Spatial segregation of four coexisting processional termites (Termitidae: Nasutitermitinae) in tropical rainforest

Yoko TAKEMATSU[1], Kohei KAMBARA[2], Takashi YAMAGUCHI[1] and Kazuaki MITSUMAKI[1]

[1]Department of Biological and Environmental Sciences, Faculty of Agriculture, Yamaguchi University, Yamaguchi, Japan and [2]The United Graduate School of Agricultural Sciences, Tottori University, Tottori, Japan

Correspondence: Yoko Takematsu, Department of Biological and Environmental Sciences, Faculty of Agriculture, Yamaguchi University, 1677-1 Yoshida, Yamaguchi 753-8515, Japan.

Email: takematu@yamaguchi-u.ac.jp

Abstract

In Lambir Hills National Park, Sarawak, Malaysia, there are four species of processional termites coexisting: *Hospitalitermes hospitalis, H. lividiceps, H. rufus*, and *Longipeditermes longipes*. This paper presents the results of our investigation on the spatial distribution of nests and foraging activities of the four species in coexistence. The results show that there are fairly marked differences in nesting sites as well as in foraging activities among the four species. It is noteworthy that *H. rufus* inhabits only the canopy area over 20m above the ground, apparently segregated from the other three species, and that their foraging activities are limited also to tree canopies over 10m above the ground. By contrast, *L. longipes* nests underground and forages exclusively on the forest floor. *Hospitalitermes hospitalis* and *H. lividiceps* inhabit and forage over wide areas from the forest floor to the tree canopies. The upper parts of the tree canopy (over 10m) are also foraging territories of the secluded *H. rufus*, but there were no observations of simultaneous foraging of the three *Hospitalitermes* species in the same canopy areas.

Key words: foraging column, *Hospitalitermes*, *Longipeditermes*, tree canopy

Termites are important insects that act as decomposers in forest ecosystems. In order to evaluate the role of termites in the forest decomposition system, it is necessary to understand food sources, life types and foraging activities of individual species, which are quite diverse among species. Termites feed not only on wood but also on leaf litter, lichen, humus, fungus, grass, dung and vertebrate corpses (Bignell & Eggleton 2000). Life types also vary among species. Some termites feed on wood in which they inhabit ("one piece type") and others forage for food outside their nests ("separate type") (Abe 1979). The majority of separate-type species travel in search of food through tunnels or galleries in soil and wood. However, there are "processional termites" that forage processionally, like ants, in exposed columns on tree trunks and in tree canopies in

tropical forests (Kalshoven 1958; Jander & Daumer 1974; Collins 1979). These termites are characterized by a dark body color and long legs. *Hospitalitermes*, *Laccessititermes* and *Longipeditermes* are three nasutitermitine genera of processional termites found in Southeast Asia. Their foraging behaviors were studied previously in some detail: Miura and Matsumoto (1995, 1997, 1998a, b) investigated the foraging activities of species of *Hospitalitermes* and *Longipeditermes*, including the column organization and the chemical composition of their diets; Jones and Gathorne-Hardy (1995) studied the foraging activity of *H. hospitalis* (Haviland) in Brunei, Borneo; and Hoare & Jones (1998) described the foraging behavior of *L. longipes* (Haviland) in southern Kalimantan, Borneo. However, each of these studies dealt with each species separately, without considering the existence of other species. Usually more than one species of termites coexist in a forest, and there is a possibility that their nesting sites as well as foraging habits are affected by the interaction with each other. The present paper is concerned with this aspect of processional termites.

This study was performed at Lambir Hills National Park (LHNP) (4˚20'N, 113˚50'E), Sarawak, Malaysia, where the canopy observation system of Canopy Biology Plot (8ha quadrate area, plot size is 200m x 400m) is available. The National Park is an extremely diverse lowland dipterocarp forest with a high average annual temperature (26.7˚C) and heavy precipitation (2685m per year). In this forest, there inhabited four processional termites sympatrically; they are three species of *Hospitalitermes* and one species of *Longipeditermes*. The three species of *Hospitalitermes* were morphologically identified as *H. hospitalis*, *H. lividiceps* (Holmgren) and *H. rufus* (Haviland), and *Longipeditermes* was identified as *L. longipes*. In order to collect data on the spatial distributions of their nests and feeding sites, we made about 30 daytime surveys in the forest over two visits to the national park.

Each colony of the processional termites sent out a single foraging column every 3-4 days and maintained the column for about half a day each time. We searched for foraging columns of the four species around the trails of the park and its canopy

observation system, and spotted their nests and feeding sites by tracing the columns. In this manner 12, 8 and 9 nests were found for *H. hospitalis*, *H. lividiceps* and *L. longipes*, respectively. For *H. rufus*, however, only 5 nests were found in a very limited canopy area accessible only by the canopy observation system, and one of the five nests could not be traced to the feeding site because its foraging column extended far into inaccessible tree canopies. Probably *H. rufus* is distributed widely in the tree canopy areas of the forest, but it was only around the canopy observation system that we could observe both their nests and the feeding sites including the foraging columns. Therefore, we visited the canopy observation system almost every day during our stay in the national park and found 12 foraging columns and feeding sites (no such repeated observations were made for the other three species). The 12 foraging columns of *H. rufus* were eventually traced back to the original 4 nests around the canopy observation system. For each nest, we recorded the heights of the nest site and its feeding site. The lengths of the foraging columns connecting the two sites were also recorded. When a foraging column passed through various heights, as is the case for most columns, the whole column was divided into segments according to the five ranges of height (<0.5m, 0.5-10m, 10-20m, 20-30m and 30m<) and the lengths of the individual segments were measured. Some termites (e.g. *L. longipes*) build their nests underground, and it was impossible to exactly locate these subterranean nest sites and measure the foraging column lengths. In such cases, we only measured the foraging columns on or above the ground.

Table 1 shows the distribution of the nest heights of the four species. The nests of *H. lividiceps* were located at heights of less than 3 m. About 60% of the nests were found at the base of trees (nest height is less than 0m). The nest heights of *H. hospitalis* were less than 15 m. Although the distribution of the nest heights of *H. hospitalis* was nearly the same as that of *H. lividiceps*, some *H. hospitalis* could build their nests over 10m. From our field observations, we found that *H. hospitalis* nested at various places including under tree bases, in canopy ferns and in tree cavities. *Hospitalitermes*

lividiceps nested mainly at the tree base. On the other hand, the nests of *L. longipes* were located only under the ground and their nest openings were on the ground. In contrast to the above three species, *H. rufus* exhibited a specific nesting site characteristic. All the nests of *H. rufus* were located in trunks only in the tree canopy (more than 20m).

Table 2 shows the distribution of feeding site heights of the four species. All of the feeding sites of *H. lividiceps* were located over 10m above the ground. About 90% of the feeding sites for *H. lividiceps* were located at heights of 10-20m and a nest was found over 20m above the ground. *Hospitalitermes hospitalis* foraged from the ground level to the canopy. About 8% of them had feeding sites below 0.5m and foraged for fallen leaves on the ground. About 60% of the feeding sites of this species were located 0.5-10m and one third of the feeding sites were 10-20m. The feeding sites of *H. rufus* were exclusively on tree trunks, twigs and epiphytes, whose heights ranged from 12.1m to 56.6m (For *H. rufus*, all 12 feeding sites from the 4 nests are included in the Table). About 40% of their feeding sites were located over 30m above the ground where no other species inhabited nor foraged. In contrast, *L. longipes* foraged mostly on forest floors and their feeding sites were also confined to the ground level (less than 0.5m).

The foraging column lengths of *H. lividiceps* were 21.0 - 44.7m (mean 35.3m) and those of *H. hospitalis* were 19.5 - 54.8m (mean 32.9m). The lengths of foraging columns of *H. rufus* were highly variable, ranging from 5.8 to 33.2m. On the other hand, foraging columns of *L. longipes* were rather short as measured here, ranging from 3.0 to 15.8m (mean 9.2m); this was likely an underestimation since underground path lengths were not measured as mentioned above. The heights of the foraging columns were related to the heights of nests and feeding sites. Figure 1 illustrates the height distribution of the foraging columns for the four species. The distribution of the foraging columns of *H. lividiceps* and *H. hospitalis* were nearly similar, although the range of *H. lividiceps* was somewhat higher than *H. hospitalis*. The heights of foraging columns of *H. lividiceps* ranged from 0m to 30m. On the other hand those of *H.*

hospitalis ranged from 0m to 20m, and more than 90% of the columns were located at a height of less than 10m. These two species foraged on tree trunks, leaves and twigs. In contrast, the foraging columns of *H. rufus* were confined to heights above 12m. This species foraged only on tree trunks. In particular, one third of the columns of this species were located above 30m where the other three species were not found. We never found foraging columns of *H. rufus* on the forest floor during our observation. Naturally, all foraging columns of *L. longipes* were located at ground level (0m).

We investigated the spatial distribution of nests and foraging columns of four processional termite species coexisting in LHNP with an objective of finding any signs of mutual interactions among those coexisting species. The results of this study showed that there are indeed fairly marked differences in nesting sites as well as in foraging activities among the four species. First of all it is worth noting that one of the four species, *H. rufus*, builds their nests only at heights of over 20m above the ground and is completely separated from the nests of the other three species. The foraging activity of *H. rufus* is also remarkable; they never foraged at heights of less than 10m on tree canopies and traveled only on tree trunks. This species was morphologically identified as *H. rufus*, but such an isolated life style on tree canopies as was found here has not previously been described for *H. rufus*. Miura & Matsumoto (1998b) focused on the temporal aspect of their activities in LHNP, but no mention was made of the specific life style on tree canopies (over 10m above the ground). Is this a new species? There is a possibility that *H. rufus* has changed its nature under the influence of competition in the forest. In order to answer the question, further comprehensive studies focusing on this species are needed. The nesting sites of *H. hospitalis* and *H. lividiceps* were quite similar, ranging from underground to 20m high, and the foraging columns of both species were also similar and ranged from the forest floor to the canopy. It is to be noted that the upper parts of tree canopies over 10m above the ground are also foraging territories of *H. rufus*. However, among the 32 foraging columns in the present study there were no observations of simultaneous foraging of the three *Hospitalitermes*

species in the same canopy areas, although the foraging territories of some nests of different species and different colonies overlapped. To clarify the precise niche segregation over 10m above the ground and to provide the provability of interaction between species, temporal as well as spatial foraging activities should be investigated. In contrast, *L. longipes* foraged only on forest floors, and the nests of the species were located only underground.

From the results, we found that processional termites can be classified into three different types according to the locations of nests and foraging sites: These are ground territory type, canopy territory type and general territory type. *Hospitalitermes rufus* belongs to the canopy territory type. *Longipeditermes longipes* belongs to the ground territory type. *Hospitalitermes hospitalis* and *H. lividiceps* belong to the general territory type. These differences in foraging activities may affect the transportation of cellulose materials in the forest. In LHNP, *H. rufus* foraged only in the canopy area, and thus this species contributes to the material cycling of the forest canopy. In contrast, *L. longipes* foraged only on the forest floor, and this indicates that this species contributes to the materials cycling of the forest floor as a decomposer of humus and dead wood. *Hospitalitermes hospitalis* and *H. lividiceps* contribute to the overall material recycling. Termites forage for cellulosic resources and the food sources of termites are generally rich in carbon and hydrogen but poor in nitrogen (Traniello & Leuthold 2000). *Hospitalitermes* species have shown a preference for lichens and the nitrogen content of *Hospitalitermes* diet was 10-60 times greater than that of wood (Miura & Matsumoto 1997). Miura & Matsumoto (1998b) reported that *L. longipes* prefer the lower, nitrogen-rich layer of the litter. To explain the bias in spatial distribution, the differences in the chemical composition of foraged foods should be compared among the four species in conjunction with foraging activities.

The density of each species, temporal dynamics of foraging activities and the total amount of material transported remain to be investigated and compared among the four species.

ACKNOWLEDGMENTS

We are grateful to the Forest Research Centre, Sarawak Forestry Corporation, Sarawak, for support and the permission to conduct this research. We also thank the staff of the Lambir Hills National Park for kind help and support. This research was supported by JSPS KAKENHI Grant Number 16405009.

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 Journal of Ecology* **29**, 121–135.

Bignell DE, Eggleton P (2000) Termites in ecosystem. In: Abe T, Bignell DE, Higashi M (eds) *Termites: Evolution, Sociality, Symbioses, Ecology*, pp. 363-387. Kluwer Academic Publishers, Dordrecht.

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

Hoare A, Jones DT (1998) Notes on the foraging behaviour and taxonomy of the southeast Asian termite *Longipeditermes longipes* (Termitidae: Nasutitermitinae). *Journal of Natural History* **32**, 1357–1366.

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

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

Kalshoven LGE (1958) Observations on the black termites, *Hospitalitermes* spp., of Jawa and Sumatra. *Insectes Sociaux* **5**, 9–30.

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

Miura T, Matsumoto T (1998a) Foraging organization of the open-air processional lichen-feeding termite *Hospitalitermes* (Isoptera, Termitidae) in Borneo. *Insectes Sociaux* **45**, 17–32.

Miura T, Matsumoto T (1998b) Open-air litter foraging in the nasute termite *Longipeditermes longipes* (Isoptera: Termitidae). *Journal of Insect Behavior* **11**, 179–189.

Traniello JFA, Leuthold RH (2000) Behavior and ecology of foraging in termites. In: Abe T, Bignell DE, Higashi M (eds) *Termites: Evolution, Sociality, Symbioses, Ecology*, pp. 141–168. Kluwer Academic Publishers, Dordrecht.

Figure legends

Figure 1 Height distribution of the foraging columns (%±SE) of four coexisting processional termites, *Hospitalitermes lividiceps* (A), *H. hospitalis* (B), *H. rufus* (C) and *Longipeditermes longipes* (D).

Table 1 Distribution of the nest heights of four coexisting processional termites

Species	N	Height ranges (m)*				
		<0.5	0.5-10	10-20	20-30	30<
H. lividiceps	8	5 (62.5)	3 (37.5)	0 (0.0)	0 (0.0)	0 (0.0)
H. hospitalis	12	7 (58.3)	4 (33.3)	1 (8.3)	0 (0.0)	0 (0.0)
H. rufus	5	0 (0.0)	0 (0.0)	0 (0.0)	3 (60.0)	2 (40.0)
L. longipes	9	9 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)

*Number of nests and the proportion (%) in parentheses.

Table 2 Distribution of the heights of feeding sites of four coexisting processional termites

		Height ranges (m)*				
Species	N	<0.5	0.5-10	10-20	20-30	30<
H. lividiceps	8	0 (0.0)	0 (0.0)	7 (87.5)	1 (12.5)	0 (0.0)
H. hospitalis	12	1 (8.3)	7 (58.3)	4 (33.3)	0 (0.0)	0 (0.0)
H. rufus	12	0 (0.0)	0 (0.0)	5 (41.7)	2 (16.7)	5 (41.6)
L. longipes	9	9 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)

*Number of feeding sites and the proportion (%) in parentheses.