

Paper:

Mathematical Model of Proportion Control and Fluctuation Characteristic in Termite Caste Differentiation

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Self-organization of hierarchy of system has been focused in task allocation of distributed autonomous systems and network analysis. It is important to realize the mechanism of hierarchy generation for implementation in artificial systems. In order to know the principle, we try to model the control of caste differentiations in the termite ecology. Equations of evolution are created, using both of biological data and assumptions obtained by mathematical analysis. In addition, the model is validated by computer simulations. In this study, we propose that the probability migration of individuals and modulations of fluctuation are operated as a differentiation control strategy.

Keywords: termite, caste differentiation, proportion control, self-organization, fluctuation

1. Introduction

It is important to realize functional differentiations and task allocations in distributed autonomous systems [1] for adaptability of systems. Adaptive behavior requires both stability to be appropriate for the purpose and instability to create new order. Dynamics for creations and destructions should be existed in self-organization systems owning purposes. It means that one of important factors is an autonomous control of irreversible fluctuations dynamics such as multiparticle random walk and diffusion phenomenon. No one knows how such a system should be systematized. One of the approaches to develop is starting to model from phenomenological theory. Phenomenon in the living thing system prove that the system equipped adaptability is especially excellent. The focus of this research is to learn how living things adaptively control differentiation and fluctuation for creation and reconfigure order.

Self-organized proportion control is treated as functional differentiations of individuals in a system according to environment conditions and given tasks. The function differentiation process is seemingly regarded as tran-

sition from a homogeneous state to a heterogeneous one in multibody system against the second law of thermodynamics. Although the behaviors of particle in equilibrium systems have been discussed enough, nonequilibrium open systems have not been systematized from the perspective of thermodynamics yet. One reason seems to be that the principle must be modeled by enforced approximation of phenomenon and the experiment data because potentials are not expressly given such as mechanical energy and free energy. Formulations and analysis of general mathematical models without degeneracy is a short cut to find out universal principle for implementations to artifact by excerpting from various biological phenomenon. In other words, it is required that cooperation between phenomenological data obtained from biological experiments and working assumptions derived from mathematical analysis. It is wise to determine the equations of evolution of systems with generality from the mutual integration chains.

Among living things termite society should be paid special attention, because they possess the communal life styles called "eusociality," in which various types of individuals in colonies. Those types are called "castes," include worker, soldiers, kings and queens. Each caste plays functional roles for the fitness of a colony. However, eusocial insects do not have any highly-advanced cognitive function even though they possess highly social systems, so that the termite colony is a valuable model target for considering functional differentiations in a organized system.

In this research, we model the control of caste differentiations in termite ecology. Especially, the adaptive proportion control between worker and soldier are focused. As related research, there are mathematical models based on reaction diffusion systems by Mizuguchi [2] and Sakaguchi [3]. Mizuguchi and Sugawara additionally apply to distributed autonomous robotic systems [4]. Bonabeau et al. experiment mathematical model of a hierarchies expression in society by computer simulations [5]. This research proposes mathematical model, focusing attentions on fluctuation characteristic generated by probabilistic spatial migration of individuals. In addition, the strat-

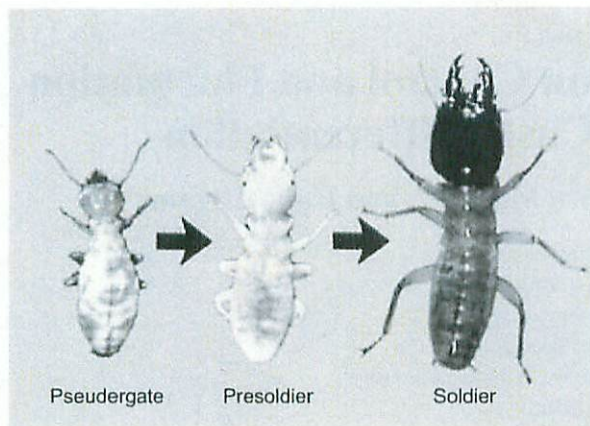


Fig. 1. Soldier differentiations in the damp-wood termite *Hodotermopsis sjostedti*.

egy of interaction using pheromone is assumed and it is shown that the important role of fluctuation inherent in a system as global feedback to control caste proportion by computer simulations at individuals behavior level.

2. Biological Datas and Assumptions

2.1. Control of Termite Caste Differentiation

The termite (Order Isoptera, Class Insecta) is categorized into a eusocial insect that lives in a group based on kinship and forms a colony with a certain size. In a termite colony, there are several castes called worker, soldier, nymph, king and queen in addition to immature larvae. The developmental pathways to caste differentiation are diverse from species to species [6–11]. Even though each individual has the similar genetic background, they present different phenotypes through anatomical specialization according to the castes [12–14].

Among the various castes, soldier castes is a peculiar one because soldiers are completely sterile and perform altruistically to attack against predators or intruders. The control of soldier ratio in a colony is an important regulatory system in the termite societies [15, 16]. In addition, there is a special stage called “presoldier” in the course of soldier differentiation. Soldiers are normally induced from workers via presoldier stage through two molting events. Presoldiers can be regarded as the system buffer for the early adaptations of social systems as shown in **Fig. 1**. It is mainly thought that such altruistic behaviors have been evolved by kin selection [17].

The caste differentiation had been acquired as the adaptation for the extremely precise social behaviors and self-organization. The multiple phenotypes of individuals and the caste ratio controls can be respectively regarded as the adaptations in micro and macro level. Both of the adaptations must work out under coherent relations between them. It is important for exploring the strategy of eusocial insects to consider information cycle between macro and micro layers. As Lüscher reported the following work-

ing thesis obtained by several biological experiments, the caste differentiation seems to be accomplished under the pheromonal control which is not transferred by diffusion in air of chemical substances, but through trophallaxis behaviors in which colony members exchange food materials from mouth to mouth [18]. However, there is the hypothesis that caste ratio is also controlled by exocrine volatiles [19, 20]. For example, in *Nasutitermitinae*, defense substances function as the chemical pheromones that inhibit the soldier production [21]. However, the effective pheromonal substances are not identified yet.

In order to realize the caste differentiation processes, it is necessary to approach from both physiological mechanisms in an individual and system methodology in the colony level. In an individual level, several researches succeeded to find the methods of induction from workers to soldiers by the application of juvenile hormone and its analogues [15, 22, 23]. In a colony level, it is reported that *Reticulitermes flavipes* adaptively changes the caste ratio according to season [16]. In addition, there are important reports in other eusocial insects, in which colonies increase the soldier proportion when they confront competitors, predators or intruders [24–26]. Termite colony generally seems to control the caste ratio precisely, depending on the environment conditions without global controls that means controls determined by congenitally genetic informations [27, 28].

The biological reports mentioned above are summarized as follows:

- Termite has the same genotype and present a different phenotype.
- The caste ratio is changed according to environmental conditions.
- Presoldier exits as previous instars of soldier.
- Individuals interact by transfer of pheromone through direct contact.
- Individuals metamorphose body characteristics based on caste.

2.2. Assumptions

The caste differentiations in termite is guessed to realize by physical interaction of pheromone transfer as global order state feedback as mentioned above. Each individual metamorphose using different phenotype depending on the amount of received pheromone and change how to interact in response to caste, that means adjustment of transfer pheromone. It means that caste ratio is determined by structural cycle between macro and micro state. In regard to this matter, there are some researches pointing out social expression mechanism. In the model of Mizuguchi [2] and Sakaguchi [3], globally coupled individual and global feedback using averages of a substance are assumed. However an existence of presoldier as mentioned above and a potential of activation for transition from worker to soldier are unexplained.

In this research, it is assumed that caste differentiations is realized by interaction through one kind of pheromone. The interaction is assumed to be carried out in probabilistic contact among individuals because individuals incessantly migrate in the colony. Probabilistic contact includes both who the individual interact with and how many times interactions are performed per unit time.

The mathematical model is represented including probabilistic interaction generated from not tight relations but loose relations. To analyze the mathematical model, the mechanism of adjustment of a potential of activation is expressed by inherent regulated fluctuation.

In short, we assume that:

- One kind of pheromone is used to stimulate differentiation.
- All individuals exchange pheromones by mutual interaction.
- The hormone value is changed by internal potential and mutual pheromone interaction.
- The relationship between the transmitted pheromone and hormone is linear.
- Individuals spatially migrate in colony with randomness.

3. Model

The mathematical principle model is constructed based on biological reports and the assumption in section 2. In order to discuss the basic caste differentiation control mechanism through one kind of pheromone, bare essentials of mathematical model is expressed. In fact, the states of the system consist of group of u_i that is amount of hormone in individual i and the genotype are expressed by one dimensional potential function. The genotype is described as extremal values of the potential function. In this model, therefore, the dynamics of internal hormone are on bistable potential because differentiations between two kinds of caste are focused. The equations of evolution of u_i are as follows:

$$\frac{\partial u_i}{\partial t} = -\frac{\partial V_i}{\partial u_i} - D_i \sum_{j=1, j \neq i}^N (w_{ij}u_j - d) \dots \dots (1)$$

$$\frac{\partial V_i}{\partial u_i} = (u_i - b_w)(u_i - b)(u_i - b_s) \dots \dots (2)$$

where $\partial V_i / \partial u_i$ is given as show in **Fig. 2** that describe the shape of genotype potential. N means the constant number of individuals in the colony. V_w , V_s and V_b are the constant number of potential when $u_i = b_w$, $u_i = b_s$ and $u_i = b$, respectively. b_w , b_s and b are constant, those are evolutionarily-conserved, so that they determine optimal caste ratio. D_i is the stochastic variable that mean the number of contacts among individuals over time. w_{ij} is a stochastic variable and satisfies $\sum_{j=1, j \neq i}^N w_{ij} = 1$ at any

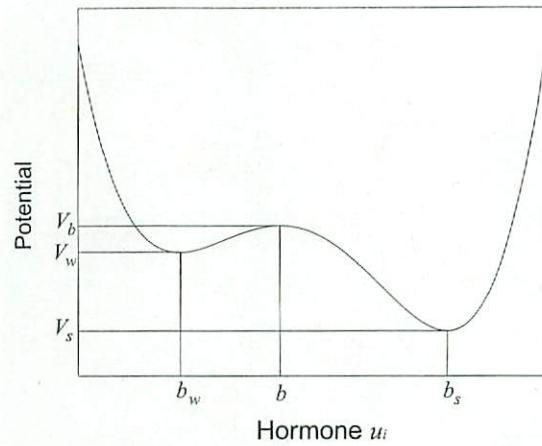


Fig. 2. Landscape by potential V_i .

time, meaning the frequency of contact between individuals i and j . d is also the constant number determining the optimum caste ratio which is evolutionarily-conserved. The equations of evolution (1) include stochastic variables depending on both a average number of contacts and which the individual has contacts with other one. The potential of activation for state transition from worker to soldier depend on $V_b - V_w$. The fluctuations are needed for transitions to climb the potential of activation.

In order to separate stochastic factor from average amount, D_i and w_{ij} are replaced in the following equations:

$$D_i = D_i^c + R_i(t) \dots \dots (3)$$

$$w_{ij} = w_{ij}^c + r_{ij}(t) \dots \dots (4)$$

$$\langle R_i(t_1)R_i(t_2) \rangle = 2M_D\delta(t_1 - t_2) \dots \dots (5)$$

$$\langle r_{ij}(t_1)r_{ij}(t_2) \rangle = 2M_w\delta(t_1 - t_2) \dots \dots (6)$$

where \cdot^c is the average concerning time in variable D_i^c and w_{ij}^c . $R_i(t)$ and $r_{ij}(t)$ are stochastic variables assumed to be Gaussian distribution without a time correlation. M_D and M_w are constant numbers that mean amplitude of fluctuation of $R_i(t)$ and $r_{ij}(t)$ respectively. Therefore, Eq. (1) is replaced in the following equations using Eqs. (3) and (4):

$$\frac{\partial u_i}{\partial t} = -\frac{\partial V_i}{\partial u_i} - D_i^c G - R_i(t)G - R_i'(t) \dots \dots (7)$$

where

$$G = \sum_{j=1, j \neq i}^N (w_{ij}^c u_j - d) \dots \dots (8)$$

$$R_i'(t) = (D_i^c + R_i(t)) \sum_{j=1, j \neq i}^N r_{ij}(t)u_j \dots \dots (9)$$

Eq. (7) is a Langevin equation depending on global feedback by parameter G . The set of individuals, that carry out interactions i.e. exchange a pheromon, and its number of individuals are defined as h and N_h , respectively. Under the condition that the number of individual is large, that is $w_{ij}^c = 1/(N_h - 1) \approx 1/N_h$, $i \in h$, the following equation is

satisfied:

$$\sum_{j=1, j \neq i, i \in h}^N w_{ij}^c u_j = \langle u \rangle \dots \dots \dots (10)$$

where $\langle u \rangle$ is the average of u_i for $i \in h$. If the number of soldiers that is included in set h decreases (increases), $\langle u \rangle$ decreases (increases) to activate (inhibit) transitions from worker to soldier. However the transition from perfectly transformed soldier to worker is unacknowledged in termite. $R_i(t)$ includes fluctuations depending on G . $R'(t)_i$ is stochastic variables give steady fluctuations to the system and depending on b_w, b_s, b and d . $R'(t)_i$ is time average 0 and Gaussian distribution without time correlation as well as $R(t)$ and $r(t)$. When the caste ratio converges to the optimum value expressed in Eq. (10), as G approaches a certain value determined by balances between the potential V_i and interaction terms in Eq. (1), the effect of fluctuation promoting to the system approaches a certain value. As show in Eq. (7), the amplitude of fluctuation for transition are amplified or attenuated by G .

Changes in G are assumed to be slower than the time evolution of u_i . This is the adiabatic approximation for analysis. When P_i is the probability distribution of u_i , Fokker-Planck of Eq. (7) and its equilibrium solution are explained as follows using normalization constant A :

$$\frac{\partial P_i}{\partial t} = \frac{\partial}{\partial u_i} \left(\frac{\partial (V_i + D_i^c G u_i)}{\partial u_i} + \sqrt{(M_D G)^2 + M^2} \frac{\partial}{\partial u_i} \right) P_i$$

$$P_{eq} = A \exp \left(\frac{-(V_i + D_i^c G u_i)}{\sqrt{(M_D G)^2 + M^2}} \right) \dots \dots \dots (11)$$

Fig. 3 shows the transition of P_{eq} according to the changes of global parameter G . If G increases or decreases, the balance of potential curve between b_w and b_s changes based on the effect of $D_i^c G$ as show in Eq. (11). The gradient also becomes loose by the effect of $\sqrt{(M_D G)^2 + M^2}$. Therefore the changes in parameter G gives the force for state transitions and the mechanism of fluctuation adjustment.

4. Experiments

4.1. Simulation Setup

Computer simulation in this research is carried out at the behavior level of individuals. The overviews of the simulation is shown in Fig. 4. The number of individuals is fixed at $N = 100$ at any time. The spatial size of the colony and the individual are given as a square, 2 on a side, and a circle of 0.05 in diameter. The initial states of all individuals are set to $u_i = 0.1$, that means all individuals in the colony are set as workers. The caste of individuals is determined as worker and soldier when $u_i < 0.5$ and $u_i \geq 0.5$, respectively. Termite actually seems to fuss around. However what group of termite are doing is unknown for caste differentiation. In this research, therefore, the individual migration is assumed as consistently

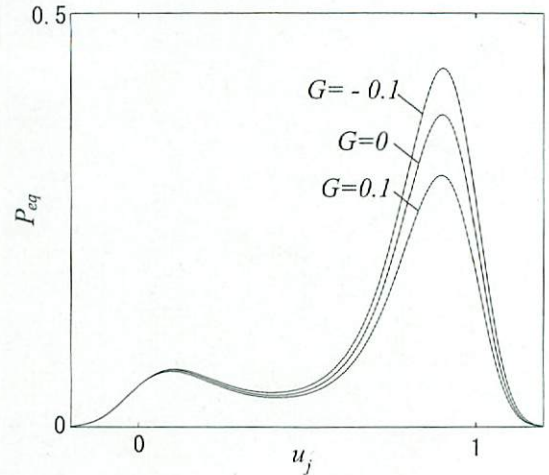


Fig. 3. Transition of probability distributions P_{eq} at $b_w = 0.1, b_s = 0.9, b = 0.4, M = 0.005, M_D = 0.01$ and $D_i^c = 0.01$. Global parameter G transits to $G = 0, G = 0.1$ and $G = -0.1$.

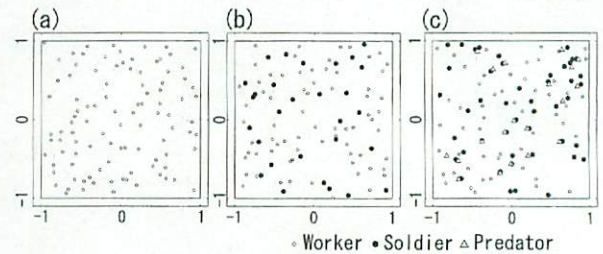


Fig. 4. Simulation view at $N = 100, b_w = 0.1, b_s = 0.9, b = 0.4$ and $d = 0.3$. White circles and black circles indicate the position of workers and soldiers, respectively. Triangles indicate predators put in at $t = 200$. (a) at $t = 0$. (b) at $t = 199$. (c) at $t = 205$.

uniform linear motion. When an individual collide with other one or colony edges, the contacts are assumed as perfectly elastic collision. By these assumptions, each individual behave as molecular motion in closed space. At $t = 200$, predators that has no relationship with termite individuals are put into the colony. It means that an incursion of predators is treated as one of the environmental variation. The predators also behaviors at random as well as termite individuals.

Figure 5 explains interaction rules among individuals in the colony. When individuals contact each other, they mutually transfer the hormone through pheromone interaction as shown in Fig. 5(a). In this simulation, the amount of hormone u_i is subsequently updated by using Eqs. (1) and (2) every iteration. At the same time, u_i is updated with $D_i = 0$ in case that the individual is contacting with an predators.

When individuals contact with an predators, there are no transfer of hormone as shown in Fig. 5(b). In this case, u_i is constantly updated using Eqs. (1) and (2) with $D_i = 0$. This assumption means that soldiers interacting with predators lose the effort for pheromone release, so that G decreases and this effect brings results of state transition as above a mathematical analysis in section 3.

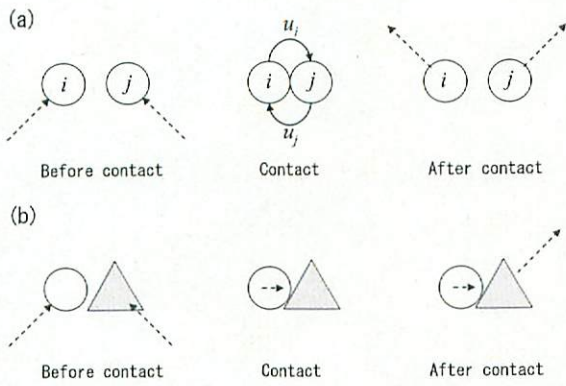


Fig. 5. Interactions between individuals. Circles indicate worker and soldier individual. Dotted arrowed lines indicate a velocity of individuals. (a) Each individual give u at one interaction. (b) Interactions between individuals and predators.

The worker individuals neglect the existence of predators and the soldier individuals follow predators that means soldier attack them. The soldiers continue to follow predators until it turns from predators by reactive force from other individuals. These behaviors are advisedly imitated from observations of real termite behaviors.

Based on above these conditions, the time evolution of u_i and $\langle u \rangle$ are evaluated by computer simulations.

4.2. Results

The simulation results are shown in **Fig. 6**. As show in **Fig. 6(a)**, the average $\langle u \rangle$ is adaptively changed on the boundary of $t = 200$. The number of soldier individuals are $N_s = 33$ and $N_s = 49$ at $t = 150$ and $t = 400$, respectively. Although actual amount of hormone can not be negative, some u_j are negative in the results. In order to realize that all values of u_j are located in positive area at any time, the parameter set needs to be changed, however, this problem seems to be nonessential in this paper. The mathematical analysis advanced in section 3 do not need any changes since there are no condition of positive and negative for u_j . As shown in **Fig. 6(b)-(d)**, the distributions of u_i dynamically change adapting to an incursion of predators. At $t = 205$, the variance of the distribution increase. The distribution eventually converge to the state of **Fig. 6(d)**.

In addition, in order to estimate the effects of fluctuations, transitions of G and variances of u_i included N_w are shown in **Fig. 7(a)** and **(b)**, respectively. The G temporarily decreases around the interval $200 < t < 220$ and the variance also increases. It means that the inherent fluctuations are increased and decreased according to incursion predators to converge to evolutionarily-conserved optimal caste ratio. In **Fig. 7(a)**, G demonstrate rapid fluctuation after $t = 200$, although the its average value are recovered to previous value. It is thought that the rapid fluctuation depends on a spatial constraint after predators putting into a colony. D_i^c , R_i^c and R_i in Eq. (2) must change and the fluctuation characteristic seems to change from rad-

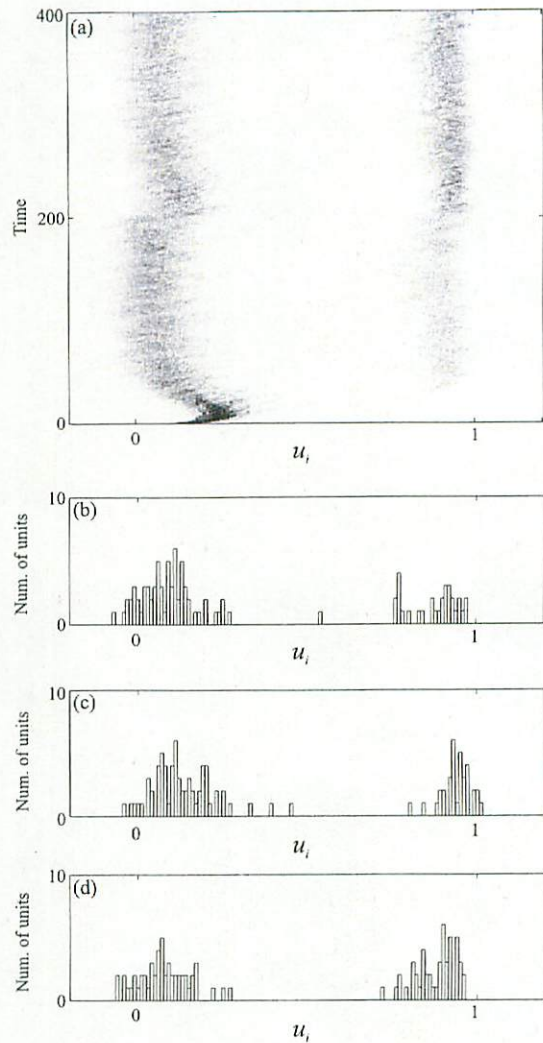


Fig. 6. Simulation results at $N = 100$, $b_w = 0.1$, $b_s = 0.9$, $b = 0.4$ and iteration size, $\Delta t = 0.05$. The number of predators, $N_e = 0$ at $0 \leq t < 200$, $N_e = 20$ at $200 \leq t < 400$. (a) Time evolution of u_i and $\langle u \rangle$. The distribution of u_i are shown by the gray scale map. (b) Distribution of u at $t = 150$. (c) Distribution of u at $t = 205$. (d) Distribution of u at $t = 400$.

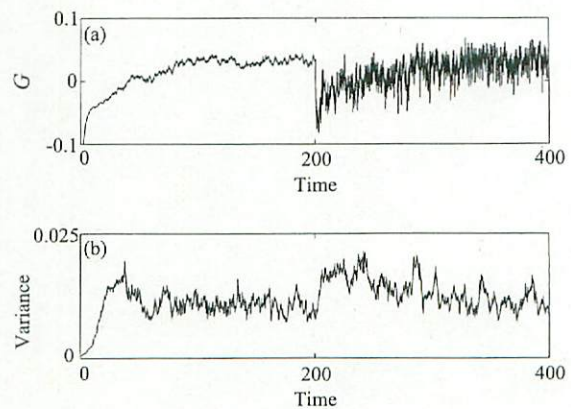


Fig. 7. (a) Transition of G given by Eq. (9). (b) Variance of u_i ($i \in w$). The variance is given by $\sigma_w^2 = \sum_{i=1}^{N_w} (u_i - \langle u_w \rangle)^2$.

ical one. In order to clarify these reasons, more developmental analysis is needed.

5. Conclusion

In this research, the mathematical model of termite caste differentiation is established based on biological evidences and assumptions which are advisedly considered to imitate biological reports. In the simulation, termite behavior like molecular motion in closed space and it seems that the simulation and mathematical analysis are carried out with specific assumption. However, strong working assumption are needed when undiscovered phenomenon are treated. Living systems are especially complex for understanding. Development of motion model of an individual should be designed by close observation and these works are included in future work. In differentiation process, the fluctuation characteristic is important role for adaptive behaviors at a colony level. It is suggested that the strategy of migration with randomness give the fluctuation to the system and the effect effectively works for caste ratio control. It can be understood that the inherent fluctuation is precisely controlled for adaptations in global order. For finding out adaptive behaviors of all living things, it would be expected that the role of fluctuation control is one of the most important factors to explain adaptabilities. The biological experiments in order to justify this conclusion are included in future work.

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