

Trophobiosis in a tropical rainforest on Borneo: Giant ants *Camponotus gigas* (Hymenoptera: Formicidae) herd wax cicadas *Bythopsyrna circulata* (Auchenorrhyncha: Flatidae)

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Abstrak. Disini kami ingin melaporkan mengenai hubungan trofobiotik diantara semut raksasa hutan, *Camponotus gigas* (Latreille, 1802) yang aktif pada waktu malam dengan *Bythopsyrna circulata* (Guerin-Méneville, 1844) daripada famili Flatidae yang kami perhatikan di Taman Negara Kinabalu, Sabah, Malaysia. *B. circulata*, yang tidak mempunyai adaptasi secara morfologi dengan interaksi trofobiotik dengan semut dilaporkan sehingga sekarang telah menghasilkan kuantiti madu yang banyak. Madu yang dihasilkan daripada larvanya adalah 24 mg/h dan dewasa 42 mg/h. Jarak masa pengeluaran madu secara berertinya lebih singkat apabila Hemiptera tersebut dijaga oleh semut. *C. gigas* menunjukkan tiga corak kelakuan semasa menjaga flatid: “mengumpul”, “membantu” dan “menerima maklumat terlebih dahulu”. *C. gigas* pekerja bertukar tugas antara satu sama lain. Semua pekerja tersebut bertukar madu secara trofolisis, dan ini seterusnya boleh mengoptimumkan beban mereka (purata beban 24.5 mg) sebelum kembali ke sarang. Walaupun purata penerimaan melalui perhubungan ini adalah lebih kurang 7.24 g madu pada satu malam, flatid tidak dilindungi oleh kebanyakan *C. gigas* dan tidak cenderung ketika waktu siang. Sebaliknya *C. gigas* melindungi Coreidae *Mictis* (cf. *longicornis* Westwood) sp. yang morfologinya telah teradaptasi untuk berinteraksi dengan semut. Coreidae merembeskan titisan madu lebih cepat daripada semut, walaubagaimanapun penilaian bagi jumlah pengeluaran madu adalah tidak mustahil.

Abstract. Here we report on a trophobiotic association of the predominantly nocturnal giant forest ant *Camponotus gigas* (Latreille, 1802) with a species of Flatidae, *Bythopsyrna circulata* (Guerin-Méneville, 1844) observed in Kinabalu National Park, Sabah, Malaysia. We investigate task sharing of the ants and quantify their nutritional benefits. *Bythopsyrna circulata*, which had no morphological adaptation to trophobiotic interaction with ants and seems to be facultatively associated with ants, produced the largest quantities of honeydew reported up to now. Honeydew output of larvae was 24 mg/h, of adults 42 mg/h. Time intervals of honeydew secretion by the Flatidae were significantly shorter when Hemiptera were tended by ants. *Camponotus gigas* showed three behavioural patterns during tending of flatids: “collecting”, “secondary gathering” and “antennating from ahead”. Workers of *C. gigas* switched among different tasks, but usually performed one task over a longer period of time.

All workers exchanged honeydew by trophallaxis, thus optimizing their load size (mean load 24.5 mg) before returning to the nest. Although total colony gain from this association was high at approximately 7.24 g honeydew per night, flatids were not guarded by majors of *C. gigas* and were not tended during daytime. In contrast *C. gigas* majors guarded the coreid bug *Mictis* (cf. *longicornis* Westwood) sp., an obligate myrmecophile, which is morphologically adapted to interaction with ants. These coreids excreted honeydew droplets at a faster rate than flatids; yet assessment of total output of honeydew was not possible.

Keywords: behaviour, Fulgoromorpha, Homoptera, honeydew production, Myrtaceae, plant hoppers, polyethism, *Syzygium* tree, trophobiosis

INTRODUCTION

Since the 1970s numerous field studies have documented that in tropical rainforests ants are a dominant animal group in terms of abundance and biomass (Fittkau & Klinge 1973) and make up about 20 to 40 % of the arthropod biomass in rainforest canopies (Tobin 1995). The nutritional basis for that dominance has been questioned. Recent results based on nitrogen isotope ratios have shown that canopy ants in particular are cryptic herbivores that feed mainly on extrafloral nectar and liquid exudates of their trophobionts (Blüthgen *et al.* 2003; Davidson *et al.* 2003; Davidson & Patrell-Kim 1996). This liquid, the “honeydew,” produced in ample quantities by speciose groups of Hemiptera (Blüthgen *et al.* 2006; Delabie 2001), is the nutritional foundation for most dominant ants in the canopy (Tobin 1994), which are often characterized by modifications of their digestive tract for the most effective use of plant sap (Davidson 1997).

While most research in the tropics has focused on the general significance of the phenomenon, there is no study of specific ant-hemipteran interactions in rain forests that elucidates behavioural interactions in detail and quantifies nutritional benefits for the ants. Here we investigated the trophobiotic interactions of the giant ant *Camponotus* (*Dinomyrmex*) *gigas* (Latreille, 1802) with the flatid *Bythopsyrna*

circulata (Guerin-Méneville, 1844) in a Bornean rainforest. Specifically we (1) observed behavioural mechanisms of honeydew collection and task-sharing of ants during honey-dewgathering and transport; (2) measured honeydew output of the Flatidae; and (3) calculated the daily input of honeydew to the *C. gigas* colony. 4) Additionally, for comparison, we present data of another trophobiosis of *C. gigas* with a coreid species.

METHODS

Observation area and time

Our observation plot was a 5-ha area of primary mixed dipterocarp lowland forest on Borneo in the Kinabalu National Park, Malaysia (around 06°03' N, 116°42' E; for details see Pfeiffer & Linsenmair 2000). As *C. gigas* is a predominantly nocturnal species (Pfeiffer & Linsenmair 1998), we usually started our observations at around 17:00 h, half an hour before the ants' main foraging activity started, and recorded data during the night, using red-filtered head-lamps to avoid disturbing the ants. Observations were conducted in two observation terms (OT) from 10 March to 7 May 1992 (OT1) and from 11 September 1992 to 18 May 1993 (OT2). Usually data was treated per OT and some experiments of OT1 were replicated in OT2; however, for some parts of the study both OTs were needed to sample sufficient data.

Species studied

Camponotus gigas is a dominant member of the ant communities of the Southeast Asian rain forests (Yamane *et al.* 1996) and one of the largest ant species in the world. We have already reported some facts of its life history and behavioural ecology (Pfeiffer 1997; Pfeiffer & Linsenmair 1998, 2000, 2001). Minors of *C. gigas* have a mean head width of 3.56 mm (SD = 0.53 mm) and a mean weight of 135 mg (SD = 43 mg, $n = 714$); majors have a mean head width of 6.9 mm (SD = 0.36 mm, $n = 122$) and a mean weight of 372 mg (SD = 57 mg, $n = 91$) (M. Pfeiffer, unpublished observations). The foraging strategy of *C. gigas* is based on its polydomous colony structure in combination with polyethism, efficient communication and ergonomic optimization, and functions according to the predictions of “Central Place Foraging Theory” (Pfeiffer & Linsenmair 1998). Our focal colony had a territory of 0.8 ha and about 7000 foragers, of which roughly 13% were majors; colonies were polydomous with between 8 and 14 nests (Pfeiffer & Linsenmair 2000).

Bythopsyrna circulata is a wax cicada (Flatidae, Hemiptera) occurring in the understorey of the rain forests of Sabah (Fig. 1). Although we did not study the development of *B. circulata* we could identify five larval stages; the winged adult hatched from the fifth (L5). Trophobiotic interactions of these planthoppers with ants have been noted as rare and unclear (Adenuga 1975), and indeed there is almost no information available, although 78 species of flatids are reported from Borneo (Medler 1996) and despite their large size and eye-catching appearance.

Interactions took place on a 12m-tall, young tree of *Syzygium* sp. (Myrtaceae) and in the immediate vicinity of a minor nest of our *C. gigas* focal colony (see Fig. 1). Observations were executed from a ladder beneath the tree. The number of wax cicadas was between 25 and 240 individuals in OT1 and 40 to 250 in OT2. The development cycle of the flatids was more or less synchronized: after OT2 all flatid larvae had been

hatched into adults and flew from the tree. After a break of about one year in 1994 we observed a *B. circulata* aggregation again sucking at the tree.

Individual marking of the ants

The large size of *Camponotus gigas* allows individual marking of these ants with durable numbered plastic tags of different colours that are otherwise used for the marking of bee queens. For marking we collected 136 ants in OT1 and 231 ants in OT2 on their way to the trophobionts, several days before the actual experiments started. Additional ants of the colony were marked during other experiments at different places. Plastic tags were fixed with acryl amid glue to the pronotum of the ant and lasted about three months.

Activity patterns of ants and flatids

We quantified ant activity at the *Syzygium* sp. tree by counting, hourly, the number of ants entering and leaving the tree between 17:00 and 08:00 h during 10-minute intervals ($n = 230$). These were recalculated to assess hourly activity. Monitoring was done at two bottlenecks that were especially suited to survey the traffic: 1) at the base of the tree, where ants entered it; and 2) on a branch seven metres high that allowed ants to climb to a neighbouring tree and further up into the canopy. During daytime activity was monitored by spot checks.

Honeydew production of *B. circulata*

We measured time intervals between honeydew excretions of larvae and adults of the planthoppers, both while ants tended them and when unattended. We recorded two to three droplets (thus one to two time intervals) per individual each night. To determine the weight of the honeydew droplets we collected 47 droplets from adults and 113 from larvae, directly from their abdomen. Droplets were sucked into a capillary tube and weighed with an electronic balance (OHAUS CT 10).

Ant interactions during honeydew gathering

During OT1 we recorded the behaviour of 136 individually marked ants over one month (91 spot checks of all ants at the tree). In OT2 we observed 231 marked ants during 42 days (149 spot checks of all ants at the tree).

In OT2, during 10 nights, each with four hours of observation, we investigated interactions of 134 individually marked ants during honeydew collecting; behaviour of each worker was studied on average for 4.2 nights. We noted grooming and trophallaxis (food exchange) among the ants. For the statistical analysis we included only those 46 ants that had been observed for a minimum of 4 nights at the tree.

For the statistical analysis of ant behaviour we calculated the time budget (as percentage of total performance) of the three behavioural patterns (see below) from the frequency counts of each individual. We used k-means clustering with Euclidean distance measure to combine groups of ants with similar behaviour (performed in STATISTICA 6.1, StatSoft, Tulsa, 2003, www.statsoft.com). K-means clustering is a multivariate explorative technique in which all elements of a group (here the individual workers) are classified into a predefined number of subgroups in such a way that they differ with regard to the target variable (here the mean performance percentage of behaviour) in a one-way ANOVA with maximal significance. Each variable is tested with a single ANOVA. While *P*-values of the ANOVAs are not valid, *F*-values give an idea about the quality of the discrimination between the clusters (STATISTICA 6.1, HELP, 2003).

Honeydew input of the ants

To measure ants' mean transport capacity we caught 421 marked and 225 unmarked ants, at the tree trunk on the ground or at 7 m height, when they left or entered the trophobiotic association, and weighed them. Between these points we

surveyed the association on the tree completely, so we were able to avoid weighing ants which had already lost weight via trophallaxis between foragers on their way to and from the nest.

RESULTS

Observation of activity patterns

In the first weeks of our observations the Flatidae were strictly nocturnal; at sunset they came down from the tree canopy to their sucking places at the stem of the tree. Immediately afterwards, minor workers of *C. gigas* appeared and started honeydew gathering. Both species stopped their activity at sunrise; the ants returned to their nest, while the flatids withdrew into the crown of the 10 m-high tree to rest during the day (Fig. 2). Some weeks later, however, most Flatidae remained at the tree trunk during daytime too, and some started sucking during daytime without being cared for by *C. gigas*, which remained nocturnal. Whereas in OT1 ants collected honeydew from the association very intensively, in OT2 when flatids were very abundant at the tree only a small portion of them were tended. Thus in day- and in night-time honeydew fell to the ground and was collected there by many other insects: wasps, stingless bees, butterflies, stalk-eyed flies and other Diptera, bugs and 18 diurnal species of ants, mostly Formicinae (for a list see Pfeiffer 1997). Workers of *C. gigas* hardly ever collected honeydew from the leaf litter, preferring direct collection from their trophobionts.

Behavioural repertoire of *C. gigas* during flatid tending

B. circulata has none of the morphological and behavioural adaptations (e.g. lengthened excretion openings, the ability to control extrusion of honeydew) that are found, for example, in aphids (Way 1963) and which ensure the direct and complete transfer of honeydew to its trophobiotic partners. The honeydew droplets were simply jerked away with vigorous flicks of the abdomen (adults did so while lifting their wings), such that other cicadas were not hit by them, unless Flatidae

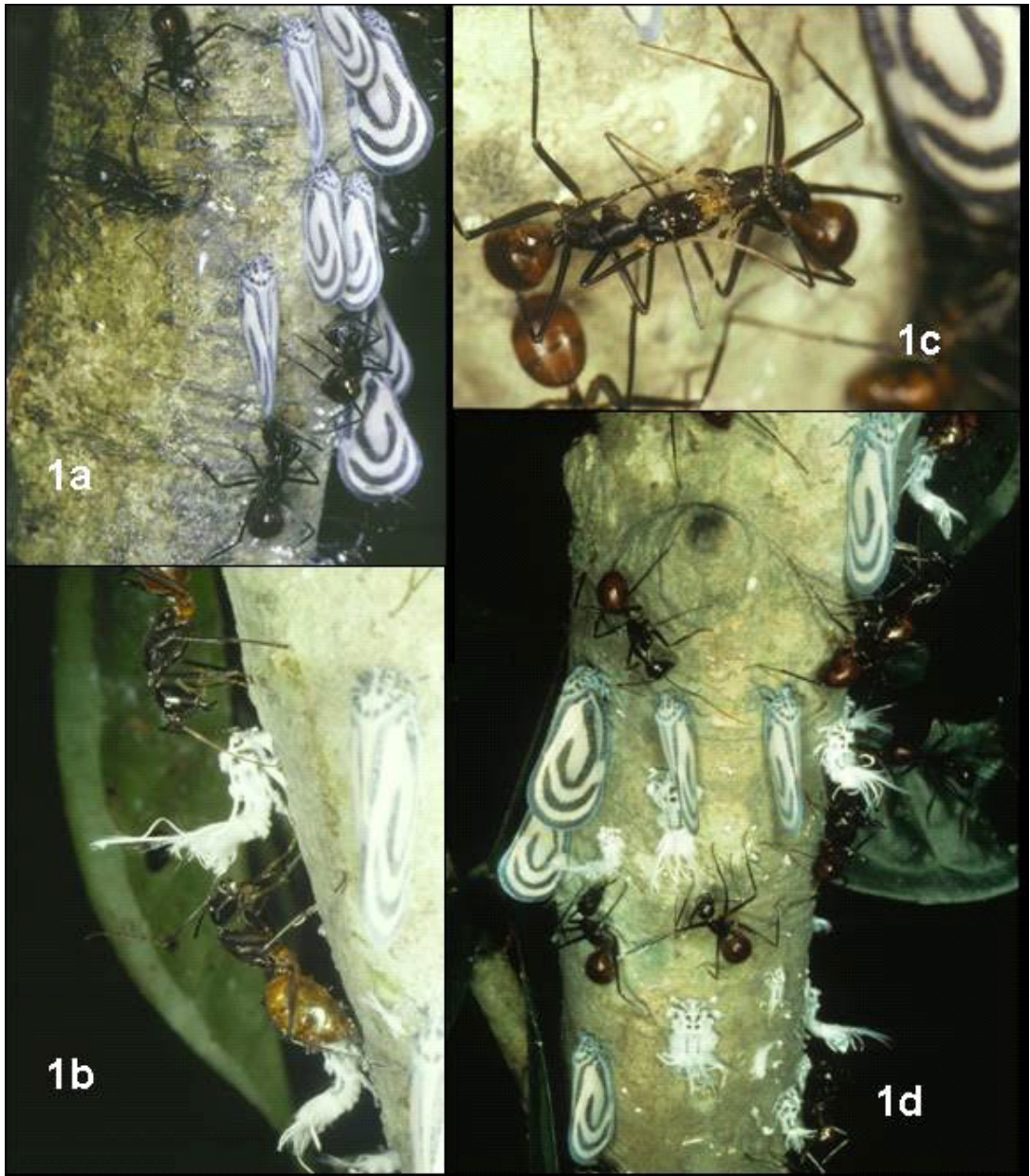


Fig. 1 Wax cicadas *Bythopsyrna circulata* in a trophobiotic association with *Camponotus gigas* on a *Syzygium* tree (Myrtaceae) in the rainforest of Sabah, Borneo. These cicadas lack any morphological adaptations that ensure controlled output of the honeydew; as a result ants have to catch the falling drops with their body surface (see 1a,b). **1a**) Workers of *C. gigas* tending *B. circulata* adults. **1b**) A collector (below) and a second ant “antennating from ahead” (above) tend a larva of *B. circulata*. **1c**) Liquid food exchange (oral trophallaxis) between two workers of *C. gigas*. **1d**) Overview picture of the association.

were sitting extremely crowded on the tree. For effective collection of honeydew the tending ants had to catch the flying drops (see Fig. 1).

Tending of trophobionts was restricted to minors of *C. gigas* which showed three different behavioural patterns suitable for executing three different tasks:

“Collecting” (C): The tending ant, waiting for falling drops of honeydew, sat directly below the hemipteran with the flatid’s abdomen between its antennae, which swung rhythmically up and down. A flatid larva treated in this way continually bent its abdomen up. Inactive flatids began sucking and after a few minutes they excreted honeydew droplets. When a flatid flicked the honeydew droplet away, the tending ant tried to catch the falling droplet with its head, or with its front legs. Then it sucked the droplets from its own body surface. So workers utilized the surface tension of the honeydew to recover it.

“Antennating from ahead” (AA): The ant sat above or lateral to the cicada and antennated its front part. In some cases up to four ants were

gathered around one cicada, performing AA. In OT2 this behavioural pattern was observed only rarely.

“Secondary honeydew gathering” (SHG): Here the worker ran between several collecting ants and groomed them if needed. They gathered those droplets that had hit the collectors such that they were unable to remove them by themselves. Often secondary gatherers prompted collectors to perform trophallaxis; four to six of them attended consecutively to collect honeydew. When they had filled their gasters they returned directly to the nest. Secondary gatherers showed no specific guarding behaviour. Secondary gatherers frequently replaced ants that performed tasks C or AA.

We observed no ant which was completely specialized on one task; however, most ants “preferred” one task to the others and performed one task over a longer period of time. Majors were hardly ever observed at the trophobiotic association. They showed aggressive behaviour towards the flatids, and minors seemed to try to keep them away from the association.

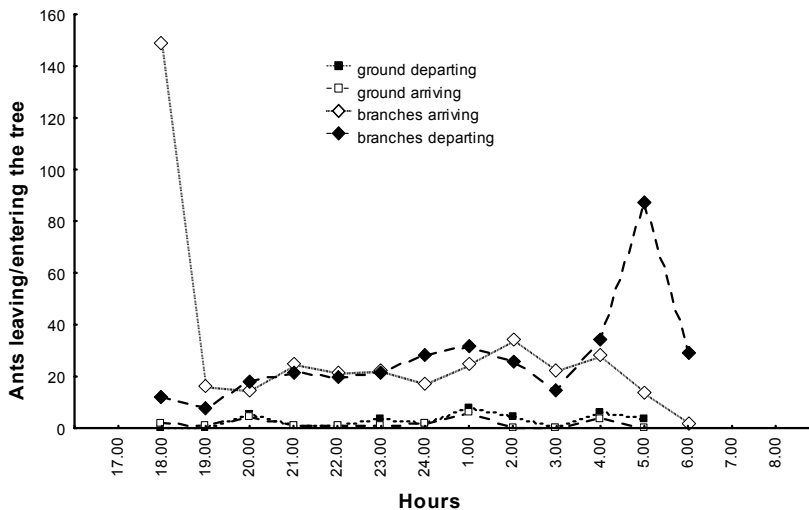


Fig. 2 Ants entering and leaving the *Syzygium* tree during their nocturnal activity phase. Most ants came down from the canopy; few travelled over ground. Listed are mean values of activity counts starting 30 minutes before and ending 30 minutes after a full hour. Ant activity at the trophobionts started at about 17:30 h and ended at approximately 06:30 h.

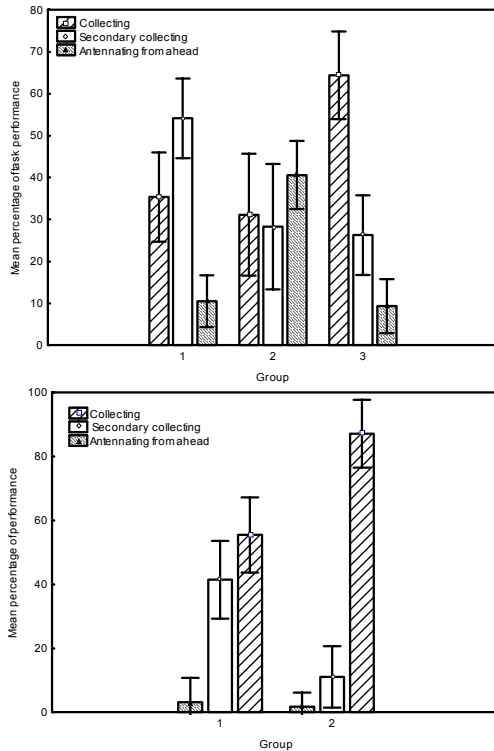


Fig. 3 Task sharing in *C. gigas* workers during flatid tending. The tasks comprise collecting (C), secondary honeydew gathering (SHG) and additional antennating from ahead (AA). **3a)** In OT1 56 workers could be sorted to three significantly different groups according to their main behavioural patterns. **3b)** In OT2 230 ants were distributed in two groups that differed significantly in the performance of two of the three tasks (not in AA). See text for the statistics. Given are the means for the single groups and the standard deviations.

Task breakdown in OT1

In OT1 52.9% of the observations were of “C” behaviour, 33% were “SHG” and 14% were “AA”. According to their task preference during our 91 spot-checks in OT1, *k*-means clustering arranged 56 individually marked workers of *C. gigas* into three groups (see Fig. 3a). Members of group 1 preferred SHG (C = 35.4%, SD = 11.2%; SHG = 54.1%, SD = 10.1%; AA = 10.5%, SD = 6.5%; $n = 13$). Ants of group 2 used most time for AA (C = 31.1%, SD = 15.3%; SHG = 28.3%, S.D. = 15.6%; AA = 40.6%, SD = 8.5%; $n = 8$). In group 3 collecting (C) was the dominant task (C = 64.4%, SD = 11.0%; SHG =

SD = 11.0%; SHG = 26.3%, SD = 10.0%; AA = 9.3%, SD = 6.8%; $n = 35$). (ANOVAs (DF for all = 2, 53) $F_1 = 179.57$, $F_2 = 35.57$, $F_3 = 6.72$).

Task breakdown in OT2

In 72% of all cases ($n = 239$) in OT2 ants “collected” honeydew (C), in 25.6 % they showed the SHG pattern, and only in 2.5 % did they antennate the cicadas from ahead (AA). A *k*-means clustering separated all ants into two groups (Fig. 3b): group 1 ($n = 101$) comprised ants that “collected” honeydew in 55.4% (SD = 12.3%) and showed the SHG pattern in 41.1% of the observations (SD = 12.8%), while group 2 ($n = 129$) “collected” in more than 87 % of the observations (SD = 11.2%) and performed SHG in only 11% (SD = 10.1%) (ANOVAs (DF for all = 1, 228), $F_1 = 413.4$, $F_2 = 404.1$, $F_3 = 2.5$).

Interactions of the ants while gathering honeydew

Detailed behavioural observations of trophallaxis between tending ants in OT2 showed that several ants gave honeydew to specialist workers (Fig. 4). We used the following variables for a description of the behaviour: GR-PAS = number of received groomings; GR-ACT = number of active groomings; TR-GIV = number of trophallactic interactions in which ants gave food to other workers; TR-TAK = number of trophallaxes in which ants took food from other workers. According to their task behavioural patterns of ants were more or less restricted: in most cases of trophallaxis secondary gatherers took the honeydew; GR-ACT was only possible for ants with AA and SHG behaviour; only collectors received GR-PAS; TR-GIV was performed by all groups. Based on their behaviour *k*-means clustering divided ants into two groups (Fig. 5): group 1 ($n = 26$) comprised the collectors with high values for GR-PAS and TR-GIV, and low values for GR-ACT and TR-TAK. Group 2 ($n = 20$) consisted of secondary gatherers that showed the opposite behaviour with high values for GR-ACT and TR-TAK. Groups were separated according to the variables GR-ACT and TR-TAK, not the other two

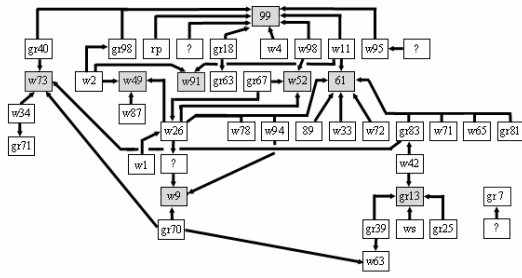


Fig. 4. Flow chart of honeydew exchange by trophallaxis between “secondary gatherers” and “collectors” at the *Syzygium* tree. The numbers of the boxes refer to the markings of the ants. Arrows represent the flow of the honeydew that had been gathered by “collectors” (white boxes) during tending of flatids and is transferred to “secondary gatherers” (grey shaded boxes) by trophallaxis for further transport to the nest. In some cases trophallaxis was also performed between collecting ants. Data of 29/30 January 1993 from 21:00 to 02:15 h.

variables (ANOVAs (DF for all= 1, 44), $F_{GR-ACT} = 77.2$, $F_{TR-TAK} = 19.7$, $F_{GR-PAS} = 3.0$; $F_{TR-GIV} = 3.1$).

These observations quantified the behaviour of the discriminated groups more exactly: the collectors sat below the cicadas and gathered honeydew, the secondary gatherers groomed them and collected honeydew drops from their integuments and by trophallaxis. So the collectors could stay at the tree for a longer time without interrupting their work for the transport of honeydew to the nest. Site fidelity of collectors and flatids was high; if they were not disturbed, usually both returned to the same place and arriving workers searched for individual flatids nearby if they had changed their sucking places (M. Pfeiffer, pers. observations with marked individuals).

The honeydew output of *B. circulata*

Influence of tending. Ants started tending of flatids at the L2 larval stage. Time intervals of honeydew secretion by the Flatidae were significantly shorter when tended by ants (see Table 1): in untended adults time intervals between single droplets were on average 340 seconds

longer than in tended ones (U -test: $U = 82.5$, $Z = -5.56$, $P < 0.001$). Similarly in untended larvae droplet intervals were 54 seconds longer than in larvae tended by ants (U -test: $U = 3525.5$, $Z = -318$, $P < 0.01$). In all tended larvae droplet intervals were 54 seconds longer than in larvae tended by ants (U -test: $U = 3525.5$, $Z = -318$, $P < 0.01$). In all tended larvae droplet intervals were positively correlated with larval stage (Spearman correlation $r_s = 0.63$, $t(164) = 10.5$, $P < 0.0001$, $n = 166$), and the same was true for the untended flatids (Spearman correlation $r_s = 0.85$, $t(66) = 13.5$, $P < 0.0001$, $n = 66$). In adults time intervals between droplets were significantly longer than in larvae, whether flatids were tended by ants (Table 1, U -test: $U = 1240$, $Z = 4.18$, $P < 0.001$) or not (U -test: $U = 139$, $Z = 6.64$, $P < 0.001$).

Tending by several workers. Most of the tree-sucking *B. circulata* individuals were tended by only one *C. gigas* that was sitting directly behind the cicada (C). However, in OT1 in about 5 % of all cases a second worker tended the flatid from ahead over long periods of the night (AA). We investigated this phenomenon with data of the L3 larvae: droplet intervals of larvae tended by two workers (54.3 s, SD = 42.4 s, $n = 15$) were significantly shorter than those tended by a single one (65.4 s, SD = 32.8 s, $n = 65$; U -test: $U = 201$, $Z = -3.53$, $P < 0.001$). Compared to them droplet intervals of untended L3 larvae were significantly longer (99.5 s, SD = 6.1 s, $n = 4$, U -test: $U = 19$, $Z = 2.85$, $P < 0.01$).

Droplet weight. The weight of the droplets produced by larvae (mean = 0.62 mg, SD 0.01 mg, $n = 113$) and adults (mean = 1.95 mg, SD 0.05, $n = 47$) of *B. circulata* differed significantly (U -test: $U = 0.0$, $Z = -3.46$, $P < 0.001$). Honeydew output of tended adults was 42 mg/h, while for tended larvae of all stages we calculated a mean of 24 mg/h. Related to body weight (see Table 2) we found for adults an hourly honeydew output of 35.4 % of their body weight, for larvae 24.6 %.

Table 1 Time intervals between drops of honeydew in *B. circulata* with and without tending by ants *C. gigas*. Given are the lengths of the intervals, the standard deviation and the number of intervals.

	Time interval [s]	SD	<i>n</i>
Larvae with ants ^{1,3}	94	62.5	136
Larvae without ants ^{1,4}	148	112.4	71
Adults with ants ^{2,3}	168	130.5	34
Adults without ants ^{2,4}	508	257.4	28
Larvae total	113	86.5	207
Adults total	322	260.2	62

^{1,2,3,4} significant differences, *U*-test, *P* < 0.01, see text.

Table 2 Weight of different stages of flatids and the time intervals between honeydew drops during tending by *C. gigas*.

	Weight [mg]	SD	<i>n</i>	Interval [s]	SD	<i>n</i>
ADULT	118.20	4.00	9	168.21	130.50	34
L5	102.53	3.22	4	169.83	72.64	24
L4	97.93	1.42	4	105.81	59.91	31
L3	94.48	1.09	4	70.67	37.33	72
L2	92.52	0.21	6	50.22	5.85	9
Mean larvae	96.86	-	18	94.0	62.5	136

Which worker caste is responsible for the honeydew transport back to the nest?

The observations above (Fig. 4) led to the hypothesis that the secondary gatherers transported most of the honeydew. We tested this with data from OT1 of individually marked ants that had been 1) observed during spot checks at the trophobiotic association and 2) weighed between 19:00 and 04:45 h (before the mass return of the ants to the nest). Again, three groups of ants could be discriminated by k-means clustering (Fig. 6, ANOVA (DF for all = 2, 53), $F_1 = 45.25$, $F_2 = 31.62$, $F_3 = 67.51$). Members of cluster 1 tended to perform SHG (54.1 %, SD = 16 %; $n = 13$), making on average 2.1 transports ant⁻¹ night⁻¹. Ants of cluster 2 ($n = 35$), which mostly (64.4 % of all observations, SD = 11 %) collected honeydew (C) directly at the Flatidae, each averaged 3.3 transports per night. Workers of cluster 3, which tended to antennate the flatids from ahead (41 % AA, SD = 9.2 %; $n = 8$) averaged only 1.3 transports ant⁻¹ night⁻¹ (Fig. 6).

The eight ants we weighed most often together performed 36.4% of all transports. They were “collecting” on 67.7 % of trips (SD = 6.2 %) and “secondary gathering” on 32.3 % (SD = 9.4 %). These ants mostly collected honeydew and were the most active transporters; as a general characteristic they did not perform AA.

The weight of the ants during transport of honeydew

To quantify honeydew retrieval we weighed ants entering the trophobiotic association (118.4 mg, SD = 32.3 mg, $n = 310$) and returning to the nest (134.4 mg, SD = 38.1 mg, $n = 366$), finding the two groups differed significantly (*U*-Test, $U = 41119$, $Z = -6.17$, $P < 0.001$). However, ants that returned to the nest during the communal return period (5:00 to 7:00 h) at the end of the nocturnal activity period (see Fig. 1) may not have had filled their gasters completely. By excluding them we calculated the weight of ants that transported the honeydew to the nest during 20:00 to 5:00 h; returning ants

weighed 142.9 mg (SD 43.9 mg, $n = 185$) so their average load was 24.5 mg, constituting 21% of body weight. To corroborate our findings we weighed 74 individually marked ants in the same time period on their way to the trophobionts and back to the nest to determine their average honeydew load directly: mean mass of honeydew per ant was 27.3 mg (SD = 36.2 mg). On the other hand those ants ($n = 181$) that returned partially loaded in the morning (5.00 hours to 7.00 hours) brought back an average of only 7.3 mg honeydew.

An estimation of the input of honeydew

During the activity counts of OT1 (Fig. 2) we counted 260 transporter ants returning to the nests within one night and additionally 119 collectors that returned to the nests during the communal return in the morning. Using the smallest values for our estimation we calculated a common input of 6.37 g honeydew by ants' transport during a night and of 0.87 g input from returning collectors in the morning; so the colony's earnings from this trophobiotic association was 7.24 g honeydew per night. For a rough mean of 100 foragers at the tree, each of these ants collected two-thirds of its weight in honeydew.

Other trophobioses

In January 1994 we discovered two individuals of Coreidae, subfamily Meropachyinae (possibly *Mictis* (cf. *longicornis*) sp.) that were tended by five workers of *C. gigas*. This trophobiotic association grew to 21 bugs in June 1994. While tending, the ratio of bugs to ants varied between 0.4 to 1.0 and 1.2 to 1.0 ($n = 26$ associations). The coreids were well adapted to tending by ants. Their excretion openings were lengthened in a spout like style. Droplets of honeydew were delivered slowly and kept hanging there until removed by a collecting ant. If no ant appeared the droplet was sucked in again. Bugs could elicit honeydew even when sucking head foremost and were able to sit extremely aggregated, without becoming stuck together by their excretions.

Coreids were guarded continually by *C. gigas* (major) workers. As proved by individual marking, ants showed a polyethism between diurnal and nocturnal workers. During the day coreids mostly sat crowded at about 8 m height, without sucking, and were surrounded by several *C. gigas*. When coreids were outside this "herd", *C. gigas* workers tried to drive them back to the group. Only when moulting did bugs stay apart. At dusk both species came down and the coreids started sucking. Task organization of ants was similar as in tending Flatidae, but there was no grooming of the collectors, because droplets were directly taken from the bugs' excretion tubes. Temporal output of honeydew droplets between nymphs and adults did not differ (see Table 3) and was much quicker and more continuous in coreids than in flatids (both group with tending ants; Coreidae: 43.5 s, $n = 81$, SD = 34.3 s; Flatidae: 109.5 s, $n = 170$, SD = 85.5 s; *U*-Test: $U = 2817$, $Z = -8.86$, $P < 0.0001$).

We also observed *C. gigas* attending other Hemiptera: Fulgoridae and different species of Membracidae (e.g. with *Eufairmairia* sp., U. E. Stegmann, University of Würzburg, pers. comm., May 1998).

DISCUSSION

The production of honeydew by *B. circulata* was extraordinarily high compared to other trophobionts. While data on Flatidae are not available, Auclair (1963) compiled data on aphids and reports on hourly honeydew production rates ranging between 1.9 and 13 % of body weight for most aphid species. Extremely high compared to other aphids is the production in the temperate *Tuberolachnus salignus* (Gmelin, 1790) in which L1 larvae produce honeydew weighing up to 133 percent of their body weight each hour (0.45 mg/h); adults produce 1.7 mg honeydew per hour, 33 percent of their body weight. However, in absolute terms, this is 24 times less than adults of *B. circulata*! If all large trophobionts in the tropics produce similar rates, as may be expected based on their physiological needs, then they would be "bonanzas" (Hölldobler & Wilson 1990) that provide superabundant food for ants. Indeed there were at least some hints that ants of the observed

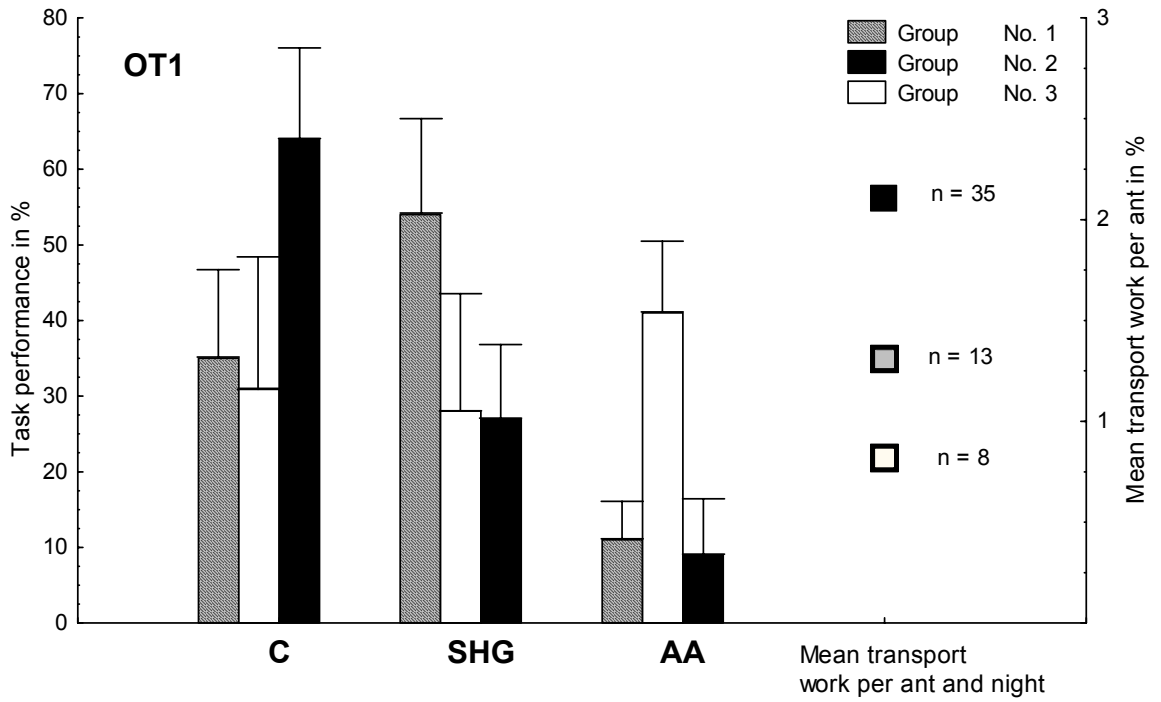


Fig. 6 Task sharing of those ants that were observed to transport the honeydew to the nest in OT1. Given are the different tasks, as noted in Fig. 3 and three groups of workers that performed them in different percentages (means and standard deviation) (left Y-axis). On the right Y-axis the mean percentage of transport work is given for the workers of each group. Those workers that did most collecting also did most of the transporting. Data in OT2 are similar but not shown.

colony had surplus honeydew food from this trophobiotic association: 1) *C. gigas* only tended the trophobionts at night, leaving the lower diurnal production of honeydew for other ant species, 2) they did not retrieve the ample amounts of honeydew that fell to the ground; 3) during OT2, when flatids were very abundant at the tree only a small portion of them were tended; 4) flatids were not guarded by majors and we observed several occasions when other ant species caught L1 larvae and removed them from the association without being hindered by any of the abundant *C. gigas* at the place. While the night activity of the ants may be also explained by the activity of diurnal phorids that are parasitoids of the ants (Disney & Schroth 1989) rather than demonstrating the surplus provision of the colony, the other arguments provide strong support for superabundance of this food supply. Avoidance of parasitoids may also explain the hiding of the flatids in the tree canopy during the day in the first weeks of our observations.

As we have shown, the tending of flatids by ants significantly reduced time intervals between droplets and may thus enhance their production of honeydew. We could not verify whether drop weight was kept constant or increased during ants' presence, because taking off the drops from ants' integuments led to aggressive reactions that affected the whole association. However, increased honeydew production during ant attendance has also been demonstrated in the mealybug *Trabutina* sp. (Degen & Gersani 1989) and certain aphid species (Douglas & Sudd 1980; Katayama & Suzuki 2002) and is likely in *C. gigas*, too.

Ants' tending of the Flatidae was well organized; we could differentiate three tasks that were necessary to fully utilize the trophobionts. With k-means clustering we distinguished worker groups that showed different task preferences:

1) The "collectors" that sat for up to 80% of their time below the cicadas and devoted little time to the other tasks. Obviously this was the best method to collect most of the honeydew. As flatids had no morphological adaptation for transfer of honeydew, ants simply had to wait for the falling

drops that were flicked at unpredictable intervals by the Flatidae. These collectors may have "adapted" their behaviour to individual flatids in order to optimize their collecting yield. This was corroborated by our observations with individual marking of ants and Hemiptera showing that newly arriving collectors had a tendency to return to the same flatids (and / or places) they had tended before.

2) A less specialized group of ants worked for more than 40 % of their time as "secondary gatherers," by removing honeydew droplets from the cuticula of the collectors and "collecting" honeydew via trophallaxis. By performing these tasks they enabled the collectors to stay at the flatids for a longer time. As the time interval between droplet-flicking by flatids was shortened by tending, it may be a good strategy to continue the tending for a longer period in order to avoid inducing the more intensive excretion of honeydew several times and to optimize the collector's position for catching the drops. By continually giving honeydew to the nestmates the collector is not forced to leave the flatid when its gaster is full, but has the chance to leave it at the optimal time (with respect to the excretion behaviour of the flatid).

3) Tending of flatids by an additional worker from ahead (AA) had an extra effect on their excretion frequency; however, this was a behaviour that was commonly performed only in OT1. In that phase flatid abundance was much lower than in OT2 and most individuals were continually tended by ants. In this situation when honeydew was more limiting and all work places were occupied, it may be a good strategy to increase the honeydew yield, assuming higher excretion frequency was coupled with an increased honeydew production (an assumption we could not prove in our experiments). However, in OT2 when flatids were highly abundant and honeydew was plentiful, this behaviour was only rarely observed. As workers that performed mainly AA brought less honeydew to the nest, the disregard for AA in OT2 may also be the result of an optimization process in ants that maximized their gains within time.

Table 3 Time intervals [s] during the output of honeydew drops of the Coreidae in the presence of *C. gigas*. Intervals of adults and nymphs did not differ significantly (*U*-Test, $U = 633$, $Z = 0.96$, $P > 0.5$).

	Mean interval between two drops [s]	Minimum interval [s]	Maximum interval [s]	SD	<i>n</i>
Adults	45.22	5.00	145.0	38.85	54
Nymphs	39.96	11.00	122.0	22.86	27
All	43.47	5.00	145.0	34.29	81

The behavioural repertoire within trophobiotic interactions of different species of ants and Hemiptera seems to be limited. The recorded tactile signals (attending workers palpating the dorsal abdominal glands of the Hemiptera; Hemiptera ready to excrete honeydew raising their abdomen) were similar between flatids and coreids and have been reported from other associations too (Dejean *et al.* 2000a). Associations between ants and heteropterans are infrequent (Dejean *et al.* 2000a, Maschwitz *et al.* 1987, Metzger & Blüthgen in press, this issue of *Asian Myrmecology*). Contrary to the flatids the Coreidae were morphologically adapted to interaction with ants. They were able to alternate extrusion and withdrawal of a honeydew droplet when the workers failed to immediately absorb the honeydew. We did not observe a single drop of honeydew that was extruded by a coreid without being taken by a worker ant. This points towards a closer association between these partners, while the interaction between *C. gigas* and *B. circulata* seems to be less specific (Zwölfer 1958). This difference was also shown by ants' guarding of the trophobionts, which happened only in the Coreidae, while *B. circulata* was unattended during the daytime, thus being prone to attack by parasitoids (M. Pfeiffer pers. observation). Guarding of Fulgoromorpha colonies by ants can significantly reduce loss to predators (Dejean *et al.* 2000b). Phloem-feeding bugs need extra long stylets to pierce the thick bark of their host tree (Maschwitz *et al.* 1987), so they are especially susceptible to wounding by their enemies, as they are unable to flee within a short time. Therefore parasitoid pressure may be higher in coreids

and predation pressure on flatids seems to be limited, possibly due to the excretion of indigestible wax. Many wax-producing Homoptera, e.g. Fulgoridae, are large and extremely conspicuous; nevertheless they are long-lived. A third argument for an unspecific association is that in *B. circulata* development of all stages was synchronized, whereas a desynchronized cycle of development would allow *C. gigas* to live continually on the honeydew output of their "cattle". This was not the case: after OT2 all larvae had hatched into adults and flew off the *Syzygium* tree, thus terminating the association. This shows that ants were only opportunists, which used the honeydew of this association facultatively.

Interestingly, most specific interactions of ants and Hemiptera seem to happen between smaller species, while large species with a potentially higher excretion rate may be mostly facultatively associated with ants (M. Pfeiffer, pers. observations 1991-2007). This holds at least in the Bornean rainforest for Flatidae, as well as for Fulgoridae and other groups of Auchenorrhyncha. However, due to the high diversity of ants (Brühl 1998) and Hemiptera (Medler 1996; Novotny & Missa 2000) in the tropical rainforest, low specialization may often be the best strategy to ensure the association of trophobiosis partners.

During tending of flatids the remarkable behavioural elasticity of *C. gigas* (see Pfeiffer & Linsenmair 1998) became obvious. Although single ants showed a high affinity towards particular duties, none of them performed only one task. In a former study of *C. gigas* (Pfeiffer &

Linsenmair 1998) we found a specialized cast of transporter ants that were larger than the average workers and carried a load five times larger than them (full weight about 240 – 290 mg); they were responsible for transporting honeydew between the nests over distances of about 15 metres. However, this worker caste was not observed at the flatids. There may be several reasons for this: on the one hand, the flow of the honeydew at the association may be too slow to use the transporter cast efficiently, and on the other hand, those big transporter ants may be too large to perform any other tasks as well (e.g. “secondary gathering”). Rather, a group of much smaller, equal sized workers showed a very flexible division of labour in different tasks and optimized their load size by use of trophallaxis before returning to their nest (Fig. 1c, 4).

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