A Mathematical Model for Caste Differentiation in Termite Colonies (Isoptera) by Hormonal and Pheromonal Regulations

by

Yusuke Ikemoto[1], Yuki Ishikawa[2], Toru Miura[2] & Hajime Asama[1]

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 ratios 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 propose a model for the regulatory mechanism controlling caste differentiation, focusing on the physiological states and inhibitory interactions among individuals. 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. The results of computer simulations based on the proposed model suggested that the two types of interactions were sufficient to enable a colony to maintain the appropriate caste ratio. These results should help to find the primer pheromones and to infer their functions in the caste differentiation in termites.

Key-words: lower termites, caste differentiation, inhibitory pheromones, mathematical model

INTRODUCTION

In any of the eusocial insects, the divisions of labor among castes are well organized, based on interactions among colony members, via pheromonal communications (Wilson 1971, Billen & Morgan 1998). For optimized

---

[1] Department of Research into Artifacts, Center for Engineering, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba, 277-8568, Japan.

[2] Laboratory of Ecological Genetics, Graduate School of Environmental Science, Hokkaido University, N10 W5, Kita-ku, Sapporo, 060-0810, Japan.

performance of social behavior, the control of colony caste ratio is one of the most important social systems (Oster & Wilson 1978). In many social insects, it is known that the caste ratio is affected by various extrinsic factors. In ants, for example, when the predation risk is high, the proportion of major workers rises (Gordon 1996, Harvey *et al.* 2000, Passera *et al.* 1996). Also, in termites, temperature and seasonality affect the caste differentiation, resulting in the change of colony caste ratio (Roisin 2000).

The flexible caste differentiation pathways are thought to be adaptive under unstable circumstances. In that sense, the developmental plasticity of individuals is very important (Nijhout & Wheeler 1982, Miura 2005). In some species of termites, relatively "lower" species, a false-worker caste, termed "pseudergate", plays important roles (Grassé & Noirot 1947), for two reasons; they function as workers, like engaging in foraging and/or nursing tasks, in addition to that pseudergates possess "totipotency", i.e. the ability to differentiate into any other castes including reproductives and soldiers. They also perform 'stationary molts' into the same stage, i.e. molt from pseudergate to pseudergate (Roisin 2000, Miura 2005). Such plastic natures of post-embryonic development are thought to play important roles in adjusting 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 (Nijhout & Wheeler 1982, Billen & Morgan 1998). For example, the existence of solders (or reproductives) is known to inhibit the soldier (or reproductive) differentiations from other colony members (Bordereau 1985). Those inhibitory interactions are thought to be based on chemicals secreted from soldiers (or reproductives). Such chemicals that affect physiological conditions of recipients are designated as "primer pheromones" although only a few chemicals have so far been identified (Henderson 1998). These chemicals can be transferred among individuals through trophallaxis and/or grooming behaviors (McMahan 1969, Machida *et al.* 2001).

In addition to social interactions, 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 (Nijhout 1994, Hartfelder & Emlen 2005). In the case of termite caste differentiation, the patterns of JH titer during intermolt stages are known to determine the caste developmental fates (Lüscher 1960, Howard & Haverty 1979, Nijhout & Wheeler 1982). It is also known that lots of JH analogs (JHAs) can induce specific caste differentiation, especially soldier differentiation (Howard & Haverty 1979). Some of those studies have shown that the caste-specific traits, like mandibles of soldiers, or wings of alates, were exaggerated or reduced in JH-dependent manners (Miura *et al.* 2003, Miura 2005). In addition, recent advances in the quantification of JH titer in termite bodies help us to understand the endocrinological regulations of caste developmental fates (Park & Raina 2005, Cornette *et al.* 2008; Fig. 1).

Although some works proposing methematical models for caste differentiation in social insects (e.g. Naug & Gadagkar 1999), few models have been proposed focusing on the plastic developmental systems in the termite

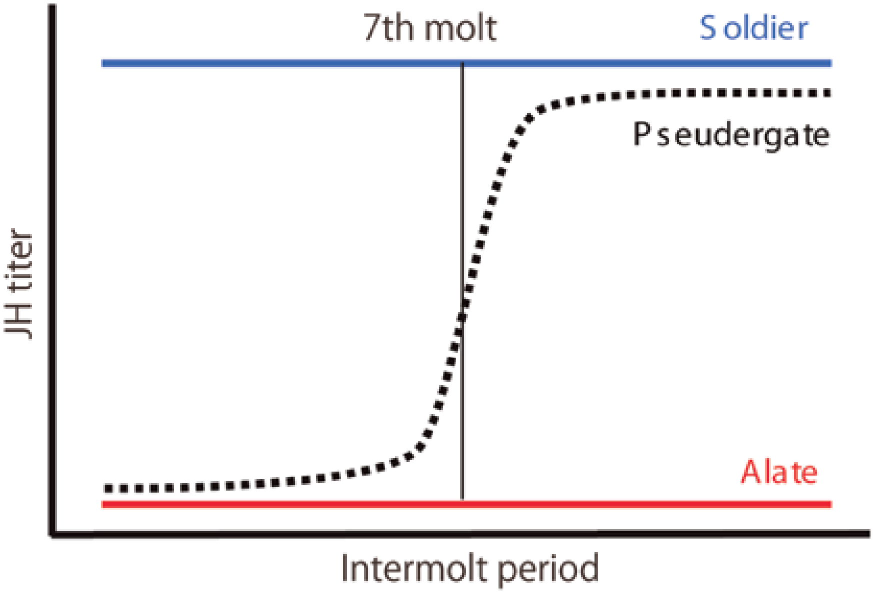

Fig. 1 . JH titer transitions during an intermolt stage, quantified in a lower termite species, *Hodotermopsis sjostedti* (Cornette *et al.* 2008). The constant high JH titer during the period induces soldier differentiation, while low titer induces alate differentiation. If the JH titer changes from low to high level during this period, those individuals molt into pseudergates, i.e. they perform stationary molts (dot-line).

caste differentiation. In this study, we propose a mathematical model for the 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 termite caste differentiation.

MODEL

The purpose of this study is to construct a mathematical model for termite caste differentiation, incorporating ontogeny, developmental plasticity and phenotypic changes. In this model, we hypothesize the endocrine system based on JH and ecdysone actions as intrinsic factors, and pheromonal communications as extrinsic factors (Fig. 2).

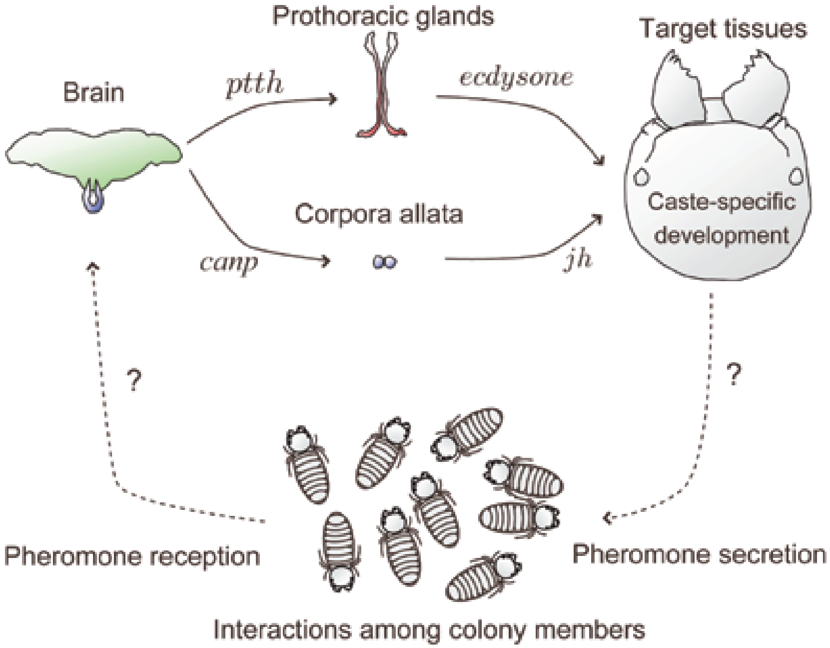

Fig. 2. Diagram showing the termite endocrine system in relation to the caste differentiation. PTTH signal secreted from brain facilitates ecdysone secretion. Ecdysone secreted from prothoracic glands is the one of the major hormones which regulates molting events in insects. In contrast, it is generally known that juvenile hormone secreted from the corpora allata negatively affects insect development. The secretion is controlled by neuropeptides from the brain. Colony members can perceive colony states such as caste ratio, through interactions among individuals (dotted arrows).

In response to the secretion of PTTH (prothoracicotropic hormone) from the brain, ecdysone is secreted from prothoracic glands (or molt glands) and the ecdysone pulse in hemolymph controls the timing of molting events and metamorphosis; i.e. ecdysone generally promotes exuviations (Nijhout 1994). On the other hand, juvenile hormone is secreted from the corpora allata, which receive neuropeptides from the brain, termed allatotropins and allatostatins. In general, JH is thought to be a status quo hormone that makes insects remain in juvenile stages (Riddiford 1996).

The crosstalk between ecdysone and JH actions coordinate insect development, although the detailed mechanism underlying the interactions between the two hormonal actions has yet to be elucidated (Dubrovsky 2005). Whereas the pathways downstream of the JH actions in termites are still unclear, it is definitely expected that JH would eventually stimulate and/or repress gene expressions of developmental factors (Noirot 1991, Miura 2001). Probably, some cooperative and competitive actions of ecdysone and JH make some temporal patterns that would eventually lead the specific differentiation patterns of termite castes. The caste-specific hormonal patterns may be generated by extrinsic factors, including social interactions among colony members probably via pheromonal communications (Vargo 1998, Henderson 1998). Some neuronal mechanisms are expected to reside in between pheromone receptions and hormonal changes (Nijhout 1994). As shown in Fig. 2, such feedback loops are expected to control the caste ratio in a termite colony.

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} ($caste=\{A, S, E\}$), 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 values 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 the 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.

Prothoracic gland function

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

$${}^{PG}f = {}^{d}\!/_{dt}\, ecdysone$$

and the time evolution of ecdysone secretion is as follows;

$${}^{PG}f = -ecdysone + ptth \qquad (1)$$

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.

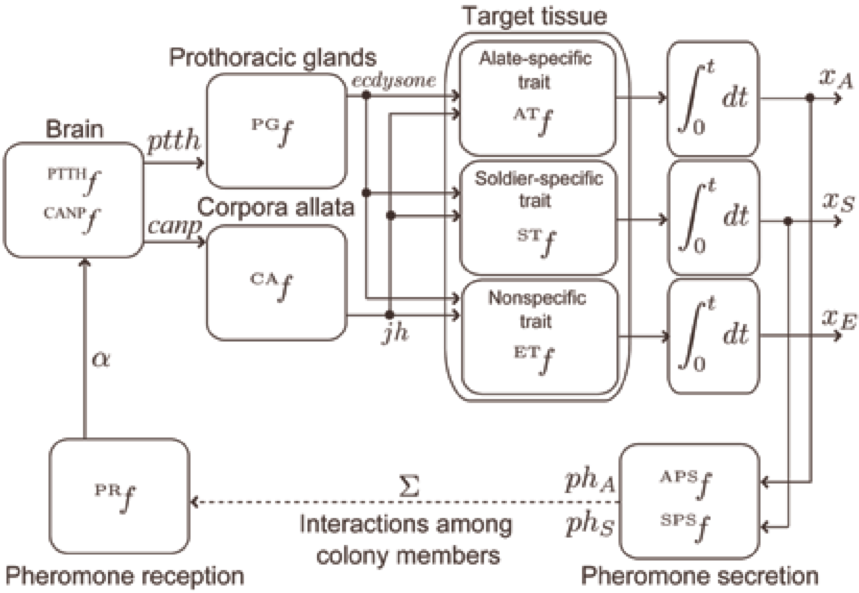

Fig. 3. Block diagram indicating a model for the endocrine system in a termite individual. Boxes indicate functions of internal tissues, while solid arrows show amounts of signaling factors like hormones, pheromones, and phenotypical values. A dotted arrow means the summation of pheromonal interactions including total amounts of pheromones

Corpora allata function

Similar to the ecdysone secretion, a corpora allata model was also constructed, because JH is secreted by the corpora allata by being stimulated by some neuropeptide hormone, which generally include allatostatin that inhibits the JH secretion, and allatotropin that stimulates the corpora allata to secrete JH (Nijhout 1994), although such neuropeptides have been identified only in a termite species (Yagi *et al.* 2008). In this model, we assumed that the JH secretion is controlled by the corpora allata neuropeptide signal from the 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 assumed that JH secretion is the only function of the corpora allata. The amount of secreted JH per unit of time is described as

$$^{CA}f = {}^{d}\!/_{dt}\, jh$$

and the time evolution of JH secretion is represented as follows;

$$^{CA}f = -jh + canp \qquad (2)$$

where *jh* and *canp* respectively mean the JH and the CANP titers inside the corpora allata. The time evolution also depends on the same manner with the prothoracic gland model. The first and second terms on the right side mean the decrement and increment of JH in the corpora allata, respectively.

Caste-specific trait function

Ecdysone and JH are thought to activate gene expressions in the target tissues (Henrich 2005, Goodman & Granger 2005), so that the downstream gene expressions are thought to regulate caste-specific tissue development in the termite caste differentiation (Miura 2004, 2005).

Therefore, 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 $caste = \{A, S, E\}$ mean alate, soldier, and nonspecific characters, respectively. The proliferating rate of caste-specific trait is described as

$${}^{d}\!/_{dt}\, x_{caste} = {}^{(caste)T}f$$

and the caste-specific trait amount x_{caste}, at time t is exhibited as follows;

$$x_{(caste)} = \int_0^t {}^{(caste)T}f\,dt \qquad (3)$$

While ecdysone generally activates the downstream gene expressions, JH also inhibits or activates gene expressions as well in a caste-specific manner. In the model, it is assumed that JH inhibits alate growth while it activates soldier growth. These assumptions are phenomenologically based on actual experimental data on the caste-specific development (e.g. Miura *et al.* 2003). In this model, we also tried to simulate experiments that artificially induced soldier differentiation by the topical application of JH (Miura *et al.*2003). Thus, the frequencies of caste-specific expressions are yielded as follows;

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

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

$$^{ET}f = ecdysone \qquad (6)$$

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 amounts among castes.

Function for interactions among individuals

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 that is secreted by an alate or a nymph is defined as ph_A. These amounts are assumed to be determined by each caste as described as follows;

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

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

Some empirical studies in termites have reported that individuals differentiated to a specific caste inhibit the differentiation to the same caste (reviewed in Henderson 1998). 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;

$$\alpha = {}^{PR}f = \frac{1}{1+\exp(-\sum ph_A)} - \frac{1}{1+\exp(-\sum ph_S)} \qquad (9)$$

where $\sum$ means the summation of ph_A or ph_S within an individual. The reception of each pheromone consists of sigmoid function because the pheromone receptions are assumed to be saturated. 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. Namely, the alate pheromone has the positive effect on the soldier differentiation, while the soldier pheromone does the opposite.

Regulatory network of ecdysone and JH

Both PTTH and neuropeptides are key factors controlling the upstream of ecdysone and JH titers in termites. Although it is not clear how those upstream factors are secreted from brain, both of them are generally secreted as pulses at the time of moltings in insects (Nijhout 1994). Therefore, this model assumes that secretions of PTTH and neuropeptides show patterns with simple dynamical systems, inducing molting events. The JH titer is affected by α, that is a variable determined by the pheromonal interactions among individuals.

In order to correspond our model to the actual hormonal dynamics, the endocrine systems via ecdysone and JH are modeled to have limit cycles with variables v_p and v_c, which mean virtual substances controlling PTTH and CANP secretions respectively. Thus, the following equations are proposed to represent the pulse patterns.

$$\frac{d}{dt}ptth = {}^{PTTH}f = ptth(1+ptth)(1-ptth) - v_p \qquad (10)$$

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

$$\frac{d}{dt}canp={}^{CANP}f=canp(1+canp)(1-canp)-v_c \qquad (12)$$

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

where ${}^{PTTH}f$ and ${}^{CANP}f$ represent the secretion frequencies for PTTH and CANP per unit time. To explain the behaviors of their dynamical systems for PTTH and CANP, a phase plane is illustrated in Fig. 4. The cubic curve indicates the nullclines of equations (10) and (12). The straight lines also indicate the nullclines of equation (13) in cases of *α=-1*, *α=0*, and *α=1* from the left. The intersections of nullclines are the fixed points at which the PTTH and CANP values can converge.

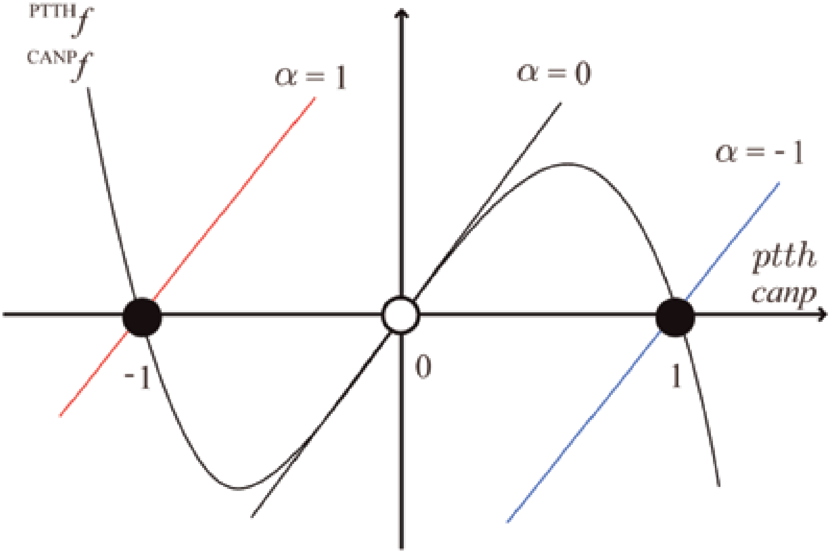

Fig. 4. A phase plane determining the time evolution of PTTH and CANP titers, to generate the oscillations of ecdysone and JH titers. The cubic curve indicates the nullclines of equations (10) and (12). The straight lines also indicate the nullclines of equation (13) in cases of *α*=-1, *α*=0, and *α*=1 from the left. When *α*=-1 and *α*=1, the intersections of nullclines are stable fixed points. Then, the canp converges to -1 or 1, respectively. It means that the JH secretion is maintained around high (or low) level at *α*=1 (or *α*=-1) with canp input. When *α*=0, the intersection of nullcline is an unstable fixed point and a limit cycle is generated around the fixed point. In this case, the JH titer oscillates with constant frequency. When the JH titer is oscillating at *α*=0, the ecdysone titer also oscillates regardless of the value of *α* because the PTTH titer does not depend on *α*. It represents the pattern of ecdysone titer that determines molt timings.

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. It mimics the JH titer profiles observed in many insects (Nijhout 1994). This oscillation pattern of JH affects the caste-specific traits (4-6), resulting in the induction of pseudergates. On the other hand, in case of $\alpha=-1$ or $\alpha=1$, the intersections of nullclines are stable fixed points, when the *canp* eventually converges to -1 or 1, respectively. It means that the JH titer is maintained around high (or low) level at $\alpha=1$ ($\alpha=-1$) with CANP input. In these cases, the functions of caste-specific traits are also affected; high and low JH titers induce soldiers and alates, respectively.

Life cycle and colony size definition

Based on empirical studies (e.g. Miura *et al.* 2000, 2004), 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. Namely, the JH profiles during the PE period depend on α as explained in equation (9) that is determined by pheromone concentrations affected by colony caste-ratio.

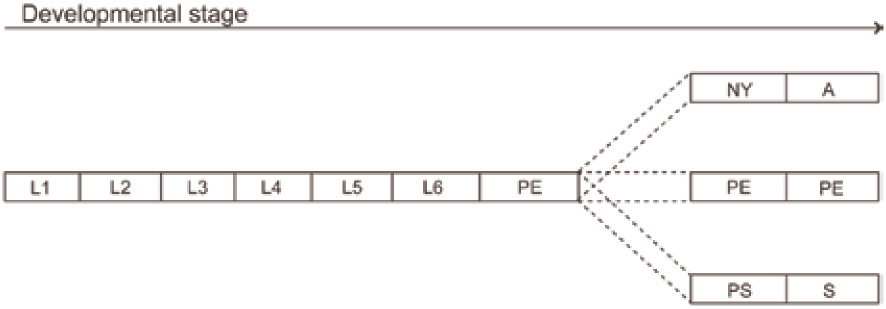

Fig. 5. Caste differentiation pathways during an individual life cycle. Developmental stages are divided by moltings. L1 – L6 indicate the 1st to 6th larval instars, and the abbreviations, i.e. PE, NY, A, PS and S, indicate pseudergate, nymph, alate, pre-soldier and soldier stages, respectively. The developmental pathways are classified into three pathways to differentiate into alates or soldiers, or go through stationary molts to remain pseudergates.

At the 8th instar, an individual can differentiate into a nymph (NY), presoldier (PS), or psuedergate (PE), which respectively molt into alates (A), soldiers (S), or pseudergates (PE) as the 9th instar stage. Eighth- and 9th-instar pseudergates develop through stationary molts. Thus, all individuals have the potential to differentiate into three different castes. The differentiated castes possess caste-specific traits with x_{caste}, which represents the trait amount exaggerated in caste-specific manners. 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. Therefore, the colony size gradually increases from $0_{[s]}$ to $90_{[s]}$, while the number of individuals in the colony is constantly *90* after *90* seconds. The total time of the simulation is $1000_{[s]}$.

SIMULATION RESULTS

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). Two types of simulation were carried out. Firstly, 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 a stationary molt to pseudergates, and by the pheromones secreted by soldiers and alates. Secondly, an empirical study focusing on the intercaste induction by a JH analog (Miura *et al.* 2003) was simulated, by assuming a parameter β that represents the amount of applied JH in equations 4-6. Comparing the simulation results with the empirical data, the adequacy of proposed model was evaluated.

Colony simulation

Fig. 6 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 ($60\text{-}70_{[s]}$) there 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. In addition, the transition from pseudergate to pseudergate (PE-PE-PE) was also represented, although only two types of inhibitory pheromones were given. This suggests that stationary molts by pseudergates can be generated by the interactions balance based on the inhibitory effects by alates and soldiers on pseudergates.

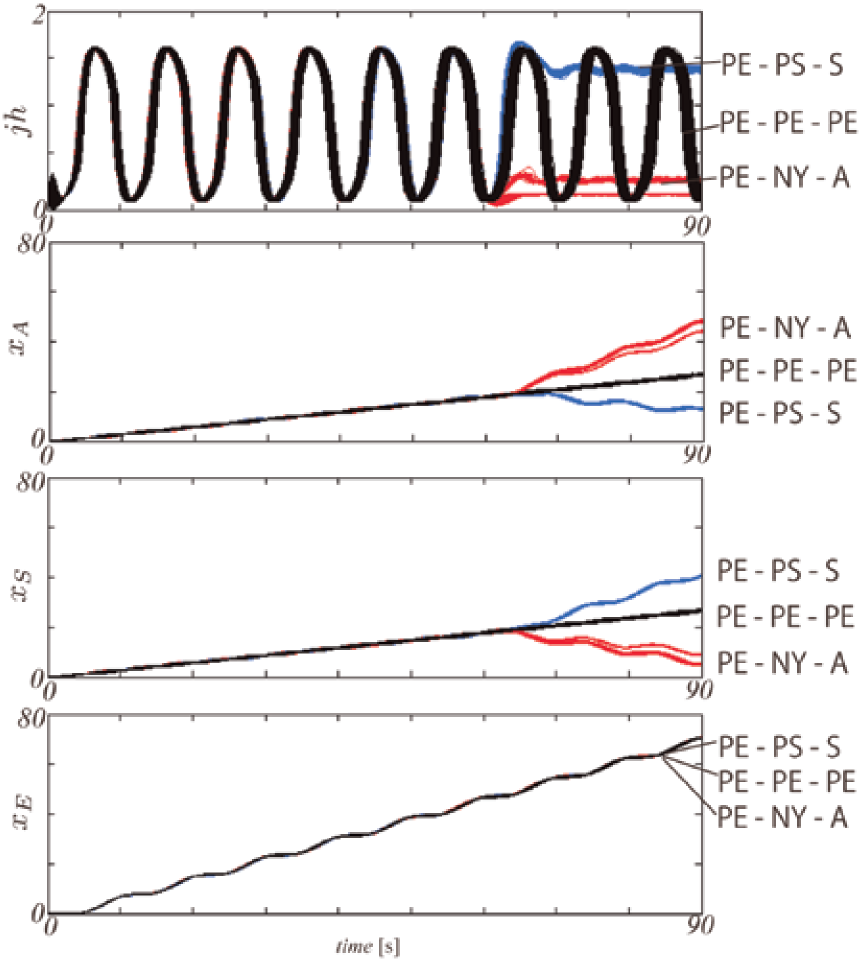

Fig. 6. Simulation results showing individuals' internal states during postembryonic development. The graphs show the time evolutions of JH titer jh and each phenotypic value of xA, xS, and xE of all simulated individuals. At 7th instar (60-70[s]), the critical period in which caste fates are determined, the JH titer trifurcates into PE-PE-PE, PE-NY-A, and PE-PS-S pathways.

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 converged 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. 7) correspond to the empirical data examining actual JH titer transitions (Cornette *et al.* 2008). 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.

Induction of intercastes by JH application

Based on the previous empirical studies showing that topical applications of JH analog can induce intercastes with intermediate phenotypes between

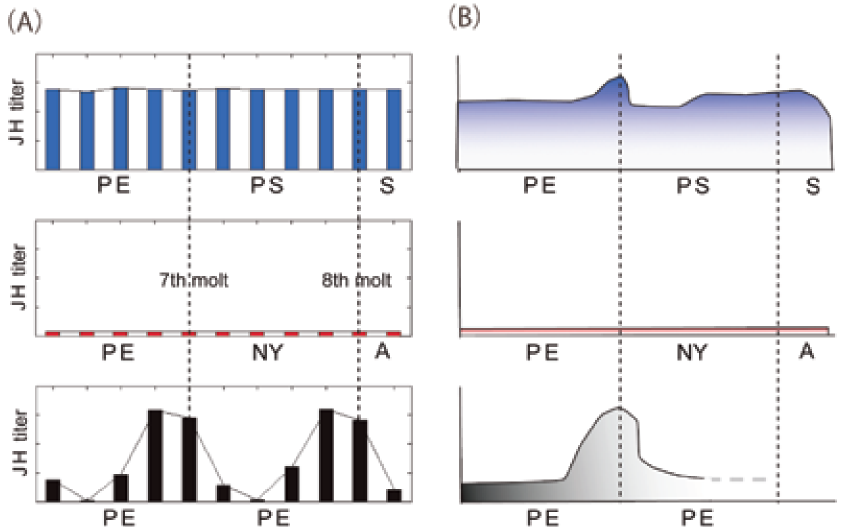

Fig. 7. The comparisons of JH profiles during the caste differentiation between simulation results and empirical data; (A) simulation results calculated with the proposed model, (B) experimental data based on Cornette *et al.* (2008). Both graphs show the time evolutions of JH titer from 6th molt to death. Dotted lines show moltings. In the graph of the simulation results (A), the bars show the averages of JH titer among individuals. Close agreement of the simulation results with empirical data is shown from a qualitative standpoint.

soldiers and alates (Miura *et al.* 2003), the simulation of intercaste induction was carried out. This attempt also confirms the adequacy of the proposed model. As in the actual experiments (Miura *et al.* 2003), nymphal individuals were picked up in the midst of above simulation, when the additional JH (β) was applied. This situation is explained by the equations (4) and (5). As the simulation result, phenotypic value x_S increased depending on the increase of β (Fig. 8A). If the phenotypic value x_S was regarded as the mandibular length and x_A as the eye diameter, the resultant phenotypes qualitatively corresponded to the intercastes obtained in the empirical study (Miura *et al.* 2003); NY, SWA (shrunk-winged alate), LWPS (long-winged presoldier), SWPS (short-winged presoldier), WSPS (wing-budded presoldier), by the conditions set to $\beta=0.0$, $\beta=0.4$, $\beta=0.8$, $\beta=1.2$, and $\beta=1.6$, respectively. These results show the phenotypic regulations of caste-specific growth by JH and the trade-off relationships between soldier- and alate-specific traits in intercastes are properly modeled, as shown in Fig. 8B.

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.

In terms of endocrinological regulations, we postulated caste-specific trait expressions depending on the JH and ecdysone actions, so that in the model, the caste phenotypes are generated based on equations (4-6). However, the actual endocrine systems in termite bodies might be more complicated. Therefore, to evaluate the validity of the proposed model, we simulated the intercaste induction by extra addition of JH titer, and compared the results with empirical data (Miura *et al.* 2003). As the result, the adequacy of the model was supported.

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

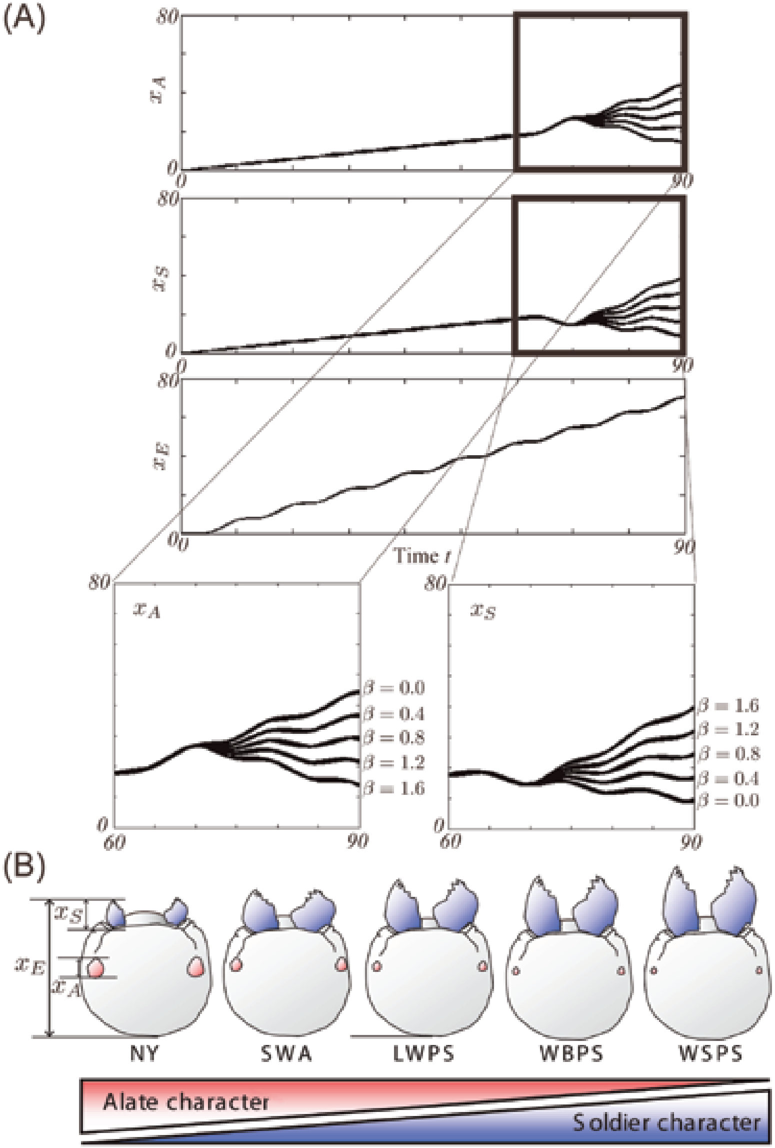

Fig. 8. Simulation results for the intercaste induction by adding extra JH titer during postembryonic development. (A) Time evolutions of phenotypic values xA, xS, and xE. The simulation conditions are the same as previously mentioned. In this simulation, extra JH (β) was added to nymphs according to equations (4) and (5). As the amount of β increases, the phenotypic value xS increases while xa decreases. (B) Resultant phenotypes of intercastes, showing intermediate sizes of mandibles and compound eyes in case of β=0.0, β=0.4, β=0.8, β=1.2, and β=1.6. These results also correspond well to an empirical study (Miura *et al.* 2003).

the caste-ratio regulation. Considering actual termite societies, there should be more complicated interactions among colony members under various ecological circumstances, so that more empirical and experimental data would be required to understand the social-regulatory systems in detail.

Therefore, to obtain deeper insights into the endocrine mechanisms affecting caste differentiation in termites, other endocrinological and pheromonal factors should be incorporated into future studies. Although the current 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 caste differentiation via social interactions in social insects.

ACKNOWLEDGMENTS

We would like to thank K. Kawabata, S. Koshikawa, R. Cornette, S. Yano, and M. Ikeda for useful comments and discussions. This research was supported by a Grant-in-Aid for Scientific Research on Priority Areas "Emergence of Adaptive Motor Function through Interaction between Body, Brain and Environment" (No. 20033002), and by a Grant-in-Aid for Scientific Research for Young Scientists (S) (No. 21677001) from the Japanese Ministry of Education, Culture, Sports, Science and Technology.

REFERENCES

Billen, J. & E. D. Morgan. 1998. Pheromone communication in social insects: sources and secretions. In R. K. V. Meer, M. D. Breed, K. E. Espelie & M. L. Winston (eds.). Pheromone Communication in Social Insects : Ants, Wasps, Bees, and Termites. Westview Press, Boulder, pp. 3-33.

Bordereau, C. 1985. The Role of Pheromones in Termite Caste Differentiation. In J. A. L. Watson, B. M. Okot-kotber & C. Noirot (eds.). Caste Differentiation in Social Insects. Pergamon Press, Oxford, pp. 221-226.

Cornette, R., H. Gotoh, S. Koshikawa & T. Miura 2008. Juvenile hormone titers and caste differentiation in the damp-wood termite *Hodotermopsis sjostedti* (Isoptera, Termopsidae). J Insect Physiol 54: 922-930.

Dubrovsky, E. B. 2005. Hormonal cross talk in insect development. Trends Endocrinol Metab 16: 6-11.

Goodman, W. & N. Granger. 2005. The juvenile hormones. In L. I. Gilbert, K. Iatrou & S. S. Gill (eds.). Comprehensive Molecular Insect Science Elsevier, Oxford, pp. 319-408.

Gordon, D. M. 1996. Soldier production under threat. Nature 379: 583 - 584.

Grassé, P. P. & C. Noirot 1947. Le polymorphisme social du termite à cou jaune (*Calotermes flavicollis* F.). Les faux-ouvriers ou pseudergates et les mues régressives. C.R. Acad. Sci. 224: 214–221.

Hartfelder, K. & D. Emlen. 2005. Endocrine control of insect polyphenism.. In L. I. Gilbert, K. Iatrou & S. S. Gill (eds.). Comprehensive Molecular Insect Science. Elsevier, Oxford, pp. 651–703.

Harvey, J. A., L. S. Corley & M. R. Strand 2000. Competition induces adaptive shifts in caste ratios of a polyembryonic wasp. Nature 406: 183-186.

Henderson, G. 1998. Primer pheromones and possible soldier caste influence on the evolution of sociality in lower termites. In R. K. V. Meer, M. D. Breed, K. E. Espelie & M. L. Winston (eds.). Pheromone Communication in Social Insects : Ants, Wasps, Bees, and Termites. Westview Press, Boulder, pp. 314-330.

Henrich, V. 2005. The Ecdysteroid Receptor. In L. I. Gilbert, K. Iatrou & S. S. Gill (eds.). Comprehensive Molecular Insect Science. Elsevier, Oxford, pp. 243-285.

Howard, R. & M. Haverty 1979. Termites and Juvenile Hormone Analogues: A Review of Methodology and observed effects. Sociobiol 4: 269-278.

Lüscher, M. 1960. Hormonal control of caste differentiation in termites. Ann NY Acad Sciw 89: 549-563.

Machida, M., O. Kitade, T. Miura & T. Matsumoto 2001. Nitrogen recycling through proctodeal trophallaxis in the Japanese damp-wood termite *Hodotermopsis japonica* (Isoptera, Termopsidae). Insect Soc 48: 52-56.

McMahan, E. A. 1969. Feeding Relationships and Radioisotope Techniques. In K. Krishna & F. M. Weesner (eds.). Biology of Termites. Academic Press, New York, pp. 387-406.

Miura, T. 2001. Morphogenesis and gene expression in the soldier-caste differentiation of termites. Insect Soc 48: 216-223.

Miura, T. 2004. Proximate mechanisms and evolution of caste polyphenism in social insects: From sociality to genes. Ecol Res 19: 141-148.

Miura, T. 2005. Developmental regulation of caste-specific characters in social-insect polyphenism. Evol Dev 7: 122-129.

Miura, T., Y. Hirono, M. Machida, O. Kitade & T. Matsumoto 2000. Caste developmental system of the Japanese damp-wood termite *Hodotermopsis japonica* (Isoptera : Termopsidae). Ecol Res 15: 83-92.

Miura, T., S. Koshikawa, M. Machida & T. Matsumoto 2004. Comparative studies on alate wing formation in two related species of rotten-wood termites: *Hodotermopsis sjostedti* and *Zootermopsis nevadensis* (Isoptera, Termopsidae). Insect Soc 51: 247-252.

Miura, T., S. Koshikawa & T. Matsumoto 2003. Winged presoldiers induced by a juvenile hormone analog in *Zootermopsis nevadensis*: Implications for plasticity and evolution of caste differentiation in termites. J Morphol 257: 22-32.

Naug, D. & R. Gadagkar 1999. Flexible division of labor mediated by social interactions in an insect colony-a simulation model. J Theor Biol 197: 123-133.

Nijhout, H. F. 1994. Insect Hormones. Princeton Univ Press, Princeton.

Nijhout, H. F. & D. E. Wheeler 1982. Juvenile-Hormone and the Physiological-Basis of Insect Polymorphisms. Q Rev Biol 57: 109-133.

Noirot, C. 1991. Caste Differentiation in Isoptera - Basic Features, Role of Pheromones. Ethol Ecol Evol: 3-7.

Oster, G. F. & E. O. Wilson. 1978. Caste and Ecology in the Social Insects. Princeton University Press, Princeton.

Park, Y. I. & A. K. Raina 2005. Regulation of juvenile hormone titers by soldiers in the Formosan subterranean termite, *Coptotermes formosanus*. J Insect Physiol 51: 385-391.

Passera, L., E. Roncin, B. Kaufmann & L. Keller 1996. Increased soldier production in ant colonies exposed to intraspecific competition. Nature 379: 630−631.

Riddiford, L. M. 1996. Juvenile hormone: The status of its "status quo" action. Arch Insect Biochem 32: 271-286.

Roisin, Y. 2000. Diversity and Evolution of Caste Patterns. In T. Abe (ed.) Termites: Evolution, Sociality, Symbioses, Ecology. Kluwer academic publishers, Dordrecht, pp. 95-119.

Vargo, E. L. 1998. Primer pheromones in ants. In R. K. V. Meer, M. D. Breed, K. E. Espelie & M. L. Winston (eds.). Pheromone Communication in Social Insects : Ants, Wasps, Bees, and Termites. Westview Press, Boulder, pp. 293-313.

Wilson, E. O. 1971. The Insect Societies. The Belknap Press of Harvard University Press, Cambridge.

Yagi, K. J., K. L. Elliott, L. Teesch, S. S. Tobe & B. Stay 2008. Isolation of cockroach Phe-Gly-Leu-amide allatostatins from the termite *Reticulitermes flavipes* and their effect on juvenile hormone synthesis. J Insect Physiol 54: 939-948.