

Task-partitioned nectar transfer in stingless bees: work organisation in a phylogenetic context

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Abstract. 1. The eusocial corbiculate bee tribes comprise the Apini (honey bees), Bombini (bumble bees), and Meliponini (stingless bees). Honey bee foragers (*Apis*) transfer nectar to receiver bees within the nest. This is an example of task partitioning, in which a task is split into sub-tasks connected by material transfer. Nectar transfer does not occur in Bombini. Although it is reported in some species of Meliponini, it has not been subject to detailed study.

2. Nectar transfer was investigated in five genera of Meliponini from Yucatan, Mexico (*Melipona*, *Trigona*, *Scaptotrigona*, *Nannotrigona*, and *Plebeia*). Nectar transfer occurred in all species and for >99% of foragers. Multiple transfer, in which a forager unloads nectar to more than one receiver, occurred but at a lower level than in *Apis*. In *M. beecheii*, multiple transfer was associated strongly with putative recruitment dances.

3. The data provide some support for the hypothesis that task partitioning is favoured by large colony size, in that the Meliponini never have small colonies because colonies are swarm founded. This ensures that colonies are always large enough to prevent delays in finding a transfer partner imposing high costs. Further tests of this hypothesis are suggested.

4. Viewed in a phylogenetic context, the most parsimonious interpretation is that nectar transfer evolved once in the clade (Apini + Meliponini).

Key words. Foraging, *Melipona*, Meliponini, *Nannotrigona*, nectar transfer, *Plebeia*, *Scaptotrigona*, task partitioning, *Trigona*.

Introduction

Work in insect societies is organised along two main principles: division of labour, in which the workforce is divided among the various tasks or groups of related tasks (e.g. Oster & Wilson, 1978; Gordon, 1996), and task partitioning, in which a task itself is divided into sub-tasks (Jeanne, 1986a). Task partitioning is important in material handling, particularly in bringing forage into the nest but also in removing waste and excavated soil from the nest (Ratnieks & Anderson, 1999; Anderson & Ratnieks, 2000; Hart & Ratnieks, 2001a). The honey bee *Apis mellifera* (L.) (Hymenoptera: Apinae) forages for four basic materials: water, nectar, plant resin (propolis), and pollen (Seeley, 1995). All except pollen are

transferred directly from the forager to receiver bees within the nest (Ratnieks & Anderson, 1999). In particular, nectar is regurgitated to one or more receivers, which then store it in honeycomb cells (Park, 1925; Seeley, 1995). In contrast, bumble bee (*Bombus*) foragers store their nectar directly into cells without transfer to receivers (Michener, 1974).

By requiring the pairing of transfer partners, task partitioning with direct transfer causes queuing delays while waiting for a suitable partner (Jeanne, 1986a,b; Anderson & Ratnieks, 1999a,b). Even when the collective work capacities of the foragers and receivers are matched perfectly, queuing delays still occur because of short-term stochastic fluctuations in the arrival of individual foragers and receivers to the transfer area. Computer simulations show that the extent of these short-term queuing delays decreases with increasing colony size, suggesting that task partitioning is more likely to occur in large-colony species, where it will have a lower ergonomic cost (Anderson & Ratnieks, 1999b). (Task partitioning also has various ergonomic benefits, which were

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reviewed by Ratnieks and Anderson, 1999.) This hypothesis is strengthened by comparisons of bees and wasps with small and large colonies. In the Apidae bees, nectar is transferred in *Apis* (which has large colonies; Seeley, 1995) but not in *Bombus* (which has small colonies; Michener, 1974). In *Ves-pula* wasp colonies, nectar is transferred in large colonies but is not transferred in small colonies (Akre *et al.*, 1976; Jeanne, 1986b). A similar situation occurs in *Ectatomma ruidum* ant colonies, with task partitioning in insect prey transport occurring only in colonies with more than 21 workers (reported by Ratnieks and Anderson, 1999). The difference in colony size is increased further by the different mechanisms of colony founding in these two groups. Honey bees found colonies by swarming so their colonies are always large, while bumble bee colonies are founded by lone queens (Michener, 1974). Thus, even though a bumble bee colony may grow to have 100 or more workers, it will be much smaller than this for most of its annual life cycle (Michener, 1974). A similar contrast occurs in wasps in the collection and use of wood pulp for nest building. In Vespinae wasps, which have lone-queen-founded nests, a worker both collects wood pulp and builds with it (Edwards, 1980); but in *Polybia occidentalis* (Polistinae: Epiponini), a species with swarm-founded nests, foragers transfer their wood pulp to builders at the nest (Jeanne, 1986b).

The Meliponini (Hymenoptera: Apinae) is a large group of bees, comprising some 300 + species in 23 genera (Michener, 2000). Colonies are large (typically >500 workers) and founded by swarms (Michener, 1974). As such, task partitioning in nectar collection is predicted to occur. Much work has investigated Meliponini foraging communication systems, which can be highly sophisticated, e.g. the food recruitment behaviours found in *Melipona* (Lindauer & Kerr, 1960a,b; Nieh & Roubik, 1995, 1998; Nieh, 1998). Although nectar transfer from foragers to receivers has been reported in *Trigona carbonaria* (Nieh *et al.*, 1999/2000), *M. panamica* (Nieh, 1998), and *M. favosa* (Sommeijer *et al.*, 1983), nectar handling has never been subject to detailed quantitative study. In the work reported here, behavioural observations of nectar handling were made in five genera, one species per genus, of Meliponini. Nectar transfer from foragers to receivers was universal, occurring in all species, all colonies, and indeed all individual foragers, with the exception of one lone observation of a *M. beecheii* forager that transferred its nectar directly into a storage pot. The results support the hypothesis that large colony size favours task partitioning and show that, in *Melipona*, performance of a special communication signal (the spinning dance) by a forager is associated with a much larger number of nectar transfers.

Methods

Study site and study organisms

The study was conducted at the Department of Apiculture, University of Yucatan, Merida, Mexico in January

and February 2001, during a nectar flow from tajonal *Viguiera dentata* (Asteraceae). Two healthy queen-right colonies each of *Trigona (Frieseomelitta) nigra nigra* (\approx 1500 workers per colony), *Scaptotrigona pectoralis* (\approx 1000 workers), *Nannotrigona perilampoides* (\approx 600 workers), and *Plebeia frontalis* (\approx 1000 workers), and three of *Melipona beecheii* (\approx 800, 1200, and 1800 workers) were studied.

Nest structure

Natural nest layout. Most meliponine bees build nests in existing cavities, which are entered and exited via a small hole, often elaborated with a cerumen tube (wax and resin; Michener, 1974). Brood cells are mass provisioned and are either arranged in combs of hexagonal cells or in grape-like clusters of ovoid cells. In contrast to *Apis*, which uses the same cells both to store food (nectar and pollen) and rear brood, in Meliponini food is stored exclusively in egg-shaped wax storage pots, which are larger than brood cells and of different shape. Storage pots, which are generally located close to brood cells towards the edges of the cavity, have an opening at the top through which a bee may enter to deposit its load. Michener (1974) provided a review of nest architecture.

Experimental nest layout. The colonies were kept in box hives in the Department's meliponary and had been collected from the wild. A few weeks prior to the study, the colonies were transferred individually into shallow observation nests consisting of a wooden box (25 × 20 × 2 cm) covered with a clear glass lid (after Lindauer & Kerr, 1960a). The shallow boxes facilitated observation and were sufficiently deep for storage pots and at least two layers of brood (in species with combs). Foragers entered and exited the nest box through a 10-mm hole on the side. The colony layout was similar to natural nests, with storage pots for nectar and pollen surrounding the brood combs. The pots and brood were arranged so that the area nearest the entrance was clear of any nest structures, enabling the marked foragers and nectar transfers to be seen clearly. Each day, before observations were made, any wax or cerumen was removed from the entrance area and the glass lid was cleaned to improve visibility.

Determining whether nectar transfer occurred

In order to compare nectar transfer in the Meliponini with honey bees and bumble bees, it was necessary to know whether, and how many times, foragers transferred nectar to bees within the nest. Two basic methods were used to do this. The main method was direct observation of nectar transfer from marked foragers to hive bees, but, for one colony of *N. perilampoides*, indirect observations of nectar transfer were made by monitoring the position and behaviour of marked foragers within the nest to determine whether they deposited their nectar into storage pots. It was not necessary to quantify all aspects of nectar transfer

under natural conditions. For example, the delay that foragers experienced in finding a transfer partner was not timed.

Direct observation

The nest entrance was blocked with wax and two to five returning foragers were captured and placed individually in small vials. The nest entrance was then opened. To ensure that all captured foragers had nectar, they were offered 2M sucrose syrup via a Pasteur pipette. All foragers extended their proboscis into the pipette and took syrup. When a forager consistently refused more syrup, it was marked with a unique combination of paint dots on the thorax. Foragers were then released singly at their nest entrance 5–60 min after marking and followed for ≤ 20 min within the nest. Transfer of nectar to other bees or into storage pots was noted. A nectar transfer was defined as a bee extending its proboscis into the mouth of the focal forager for > 1 s (Korst & Velthuis, 1982).

Melipona beecheii foragers frequently performed dance behaviours (with the long axis turning clockwise and anti-clockwise, as described by Nieh, 1998), which were not observed in any other species. Data were collected on the incidence of these dances to determine whether they were related to multiple nectar transfer.

Indirect observation

It was impossible to carry out direct observation on one of the two colonies of *N. perilampoides* because foragers ran under the brood comb immediately after introduction and disappeared for several minutes. An indirect method was therefore adopted to determine whether nectar transfer occurred. If nectar transfer was occurring, foragers would not be observed regurgitating nectar into storage pots. This was investigated by dividing the nest into five sections (entrance area, left area, right area, brood comb, storage pots) and tracing the sections onto an acetate sheet from which section area was determined. Thirty foragers were captured, fed 2M sucrose solution as above, marked with a single colour paint spot, then released at the nest entrance. The nest was scanned for 30 s at 10-min intervals for 190 min, and the number of marked and unmarked bees in each nest section was counted. This was repeated on a second day, with 30 different foragers, which were marked with a different colour paint spot.

Results

Melipona beecheii

One hundred and fifteen of 116 foragers (99.1%) transferred nectar to nest-mates within 20 min of entering the nest. The single bee that did not transfer nectar went directly to a nectar storage pot, where it regurgitated. Transfer of nectar to multiple receivers was associated

strongly with dancing in all colonies (Table 1). Colony data were pooled because there were no differences between the number of transfers for both non-dancing and dancing bees across colonies [non-dancing: Kruskal–Wallis test (adjusted for ties), $H_2 = 0.76$, $P = 0.68$, NS; dancing: Kruskal–Wallis test (adjusted for ties), $H_2 = 1.32$, $P = 0.52$, NS]. Pooling data gave a mean number of transfers of 1.47 (SE = 0.10, transfer range = 1–4, $n = 71$) for non dancing bees and 5.68 (SE = 0.34, transfer range = 2–12, $n = 44$) for dancing bees.

Trigona nigra, *Plebeia frontalis*, and *Scaptotrigona pectoralis*

All foragers transferred nectar to nest-mates and multiple transfers were observed. There were no significant inter-colony differences in the number of transfers within a species (Mann–Whitney test, Kruskal–Wallis test, $P > 0.4$ in all cases; Table 2). There were also no significant differences for the medians of the number of transfers between *Trigona*, *Plebeia*, *Scaptotrigona*, and *Melipona* colonies when non-dancing *Melipona* foragers were considered [Kruskal–Wallis test (adjusted for ties), $H_3 = 6.55$, $P > 0.05$, NS; Table 2], however *Melipona* dancers made significantly more transfers than any other species [Kruskal–Wallis test (adjusted for ties), $H_3 = 98.4$, $P < 0.001$; Table 2].

Nannotrigona perilampoides

In the colony that was observed directly, all 20 marked foragers transferred nectar to nest-mates at least once. At least seven bees went on to make a second transfer but the remaining 13 went under the combs after the first transfer and could not be observed. In the colony observed using the indirect method, marked foragers were *never* seen in the storage pot area. The number of bees around the storage pots was taken as one category and the combined number of bees in the rest of the nest as the other category. The number of bees expected in each category was generated by multiplying the total number of bees by the proportion of nest area for each category occupied. Unmarked bees distributed themselves around the two nest areas in the same proportion as expected (day 1: $\chi^2 = 0$, d.f. = 1, $P = 1$, NS; day 2: $\chi^2 = 1.32$, d.f. = 1, $P = 0.25$, NS; Table 3). The distribution of marked foragers differed highly significantly from the expected distribution, however, with none being observed in the pot area (day 1: $\chi^2 = 82.8$, d.f. = 1, $P < 0.001$; day 2: $\chi^2 = 101.3$, d.f. = 1, $P < 0.001$; Table 3). Additionally, unmarked bees in the storage pot area were observed regurgitating nectar into pots, suggesting strongly that nectar transfer must have occurred during the observation period.

Discussion

The data show clearly that foragers transferred their nectar to bees inside the nest in all five species of Meliponini.

Table 1. Frequencies of single and multiple transfer of nectar to receivers for dancing and non-dancing *Melipona beecheii* foragers.

Colony	Forager dances		Forager does not dance		X ² ₁	P
	Single transfer	Multiple transfers	Single transfer	Multiple transfers		
1	0	12	21	7	18.9	< 0.001
2	0	19	13	8	17.4	< 0.001
3	0	13	15	7	15.5	< 0.001
Total (%)	0 (0)	44 (100)	49 (75)	22 (25)	50.1	< 0.0001

Thus, in the Meliponini, task partitioning in nectar foraging closely resembles *Apis*. One incidence of non-transfer occurred in *Melipona beecheii* but this was not observed in any other species. This also resembles *A. mellifera*, in which occasional non-transfer of nectar has been reported (e.g. 1.5% of foragers regurgitated nectar directly into cells; Hart & Ratnieks, 2001b). Sommeijer *et al.* (1983) reported that returning *M. favosa* foragers distribute nectar to nest-mates for ≈ 1.5 min before regurgitating nectar into the storage pots. Thus, they did not observe task partitioning in nectar foraging in this species; however, incoming foragers were observed for up to 20 min and, with one exception, foragers of any genera were never observed depositing nectar in pots. It can therefore be concluded that nectar foraging is a partitioned task in the stingless bees. Furthermore, multiple nectar transfer occurred in all colonies of all species observed directly, although generally at a lower level than found in *A. mellifera* (minimum and maximum mean values of 1.47–1.85, *M. beecheii* (non-dancing) and *Plebeia frontalis*, compared with 1.9–2.7, *A. mellifera*; Kirchner & Lindauer, 1994; Hart & Ratnieks, 2001b).

Multiple transfer compounds the transfer and queuing costs that task partitioning imposes – why then is it found in both *Apis* and now Meliponini? In *A. mellifera*, multiple transfer of nectar is hypothesised to improve the information available to foragers on the relative work capacities of foragers and receivers (Anderson & Ratnieks, 1999a,b; Hart & Ratnieks, 2001b). When a forager enters the nest, it experiences a delay in finding a receiver bee and this delay conveys information on the balance of work capacities between foragers and receivers (Seeley, 1995). Short delays indicate that foragers are in deficit whereas long delays indicate that receivers are in deficit (Anderson & Ratnieks,

1999c). By partitioning its load among several receiver bees, foragers obtain multiple samples of the delay experienced by foragers, thereby improving their information on the balance between foragers and receivers and whether to adjust this by recruiting more foragers or receivers (e.g. Anderson & Ratnieks, 1999c).

In the Meliponini, it was found that although multiple transfer occurred, it was to fewer partners on average than in *A. mellifera*; however, individual Meliponini foragers transferred nectar to as many as five nest-mates in a single transfer bout (12 nest-mates if dancing *M. beecheii* are considered), coinciding with the maximum reported in *A. mellifera* (Hart & Ratnieks, 2001b). Because *Melipona* have a forager recruitment system (Lindauer & Kerr, 1960a,b; Nieh & Roubik, 1995, 1998; Nieh, 1998), it is possible that multiple nectar transfer is involved with this, as seems to be the case in *A. mellifera*. Alternatively, it may be that nectar transfer is involved with the communication either of nectar source profitability or nectar source odour, as has been suggested in *A. mellifera*, although the data do not support this hypothesis explicitly (e.g. Nuñez, 1970; Farina, 1996). It may also be that multiple transfers are merely an indication that intra-nidal demand for nectar has decreased so nectar foragers are unable to offload nectar to nest-mates. Although there is good evidence that multiple nectar transfer in honey bees may be an information improvement strategy, it cannot be assumed that multiple transfer in other bees may be adaptive.

A very strong relationship was found between the spinning dance behaviour of *M. beecheii* and multiple transfer. Furthermore, many transfers made by dancing *M. beecheii* foragers occurred when the forager was *dancing* (as described by Nieh, 1998, for *M. panamica*). The spinning

Table 2. Number of nectar transfers made by foragers for the two study colonies. The median number of transfers pooled across colonies is compared with *Melipona beecheii* foragers that were categorised either as dancing (D) or not dancing (ND). IQR is the inter-quartile range. In the final column, species or categories with the same letter do not differ significantly from each other.

Species	Median transfers (IQR), N			Difference between colonies	
	Colony 1	Colony 2	Colony 3	Statistical test P > 0.4	Pooled transfer mean (SE)
<i>Trigona nigra nigra</i>	1 (1,2), 41	1 (1,2), 40		Mann–Whitney W = 1689	1.63 (0.12) a
<i>Scaptotrigona pectoralis</i>	1.5 (1,2), 20	2 (1,2.75), 20		Mann–Whitney W = 396	1.83 (0.15) a
<i>Plebeia frontalis</i>	1 (1,2), 20	2 (1,2.75), 20		Mann–Whitney W = 382	1.75 (0.15) a
<i>Melipona beecheii</i> ND	1 (1,1.5), 29	1 (1,2), 21	1 (1,2), 25	Kruskal–Wallis H ₂ = 0.76	1.47 (0.10) a
<i>Melipona beecheii</i> D	5.5 (4,6.75), 12	6 (4,8), 19	6 (4.5,7.5), 13	Kruskal–Wallis H ₂ = 1.32	5.68 (0.34) b

Table 3. Indirect observation of a *Nannotrigona perilampoides* colony over 2 days. χ^2 tests were performed on the number of bees in the storage pot section versus the number of bees in all the other sections of the nest combined. Expected values were generated using the proportions of nest area occupied by each section multiplied by the total number of bees observed (thus, on day 1, unmarked bees had expected values of 5890×0.36 bees in the pot section, 5890×0.64 bees in the rest of the nest).

Nest section	Proportion of total area	Proportion of unmarked bees in area		Proportion of marked bees in area	
		Day 1	Day 2	Day 1	Day 2
Left	0.19	0.16	0.17	0.20	0.21
Right	0.22	0.20	0.21	0.13	0.20
Entrance	0.14	0.18	0.16	0.67	0.58
Brood	0.09	0.10	0.11	0.00	0.01
Pots	0.36	0.36	0.35	0.00	0.00
Total bees seen over 20 counts		5890	6010	190	230
χ^2 (bees in pots versus rest of nest)		0	1.32	82.8	101.3
<i>P</i>		1 (NS)	0.25 (NS)	< 0.0001	< 0.0001

behaviours interpreted as communication dances in *Melipona* might have originated (and persisted in some Meliponini) as a mechanism for distributing nectar samples to unemployed foragers as they surround the dancing forager. This distribution behaviour would be an elaboration of simple forager-receiver nectar transfer occurring within partitioned foraging. It is important to state at this point, however, that *nectar transfer* can describe two types of behaviour. Transfer to nectar storing bees can be regarded as task partitioning whereas transfer to non-storing bees (e.g. small *tasting* transfers to unemployed foragers) is not part of a partitioned nectar foraging system; rather it is part of a foraging communication or recruitment system.

The universal occurrence of nectar transfer in the Meliponini genera studied lends further support to the hypothesis that task partitioning is more likely to evolve in swarm-founding species than in species with lone-founding queens (Anderson & Ratnieks, 1999b); however the Meliponini and Apini are generally considered to be sister groups (Schultz *et al.*, 1999, 2001; Ascher *et al.*, 2001; Engel, 2001a, b) and both tribes have swarm-founded nests. It could, therefore, be argued that swarm founding of nests is a shared derived character and that the existence of task partitioning in Meliponini adds no further independent evidence for the swarm-founding hypothesis than is provided by *Apis*; however the swarming characteristics of Apini and Meliponini are widely divergent (Michener, 1974) and swarm foundation may have evolved independently in each tribe. Apini form new colonies by complete colony fission, with the old queen and a group of workers leaving the nest to find a new site. Meliponini establish daughter colonies gradually, with workers going back and forth from an existing nest carrying the food and building materials required to establish a new nest. Eventually a new queen goes to the new nest and workers remain with the new queen, with the new nest slowly becoming independent of the mother nest. Importantly, if

task partitioning had not been found in the Meliponini, the colony size/swarm-founding hypothesis would have been weakened severely. A comparative analysis of the collection and handling of building materials, in swarm founding and independent-founding wasp genera of different colony sizes, would be useful in testing further the associations among swarm foundation, colony size, and task partitioning. Additionally, it would be worthwhile to study *Bombus atratus*, a South American bumble bee, which has large perennial colonies (Michener, 1974). Were task partitioning to occur in any Bombini, it might be expected there.

There is now information on the occurrence and nature of nectar transfer in the three eusocial tribes of corbiculate bees. Nectar transfer is not reported in the Bombini (Michener, 1974) but occurs in all genera of Meliponini studied so far and in the Apini (nectar transfer occurs in *Apis mellifera*, *A. cerana*, and *A. florea*; W. Towne, pers. comm.). The fourth and final tribe of corbiculate bees, the Euglossini, is not eusocial although several females may be present in a nest (e.g. some species of *Euglossa* and *Eulaema*; Michener, 1974). There are no storage pots as such but brood cells are filled with food before closure. Task partitioning could be present during brood cell provisioning and would provide a mechanism by which a dominant female could exercise control over reproduction. Further study of the Euglossini is required to investigate this. While the monophyly of the corbiculate bees within the subfamily Apinae (family Apidae) is well established, the phylogeny of the four corbiculate tribes has been controversial. Different methodologies have produced conflicting resolutions, with eight of the 15 possible rooted trees being supported over recent years (Schultz *et al.*, 1999); however a consensus of {Euglossini [Bombini (Meliponini, Apini)]} has emerged based on an approach combining molecular and morphological data (Schultz *et al.*, 1999, 2001; Ascher *et al.*, 2001). This consensus supports the (Meliponini + Apini) sister grouping and a single origin for advanced eusociality in the corbiculate bees. Accepting the Meliponini,

Apini sister grouping, the most parsimonious explanation for the evolution of task partitioning in nectar foraging is a single origin in their common ancestor.

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