A Termite Internal State Model for Elucidating Caste Differentiation

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Abstract: Eusocial insects form colony and adapt environmental fluctuations. Colony is maintained with caste differentiation, which is a self-organized task allocation. We researched termite caste differentiation. Termites have several specialized castes. The pseudergate, one of those, has some differentiation possibilities. It is suggested that Juvenile Hormone (JH) is concerned in termite caste differentiation. Our research emphasized focus on the relationship between the pseudergate caste differentiation and time evolution of JH titer. We built an termite internal state model through development for understanding of caste differentiation mechanism. This model was evaluated with mathematical analysis and computer simulation.

Keywords: Multiagent System, Termite, Caste differentiation

1. OVERVIEW

Eusocial insects form a social group called a colony [10]. They adapt to changes in the environment through changes in the colony. The colony is maintained through caste differentiation. Self-organization is supported by specialization of roles in behavior and morphology.

Eusocial insect colonies have been studied as an example of swarm intelligence [1]. Clarification of caste differentiation mechanisms engenders not only understanding of eusocial insect colonies, but also understanding of the design of multiagent systems. This study clarifies the termite caste differentiation mechanism. Termites are known to have multiple castes and display many caste differentiation phenomena. Nevertheless, the internal state of individuals with respect to caste differentiation remains unclear. Mathematical modeling that reproduces caste differentiation was used to solve the problem. An earlier termite caste differentiation model [3] was investigated, but that study did not include a developmental process. Measured chemical amounts of termites' standalone chemicals are technically too difficult to evaluate using a model. Therefore, an internal state model using the colony and a colony mathematical simulation model is introduced for mathematical analysis of caste global behavior by inspecting the internal state model to evaluate.

2. ECOLOGY OF TERMITES

The termite caste differentiation pathway differs by species. For this study, *Hodotermopsis sjostedti* is used as a model for construction of a model. *Hodotermopsis sjostedti* includes major castes whose individuals are developed according the following differentiation pathway (Fig. 1).

A termite is hatched from an egg and becomes a larva. Larvae molt six times repeatedly, then become differentiated pseudergates. Pseudergates are workers that potentially have reproductive capacity. In a termite colony, non-reproductive workers do not exist. Alternately, lar-
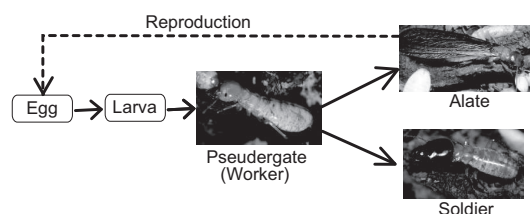

Fig. 1 Caste differentiation pathways of termites (*Hodotermopsis sjostedti*).

vae and pseudergates play roles as workers.

After several repetitions of molting, pseudergates differentiate mainly into alates and soldiers during the final caste differentiation. On the other hand, pseudergates remain pseudergates after molting. This phenomenon is called stationary molting. Alates are the next colony's reproductive insects. Soldiers are aggressive and serve as soldiers for the colony.

A response to a changing environment has been confirmed by an increase in the ratio of soldiers to other termites when the colony encounters an enemy invasion. [2, 9]

Juvenile hormone (JH) is involved with maintaining insects' larval characteristics. In termites, JH inhibits pseudergates from becoming reproductive [6]. Nijhout argues that a relationship pertains between the individual internal JH titer in the pseudergate instar and caste after pseudergate's molting [7] (Fig. 2)). Their theory shows that pseudergates which became alates (soldiers) exhibited a high (low) JH titer and pseudergates' JH titer has temporary changes, thereby pseudergates is caused stationary molting. The individual internal JH titer is too minute to record temporal variations of the titer. Consequently, it is difficult to underpin the hypothesis quantitatively. Artificial spraying of JH raises the rate of differentiation from pseudergate to soldier [8]; the individual internal JH titer changes with the seasonal change [5]. The individual internal JH titer is deeply involved in environmental changes.

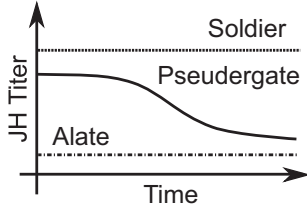From these biological findings, we can advance three

Fig. 2 Temporal variation of JH titer in pseudergates and the post-molting hypothesis about castes (modified from Nijhout 1982).

hypotheses. Pseudergates caste differentiation reflects environmental changes. Pseudergates' JH titer is of an intermediate level between that of alates' and soldiers'. An individual internal model which incorporates pseudergates, soldiers, and alates can be constructed.

3. MODEL

3.1 Caste Differential Model by JH Titer

We construct a pseudergate caste differentiation model. The important aspect of this model is that the differentiation to alates and soldiers is fundamentally irreversible: the pseudergate caste is a buffer state of other castes that can form different multiple castes flexibly. Pseudergates adjust the caste ratio of the entire colony. Based on the conjecture given above, if the individual internal JH titer is high, pseudergates become soldiers with a high probability. On the other hand, if the titer is low, pseudergates become alates. There are two threshold amounts in the individual internal JH model; θ_{Ala} and θ_{Sol}. If the JH titer is upper θ_{Ala}, pseudergates become alate. If the JH titer is above θ_{Sol}, pseudergates become soldier. If the JH titer is intermediate, pseudergates remain as pseudergates, stationary molting. The three ranges of response to JH is defined, to pseudergates, soldiers, and alates.

Through numerous experiments, the soldier's differentiation-inhibitory effect was derived. The rate of differentiation from pseudergate to soldier is lowered if soldiers are numerous. Pseudergates apparently receive an inhibitory effect from soldiers [4]. The effect was realized by the JH titer change with the contact between individuals in the model. In this study, alates have similar inhibitory effects.

3.2 Developmental Process

In eusocial insects, multiple generations live together in the same colony, which allows the termite colony members to lead differentiated and undifferentiated individual lives. The colony's stability is derived from living together. The model was given the developmental process; the colony was able to continue for multiple generations of living together. Individual developmental processes have a life cycle, which includes birth, growth, and death. Growth was set as a given length of time (instar) per molting and accompanying caste differentiation. First, the eggs hatch and become larvae. After larvae molt six times, they become differentiated into pseudergates

(7th instar). Pseudergates undergo post-caste differentiation to alates, soldiers, and pseudergates according to their internal JH titer when pseudergates molt. Pseudergates become soldiers if the JH titer is high. Pseudergates become alates if the JH titer is low. If the JH titer is intermediate, pseudergates remain as pseudergates, even after molting (Fig. 3).
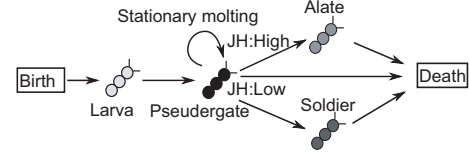

Fig. 3 Development of the model.

The individual's life is set as shown in Eq.(1) randomly using the Weibull distribution.

$$\frac{\nu}{m} \log \frac{1}{1-p} \qquad (1)$$

In that equation, ν denotes the average life expectancy, p is a random number of $[0, 1]$, and m is a shape coefficient.

3.3 Interaction between Individuals

In this model, termite individuals move and collect external information through mutual interaction. Interaction among them comprises two elements. The first is JH titer. This follows the differential equation described above. The initial state is in the pseudergate's JH titer. Through larva and pseudergate contacts, individuals' JH titer change. Larger values become larger; smaller values become smaller. The second element is a caste differentiation inhibitory effect. When the pseudergate and larva meet alates and soldiers, they receive inhibitory effects with a coefficient $\gamma_{\text{Sol}}, -\gamma_{\text{Ala}}$. This effect decreases with time.

$$\frac{d\beta}{dt} = -\gamma\beta \qquad (\gamma > 0) \qquad (2)$$

4. EVALUATION

4.1 Mathematical Analysis

In this study, a mathematical model related to the individual internal state was constructed as above. We model the entire colony of caste ratio changes mathematically and find the global time change of the caste ratio to evaluate the model.

Following the caste differentiation pathway, a relationship like Fig. 4 is evident. The caste differentiation ratio changes depending on the environment in the relationship. As a result, a mathematical model of caste popula-
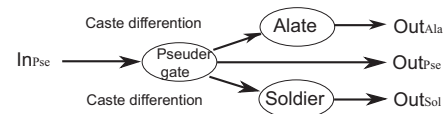

Fig. 4 Caste differentiation model in the termites' colony.

tion is represented below. Interaction between individuals is treated with average JH titer. Each caste's JH titer

range is $[0, 1]$ and corresponds to that represented by the sigmoid function.

$$\dot{n}_{\text{Pse}} = -\{\alpha_{\text{Ala}} + \alpha_{\text{Sol}}\,\text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})\}\,n_{\text{Pse}}$$
$$+ In_{\text{Pse}} - Out_{\text{Pse}}$$
$$\dot{n}_{\text{Sol}} = (\alpha_{\text{Sol}} + \alpha_{\text{Pse}})\,\text{sig}\,(x_{\text{JH}} - \theta_{\text{Sol}})n_{\text{Pse}} - Out_{\text{Sol}}$$
$$\dot{n}_{\text{Ala}} = \{\alpha_{\text{Ala}} - \alpha_{\text{Pse}}\,\text{sig}\,(x_{\text{JH}} - \theta_{\text{Sol}})\}\,n_{\text{Pse}} - Out_{\text{Ala}}$$
$$(3)$$

Variables are explained hereinafter. The caste's population is represented as: n_i (pseudergate, n_{Pse}; soldier, n_{Sol}; alate, n_{Ala}). The new population (caste differentiation, birth) is In_i; the caste from the remaining population (caste differentiation and death) is Out_i. The interaction representing the average amount is x_{JH}. Then, coefficients are explained. The variable of d_i represents caste mortality. Out_i is defined as $Out_i = d_i n_i$. α_i is the differentiation coefficient, caste differentiation in the rate respectively. The effect of the average JH titer in Eq.(3) is represented as a sigmoid function $\text{sig}(x) = 1/1 + \exp(-Kx)$ The sigmoid function has a $[0, 1]$ range of value. θ_{Sol} is a threshold amout; it was set as $\text{sig}(x) = 0.5$ when $x = \theta_{\text{Sol}}$. K is the gain of the sigmoid function, which can be regulated to a near-threshold slope.

As shown in Eq.(3), x_{JH} controls the pseudergate individual formation to alates and soldiers. This is the hypothesis by which the individual JH titer changes according to individual interactions and effects of environment, and which causes caste differentiation. Actually, x_{JH} increases if the alate population is large, and x_{JH} decreases if the soldier population is large. Under these conditions, x_{JH} time development is represented as shown in Eq.(4)

$$\frac{dx_{\text{JH}}}{dt} = \frac{-\gamma_{\text{Sol}}n_{\text{Sol}} + \gamma_{\text{Ala}}n_{\text{Ala}}}{n_{\text{Pse}} + n_{\text{Sol}} + n_{\text{Ala}}}. \qquad (4)$$

As shown in Eq.(4), the inhibition effect size can be adjusted using the caste differentiation inhibiting coefficient γ_i.

This mathematical model has a nonlinear term, which represents the reaction of the average JH titer. Let us analyze the model and derive a fixed point. Under $In_{\text{Pse}} = $ const, the variables in the fixed point are represented as Eq.(5).

$$\begin{cases} n_{\text{Pse}}^* = \frac{In_{\text{Pse}}}{d_{\text{Pse}} + \alpha_{\text{Ala}} + \alpha_{\text{Sol}} + \text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})} \\ n_{\text{Sol}}^* = \frac{(\alpha_{\text{Sol}} + \alpha_{\text{Pse}})\,\text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})\,In_{\text{Pse}}}{d_{\text{Sol}}\{d_{\text{Pse}} + \alpha_{\text{Ala}} + \alpha_{\text{Sol}} + \text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})\}} \\ n_{\text{Ala}}^* = \frac{\{\alpha_{\text{Ala}} - \alpha_{\text{Pse}}\,\text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})\}\,In_{\text{Pse}}}{d_{\text{Ala}}\{d_{\text{Pse}} + \alpha_{\text{Ala}} + \alpha_{\text{Sol}} + \text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})\}} \\ x_{\text{JH}}^* = \frac{1}{K}\log\frac{y^*}{1 - y^*} + \theta_{\text{Sol}} \end{cases} \qquad (5)$$

$$y^* = \frac{d_{\text{Sol}}\gamma_{\text{Ala}}\alpha_{\text{Ala}}}{d_{\text{Ala}}\gamma_{\text{Sol}}(\alpha_{\text{Pse}} + \alpha_{\text{Sol}}) + d_{\text{Sol}}\gamma_{\text{Ala}}\alpha_{\text{Pse}}} \qquad (6)$$

The Jacobi matrix of the fixed point and that eigenvalue are derived. The entire colony population was defined as $n_{\text{Pse}} + n_{\text{Sol}} + n_{\text{Ala}} = C$. Then, C follows a different equation $\dot{C} = -dC + In_{\text{Pse}}$.

The dynamic system Eq.(3) is restricted on manifold $n_{\text{Pse}} + n_{\text{Sol}} + n_{\text{Ala}} = \frac{In_{\text{Pse}}}{d}$. We linearized the Jacobi matrix around the fixed point $(n_{\text{Pse}}^*, n_{\text{Sol}}^*, n_{\text{Sol}}^*, x_{\text{JH}}^*)$; the Jacobi matrix is $\mathbf{J}$.

$$\mathbf{J} =$$

$$\begin{pmatrix} -\alpha_{\text{Sol}}s - d - \alpha_{\text{Ala}} & 0 & -\alpha_{\text{Sol}}n_{\text{Pse}}^*\frac{\partial s}{\partial x_{\text{JH}}} \\ (\alpha_{\text{Sol}} + \alpha_{\text{Ala}})s & -d & (\alpha_{\text{Sol}} + \alpha_{\text{Pse}})n_{\text{Pse}}^*\frac{\partial s}{\partial x_{\text{JH}}} \\ -\frac{\gamma_{\text{Ala}}d}{In_{\text{Pse}}} & -\frac{(\gamma_{\text{Ala}} + \gamma_{\text{Sol}})d}{In_{\text{Pse}}} & 0 \end{pmatrix}$$
$$(7)$$

Here, we derived $s = \text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})$. Under the y^* domain definition $(0 < y^* < 1)$, the eigen value of $\mathbf{J}$ has an all-negative real part; the fixed point is stable.

This model is that $\text{sig}(x_{\text{JH}} - \theta_{\text{Sol}})$ value of the pseudergate alate from the soldier to a change in the ratio of the population differentiation model. In a fixed point, soldiers and alates ratio is $n_{\text{Sol}} : n_{\text{Ala}} = \gamma_{\text{Ala}} : \gamma_{\text{Sol}}$. When alates are much, the JH titer is under x_{JH}^* and $dx_{\text{JH}}/dt > 0$. When soldier are much, the JH titer is above x_{JH}^* and $dx_{\text{JH}}/dt < 0$. The fixed point is maintained through these inhibitory effects. A stable environment is maintained in a real colony through multiple suppression.

4.2 Simulation

4.2.1 Setting

The individual internal model described above was combined with a termite model to create a simulation of multiple individuals as they affect the entire internal state of the individual's behavior. We can observe changes through computational experiments.

Variables in the experiment: birth ratio, 0.15 [individual/step]; average life expectancy, 10 instar (1 instar = 100 [step]); hours of work, the average life expectancy $\times$ 10 (1000 [step]); field work, 256×256 [pixel]. One step represents the minimum time during which each individual takes some kind of action. The individual goes straight, rotates, or stops at during one step.

Each different caste population and the individual internal JH titer were recorded at each step. Caste populations of alates, soldiers, and pseudergates were recorded. Individual internal JH titer was recorded for all individuals.

4.2.2 Stability of Soldier Caste in the Colony

We reproduced the experimental facts using the simulation: the differentiation rate was increased and the number of soldiers reverted to the original when soldiers were removed. When we judged the caste ratio was stable (5000 [step]), we removed all soldiers.

Figure 5 presents results of the experiments. The model based on caste is judged as stable from the result that the number of soldiers are recovered in about 500[step]. Results show that larvae and pseudergates affect caste ratios in the colony.
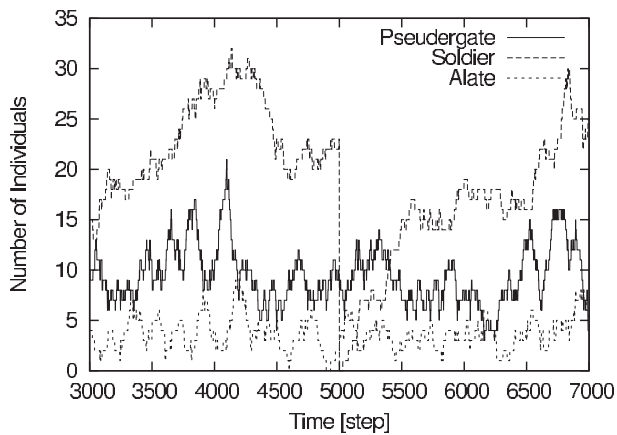
Fig. 5 Time variation of caste numbers.

4.2.3 JH Titer in Pseudergates and Differentiated Castes

The simulation result was compared to Nijhout's hypothesis [7] for purposes of recording the average of individual internal JH titer time variable and its standard deviation by each differentiate caste. Only the seventh instar pseudergates' JH titers were recorded.

Figure 6 shows results for the pseudergate seventh instar at normalized time, and the each post-caste differentiation within each individual JH average and standard deviation of the amount of time to change that record. Nijhout's experimental results and hypotheses [7] compared to soldiers and alates the match. However, pseudergates showed that there was a mismatch in the seventh instar JH amount of change. Nijhout's hypothesis hints at the nature of the actual body from facts obtained from experiments and does not show individual internal JH titer before caste differentiation. It is important that pseudergates fluctuate and be able to translate other castes with interaction in Nijhout's hypothesis.
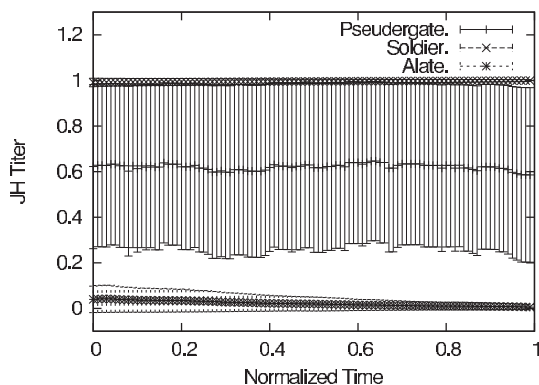

Fig. 6 Time variation of the pseudergate's JH titer and differentiated castes after molting.

5. CONCLUSION

Results of this study clarified termite caste differentiation mechanisms and termite ecology that is used to organize the entire colony. A model was created, which reflects individualsf internal states. This model was derived from two phenomena. The threshold of individual internal JH titer. The developmental process. A model that can reflect the global caste ratio change in the entire colony was built and analyzed to evaluate the individual internal model. Results of this study showed that the fixed point was consisted of caste differentiation and inhibitory effects.

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