



Soldier Production Strategy in Lower Termites: From Young Instars or Old Instars?

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We constructed a mathematical model to explain from which instars soldiers should be produced to maximize the growth rate of a termite colony. The model is based on the demography of the lower termite's colony: many of them feed inside the nest. The model predicts the following: (1) When the colony is young (it still has enough food and needs a high ratio of soldiers to workers) it will produce soldiers from young instars. (2) When the colony is old (it does not have enough food any more and needs a lower ratio of soldiers to workers) it will produce soldiers from old instars. This prediction fits well with the fact investigated by past empirical researches. With the samples of colonies of *Neotermes koshunensis*, we measured the antennal joint number of soldiers of each colony. We plotted the antennal joint number (1) of the average and (2) of the maximum one for each colony, against the total number of colony members. For both in each colony, we confirmed the consistency between the model and the samples: *as the colony matures, it produces soldiers from older instars*. The model also explains why higher termites produce soldiers from fixed instars. Their life style, in which they go outside to collect food, does not require a change in their soldier production strategy.

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Introduction

Caste differentiation is a major phenomenon, which helps to reveal the adaptive meaning of the social organization of eusocial insects (Oster & Wilson, 1978). Because of the existence of sterile castes, which is an essential trait of eusociality (Wilson, 1971), many theoretical researches have tackled how sterile castes can evolve and be maintained in general social

insects (Hamilton, 1964; Alexander, 1974; Charnov, 1978). This research trend has prevailed also in termites (Bartz, 1979; Higashi *et al.*, 1991, 1992; Roisin, 1994). In many species of the Hymenoptera, soldier caste is rare, and there appear small distinct differences between workers and soldiers in their morphology and function. These tendencies might conceal the significance and importance of the existence of a soldier, not as the sterile caste but as the defender for the colony. The soldier is, however, an essential component in termite societies, and needs more specific attention, because all termites satisfy the condition of eusociality, not by the existence of sterile workers but by the existence of sterile soldiers (but see Sands, 1972;

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Miller, 1984; Myles, 1986). Various defense mechanisms of termite soldiers (Prestwich, 1984), and recent discoveries of soldiers in some animal societies such as aphids (Aoki, 1977), thrips (Crespi, 1992) and shrimps (Duffy, 1996), reveal the importance of soldiers. Ecological and genetic factors promoting the evolution of soldiers and workers seem to be different (Yamamura, 1993).

Termites produce soldiers developing from alate line or apterous line. Lower termites tend to produce soldiers from young instars when the colony is incipient, and from old instars as time passes (Watson *et al.*, 1977; Sewell & Watson, 1981; Watson & Sewell, 1981, 1985; Noirot 1985a; Renoux, 1985; Noirot & Pasteels, 1987; Roisin & Pasteels, 1991). This phenomenon was discussed theoretically only by Shellman-Reeve (1997), focusing on the life history of individual colony members.

Our present aim is to make a mathematical model, based on the ecology and demography of the colony, in order to predict who should become the soldier for the colony. Colony members always need soldiers to defend themselves, so they must select the best individuals as soldiers at any time. For simplicity, we compare two strategies, “young soldier production strategy” and “old soldier production strategy”, regarding the growth rate of the colony as the fitness of each strategy. We assume that if young soldier production strategy shows a higher growth rate than old soldier production strategy, the colony should produce soldiers from young instars, and vice versa.

One-piece-type termites (Abe, 1987), including all genera in Termopsidae, most genera in Kalotermitidae and one genus in Rhinotermitidae, make their nests in a piece of wood, which also serves as their food. Unless they molt to alates and start new colonies, they spend their entire life as instars inside the nest. Most instars do not molt to alates but work for the colony, until the colony matures (Zimmerman, 1983; Lenz, 1994; Shellman-Reeve, 1997). During this period, deaths of workers and soldiers can be regarded as energy or labor debit, rather than a destruction of reproductive agents, as in ants (Hölldobler & Lumsden, 1980). Until the colony matures, the main interest for the colony

members is to have a high population growth rate, so that the colony can become mature within a short time to avoid accidental death of the colony, and will produce many alates after it matures. The colony size does not increase so much after maturation, and it does not need more soldiers (Luykx, 1993). This is why we regard the population growth rate as the fitness of the colony, for considering the soldier production strategy.

Generally speaking, collecting whole members of a colony in ants and termites is quite difficult, except for some species of termites, which nest in dead parts of living trees (Shellman-Reeve, 1994). We have the whole members (including eggs in incipient colonies) of some colonies of *Neotermes koshunensis* (Kalotermitidae) which nest in the dead branches of living trees in Okinawa Island, collected by Maki & Uetzu during 1978–1979 (Maki, 1980). Because of their oldness, we cannot use some colonies. We have to test the colonies, which can potentially take both soldier production strategies, that is, which have both young instars and old instars. Therefore, we excluded the incipient colonies of less than 100 colony members, and use the other 18 colonies to test the consistency of our model with these samples. *N. koshunensis*, with other species of Kalotermitidae and Termopsidae, is a proper material to study this topic, because it has a very flexible social system; newly born individuals seem to choose their best fitness option (soldier, pseudergate, neotenic or alates) in response to social or resource conditions (Shellman-Reeve, 1997).

Description of the Model

In order to formulate the model, we consider a colony as constituting three age classes,—“young instars”, “old instars” and “grown instars”—and two castes,—“workers” and “soldiers” (see Fig. 1). Young instars become old instars, old instars become grown instars, and grown instars disappear at the next time step. Workers serve the colony, contributing to produce and care for new eggs, which become young instars. Soldiers are produced to defend other colony members, mainly workers. As shown in Fig. 1a, in young soldier production

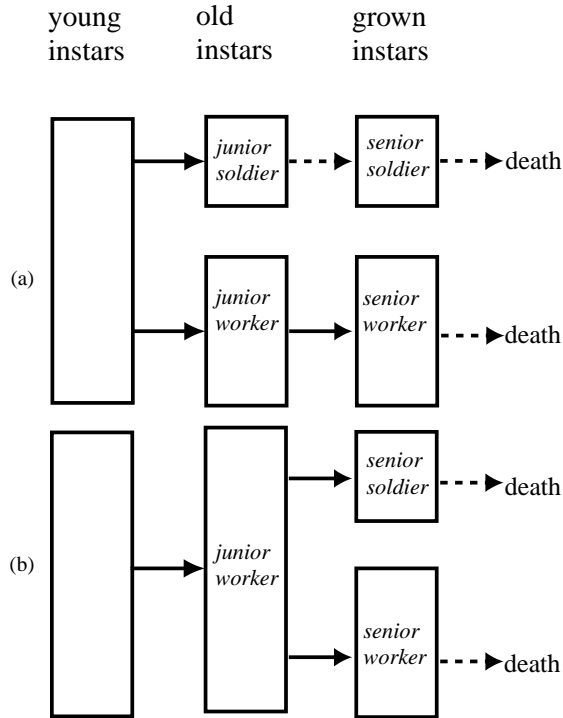


FIG. 1. (a) Scheme of the demographic model of young soldier production strategy. Young instars become junior soldiers or junior workers at the next time step. Junior soldiers become old soldiers while junior workers become senior workers at the next time step. Both senior soldiers and senior workers disappear at the next time step. (b) Scheme of the demographic model of old soldier production strategy. Young instars become junior workers at the next time step. Junior workers become senior soldiers or senior workers at the next time step. Both senior soldiers and senior workers disappear at the next time step. In both figures, arrows mean the pass of time: solid arrows, with molting; dotted arrows, without molting.

strategy, soldiers depart from the workers line at the young instars stage, while as shown in Fig. 1(b), in old soldier production strategy, soldiers depart from the workers line at the old instars stage. By this difference, two strategies are distinguished. The amount of soldiers produced depends on the strength of each soldier and the total number of workers to be defended.

Workers are divided into junior workers and senior workers based on their age stage, which is in old instars or in grown instars. The number of junior workers and senior workers at time step t is $W_{j,t}$ and $W_{s,t}$, respectively, for both strategies. Here, we assumed that senior workers serve more than junior workers because of their greater jaws from molting (Noirot & Pasteels,

1987; Rosengaus & Traniello, 1993; Crosland & Traniello, 1997; Crosland *et al.*, 1998). The contribution of each junior worker or senior worker for producing and caring for eggs, which become young instars, is c or C ($C > c > 0$), respectively.

In young soldier production strategy, soldiers develop from the young instar stage, and the colony has small soldiers. They are divided into junior soldiers and senior soldiers, similar to workers. The numbers of junior soldiers and senior soldiers at time step t are $S_{j,t}$ and $S_{s,t}$, respectively. In old soldier production strategy, soldiers develop from old instars, and the colony has large soldiers. These soldiers consist of one age stage because they die at the next time step. The number of (senior) soldiers at time step t is $S_{s,t}$. Luykx (1993) reported that soldiers are relatively long-lived within the colony, and that individuals becoming soldiers are expected to live at least as long as those becoming workers, regardless of their dangerous tasks. As further details are not known, we assumed for simplicity that all individuals have the same life span. We assume that large soldiers are stronger than small soldiers, because of their greater jaws from molting, and that the strength is not different between junior soldiers and senior soldiers in young soldier production strategy, because instars do not molt after they become soldiers (Watson *et al.*, 1977; Sewell & Watson, 1981; Watson & Sewell, 1981; 1985; Noirot, 1985a; Renoux, 1985; Noirot & Pasteels, 1987). The strength of each small soldier or large soldier is d or D ($D > d > 0$). The defensive strength needed for one worker is b ($b > 0$). With these dimensionless parameters, we can formulate demography of the two strategies.

In young soldier production strategy, the demography can be written as follows, following Fig. 1(a).

$$\begin{aligned} W_{s,t+1} &= W_{j,t}, \\ S_{s,t+1} &= S_{j,t}, \\ W_{j,t+1} + S_{j,t+1} &= cW_{j,t} + CW_{s,t}, \\ d(S_{j,t+1} + S_{s,t+1}) &= b(W_{j,t+1} + W_{s,t+1}). \end{aligned} \quad (1)$$

The first equation tells us that junior workers become senior workers at the next time step. The

second equation tells us that junior soldiers become senior soldiers at the next time step. The third equation tells us that young instars produced and cared for when they were eggs by workers become old instars, that is junior workers and junior soldiers at the next time step. The fourth equation tells us that the number of soldiers produced is determined by the number of workers defended at the next time step. From these equations, we can deduce a recursion formula with a projection matrix:

$$\begin{bmatrix} W_s \\ W_j \\ S_s \\ S_j \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 1 & 0 & 0 \\ Cd/(d+b) & (cd-b)/(d+b) & 0 & d/(d+b) \\ 0 & 0 & 0 & 1 \\ Cb/(d+b) & (cb+b)/(d+b) & 0 & -d/(d+b) \end{bmatrix} \begin{bmatrix} W_s \\ W_j \\ S_s \\ S_j \end{bmatrix}_t. \quad (2)$$

The matrix elements in the first and third rows are straightforward. The other elements are deduced by solving the third and fourth equations in eqn (1) after inserting the first and second equations. The characteristic equation of this 4×4 matrix is

$$\lambda(\lambda+1)\{(b+d)\lambda^2 - cd\lambda - Cd\} = 0. \quad (3)$$

In old soldier production strategy, the demography can be written as follows, following Fig. 1(b):

$$\begin{aligned} W_{s,t+1} + S_{s,t+1} &= W_{j,t}, \\ W_{j,t+1} &= cW_{j,t} + CW_{s,t}, \\ DS_{s,t+1} &= b(W_{j,t+1} + W_{s,t+1}). \end{aligned} \quad (4)$$

The first equation tells us that junior workers become senior workers or (senior) soldiers at the next time step. The second equation tells us that young instars produced and cared for when they were eggs by workers become old instars, that is junior workers at the next time step. The third equation tells us that the number of (senior) soldiers produced is determined by the number of defended workers at the next time step. From these equations, we can deduce a recursion

formula with a projection matrix:

$$\begin{bmatrix} W_s \\ W_j \\ S_s \end{bmatrix}_{t+1} = \begin{bmatrix} -Cb/(D+b) & (D-cb)/(D+b) & 0 \\ C & c & 0 \\ Cb/(D+b) & (Cb+b)/(D+b) & 0 \end{bmatrix} \begin{bmatrix} W_s \\ W_j \\ S_s \end{bmatrix}_t. \quad (5)$$

The matrix elements in the second row are straightforward. The other elements are deduced by solving the first and third equations in eqn (4) after inserting the second equation. The characteristic equation of this 3×3 matrix is

$$\lambda\{(b+d)\lambda^2 + (Cb - cb - cD)\lambda - CD\} = 0. \quad (6)$$

Here, we substitute $C = K_c c$ and $D = K_d d$ where $K_c > 1$ and $K_d > 1$, and $b = dl$. K_c is the comparative ability of senior workers against junior workers for serving the colony. K_d is the comparative strength of large soldiers against small soldiers. As the colony needs more defensive power for each worker, l is larger.

As shown in Appendix A, colonies with young soldier production strategy cannot increase when

$$(K_c + 1)c < 1 + l, \quad (7)$$

while colonies with old soldier production strategy cannot increase when

$$K_d < (K_c - 1)l, \quad (8)$$

or when

$$K_d\{(K_c + 1)c - 1\} < \{(K_c - 1)c + 1\}l. \quad (9)$$

As long as none of eqns (7)–(9) hold, we can compare the population growth rates of both strategies, or the maximum solutions of eqns (3)

and (6). Young soldier production strategy should be taken when

$$c \left(l - \frac{K_d - K_c}{K_c - 1} \right) > K_c \left(\frac{K_d - 1}{K_c - 1} \right)^2, \quad (10)$$

while otherwise old soldier production strategy should be taken. The proof is shown in Appendix B.

When $K_d = K_c = K$, eqn (10) becomes simpler:

$$cl > K. \quad (11)$$

Prediction from the Model

The result of the model, presented by inequalities eqns (7)–(10), can be illustrated as regions in parameter space (c, l), where regions A, B and C represent the case where young soldier production strategy is taken, old soldier production strategy is taken, and colonies with neither strategy increase (Fig. 2). The three curves corresponding to eqns (7), (9) and (10) cross at one point. Depending on whether the value of l at the point is smaller than $K_d/(K_c - 1)$, or whether or not K_d is smaller than 2, slightly different patterns are obtained [see Fig. 2(a) and

(b)]. Region C always exists where c is small and l is large. It is easily understandable that the colony cannot increase in such conditions where the caring ability of workers is low and the necessary numbers of soldiers for defending one worker is large.

The difference between Fig. 2(a) and (b) is not important to understand the result. Whichever is the case, when c or l is large within regions A and B, as depicted in eqn (10), young soldier production strategy is more advantageous than old soldier production strategy. Moreover, when K_c is large compared to K_d , young soldier production strategy is more advantageous because the boundary of the two regions moves downwards then, which is proved in Appendix C. The condition with which the colony decides soldier production strategy can be depicted concretely as below. (1) With a high value of c and C , the colony has a relatively high ratio of young instars to old instars. In this situation, the colony should make soldiers from young instars (young soldier production strategy), in order to have a high population growth rate with steady growth. As c and C get smaller, the colony has a relatively low ratio of young instars to old instars. Then the colony should make soldiers from old instars (old soldier production

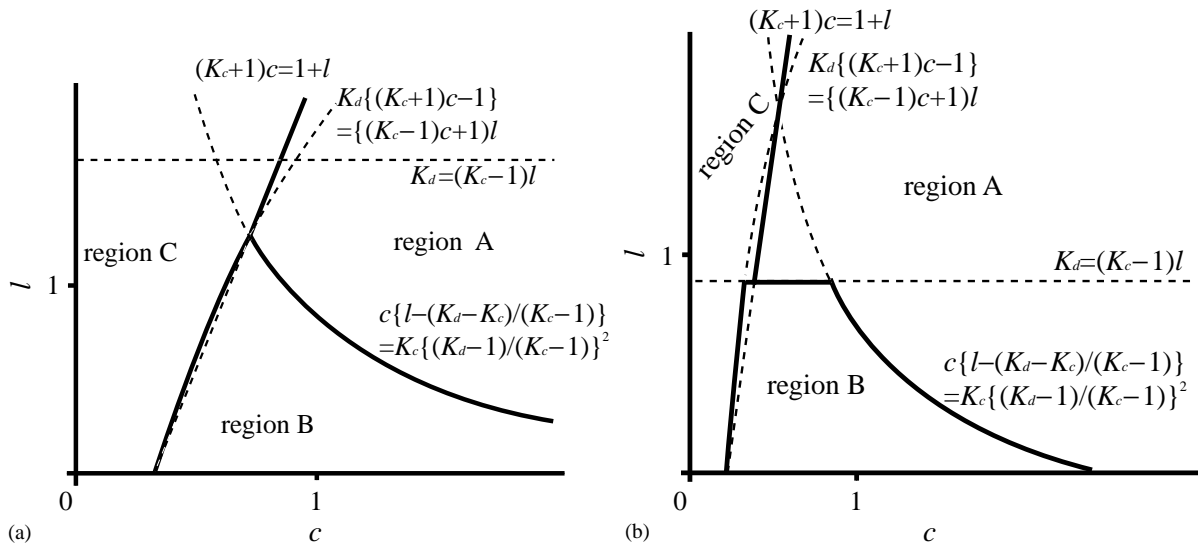


FIG. 2. Parameter space of (c, l) which classifies different optimal strategies. In region A, the colony should take young soldier production strategy. In region B, the colony should take old soldier production strategy. In region C, colonies with either strategy cannot increase. (a) K_d is smaller than 2 ($K_c = 2.1, K_d = 1.8$); (b) K_d is larger than 2 ($K_c = 4, K_d = 2.6$). Although patterns of the region division are slightly different between cases (a) and (b), in either of the cases region A exists where c and l are relatively large while region B exists where they are relatively small.

strategy). (2) With a high value of l , the colony needs a relatively high number of soldiers. In this situation the colony should make small soldiers from young instars (young soldier production strategy), which serve longer than large soldiers derived from old instars. As l gets smaller, the colony does not need so many soldiers. The colony should now make large soldiers from old instars and have strong soldiers of small number (old soldier production strategy). (3) If molting, i.e. increasing the size, is more useful for workers to serve the colony than for soldiers to defend the colony (high K_c/K_d), the colony should take young soldier production strategy and vice versa.

In *Zootermopsis* (Termopsidae), Shellman-Reeve (1997) showed that, as the colony is filled with many colony members, offspring gained per allopARENT per year decreases from 5.00 to 0.60 in six years. This phenomenon corresponds to the decrease of the parameter c in the model. The reason is supposed to be that (1) the food intake rate of each worker becomes less as the number of workers increases, because the total amount of food workers can get has the upper limit (Abe, 1987; Lenz, 1994), and (2) the queen cannot produce enough eggs for each worker's workload in a large colony because of her limited egg productive capacity (Brian, 1983, p. 180).

In *N. Koshunensis* (Kalotermitidae), Maki & Abe (1986) showed that as the colony gets larger, the ratio of soldiers within a colony becomes smaller. This phenomenon corresponds to the decrease of the parameter l in the model. They explain the reason as due to the fact that the surface area of the nest where defense is needed increases more slowly than the volume of the nest, which is proportional to the number of colony members, that is, the defensive power needed for each colony member decreases as the colony expands.

The cases of *Zootermopsis* and *Neotermes* seem to hold generally for lower termites whose nests are settled in the single wood, that are one-piece type termites. By the change of soldier production strategy, the colony changes population growth rate and population structure, that is, matrix eigenvalues and matrix eigenvectors, respectively.

Lower termites, especially Kalotermitidae, produce soldiers from young instars when the colony is incipient, and from old instars as time passes (Watson *et al.*, 1977; Sewell & Watson, 1981; Noirot, 1985a; Renoux, 1985; Watson & Sewell, 1981; 1985; Noirot & Pasteels, 1987; Rosin & Pasteels, 1991). Therefore, prediction of the model fits well with their pattern of soldier production along the colony development.

Test of the Model with Samples

In order to test our model, we measured the joint number of antenna of soldiers in the colonies of *N. koshunensis*, which were collected in Okinawa by Maki & Uetzu during 1978–1979 (Maki, 1980). Antennal joint number increases by one or two with each successive molt in numerous Termopsidae and Rhinotermitidae (Heath, 1927; Renoux, 1985). We assumed *N. koshunensis* also has this tendency. Because the collection was old, many samples of soldiers lost their antenna. We selected colonies in which more than half of the soldiers still have over 12 joints, which is the least number if they did not lose their antennal joints. We excluded incipient colonies whose total number of colony members is less than 100. Therefore we used the other 18 colonies to test our model.

As the colony matures and has many colony members, each worker cannot work efficiently (Shellman-Reeve, 1997). It is empirically known that as the colony matures and has many colony members, the colony has relatively fewer soldiers (Maki & Abe, 1986). Therefore the total number of colony members is inversely correlated to c and l .

We plotted the average number of antennal joints of soldiers, which have more than 12 joints, on y -axis for each colony, against the number of total colony members (Fig. 3) with least-squares regression. In Fig. 3, as the colony is larger, it has a tendency to produce soldiers from old instars. The correlation between the number of colony members and the average number of antennal joints is significantly positive ($r^2 = 0.540$, $P < 0.001$, $n = 18$).

We plotted the number of antennal joints of the soldier, which has the maximum number of it in each colony, on y -axis, against the number

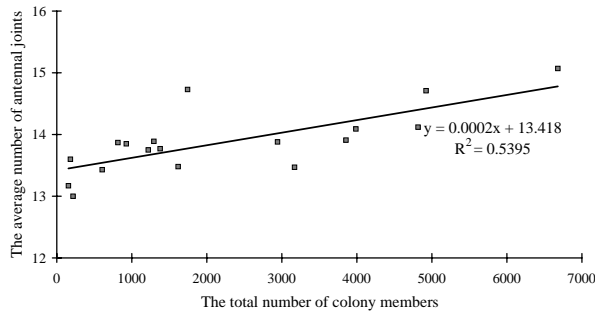


FIG. 3. Relationship between colony size and the average number of antennal joints of soldiers for each colony. Colonies with large population have a trend to produce soldiers from old instars.

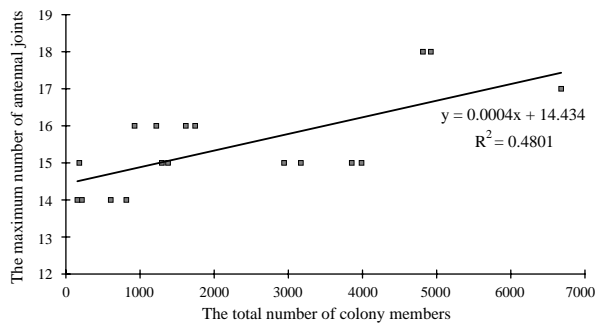


FIG. 4. Relationship between colony size and the maximum number of antennal joints of soldiers for each colony. Colonies with large population have a trend to produce soldiers from old instars.

of total colony members (Fig. 4) with least-squares regression. Considering that some soldiers lose their antennal joints partly, the maximal joint number may be a more adequate index for the instars molting to the soldiers. In Fig. 4, as the colony is larger, it produces the soldier from an old instar. The correlation between the number of colony members and the maximum number of antennal joints is significantly positive ($r^2 = 0.480$, $P < 0.005$, $n = 18$).

The above data suggest that as the colony matures, it certainly has a trend to produce soldiers from old instars.

Discussion

Soldiers are quite rich in the variety of morphology, showing the importance of soldiers in the life of termites. Many studies have been done on the biology of soldiers, the process of

soldier differentiation (Watson *et al.*, 1985), soldier defense secretion (Prestwich, 1984) and the proportion of soldiers in a colony (Haverty, 1979; Maki & Abe, 1986). However, few studies have been done on the problem of who become soldiers. This article proposed the first mathematical model predicting soldier production in termite colonies.

Large workers work better than small workers, and large soldiers defend the colony better than small soldiers (Watson *et al.*, 1977; Sewell and Watson, 1981; Watson & Sewell 1981; 1985; Noirot, 1985a; Renoux, 1985; Noirot & Pasteels, 1987; Rosengaus & Traniello, 1993; Crosland & Traniello, 1997; Crosland *et al.* 1998). Colonies meet trade-off of how to divide large instars between workers and soldiers. Our model shows how colonies solve the trade-off in order to have a high population growth rate during their growth. The soldier production strategy might be explained by a simpler reason: for example, colonies should produce small soldiers or large soldiers just to fit the head of soldiers to plug up the galleries for the defensive activity. It is known in some termite species that as termite colonies age, the workers become progressively larger (Grace *et al.*, 1995; Darlington, 1991). However, we do not know whether the head-width of soldiers fit for galleries in general termite species. In order to test this hypothesis, we need further extensive studies.

As for one-piece-type termites, the model and the fact fitted well: along the development of a colony, soldiers will depart from the worker line at different stages, because finiteness of their nest and their food brings a change in the parameters of colony demography. If their nest and their food are infinite, however, the condition for colony members will never change (Lenz, 1994). Separates-type termites (Abe, 1987), including Hodotermitidae, some Rhinotermitidae, Serri-termitidae and Termitidae, differ from one-piece-type termites as shown below. (1) Workers go outside and gather food such as fallen leaves, dead wood pieces, lichens and humus, and each worker can always get enough food corresponding to its workload (Abe, 1987). (2) The queen becomes bigger as time passes, and can produce many eggs, so that each worker can always contribute to egg production enough (Brian,

1983, p. 180). (3) When workers go outside the nest, soldiers must defend them, so that soldiers approximately proportional to the number of colony members are needed (Maki & Abe, 1986). In Conclusion, the condition for each colony member does not change as the colony becomes large. In fact, separates-type termites always produce soldiers from defined and less numerous instars (Noirot, 1989). For example, Macrotermitinae always produce soldiers from larvae—thus they always take young soldier production strategy (Okot-Kotber, 1985; Noirot, 1985b)—and Nasutitermitinae always produce soldiers from workers—thus they always take old soldier production strategy (Roisin, 1992, 1996). Our model predicts that both of these do not have to change soldier production strategy during their colony life, and it fits well with the fact.

The problem of “who should be the soldier” was once discussed by Shellman-Reeve (1997). According to her, soldiers should be the oldest ones, because they have gained enough inclusive fitness during their young age’s work and do not want to reproduce anymore. However, colony members do not consider the inclusive fitness they have gained, but rather the inclusive fitness they can get now and in the future if they behave rationally. Furthermore, her theory cannot explain why one-piece termites take young soldier production strategy in incipient colonies. Our model does not analyse why a part of the colony members become sterile soldiers to defend the colony altruistically. They may defend the colony because they can increase their inclusive fitness through their brothers and sisters (Hamilton, 1964; Shellman-Reeve, 1997), or because other colony members manipulate them to become sterile (Alexander, 1974; Zimmerman, 1983). Whichever the case, once a part of the colony members are determined to become sterile soldiers, the maximum reproductive output from the colony is the very interest of all members. Thus we used the growth rate of the colony as the fitness measure. Such an approach is common in evolutionary models for social animals (Macevicz & Oster, 1976; Oster & Wilson, 1978; Wakano *et al.*, 1998).

Our model can be applied on other animal societies, which have age structure, to predict the

soldier production in their society, but some corrections are required. For example, some gall-making aphids have sterile soldier castes (Aoki, 1977; Foster, 1990) and several researches have tackled problems of sterile soldiers (Ito 1989; Stern *et al.*, 1994; Tanaka & Ito, 1994; Akimoto, 1996). Some eusocial gall-making aphids produce sterile soldiers from the first instar, while others produce these from the second instar. The two groups live on hosts of different types (Stern & Foster, 1997). Therefore the difference of the two groups is likely to be analysed by our model to predict the soldier production strategy. However, they do not have workers as termites. Colony members excluding soldiers feed by themselves and disperse afterwards. The assumption on workers in our model must be changed in order to apply the model to eusocial gall-making aphids. Our model must be applied to other animal societies with some appropriate changes in the model.

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REFERENCES

- ABE, T. (1987). Evolution of life types in termites. In: *Evolution and Coadaptation in Biotic Communities* (Kawano, S., Cornell, J. & Hidaka, T., eds), pp. 159–209. Tokyo: University of Tokyo Press.
- AKIMOTO, S. (1996). Ecological factors promoting the evolution of colony defense in aphids: computer simulations. *Insectes Soc.* **43**, 1–15.
- ALEXANDER, R. D. (1974). The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383.
- AOKI, S. (1977). *Colophina clematis*, an aphid species with “soldiers”. *Kontyu* **45**, 276–282.
- BARTZ, S. H. (1979). Evolution of eusociality in termites. *Proc. Natl Acad. Sci. U.S.A.* **76**, 5764–5768.
- BRIAN, M. V. (1983). *Social Insects: Ecology and Behavioral Biology*. Cambridge: Chapman & Hall.
- CHARNOV, E. L. (1978). Evolution of eusocial behavior: offspring choice or parental parasitism? *J. theor. Biol.* **75**, 451–465.

- CRESPI, B. J. (1992). Eusociality in Australian gall thrips. *Nature* **359**, 724–726.
- CROSLAND, M. W. J. & TRANIELLO, J. F. A. (1997). Behavioral plasticity in division of labor in the lower termite *Reticulitermes fukienensis*. *Naturwissenschaften* **84**, 208–211.
- CROSLAND, M. W. J., LOK, C. M., WONG, T. C., SHAKARAD, M. & TRANIELLO, J. F. A. (1997). Division of labor in a lower termite: the majority of tasks are performed by older workers. *Anim. Behav.* **54**, 999–1012.
- CROSLAND, M. W. J., REN, S. X. & TRANIELLO, J. F. A. (1998). Division of labor among workers in the termites *Reticulitermes fukienensis*. *Ethology* **104**, 57–67.
- DARLINGTON, J. P. E. C. (1991). Relationship of individual weights to nest parameters in termites of the genus *Macrotermes*. *Sociobiology* **18**, 167–176.
- DUFFY, J. E. (1996). Eusociality in a coral-reef shrimp. *Nature* **381**, 512–514.
- FOSTER, W. A. (1990). Experimental evidence for effective and altruistic colony defense against natural predators by soldiers of the gall-forming aphid *Pemphigus spyrothecae*. *Behav. Ecol. Sociobiol.* **27**, 421–430.
- GRACE, J. K., YAMAMOTO, R. T. & TAMASHIRO, M. (1995). Relationship of individual worker mass and population decline in a Formosan subterranean termite colony. *Environ. Entomol.* **24**, 1258–1262.
- HAMILTON, W. D. (1964). The genetical evolution of social behavior I. *J. theor. Biol.* **7**, 1–16.
- HAVERTY, M. I. (1979). Soldier production and maintenance of soldier proportions in laboratory experimental groups of *Coptotermes formosanus*. *Insectes Soc.* **26**, 69–84.
- HEATH, H. (1927). Caste formation in the genus *Termopsis*. *J. Morphol. Physiol.* **43**, 387–425.
- HIGASHI, M., YAMAMURA, N., ABE, T. & BURNS, T. P. (1991). Why don't all termites have a sterile worker caste? *Proc. R. Soc. London B* **246**, 25–29.
- HIGASHI, M., ABE, T. & BURNS, T. P. (1992). Carbon–nitrogen balance and termite ecology. *Proc. R. Soc. London B* **249**, 303–308.
- HÖLDOBLER, B. & LUMSDEN, C. J. (1980). Territorial strategies in ants. *Science* **201**, 732–739.
- ITO, Y. (1989). The evolutionary biology of sterile soldiers in aphids. *Trends Ecol. Evol.* **4**, 69–73.
- LENZ, M. (1994). Food resources, colony growth and caste development in wood-feeding termites. In: *Nourishment and Evolution in Insect Societies*. (Hunt, J. H. & Nalepa, C. A., eds), pp. 159–209. Boulder, New Delhi: Westview Press.
- LUYKX, P. (1993). Turnover in termite colonies: a genetic study of colonies of *Incisitermes schwarzi* headed by replacement reproductives. *Insectes Soc.* **40**, 191–205.
- MACEVICZ, S. & OSTER, G. F. (1976). Modeling social insect populations II: optimal reproductive strategies in annual eusocial insect colonies. *Behav. Ecol. Sociobiol.* **1**, 265–282.
- MAKI, K. (1980). Studies on the caste composition of *Neotermes koshunensis*. Graduation Thesis, University of the Ryukyus, 93pp. (in Japanese).
- MAKI, K. & ABE, T. (1986). Proportion of soldiers in the colonies of dry wood termite. *Neotermes koshunensis*. *Physiol. Ecol. Japan* **23**, 109–117.
- MILLER, L. R. (1984). *Invasitermes*, a new genus of soldierless termites from Northern Australia. *J. Aust. Entomol. Soc.* **1984**, 33–37.
- MYLES, T. G. (1986). Reproductive soldiers in the Termopsidae. *Pan-Pacific Entomol.* **62**, 293–299.
- NOIROT, C. (1985a). Pathways of caste development in the lower termites. In: *Caste Differentiation in Social Insects* (Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C., eds), pp. 41–58. Oxford, New York: Pergamon Press.
- NOIROT, C. (1985b). The caste system in higher termites. In: *Caste Differentiation in Social Insects* (Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C., eds), pp. 75–86. Oxford, New York: Pergamon Press.
- NOIROT, C. (1989). Social structure in termite societies. *Ethol. Ecol. Evol.* **1**, 1–17.
- NOIROT, C. & PASTEELS, J. M. (1987). Ontogenic development of the worker caste in termites. *Experientia* **43**, 851–860.
- OKOT-KOTBER, B. M. (1985). Caste polymorphism in a higher termite, *Macrotermes michaelseni*. In: *Caste Differentiation in Social Insects* (Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C., eds), pp. 87–104. Oxford, New York: Pergamon Press.
- OSTER, G. F. & WILSON, E. O. (1978). *Caste and Ecology in the Social Insects*. Princeton, NJ: Princeton University Press.
- PRESTWICH, G. D. (1984). Defense mechanisms of termites. *Annu. Rev. Entomol.* **29**, 201–232.
- RENOUX, J. (1985). Dynamic study of polymorphism in *Schedorhinotermes lamanianus*. In: (Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C., eds), pp. 59–74. *Caste Differentiation in Social Insects*. Oxford, New York: Pergamon Press.
- ROISIN, Y. (1992). Development of non-reproductive castes in the neotropical termite genera *Cornitermes*, *Embiratermes* and *Rhynchotermes*. *Insectes Soc.* **39**, 313–324.
- ROISIN, Y. (1994). Intragroup conflicts and the evolution of sterile castes in termites. *Am. Nat.* **143**, 751–765.
- ROISIN, Y. (1996). Castes in humivorous and litter-dwelling neotropical nasute termites. *Insectes Soc.* **43**, 375–389.
- ROISIN, Y. & PASTEELS, J. M. (1991). Polymorphism in the giant cocoa termites, *Neotermes papua*. *Insectes Soc.* **38**, 263–272.
- ROSENGAUS, R. B. & TRANIELLO, J. F. A. (1993). Temporal polythetism in incipient colonies of the primitive termite *Zootermopsis angusticollis*. A single multiage caste. *J. Insect Behav.* **6**, 237–252.
- SANDS, W. A. (1972). The soldierless termites of Africa. *Bull. Br. Mus. Nat. Hist. (Suppl)* **18**, 1–244.
- SEWELL, J. J. & WATSON, J. A. L. (1981). Development pathways in Australian species of *Kalotermes hagen*. *Sociobiology* **6**, 243–323.
- SHELLMAN-REEVE, J. S. (1994). Limited nutrients in a dampwood termite: nest preference, competition and cooperative nest defense. *J. Anim. Ecol.* **63**, 921–932.
- SHELLMAN-REEVE, J. S. (1997). The spectrum of eusociality in termites. In: *The Evolution of Social Behavior in Insects and Arachnids* (Choe, J. C. & Crespi, B. J., eds), pp. 52–93. New York: Cambridge University Press.
- STERN, D. L. & FOSTER, W. A. (1997). The evolution of sociality in aphids: a clone's-eye view. In: *The Evolution of Social Behavior in Insects and Arachnids* (Choe, J. C. & Crespi, B. J., eds), pp. 150–165. Cambridge University Press, New York.

STERN, D. L., AOKI, S. & KUROSU, U. (1994). A test of geometric hypotheses for soldier investment patterns in the gall producing tropical aphid *Cerataphis fransseni*. *Insectes Soc.* **41**, 457–460.

TANAKA, S. & ITO, Y. (1994). Reversal of caste production schedule in a eusocial aphid, *Pseudopregma koshunensis*. *Naturwissenschaften* **81**, 411–413.

WAKANO, J. Y., NAKATA, K. & YAMAMURA, N. (1998). Dynamic model of optimal age polyethism in social insects under stable and fluctuating environments. *J. theor. Biol.* **193**, 153–165.

WATSON, J. A. L. & SEWELL, J. J. (1981). The origin and evolution of caste systems in termites. *Sociobiology* **6**, 101–108.

WATSON, J. A. L. & SEWELL, J. J. (1985). Caste development in *Mastotermes* and *Kaloterms*: which is primitive? In: *Caste Differentiation in Social Insects* (Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C., eds), pp. 27–40. Oxford, New York: Pergamon Press.

WATSON, J. A. L., METCALF, E. C. & SEWELL, J. J. (1977). A re-examination of the development of castes in *Macrotermes darwiniensis*. *Aust. J. Zool.* **25**, 25–42.

WATSON, J. A. L., OKOT-KOTBER, B. M. & NOIROT, C. (eds) (1985). *Caste Differentiation in Social Insects*. Oxford, New York: Pergamon Press.

WILSON, E. O. (1971). *The Insect Societies*. Cambridge: The Belknap Press of Harvard University Press.

YAMAMURA, N. (1993). Different evolutionary conditions for worker and soldier castes: genetic systems explaining caste distribution among eusocial insects. *J. theor. Biol.* **161**, 111–117.

ZIMMERMAN, R. B. (1983). Sibling manipulation and indirect fitness in termites. *Behav. Ecol. Sociobiol.* **12**, 143–145.

APPENDIX A

Two solutions of eqn (3) satisfy $f(\lambda) = 0$, where

$$f(\lambda) = (1 + l)\lambda^2 - c\lambda - K_c c. \quad (A.1)$$

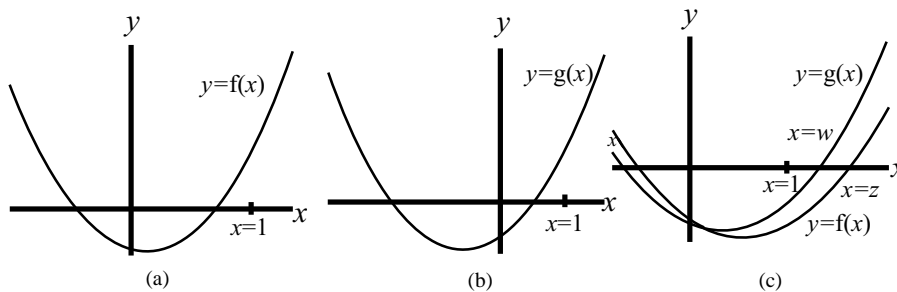


FIG. 5. (a) Condition where young soldier production strategy cannot be taken. If the function $f(x) = 0$ has the maximum solution smaller than 1, the colony does not increase. (b) Condition where old soldier production strategy cannot be taken. If the axis of $y = g(x)$ is smaller than 0, $g(x) = 0$ has a negative solution with the maximum absolute value, when the population fluctuates and reaches 0. If the function $g(x) = 0$ has the maximum solution smaller than 1, the colony cannot increase. (c) Condition where young soldier production strategy should be taken because it has a higher population growth

As shown in Fig. 5(a), the graph $y = f(x)$ has two cross points with the x -axis (one is positive and one is negative) because $f(0) < 0$. When $f(1) > 0$, or $(K_c + 1)c < 1 + l$, the absolute values of two solutions for $f(x) = 0$ are both less than 1 because the axis of the parabola $y = f(x)$ is positive. Therefore the solution of eqn (3) with the maximum absolute value is -1 . In this case, the number of colony members shows an oscillation and does not increase.

Two solutions of eqn (6) satisfy $g(\lambda) = 0$, where

$$g(\lambda) = (K_d + 1)\lambda^2 + \{(K_c - 1)l - K_d\}c\lambda - K_c K_d c. \quad (A.2)$$

As shown in Fig. 5(b), when $K_d < (K_c - 1)l$, the axis of the parabola $y = g(x)$ is negative, the solution with the maximum absolute value is negative and the number of colony members shows an oscillation and reaches a negative value. When $K_d > (K_c - 1)l$ and $g(1) > 0$, or $K_d \{(K_c + 1)c - 1\} < \{(K_c - 1)c + 1\}l$, the solution for eqn (A.2) with the maximum eigenvalue is positive but less than 1.

Therefore, colonies with young soldier production strategy cannot increase when

$$(K_c + 1)c < 1 + l, \quad (A.3)$$

while colonies with old soldier production strategy cannot increase when

$$K_d < (K_c - 1)l \quad \text{or} \quad K_d \{(K_c + 1)c - 1\} < \{(K_c - 1)c + 1\}l. \quad (A.4)$$

APPENDIX B

When none of eqns (7)–(9) are satisfied, we can compare maximum eigenvalues of two strategies. Under these conditions, some elements of the projection matrix in eqns (2) and (5) are negative so that some positive initial values may make some of the subsequent values negative. We assume that the king and the queen can prepare the initial distribution of workers and soldiers, which make the subsequent values positive.

The maximum solutions of eqn (3), or the positive solution of eqn (A.1), that is the population growth rate of young soldier production strategy, is

$$z = \frac{c + \sqrt{c^2 + 4K_c c(1+l)}}{2(1+l)}. \quad (\text{B.1})$$

As shown in Fig. 5(c), when $g(z) > 0$, z is larger than w , which is the positive solution of $g(x) = 0$. Therefore, the colony should take young soldier production strategy when $g(z) > 0$. This relation leads to

$$\left\{ c + \sqrt{c^2 + 4cK_c(1+l)} \right\} \{ (K_c - 1)l - (K_d - K_c) \} > K_c(K_d - 1)(1+l). \quad (\text{B.2})$$

This is equivalent to

$$(K_c - 1)l - (K_d - K_c) > 0$$

and

$$c \left(l - \frac{K_d - K_c}{K_c - 1} \right) > K_c \left(\frac{K_d - 1}{K_c - 1} \right)^2.$$

Because the former equation is automatically satisfied when the latter one is satisfied, we can conclude that the young soldier production strategy should be taken when

$$c \left(l - \frac{K_d - K_c}{K_c - 1} \right) > K_c \left(\frac{K_d - 1}{K_c - 1} \right)^2, \quad (\text{B.3})$$

while otherwise old soldier production strategy should be taken.

APPENDIX C

The boundary of the two regions, A and B, is depicted in eqn (10). The boundary moves downward when $(K_d - K_c)/(K_c - 1)$ gets smaller or $K_c \{ (K_d - 1)/(K_c - 1) \}^2$ gets smaller. It is easily confirmed that both become smaller when K_d gets smaller or when K_c gets larger.