (r_x xz + r_y yz)(1-x-y-z)(1-\alpha), \quad (2c)$$

where the first (second) term in the right hand side of equation (2) represents the death (birth) process. The factor $(1-x-y-z)$ in the birth term means the density of empty site (O). If $y = 0$ (or $\beta = 1$), equation (2) represent the single-male system (e.g. Tainaka *et al.*, 2007; Boukal and Berec, 2002). In the present paper, we consider the case of equal mortality rates: $m_x = m_y = m_z = m$.

The final density in stable equilibrium can be obtained as follows. From the definition of sex ratio, the equilibrium state must satisfy the condition:

$$(x + y) / z = \alpha / (1 - \alpha), \quad (3)$$

Similarly, from the ratio of dominant male, we have the following equilibrium condition:

$$x / y = \beta / (1 - \beta). \quad (4)$$

For the simplicity, we consider the special case of $r_y = 0$. Inserting equations (3) and (4) into (2), we can obtain

$$\frac{dx}{dt} = Rx(x-a)(b-x), \quad (5)$$

where

$$R = r_x (1 - \alpha) / (\alpha\beta), \quad (6a)$$

$$a = \alpha\beta(1 - \sqrt{D})/2, \quad b = \alpha\beta(1 + \sqrt{D})/2, \quad (6b)$$

$$D = 1 - \frac{4m}{r_x\beta} \left(\frac{1}{1-\alpha} + \frac{1}{\alpha} \right) \quad (6c)$$

The population dynamics of equation (5) depends on the sign of D . When $D \leq 0$, both a and b become imaginaries. In this case, equation (5) has a single equilibrium ($x = 0$), and the extinction always occurs ($x \rightarrow 0$ for $t \rightarrow \infty$). In contrast, when $D > 0$, equation (5) has three equilibria; both $x = 0$ and $x = b$ are stable, while $x = a$ is unstable. Depending on initial conditions, the system eventually reaches one of two stable equilibria. When both male and female have sufficiently high densities at initial state, the system reaches the survival equilibrium ($x = b$). Otherwise, the system goes to the extinction ($x = 0$). The dynamics in SE phase represents the Allee effect which means the threshold between survival and extinction. In summary, a phase transition is predicted according to the sign of D : unconditional extinction (UE) for $D \leq 0$, and the survival/extinction (SE) for $D > 0$.

To explore the sustainability of population, we obtain the steady-state densities in the SE phase ($D > 0$). It is obvious from equation (5) that the male density finally reaches $x = b$. By the use of equations (6), the steady-state densities can be explicitly expressed as follows:

$$x = \alpha\beta(1 + \sqrt{D})/2, \quad (7a)$$

$$y = \alpha(1 - \beta)(1 + \sqrt{D})/2, \quad (7b)$$

$$z = (1 - \alpha)(1 + \sqrt{D})/2. \quad (7c)$$

The total population size ($x + y + z$) at survival equilibrium is given by

$$x + y + z = (1 + \sqrt{D})/2. \quad (8)$$

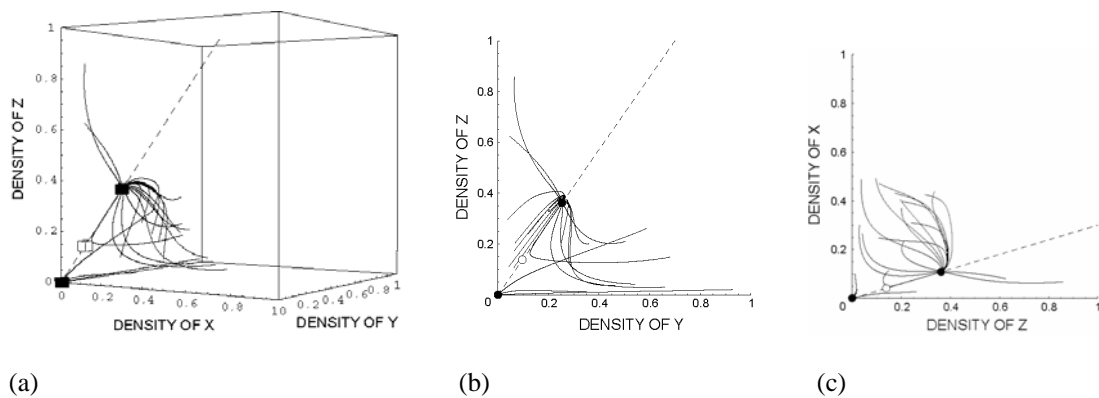


Figure 2. Typical population dynamics in the SE phase for global interaction (mean-field theory). (a) The orbits on 3-dimensional space (x, y, z). (b) and (c): The projections into 2-dimensional spaces. The black and white boxes respectively denote the stable and unstable equilibria. The dotted lines indicate the equilibrium conditions (3) and (4). The orbits start from 20 initial conditions which are randomly chosen, and they eventually reach one of stable equilibria. Model parameters are set as $(r_x, r_y, m, \beta) = (1, 0, 0.015, 0.3)$.

4. SIMULATION RESULTS

4.1. Results of Global Interaction

First, we report the simulation results for global interaction. Results obtained by computer simulations completely agree with the prediction of mean-field theory, so long as the lattice size is sufficiently large. The population dynamics can be classified into two phases: unconditional extinction (UE) and survival/extinction (SE). In the UE phase, the species always goes extinct. On the other hand, in the SE phase, the Allee effect can be observed. Fig. 2 illustrates the population dynamics for the SE phase. We here consider the special case that the reproductive rate r_Y of Y is zero. In Fig. 2, twenty initial conditions are randomly chosen. In the case of global interaction, simulation results completely agree with the predictions of mean-field theory. The SE phase has three equilibria; two are stable (extinction and survival), while one is unstable. To explore the population sustainability, we obtain the final survival densities in SE phase. In Fig. 3, the equilibrium densities are plotted against sex ratio α . Even when $r_Y \neq 0$, overall profiles of population dynamic never change. Fig. 4 shows the total density for different values of reproductive rate r_Y of Y. When r_Y increases, the total density slightly increases.

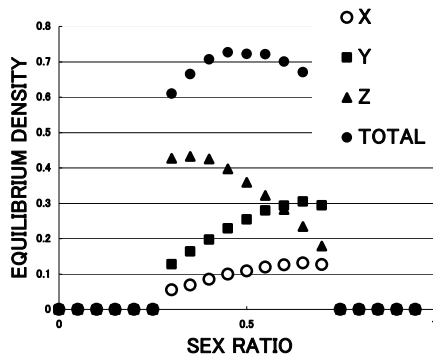


Figure 3. The equilibrium densities for global simulation is plotted against sex ratio α . Model parameters are the same as used in Fig. 2.

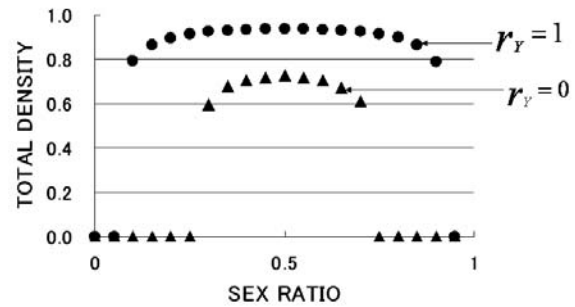


Figure 4. The total density at equilibrium for global simulation. The increase of reproductive ratio of sneaker (Y) gives slight change for equilibrium density.

4.2. Results of Local Interaction

Next we report the simulation results for local interaction. As predicted by the mean-field theory, the population dynamics is classified into unconditional extinction (UE) or survival/extinction (SE) phase. In the latter phase, the system also reaches either extinct or surviving equilibrium. The final equilibrium in SE phase sensitively depends on initial spatial patterns. The boundary (separatrix) in initial condition is still unclear. To obtain steady-state densities at surviving equilibrium, we set the initial condition without the empty site. For instance, Fig. 5 displays population dynamics under such initial condition. In Fig. 5, we use a higher value of reproduction rate ($r_X = 5$) and a lower value of mortality rate ($m = 0.0015$), compared to the

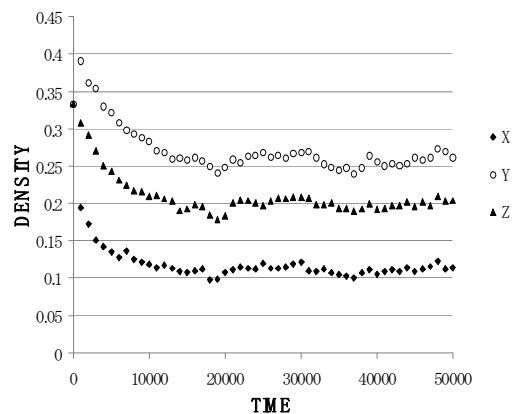


Figure 5. The population dynamics for local simulation ($\alpha = 0.65$). Model parameters are set as $(r_X, r_Y, m, \beta) = (5, 0, 0.0015, 0.3)$.

value used in Figs. 2, 3 and 4 ($r_x = 1$, $m = 0.015$).

This is because the system under the local interaction easily becomes extinct.

In Fig.6, the total equilibrium densities for local simulation are plotted against sex ratio α , where each plot is obtained by averaging densities over the period $48000 < t \leq 50000$. It is found from Fig. 6 that the total density largely increases with the increase of r_Y .

In most cases of local simulation, the surviving region is very narrow as indicated in Fig. 6 (see the case of $r_Y = 0$).

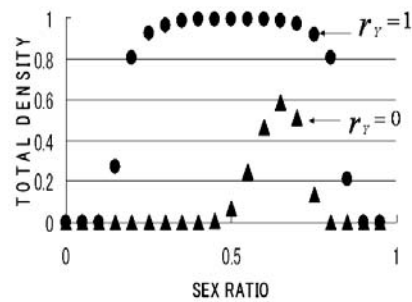


Figure 6. Same as Fig. 4, but in the case of local interaction. Model parameters are the same as used in Fig. 5. The increase of reproductive rate r_Y of Y gives a large change for equilibrium density (see Fig. 4). Hence the increase of r_Y is adaptive for the sustainability of all individuals.

5. DISCUSSIONS & CONCLUSIONS

We have developed the lattice model of mate-choice system and obtained the population dynamics. We find the Allee effect. Namely, when the initial abundances of X, Y and Z are lower than certain thresholds, the population goes extinct. In contrast, when they are higher than the thresholds, the population can survive reaching in a stable equilibrium (see Fig. 2). Computer simulations are carried out by two methods: global and local interactions. In the case of global simulations, the population dynamics can be completely represented by mean-field theory.

To explore the population sustainability, we obtain densities of X, Y and Z at stable equilibrium. It is found for global interaction that the population can survive in the wide range of parameter space (sex ratio) as illustrated in Fig. 4. In contrast, the survivable sex ratio is narrow in the case of local simulations (Fig. 6). In the local simulation, the density peak usually stands out sharply.

We discuss the evolution of sneakers based on the sustainability (Tanaka *et al.*, 2009b). It is found that the total density increases, when reproductive rate r_Y of small male (Y) increases, or when the ratio β of dominant male increases. Under local simulations, the average density of the overall population is close to zero (see Fig. 6). When the reproductive rate of small male (Y) increases, it acts as the avoidance of population extinction. This implies that sneaker is adaptive for the sustainability of all individuals.

Finally the optimality of sex ratio α is discussed. In the case of local simulations, the optimal sex ratio becomes larger than 1/2 for small value of β . This result looks different from the cases of real animals ($\alpha \approx 1/2$). We consider our model has some oversimplifications. In particular, we neglect a sterile period in female. For instance, females have a long pregnant period. Moreover, in real animals, eggs of females are energetically more costly than sperms (e.g. Togashi *et al.*, 2006; Togashi *et al.*, 2004). Hence, it takes long period for female to mature. If we modify our model to take into account such sterile properties of female, then the optimal sex ratio may become close to 1/2.

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