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Research article

Contributions to the life history of the Malaysian giant ant *Camponotus gigas* (Hymenoptera, Formicidae)

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Summary. We studied 4 polydomous colonies of the giant ant *Camponotus gigas* living on ca. 5 ha of primary rain forest in Borneo. Colony structure was flexible, comprising between 8 and 14 mostly subterranean nests. During the course of the study some nests were abandoned and others were established. Colonies appeared territorial with nests being connected by trails through the forest canopy. The best studied colony had a territory of 0.8 ha and a population of ca. 7000 workers, distributed unevenly among an average of 11 nests. Workers were bimorphic, majors on average weighed 372 mg and minors 135 mg. The castes differed in the morphology particularly by allometric growth of the head (mean head width 6.93 mm and 3.56 mm).

Foraging was mainly nocturnal. At dusk large numbers of foragers (between 35 and 2287 left single nests within 75 minutes of the onset of foraging) invaded the canopy, many workers commuting between the canopy and the nests and all returning home by dawn. During the daytime foraging was reduced and was restricted to a much smaller number of workers which roamed the forest floor. *C. gigas* foragers collected mainly honeydew (90%) with the remainder consisting of insect prey and bird droppings. Hunting success was increased by rainfall. The numbers of foragers in each nest frequently changed naturally, but could be manipulated by altering local food supply.

Key words: Formicidae, polydomy, ecology, social structure, rain forest canopy.

Introduction

Camponotus gigas Latreille 1802 (subgenus *Dinomyrmex*) is one of the largest ant species of the world living in the South-East Asian rain forests, from Sumatra to Thailand. Its habitat ranges from peat swamps of the mangrove forests up to the mountain forests at 1500 m above sea level. In South Borneo it is replaced by *Camponotus gigas* var. *borneensis*, a subspecies with yellow legs. Although it is a conspicuous element of the Malaysian fauna (Tho, 1981; Gault, 1987; Chung and Mohamed, 1993; Levy, 1996; Orr and Charles, 1994; Orr et al., 1996), a comprehensive study of its life history is still lacking.

We studied the behavioral ecology of *C. gigas* in the tropical lowland rain forest of Sabah and gathered basic ecological data as a part of a long term investigation (Pfeiffer, 1997). *Camponotus gigas* is a central place forager which has a polydomous colony structure, combining efficient communication, ergonomic optimization, polyethism and effective recruitment systems (Pfeiffer and Linsenmair, 1998). A subcaste of specialist transport workers carries food from peripheral nests to the central nest of the queen. The aseasonal nuptial flight pattern of *C. gigas* shows phase shifted reproductive cycles and a circasemiannual rhythm with a period of 188 ± 5 days (Pfeiffer and Linsenmair, 1997). Its territorial behavior consists of long lasting ritual fights between a few specialist majors that meet at fixed tournament places (Pfeiffer and Linsenmair, in prep.). In this paper we summarize some fundamental data on territory, colony structure, biometry, activity, diet, and foraging behavior of this remarkable giant ant.

Material and methods

Observation object, area, and time

We studied a total of 50 nests from four colonies of *Camponotus gigas* in different parts of Kinabalu National Park near Poring Hot Spring (N 6°2′, E 116°42′, District of Ranau, Malaysia) where the ant community contains 524 morphospecies from seven subfamilies and 73 genera (Brühl et al., 1998) and is the most species rich yet described for a tropical rain forest. The main observation plot was a five hectare area of primary mixed dipterocarp rain forest at ca. 580 m above sea level. We studied the plot continually between July 1991 and November 1995, except for August in each year. Most behavioral recordings were made at night, using red-filtered head lamps (Petzl "Mega", with filter about 20 lux), starting at 17:00 hours (1/2 h prior before ants' main foraging activity). Annual rainfall ranges from 2000 to 3800 mm (1975–83) (Kitayama, 1992), and we measured 3218 mm in 1993. One of the polydomous colonies of *C. gigas* within our plot was located in a comparatively flat area with a 6 to 16% inclination, and was chosen as focus colony.

Territorial mapping

Nests of *C. gigas* were mapped by examing the trunks of all large trees in the plot at night time, the 10,000 m^2 plot around the borders of colonies A and B (see Fig. 1) was scrutinized with special care. In addition, we laid out 20 100-m-transects, at approximately 10 m intervals, each with 15 baits, consisting of petri-dishes filled with human urine (this was very attractive to *C. gigas* and other ant species). Two further lines (24 baits each) were set with sugar water and two lines set with tuna. On each of 11 successive nights two baited transects were set, the baits were examined hourly and foragers were followed back to their nests.

Territory borders of the polydomous colonies were determined by collecting samples of foragers from all nests and forcibly presenting individuals to conspecifics at other nest sites or on trunk trails, at places where the ants were not able to flee (e.g., twigs). Within a short time several ants touched the newcomer with their antenna. The examined ant was considered to be a member of the colony if we observed peaceful interactions – after some short contact – ranging from no reaction to grooming and trophallaxis. Ants from very distant nests of the same polydomous colony caused extended and intensified antennation, but were never attacked. Ants from alien colonies released avoidance behavior or immediate aggression, resulting in several ants circling and attacking the alien, which was killed and/or carried to the nest. As a control five ants from each nest were kept in captivity for about 1/2 hour and presented at their own nests. These were accepted in all cases. In this way all nests could be attributed to one of the polydomous colonies. We climbed more than 30 trees to explore the foraging trails into the canopy. To study the interactions between the nests more closely, we established a well to observe trail system of artificial bamboo bridges measuring 430 m that connected the nests of the focus colony A. These bridges shortcutting the tree trunk trails of the ants were readily accepted by *C. gigas* within a few days. The foraging range of individuals and the interactions between the nests were studied by individually marked foragers. The speed of locomotion was estimated for ten ants (five ants with load and five unloaded) running up and down a three meter section of the bamboo trail (at about 21 °C).

Studying foraging activity

The dial activity of *C. gigas* was studied by five 24-hours activity countings at different nests, eight 12-hours night time examinations (starting at 17:00 hours), and dozens of shorter studies at different daytimes. Altogether we observed 322 hours at 24 nests from five colonies. We noted time and weather conditions and in periods of 15 minutes we recorded: number of foragers and majors leaving and entering the nests, the transport of larvae, prey and honeydew.

The number of foragers of colony A was determined by counting the number of foragers leaving the nests within 1 1/2 hours after the sudden begin of foraging activity at about 17:30 hours (n = 140 observations). After this period exodus of the foragers stopped (see Fig. 2). A longer observation would have falsified the results because of returning foragers, leaving the nests again. A best estimate of the total number of foragers was obtained by data that were recorded by subsequent and partly simultaneous countings at different nests within six days.

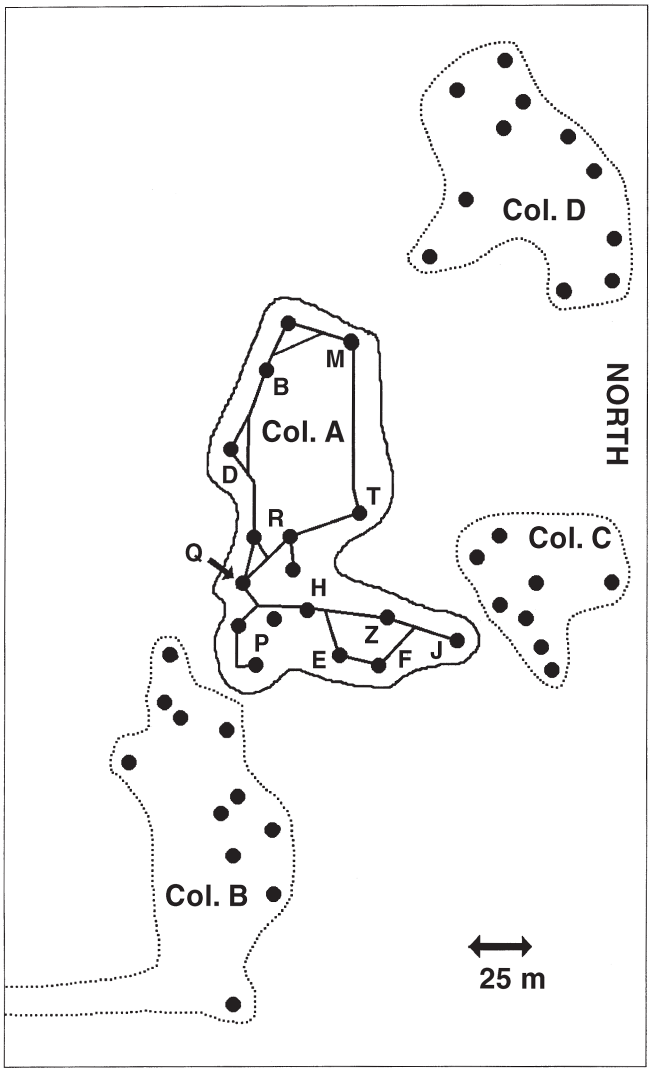

Figure 1. Distribution of four colonies of *Camponotus gigas* in our study area. Nests are symbolized by black dots. At colony A borders could be verified exactly (continuous lines), borders of colonies B, C, D could only be roughly determined (broken lines).The straight lines connecting the nests of colony A are indicating the bamboo runway system. An arrow (Q) points to the putative nest of the queen. Some nests of this colony are named with uppercase letters. In the southern part of colony B there were three additional nests, not shown on this map

Changes within the worker force of the nests were investigated by a set of experiments. In these we measured net exodus activity (number of ants leaving the nest minus number of ants entering the nest) between 17:00 and 19:00 hours under two conditions: without or with extra food supply near the nests.

Experiment 1. Are changes in the number of foragers leaving the nest during the exodus phase a consequence of a changing food supply? We counted exodus activity at nest F over eight days to measure its natural variance. Then we hung eight infusion systems filled with sugar water (flow rate: two drops/minute) to the surrounding trees to provide a continual food supply. The trees were connected to the nest with bamboo trails, the apparatus were refilled daily and kept functioning over five nights. At the 4th and 5th evening we counted activity at nest F again.

Experiment 2. Are changes in the number of foragers leaving the nest during the exodus phase a consequence of worker exchange between different nests of a colony?

We counted exodus activity (simultaneously) at nest B on five days and at nearby nest M over one week to measure its natural variance.

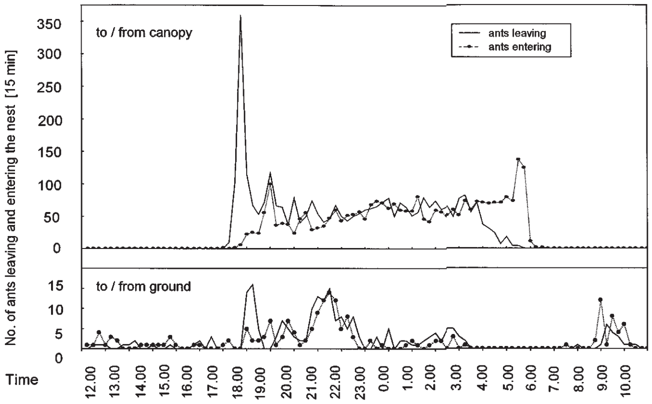

Figure 2. Activity pattern of *C. gigas* at central nest Q on 10 November 1991 during a 24 hours recording. Shown is the number of ants leaving or entering the nest within a periods of 15 minutes. Above: Arboreal activity. Below: Activity at the ground. At daytime foraging was restricted to the forest floor, then the arboreal home range was used by other ant species

Then we marked 35 ants at nest B individually with plastic tags. At nest M we provided sugar water in two infusion systems and in several petridishes as an extra food supply over five days. We measured exodus activity at nest M starting from the second day of the experiment.

Experiment 3. Does extra food supply at a deserted nest attract workers of other nests to stay there?

At the beginning of 1995 nest H, a cavity in a tree, was deserted. Within 1 m distance to the nest's entrance we installed an infusion system with sugar water (simulating a large trophobiont) and connected the nest to the bamboo trail system.

Nest excavations and biometric investigations

In 1995, after we had finished all other studies, we dug up three of the nests of colony A, killed the inhabitants by spraying insecticide ("Shelltox") and collected them to sample biometric data. Additional ants were sampled from nest Q, during a failed attempt to dig it up. Collected ants were fresh weighed (with an electronic balance "Ohaus CT 10") and measured (using a digital-vernier calipers "Mahr 16 ES").

Investigation of the diet and foraging tactics

All records of foraging activity were evaluated to determine the diet of *Camponotus gigas*. Most of the food was carried in the ants' gasters. "Transporter" ants carried the load of several foragers (Pfeiffer and Linsenmair, 1998). After dissecting 20 of them we calculated that honeydew or extrafloral nectar had a share of 95% of all food carried in the gaster (see Results). Although this will have led to a considerable underestimation of the share of liquid food in the diet of *C. gigas* we classified only transporter ants with bursting full gasters as fluid carriers to be on the very safe side.

Most of the droppings and insect prey were carried between the mandibles, thus easy to recognize. Samples were taken from the prey for taxonomical determination. Samples of the "birds' droppings" were chemically analyzed in the laboratory.

The foraging yield depending on different intensities of precipitation, was examined by evaluating 130 hours of observation, conducted at four different nests. A period of 78 hours was dry or with only light precipitation (no rain drops arriving at the forest floor), while during 52 hours there was heavy rain, but not so heavy to stop *C. gigas* from foraging. The differences were tested with a chi-square test.

Founding experiments

Six young queens were caught after their mating flight and transferred to six terraria, filled with soil, plants, decaying wood and small tubes of bamboo that offered shelter and nesting place. Fresh food (honey water, dead insects, tuna fish) was offered regularly. First control took place after three months, thereupon nests with queens and brood were brought to Germany and kept under similar conditions in nests of plaster of Paris within a climatic chamber (25 °C, 88–95% air humidity, 12 h light rhythm).

Results

Activity patterns

Camponotus gigas was a mostly nocturnal animal. With the beginning of dusk foragers left their underground nests jointly. We counted between 40 to more than 2000 foragers that left single nests until 1900 hours, with more than 95% (e.g., at nest Q 97%, S.D. = 2.62, n = 11) running up the trunks of huge trees to swarm out into the canopy. Then activity level declined sharply and the numbers of incoming and outgoing foragers remained balanced. At dawn most ants returned to their nests. At 06:30 hours peak activity stopped and till 08:00 hours we recorded hardly any ant leaving the nest. During daytime, after 08:00 hours, activity was very low: usually only few minors departed from the nests within hours. These diurnal solitary foragers generally did not climb trees, they mostly searched on the ground or within the lower vegetation. Only very rarely foragers that gathered honeydew in trophobiotic associations stayed at their trophobionts on small trees and continued gathering. Thus, activity pattern showed a strong day-night rhythm (Fig. 2).

The location of the nest

Camponotus gigas built its nests mostly in the soil between the buttress roots of emergent trees. From 55 nests of seven colonies that we examined, 43 were built in this way, three laid at the base of smaller trees, six were situated in hollow trunks of small trees, with the nest entrances between one to 2.50 m above the ground, and three in decaying logs lying on the ground.

The colony structure and foraging range of Camponotus gigas

All *Camponotus gigas* colonies in our plot were polydomous. Single colonies comprised between eight to 14 nests. At colony A we first counted 11 nests and calculated a "nearest neighbor distance" of 19.75 m (S.D. = 6.91), at a later stage colony structure changed, four nests were abandoned, five newly established (nearest neighbor distance 19.6 m; S.D. = 7.5; n = 12). At the other three colonies with 14, eight, and 11 nests, we noted nearest neighbor distances of 22.6 m (S.D. = 12.6), 12.8 m (S.D. = 6.6), and 19.1 m (S.D. = 4.8).

The foraging range[1] of colony A covered an area of approx. 8000 m^2. This was determined by hundreds of observations during our field work: of marked foragers, induced recruitments, or territorial conflicts. The territorial borders of the other, less closely observed colonies could only be guessed at, their foraging ranges were estimated to amount to at least 0.57 ha in colony B, and 0.35 ha, and 0.66 ha, respectively, in colonies C and D (Fig. 1). *C. gigas*' polydomous nesting system facilitated the foraging within a large area. We had two hypotheses on why ants needed a large territory: (1) they use large and stable resources that occur widely dispersed or (2) they use resources that are stochastically scattered over the whole area. Both hypotheses were confirmed by our observations. (1) During the whole time of our research we found only two large trophobiotic associations that were exploited by giant ants, though we searched intensively on the ground and in the trees. The fact that trophobionts are rather scarce in this area is confirmed by the extensive investigations of A. Floren, who found only few Homoptera when he fogged dozens of trees (Floren, pers. comm.).

(2) On the other hand, we detected giant ants everywhere in their huge three-dimensional foraging area: in the arboreal stratum as well as on the ground. When we tested the search efficiency of *C. gigas* by a ground level transect with 7 m × 10 m spaced baits, 62% of 160 baits within the foraging area of colony A and 57% of 107 baits in the foraging range of colony B were found within 4 hours after their presentation. These results corroborate the second hypothesis.

The nests of the colonies were connected by trails leading through the canopy. We explored about 200 m of arboreal trails of different colonies by tree climbing. Even when the way on the ground would have been much shorter ants used trails leading through the canopy. The smooth surface of the trees provided an easy way, compared to the litter on the ground. We measured a mean speed of about 6 m/minute (= 331.7 body lengths[2]/ min.) for giant ants on our horizontal bamboo trails (maximum: 10.7 m/min, minimum: 4 m/min, mean time needed to run a distance of 3 m: 29.85 s, S.D. = 6.29, n = 20 individuals). Comparative measurements on the leaf litter showed that ants reached less than half the speed there (n = 15, mean 2.5 m/min., S.D. = 0.21, minimum = 2.20 m/min., maximum = 2.83 m/min.). When we established our artificial trail system we observed that *C. gigas* needed on average merely two days to find the much shorter ways along our bamboo trails. Then, within one night, most ants switched to these shortcuts.

In the next step we wanted to know, whether the members of a *C. gigas* colony were equally distributed among the nests of a colony or changing due to circumstances. To compare ants' abundance at distinct nests of colony A, we analyzed their activity during the nocturnal exodus of the foragers (see Table 1). We determined the total number of foragers of colony A to amount to about 7000 in May 1994, later countings verified this figure.

Table 1. The abundance of foragers at all nests of colony I from July 1991 to July 1994. Given are nest names, the number of countings, the median, minimum and maximum of the countings. Apart from fluctuations in the colony and site, shifting of workers among the nests led to variations within the number of foragers at different nests

NEST	N	MEDIAN	MIN	MAX
Q	28	745.5	231	1287
H	19	536.5	209	1099
E	31	550	223	1100
T	6	1234	191	2287
F	19	269	94	415
TW	2	164	146	182
M	3	643	525	961
B	2	220	160	280
D	2	696.5	444	949
Z	7	306.5	13	446
S	2	41	39	41
R	4	185	112	331
LI	6	280	201	336
BIW	3	83.5	51	105
LI	3	250	37	463
J	1	220	–	–
P	1	60	–	–
O	1	190	–	–

Within our observation time the structure of the colony changed repeatedly. Table 1 shows the variance of the "exodus counts" within the observation time. Some nests seemed to grow rapidly, others declined. Several nests were abandoned, others were newly established. These changes were so quick and nest specifically that they were not due to natural changes of ants' abundance, but mainly to wanderings of ants among different nests of the colony that were influenced by stochastic events, like, e.g., tree fall, and probably also by the distribution of resources: Nest Z, e.g., laid beneath an old *Shorea* tree that had to be felled for security reasons. Within one year the number of foragers leaving this nest declined from formerly 352 (n = 5, S.D. = 77.5) to 13 (n = 1), three months later the nest was deserted. Nest T grew within one year from 191 active foragers at 11 May 1993 to 2287 foragers at 3 June 1994 (mean for 1994: 1456; n = 5; S.D. = 583). Nest H that was situated in a hole of a tree had 264 foragers in spring 1993 (n = 3, S.D. = 68) and was left in June 1993 (0 foragers, n = 5, S.D. = 0). In 1994 we counted an average of 843 foragers leaving the nest (n = 5, S.D. = 224), but in 1995 it was empty again. In one case we observed the relocation of a nest directly.

We could distinguish different types of nests according to their size and different significance within the colony: Nest Q laid in the center of the trail system and was the focal point of specialized transport-workers that carried food items and honeydew as well as larvae and callows from nest to nest. Most food was concentrated at nest Q (Pfeiffer and Linsenmair, 1998) that was the only nest of the colony where we registered nuptial flights (Pfeiffer and Linsenmair, 1997). Eggs were only brought from Q to other nests, therefore we assume that it was the nest of the (single) queen of the colony. Six large nests comprised more than 2/3 of the foragers' force, each of them was left in mean by more than 400 foragers at

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[1] In a further publication we will show that *C. gigas* established and defended true territiories (Pfeiffer and Linsenmaier, in prep.).

[2] Of minors in natural position = 18.09 mm (n = 90).

night. At these nests we also observed patrolling majors and transport of larvae and workers (Pfeiffer, 1997). The minor nests often lacked these features, they had a smaller worker force and their inhabitants pursued special tasks. Most of these nests were established below foraging trees (e.g., near birds' nests or trophobiotic associations), others were specialized "barrack-nests" containing a high percentage of majors guarding the near borders (Pfeiffer and Linsenmair, in prep.).

Experimental induced changes in colony structure

We wanted to learn whether changes in resource access would induce changes in forager abundance at single nests of a *C. gigas* colony and investigated this question by offering extra food near the nests (see methods).

1) At nest F exodus of the foragers was significantly influenced by the extra food we submitted (exact Mann-Whitney U-test, $p < 0.05$). In the first eight days we measured an average of 250 ants ($n = 8$, S.D. = 43.7) leaving the nest under natural conditions, after we had provided extra food for four days, we counted 359 ants ($n = 2$, S.D. = 19.8) during the next two days.
2) At nests B and M ants' numbers fluctuated extremely for unknown reasons: at nest B exodus activity grew on five subsequent nights from 90 to 351, at nest M it declined from 494 to 166. Net exodus activity at both nests correlated significantly negatively among each other ($R(x,y) = -0.89$, $p < 0.05$, $n = 5$). Within the four days of extra food supply, exodus activity at nest M grew from 155 to 369 leaving ants. But due to the former decline, there was no significant difference in the exodus at nest M before and during our extra feeding (U-test, $p = 0.43$). However, between seven and 22 (mean 12) of the foragers, we had marked at nest B a week before, were re-observed at nest M after extra food supply.
3) Nest H had been completely abandoned for at least 4 weeks when we started feeding. After three weeks of the extra food supply 74 ants ($n = 3$, S.D. = 18) left it during the nocturnal exodus, $^1/_4$ of them could be observed at our bait.

Nest excavations and biometrical investigations

In order to learn more about the social structure of *C. gigas* colonies we tried to dig out four nests of colony A. Since we measured a monogynous colony with nest Q containing the queen, we supposed differences in the worker forces. "Source" nests of the periphery should mostly accommodate foragers while central "sink" nests should contain larvae, eggs, brood caring minors, and major workers.

However, we failed in digging out the putative queen nest Q, for its most parts inaccessibly situated within the root system of a huge *Shorea* tree. We could not reach the deeper parts of the nest with larvae, brood tending workers, and the queen and caught less than 30% of the number of ants that had regularly left the nest during exodus time. We had similar problems with nest D, there, however, we caught 94% of the foragers counted before. The other two nests were holes in tree trunks and could be sampled completely.

In nest M we found 319 workers, in nest E 297 workers, and in nest D 216. Nests E and M were nests of the periphery, they differed significantly in mean head width and mean weight of the workers from the more central nest D where we found a greater portion of major workers (see Table 2). As expected no queen was found in these nests.

The distribution of head widths of 1085 workers of four nests from one colony of *Camponotus gigas* is presented in Fig. 3. The size frequency distribution within the colony was bimodal, minors were predominating, they made up 87.3% of the ants we caught (948 minors to 137 majors). The two modal groups overlap, since majors and minors were connected by a small group of intermediate-sized workers. Mean head width of minors was 3.56 mm ($n = 948$, S.D. = 0.53), of majors 6.93 mm ($n = 137$, S.D. = 0.36), the mean weight of minors was 135 mg ($n = 365$, S.D. = 43) and of majors 372 mg ($n = 58$, S.D. = 57).

Besides ants we also found two species of ant guests inside the nests of *C. gigas*: *Camponophilus irmi* Ingrisch 1995, a newly described genus of myrmecophilous crickets (Ingrisch, 1995), and the cockroach *Eroblatta borneensis* Shelford (Fam. Archiblattidae).

The foraging behavior

We observed *C. gigas* in different trophobiotic associations, with wax cicadas *Bythopsyrna circulata* Guèrin-Meéneville (Homoptera/Flatidae), with Coreidae (Heteroptera), different Membracidae (e.g., with *Eufairmairia* sp., pers. comm. U. E. Stegmann), and with Fulgoridae. Ants collected very large amounts of honeydew, excreted by these Homoptera.

Table 2. Weight and head width of workers from three nests of colony A. In the first line the share of minors and majors is given. Nest E and M differed significantly from nest D (Mann-Whitney U-test; weight: M vs. D, $U = 14387$, $p < 0.001$; E vs. D, $U = 12599$, $p < 0.001$; head width: M vs. D, $U = 18133$, $p < 0.001$; E vs. D, $U = 14678$, $p < 0.001$)

	NEST M			NEST D			NEST E		
Minors/Majors	301/19			149/67			291/6		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
Weight [mg]	14.5	8.4	320	23.2	11.4	186	13.5	4.8	295
Head width [mm]	3.66	0.89	320	4.69	1.53	216	3.50	0.61	297

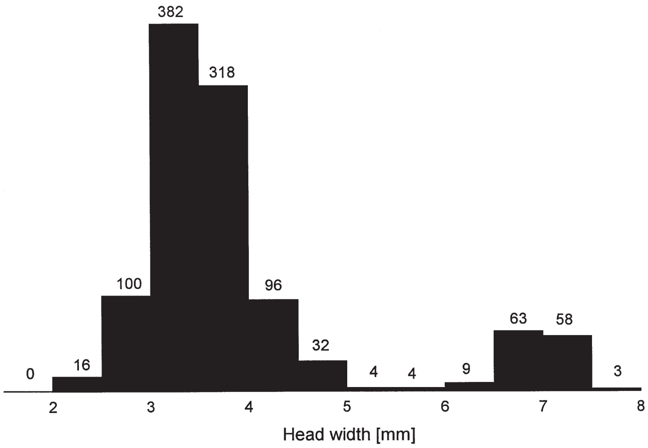

Figure 3. The size frequency distribution of head width (mean = 3.94 mm, min. = 2.10 mm, max. = 7.96 mm, S.D. = 1.22 mm, n = 1085) of *Camponotus gigas* was bimodal, but minors and majors were connected by a small group of intermediates. The minors' distribution is slightly skewed to the left (K-S-test d = 0.108, p < 0.01)

We also observed ants sucking drops from the ground that were excreted by large cicadas sitting somewhere in the tree crowns. *C. gigas* frequently collected extrafloral nectar and sucked plant sap or took rubber directly from plant wounds. Rarely *C. gigas* acted as a scavenger and cut vertebrate cadavers into pieces.

The trophobiotic associations were exploited by a complex system of labor division (Pfeiffer, 1997), the same was true for the transport of food between the nests (Pfeiffer and Linsenmair, 1998). Ants recruited large numbers of nestmates to our artificial baits or to vertebrate cadavers, but foragers were unable for co-ordinated retrieval, however, for their large size individuals could carry heavy pieces of food.

Arthropods' and birds' droppings contributed to the ants' nitrogen supply. At the beginning of the rainy season, when termites and ants had their nuptial flights, *C. gigas*' hunting success rose. Much prey was brought to the nest when rain immobilized the winged sexuals. Birds' droppings, however, were washed from the leaves, so we expected *C. gigas* in rainy nights to find less excrements, but to hunt more insects. Evaluating 130 hours of recordings at nest entrances, we could prove our hypothesis. In 30 nights without rain we measured a mean input of 2.84 pieces of birds' droppings per hour (S.D. = 7.6) and of 1.7 pieces of prey per hour (S.D. = 4.1), in 15 rainy nights we counted a mean input of 1.5 pieces of birds' droppings per hour (S.D. = 2.8) and of 5.0 pieces of prey per hour (S.D. = 8.9). The ratio between droppings and prey during rain laid at 1:3.3 and differed significantly from the ratio of 1.7 : 1 during dry nights (chi square test, $\chi^2 = 104.78$, df = 1, $p < 0.001$).

The diet of Camponotus gigas

Before we started our countings we had dissected 20 transporter ants. In 15 cases we found a sweet tasting, clear liquid inside the gasters (most probably honeydew), in 4 cases small particles of other substances were dissolved in this liquid. In one case when ant's gasters seemed white coloured, we found a hard ball of birds' droppings inside it. Obviously *C. gigas* was able to dissolve it during the regurgitation. These small white balls were also carried by the ants in their mandibles and seemed to be the transport form for birds' droppings. As a result of these dissections, in combination with our behavioral data (Pfeiffer, 1997), we guess that probably 95% of the transport workers that brought food to the nests in their gasters carried honeydew or nectar from extrafloral nectaries.

During the entire time of our field observations we recorded 29,404 foragers that returned to their nests. In 6254 cases we could exactly determine their yield. Table 3 shows the most important taxonomic groups of the prey. The biomass of the different items is listed in Table 4. Most of the food input were liquids that were carried inside the ants' gaster, only in 13% of our records food was transported between the mandibles. Table 5 explains the detailed composition of *C. gigas*' diet.

C. gigas *as a prey*

We identified several predators of the giant ant. At daytime we once observed parasitic Phoridae attacking a major that returned to its nest. During the night we repeatedly observed ground living spiders attacking foragers and Chilopoda (*Scolopendra* spec.) that hunted for young queens. Vertebrate predators like *Manis javanica* (the ant eater) and *Varanus salvator* (monitor lizard) attacked the nests several times, even Geckos (*Cyrtodactylus* spec.) did so. The most common predator of *C. gigas*, however, was the nocturnal giant river toad (*Bufo juxtasper*) that can grow up to 21 cm and attacked nests periodically. Then it was motionless sitting at the nest entrances, "shooting" its long tongue at the returning foragers at a frequency of one per minute.

Results of the founding experiments

After three months in their isolated nests five queens of *C. gigas* were still alive, two of them had eggs and one of these also one pupa. One of these queens survived the next

Table 3. The prey of *Camponotus gigas* consisted of different groups of Articulata. The main group were termites (Isoptera), mostly winged sexuals

Group	Number	Percentage
Isoptera	180	53.1
Ensifera	40	11.8
Lepidoptera	35	10.3
Formicidae	27	8.0
Homoptera	7	2.1
Coleoptera	7	2.1
other Insecta	28	8.3
Aranea	9	2.7
Annelida	6	1.8
Total	339	100

Item	N	Weight	Min.	Max.	S.D.
Birds' droppings	49	48.4 mg	0.5 mg	344.0 mg	76.0
Other excrements	45	22.2 mg	1.0 mg	95.4 mg	25.0
Prey	134	18.6 mg	0.2 mg	256.0 mg	30.6
Vegetation parts	13	8.1 mg	1.0 mg	36.0 mg	9.8
Honeydew carriers:					
Gross weight	220	255 mg	186.7 mg	323.2 mg	68
Net weight	143	139 mg	108.3 mg	170.0 mg	31
Load	–	116 mg	–	–	–

Table 4. Above: Mean fresh weights per ant's load of the main solid components of the diet of *C. gigas*. Total n: 241, mean weight per load: 24.7 mg. **Below:** Mean gross weight, net weight and load of transporter ants of colony A that carried honey dew from trophobiotic Flatidae (from Pfeiffer and Linsenmair 1998). These data were used for the calculation of the data in Table 5

Table 5. The main part of the diet of *C. gigas* consisted of honeydew and nectar, which was brought into the nest in the ants' gasters. Insect prey, droppings and vegetation parts were mostly carried between the mandibles. The table shows the load of 6254 individually checked ants, the percent of all countings and the percentage of the entire biomass (calculated with data of Table 4)

Item	Pieces	Percent of counting	Percent of biomass
Honeydew, extrafloral nectar	5438	86.4	95.4
Birds' droppings	464	7.8	3.6
Other excrements	83	1.4	0.3
Arthropod prey	248	4.1	0.7
Vegetation parts	20	0.3	0.02

months in Germany and established a small colony. Growth was slow: 10 months after we had caught it we counted six workers, four pupae and three larvae. The first workers were typical nantics (head width 2.31 mm, $n = 10$, S.D. 0.12), much smaller than minors of old colonies (U-Test, $U = 17$, $n = -948$, $p < 0.001$). Founding in *Camponotus gigas* seemed to be claustral, none of the six queens took anything of the offered food. Nantics, however, were regularly seen at the feeding stations.

Discussion

Three main factors determined ecology and behavior of the Malaysian giant ant:

1) Its large body size (majors can grow up to 3 cm and weigh up to 400 mg), combined with polymorphism and ergonomic optimization.
2) The relatively low number of individuals (about 7000 foragers) living within one colony.
3) The huge three-dimensional foraging range of this species, combined with the use of clumped and stochastically dispersed resources.

Camponotus gigas is one of the largest ant species of the world and can be compared to the huge South-American ant species *Paraponera clavata* or *Dinoponera gigantea*, both with head widths of more than 4 mm (Bolton, 1994). The enormous size of these species opens them new niches within their rainforest habitats that are characterized by a great diversity of ant species (e.g., Floren and Linsenmair, 1997) and a strong competition among them. Large sized ants are better adapted to forage during heavy rain, and may more easily interact with extra large Homoptera, e.g., Fulgoridae.

In *C. gigas* we found a bimodal size frequency pattern and a diphasic allometry of the head width (Pfeiffer, 1997). Both findings point to an advanced stage of polymorphism (Oster and Wilson, 1978). A bimodal size frequency pattern was also found by Orr et al. (1996), who sampled a central nest of this species.

Although *C. gigas* had a polydomous nesting pattern, we postulate that *C. gigas* was monogynous, as can be concluded from our founding experiments, genetic investigations (Gadau 1997), excavations, and observations of the mating flight that occurred only at one nest of the colony (Pfeiffer and Linsenmair, 1997). Orr and Charles (1994) and Orr et al. (1996), who observed *C. gigas* in Brunei, counted nine to 15 nests in one hectare of forest which is about the density we found in Poring. However, they did not recognize polydomy of *C. gigas* and therefore underestimated its territory size and the population of its colonies by far.

A common reason for polydomy that is found in various ant species (e.g., Buschinger et al., 1994), are too small nest sites that can not be enlarged in any way (e.g., silk nests, tree holes). This is not the case in the ground nesting giant ants that should be able to dig nests of any size. Rather, in *C. gigas* polydomy seems to be an integral part of its "dispersed central-place foraging" strategy, based on foragers searching the forest from single nests that are connected via trunk roads to the central nest of the queen. Transport workers that optimize travel time and load size carry food between the nests, a very flexible "cascade" recruitment allows the quick movement of workers from different nests to every point of the territory, all nests of a colony are interacting intensively (Pfeiffer and Linsenmair, 1998). Nesting structure can only be discussed in connection with the diet of this species that combined stochastically distributed food (insects, bird droppings) as well as clumped resources (honeydew from trophobionts). Foragers had either to be distributed equally over the territory, or had to be concentrated at several focal points. Our experiments testing ants' reaction towards an improved food supply, showed clearly that *C. gigas* reacted very flexible: foragers were attracted to nests where we offered extra food and stayed there, thus obtaining a better access to these resources. This steady process of adaptation led to a continual reorganization of the colony.

The behavioral elasticity of *C. gigas* towards habitat changes is also stressed by the quick and almost complete switching from old arboreal trails to our shorter bamboo trail system. This flexibility is of great adaptive value, e.g., in regard to the common and massive environmental changes caused by treefalls in rain forests. The mean speed of 360 m/h (= 331.7 body lengths/ min.) of *C. gigas* foragers on their arboreal trails was relatively high and facilitated their access to their large foraging areas. Ants of temperate zones are much slower: e.g., the European *Formica polyctena* runs only with 29 m/h (= 60.4 body lengths/min.) at 15 °C (Horstmann, 1974).

The diet of *C. gigas* has been subject of several studies, although extensive investigations have not been made before. Tho (1981) and Chung and Mohammed (1993) described *C. gigas* as omnivore, depending on dead insects, fruits, cadavers and excrements. Rabenstein et al. (1994) and Fiala (pers. comm.) watched *C. gigas* frequently at extrafloral nectaries. Two studies from Brunei do not mention liquid food and stress the importance of fungi: Levy (1996) found fungi to be the main part (39%) of *C. gigas*' diet, followed by ants (7%) and termites (5%), and according to Orr and Charles (1994) fungi contribute to about 60% of the input, approximately 25% of it was arthropod prey. Because ants in Poring took fungi only occasionally and both Brunei studies do not mention at all birds' droppings that look a bit similar to fungi, these items may have been confused. Comparable to us, Gault (1987), in Pasoh, found the solid components of *C. gigas*' diet were 50% insects and 45% birds' droppings and noticed a "sweet liquid" (supposed honeydew) as the main food of *C. gigas*. The importance of honeydew in the diet of *C. gigas* is confirmed by many reports of other scientists from various places of South East Asia (B. Fiala, M. Dill, U. Maschwitz, G. Waldkircher; pers. comm.) and may be largely underestimated even in our study, due to the problems with the exact determination of its quantity.

Honeydew as a main source of food for rainforest ants has been recently stressed by Davidson (1997) and seems to be a general trend within the Camponotini (e.g., Sanders, 1970). At least two of these *Camponotus* species, the Mediterranean *C. cruentatus* (Alsina et al., 1988), and the Namib Desert dune ant *C. detritus* (Curtis, 1985) feed also on excrements of vertebrates. Curtis discusses stomach living micro-organism that should allow the Camponotini the use of excrements as a source of nitrogen.

Why was *C. gigas* mostly active at night, and why stayed the foragers at the ground or the lower vegetation in daytime? We have three hypotheses that complement one another: night activity and avoidance of the canopy during daytime should be a result of (1) climate, (2) predation, and (3) competition.

(1) We agree with most authors (Gault, 1987; Chung and Mohamed, 1993; Orr and Charles, 1994; Levy, 1996) that the high temperature and the relatively low humidity in the canopy during daytime may be one reason for this behavior. Rather constant temperatures and humidity might – among other reasons – also be the explanation for ground nesting of this species. There are, however, some arguments against this hypothesis: (a) if microclimate would be the only reason for night activity, we would expect a much more opportunistic foraging activity, with ants using the canopy in the rainy seasons also during daytime, when temperatures are down and humidity is – also in the canopy – about 100% for weeks. This we had never observed. (b) According to our few measurements in the dry season humidity in understory trees (up to 15 m) during the day is as high and more constant than at the ground, while temperature in this stratum correspond to the temperatures in upper canopy during night time (see Fig. 4). (c) In the early morning after sunrise, conditions are still similar to early evening, when *C. gigas* starts its activity, however, especially in the time from 6.30 hours to 8.00 hours, *C. gigas* showed almost no foraging activity.

(2) The sudden stop of foraging activity in the canopy after sunrise may also be an avoidance of predation by ant-eating birds. While most of the larger *Camponotus* species in Kinabalu park are nocturnal, diurnal arboreal activity is found in many species of *Polyrhachis*, a genus that is better protected against being eaten through large spines, teeth, or hooks on the alitrunk.

Diurnal ant parasites may be another important factor that reduces *C. gigas'* activity during the day. Like Disney and Schroth (1989) in West Malaysia, we also observed phorid flies which attacked a wounded major of *C. gigas*. From phorid flies it is known that they influence the activity and the foraging behavior of their host ants (e.g., Feener, 1988). They are attracted by haemolymph from wounds and lay their eggs into the body of the ants. As the positioning of the ovipositor is controlled optically (Disney and Schroth, 1989), it is likely that these parasites endanger *C. gigas* only in daytime. In *Atta cephalotes* phorid flies influence the size of the diurnal

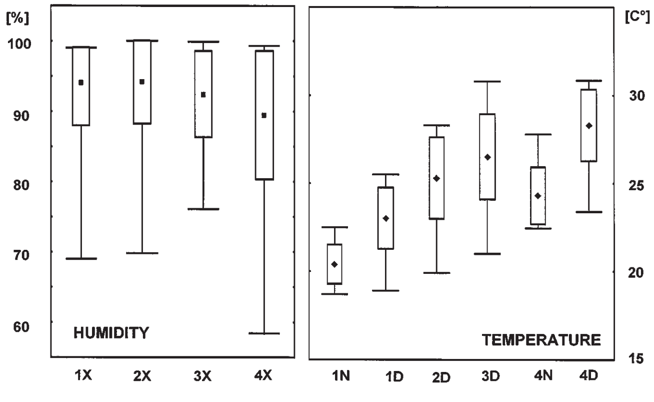

Figure 4. In April 93 we measured temperature and humidity in different strata of the rain forest on four days running, by use of a Grant 1200 Series (12-Bit) "Squirrel" Logger. Means are given as squares, boxes symbolize the standard deviations and the ranges are given by whiskers. The left Y-axis indicates humidity in percent, the right temperature in C°. The X-axis shows the different strata that are labeled with numbers, different time intervals with letters: (1) = 1.20 m above ground, (2) = 8 m above ground, (3) = 15 m above ground, (4) = 21 m above ground, (N) = Night (17.30–7.00 hours), (D) = Day (7.00–17.30 hours). (X) = (0.00–24.00 hours). Humidity at ground level is roughly identical to that in the smaller trees, temperature at the level of understory trees during daytime is only 1–2 degree C higher than in the lower canopy during the night

foragers that are significantly smaller than those at night (Orr, 1992), the same is true in *C. gigas* where we found mostly minors to leave the nests during daytime. It is probable that majors that often suffer small wounds when standing sentry at the colonies borders (pers. observations) are especially threatened. Probably these costs are too high to control the large arboreal territories of *C. gigas* in daytime, when 90% of all ant species in our observation area are active (Götzke, 1994).

(3) The strong impact of diurnal ant species may be one more reason for the observed temporal pattern of foraging activity in *C. gigas*. During the day we found many sympatric ant species running on the arboreal trails that *C. gigas* used at night, e.g., *Polyrhachis ypsilon*, *Dolichoderus sulcaticeps*, and other – more populous – species of *Polyrhachis, Camponotus* (*Colobopsis*) and *Dolichoderus* (Pfeiffer and Linsenmair, in prep.). Although most of these species were much smaller than *C. gigas*, their dense "traffic" obstructed the arboreal trails of the giant ants during daytime and we observed at several occasions that some of the few dayactive foragers of *C. gigas* had to jump off the bamboo trail. In combination with the factors mentioned above *C. gigas* was replaced on its arboreal trails and resources.

The remarkably orderly changeover in tropical regions from a nocturnal to a diurnal fauna has been noticed already by Wilson (1971) who stressed the importance of food competition. In the case of *C. gigas*, however, activity pattern seemed to be related to several interacting factors.

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