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Polydomy and the organization of foraging in a colony of the Malaysian giant ant *Camponotus gigas* (Hym. / Form.)

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Abstract In Kinabalu National Park, Borneo we observed four colonies of the Malaysian giant ant *Camponotus gigas* in a primary forest. These predominantly nocturnal ants have underground nests, but forage in huge three-dimensional territories in the rain forest canopies. The colony on which our study was mainly focused had 17 nests with about 7000 foragers and occupied a territory of 0.8 ha. To improve observation and manipulation possibilities, these nests were linked at ground level by 430 m of artificial bamboo trail. A group of specialist transport worker ants carried food from 'source' nests at the periphery to the central 'sink' nest of the queen. Transport of food between nests started immediately after the evening exodus of the foragers. Transporter ants formed a physical subcaste among the minors and behaved according to predictions of the central-place foraging theory. Their load size was about five times that of the average forager and grew proportionally with head width. Longer distances were run by ants with greater head width and larger gross weight. Transporter ants that ran more often took heavier loads. Experiments with extra-large baits revealed that *C. gigas* used long-range recruitment to bring foragers from different nests to "bonanzas" at far distant places. The foraging strategy of *C. gigas* is based on a polydomous colony structure in combination with efficient communication, ergonomic optimization, polyethism and an effective recruitment system.

Key words *Camponotus* · Polydomy · Dispersed central-place foraging · Polymorphism · Borneo

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Introduction

The problem of how to optimize individual behavior within the different contexts of the "struggle for life" led to the introduction of economic theories into ecology. Among the essential problems studied with these methods are many questions concerned with resource allocation in organisms (e.g., Pyke 1984). The central-place foraging theory describes the behavior of animals gathering food by starting from and returning to a central point, their nest (e.g., Orians and Pearson 1979; Schoener 1979; Cheverton et al. 1985). The problem to be solved here is to minimize foraging costs while optimizing yield. Ant colonies have complex social structures enabling them to reduce their total energy costs by cooperative foraging (e.g., Oster and Wilson 1978). Detailed studies of the ergonomics of foragers have shown that polymorphism in ants is an appropriate means to optimization. Especially well studied are the relations between load size and body size in foragers of harvester ants (e.g., Bailey and Polis 1987) or leaf-cutting ants (e.g., Roces and Hölldobler 1994; Wetterer 1994). Observation of honeydew-feeding ants revealed in some species the existence of two physical subcastes: small honeydew gatherers and greater "tankers" that transport the honeydew to the nest (e.g., Fowler 1985). Polydomous ants are thought to achieve energetic savings by decentralization (Hölldobler and Lumsden 1980), especially by reducing the overlap in the foraging paths of individual workers (Davidson 1997). However, little is known of how polydomy actually influences foraging yield (McIver 1991) and nothing is known about the mechanisms of this "dispersed central-place foraging." Splitting of the colony may cause problems with nest interaction. Especially in monogynous species, polydomy may result in nests with queen and brood, and satellite nests that contain mostly foraging workers. This asymmetric distribution would require a steady flux of energy between the different nest types.

Camponotus gigas Latreille 1802 is one of the largest ant species of the world and a common inhabitant of South-East Asian rain forests. The mainly nocturnal ants live in underground nests and forage in the forest canopy (Gault 1987; Chung and Mohamed 1993). During the day, foraging is restricted to a few ants searching the floor of the rain forest (Tho 1981; Orr and Charles 1994). These ants have two clearly distinguishable worker subcastes: minors (head width 1.6–5 mm) and majors (head width 5–8 mm) (Orr et al. 1996; Pfeiffer 1996). Although monogynous, *C. gigas* lives in polydomous colonies, with only some of the peripheral nests containing brood (more details in Pfeiffer 1996; Pfeiffer and Linsenmair 1997).

Three main factors seem to determine the foraging ecology and behavior of this ant: (1) its extraordinary body size and the wide range of size classes (minors weighed between 52 mg and 362 mg, mean = 133 mg, SD = 39, n = 708; majors weighed between 200 mg and 480 mg, mean = 372 mg, SD = 50, n = 89; M. Pfeiffer and K.E. Linsenmair, unpublished data), (2) the modest population size of its polydomous colonies, and (3) its huge three-dimensional territories including clumped and randomly dispersed food resources.

The diet of *C. gigas* within the studied population consisted of 87% honeydew (or other liquid food, e.g., nectar of extrafloral nectaries), 7.4% bird droppings, 1.3% other droppings, and 4% arthropods from hunting or scavenging (n = 6254). Occasionally, *C. gigas* scavenges at vertebrate carcasses and gathers vertebrate excrements (Pfeiffer 1996). Slightly different diet compositions (especially utilization of fungi as food) have been reported by Orr and Charles (1994), and Levy (1996) from Brunei.

In this study of the organization of foraging in *C. gigas*, we asked the following questions. (1) Is food transported between the nests of a polydomous colony? (2) Does this transport function according to central-place foraging theory, regarding travel time and/or load size? (3) Are the different nests of a colony autonomous units, or is their any coordination of recruitment behavior among them?

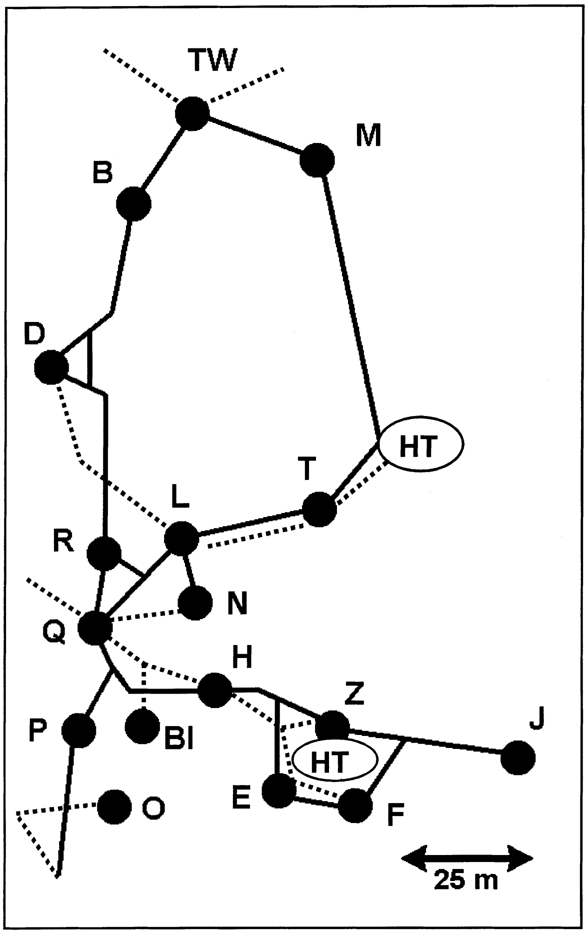

Fig. 1 Map of the observed colony. The nests are marked with *uppercase letters*, nest *Q* is the nest of the queen. The bamboo trail system is drawn with *black lines*, *broken lines* indicating 'natural' paths through the canopy that were mostly abandoned after our trail system had been installed. *HT* marks foraging trees with large groups of associated trophobionts

Methods

Our observation plot was a 5-ha area of primary mixed dipterocarp forest in Kinabalu National Park (KNP) near Poring Hot Spring (District of Ranau, Sabah, Malaysia). Annual rainfall in KNP Headquarters ranges from 2000 to 3800 mm (Kitayama 1992); in Poring we measured a total of 3218 mm of rain in 1993. We performed our field work during five periods totaling 2 years between July 1991 and November 1995. Most of our observations were conducted at night, using red-filtered head lamps (Petzl "Mega", approximately 20 lux) in order not to disturb the ants.

We observed four colonies of *C. gigas* with 8–17 nests. At one of these colonies we established 430 m of bamboo bridges connecting the nests and foraging trees at ground level (Fig. 1), so that ants did not have to climb up and down the trees. These bridges followed the ants' natural trunk trails through the tree canopies. They were readily accepted and ants abandoned their longer, arboreal routes. This system offered many possibilities to observe and manipulate the ants. The 17 nests of the most observed colony were situated within a territory of 0.8 ha and had only about 7000 foragers. The colony seemed to be monogynous with nest Q being inhabited by the queen. In our study, we focused on nests Q, E, H, F, and T; they showed the most intense interactions and the highest activity.

In preliminary tests we weighed the ants leaving and entering nests Q, H, and E between 1845 and 1945 hours. We carefully observed transport of food for several days and collected the following data during 260 h of observation at seven nests of the colony: (a) activity of ants, (b) transport of eggs and larvae, (c) worker transports leaving and entering the nest, and (d) input and output of prey and honeydew.

To record the distribution of size classes during the exodus phase, we videofilmed the exodus of the foragers (from 1730 to 1900 hours) at three nests (Q, H, T) (Panasonic NV-MS95 E, red video light). The length of 859 ants was measured from a TV screen with digital sliding calipers. They were compared with 60 ants that were filmed at the bamboo bridges running from nest Q to other nests at 0030 hours. We determined the error in measurement to 0.1 mm by filming ten screw caps with a mean diameter of 2.48 cm.

We observed a trophobiotic association and weighed 676 foragers gathering honeydew from a large group of Flatidae when they climbed or left the host tree that was about 4 m away from nest E. To study transport of food between nests, 116 ants that transported liquid food between nests Q, H, and E were caught, measured and individually marked with small numbered plastic tags that were glued on their thoraces. These ants were weighed several times to determine mean gross weight and net weight of each marked ant (electronic scales Ohaus CT 10). For quick classification of size groups in the field, we made a template: we fixed the cut-off heads of ants of different size groups on cardboard and covered them with cellophane. This method (B. Hölldobler, personal communication) proved to be very exact when we reexamined samples of ants with digital sliding calipers (Mahr 16 ES). We observed ants on five nights (January/February 1994) from 1800 to 0200 hours simultaneously at nests Q, H, and E and made 615 recordings of place, time, and path of the ants. We also measured head width, filling of their gasters and weight of unmarked ants transporting food on different sections of the trail (Fig. 1): section 1, from nest E to nest Q (57 m); section 2, from nest H to nest Q (30 m); section 3, from nest E to nest H (27 m); section 4, from nest Q to nest H (30 m); section 5, from nest H to nest E (27 m). Only those ants were included in our study that could be observed throughout their use of the trail to be sure about their starting point and destination.

To examine long-range recruitment, a table with a petri dish filled with human urine as a bait was isolated from the ground by "tangle foot" insect glue and connected to the runway by a bamboo bridge. Light barriers were installed at this bridge and at other sections of the runway system between the nests. Signals thus triggered were amplified and read into a single-board computer (BDE-module-535, PHYTEC Messtechnik, Mainz, Germany). The countings were performed continuously, stored in periods of 5 or 15 min on a magnetic card (Panasonic BN-MC-E) and were read out by a laptop computer. Average traffic on the runway was controlled for several days without baiting. One experimental setting was repeated at least five times. To avoid habituation of the ants we alternated different experiments.

Data were processed with CSS Statistica or SPSS.

Results

Activity pattern and transport of food

Foragers of the nocturnal *C. gigas* left the nest within a very narrow time window of about 50 min at around 1740 hours. Most of them climbed into the canopy. First retrieval of food to the nests by these ants normally took place not before 1900 hours as proved by marked foragers. Foragers returning to the nests during the night generally went out a second time. Shortly before sunset, the ants returned jointly to their nest, about 90% of them within 30 min.

Timing of input at central nest Q showed an interesting feature (Fig. 2). At 1830 hours, immediately after termination of the exodus of foragers, we observed a strong influx of workers carrying honeydew in their widely expanded gasters, some of them also transporting bird droppings and insect prey in their mandibles. This amount of food could not have been collected in that activity period – too little time had elapsed for such successful foraging. Rather, it must have been collected the night before (and/or during daytime) and been stored in the peripheral nests after the nocturnal activity phase had ended. Behavioral observations proved this assumption. The transporter ants seemed to differ from returning foragers by their higher load and we suspected that they might be a larger subcaste of minor workers. At nest H, which lay inside the hollow trunk of a tree and had a wide opening allowing easy inspection of a part of the nest, we often observed several returning foragers transferring their load by trophallaxis to one transporter ant that waited behind the entrance.

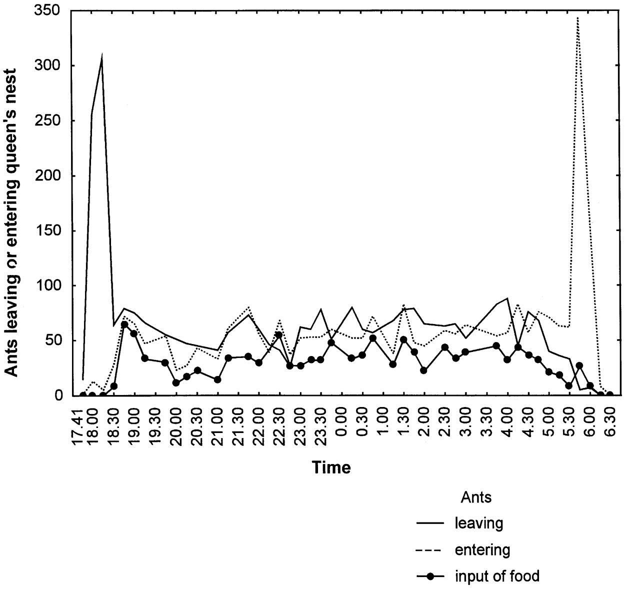

Fig. 2 Nocturnal activity of *Camponotus gigas* recorded at the entrance of the main nest Q on 11 September 1992. Foragers left the nest at sunset, and searched for food until sunrise. Input of food started immediately after the end of the exodus phase at about 1830 hours and fell shortly before the start of the run-in. We counted only those ants carrying food between the mandibles or in their enlarged gasters, thus differing clearly from their unloaded nestmates

In a weight analysis, comparing ants leaving the nests with those entering it, from 1845 to 1945 hours, ants leaving nest E and H were heavier than ants entering it (Fig. 3). Our investigations showed that the weight difference of these workers came about because ants leaving nests E and H at this time were mostly transport workers carrying food to nest Q, whereas ants leaving nest Q carried nothing. Ants entering nests E and H, however, were only foragers returning from their search for food in the canopy or transporter ants returning from Q with empty gaster. These results substantiated liquid food transport between the nests.

Most of the observed food transports took place from nest E to nests H and Q, and from nest H to nest Q (see Fig. 1). As nest Q was the aim of transport workers coming from different nests, mean total activity (MTA, number of ants leaving and entering the nest within 15 min) during the night (1845–0500 hours) at nest Q was much higher (109.7, SD = 38.11, n = 138), than at nests H, E, and F (28.4, SD = 24.6, n = 284). The ration of MTA during exodus (1740–1845 hours) at nest Q (164.4, SD = 152.9, n = 127) and at the other nests (113.4, SD = 133.8, n = 292) versus MTA during the rest of the night (1845 to 0500 hours) was 1.5:1 at nest Q and 4:1 at the other nests.

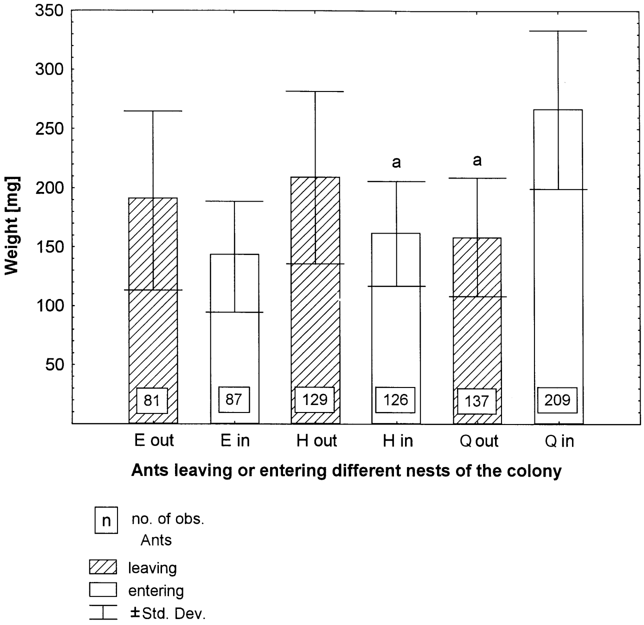

Fig. 3 Weight of ants leaving and entering different nests. These measurements were taken *after* the exodus phase, so weight differences depend on food transport between the nests [Kruskal-Wallis ANOVA by ranks: $H(5,\ n\ =\ 769)\ =\ 261.6$, $P < 0.001$; multiple comparisons with the Nemenyi test (Zar 1996), *a* n.s., $P < 0.001$ for all other test combinations]

Distribution of size classes during the exodus

The mean length of all minor workers entering and leaving the nests during our video scannings ($n\ =\ 1306$) was 17.5 mm (natural body position from above). Mean body length of minor workers leaving nests Q, T, and H during the exodus time was 17.27 mm ($n\ =\ 859$, SD = 1.56 mm), significantly smaller than the mean body length of transport workers that were filmed at the bamboo bridges running from nest Q to other nests from 0030–0100 hours ($n\ =\ 60$, mean = 17.85, SD = 1.64 mm; U-test, $U\ =\ 28{,}931$, $Z\ =\ -7.22$, $P < 0.001$).

We then focused on single nests and divided the data of the worker ants leaving the nest during exodus time with respect to the evening start of activity: group 1 included all ants leaving the nest until 45 min after the start of activity at about 1745 hours, group 2 comprised all ants leaving the nest after about 1830 hours (exactly 45 min after the start) to 1900 hours. So, group 1 comprised foragers leaving the nest during the peak time of exodus, while group 2 contained all ants leaving the nest after this period, which should be mostly transporter ants (both groups were separated by a short characteristic drop in activity, which could be found in all our records (for Q, $n\ =\ 28$); see Fig. 2).

At nest Q, both groups could be discriminated with high significance (for statistics see below): group 1 comprised workers with a mean size of 17.4 mm ($n\ =\ 290$, SD = 1.63), group 2 had a mean size of 17.9 mm ($n\ =\ 96$, SD = 1.77). The latter group left nest Q after the input of food from other nests had begun (see Fig. 2). These ants were larger than the mean foragers and seemed to walk mostly on the trails connecting the different nests of the colony. Transporter ants leaving nest Q after 0030 hours (group 3) were significantly larger than group 1 ants leaving nest Q during the exodus (17.9 vs 17.4 mm), but did not differ from ants of group 2 [Kruskal-Wallis ANOVA $H(2,\ n\ =\ 446)\ =\ 12.01$, $P < 0.01$; multiple comparisons with the Nemenyi test (Zar 1996): group 1 vs group 2, $P < 0.01$; group 1 vs group 3, $P < 0.01$].

These results were confirmed at nest H where ants of group 2 were also significantly larger (18.0 mm, $n\ =\ 41$, SD = 2.0) than those of group 1 (17.0 mm, $n\ =\ 167$, SD = 1.2). Transport workers leaving nest Q after 0030 hours (mean 17.9 mm) differed significantly in size from group 1 foragers, but not from group 2 [Kruskal-Wallis ANOVA $H(2,\ n\ =\ 268)\ =\ 23.671$, $P < 0.001$; multiple comparisons with the Nemenyi test: group 1 vs group 2, $P < 0.001$; group 1 vs group 3, $P < 0.001$; group 2 versus group 3, n.s.].

At nest T, all workers were rather small in size and group 1 versus group 2 differed by only about 0.2 mm (16.9 vs 17.1 mm, n.s.). Compared to these ants, transport workers were much larger (group 3: 17.9 mm) and differed from all ants leaving nest T during exodus time [Kruskal-Wallis ANOVA $H(2,\ n\ =\ 325)\ =\ 20.15$, $P < 0.001$; multiple comparisons with the Nemenyi test: group 1 vs group 2, n.s.; group 1 vs group 3, $P < 0.01$; group 2 vs group 3, $P < 0.001$].

Taken together these results corroborate our observations of two physical subcastes of minors in *C. gigas*: the "foragers" and the "transporter ants."

Observation of foragers in a trophobiotic association

Foragers, collecting honeydew from a group of associated *Bythopsyrna circulata* Guerin-Meéneville (Flatidae, Homoptera) on a young *Eugenia* tree (Myrtaceae) 4 m away from nest E, were weighed when entering or leaving the tree. Their weight when climbing up the tree was 118 mg ($n\ =\ 310$, SD = 32.3). Foragers that left the tree to carry honeydew to their nests could be sorted into two groups: those that left the tree until 0500 hours were heavier (143 mg, SD = 44, $n\ =\ 185$) than those that left the tree jointly in the morning, when foraging activity stopped (126 mg, SD = 29, $n\ =\ 181$; U-test, $U\ =\ 12{,}927$, $Z\ =\ -\ 3.77$, $p < 0.001$). Most probably, the cessation of activity in the morning prevented the second group from becoming completely filled up. Ant loads were 25 and 8 mg, respectively.

Transport system

Weight of workers at different nests

In preliminary experiments, we weighed unmarked workers after 1845 hours at nests E, H, and Q when leaving or entering the nest (see Fig. 3). The difference between these measurements represents the mean load of the transport workers leaving the peripheral nests and entering central nest Q (E out, H out, Q in): 47.1 mg at nest E, 47.5 mg at nest H, and 108 mg at nest Q. Nest Q was at the end of this transport chain. Ants leaving Q shortly after 1845 hours should be mostly "empty" transporter ants returning to their nests, because the exodus of the foragers had already ceased and input of food had started (see Fig. 2). Ants leaving nests E and H at that time were loaded transporters. However, nest H in particular was not only a filling station but also a "place of transshipment," with many loaded transporter ants entering it. So absolute load at nest H should have been higher, because loaded transport workers were found in both samples of this nest. We also may have included some foragers in our random samples, especially at nests E and H that were situated near to the foraging tree; this may to some extent explain the large difference between "H out" and "Q in."

When we measured only transporter ants, observed moving between nests, mean gross weight was higher at nest Q and H than at the more peripheral nests E and T. Net weight was the same at all nests; mean load became heavier from the periphery to the center (see Table 1).

Transporter load, transporter size, and distance of transport

A total of 103 weight measurements were made of unmarked carriers that ran different sections of the bamboo trail system. As shown in Fig. 4, transporters that had the longest path (from E to Q) were the heaviest, heavier than those running only a section of the trail. The difference between ants that came from H to Q and those going from E to H depended not only on the path length, but seemed to be a result of load transfer at nest H. Empty carriers returning to their nests had equal weights.

The mean head width of 16 transporter ants that went the whole way from nest E to nest Q was 4.2 mm (SD = 0.49), significantly larger than that of the remaining 87 ants that only went a section of this course (3.86 mm, SD = 0.51; *U*-test, $U = 195$, $Z = -4.56$, $P < 0.001$).

Table 1 Weight and load of transporter ants at different nests of colony A. The ants differed significantly in gross weight between Q and E ($P \le 0.01$), Q and T ($P \le 0.001$), and H and T ($P < 0.05$) [ANOVA $F(3,215) = 8.05$, $P < 0.001$; Hochberg GT2 post hoc test]. Net weight was equal at all nests [ANOVA $F(2,143) = 2.70$, n.s.]

Nest	Gross weight			Net weight			Load mean (mg)
	mean (mg)	SD	*n*	mean (mg)	SD	*n*	
Q	274	64	94	140	34	78	134
H	255	69	78	140	26	40	115
E	224	64	20	127	29	28	97
T	212	60	27	–	–	0	–

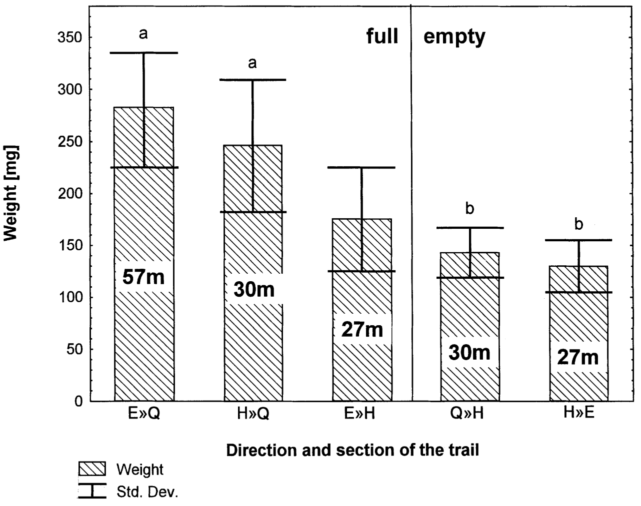

Fig. 4 Weight of honeydew carriers to (and from) the central nest Q, relative to the length of their path between the nests (marked on the column). Those with the longest path are the heaviest, as predicted by central-place foraging theory [*n* for the different groups: E to Q, 16, H to Q, 35, E to H, 14, Q to H, 18, H to E, 20; Kruskal-Wallis ANOVA by ranks $H(4, n = 103) = 64.73$, $P < 0.001$; multiple-comparison testing with the Nemenyi test (Zar 1996) *a* $P < 0.05$, *b* n.s., other groups, $P < 0.01$]

In a 5-day study of 116 marked transporter ants, 21 were found at all three observed nests (Table 2, G1, transport distance 55 m), 20 shuttled only between two (G2, transport distance 30 or 25 m), and 75 of the marked ants were observed at only one nest (G3). Group 1, the long-distance carriers, differed from group 3 in their mean gross weight and also from all other marked workers (G2 + G3), however, presumably because of their low number, not from group 2 alone. If we pooled group 1 and 2, and tested them against 3, the gross weights were significantly different.

Transporter size and frequency of transports

During 38 h of observation on five nights, we recorded 160 transports of liquid food that were carried out by 41 marked transport workers. Transport frequency correlated with head width [Pearson correlation: $r(X,Y) = 0.51$, $r^2 = 0.26$, $t = 3.24$, Bonferroni-corrected $P < 0.01$ (see Sokal and Rohlf 1995)] and with gross weight [Pearson correlation: $r(X,Y) = 0.53$, $r^2 = 0.28$, $t = 3.39$, Bonferroni-corrected $P < 0.01$], however not with net weight [Pearson correlation: $r(X,Y) = -0.04$, $r^2 = 0.001$, $t = -0.17$, $P = 0.866$, n.s.]

Regression analysis of ant weight

Mean gross weight and net weight of marked transporter ants depended on head width, and their carrying capacity

Table 2. Transport workers with different working sections differed significantly in their gross weight. *G1* differed from *G3* ($P < 0.05$), but not from *G2* ($P = 0.74$, n.s.) (ANOVA, *df* 2,96, $F = 3.69$ $P < 0.05$, Hochberg GT2 post hoc test). *G1* + *G2* differed from *G3* (*t*-test, $t = 2.56$, $df = 97$, $P < 0.013$) and *G1* differed from *G2* + *G3* (*t*-test, $t = 2.39$, $df = 80$, $P < 0.05$)

	Working section	*n*	Head width (mm)	SD	Gross weight (mg)	SD	Net weight (mg)	SD	Load (mg)
G1	at three nests	21	3.9	0.61	284	48	148	27	136
G2	at two nests	20	3.7	0.37	264	37	135	21	129
G3	at one nest	75	3.8	0.56	240	67	130	16	110

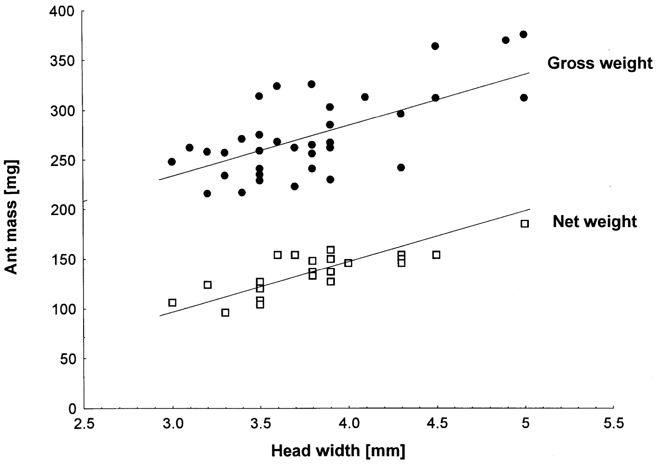

Fig. 5 Linear regressions of head width on ant mass, the two data sets showing ants with full and empty gasters. Data were collected from marked transporter ants that were observed on average 13.2 times within 5 days. The curves in the figure are based on the common regression coefficient. Least-square fit for gross weight (*filled circles*): $Y = 0.081 + 0.509X$; for net weight (*open squares*): $Y = -0.056 + 0.509X$, common $r^2 = 0.54$

grew proportionally with their size (see Fig. 5). As data of both regressions showed replications (multiple values of Y on each value of X), we first tested them for linearity in a one-way analysis of variance (Zar 1996) and found that the null hypothesis of linear regression could not be rejected: gross weight $F(1)13,14 = 0.44$, $p > 0.25$; net weight $F(1)10,11 = 1.88$, $p > 0.10$. We calculated a least-square fit for gross weight of the ant: $Y = 0.055 + 0.577X$ [$r^2 = 0.45$, $n = 39$, $F(1,37) = 30.5$, $P < 0.001$] and for net weight: $Y = -0.005 + 0.374X$; [$r^2 = 0.60$, $n = 27$, $F(1,25) = 37.8$, $P < 0.001$]. The slopes of the regression lines did not differ significantly in a two-tailed *t*-test [Zar 1996; $t(2)$ 62 = 1.37, $P > 0.2$, n.s.], but elevations of both regressions differed significantly (Zar 1996; *t*-test, $t(2)$ 63 = 6.64, $P < 0.001$). This showed that the carrying capacity of ants grew proportionally with their size. We calculated a common regression coefficient bc = 0.509 and a common $r^2 = 0.54$.

Mean weight of transport workers compared to foragers

In pooling weight data of marked and unmarked transporter ants, we obtained the following results: mean gross weight, 255 mg (SD = 68, $n = 220$); mean net weight, 139 mg (SD = 31, $n = 143$); thus mean load: 116 mg. In 28 cases, we measured the weight of marked ants directly before entering and after leaving nest Q: the difference was 137 mg (SD = 49.8). The mean head width of 222 transporter ants was 3.78 mm (SD = 0.05), significantly larger (*U*-test, $U = 0.0$, $Z = -23.29$, $P < 0.01$) than that of the average minor worker (3.56 mm, $n = 853$, SD = 0.53; M. Pfeiffer and K.E. Linsenmair, unpublished results). Foragers collecting honeydew in the trophobiotic association differed in gross and net weight from transporter ants (Fig. 6).

Differences between nests: energetic 'sinks' and 'sources' in a polydomous colony

The records of long-term observations revealed significant differences between 'sink' nests, showing a large input of honeydew, insects, and bird droppings, and 'source' nests exporting food (Table 3). The largest 'sink' within the colony was the nest with the queen showing an input/output relationship of 41.6:1. However, only ants with largely extended gasters or with food between their mandibles were classified as transporter ants. Foragers that arrived with smaller gasters were not categorized as transporters, but contributed only to 'total activity'. Small loads did not puff up the gasters, therefore we were unable to estimate the foragers' contribution to food input.

The queen's nest Q showed high transport rates of workers and larvae that were carried to other nests or brought back from there. Eggs, however, were only carried from nest Q to other nests but never vice versa. Within colony bidirectional transport rates of workers and larvae were correlated with a high input/output ratio (Spearman correlation $R = 0.76$ for worker transport, $R = 0.77$ for larval transport, both $P < 0.001$). At typical 'source' nests that had input/output relations (by transporter ants) smaller than 1, we never found brood.

Long-range recruitment

Excrement or cadavers of larger vertebrate are huge resources that cannot be effectively exploited by single workers. They require the cooperation of hundreds of

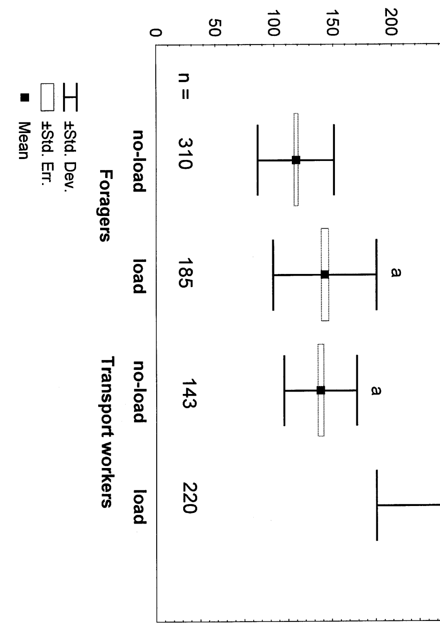

Fig. 6 Division of labor in *C. gigas*. Given is the weight of the ants in milligrams. *Foragers*, which gathered honeydew at the trophobionts and brought it into nest E, about 4 m away, were the smallest minors. *Transport workers* were the largest of the minor caste – they carried heavy loads of liquid food in their gasters. Their mean load was about five times that of the foragers. (U-tests, significance levels are corrected with the Bonferroni method because of multiple testing: net transporters vs gross transporters $U = 2135$, $Z = -13.92$, $P < 0.01$; net foragers vs gross foragers $U = 18{,}250$, $Z = -6.77$, $P < 0.01$; net foragers vs net transporters $U = 11{,}097$, $Z = -8.5$, $P < 0.01$; gross foragers vs gross transporters $U = 3713$, $Z = -14.2$, $P < 0.01$; net foragers vs gross transporters $U = 2238$, $Z = -18.3$, $P < 0.01$, gross foragers vs net transporters $U = 13{,}169$, $Z = -0.07$, $P = 0.95$)

ants. Because of its large range and its polydomous colony structure, *C. gigas* seemed to be especially suited to locate and exploit such "bonanzas." However, because of polydomy, worker force is distributed among many nests. Large resources may thus overcharge the foraging capacity of single nests. We wanted to know whether *C. gigas* had developed mechanisms to overcome this problem by recruiting workers from more than a single nest. To check this we worked with a computer-recorded system of light barriers to supervise the trunk trails at different sections between the nests.

Figure 7a shows the experimental setting, and a corresponding 2-day record without experimental recruitment is given in Fig. 8a. The correlation coefficients of data from bidirectional activity countings at different light barriers are listed in Table 4. Correlation without recruitment was poor and only weakly significant.

When we offered a bait at X, workers recruited to it. Activity at the adjacent nest (E) rose, then recruitment spread to the next nests (first H, then Q). Within a period of 15 min, 270 min after the presentation of the bait, we counted 348 ants crossing the bridge to/from the food table. At the same time, activity rose to 275 at nest H and to 118 at the queen's nest. The propagation of this activity peak is shown in Fig. 8b. Activity at

Table 3 Activity and transport of food, workers and larvae at different nests of the most intensively studied colony. [Only ants with bursting full gasters were classified as honeydew carriers. Output could be larger than input because (1) several entering foragers with smaller gasters (that were counted here only as a part of the total activity) gave their load to carrier ants that were counted as 'output' when leaving the nest, and (2) counting covered many periods during transport peak time, when stored food was transported.] Shown are mean values in observation units of 15 min. All nests differed significantly in mean transport rates of larvae, workers, honeydew, and nitrogenous food (Kruskal-Wallis ANOVA, H_0: same transport rates at all nests). The queen's nest *Q* was the center of transport. Carriers of other nests (e.g., *E*, *H*) brought food to Q, which had only moderate total activity, but the highest input/output relationship. In a Nemenyi test we looked for differences between Q and all other nests. Q differed significantly ($P < 0.05$) from most other nests, non-significant differences are marked °

Nest	*n* in 15 min	Total activity (bidirectional)		Worker transport (bidirectional)		Transport of larvae (bidirectional)		Input of honeydew		Output of honeydew		Input of insects or droppings		Output of insects or droppings		Input/output
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	
Q	359	112.4	111.8	1.2	1.7	1.0	1.6	17.6	17.4	0.4	1.6	1.51	2.48	0.06	0.44	41.58
E	298	84.8	120.6	0	0	0	0	6.6	13.7	2.1	3.8	0.23	0.63	0.20	0.68	2.97
H	230	65.7	95.3	0	0	0	0	3.1	3.2	3.9	5.1	0.31	0.68	0.23	0.62	0.83
F	149	43.1	53.7	0.18	0.55	0.12	0.38	3.7	5.3	1.2	2.2	0.23	0.60	0.49	1.28	2.32
Z	35	35.8	71.3	0	0	0	0	0.9	1.5	3.3	5.4	0.57	0.23	0.57°	0.23	0.37
T	30	195.7	337.7	0.6°	1.3	0.8	1.2	2.4	5.7	0.1°	0.4	0.80	2.47	0.00°	0	24.62
L	23	40.0	80.1	0	0	0	0	0.63	1.6	2.2	4.7	0.21	0.92	0.67°	0.25	0.30
Kruskal-Wallis		–		$H(6, n = 1114) = 329.7$		$H(6, n = 1114) = 296.4$		$H(6, n = 713) = 117.5$		$H(6, n = 826) = 192.2$		$H(6, n = 952) = 90.1$		$H(6, n = 927) = 53.4$		–
ANOVA by ranks				$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$		

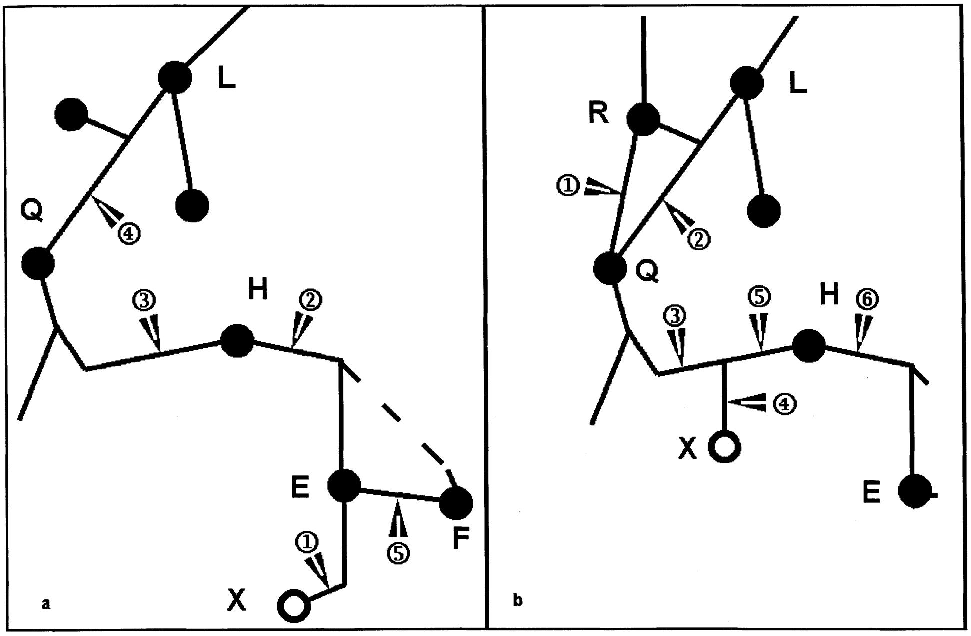

Fig. 7a, b The nests were connected by the bamboo trail system (shown by the *continuous line*; the *broken line* indicates the natural path through the canopy). The *numbers* mark the light barriers that were connected to the single-board computer during the first assay. **a** First part of the recruitment experiments. We installed a table with a bait (*X*) near nest E. Measuring points *4* and *5* were used alternately. **b** Second part of the recruitment experiments. The table with the bait was shifted to a place between nests *Q* and *H*

different sections of the trail was highly correlated (Table 4). The long-distance recruitment was released by single workers that laid trails between the nests. Trails were laid by ants with full gasters returning to their nests, and also by unloaded ants on their way to the bait. These were sometimes followed by small groups of workers, the typical picture of group recruitment. As we counted the activity in both directions, we observed not only recruitment of workers to the bait, but also transport of food back to their nests. Both stopped in most cases finally at central nest Q. A comparison of the activity during our experiment (Fig. 8b) and during normal nights (Fig. 8a) shows the very pronounced response of the ants to our bait. This experiment proved that several nests cooperated in foraging and a "bonanza" could trigger recruitment activity that spread from the nearest to several further distant nests.

In the next assay we examined the spread and direction of recruitment further: the bait was moved to a point between nests Q and H (Fig. 7b, Table 5). Although the bait was very near to nest H, recruited workers came mostly from nest Q and recruitment stopped there. Light barriers no. 1 and no. 2, which would have indicated its spread to other nests, showed no significantly correlated increases of activity. This shows that Q determined the demand of food within the colony and was able to satisfy this – within near range – by recruitment of its own workers.

Discussion

Central-place foraging theory has been applied to a wide range of organisms that feed offspring at a central place, or store food there for times of reduced prey availability, e.g., birds (Leopold et al. 1996), bees (van Nieuwstadt and Iraheta 1996), or ants (Roces 1990). Our study focused on two of the predictions of the central-place foraging theory: (1) the optimal central place should minimize traveling time during resource allocation and (2) the optimal load should increase with increasing distance of transport (Orians and Pearson 1979; Schoener 1979).

In *C. gigas* we have a special case of "dispersed central place foraging" (McIver 1991), because observed colonies were polydomous. Foragers brought the food to nests that were scattered inside the territory. A specialized group of transporter ants carried it from 'source' nests, which lay near the foraging trees, to the 'sink' nests in the center of the colony, especially to the nest of the queen that seemed to contain most brood.

Polydomy may be – among other reasons – a reaction to patch quality variation within the territory, concentrating foragers in patches with high food quality, or to low food density, spreading the worker force over a large area to more effectively gather randomly distributed resources. In *C. gigas*, both conditions were met, as this ant foraged for clumped food (honeydew from associated Homoptera) as well as for randomly dispersed food (bird droppings, insects, cadavers). In either case, polydomy results in a reduced total travel time of all foragers when food is transported to the central nest by specialist transport workers that carry the loads of several foragers. This also reduces the number of "empty" ants running back without load, and may optimize the transport capacity. *C. gigas* transport workers became heavier from the periphery to the central nest; this may be partly due to better use of transport capacity during nest-to-nest transport, when ants with smaller loads gave their honeydew to other transport workers. Another reason was the arrival of heavily loaded transporter ants at nest Q that came from far distant nests.

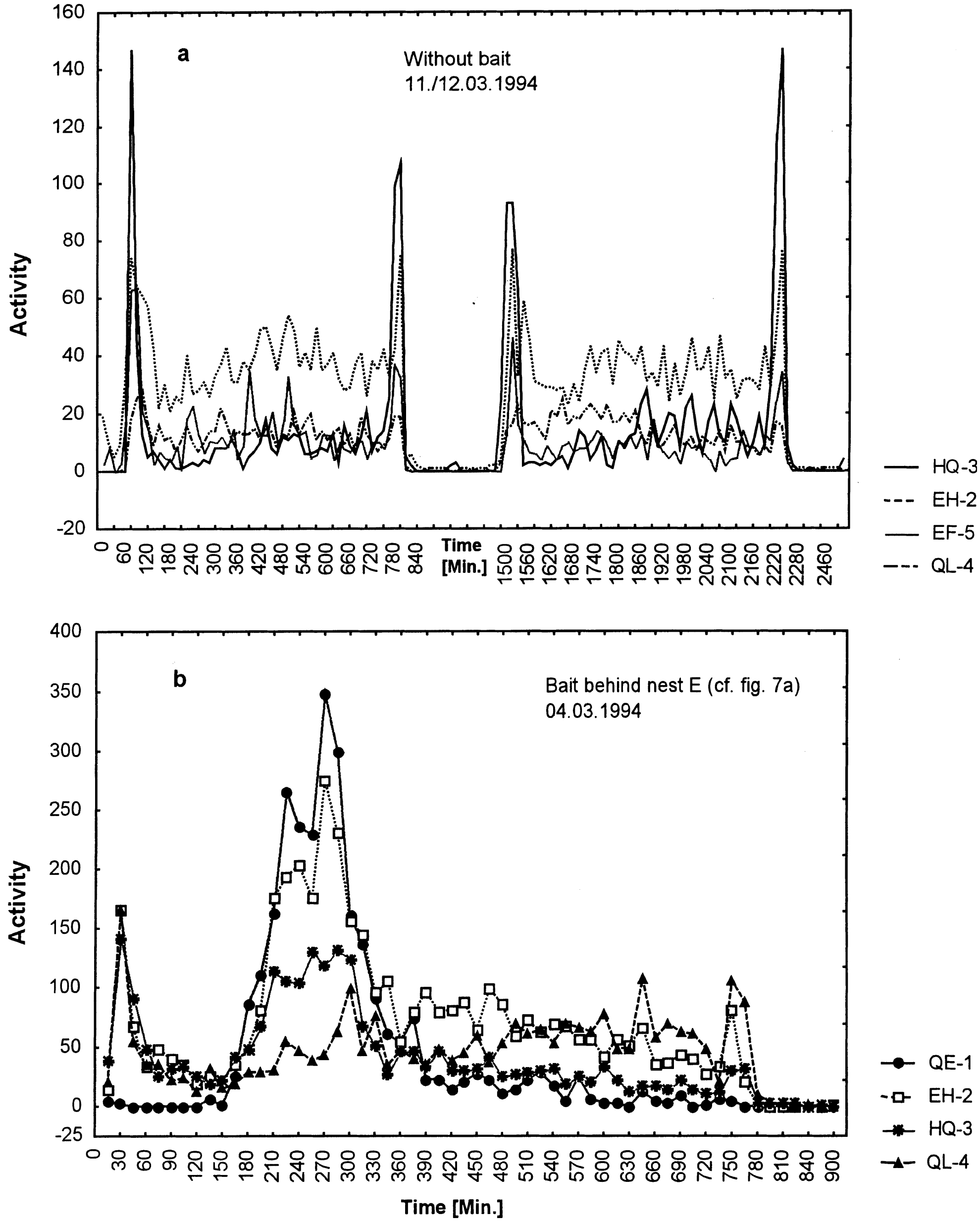

Fig. 8a Two-day record of activity at the trail system without experimental recruitment. All ants that ran on the bamboo trail in both directions were counted when passing the light barriers. The trail sections and numbers of the light barriers in the legend are mapped in Fig. 7a. Because the recorder reacted only to activity, the period between the two nocturnal activity periods is shortened. **b** Recruitment to a "bonanza." The arrangement of light barriers is similar to that in **a**. The activity at the bait increased in one onslaught. The highest activity was measured at the trail to nest E (*QE*), the curves below show activities at sections *EH* and *HQ*. At section *QL*, activity was not correlated with that at QE (see Table 4). On section EH, activity was high even after the end of recruitment, indicating transport of food from E to H. The small peak at the start (at 30 min) is a part of transport activity after the exodus phase and has nothing to do with the experiment. Note the different scale of the *y*-axis cf. **a**

The large transporter ants carried the load of five foragers, while their biomass was only 1.16 times that of a honeydew gatherer. In addition, the energetic cost/benefit relationship for many ant species improves with rising load. This was demonstrated for *C. herculeanus* by Nielsen et al (1982), by Duncan and Lighton (1994) for two species of *Myrmecocystus*, and by Bartholomew et al. (1988) for *Eciton*. Compared to transport by foragers, food transport by carrier ants will reduce foraging costs.

Ant species that are opportunistic foragers should maximize their number of foragers (while minimizing the costs of a single forager); in polymorphic species, therefore, smaller workers should search for food and alarm their larger nestmates to transport it (Carroll and Janzen 1973). This was shown, e.g., in the leaf-cutting *Atta cephalotes*, where Hubbell et al. (1980) found a two-stage harvesting method, with smaller ants cutting the leaves and larger ants transporting them. In the polydomous Australian *Iridomyrmex* ants, foragers show a division of labor between smaller food gatherers and larger transporter ants (McIver 1991). We found a similar polyethism in *C. gigas*. Foragers were significantly smaller than transporter ants that run the trails after 1845 hours. Videofilming corroborated the hypotheses of two physical subcastes among the minor workers of *C. gigas*.

The transport system of *C. gigas* also fulfilled the second prediction of the central-place foraging theory: the gross weight of the carriers rose with larger transport distance and increasing activity of the carriers. Longer distances were run by larger ants. Goss et al. (1989)

Table 4 Long-distance recruitment in *C. gigas*. Correlation coefficients of bidirectional activity countings at different trail sections. Column headings indicate the numbers of the light barriers (Fig. 7a) and the corresponding sections of the trail system. The first two records are without baiting, the rest are with a bait at X. Three records were made with a counter between nests Q and L. However, after we observed recruitment of workers much more often at nest F, we changed this counter to section EF. On 1 March 1994, two counters broke down because of heavy rain. The data for 22 March 1994 did not show a normal probability distribution, and we therefore calculated the nonparametric Spearman correlation coefficient (S*P*). Activities of single sections were better correlated during long-distance recruitments, and most sections also showed correlations with activity between nest E and the bait (XE). Allowing for multiple testing, we used the Bonferroni method to correct significance levels by dividing them by the number of tests (*k*). Significances remained high, even after correction (**P* < 0.05/*k*; ***P* < 0.01/*k*; ****P* < 0.001/*k*)

Date	*n*	③/④ HQ/QL	③/② HQ/HEF	③/⑤ HQ/EF	②/④ EH/QL	①/③ XE/HQ	①/② XE/HEF	①/⑤ XE/EF	①/④ XE/QL
11 March 1994	38	n.s.	n.s.	–	n.s.	–	–	–	–
12 March 1994	39	−0.44 *	n.s.	–	n.s.	–	–	–	–
4 March 1994	48	n.s.	0. 851 ***	–	n.s.	0.902 ***	0.932 ***	–	n.s.
7 March 1994	24	0.740 **	0.855 ***	–	0.690 **	0.794 ***	0.814 ***	–	0.860 **
01 March 1994	99	–	–	–	–	0.663 ***	–	–	–
17 April 1994	15	n.s.	n.s.	–	n.s.	0.947 ***	n.s.	–	n.s.
21 March 1994	27	–	0.858 ***	0.839 ***	–	0.858 ***	0.677 ***	0.944 ***	–
22 March 1994	26	–	0.765 S*P******	0.507 S*P*****	–	0.643 S*P*****	0.637 S*P******	0.825 S*P*****	–
26 March 1994	34	–	0.741 ***	0.884 ***	–	0.759 ***	0.498 **	0.756 ***	–

Table 5 Long-distance recruitment in *C. gigas*. The bait was sited between nests Q and H (Fig. 7b), and shown are the correlation coefficients of different trail sections. Column headings as in Table 4. The first two records were made without baiting, the rest with a bait at X. In baited assays, ants recruited in the direction of nest Q. Ant activity at X correlated strongly with counter no. 3. Counter no. 5 that should register transport of food to the nearer nest H was correlated negatively or not significantly, as were counters no. 1 and 2 (Bonferroni-corrected significances: **P* < 0.05/*k*; ***P* < 0.01/*k*; ****P* < 0.001/*k*)

Date	*n*	③/⑤ QH/QH	④/③ X/QH	④/⑤ X/QH	④/① X/QR	④/② X/QL	④/⑥ X/HEF
22 April 1994	39	0.736 ***	n.s.	n.s.	n.s.	n.s.	n.s.
29 June 1994	39	0.754 ***	n.s.	n.s.	n.s.	n.s.	n.s.
18 April 1994	47	0.4 *	0.429 **	n.s.	n.s.	n.s.	n.s.
20 April 1994	53	−0.328 *	0.84 ***	−0.396 **	n.s.	n.s.	−0.357 *
21 April 1994	36	0.464 *	0.929 ***	n.s.	n.s.	n.s.	n.s.
1 July 1994	11	n.s.	0.908 **	n.s.	n.s.	n.s.	n.s.
3 July 1994	17	−0.706 *	0.602 **	−0.808 **	n.s.	n.s.	n.s.

showed in a modeling study that larger workers gain most profit in large territories.

As our experiments revealed, the colony was organized as a unit, although polydomy persisted over years (Pfeiffer 1996). The single nests were well coordinated in their actions. Recruitment stimuli given at one nest were easily passed on to the central nest. Long-distance recruitment makes polydomy possible for species with only moderate colony size, like *C. gigas*. It helps them take advantage of the positive sides of polydomy, e.g., a better distribution of the foragers, which therefore have shorter paths to foraging areas and know well the exact position of the permanent resources inside the large territory. It also avoids most of the disadvantages of polydomy, e.g., poor flow of information, too small worker groups, and unfavorable defense opportunities. Within a few minutes, an alarm shifted from nest to nest. As our observations of territory defense revealed (Pfeiffer 1996), this also happened when conspecific enemies attacked colonies at the borders. Long-distance recruitment has also been found in colonies of other ants, e.g., the African *Oecophylla longinoda* (Hölldobler and Wilson 1978); however, in *C. gigas* we demonstrated interaction of nests by quantitative countings for the first time in the field.

Fewell et al. (1992) examined the influence of distance on recruitment behavior of the South American *Paraponera clavata* that lives in colonies of 2500 workers. Foragers gathering food far from the nests often give the nectar to other workers that transport it to the nest. With growing distance, they recruit reserve workers from the canopy that spend 98% of their time outside the nest. This mechanism reduces recruitment time to a quarter. It is possible that these extra-nidal worker groups are a precursor of a polydomous nesting system like that of *C. gigas*.

Most of our experiments were carried out only at one colony; however, behavior of three other colonies of *C. gigas* within our observation area seemed to be fully consistent with the studied colony. In many observations and minor experiments, we never found any hint of mechanisms other than those described here. However, due to the large experimental setting (runway system, computer countings, large numbers of marked foragers) and long-term observation, including up to 5 years of data (e.g., of nest input), we were not able to observe these colonies as thoroughly as the one on which we concentrated our observations. For some of the problems facing behavioral studies on social insects, an individual-based assay seems to be the only possible way of collecting data.

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References

Bailey KH, Polis GA (1987) Optimal and central-place foraging theory applied to a desert harvester ant, *Pogonomyrmex californicus*. Oecologia 72:440–448

Bartholomew GA, Lighton JRB, Feener DH Jr (1988) Energetics of trail-running, load carriage, and emigration in the column-raiding army ant *Eciton hamatum*. Physiol Zool 61:57–68

Carroll CR, Janzen DH (1973) Ecology of foraging by ants. Annu Rev Ecol Syst 4:231–257

Cheverton J, Kacelnik A, Krebs JR (1985) Optimal foraging: constraints and currencies. In: Hölldobler B, Lindauer M (eds) Experimental behavioral ecology. Fischer, Stuttgart, pp 109–126

Chung AYC, Mohamed M (1993) The organisation and some ecological aspects of the giant forest ant, *Camponotus gigas*. Sabah Soc J 10:41–55

Davidson DW (1997) The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biol J Linn Soc 61:153–181

Duncan FD, Lighton JRB (1994) The burden within: the energy cost of load carriage in the honeypot ant, *Myrmecocystus*. Physiol Zool 67:190–203

Fewell JH, Harrison JF, Stiller TM, Breed MD (1992) Distance effects on resource profitability and recruitment in the giant tropical ant, *Paraponera clavata*. Oecologia 92:542–547

Fowler HG (1985) Alloethism in the carpenter ant, *Camponotus pennsylvanicus* (Hymenoptera Formicidae). Entomol Gen 11:69–76

Gault D (1987) Feeding and foraging behaviour of the giant forest ant, *Camponotus gigas*, in a Malaysian rain forest. Trop Biol Newsl 52:2

Goss S, Deneubourg JL, Pasteels JM, Josens G (1989) A model of noncooperative foraging in social insects. Am Nat 134:273–287

Hölldobler B, Lumsden CJ (1980) Territorial strategies in ants *Oecophylla longinoda*, *Pogonomyrmex*, *Myrmecocystus mimicus*. Science 210:732–739

Hölldobler B, Wilson EO (1978) The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). Behav Ecol Sociobiol 3:19–60

Hubbell SP, Johnson LK, Stanislav E, Wilson B, Fowler HG (1980) Foraging by bucked-brigade in leaf-cutter ants. Biotropica 12:210–213

Kitayama K (1992) An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. Vegetatio 102:149–171

Leopold MF, Vanelk JF, Vanheezik YM (1996) Central place foraging in oystercatchers *Haematopus ostralegus* – can parents that transport mussels *Mytilus edulis* to their young profit from size selection. Ardea 84A:311–325

Levy R (1996) Interspecific colony dispersion and niche relations of three large tropical rain forest ant species. In: Edwards DS, Booth WE, Choy SC (eds) Tropical rainforest research. Kluwer, Dordrecht, pp 331–340

McIver JD (1991) Dispersed central place foraging in Australian meat ants. Insect Soc 38:129–137

Nielsen MG, Jensen TF, Holm Jensen I (1982) Effect of load carriage on the respiratory metabolism of running worker ants of *Camponotus herculeanus* (Formicidae). Oikos 39:137–142

Nieuwstadt MGL van, Iraheta CER (1996) Relation between size and foraging range in stingless bees (Apidae, Meliponinae). Apidologie 27:219–228

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ (ed) Analyis of ecological systems. Ohio State University Press, Columbus, pp 155–177

Orr AG, Charles JK (1994) Foraging in the giant forest ant, *Camponotus gigas* (Smith) (Hymenoptera: Formicidae): evidence for temporal and spatial specialisation in foraging activity. J Nat Hist 28:861–872

Orr AG, Charles JK, Yahya Hj HR, Sharebini Hj N (1996) Nesting and colony structure in the giant forest ant *Camponotus gigas* (Latreille) (Hymenoptera: Formicinae). Raffles Bull Zool 44:247–251

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Monogr Popul Biol 12. Princeton University Press, Princeton, NJ

Pfeiffer M (1996) Sozialstruktur und Verhaltensökologie von Riesenameisen *Camponotus gigas* Latreille 1802 im Regenwald Malaysias auf Borneo. Thesis, Bayerische Julius-Maximilians-Universität Würzburg

Pfeiffer M, Linsenmair KE (1997) Reproductive synchronization in the tropics: the circa-semiannual rhythm in the nuptial flight of the giant ant *Camponotus gigas* Latreille (Hym./Form.). Ecotropica 3:21–32

Pyke GH (1984) Optimal foraging theory: a critical review. Annu Rev Ecol Syst 15:523–575

Roces F (1990) Leaf-cutting ants cut fragment sizes in relation to the distance from nest. Anim Behav 40:1181–1183

Roces F, Hölldobler B (1994) Leaf density and a trade-off between load-size selection and recruitment behavior in the ant *Atta cephalotes*. Oecologia 97:1–8

Schoener TW (1979) Generality of the size-distance relation in models of optimal feeding. Am Nat 114:902–914

Sokal RR, Rohlf FJ (1995) Biometry – the principles and practice of statistics in biological research, 3rd edn. Freeman, New York

Tho YP (1981) The giant forest ant *Camponotus gigas*, Malaysia. Nat Malaysiana 6:32–35

Wetterer JK (1994) Forager polymorphism, size-matching, and load delivery in the leaf-cutting ant, *Atta cephalotes*. Ecol Entomol 19:57–64

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice Hall, Englewood Cliffs, NJ