

A Mathematical Model for the Caste Differentiation in Termite Colonies by Hormonal and Pheromonal Regulations

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Abstract: In social insects, the division of labor among castes is one of the fundamental natures for establishing social behaviors. In termites, because of their hemimetaboly, the regulations of postembryonic development should be important to regulate appropriate caste ratio in a colony. Although the caste differentiation can be triggered by social interactions among colony members, the interactions via primer pheromones and the physiological mechanisms underlying caste determination or differentiation are poorly understood. In this study, therefore, we proposed a model for the regulatory mechanism controlling caste differentiation, focusing on the physiological states and inhibitory interactions among individuals. We suggested that the two types of interactions were sufficient to enable a colony to maintain the appropriate caste ratio with the results of computer simulations based on the proposed model. The proposed model incorporates an internal physiological system like JH and ecdysone actions, together with two types of inhibitory interactions by pheromones secreted by soldiers and alates. These results would help to find primer pheromones and to infer the functions in the caste differentiation in termites.

Keywords: termite, caste differentiation, juvenile hormone, mathematical model.

1. INTRODUCTION

Termites conduct their behaviors with a group, called as colony, which includes a certain number of individuals and which dynamically produces a division of labor. Termite have groups of polymorphic individuals called castes[1](Fig. 1). Three typical castes consist of reproductives, soldiers, and workers. Division of labor by caste is called caste differentiation.

In a termite colony, here is a special stage called "pseudergate". Soldiers are normally induced from pseudergates via presoldier stage through two molting events. Pseudergates also perform "stationary molt" into the same stage, i.e. molt from pseudergate to pseudergate. Therefore, they can be regarded as the system buffer for the rapid adaptations of social systems. Polyphenism means discrete variations of phenotypes, even for the same genotype in a colony. During their postembryonic development, termite individuals do not only modify morphological characteristics but also behavioral patterns, i.e. they change nervous systems, during caste differentiation to specialize in a certain task. The caste differentiation pathway varies greatly among termite lower species[2]. Such plastic natures of post-embryonic development are thought to play important roles to adjust the colony caste ratio.

Considering the regulation of caste ratio, the caste determination and differentiation systems should be important. The caste determination is thought to take place in response to extrinsic cues, resulting in the optimal caste ratio. Although the detailed mechanisms of caste determination have not been revealed yet, interactions among colony members via chemical communication have been thought to be fundamental.

In this study, we propose a mathematical model for the

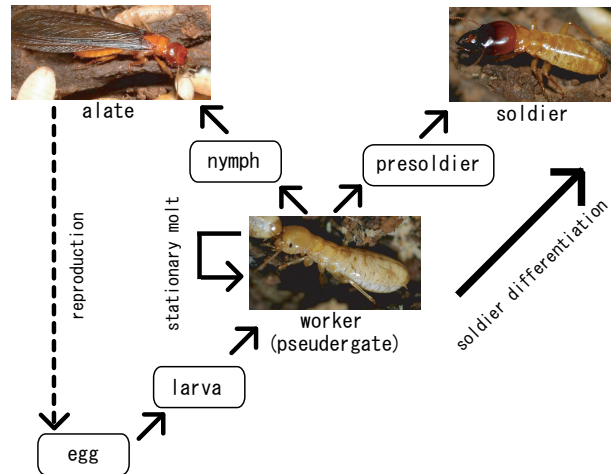


Fig. 1 Developmental pathway of damp-wood termite *Hodotermopsis sjostedti*.

caste development in lower termites, by incorporating endocrinological and ecological factors, which are responsible for the developmental regulation of caste differentiation. Furthermore, the constructed model was evaluated by the comparison of the simulation results with previous observations on the termite caste differentiation.

2. MODEL

In social interactions of termites, endocrine regulations by hormones cannot be neglected. The juvenile hormone (JH) is the most famous and important insect hormone in relation to the polyphenic development [3]. In the case of termite caste differentiation, the patterns of JH titer during intermolt stages are known to determine the caste developmental fates [4]. One of those study has

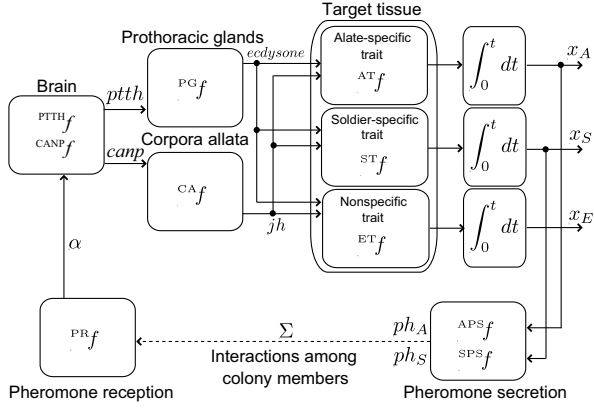


Fig. 2 Block diagram of individual's endocrine system

shown that the caste-specific traits, like mandibles of soldiers, or wings of alates, were exaggerated or reduced in the JH-dependent manners[5]. In addition, recent advances in the quantification of JH titer in termite bodies help us to understand the endocrinological regulations of caste developmental fates [6].

In proposed model, we hypothesize the endocrine system based on JH and ecdysone actions as intrinsic factors, and pheromonal communications as extrinsic factors (Fig. 2).

The state variables used in this model are defined as follows; the internal titers of ecdysone and JH are ecdysone and jh respectively. The phenotypic value is exhibited by x_{caste} ($\text{caste} = \{A, S, E\}$), which represents the amount of cell proliferations or gene expressions required for caste-specific traits. The subscripts A , S and E respectively indicate "alate", "soldier" and "others". The values for alate- and soldier-specific traits are designated by x_A , x_S , and other trait value by x_E . In addition, we hypothesized two types of pheromones, i.e. alate- and soldier-specific pheromones. The amounts released by an individual are designated as ph_A or ph_S . It is also hypothesized that colony members perceive total amount of pheromones, i.e. ph_A and ph_S , that are accumulated inside a colony, as social factors, although the neuronal mechanisms interconnecting between pheromone perceptions and brain remain to be elucidated. In this model, we hypothesized an unknown factor α , which transforms pheromonal stimuli into neuronal signals like neuropeptides such as PTTH or corpora allata neuropeptides.

The amount of secreted ecdysone and JH per unit of time is described as ^{PG}f and ^{CA}f , respectively. Ecdysone and JH are thought to activate gene expressions in the target tissues, so that the downstream gene expressions are thought to regulate caste-specific tissue development in the termite caste differentiation. Therefore, three types of caste-specific tissues are focused, two of which are alate- and soldier-specific and the other shows no caste-specificity.

While ecdysone generally activate the downstream gene expressions, JH also inhibits or activates gene expressions as well in the caste-specific manner. In the

model, it is assumed that JH inhibits the alate growth while activates the soldier growth. These assumptions are phenomenologically based on the actual experimental data on the caste-specific development[5]. This function assumes that interactions among individuals are carried out by two kinds of primer pheromones. One is secreted from soldiers and has an inhibitory effect on the soldier differentiation of other individuals. The amount of soldier-inhibition pheromone is defined as ph_S that is secreted by a soldier or a pre-soldier. By contrast, the other is secreted by alates and has an inhibitory effect on the alate differentiation of other individuals. The amount of alate-inhibition pheromone is defined as ph_A that is secreted by an alate or a nymph. During postembryonic development, an individual passes through 9 instars divided by 8 molting events. In this model, an instar period is defined as $10_{[s]}$, and an individual dies at $90_{[s]}$. During the life cycle, the 1st to 6th instar stages are thought to be larvae so that they are respectively termed as L1 to L6. The individuals at 7th instar become pseudergates (PE), when the individual is affected by pheromonal interactions. Namely, the JH profiles during the PE period depend on α that is determined by pheromone concentrations affected by colony caste-ratio.

2.1 Prothoracic gland function

We postulated a prothoracic gland function, because this gland secretes ecdysone in response to PTTH secreted from brain. The amounts of secreted ecdysone per unit of time are described as and the time evolution of ecdysone secretion is as follows;

$$^{PG}f = -\text{ecdysone} + \text{ptth}, \quad (1)$$

where ecdysone and ptth respectively mean the ecdysone and PTTH titer in the prothoracic glands. The first and second terms on the right side respectively indicate the decrement and increment of ecdysone in the prothoracic glands, which are explained by the secretion (and degradation) of ecdysone or by the synthesis activated by the PTTH signal, respectively.

2.2 Corpora allata function

In this model, we assumed that the JH secretion is controlled by the corpora allata neuropeptides signal from brain. Here, we treated the "CANP (corpora allata neuropeptides)" as the summative factor of both allatostatin and allatotropin, which stimulate the CA action. Furthermore, it is assume that the JH secretion is the only function of corpora allata. The amount of secreted JH per unit of time is described as and the time evolution of JH secretion is represented as follows;

$$^{CA}f = -jh + \text{canp}, \quad (2)$$

where jh and canp respectively mean the JH and the CANP titers inside corpora allata. The time evolution also depends on the same manner with the prothoracic gland model.

2.3 Caste-specific trait function

Three types of caste-specific tissues are focused, two of which are alate- and soldier-specific and the other shows no caste-specificity. The amount of caste-specific traits, e.g. number of cells involved in the caste-specific traits, are presented as x_{caste} , where $\text{caste} = \{A, S, E\}$ mean alate, soldier, and nonspecific characters, respectively. The proliferating rate of caste-specific trait is described as and the caste-specific trait amount x_{caste} , at time t is exhibited as follows;

$$x_{(\text{caste})} = \int_0^t {}^{(\text{caste})}Tf dt, \quad (3)$$

The frequencies of caste-specific expressions are yielded as follows;

$${}^{AT}f = \text{ecdysone} - (jh + \beta) + 0.3 \quad (4)$$

$${}^{ST}f = -\text{ecdysone} + (jh + \beta) + 0.3 \quad (5)$$

$${}^{ET}f = \text{ecdysone}, \quad (6)$$

where β shows the amount of JH that is externally induced in the following comparative simulation. The third term of right side in the equation (4-5) is given for the bias in the expression systems. This value determines the relative phenotypic amount among caste.

2.4 Function for interactions among individuals

The amount of soldier-inhibition pheromone is defined as ph_S that is secreted by a soldier or a pre-soldier. By contrast, the other is secreted by alates and has an inhibitory effect on the alate differentiation of other individuals. The amount of alate-inhibition pheromone is defined as ph_A that is secreted by an alate or a nymph. These amounts are assumed to be determined by each caste as described as follows;

$$ph_A = {}^{APS}f = x_A \quad (7)$$

$$ph_S = {}^{SPS}f = x_S \quad (8)$$

This model assumes that reproductives and soldiers release the above inhibition pheromone while only pseudergates receive the pheromones during their pheromone-sensitive period. The effect of pheromone α is described as following;

$$\begin{aligned} \alpha &= {}^{PR}f \\ &= \frac{1}{1 + \exp(-\sum ph_A)} - \frac{1}{1 + \exp(-\sum ph_S)}, \end{aligned} \quad (9)$$

The first and second term of the right side mean the inhibitory effects of alate and soldier individuals, respectively. However, the increase of alate pheromone induces the increase of alpha, which induces high JH titer resulting in the soldier induction.

2.5 Regulatory network of ecdysone and JH

Both PTTH and neuropeptides are key factors controlling the upstream of ecdysone and JH titers in termites. In order to correspond our model to the actual hormonal dynamics, the endocrine systems via ecdysone and JH are

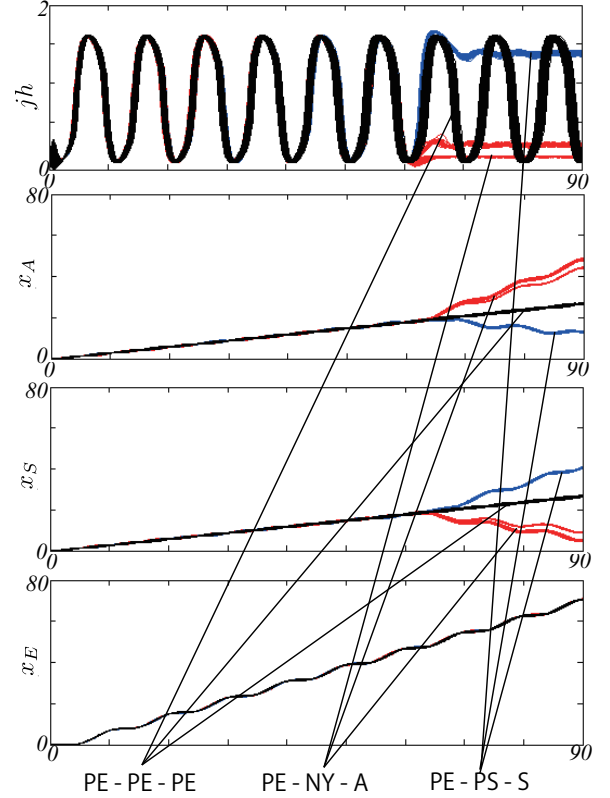


Fig. 3 Result of caste differentiation simulation

modeled to have limit cycles with variables vp and vc , which mean virtual substances controlling *PTTH* and *CANP* secretions respectively.

$$\frac{d ptth}{dt} = ptth (1 + ptth) (1 - ptth) - v_p \quad (10)$$

$$\frac{d v_p}{dt} = ptth - v_p \quad (11)$$

$$\frac{d canp}{dt} = canp (1 + canp) (1 - canp) - v_c \quad (12)$$

$$\frac{d v_c}{dt} = canp - v_c + \alpha, \quad (13)$$

where α represents the secretion frequencies for PTTH and CANP per unit time. The regulation of PTTH secretion is not affected by α . In the case of JH profiles, $\alpha=0$ induces the oscillation of JH titer. Then, the intersection of nullclines is an unstable fixed point and a limit cycle is generated around the point. In this case, the JH titer oscillates with a constant frequency.

3. SIMULATION

The life cycle of a termite individual can be depicted as Fig. 5. During postembryonic development, an individual passes through 9 instars divided by 8 molting events. In this model, an instar period is defined as 10[s], and an individual dies at 90[s]. During the life cycle, the 1st to 6th instar stages are thought to be larvae so that they are respectively termed as L1 to L6. The individuals at 7th instar become pseudergates (PE), when the individual is affected by pheromonal interactions.

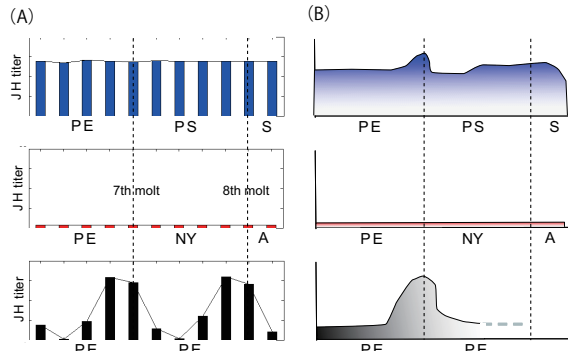


Fig. 4 JH titer level transitions: comparison between (A) proposed model and (B) Cornette model

At the time to become the 8th instar, an individual can differentiate into nymph (NY), pre-soldier (PS), or pseudergate (PE), which respectively molt into alate (A), soldier (S), or pseudergate (PE) as the 9th instar stage. Eighth- and 9th-instar pseudergates develop through stationary molts. Thus, all individuals have potential to differentiate into three different castes. In the simulation, from 0[s] to the end of simulation, L1 individuals are added one by one to a colony every 1[s]. Based on the assumptions mentioned above, each individual dies at 90[s] after birth.

In the simulation, the data for the total of 909 termite individuals was obtained during 1000[s]. The internal state of an individual was represented by the data (i.e. hormone titers, trait values) from 0[s] (birth) to 90[s] (death). The patterns of caste differentiation in response to pheromonal interactions were simulated, suggesting that the caste-ratio in a colony was maintained by the developmental fates of pseudergates, to differentiate into soldiers or alates, or to perform stationary molt to pseudergates, and by the pheromones secreted by soldiers and alates.

Figure 3 shows the simulation result, in which the time evolution of JH titer (jh) and values for alate-specific traits (x_A), soldier-specific traits (x_S), and non-specific traits (x_E) are shown. As the seventh instar (60-70[s]) is a pivotal phase differentiating into various castes, the time evolution of JH titers were trifurcated into three levels that correspond to the developmental pathways of PE-PE-PE, PE-NY-A, and PE-PS-S. At the steady state after 90 seconds, the caste-ratio in a colony converged to alate:soldier:pseudergate = 23:6:61, indicating that the caste differentiation was authentically realized and the cast ratio was maintained in the proposed model. This result suggests that stationary molts by pseudergates can be generated by the interactions balance based on the inhibitory effects by alates and soldiers on pseudergates.

The transitions of JH titer in association with the caste differentiation are summarized as follows. The JH titer continuously oscillated and the phenotypic values were increased. In the alate pathway (PE-NY-A), the JH titer converged to a low level. Then, depending on JH titer, the phenotypic value x_A increased while x_S decreased. In contrast, in the pathway (PE-PS-S), the JH titer con-

verged to a high level and the phenotypic value x_A decreased while x_S increased. Interestingly, the JH titer transitions in the simulation results (Fig. 4) correspond to the empirical data examining actual JH titer transitions[6]. On the graph of the simulation results, the bars indicate the average JH titers observed in individuals during the developmental course. The qualitative agreement between simulation results and empirical data indicates that the proposed model is appropriate at least in terms of phenotypic values and JH titer transitions.

4. DISCUSSION

In this study, we proposed a model of the caste differentiation in termites, based on the physiological and ecological data. In the proposed model, the developmental plasticity, i.e. totipotency, of pseudergates was focused and the two types of inhibitory interactions by the existence of soldiers and alates were assumed. In addition, the insect endocrine systems, mainly based on JH and ecdysone actions, were incorporated into the model.

By using computer simulations, the colony caste-ratio was appropriately regulated by the pheromonal inhibitions among colony members. Interestingly, it was shown that at least two types of pheromonal factors possessing inhibitory effects, such as those secreted from soldiers and alates, are sufficient for the caste-ratio regulation. Although the recent molecular and chemical techniques enable us to identify factors involved in hormonal and pheromonal regulations, it is still difficult to understand overall mechanisms of social systems. In that sense, mathematical approaches as shown in this study will help us to unravel unknown mechanisms controlling the caste differentiation via social interactions in social insects.

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