Insectes soc. 45 (1998) 17 – 32
0020-1812/98/010017-16 $ 1.50+0.20/0

Insectes Sociaux

Research article

Foraging organization of the open-air processional lichen-feeding termite *Hospitalitermes* (Isoptera, Termitidae) in Borneo

T. Miura* and T. Matsumoto

Department of Biology, University of Tokyo, 3-8-1 Komaba, Meguro-ku, Tokyo 153, Japan, e-mail: ss67246@hongo.ecc.u-tokyo.ac.jp

Key words: Caste-ratio dynamics, division of labor, foraging frequency, open-air foraging, social behavior.

Summary

The temporal dynamics and social interaction in the foraging activities of the open-air processional termite *Hospitalitermes* (Termitidae, Nasutitermitinae) were studied in Borneo, Southeast Asia. *H. medioflavus* and *H.* sp. A tended to forage from evening to the next morning. On average foraging activity occurred every 3.2 days. Some synchronization of foraging events among colonies was observed, which appeared to be caused by rainfall levels.

Temporal dynamics during foraging activity was observed in detail using a photographic method for two species; *H. medioflavus* and *H. rufus*. Roughly 300,000 to 500,000 individuals participated in a single foraging event in both species. The soldier ratio was highest at the beginning and the end of the activity. Temporal patterns of behavior were different between soldier, major worker, medium worker and minor worker during foraging. The patterns of behavior are consistent with their tasks in the foraging activity. Soldiers lead the foraging column and protect it, major workers act as food carriers in the earlier stage while medium workers become the dominant food ball carriers in the later stage, and minor workers play the role of gnawers. Therefore, caste composition changes during foraging activity. Similar behavioral tendencies were recognized in both species. Measurement of workers' body weights revealed that workers not only carry balls of food from foraging sites but also feed directly at the foraging sites.

Introduction

There are few studies on the behavior of termites because most species live cryptically in nests, galleries, and subterranean tunnels etc., and therefore, observations of termites operating under natural conditions are difficult to obtain. However, world wide there are several species of termites which forage in the open, thus making their foraging behavior relatively easier to observe. The termite genus

* Author for correspondence.

Hospitalitermes is distributed throughout Southeast Asia (18 species are known; Tho, 1992) and is one such open-air foraging genus, foraging in large columns to feed on lichens. There have been studies of their foraging activity and behavior by Escherich (1911), Kalshoven (1958), Roonwal (1970), Jander and Daumer (1974), Abe (1979), Collins (1979), and Jones and Gathorne-Hardy (1995).

Hospitalitermes forages in the open, and at the start of an expedition, the nasute soldiers are the first to move out from the nest opening at the base of a tree. During foraging, soldiers play the roles of scouts and defenders protecting workers against predators using terpenic substances secreted from their nasus (Chuah et al., 1983; Prestwich, 1984). The continuous column is oriented by means of "crest line trailing" and odor trails, often along trees and fallen boughs (Jander and Daumer, 1974). The column of mixed workers and soldiers follows closely behind the scouts, and occasionally clumping to pluck at lichens or mosses on the edge of the path. The column builds up, and begins to move forward in a continuous stream, deploying soldiers to guard the flanks as it lengthens. Some of the workers returning to the nest carry food balls in their mandibles (Kalshoven, 1958). These behavioral observations were descriptive, not quantitative.

Jander and Daumer (1974) reported that marching in these termites was based on crest line trailing, whereby foraging individuals use gravity orientation to follow their column. The authors indicated that the orientation strategy and the organization of the marching column of *Hospitalitermes* species bear some striking resemblances to those of some Neotropical *Eciton* species (army ants). Abe (1979) measured approximately daily changes of foraging activity in an unidentified species of *Hospitalitermes.* Collins (1979) took photographs of a marching column of *H. umbrinus*, estimated the number of individuals that foraged outside the nest, and calculated the amount of food they carried into the nest. According to Collins (1979), 500,000 individuals took part in the foraging activity, and the colony brought back an estimated 46.4 g (dry weight) of food in 4 days. The biomass of the colony was estimated at 349 g (d.w.) (1396 g wet weight) and the consumption at 8.3 mg (d.w.)/g(w.w.) day. The food actually contained more nitrogen ($1.57 \pm 0.49\%$; mean ± s.d.) than wood on which most termites feed (Miura and Matsumoto, 1997). Jones and Gathorne-Hardy (1995) reported that colonies of *H. hospitalis* foraged on 46% to 72% of nights and utilized trees with a significantly larger diameter than the mean diameter of trees in the population at their study site.

In *H. medioflavus* there are distinct major, medium and minor workers. Miura and Matsumoto (1995) observed a division of labor among the trimorphic workers, during which minor workers gnaw food material while major workers repeatedly receive small pieces of food with their mandibles from the gnawing workers and carry the food balls to the nest. Medium workers are engaged in both tasks. This worker trimorphism is related to their developmental stages (instars) (Miura and Matsumoto, 1995). Other *Hospitalitermes* species, including *H. rufus* and *H.* sp. A in this study, also have trimorphic workers.

Although the foraging behavior as a whole colony was studied as described above, the social organization, especially on dynamics of the castes in the foraging activities, has never been studied. In order to examine the colony integrity in foraging, we investigated the foraging activity of *Hospitalitermes* in detail at both colony-level and individual-level. In this paper the frequency of the foraging activities of *H. medioflavus* and *H.* sp. A, and the temporal dynamics of caste ratio during the foraging of *H. medioflavus* and *H. rufus* are reported. We used the photographic method employed by Collins (1979), and focused on caste ratio dynamics among major, medium, and minor workers, and soldiers.

Materials and methods

Frequency of foraging activities

Eleven nests of *H. medioflavus* (Holmgren) and five nests of *H.* sp. A were selected in Bukit Soeharto Protection Forest, East Kalimantan, Indonesia. More than 40 nests of both species had been found along the observation trails in the forest (31 nests of *H. medioflavus* and 9 nests of *H.* sp. A).

Twice a day, at 09:00 and 21:00, we checked the nests for foraging activity. We evaluated the intensity of foraging activity on a 5 grade scale;

– (0): no foraging column was present,
± (1): a few soldiers seen outside the nest opening,
+ (2): small column composed only of soldiers was observed,
++ (3): a moderately sized column comprising of both soldiers and workers, sometimes the workers were carrying food balls,
+++ (4): large sized foraging columns (full scale foraging column).

If the foraging column was small and composed only of soldiers, tiny disturbances could occasionally make them return to the nest and cease their foraging. Therefore, we considered only grades 3 and 4 as foraging activity. In the cases where foraging continued from a night to the next morning, these were regarded as the same foraging event. Cumulative activities of all the observed nests were examined to ascertain whether synchronization among colonies occurs.

Temporal dynamics of foraging activity

Using the photographic method employed by Collins (1979), we quantified foraging activity by counting the number of individuals which leave and return to the nest.

The investigated nest of *H. medioflavus* was inside a living tree near Mentoko field station in Kutai National Park, East Kalimantan, Indonesia. The activities of the colony were recorded every half hour from 18:00 on 15th to 10:00 on 16th June 1995. When foraging activity began, we started to take two photographs every 30 minutes. In addition, speed of outgoing and ingoing individuals was calculated from the measurements of time to cover 10 cm. After developing and printing photographs, outgoing and ingoing individuals were counted. Stationary soldiers or workers on the flanks of the column were ignored.

A nest of *H. rufus* (Haviland) was investigated in Lambir Hills National Park, Sarawak, Malaysia, from the evening on 13 July to the next morning on 14 July 1996.

In this case, photographs were taken every 10 minutes to record more detailed activity.

The number of individuals passing a fixed point per half hour (or 10 minutes for *H. rufus*) in each direction was calculated from the equation (modified from Collins, 1979):

$$N = \frac{n \times t \times v}{l}$$

where N = number of outgoing or ingoing per half hour or per 10 minutes, n = number of outgoing or ingoing in column as seen on photograph, t = time interval between photographs (1800 or 600 sec), l = length of column in the photograph (cm), and v = marching speed of outgoing or ingoing individuals (cm/sec).

The calculation was done separately for outgoers and ingoers on each photograph, and within each category, all measurements were added to give cumulative totals. The net number outside the nest at any one time was estimated by subtracting the cumulative ingoing total from the cumulative outgoing total. We distinguished among soldiers and trimorphic workers to estimate the outgoing and ingoing number of each caste.

Difference of body weight between outgoers and ingoers

To examine whether the workers feed directly at the foraging sites as well as carrying food balls, the dry body weights of foraging castes were measured in *H. rufus*, using a CAHN balance after dehydration of specimens with acetone and desiccation in a drying oven (50 °C, overnight). The investigated colony in Lambir Hills National Park was the same one in which temporal dynamics were investigated.

Results

Frequency of foraging activities

Table 1 shows the results of the frequency of foraging activity, in which each foraging event is enclosed by a box. In *H. medioflavus*, during the 11 days of observation, foraging activity occurred 4.3 times per colony on average; therefore, one foraging event was performed every 3.4 ± 2.7 days (mean ± s.d.). In the case of *H.* sp. A., foraging event occurred 5.2 ± 2.3 times/11 days (mean ± s.d.); one event was performed every 3.4 ± 2.7 days (mean ± s.d.). Foraging tended to commence in the evening and finish the next morning. It could be diagnosed from the direction of foraging columns.

To examine the synchronization of foraging activity among colonies, the five-grade intensities of all colonies were summed together (Fig. 1). In both species, 4 to 5 peaks occurred during 11 days. On the rainy night of 5th December, only two colo-

Table 1. Foraging activities of *Hospitalitermes medioflavus* and *H.* sp. A.

date	1	1	2	2	3	3	4	4	5	5	6	6	7	7	8	8	9	9	10	10	11	11		
time*	m	n	m	n	m	n	m	n	m	n	m	n	m	n	m	n	m	n	m	n	m	n	frequency	
weather**	◎	◎	◎	◎→○	◎	◎→○	◎	◎	◎	●	◎	◎→○	○	◎→●	◎	○	◎/●	◎/○	◎	◎→○	○	○	(/11days)	(days/one foraging)
Hospitalitermes medioflavus																								
H-I1	-	+++	+++	-	-	+++	+++	-	-	+	-	+++	+++	-	-	+++	+++	-	-	+++	-	+++	6	1.8
H-I6	-	+++	-	-	-	+++	-	-	-	-	-	-	+++	-	-	-	+++	-	-	+++	-	-	5	2.2
H-I8	-	+++	+++	+++	+++	+++	-	-	-	-	-	-	-	-	-	+++	+++	-	-	+	-	-	4	2.8
H-I9	+++	-	-	++	-	-	-	++	++	-	-	+	+++	+++	+++	-	-	-	±	+++	+++	-	6	1.8
H-I14	-	-	-	-	-	-	-	-	-	-	-	-	-	+++	-	-	-	-	-	-	-	-	1	11.0
H-I17	ND	ND	++	-	-	+	±	-	-	-	-	-	-	+++	-	-	-	-	-	-	+++	+++	3	3.7
H-I18	ND	ND	-	ND	-	+++	-	-	-	-	-	-	-	-	-	-	-	+++	+++	+	-	+++	3	3.7
H-L1	-	++	-	-	-	+++	-	+++	±	-	-	+++	-	++	++	-	-	-	-	+++	-	+++	7	1.6
H-L5	-	+++	+++	+++	+++	+++	+	+++	±	-	-	-	-	+++	+++	+	-	+	++	-	-	-	6	1.8
H-L6	-	-	-	+++	+++	-	-	-	-	-	-	-	-	+++	+++	-	-	-	-	-	+++	+++	3	3.7
H-L10	-	++	+++	-	-	-	+++	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+++	3	3.7
																					mean ± s.d.		4.3 ± 1.8	3.4 ± 2.7
Hospitalitermes sp. A																								
H-I2	-	+	±	+++	±	+++	+++	-	-	-	-	+++	-	±	+++	-	-	+++	+++	+++	-	-	6	1.8
H-I11	-	++	-	-	++	+++	+++	-	-	-	-	-	+++	-	-	+++	-	+++	+++	+++	+++	+++	8	1.4
H-I15	-	+++	+++	-	-	-	-	+++	+++	-	-	+++	++	-	++	-	-	-	+++	+++	+	+	6	1.8
H-L3	+	+++	-	+++	+	-	-	-	-	+++	+++	-	-	-	-	-	-	+++	+++	-	-	-	4	2.8
H-L4	-	-	-	-	-	++	+++	-	-	-	-	-	-	-	-	-	-	+++	+++	-	-	-	2	5.5
																					mean ± s.d.		5.2 ± 2.3	2.7 ± 1.7

Observations were made from December 1 to 11, 1994. ¹, 1994.
A single foraging event is enclosed by a box..
Intensity of foraging activity is indicate in five ranks.
-: no foraging activity, ±: only a few soldiers out, +: small column of soldiers, ++: moderate column with soldiers and workers,
+++: large foraging column, ND: no data.
* m : morning (09:00), n : night (21:00)
** ○: clear, ◎: cloudy, ●: rainy

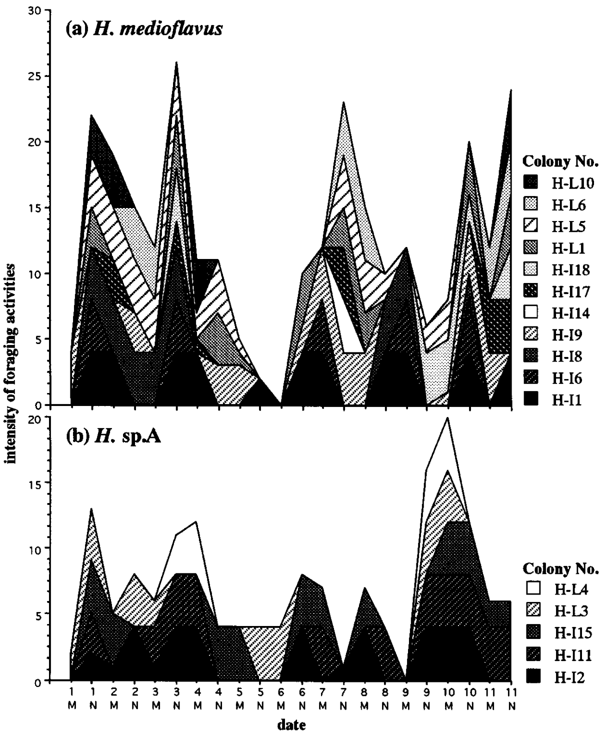

Figure 1. Cumulative intensity of foraging activity of 11 colonies of *Hospitalitermes medioflavus* (a) and 5 colonies of *H.* sp. A (b) in Bukit Soeharto Protection Forest. The nests were monitored from 1 to 11 December 1995 (M = morning 09:00; N = night 21:00). The value on the Y axis is based on the 0–5 scores (see text), including scores 1 and 2. A high degree of synchronization of foraging activity among colonies was observed

nies foraged. The next morning, though it was clear, only one of the two colonies (H-L3, *H.* sp. A) was still foraging. This suggests that foraging activity of *Hospitalitermes* begins in the evening and continues until the next morning. Besides the night of 5th December, there were other periods of low activity. These results suggest that climatic conditions affect foraging activity, and thereby give rise to some synchronization between colonies.

Temporal dynamics of foraging activity

On the night when the activity of *H. medioflavus* was observed in Kutai National Park, a foraging column climbed the host tree to the canopy. The weather that night was clear. The foraging event was performed for total of 15.5 hours from 18:30 to 10:00 in the next morning. Foragers left from three nest exits, and the three small columns joined together on the upper part of the trunk. Photographs were taken of the combined column. Some examples of the photographs are shown in Figure 2. Significant differences of marching speed were found between outgoers

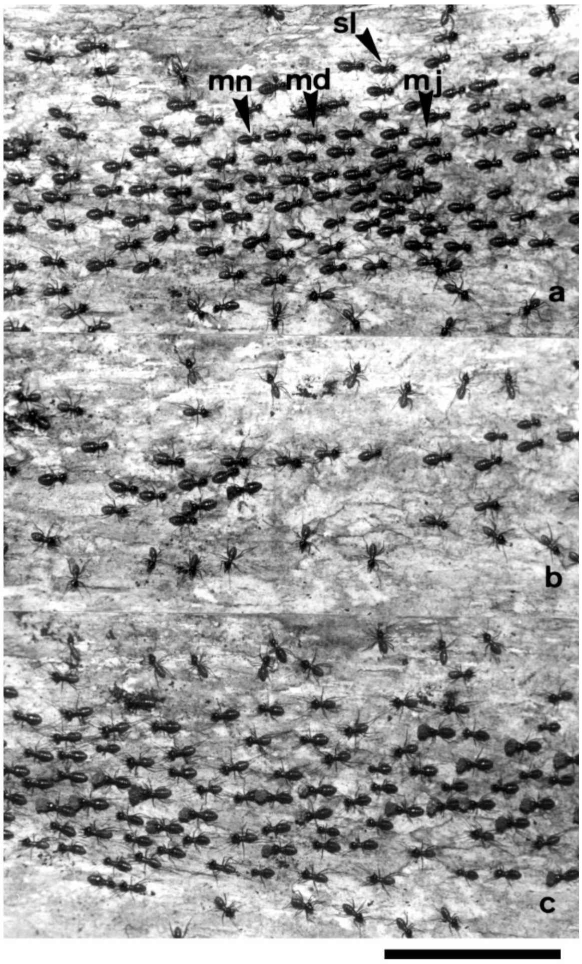

Figure 2. Photographs used for counting the number of foraging individuals in *H. medioflavus*; (a) 22:00, (b) 3:00, (c) 7:00. Note the change in marching direction of the column with time. Each caste is exampled by arrows; mj: major worker, md: medium worker, mn: minor worker, sl: soldier. Bar = 3 cm

and ingoers (n = 40, t-test: $p < 0.01$). Ingoers marched faster than outgoers. The average speed of outgoers was 1.67 cm/sec (n = 30), and that of ingoers was 2.04 cm/sec (n = 10). These data were used for the subsequent estimation of number of foragers.

The foraging activity of *H. rufus* at Lambir Hills National Park was observed from 13 to 14 July 1996. Termites began to forage from 16:30 until 13:00 on the next day. Therefore the duration of the activity was 20.5 hours. The termites climbed a big tree (diameter at breast height: about 90 cm) 20 m distant from the host tree, and the camera was focused on the climbing column. On the way to the foraging tree, some workers gnawed food, but almost all foragers climbed the main foraging

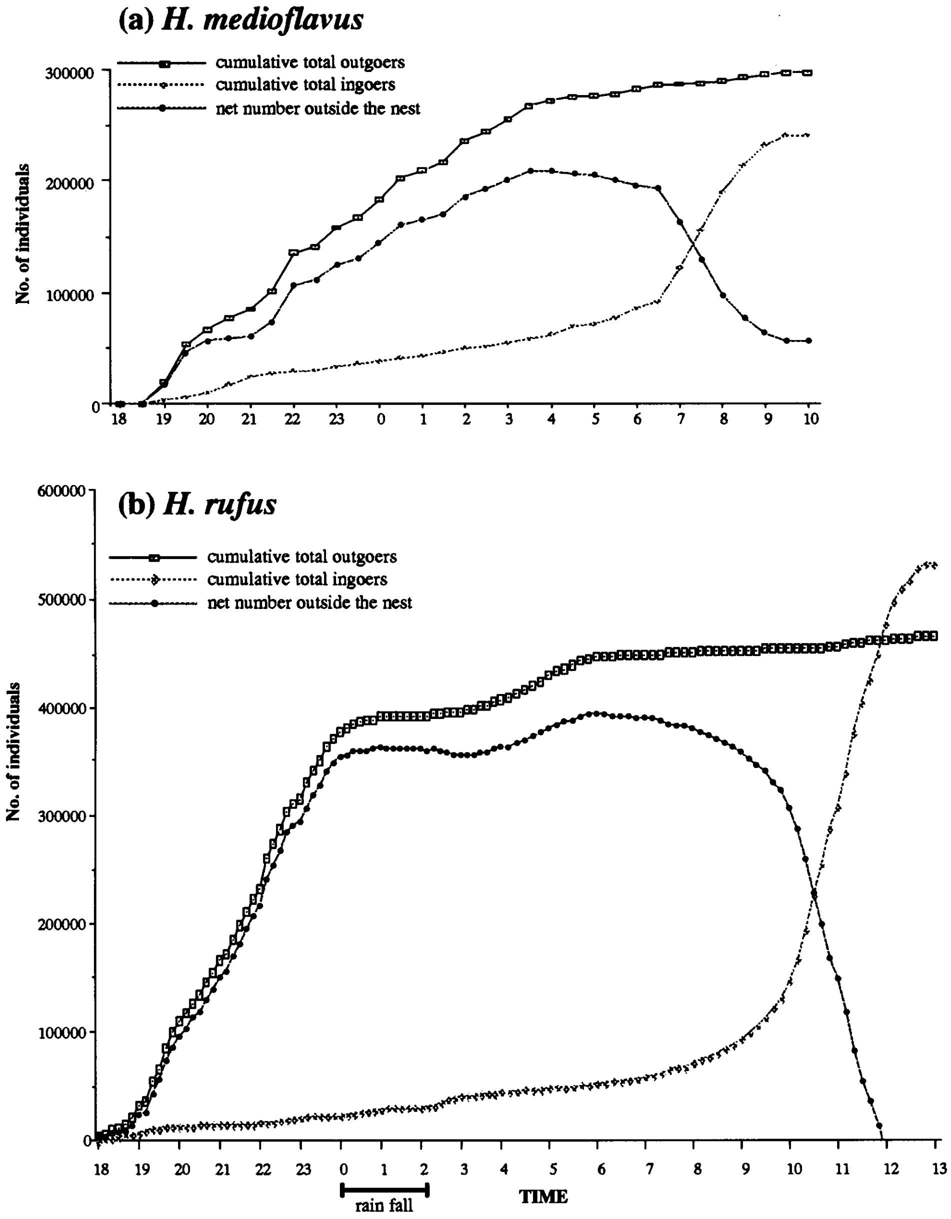

Figure 3. The cumulative number of outgoing and ingoing termites and net population outside the nest. (a) *H. medioflavus* in Kutai National Park, (b) *H. rufus* in Lambir Hills National Park

tree. From 00:00 to 02:00 there was rain, and the foragers ceased marching to take shelter under the bark of tree trunk, etc. The speed of foragers was measured every two hours from the beginning to the end of the activity. Some differences in speed were observed, but in total there was no significant difference between outgoers and ingoers (n = 80, t-test: $p > 0.1$). The average speed every two hours was used for the estimation of numbers of individuals.

Figure 3 shows the cumulative number of outgoers, ingoers and net number of individuals outside the nest during foraging activity. In *H. medioflavus*, about 300,000 individuals left the nest to participate in the foraging event. Workers returned to the nest intensively from 06:00 to 09:00. Total number of ingoers was about 240,000. The maximum number of individuals outside the nest was 200,000 at 04:00. In *H. rufus,* nearly 500,000 individuals left the nest, and the maximum number outside the nest was more than 350,000 at about 06:00. Workers returned most

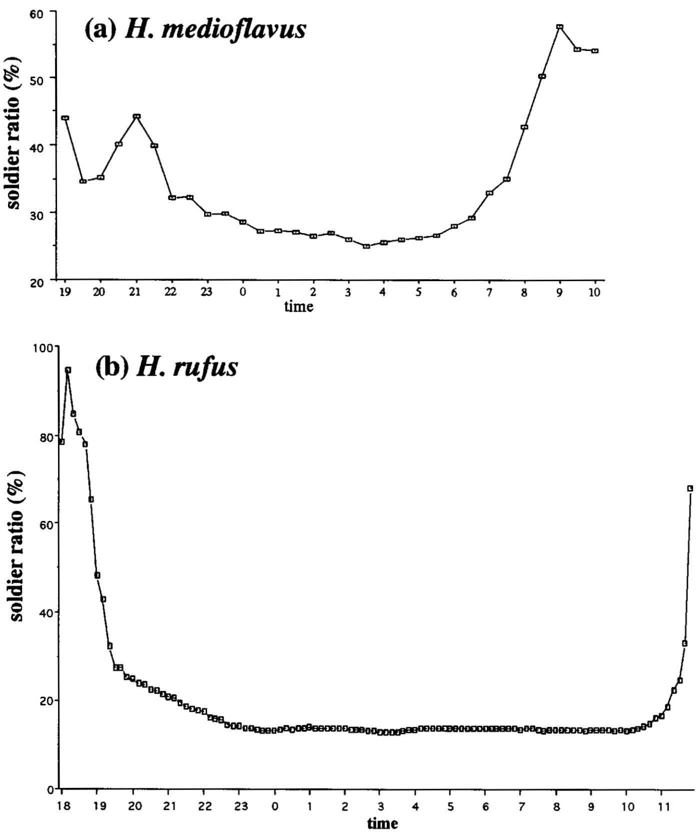

Figure 4. Temporal dynamics in the percentage of soldiers outside the nest during foraging activity. (a) *H. medioflavus*, (b) *H. rufus*. Soldier ratio = cumulative number of soldiers / cumulative number of total foragers × 100 (%). At the beginning and the end of the activity the percentage is relatively high

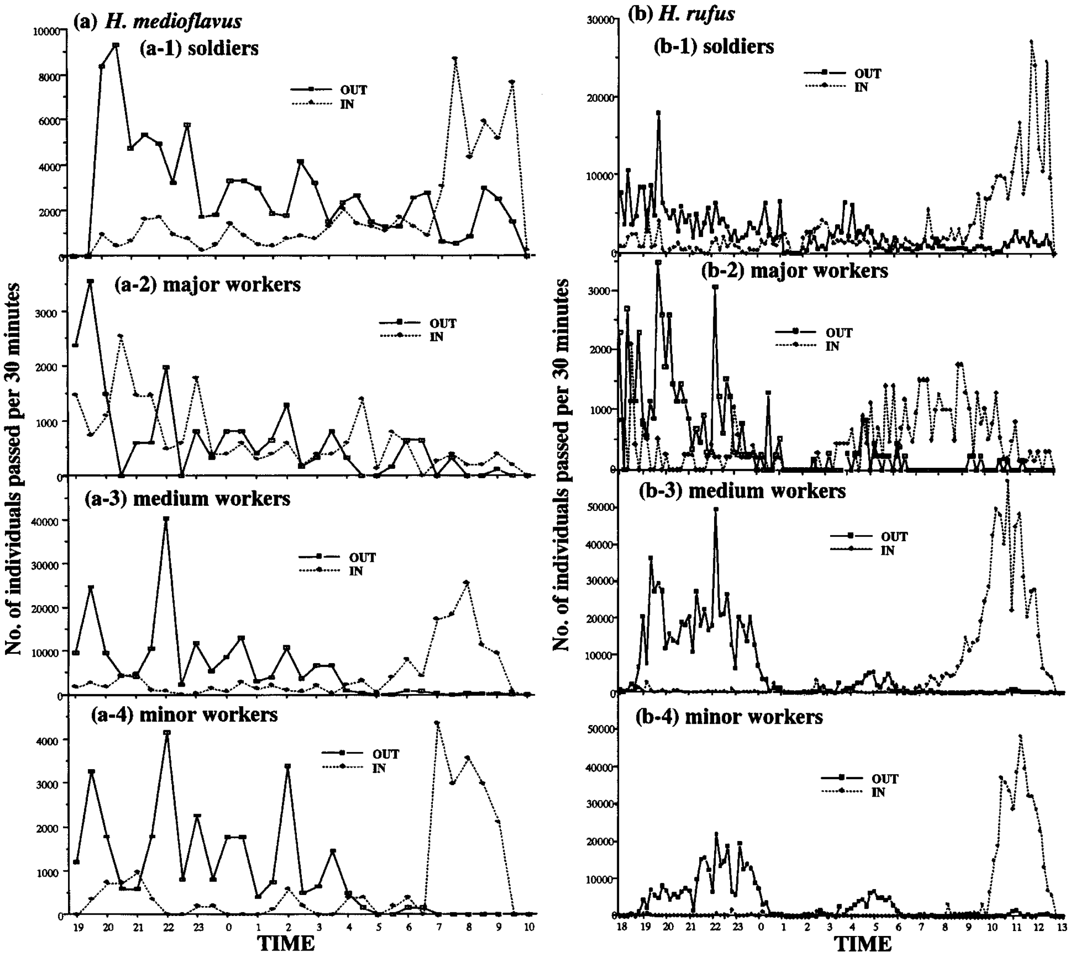

Figure 5. Temporal pattern of outgoing and ingoing soldiers and three types of workers. Number of individuals passing per half hour are shown; (a) *H. medioflavus*, (b) *H. rufus*. Differences between the castes are seen

intensively from 10:00 to 12:00. It was later than in the case of *H. medioflavus*, possibly because midnight rainfall delayed their return.

The percentage of soldiers outside the nest changed during the foraging activity (Fig. 4). As expected, the proportion of soldiers was high at the beginning and at the end of the activity. Ideally the proportion should be 100% at the beginning and at the end because the first individual leaving out or the last individual returning to the nest should be a soldier. In *H. medioflavus*, from 22:00 to 06:00 the ratio was low (around 25%), due to a higher number of workers. In the case of *H. rufus*, the ratio was low (around 17%) from 22:00 to 10:00.

Figure 5 shows the temporal patterns of outgoing and ingoing individuals passing per 30 minutes. Both *H. medioflavus* and *H. rufus* show very similar patterns. In medium and minor workers, periods of outgoing and ingoing were distinctly separated; for example, the majority of medium and minor workers were outgoing until 04:00, and then ingoing from 05:00 in *H. medioflavus*. Little conspicuous difference between medium and minor workers is recognized, though many medium workers carried food balls when returning to the nest. Minor workers were seldom engaged in the task of carrying food balls. However, the pattern for major workers was distinctive. Major workers went back and forth throughout the activity. They played a role as carrier of food balls from an early stage of the activity, while medium workers carried food balls only in the later stages. In soldiers there was less obvious separation of outgoing and ingoing activity than that in medium and minor workers. Soldiers went out of the nest even at the latest stage of the activity and escorted workers back to the nest. From these results it is clear that the temporal pattern of behavior differed among castes.

Based on all foragers in the foraging column, composition of castes was 27.8% soldiers, 7.1% major, 56.3% medium and 8.8% minor workers in *H. mediflavus*, 22.5% soldiers, 3.5% major, 46.1% medium and 27.9% minor workers in *H. rufus*. These proportions are the averages of outgoing and ingoing populations.

In *H. medioflavus*, the cumulative number of food ball carriers was 46,600, in which 15.9% were major workers and 83.8% were medium workers. Few minor workers (0.3%) were engaged in carrying food balls. Twenty-five % of ingoing workers were carriers. The number of food balls was equal to the number of carriers. Since the average weight of food balls (of 3 other colonies) was 0.86 ± 0.27 mg (d.w.; mean ± s.d.; n = 30), the colony brought back an estimated 40.1g (d.w.) of food in a night. In the case of *H. rufus*, the cumulative number of carriers was 95,200 (12.2% major workers, 85.9% medium workers, 1.9% minor workers). Twenty-three % of ingoing workers were carriers. The colony brought back an estimated 81.9 g (d.w.) of food in a night.

Difference of body weight between outgoers and ingoers

Figure 6 shows the dry body weight of foragers in *H. rufus*. The mean body weight of ingoing workers was significantly heavier than that of outgoing workers (Fig. 6a, t-test: $p < 0.001$). Comparing the body weights of ingoers and outgoers within each foraging caste, outgoers and ingoers show large significant differences in medium and minor workers (Fig. 6b, t-test: $p < 0.001$). The ingoing major workers may be heavier than outgoers, but the number of measured individuals is too small to analyze.

Discussion

The data on frequency of foraging activities (Table 1) suggest that food provisions for about three days are carried to the nest of *Hospitalitermes* in a single foraging event. From our results, 39% of nights were spent for foraging in *H. medioflavus*

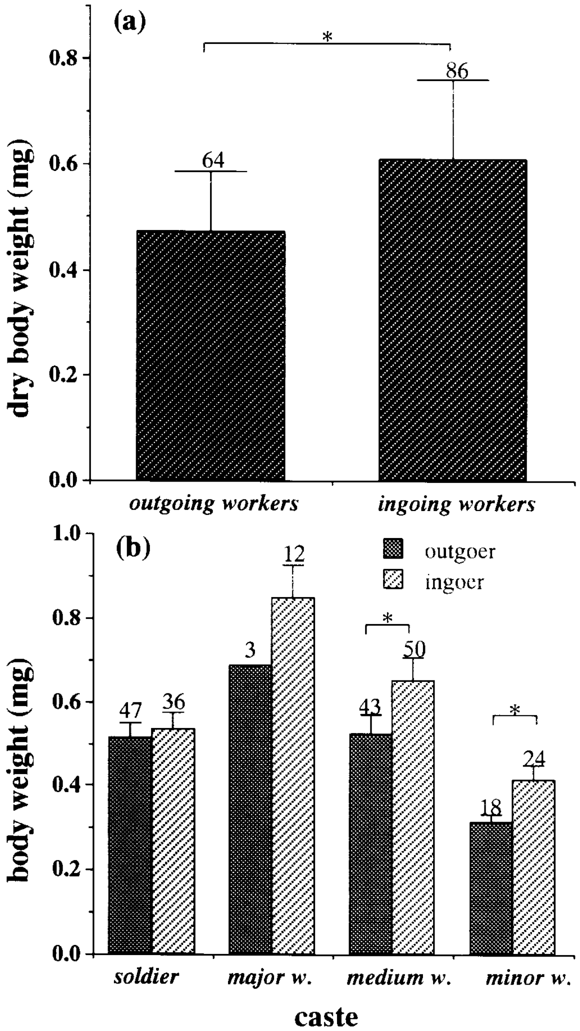

Figure 6. (a) Dry weight of outgoing and ingoing workers in *H. rufus*. All of the trimorphic workers are included. A significant difference between them is recognized. (b) Dry weight of each caste in outgoing and ingoing columns. In medium and minor workers, significant differences between outgoers and ingoers are recognized (asterisks indicate t-test: $p < 0.0001$). Numbers on columns indicate the numbers of measured individuals. Bars indicate standard deviation

and 47% in *H.* sp.A on the average. These frequencies of the foraging events are similar to *H. hospitalis* studied by Jones and Gathorne-Hardy (1995). Food balls carried to the nest were stored in specific chambers. We found food storage chambers in the nest of *H. medioflavus* (Miura and Matsumoto, 1997) and *H. rufus*. Depletion of food stores may trigger foraging events. Judging from the pattern of frequency, foraging tended to start in the evening and continue to the next morning. Daily foraging activity may be initiated by darkness or temperature. Recorded foraging events (Fig. 1) showed a high degree of synchronization among the investigated colonies of *Hospitalitermes.* As the termites did not forage during rainfall, we suggest that climatic conditions cause the observed synchronization. From these results, we conclude that the quantity of food remaining in the nest and climatic conditions are the main determinant factors of whether foraging occurs.

Although Collins (1979) found the walking speed to be almost constant irrespective of direction and load in *H. umbrinus*, significant differences were found in *H. medioflavus.* However, in *H. rufus* no difference of marching speed was detected between the two directions. According to our estimates, about 300,000 to 500,000 individuals left their nest to forage. However, the actual number of foragers will depend on colony size. We have never found incipient colonies of *Hospitalitermes,* so it is unknown how they accomplish their foraging when a colony has a small population.

The soldier to worker ratio was high at the beginning and end of the activity (Fig. 4), which indicates that soldiers play important roles in leading other foragers to the feeding site, and protecting the column until the end of the foraging activity. Soldier ratio outside the nest was about 20% even at the lowest level of activity, but only 13–14% in the nest (Miura and Matsumoto, unpublished) which is higher than previously reported (Haverty, 1977). In this respect, the soldier caste is thought to play a more important role as defender when foraging than while in the nest. As shown in Figure 5a-1 and Figure 5b-1, soldiers pass back and forth throughout the activity period. This observation may indicate that soldiers also play a role as messengers between the nest and the foraging site.

For major workers, the time of peak outgoing and ingoing overlapped. From the early stage of the activity, ingoing major workers were frequently observed. In the early stages of the foraging event the major workers were the predominant carriers of food balls. Major workers which left the nest at later stages of the foraging event may have previously returned from the foraging site with a food ball and deposited it in the food store. However, we do not have any proof that major workers make repeated visits to the feeding site during one foraging event. To investigate this possibility, it would be necessary to mark workers. Since major workers are older than medium and minor workers (Miura and Matsumoto, 1995), the fact that major workers actively forage outside the nest, i.e., age polyethism, is similar to the phenomenon seen in some ants and other termites (Pasteels, 1965; McMahan, 1977; Watson and McMahan, 1978; Tsuji, 1992).

The largest proportion (about 50%) of foragers were medium workers. The mean flow of medium workers changed from outgoing to ingoing in the early morning. Although medium workers act as both carriers and gnawers, carrying became their dominant activity in the later stages. This observation might support the hypothesis that medium workers first work as gnawers and afterwards change their task to carry food balls when they return to the nest. Most of the food acquired during foraging was carried to the nest by medium workers.

Minor workers tended to return to the nest all at the same time, after 07:00 for *H. medioflavus* and after 09:00 for *H. rufus*. They were seldom engaged in the task of carrying but instead only gnawed at the foraging sites. As minor workers are at a relatively young stage of development (Miura and Matsumoto, 1995), it is reasonable that their activity is concentrated in a short time and they move together in a group, which may be a behavioral adaptation against predation.

Calculated from our data, the number of food balls (= number of carriers) was 14.6% of the total number of foragers in *H. medioflavus*, and 17.9% in *H. rufus*. From Collins' (1979) data on *H. umbrinus,* it was 9%. The requirement for food resources may be different according to the colony size, with demand being greater in larger colonies. From our results of the measurement of worker body weight before and after foraging (Fig. 6), it is clear that workers returning to the nest without food balls (about 75% of ingoing workers) ate food at the feeding site as well as helping to make food balls. Soldiers, nymphs and reproductives, cannot take food by themselves but must receive food material from workers through trophallaxis or secretion. The average increase in weight of all worker bodies is 0.14 mg (d.w.), and total number of ingoing workers is about 500,000. Therefore, the total amount of food in the guts of ingoers is approximately 70 g. As the estimation of food balls acquired was about 80 g, the total amount of food carried back to the nest during the foraging event was estimated to be about 150 g (d.w.). The demand for food will vary according to factors such as colony size, seasonality and the production of alates. The relationship between amount of food and colony size needs further investigation.

Although some studies on social insect foraging dynamics have been published on bees and ants (e.g., Menzel and Greggers, 1992; Simon and Hefetz, 1992), studies on termites are very few. However, some studies have been performed on termites which forage in the open. Studies on the foraging behavior of *Trinervitermes* were reported by Sands (1961, 1965), Nel (1968), Leuthold and Lüscher (1974), Ohiagu (1979) and Oloo (1981). However, none of the above studies focused on caste ratio in the foraging population. Behavioral differences among castes (instars) was reported for *Nasutitermes extiosus* (McMahan, 1977) and *Drepanotermes* (Watson and McMahan, 1978). In the case of some *Nasutitermes* species these differences were explained as temporal polyethism (Pasteels, 1965; McMahan, 1979). In our study we focused on caste ratio dynamics by the observation of open-air-foraging termites. In the studies of social insects, it is very important to understand the behavioral differences between castes and their communication. The division of labor and the communication among these castes during foraging activity are important in termite sociality (Stuart, 1969). Further studies on them will help to uncover the mechanism and the evolution of the social behavior of termites.

Acknowledgements

We thank Dr. D. Jones for valuable comments on the manuscript. We are also grateful to Drs. A.A. Hamid, T. Inoue, S. Yasuma and S. Maman for their instructions of our field survey. This work was supported partly by Grant-in-Aid International Scientific Research Program (Nos. 07044193, 08041136) and for Scientific Research (No. 07454211) from the Ministry of Education, Science and Culture of Japan. The first author was supported by Research Fellowships of the Japan Society for the Promotion of Science for Young Scientist.

References

Abe, T., 1979. Studies on the distribution and ecological role of termites in a lowland rain forest of West Malaysia (2) food and feeding habits of termites in Pasoh forest reserve. *Japanese J. Ecol. 29*: 121–135.

Collins, N.M., 1979. Observations on the foraging activity of *Hospitalitermes umbrinus* (Haviland), (Isoptera: Termitidae) in the Gunong Mulu National Park, Sarawak. *Ecol. Entomol. 4*: 231–238.

Chuah, C.H., S.H. Goh, G.D. Prestwich and Y.P. Tho, 1983. Soldier defense secretions of the Malaysian termite *Hospitalitermes umbrinus* (Isoptera, Nasutitermitinae). *J. Chem. Ecol. 9*: 347–356.

Escherich, K., 1911. *Termitenleben auf Ceylon*. Jena: Fischer.

Haverty, M.I., 1977. The proportion of soldiers in termite colonies: a list and a bibliography (Isoptera). *Sociobiology 2*: 199–216.

Jander, R. and K. Daumer, 1974. Guide-line and gravity orientation of blind termites foraging in the open (Termitidae: *Macrotermes, Hospitalitermes*). *Insectes soc. 21*: 45–69.

Jones, D.T. and F. Gathorne-Hardy, 1995. Foraging activity of the processional termite *Hospitalitermes hospitalis* (Termitidae: Nasutitermitinae) in the rain forest of Brunei, north-west Borneo. *Insectes soc. 42*: 359–369.

Kalshoven, L.G.E., 1958. Observations on the black termites, *Hospitalitermes* spp., of Jawa and Sumatra. *Insectes soc. 5*: 9–30.

Leuthold, R.H. and M Lüscher, 1974. An unusual caste polymorphism of the sternal gland and its trail pheromone production in the termite *Trinervitermes bettonianus. Insectes soc. 21*: 335–342.

Levings, S.C. and E.S. Adams, 1984. Intra- and interspecific territoriality in *Nasutitermes* (Isopotera: Termitidae) in a Panamanian mangrove forest. *J. Anim. Ecol. 53*: 705–714.

McMahan, E.A., 1977. Mound repair and foraging polyethism in workers of *Nasutitermes exitiosus* (Hill): (Isoptera: Termitidae). *Insectes soc. 24*: 225–232.

McMahan, E.A., 1979. Temporal polyethism in termites. *Sociobiology 4*: 153–168.

Menzel, R. and U. Greggers, 1992. Temporal dynamics and foraging behaviour in honey bees. In: *Biology and Evolution of Social Insects* (J. Billen, Ed.), Leuven University Press. pp. 325–334.

Miura, T. and T. Matsumoto, 1995. Worker polymorphism and division of labor in the foraging behavior of the black marching termite *Hospitalitermes medioflavus*, on Borneo Island. *Naturwissenschaften 82*: 564–567.

Miura, T. and T. Matsumoto, 1997. Diet and nest material of the processional termite *Hospitalitermes,* and cohabitation of *Termes* (Isoptera: Termitidae) on Borneo Island. *Insectes soc. 44*: 267–275.

Nel, J.J.C., 1968. Aggressive behaviour of the harvester termites *Hodotermes mossambicus* (Hagen) and *Trinervitermes trinervoides* (Sjöstedt). *Insectes soc. 15*: 145–156.

Ohiagu, C.E., 1979. A quantitative study of seasonal foraging by the grass harvesting termite, *Trinervitermes geminatus* (Wasmann), (Isoptera, Nasutitermitinae) in Southern Guinea savanna, Mokwa, Nigeria. *Oecologia 40*: 179–188.

Oloo, G.W., 1981. Specificity of termite trails: analysis of natural trails of *Trinervitermes*, *Macrotermes* and *Odontotermes* from sympatric populations. *Entomol. exp. appl. 29*: 162–168.

Pasteels, J.M., 1965. Polyéthism chez les ouvriers de *Nasutitermes lujae* (Termitidae Isoptères). *Biologia Gabonica 1*: 191–205.

Prestwich, G.D., 1984. Defense mechanisms of termites. *Ann. Rev. Entomol. 29*: 201–232.

Roonwal, M.L., 1970. Termites of the oriental region. In: *Biology of Termites.* Vol. II, (K. Krishna and F.M. Weesner, Eds.), Academic Press, N.Y. pp. 315–391.

Sands, W.A., 1961. Foraging behaviour and feeding habits in five species of *Trinervitermes* in West Africa. *Entomol. exp. appl. 4*: 277–288.

Sands, W.A., 1965. Mound population movements and fluctuations in *Trinervitermes ebenerianus* Sjöstedt (Isoptera, Termitidae, Nasutitermitinae). *Insectes soc. 12*: 49–58.

Simon, T. and A. Hefetz, 1992. Dynamics of mass recruitment and its regulation in *Tapinoma simrothi*. In: *Biology and Evolution of Social Insects,* (J. Billen, Ed.), Leuven University Press. pp. 325–334.

Stuart, A.M., 1969. Social behavior and communication. In: *Biology of Termites.* Vol. I, (K. Krishna and F.M. Weesner, Eds.), Academic Press. N.Y. pp. 193–232.

Tho, Y.P., 1992. *Termites of Peninsular Malaysia*. Malayan Forest Records No. 36 (L.G. Kirton, Ed.), Forest Research Institute Malaysia.

Tsuji, K., 1992. Reproductive division of labour related to age in the Japanese queenless ant, *Pristomyrmex pungens*. *Anim. behav. 39*: 843–849.

Watson, J.A.L. and E.A. McMahan, 1978. Polyethism in the Australian harvester termite *Drepanotermes* (Isoptera, Termitinae). *Insectes soc. 25*: 53–62.

Received 27 May 1997;
revised 4 August 1997;
accepted 8 August 1997.