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Behavioral suites mediate group-level foraging dynamics in communities of tropical stingless bees

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Abstract Competition for floral resources is a key force shaping pollinator communities, particularly among social bees. The ability of social bees to recruit nestmates for group foraging is hypothesized to be a major factor in their ability to dominate rich resources such as mass-flowering trees. We tested the role of group foraging in attaining dominance by stingless bees, eusocial tropical pollinators that exhibit high diversity in foraging strategies. We provide the first experimental evidence that meliponine group foraging strategies, large colony sizes and aggressive behavior form a suite of traits that enable colonies to improve dominance of rich resources. Using a diverse assemblage of Brazilian stingless bee species and an array of artificial “flowers” that provided a sucrose reward, we compared species’ dominance and visitation under unrestricted foraging conditions and with experimental removal of group-foraging species. Dominance does not vary with individual body size, but rather with foraging group size.

Species that recruit larger numbers of nestmates (*Scaptotrigona* aff. *depilis*, *Trigona hyalinata*, *Trigona spinipes*) dominated both numerically (high local abundance) and behaviorally (controlling feeders). Removal of group-foraging species increased feeding opportunities for solitary foragers (*Frieseomelitta varia*, *Melipona quadrfasciata* and *Nannotrigona testaceicornis*). *Trigona hyalinata* always dominated under unrestricted conditions. When this species was removed, *T. spinipes* or *S. aff. depilis* controlled feeders and limited visitation by solitary-foraging species. Because bee foraging patterns determine plant pollination success, understanding the forces that shape these patterns is crucial to ensuring pollination of both crops and natural areas in the face of current pollinator declines.

Keywords Aggression · Dominance · Group foraging · Species removal · Superorganism

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Introduction

The availability of rich resources such as mass-flowering trees is important in shaping foraging behavior of tropical pollinators (Roubik, 1989; Wilms et al., 1996). Such resources attract a high diversity of visitors (Heithaus, 1979), and can be fiercely contested (Roubik, 1980; Nagamitsu and Inoue, 1997). Foraging shifts resulting from competitive interactions (e.g. Inouye, 1978) may alter pollination dynamics (Roubik and Villanueva-Gutiérrez, 2009). For social insects, intense inter- and intraspecific competition (Johnson and Hubbell, 1974; Hölldobler and Wilson, 1990; Dornhaus and Chittka, 2004) should favor strategies such as cooperative group foraging that improve foraging efficiency and resource defense. Group foragers are those who forage in the same location as nestmates.

They often use information provided by group members to locate food sources.

When animals compete for food, larger species tend to dominate (Schoener, 1983; Eccard and Ylönen, 2003) in both direct (e.g. interference competition) and indirect (e.g. exploitative competition) contests. For social animals, however, foraging in groups can improve yield through shared food location information (Clark and Mangel, 1984), increased hunting success (Bednarz, 1988), retrieval of larger food items (Traniello and Beshers, 1991), control of food (Holway and Case, 2001) or more efficient harvesting (Fernández-Juricic et al., 2004). Group foraging may be particularly important for highly social insects whose colonies act as “superorganisms” (Wilson, 1990), reproductive units whose parts, individuals, must work together to permit colony survival and reproduction. Thus, superorganism size (group size) may be more relevant than individual size for determining the outcome of dominance interactions.

Stingless bees (Hymenoptera, Apidae, Meliponini) provide a good system for studying the ecological importance of group foraging. All stingless bees are eusocial, but some species forage as individuals while others tend to forage in large groups (Johnson, 1983). These groups typically form through location-specific recruitment via odor trails or potentially referential vibrations (Nieh, 2004). Foraging strategies are likely constrained by colony sizes, which range from approx. 100 (van Veen et al., 1997) to at least 20,000 workers (Roubik, 1983). Stingless bee within-habitat diversity can range up to 62 species (Roubik, 1989) with considerable diet overlap (e.g. Wilms and Wiechers, 1997; Eltz et al., 2001). Limited food availability (Hubbell and Johnson, 1977; Eltz et al., 2002) can thus lead to high levels of both intra- and interspecific competition (Hubbell and Johnson, 1977; Nagamitsu and Inoue, 1997; Slaa, 2003).

Despite these bees’ important role as tropical pollinators (Heard, 1999), the ecological importance of stingless bee foraging strategies remains poorly understood. Several researchers have hypothesized that group foraging improves dominance for stingless bees (Johnson and Hubbell, 1975; Roubik, 1980; Nagamitsu and Inoue, 1997; Slaa, 2003). However, there are few tests of these hypotheses and no studies directly manipulate dominance by altering experimental conditions (e.g. species removal). In addition, most studies of stingless bee foraging behavior have focused primarily on aggression, comparing resource control of “aggressive” versus “unaggressive” species (Biesmeijer and Slaa, 2004 and sources therein). While aggression is a commonly proposed mechanism of interference competition (Reitz and Trumble, 2002), other traits also permit species to control or efficiently exploit a resource. For example, the stingless bee *Partamona*

orizabaensis (formerly *P. aff. cupira*, Pedro and Camargo, 2003) is “non-aggressive” (Biesmeijer and Slaa, 2004) yet in large groups can maintain control of a resource despite attack by *Trigona silvestriana* (Howard, 1985).

We experimentally altered an assemblage of stingless bees foraging at an array of feeders to investigate stingless bee dominance and foraging on a resource accessible to multiple species. We measured behavioral dominance, numerical dominance, displacement success and aggression of six Brazilian species. We tested three hypotheses: (H1) group foragers are dominant, as is found for other social insects; (H2) body size correlates with dominance (Johnson and Hubbell, 1974); and (H3) removal of group-foraging species increases feeding opportunities for remaining species. Finally, we examined the role of aggression in resource dominance.

Methods

Study site and species, and feeder array

This study was carried out at the Fazenda Aretuzina, a ranch in the state of São Paulo, Brazil, during July of 2006. This area is home to at least 12 native stingless bee species (*P. Nogueira-Neto*, pers. comm.). Colonies of several species were also kept in hives at the Fazenda.

We selected six species that span a broad range of foraging strategies, colony sizes, body sizes and aggression levels (based on similarity with congeners described by Biesmeijer and Slaa, 2004). These species also show overlap in plant species utilization (Table S1 in Electronic Supplementary Material): *Frieseomelitta varia* (Lepeletier, 1836), *Melipona quadrifasciata* Lepeletier 1836, *Nannotrigona testaceicornis* (Lepeletier, 1836), *Scaptotrigona aff. depilis*, *Trigona hyalinata* (Lepeletier, 1836), and *Trigona spinipes* (Fabricius, 1793). *Trigona* species were from wild colonies, each estimated to be 200–400 m from the feeder array and in opposite directions (Fig. S1 in Electronic Supplementary Material). The other four species occupied nest boxes dispersed in a meliponary occupying approximately 1 ha, at a density similar to that found under natural conditions (Antonini and Martins, 2003). We trained one colony of each species (von Frisch, 1967) to an artificial feeder array approximately 50 m from the center of the meliponary. Table 1 lists characteristics of the study species. Head widths were measured for 38–40 individuals (two to four colonies) of each species using a Leica M16 microscope with Leica camera attachment (model DFC500). Colony size estimates are based on reliable published data. We used descriptions of bees foraging on natural food sources to characterize foraging strategies, based on a functional definition that considers numbers of

Table 1 Characteristics of bee species studied

Species	Head width (mm)	Average colony size (# workers)	Recruitment mechanism	Group forager?	Estimated flight range (m)
<i>F. varia</i>	2.33 ± 0.06	875 (Tóth et al., 2004; Nunes et al., 2008)	SA?	No (Jarau et al., 2003)	705
<i>M. quadrifasciata</i>	3.89 ± 0.11	715 (Roubik, 1980; Wille and Michener, 1973; Tóth et al., 2004)	SM (Lichtenberg et al., 2009), 3-DS?	No (Kerr, 1994)	2000 (Kerr, 1996)
<i>N. testaceicornis</i>	1.90 ± 0.03	1,750 (Lindauer and Kerr, 1960; Jarau et al., 2003)	SM (Schmidt et al., 2005)	No (Jarau et al., 2003)	468
<i>S. aff. depilis</i>	2.69 ± 0.04	6,000 (Ramalho, 1990; Jarau et al., 2003)	OT (Schmidt et al., 2003)	Yes (Jarau et al., 2003)	903
<i>T. hyalinata</i>	2.81 ± 0.04	15,000 (D. W. Roubik, pers. comm.)	OT (Nieh et al., 2003)	Yes (Roubik, 1980)	969
<i>T. spinipes</i>	2.79 ± 0.05	5,500 (Wille and Michener, 1973)	OT (Lindauer and Kerr, 1960)	Yes (Cortopassi-Laurino and Ramalho, 1988)	840 (Kerr, 1959, <i>T. spinipes</i> = <i>T. ruficrus</i>)

Recruitment mechanisms are: three-dimensional communication of food location without the use of an odor trail (3-DS), odor trail deposited along visually prominent landmarks between the food source and the nest (OT), sounds and agitation inside the nest that do not indicate food source location (SA), and scent marking of the food source (SM). Flight ranges with no citation were estimated from van Nieuwstadt and Ruano Iraheta (1996)

nestmates visiting the same food source rather than on recruitment. Species whose colonies can forage in large groups at the same spatial location were categorized as group foraging. Those whose workers forage as solitary individuals at different spatial patches are solitary foraging. Many group-foraging species will not permit non-nestmate conspecifics to forage in close proximity (Johnson and Hubbell, 1974; pers. obs.), thus large groups of these species are generally foragers from one colony.

Feeders consisted of yellow 1.5 mL Eppendorf tubes from which four capillary tubes protruded by 1–2 mm (Figs. 1, S2). Each tube rested in a white nylon washer upon which bees stood when feeding and interacting.



Fig. 1 Artificial “flower” used in this experiment, with two feeding *S. aff. depilis* foragers

Sixteen feeders were suspended from a 15 m × 15 m grid, and were spaced every 5 m. This created a resource that was easily exploitable by all study species, despite differences in tongue length and body size. We filled feeders with 2.5 M unscented sucrose solution during training and 1.5 M unscented sucrose solution during experimentation, providing sucrose ad libitum.

Data collection

We monitored the feeder array in 5-min periods, observing from 0900 to 1146 (morning trials) or 1300 to 1546 (afternoon trials). Stingless bees show activity peaks at different times of day (Roubik, 1989). Observation during both morning and afternoon thus allowed us to study interactions over a broad time span. We began observation after sunrise because, during austral winter, chilly early morning temperatures delay foraging activity of many stingless bee species (Hilário et al., 2000). During non-removal trials (see below), each of four observers rotated among four feeders, moving sequentially down a row and then returning to the beginning of that same row. Movement between feeders occurred during 1-min pauses between observation periods.

To assess interspecific effects on foraging, we used aspirators to remove group-foraging species from feeders. We removed (1) *T. hyalinata*, (2) *T. hyalinata* and *T. spinipes*, (3) *T. hyalinata* and *S. aff. depilis* or (4) *T. hyalinata*, *T. spinipes* and *S. aff. depilis*. In all trials, we removed *T. hyalinata* because this species dominated the entire feeder array whenever it was present. For each removal combination and for the non-removal treatment,

we conducted one morning and one afternoon trial. Aspirated bees were released away from the feeder array at the end of each trial. Because removal requires constant attention to feeders, we used four feeders (one per observer) during removal trials. Observers did not move during the removal trials, but continued to implement the 1-min pause between 5-min observation periods. Observer row assignments and feeder positions within each row were randomly assigned. Non-removal and removal trials were interspersed with each other, and with several days during which data were not collected, across 10 days.

Each observer recorded the species visiting the focal feeder and all interspecific interactions. Feeders were also videotaped during observation periods, and bee interactions were verified from the video. We did not individually mark all bees because doing so would have disrupted recruits and altered results. Thus, we recorded the maximum number of bees simultaneously feeding during each period for each species rather than the total number of visits.

For each interspecific interaction that occurred during an observation period, we recorded (1) species identity and number of individuals, (2) interaction initiator, (3) interaction outcome and (4) intensity of aggression. Displacement was considered aggressive when one individual directed movement toward another bee that could cause injury (e.g. spreading mandibles or biting), or that potentially increased the aggressor's apparent size (e.g. wing or leg spreading). We defined non-aggressive displacement as the rapid departure of a bee when another bee arrived but showed no evident aggression. An individual won an interaction if her opponent moved away immediately after the encounter.

Data analysis

We calculated three measures of dominance and one index of aggression for each species. (1) *Behavioral dominance* indicates a colony's ability to control a resource. We determined the number of turnovers in favor of each species, a turnover being defined as a change in the species makes up at least 50% of individuals at a feeder. Behavioral dominance was weighted to adjust for the number of

trials each species was present at the array. (2) We use *numerical dominance* to indicate local abundance at the array. For each trial, we determined the largest number of bees visiting the array during a single observation period. Behavioral and numerical dominance were calculated separately for non-removal and removal trials. (3) For each species, we calculated displacement success—the ability to win fights—as the proportion of displacement interactions (aggressive and non-aggressive) won during non-removal trials. This measure is comparable to “dominance” of species where contests occur between individuals rather than groups (e.g. Dingemanse and de Goede, 2004; White et al., 2007). (4) *Attack probability* is the number of aggressive displacement interactions that each species initiated as a proportion of the total number of such interactions in which it was involved (Catlett, 1961). To more accurately represent species aggression, attack probability includes interactions from all trials. Due to the non-parametric nature of several indices and the fact that we compare species rather than individuals, we are sometimes limited to describing the effects of removal rather than using statistical tests. Analyses were conducted in R v. 2.8.1 (R Development Core Team, 2008).

Results

Species dominance patterns

Table 2 shows dominance values and ranks in non-removal trials for each species. *Trigona hyalinata* was clearly the dominant species, both behaviorally and numerically. All feeders were completely controlled by *Trigona hyalinata* at the end of each non-removal trial. *Scaptotrigona* aff. *depilis* and *T. spinipes* occasionally behaviorally dominated individual feeders before expulsion by *T. hyalinata*, but the remaining three species never did. *Scaptotrigona* aff. *depilis* was relatively abundant at the feeder array, maintaining on average a maximum of 11 bees/trial. The remaining species averaged between 0.5 and 3 bees/trial.

As predicted by H1, group-foraging species, which had larger colonies (Table 1), ranked above solitary-foraging

Table 2 Dominance and aggressive index values (and ranks) calculated for each species

Behavioral and numerical dominance values are for non-removal trials

Species	Behavioral dominance	Numerical dominance	Displacement success	Attack probability
<i>F. varia</i>	0.00 (5)	2.50 (4)	0.300 (4)	0.26 (5)
<i>M. quadrifasciata</i>	0.00 (5)	2.00 (5)	0.000 (5.5)	0.06 (6)
<i>N. testaceicornis</i>	0.00 (5)	0.50 (6)	0.000 (5.5)	0.30 (4)
<i>S. aff. depilis</i>	1.00 (2)	11.00 (2)	0.303 (3)	0.80 (3)
<i>T. hyalinata</i>	11.50 (1)	22.50 (1)	0.737 (1)	0.86 (2)
<i>T. spinipes</i>	0.50 (3)	3.00 (3)	0.332 (2)	0.89 (1)

species in all three dominance measures (Fig. 2a). Because stingless bee nest sizes are better known than foraging behavior, we also determined the relationship between dominance and colony size (Fig. 2b). Species with larger colonies were behaviorally dominant ($r = 0.94$, $N = 6$, $P = 0.005$) but only marginally more abundant at the feeder array ($r = 0.83$, $N = 6$, $P = 0.06$). Contrary to H2, body size did not correlate with either behavioral (Fig. 2c;

$r = 0.33$, $N = 6$, $P = 0.52$) or numerical (Fig. 2c; $r = 0.37$, $N = 6$, $P = 0.50$) dominance. We found no relationship between colony size and body size ($r = 0.03$, $N = 6$, $P = 1$). Probability of winning fights correlated with colony size ($r = 0.84$, $N = 6$, $P = 0.04$), but not with body size ($r = 0.29$, $N = 6$, $P = 0.58$). Thus, group-foraging species with large colonies (H1), but not species with larger worker body size (H2), are dominant.

Effects of species removal

Removal of group-foraging species increased feeding opportunities for the remaining species, supporting H3. All species except *N. testaceicornis* increased behavioral dominance during removal trials (Fig. 3a), yielding a more even spread of turnovers across non-removed species. The per-feeder turnover rate, however, was relatively constant across trials, averaging 0.91 turnovers/feeder without removal and 0.73 turnovers/feeder during removal trials. For all species, numerical dominance increased almost threefold with exclusion of group foragers (Fig. 3b; quasi-Poisson regression: $\chi^2_1 = 7.51$, $P = 0.006$, $e^b = 2.72$). Removing one or two group-foraging species resulted in dominance by a remaining group forager.

Solitary-foraging species are unlikely to show major increases in numerical dominance. Thus, for each treatment we also determined the number of observation periods during which each species fed. This provides a robust measure of species visitation and resource consumption, facilitating comparisons among species with different foraging strategies. All species except *N. testaceicornis* increased visitation in the absence of group foragers (*F. varia*: $\chi^2_4 = 37.01$, $P < 0.0001$; *M. quadrifasciata*: $\chi^2_4 = 28.82$, $P < 0.0001$; *N. testaceicornis*: $\chi^2_4 = 8.76$, $P = 0.07$; *S. aff. depilis*: $\chi^2_2 = 15.03$, $P = 0.0005$; *T. spinipes*: $\chi^2_2 = 17.78$, $P = 0.0001$). Solitary-foraging species benefited most from complete removal of group foragers, and occasionally were able to increase visitation even in the presence of one group-foraging species (Fig. 3c).

Aggression

All species showed some degree of aggression. We observed 499 interspecific displacements of which 59% involved aggression, 94% were one-on-one and 77% were initiated by group-foraging species. Group-foraging species were significantly more aggressive than solitary-foraging species (Table 2; Scheffé’s test for proportions, $S = 9.46$, $P < 0.0005$; Zar, 1999). The majority of attacks (75%) were directed toward *M. quadrifasciata* (Table S2). Most interactions involved low levels of aggression, with prolonged

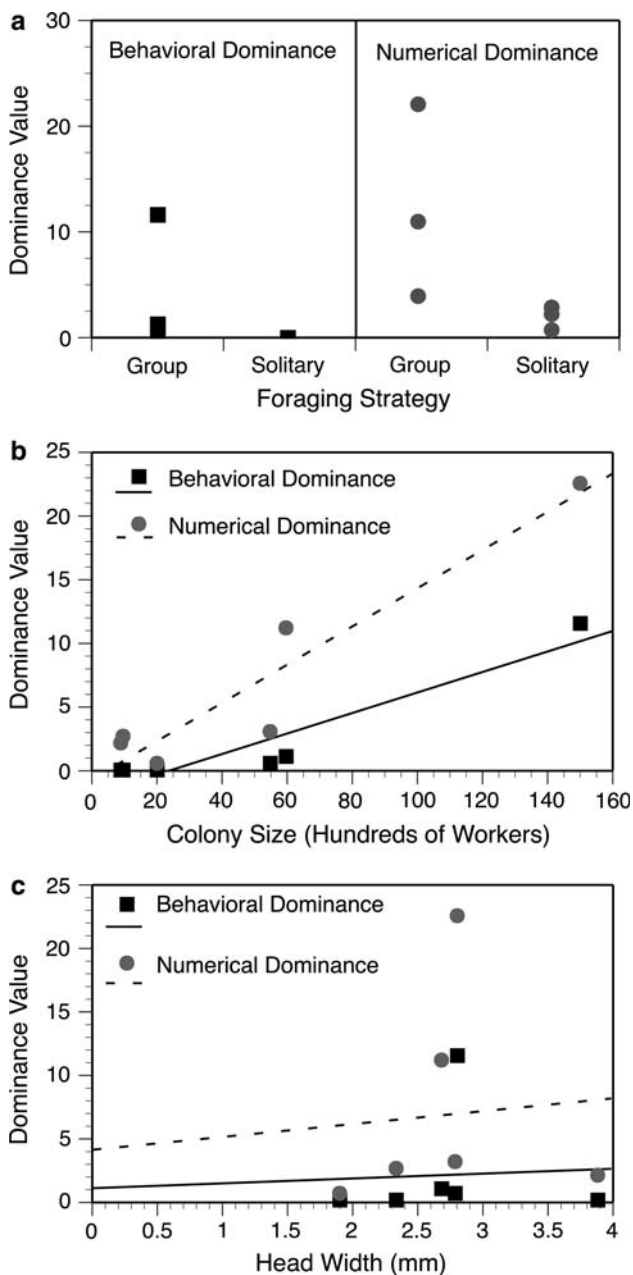


Fig. 2 a Group foragers show higher behavioral and numerical dominance than do solitary foragers. b Dominance increases with colony size. Lines were fit using least squares. c Dominance does not reflect body size. See text for statistics

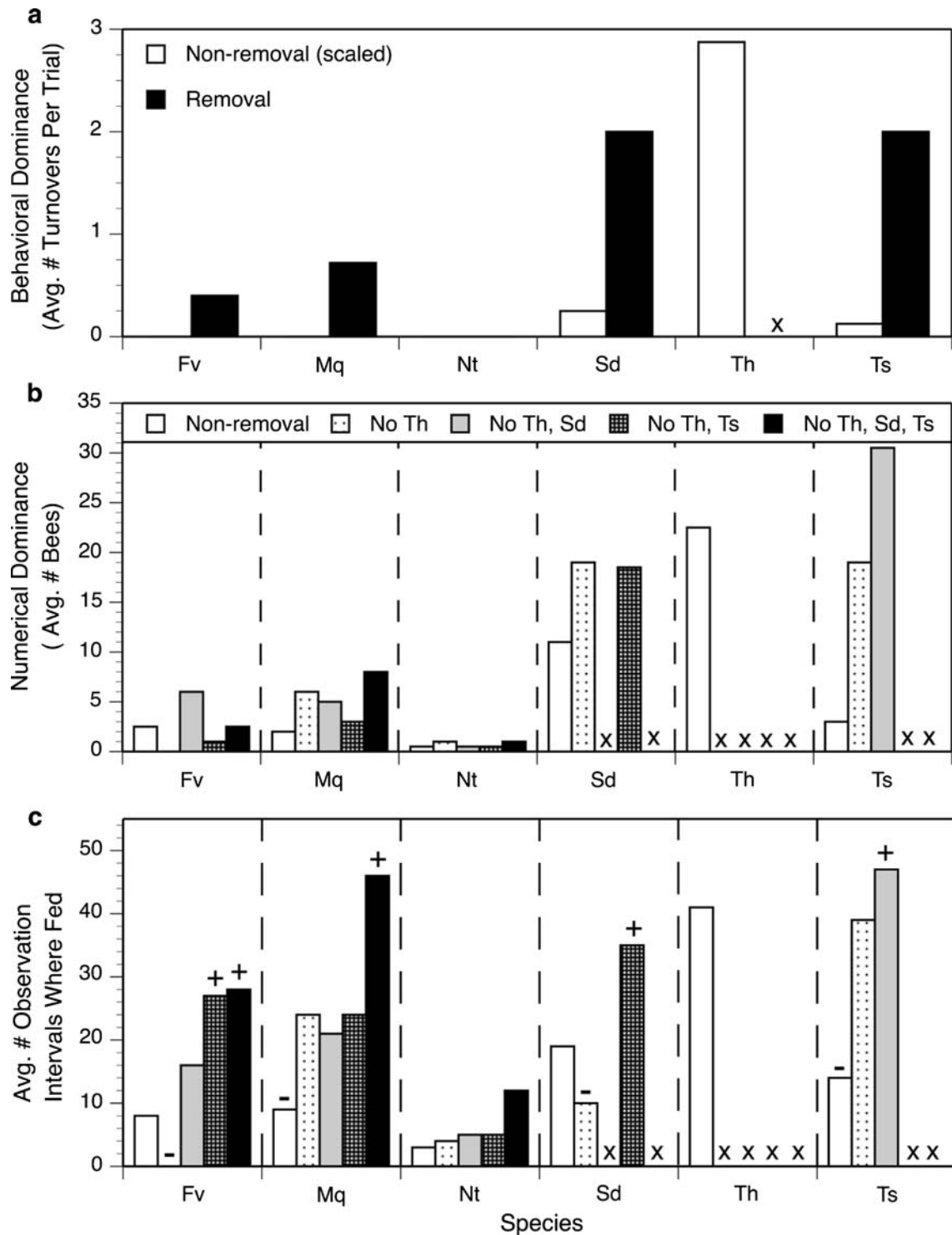


Fig. 3 *Fv*, *Frieseomelitta varia*; *Mq*, *Melipona quadrifasciata*; *Nt* *Nannotrigona testaceicornis*; *Sd*, *Scaptotrigona* aff. *depilis*; *Th*, *Trigona hyalinata*; *Ts*, *Trigona spinipes*. **a** Behavioral dominance increases with removal of group-foraging species. Non-removal values are scaled by ¼ to account for the different numbers of feeders observed

in removal and non-removal trials. **b** Numerical dominance increases with removal of group-foraging species. A “x” indicates that the species was removed during that treatment. **c** Feeder visitation increases with removal of group-foraging species. “+” and “-” indicate standardized residuals >2 or <-2, respectively. See text for statistics

fighters occurring only 13 times. Correlations between aggression and dominance were weak at the species level (behavioral dominance: $r = 0.76$, $N = 6$, $P = 0.08$;

numerical dominance: $r = 0.66$, $N = 6$, $P = 0.18$), but stronger at the individual level (displacement success: $r = 0.89$, $N = 5$, $P = 0.03$).

Discussion

We show that stingless bee species that form larger colonies and forage in large groups are able to dominate resources, altering the foraging patterns of displaced bees. Our results strongly suggest that, for highly social superorganisms, group size can have the same ecological role as body size does for non-social species. First, group-foraging species were more likely to control a resource and win individual fights than solitary-foraging species (H1). Second, worker body size did not relate to dominance (H2). Third, experimental removal of group foragers increased feeding opportunities for remaining species (H3). Numerical dominance, behavioral dominance and visitation of all species increased during removal trials. The small increases in dominance of solitary foragers after removal of group foragers enabled these colonies to feed for significantly longer. They thus likely collected more of the resource in the absence of group foragers. These experimental results are consistent with observed patterns of bee floral visitation in a Malaysian dipterocarp forest, where non-aggressive species showed increased visitation in the absence of an aggressive, dominant species (Nagamitsu and Inoue, 1997). Group-foraging species showed larger dominance increases with removal than did solitary-foraging species. However, the success of group-foraging species was not due solely to greater abundance. Feeders were often defended by a single *Scaptotrigona* or *Trigona* forager. Group forager abundance typically increased only after other species were chased away. Aggression facilitated species turnover and the subsequent increase in aggressor abundance. Our results suggest that group foraging is part of a suite of traits that evolved in several stingless bee genera as a mechanism promoting successful foraging in the face of intense competition, which can occur during times of several floral shortage (Roubik, 1989). These traits include large colonies, rapid location-specific recruitment via odor trails and aggression at food sources.

Stingless bees have likely evolved multiple strategies to improve competitive success during dearth seasons. Forming a large, aggressive group at the resource (“thug-gery”) is one strategy. Pronounced mandibular teeth, such as those characteristic of *Trigona* species (Schwarz, 1948), likely improve fighting ability of “thug” species. Some large *Melipona* species may use an alternative strategy (“tenacity”) by continuing to feed despite being the recipients of aggression. We found a high proportion of attacks directed at *M. quadrifasciata*, mainly due to this species remaining at the feeders while being bitten or returning to feeders immediately after being displaced. Very small (2–3 mm long) species likely remain competitive through a third strategy, insinuation (Johnson, 1983).

Insinulators fly away when threatened by dominant species but quickly return to nearby flowers and continue to feed.

Natural context

Aggressive and non-aggressive displacement also occurs on natural food sources. Abundance scans at a *Dombeya wallichii* tree at the Universidade de São Paulo, Ribeirão Preto revealed that *T. hyalinata* was numerically dominant, comprising 80% of bees counted (supplemental Table S3). This high abundance is somewhat surprising given the presence of over 30 honey bee colonies <50 m away. *Trigona hyalinata* bit and aggressively removed other species from flowers (0.08 displacement interactions per observer-minute versus 0.52 at the feeder array). *Trigona pallens* and *Tetragona clavipes* are also known to exhibit low to medium intensity aggression at flowers (Roubik, 1980; pers. obs.), and *Trigona cilipes* low intensity aggression (Roubik, 1980). *Trigona spinipes* (Kerr, 1959), *T. corvina* and *T. silvestriana* (Johnson and Hubbell, 1974) will fight, sometimes to the death, at flowers.

Sugar-providing feeder arrays such as those typically used for bee dominance and aggression studies are somewhat unrealistic in that they are much smaller than mass-flowering trees, important food sources for stingless bees (Endress, 1994; Ramalho, 2004). Feeder arrays may elicit more intense interactions. However, they remain useful because they permit detailed data collection of species identity and behavior.

Body size

Our results do not support H2. Body size was not a major determinant of dominance. In our study, dominant species were medium-sized. However, unlike previous research (Johnson and Hubbell, 1974), we included the *Melipona* genus, whose species have a large and robust body form (Michener, 2007) but do not forage in large groups and are non-aggressive at food sources (Biesmeijer and Slaa, 2004). Dominance studies have typically overlooked *Melipona*, although this genus is commonly found in bee–plant interaction studies (Biesmeijer and Slaa, 2006).

Aggression

Our analyses suggest that aggression can mediate dominance but should not substitute as a measure of dominance. Rather, dominance should be interpreted as the suppression of one species by another (Keddy, 2001). This may arise from aggressive interactions, unequal resource exploitation efficiency or avoidance of a food source on which the dominant species is feeding. Analysis of data from Nagamitsu and Inoue (1997) also supports using ecologically relevant

measures rather than aggression in assessing dominance. In their study, the most aggressively dominant species showed an average decrease in visitation in the presence of other species (supplemental Table S4).

Dominance and group foraging

Changes in dominance reported here and in other studies (Johnson and Hubbell, 1974; Nagamitsu and Inoue, 1997; Eltz et al., 2002; Slaa, 2003) suggest that food competition helps structure stingless bee communities. Feeding opportunities at individual resources increased with removal of group-foraging species. Group foragers typically gained control through aggression, suggesting they excel in interference competition. Solitary foragers exhibited behavioral flexibility, increasing visitation and marginally increasing local abundance in the absence of group foragers. This contradicts the prediction that foraging patterns of less aggressive species reflect floral preferences and will not be altered by removal of aggressive species (Johnson and Hubbell, 1975). Just as individuals may benefit competitively from larger body size in solitary bees (Bosch and Vicens, 2006), social bees may increase dominance with larger superorganism sizes: larger colonies whose workers forage in groups.

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