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Distribution and abundance of colonies of selected meliponine species in a Costa Rican tropical wet forest

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ABSTRACT. The goal of this study was to assess territoriality and foraging home ranges for stingless bee species; and to develop methods for censusing stingless bee colonies. Colonies of two meliponine bee species, *Trigona corvina* Cockerell and *Trigona amalthea* Vachal, were censused using carrion and honey baits. *Trigona corvina* and *Trigona amalthea* are dispersed in a Costa Rican tropical wet forest (La Selva) so that foraging ranges of the colonies are non-overlapping. The nest density was *c.* 0.25 ha⁻¹ for *T. amalthea* and 1.0 ha⁻¹ for *T. corvina*. *T. corvina* visited carrion baits exclusively, while *T. amalthea* visited both carrion and honey baits. The identities of *T. amalthea* colonies were confirmed using a nestmate recognition assay. *Partamona peckolti* Friese, *Plebeia frontalis* Friese, and *T. fulviventris* Guerin also appeared at the baits. The reliability of baiting to determine colony abundance and distribution is assessed.

KEY WORDS: agonistic behaviour, carrion, competitive interactions, distribution, feeding preferences, nectar, *Trigona*

INTRODUCTION

How are stingless bee colonies distributed in tropical wet forests? Patterns of local distribution and abundance of social insects are well studied in ants (Wiernasz & Cole 1995), termites (Jones 1993), and honey bees (McNally & Schneider 1996, Oldroyd *et al.* 1997, Seeley & Morse 1977), however they are much less studied in other flying social insects, i.e. wasps and the remaining bees. An understanding of distribution and abundance is critical to the development of models for the effects of habitat reduction and fragmentation on the population genetics and ecology of stingless bees. The aims of this study were

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to test a method for assessing population density and nest distribution in selected meliponine species, to verify that field assays could be used to distinguish colony mates from non-colony mates, and to generate additional information concerning the foraging ecology of stingless bees.

A well-known feature of meliponine biology is that many species visit faeces or carrion (Baumgartner & Roubik 1989, Cornaby 1974, Schwarz 1948). Most notable is Baumgartner & Roubik's (1989) study of the meliponines attracted to carrion baits in Peru. While most species collect faecal or decaying materials for use in nest construction, some collect the material as a food item (Roubik 1982). Meliponines also collect nectar and pollen and some species respond to honey baits (Hubbell & Johnson 1978, Johnson & Hubbell 1974, Wille 1962). Given the large number of species of meliponine bee and the variability in food visitation patterns among species, it is not surprising that our understanding of foraging behaviour and food preferences in meliponines is in need of further development.

Meliponine nests are often fairly cryptic and can be difficult to locate. Consequently the distribution of colonies is relatively unexplored. Hubbell & Johnson (1978, see also Gilbert 1973) present a map of nest distribution of *Trigona fulviventris* Guerin; their sampling area included only three colonies, but the distribution of nests and foragers from those nests suggests that colonies are evenly spaced. The possibility of overdispersion in stingless bee nests is intriguing and merits further investigation.

A number of studies have demonstrated nestmate recognition in meliponine bees (Breed & Page 1991, Hubbell & Johnson 1978, Inoue & Roubik 1990, Johnson & Hubbell 1974, Suka & Inoue 1993). The expression of nestmate recognition behaviour in a bioassay can provide a useful tool for determining whether two social insect workers derive from the same or different colonies (Breed & Page 1991). Aggression between the bees indicates membership in different colonies; this assumption is well supported in the nestmate recognition literature (Breed & Bennett 1987, see also Johnson & Hubbell 1974 and Breed & Page 1991).

To address the issues of feeding habits, foraging ranges, colony distribution and colony abundance we asked the following questions in a Costa Rican tropical wet forest: (1) Which meliponine bees are attracted to honey and carrion baits?; (2) How are foraging bees distributed over a sampling grid?; (3) Can inferences from the distributions of foragers be verified by nestmate recognition assays?; and (4) What inter- and intraspecific interactions, if any, occur between bees at baits?

METHODS

Attraction of meliponine bees to honey and carrion baits

We performed this work at La Selva Biological Station, Sarapiquí Canton, Heredia Province, Costa Rica in May 1993, January 1994, June 1994, December

1995 to January 1996 and in January 1997. In the Results section we refer to the 1995–1996 sampling, unless otherwise specified. Baits placed at 50-m intervals along transects and in grids determined the presence/absence of species. Bees were identified using the key provided by Roubik (1992); voucher specimens were deposited in the insect collection maintained by the Arthropods of La Selva project at La Selva Biological Station.

Slight modifications were made in the baits as experience was gained in baiting bees. In 1994 baits consisting of 50% honey in water (volume:volume) or anise scented 50% sucrose solution absorbed into white cloth suspended 0.5–1.0 m above ground were used while in 1995/1996 and 1997 we used honey or carrion (decomposing chicken) baits. The 1995/1996 and 1997 honey baits were presented in the same manner as the 1994 honey and sucrose baits but consisted of 25 ml of 33% honey solution (one part honey to two parts water). Honey baits did not differ from the anise-scented baits in their attractiveness. We hung carrion baits, pieces of rotting chicken weighing *c.* 75 g, at heights similar to honey baits. Placement of baits occurred between 08h00 and 10h00. We counted the number of bees present at the baits after a sampling interval of 3–5 h. We interpreted distributions of bee responses to baits by examining maps of our grids for contiguous bait sites that attracted the same species of bee.

Distribution of foraging bees in a sampling grid

The sampling grid experiments were conducted in 1996 and form the basis for most of the results. We placed either honey or carrion baits at 50-m intervals in four 100-m × 200-m grids located in primary forest. Honey and carrion were presented at the same sites, but on different days, so that the baits did not interfere with each other. The baiting strategy was to place baits early in the morning and to census bees and collect baits after several hours, allowing adequate time for discovery of baits.

Four relatively straight sections of trails at La Selva served as the central axes for the 200-m long baseline of each grid. Consistent compass bearings and a tape allowed location of bait points 50 m perpendicular to the central axis with an accuracy of ± 1 m. The grids included 59 sampling sites (one site was not baited due to the steepness of the terrain). In addition baits were placed in secondary forest and in abandoned pasture in the 'Flaminea' portion of La Selva.

Resampling of selected locations tested the repeatability of responses of bees to baits. We resampled with both carrion and honey at 20 locations at 48–96-h intervals after the initial samples were taken. Resampling after only 1 d was avoided in order to reduce the effects of learning of the bait locations on rediscovery. The same methodology (time of day, placement of baits, interval between bait placement and census) was used in the resamples as in the original samples. A replicate consisted of the outcome of the first sample (which species, if any, came to the bait) paired with the outcome of the second sample.

The replicates were arrayed in a transition matrix, with the rows representing the first sample and the columns the second sample; this matrix is an $r \times c$ contingency table. Chi-squared tests of independence were performed on the contingency tables; if the result of the second sample was dependent on the first, then the χ^2 was significant, if the result of the second sample was independent of the first, then the χ^2 was not significant.

Bee-lining

As an independent test of our measures of foraging range and our ability to estimate nest locations in 1997 we used bee-lining techniques to locate a nest of *Trigona amalthea* Vachal that had not been included in our 1996 study. Flight distances and colony foraging range for *T. amalthea* were determined for a single colony based on bee-lining (establishing flight directions from feeding stations and triangulating on a presumed nest location) and timing of foraging trips. Foragers at bait stations were marked to allow timing of foraging trips. Observations of flights of marked bees determined the direction from the bait station to the colony. Flight directions and round-trip times were then used to construct a map of the foraging home range of the colony.

The relationship between forager distribution and nestmate recognition

We tested for nestmate recognition by allowing pairs of bees collected at the baits to interact for 10 min in 5 ml glass vials. Aggressive behaviour consisted of biting, lunging and grappling; these behaviours were usually all expressed in an aggressive interaction. We recorded the presence or absence of aggression. Bees were paired from collections within bait site, between sites along the same transect, between separate transects, and between species.

Inter- and intraspecific interactions at baits

While collecting data at the baits described above we noted any within- or between-species behavioural interactions. All such interactions that were observed were recorded, but we focused on possible agonistic interactions among bees at baits. In addition to recording stingless bee visits to baits, we also noted visits by other arthropods.

RESULTS

Meliponine bees attracted to honey and carrion baits

Four species of meliponine bees were collected at carrion baits and three species at honey baits. Seven honey baits attracted workers of *Trigona amalthea* (11.9%, $n = 59$), 12 attracted *Plebeia frontalis* Friese (20.3%), and five attracted both species (8.5%); the majority attracted no bees (59.3%). Thirty-one of the carrion baits attracted *Trigona corvina* Cockerell (52.6%, $n = 59$), eight attracted *T. amalthea* (13.6%), one attracted *Partamona peckolti* Friese and one attracted *T. fulviventris* Guerin.

Table 1. Meliponine species attracted to baits at La Selva Biological Station. Each species responding to each bait type is shown with the mean number of individuals observed (\pm SE), the range in the number of individuals observed and the number of baits presented. The sample sizes, *n*, are the number of baits at which at least one individual in the species was observed. Baits which did not attract bees are not included in this analysis.

Species	Bait	Number of bees	Range	<i>n</i>
<i>Trigona amalthea</i>	Honey	4.3 \pm 5.3	1–21	19
<i>Trigona amalthea</i>	Carrion	10.7 \pm 6.5	1–20	7
<i>Plebeia frontalis</i>	Honey	3.4 \pm 4.8	1–300	29
<i>Partamona peckolti</i>	Honey	10.2 \pm 20.1	1–95	26
<i>Partamona peckolti</i>	Carrion	2	na	1
<i>Trigona fulviventris</i>	Honey	2	na	1
<i>Trigona corvina</i>	Carrion	39.7 \pm 58.1	1–300	29

Distribution of foraging bees in a sampling grid

T. amalthea was unique among the species baited in commonly appearing at both types of baits (Table 1). There was no correlation between appearance at honey baits and carrion baits at the same locations; only one bee appeared at a carrion bait in a location where honey had attracted bees (*n* = 20 locations). Also, one location that yielded *T. amalthea* at honey baits in 1994 had bees of that species at carrion baits (but not at honey) in 1996.

In the 1996 samples we found four areas of *T. amalthea* activity, one in each of the four sampling grids. When *T. amalthea* was present in a sampling grid it sometimes occupied numerous adjacent baits; *T. amalthea* was attracted to 12 contiguous honey baits in one grid, to six contiguous carrion baits in another, and to isolated carrion baits in the other two other grids. In the two cases in which *T. amalthea* was attracted to several baits in a grid, there was a clear centre of activity – a bait with large numbers of bees – and the adjacent baits attracted fewer bees. In one grid the most frequently visited bait attracted 14 bees, while five baits 50–150 m distant from this bait only attracted one or two bees each.

T. corvina workers appeared only at carrion baits and were present in large numbers (>25) at many bait stations (Table 1). *T. corvina* colonies foraged on no more than five contiguous baits in a grid (mean = 2.4, SE = 0.45, *n* = 11). Bees from a single colony never occupied baits more than 111 m apart, a maximum that was observed only twice among the 11 colonies represented on the grids.

The responses of our two principal study species, *T. amalthea* and *T. corvina*, were similar when compared between the beginning of the dry season (December and January sampling periods) and the beginning of the wet season (May and June sampling periods). Both of these species also responded to baits throughout the day.

Plebeia frontalis was present in low numbers at six honey bait stations in one grid, at eight in another, and at one in a third in 1997. In 1994 *P. frontalis* only occurred at one primary forest site.

Interannual effects were strongest for *Partamona peckolti*. The difference

between 1994 and 1996 in the distribution of *Partamona peckolti* was striking. In 1994 this species was common at honey baits in several locations. In 1996 it was not attracted to honey and was a rare visitor at carrion baits, but in 1997 *P. peckolti* was numerous at some honey bait stations. A fifth species, *T. fulviventr*is was rare, occurring only once in our honey bait samples.

Repeatability of sampling

Short-term repeatability of bait results was tested by resampling bait stations: in 29 of 42 resampled honey locations the same result was obtained (69%). In eight cases a species that was absent in the first trial appeared in the second trial, and in four cases a species that was present in the first trial was absent in the second. In only two cases was there a switch from one species present to another being present. A chi-squared test of independence for an association between the first sampling to the second showed a significant trend for the same species to appear in both samples ($\chi^2 = 20.2$, $df = 4$, $P < 0.0005$).

On the carrion baits 11 of 25 locations (44%) gave the same result in both trials. In three cases *T. corvina* was present in the first trial but not in the second. In 11 cases no bees were sampled in the first trial but bees were present in the second trial. Again, there is a significant trend for the same species to appear in both samples ($\chi^2 = 12.6$, $df = 4$, $P < 0.05$). The repeatability experiment was affected in some cases by the discovery of baits by ants, *Paraponera clavata* Fabricius or *Crematogaster* sp. (see below); these samples were excluded from the analysis.

Bee-lining

The result of the independent test of *T. amalthea* colony location by bee-lining is shown in Figure 1. Bees used the streams as flyways and consequently it was not possible to triangulate the colony location from a small number of feeding stations. Colony location was estimated based on a combination of flight times and flight directions along the streams.

Testing of inferred colony distributions by nestmate recognition assays

Nestmate recognition assays were conducted for three species, *T. amalthea*, *T. corvina* and *Plebeia frontalis*. Our most extensive testing was with *T. amalthea*, pairings of which sometimes resulted in aggression that was clearly associated with recognition of a non-nestmate. In *T. corvina* nestmate recognition behaviour was not reliably expressed; grappling was observed in only one case ($n = 17$ pairings). No aggression was observed in pairings of *P. frontalis*.

T. amalthea paired from within bait sites exhibited aggression in one of 21 pairs tested. Pairings within grids, but between sites, produced no aggressive acts among 21 tests. When bees from separate grids interacted with one another, 12 out of 18 pairings produced aggression. All possible combinations of four bait sites were used in the between-grid tests (Table 2). Incompatibility was observed in all but one of the between-grid pairings.

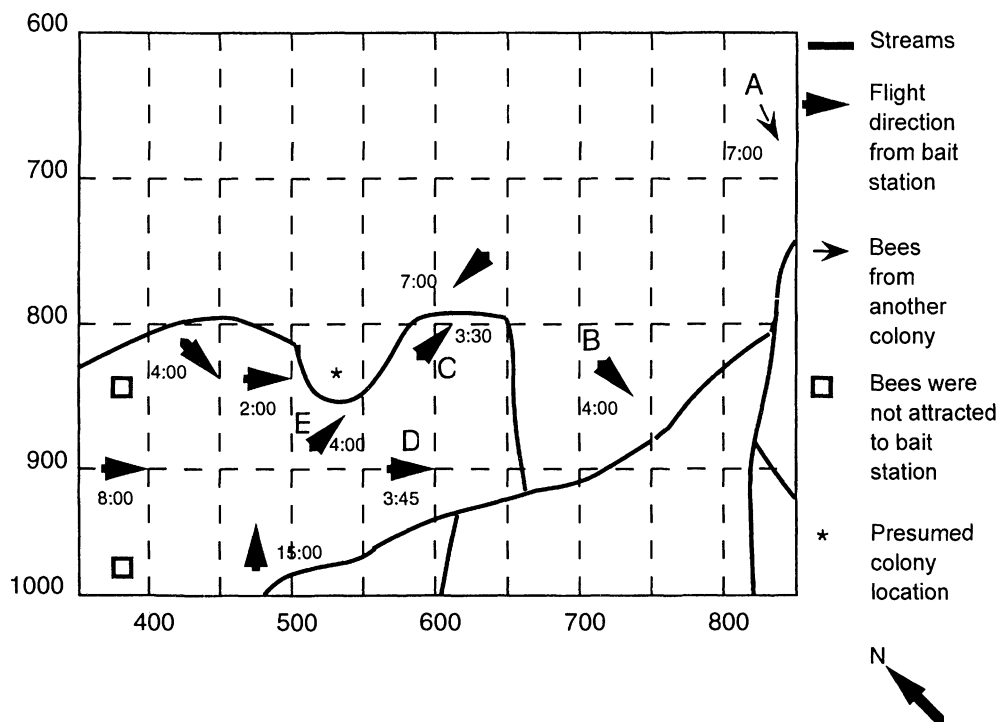


Figure 1. Flight directions and mean round-trip flight times in min (n = 3 to 10 bees) from feeding stations for bees from a colony of *Trigona amalthea*. This is a different colony than those sampled in the bait grids. Aggression tests showed that all bees except those at station A were from the same colony. Bees from some stations (B, C, D, E) used the streams as flyways and did not fly the most direct overland route to the nest. The axes are in m, and correspond to the La Selva grid system.

Table 2. Results of the tests of aggression between *T. amalthea* from four collection areas, which are designated Sites 1–4. The number to the left of the solidus in each cell indicates replicates in which fighting was observed. The number to the right of the solidus is the number of replicates without fighting. The columns and rows correspond to the sources of the bees; for example the uppermost cell in the left column represents pairings in which both bees came from Site 1 and the cell next to it is pairings of bees from Site 1 with bees from Site 2.

Site	Site			
	1	2	3	4
1	1/28	2/0	4/1	2/0
2	na	0/3	2/0	0/2
3	na	na	0/5	2/3
4	na	na	na	0/5

Four pairings of *T. corvina* with *T. amalthea* resulted in aggression in all cases.

Inter- and intraspecific interactions at baits

In 1996, the year for which the largest sample, 63 honey baits and 63 carrion baits, is available, *T. amalthea* was the sole visitor at 14 honey baits (22.2%, n = 63), and *P. frontalis* at 16 baits (25.4%). *T. corvina* was never observed at a honey

bait. *T. amalthea* and *P. frontalis* were observed at the same bait seven times (11.1%). In 1997 *T. amalthea* and *P. frontalis* co-occurred at two adjacent baits on a transect, and after a time *P. frontalis* monopolized those baits.

A similar pattern was observed at the carrion baits. In one case *T. amalthea* and *T. corvina* shared a carrion bait site, and in two cases *T. amalthea* co-occurred with *P. peckolti*. In two cases all three species occurred at the same carrion bait site. The sample size for this comparison was 63, as repeated baitings at a site are included.

Direct interactions were neither consistent nor intense enough to lead to competitive exclusion of one species by another at the bait. No escalated aggression (grappling or biting) was ever observed at carrion or honey baits. Within-species interactions were somewhat more common, consisting of displacements of feeding individuals by lunging or pouncing. In *P. frontalis*, workers often pounced on feeding workers of the same species.

Other insect visitors at the carrion baits included an epinonine wasp (*Agelaia myrmecophila*), calliphorid flies, sarcophagid flies, ants, and staphylinid beetles. The most notable ant was *Paraponera clavata*, which recruited large numbers of workers to some of the carrion baits. Bees, beetles and flies were usually absent when *P. clavata* was present. Hundreds of *Crematogaster* sp. workers were present on some baits and also effectively excluded other insects. Other ants, *Ectatomma ruidum* Roger, *Pheidole* sp. and *Neoponera (Pachycondyla)* sp., appeared at some baits but did not exclude other insects. Our impression, although unquantified, was that the presence of large numbers of *T. amalthea* or *T. corvina* reduced the number of other insects at the bait. Some direct displacements of flies by both *Trigona* species were observed.

Sampling outside the primary forest

T. amalthea and *P. peckolti* both came to baits on a transect located between a riparian zone and relatively mature second-growth forest. Neither honey baits nor carrion baits attracted bees at 16 stations at 50-m intervals along a 750-m transect in recently abandoned pasture.

DISCUSSION

Stingless bee foraging ranges and colony distribution

Roubik (1989) presents an extensive discussion of foraging ranges in tropical bees. Maximum flight ranges of meliponines are probably in excess of 2 km (Roubik & Aluja 1983). As Roubik & Aluja (1983) and Roubik (1989) point out, maximum flight range does not necessarily correspond with normal flight range nor with foraging range. Measures of foraging ranges have resulted in estimates of more limited distances, such as 84–434 m for *Tetragonula minangkabau* (Inoue *et al.* 1985). Hubbell & Johnson's (1978) Figure 7, a map of the distribution of foragers from their colonies of *Trigona fulviventris*, suggests normal foraging ranges of *T. fulviventris* of 100 to 150 m.

Our method places the burden of discovery of the resource on the bees, rather than making estimates based on translocation of foragers away from colonies (Roubik & Aluja 1983) or by progressively moving bait stations away from colonies (Michener 1974). Rate of discovery should be directly correlated with forager density, which is highest near the colony (Roubik 1989, his Figure 2.25). Longer periods of time for discovery would increase the probability of discovery at greater distances from the colony. Michener (1974) states that for *T. amalthea* the upper limit of effective communication about food resources is 800 m and the upper limit of flight distance is 980 m.

Assuming that the distribution of *T. amalthea* at baits in the five primary forest locations (the four grids plus the arboretum site) represents four colonies, the minimum foraging range for this species is 100 m (from one of the colonies which appeared to be centred in a grid to the edges of that grid). The foraging range could be 200 m if bees from outside the grid were flying the length of the grid. Similar logic applied to our data for the foraging range of *T. corvina* suggests a value of 50 to 100 m. Given the differences in methodology between our study and the studies of Inoue *et al.* (1985) and Hubbell & Johnson (1978) the foraging ranges we suggest for *T. amalthea* and *T. corvina* are reasonable, and are consistent with the published data for *Tetragonula minangkabau* (Inoue *et al.* 1985) and *T. fulviventris* (Hubbell & Johnson 1978). These limited foraging ranges have considerable importance in interpreting the role of meliponine bees as pollinators (Martínez-Hernández *et al.* 1994, Ramalho *et al.* 1994).

In most cases colonies of walking social insects have non-overlapping foraging ranges (e.g. Whitehouse & Jaffe 1996). Colony distributions of flying social insects are much less well understood, and our perceptions are probably biased by observations of *Polistes* wasps, which tend to have clumped distributions in anthropogenic habitats, social halictid bees, which often nest in aggregations (for reasons that are poorly understood) (Michener 1974), and honey bees, which may have clumped nests if nesting sites are patchily distributed (Michener 1974). None of these species are known to engage in agonistic interactions at food locations.

In contrast, agonism between stingless bees at food resources is well documented (Hubbell & Johnson 1978, Johnson & Hubbell 1974). While we did not observe intense agonistic interactions at baits within or between meliponine species at La Selva, the nestmate recognition experiment reported in this paper, which was conducted in the laboratory, indicates that such interactions are a possibility because fighting between species could be induced. Intraspecific competitive exclusion at food resources via direct agonistic interactions could, clearly, lead to dispersed colonies.

To interpret the distributions of stingless bee colonies in our studies we assume that bees attracted to contiguous baits are from the same colony. In *T. amalthea* this assumption is strongly supported by our nestmate recognition

data. Based on the grid data (a total of 8 ha sampled, yielding two colonies), the density of *T. amalthea* colonies in primary forest at La Selva is $< 0.25 \text{ ha}^{-1}$. It is important to note that *T. amalthea* was entirely absent from some of the grids in 1996 and also did not appear at baits along the same transect in 1994; thus *T. amalthea* is not at baits in all primary forest areas at La Selva. Eight *T. corvina* colonies were present in the grid samples, a density of $1.0 \text{ colonies ha}^{-1}$. All four grids contained evidence of at least one *T. corvina* colony. The distribution of *P. peckolti* may reflect foraging ranges and population densities similar to that of *T. amalthea*, but our sample size for *P. peckolti* is too small to draw strong conclusions. Our conclusion that colonies are overdispersed with non-overlapping foraging ranges is consistent with the findings of Hubbell & Johnson (1978) on *T. fulviventris* in dry forest, where they found three colonies spaced evenly, 200–220 m apart.

Baits in population assessments of stingless bees

Baits set out on grids are a promising method for assessing populations of select meliponine species. Colony foraging ranges can be defined, aggression tests can be used in some species to supplement data based on appearances at baits, and the use of different bait types results in sampling different species. Baumgartner & Roubik (1989) used a similar method, employing rotting fish, to sample meliponine bees over an elevational gradient and to compare the species compositions of meliponine guilds in habitats with and without human disturbance. They did not attempt to estimate colony numbers, or to sample small areas intensively, as we have done.

Despite our optimistic assessment of the methods we employed, some important caveats are suggested by our data. Repeatability between samples was moderate, suggesting that conclusions from grid samples should be refined by repeated sampling over longer spans of time. *P. peckolti* appeared at honey baits in 2 y and at carrion baits in another, and in one grid *T. amalthea* was attracted predominantly to honey, while in another grid *T. amalthea* came only to the carrion baits. This indicates the possibility that foraging preferences may shift according to colony need or competing natural food resources.

The species responding to baits represent a relatively small sample of the meliponine guild, and may be biased to include foraging generalists, rather than specialists. Not surprisingly, sampling with baits attracts species that are generalists; species with narrower floral preferences will require baiting with species-appropriate floral models. Roubik's (1992) treatment of Mesoamerican stingless bees suggests that *c.* 30 species should be found in north-eastern Costa Rica. Of these, only four appear at our baits, *T. amalthea*, *T. corvina*, *P. frontalis* and *P. peckolti*. How representative these species are of meliponine species in general remains to be tested. More species might be attracted to baits in the canopy. *Trigona angustula* commonly nests near ground level at La Selva, but was not attracted to either type of bait, even when baits were located near known nests.

Nestmate recognition

Johnson & Hubbell (1974), Hubbell & Johnson (1978), Breed & Page (1991) Suka & Inoue (1993) and Inoue & Roubik (1990) showed that nestmate recognition is expressed in many meliponine species. Breed & Page (1991) found that the expression of discrimination of non-nestmates varied substantially among *Melipona* species, from very consistently expressed attacks on non-nestmates to infrequent attacks. Hubbell & Johnson (1978) used field observations of aggressive interactions in *T. fulviventris* as an indicator of colony membership. Our results from *T. amalthea* show a high rate of attack, making nestmate recognition a useful tool for the study of colony distribution in this species. Johnson & Hubbell (1974) found that *T. corvina* workers fought at baits and flowers, while we observed few such interactions. This difference may reflect different colony distributions and foraging patterns in the wet forest where our study was located.

Carrion reduction

As in other tropical habitats, stingless bees are important reducers of carrion in lowland wet forest in Costa Rica, and they may have important competitive interactions with other consumers of carrion. Baumgartner & Roubik (1989) emphasize the importance of stingless bees in carrion reduction in the tropics, and document the presence of stingless bees across an elevational transect that incorporates dramatic changes in temperature, moisture and vegetation. Roubik (1982) and Camargo & Roubik (1991) amplify the importance of stingless bees in this role by reporting three species of carrion specialists, one from Panama and two from Amazonia. Our findings reinforce the importance of stingless bees in this role.

Cornaby (1974), working in Costa Rica, found differences in the reducer guild between wet and dry forest, and between toad and lizard carrion. He found seven species of stingless bee on carrion in his wet forest site (the Osa Peninsula in south western Costa Rica). Of the seven species he lists, three have been observed on carrion at La Selva (*T. amalthea*, *T. fulviventris*, and *T. corvina*) but a fourth, *P. frontalis* came to our honey baits but not to our carrion baits.

Carrion reduction to the 'dry skin' stage moves very rapidly in tropical wet forest (Cornaby 1974) and competition among arthropods for carrion appears to be intense. The rapid discovery of carrion by *T. amalthea* and *T. corvina* at La Selva is not surprising, given the number of potential fly, beetle and ant reducers. By suspending our baits on strings we purposely reduced the chances of ants and beetles competing with bees for carrion; in experiments designed to measure competition more natural placement of baits would be required.

Species richness

Baumgartner & Roubik (1989) found 33 species of stingless bee associated with filth (*sic.*) and carrion in Peru. At one bait site 15 species were collected.

They found the greatest species richness during the wet season in relatively undisturbed lowland wet tropical forest. One abundant species in their sample, *T. amalthea*, was also prominent in our study. The lower number of bee species visiting carrion at La Selva is probably associated with overall lower species richness at higher latitudes within the tropics; the number of stingless bee species declines from the equator to the subtropics, and stingless bees are not found in the temperate zone. Our surveys were done in January, May and June; slightly different results might be obtained under different seasonal conditions.

This research sets the stage for more extensive studies of resource utilization and colony distributions of stingless bees. Conservation concerns also need to be addressed by future work. Klein (1989) reported changes in species composition of carrion beetle communities after forest fragmentation in wet forest in Brazil. If pastures are barriers to movement of stingless bee populations (as suggested by our failure to attract bees in pasture) and nest densities are as low as indicated by our results, effective population sizes may be disastrously small, even in moderately sized reserves.

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