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Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest

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Abstract Interference competition by aggressive foraging often explains resource partitioning, but mechanisms contributing to partitioning have rarely been studied in Asian social bee guilds. Foraging of social bees at canopy flowers of *Santiria laevigata* (Burseraceae) and honey-water feeders was studied in a lowland mixed-dipterocarp forest in Sarawak, Malaysia. Four stingless bee species (Apidae, Meliponinae), *Trigona canifrons*, *T. fimbriata*, *T. apicalis* and *T. melina*, aggressively defended flower patches and feeders. At the flowers, *T. canifrons* excluded other bees only in the morning when nectar flow peaked. At the feeders, the aggression resulted in asymmetric interference competition, which produced a dominance hierarchy among seven social bee species. Interspecific partitioning of the feeders was detected in time and height but not quality. Only time of the first arrival after feeder presentation was negatively correlated with the dominance hierarchy: more aggressive species arrived at the feeders later than less aggressive species. This result suggests that a trade-off between searching ability and defensive ability at flower patches gives rise to resource partitioning in the social bee guild.

Key words Stingless bees · Floral resource · Interference competition · Resource partitioning · Sarawak

Introduction

Aggressive defense of foods is prevalent in animals, particularly in nectar-feeders, which use rich and compact resources at flowers. Nectar-feeding birds defend territories containing many flowers (Kodric-Brown and Brown 1978; Pyke 1979), while some tropical stingless bees (Meliponinae, Apidae, Hymenoptera) defend each flower or flower patch (Roubik 1982).

Aggressive behavior of stingless bees at flower patches has been studied mainly in the Neotropics (Johnson and Hubbell 1974, 1975; Hubbell and Johnson 1978; Johnson 1981). Aggressive foragers exclude other bees and monopolize flower patches (Johnson and Hubbell 1974). This competitive advantage meant that aggressive species had a higher frequency of foragers returning with nectar loads than unaggressive species when Africanized honey bees started to use their floral resources (Roubik et al. 1986).

Two mechanisms have been proposed for resource partitioning between aggressive and unaggressive species: (1) aggressive species may use clumped, rich resources, while unaggressive species use scattered, poor resources (Johnson and Hubbell 1974; Johnson 1981), or (2) aggressive species may have lower ability for discovering newly available patches than unaggressive species (Hubbell and Johnson 1978). Recently, such behavioral partitioning of ephemeral and patchy resources are regarded as major mechanisms for co-existence of competing species (Kotler et al. 1993; Brown et al. 1994).

Another axis for floral resource partitioning of bees is suggested to be in the vertical forest structure (Roubik 1993a; Roubik et al. 1995). The vertical structure is well-developed in lowland mixed-dipterocarp forests in Sarawak. Flowers in upper strata have different features in attractants and rewards for bees from flowers in lower strata (Apanah 1990). Most flowers in upper strata are conspicuous from a distance and often produce a large

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amount of rewards in a short period. In contrast, flowers in lower strata, except for plants specialized for birds and some trap-lining bees, are usually inconspicuous and have poor rewards, being produced slowly over a long period (Kato 1996). Consequently, we expect aggressively defending species to forage in upper strata, and unaggressive species to forage in lower strata.

Aggressive behavior of palaeotropical social bees has been poorly investigated in forests (Appanah 1981). Visits of social bees to artificial feeders were observed in Sri Lanka (Koeniger and Vorwohl 1979) and peninsular Malaysia (Khoo 1992). They showed that aggression of stingless bees compensated for the disadvantage due to smaller foraging area compared to that of honey bees, and that more aggressive stingless bees arriving later at feeders excluded unaggressive bees. These studies, however, were not designed to investigate how aggressive foraging affects floral resource partitioning among species of a local bee guild.

This paper shows which kinds of floral resource partitioning mentioned above are created by aggressive defense of flower patches. We have three aims: (1) to measure dominance hierarchy in aggressive foraging among social bee species, (2) to detect resource partitioning in time, height and quality of feeders, and (3) to examine negative correlations between the aggressive dominance and superior position on the resource axes partitioned, which indicates trade-offs between foraging traits. Finally we discuss potential factors of the trade-off that affect resource partitioning.

Materials and methods

Study site

The study site was an intact mixed-dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20'N, 113°50'E, altitude 150 m). We directly observed foraging behavior of bees at various forest strata from a canopy observation system which consisted of two towers and nine aerial walkways in a plot (200 × 400 m, 8 ha; Fig. 1; Inoue et al. 1995). In the plot, we surveyed bee nests in the basal trunks of all trees of ≥ 40 cm diameter at 1.3 m height above

the ground and in the trunks visible from the towers and the walkways. We found and mapped 14 nests of 7 stingless bee species out of 27 species recorded in the Park (Inoue et al. 1994).

Observations at flowers

Foraging of stingless bees was observed at flowers of a male tree of *Santiria laevigata* form. *glabrifolia* (Burseraceae). The flowers bloomed 35 m above the ground in November 1994 in the plot (Fig. 1). We collected flower-visiting insects with a hand net for 10 min at seven times from 0700 to 1630 hours on 17 November 1994. Aggressive behavior of bees at the flowers was observed at each collection time. Collection and observation were done from a terrace built on an emergent tree, 5 m from the edge of the foliage of the *S. laevigata* tree.

To estimate the amount of nectar produced and the standing amount of nectar in individual flowers, we collected 12 flowers from each of bagged and open inflorescences at five times from 0700 to 1630 hours on 17 November 1994. The bags were insect-collecting nets made of fine nylon mesh (Shiga Entomological Company, Tokyo), which prevents flower visitors from consuming floral rewards. The volume of nectar in a flower was measured by micro capillary tubes (Microcaps Drummond Scientific Company, Broomall, Pa., USA), and its sucrose concentration (% in weight) was measured by an Atago hand-held refractometer. Sucrose weight (mg) was calculated from the nectar volume and the sucrose concentration. Pollen grains were extracted from a flower by 10% KOH and diffused in 1 ml of 20% ethanol. The number of pollen grains in 0.0032 ml solution sampled from the 1 ml ethanol solution was counted by a hemacytometer.

Feeder experiments

We used artificial honey-water feeders to detect interference competition and resource partitioning. We filled a plastic bottle (diameter 6 cm, height 15 cm) with 300 ml solution of water and commercial honey. We perforated six holes at the bottom edge of each bottle. We completely sealed the bottles except for the holes to prevent honey-water from flowing away, unless bees imbibed honey-water through the feeding holes. The total amount of honey-water in a feeder was enough so that potential reward remained constant during the experiments. Each feeder was set on a yellow pan located on the towers.

To examine possible temporal partitioning, we measured visitation rate (the number of bees visiting a feeder per min) of each species for 5-min observations at 1- to 4-h intervals during daytime for up to 6 days after the presentation of feeders (Table 1). To examine possible partitioning in height and quality, the feeders with various sucrose concentration between 10 and 70%, and with two

Fig. 1 A map of the canopy biology plot in Lambir Hills National Park, Sarawak, Malaysia. Contour shows relative altitude from the lowest point in the plot at 10 m interval. Locations of 14 nests of seven stingless bee species, of two towers used for feeder experiments, and of a canopy tree *Santiria laevigata* are also shown

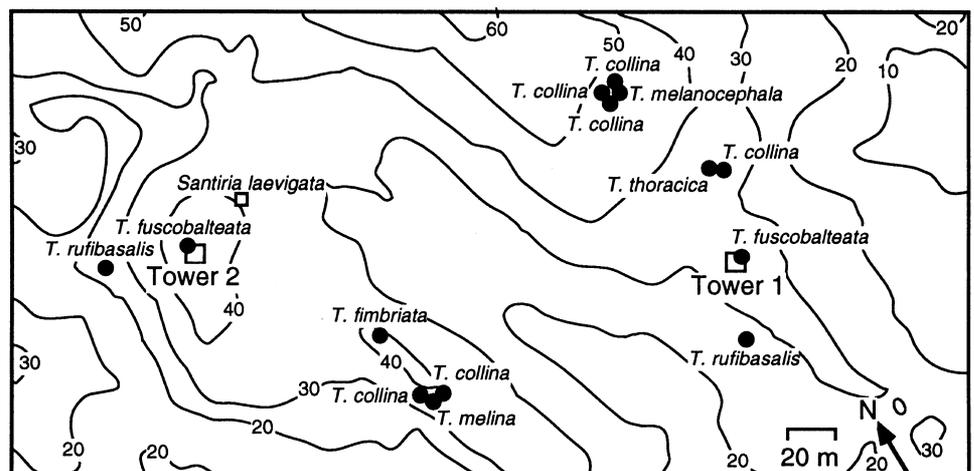


Table 1 Design of three experiments using artificial honey-water feeders

Factors (Resource axes)	No. of levels	Levels
Experiment 1 (at tower 1 in February 1994) ^a		
Day after set of feeder	2	Days 1, 2
Time of day	4	8:00, 9:00, 10:00, 11:00
Height	4	3, 16, 25, 35 m
Sucrose concentration	5	10, 25, 40, 55, 70%
Size of feeding hole	1	0.7 mm
Total no. of observations	160	
Experiment 2 (at tower 2 in March 1994) ^b		
Day after set of feeder	3	Days 1, 2 and 4
Time of day	9	9:30, 10:30, 11:00, 11:30, 12:30, 13:00, 14:00, 15:00, 16:00
Height	3	1, 25, 50 m
Sucrose concentration	2	20, 60%
Size of feeding hole	2	0.2, 0.7 mm
Total no. of observations	276	
Experiment 3 (at tower 1 in October 1994) ^c		
Day after set of feeder	6	Days 1, 2, 3, 4, 5, 6
Time of day	3	9:00, 12:00, 15:00
Height	3	1, 19, 35 m
Sucrose concentration	1	40%
Size of feeding hole	1	0.7 mm
Total no. of observations	48	

^a Five feeders with five different sucrose concentrations at 4 heights (total 20)

^b Four feeders (2 sucrose concentration \times 2 size of feeder holes) at 3 heights (total 12)

^c Two feeders at 3 heights (total 6)

different diameters (0.2 and 0.7 mm) of feeding holes, were set at different heights (1–50 m above the ground) on the towers. Three experiments were conducted at the two towers between February and October 1994 (Table 1).

We identified most bee species at feeders, using reference specimens from our collections. We measured mean head width (mm; $n = 5$) to compare body size among species. Aggressive behavior when two bees met was ranked in five levels according to Johnson and Hubbell (1974). An encounter is defined as an event where two bees landed on the same feeder during a 5-min observation when the visitation rate was measured (level 0: no aggressive behavior; level 1: threat display without body contact; level 2: brief contact attempting to bite the other; level 3: prolonged biting of the other; level 4: mortality during combat).

Data analysis

To detect interference competition between bee species, we calculated changes in the visitation rate of the focal species after an encounter with the other species between the two consecutive observations. Decrease in the visitation rate was tested by two-tailed one-sample *t*-test.

We tested whether four measures: (1) time of the first arrival after feeder presentation except for night time, (2) height of the visited feeders above the ground, (3) sucrose concentration of honey-water of visited feeders, and (4) size of feeding holes of visited feeders, differed among species, using ANOVA with two factors, species and experiments (SAS Institute 1988). Significant differences in the measures on feeder use between any species pairs were examined by Scheffé's multiple comparisons test.

We ranked bee species in aggressive dominance, based on both the aggressive behavior and the asymmetric change in the visitation

rates after encounters. To show positions of species on the four resource axes, we ranked species along the axes from superior to inferior position: (1) time of the first arrival: from earlier to later, (2) height of feeders: from higher to lower, (3) sucrose concentration: from higher to lower and (4) size of feeding holes: from larger to smaller. To detect negative correlations between aggressive dominance and superior position on each resource axis, we examined the associations between these ranks by Kendall rank correlation (Sokal and Rohlf 1981).

Results

Observations on flowers

Individual flowers of a male tree of *S. laevigata* opened before 0700 hours and bloomed for 1–1.5 days. Flowers produced both nectar and pollen as rewards. Sucrose production rate reached a plateau (6.3 mg/h) at 0900–1200 hours, and standing amount of sucrose increased until 0900 hours and remained at 5.9–6.4 mg until 1600 h (Fig. 2a). Sucrose concentration increased from 10% to 60% at 900 h, and reached to 70% in the afternoon (Fig. 2b). The number of pollen grains in a flower was 6000–9000 at 0700 hours before anther dehiscence, and decreased constantly to 2500 in the late afternoon (Fig. 2c).

We collected 444 insect visitors from five orders on *S. laevigata* flowers. Stingless bees (13 species) were the most abundant (71% in individuals) among the visitors. *Trigona canifrons* behaved aggressively on the flowers. Hovering above the flowers, *T. canifrons* turned to face newly arrived bees of other species and chased them. We did not observe *T. canifrons* attacking conspecific foragers, suggesting that they were nestmates. Other bee species did not show aggressive behavior during the observations.

Visitation of *T. canifrons* peaked from 0900 to 1200 hours when nectar production reached a plateau (Fig. 2d). In contrast, *T. itama*, *T. collina* and *T. apicalis* mostly visited the flowers before 0900 hours (Fig. 2e). *T. itama* visited the flowers again after 1500 hours when *T. canifrons* stopped foraging. Three species in subgenus *Lepidotrigona*, *T. ventralis*, *T. terminata* and *T. nitidiventris*, visited flowers throughout a day, not affected by the presence of *T. canifrons* (Fig. 2f).

Feeder experiments

At the feeders, we found 12 stingless bee species and one honey bee species varying in body size (Table 2). Among the 13 species, the seven most abundant species were analyzed in detail. Among them, *Trigona fimbriata*, *T. apicalis* and *T. melina* were aggressive to other bee species (Table 3). *Apis koschevnikovi* was aggressive only to conspecifics.

T. fimbriata displayed threat, which consisted of turning face and attempting to rush at the rival bees, opening the mandibles, and spreading the wings upward.

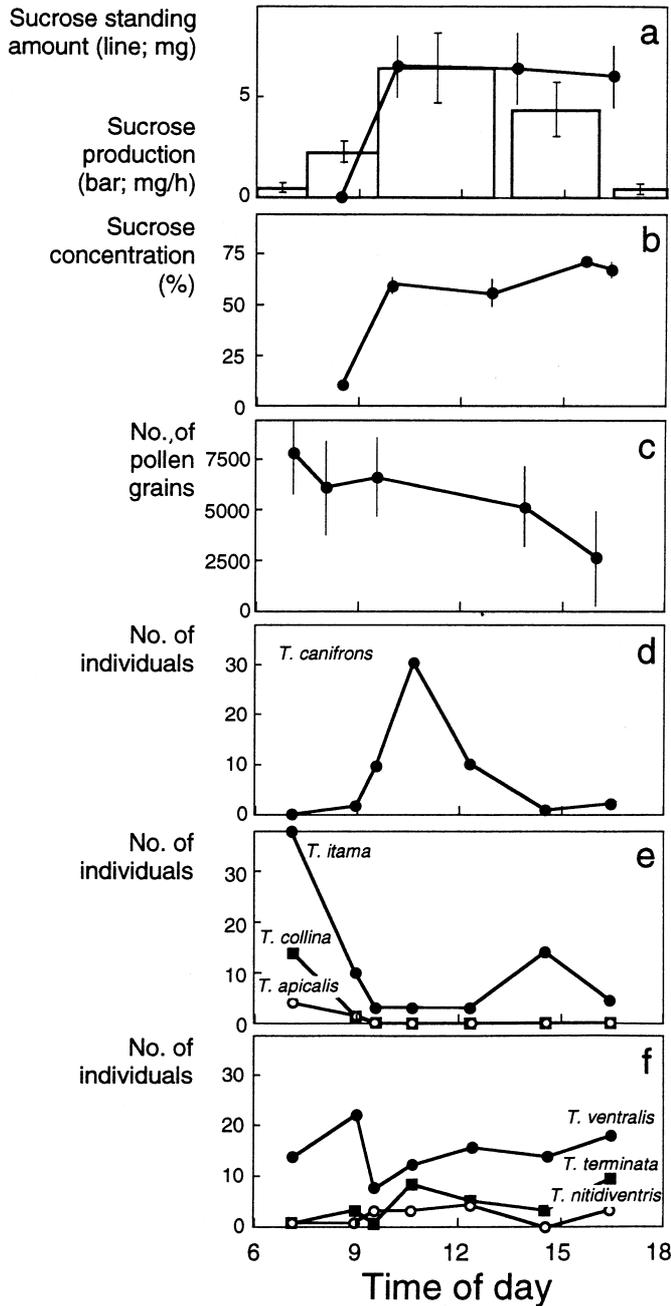


Fig. 2 a-f Diurnal changes in floral rewards and stingless-bee visits to flowers of a canopy tree, *Santiria laevigata* (Burseraceae). Floral rewards are expressed by **a** sucrose standing amount (mg per flower) and sucrose production rate of nectar (mg/h per flower); **b** sucrose concentration of nectar (% in weight); and **c** number of pollen grains per flower. Symbols indicate mean \pm 1 SD. Stingless-bee visits (number of individuals collected for 10 min at flowers) of **d** aggressive species, *Trigona canifrons*; **e** unaggressive non-*Lepidotrigona* species; and **f** unaggressive *Lepidotrigona* species are shown

Even honey bees, which were larger than *T. fimbriata*, flew away after this threat display. The threat rarely escalated to direct combat with unaggressive species. We observed, however, a battle to the death between *T. fimbriata* and *T. apicalis* on a feeder in experiment 1. *T. fimbriata* bit *T. apicalis* on the neck and legs. This

battle finished within 10 min, and *T. fimbriata* won after killing two individuals of *T. apicalis*. Once *T. fimbriata* occupied the feeders, five to ten guard bees stayed at the feeders, and two or three guard bees faced toward a feeding hole from 5 mm. These guard bees stayed at the feeders for 5–15 min and infrequently imbibed honey-water, while other nestmates foraged, staying only for 1–2 min. When guard bees of *T. fimbriata* were on the feeders, other bees left without attempting to land.

T. apicalis displayed threat to unaggressive species in the same way as *T. fimbriata*. No encounter between *T. apicalis* and *T. melina* was observed.

T. melina threatened other bee species less frequently than *T. fimbriata* and *T. apicalis*. *T. melina* often bit rival bees on neck and legs, and brought up the body of the rivals, and then removed them from the feeders. In spite of the direct body contact, the removed bees were rarely injured. After *T. melina* monopolized the feeders, two or three guard bees defended a feeding hole and stayed for 3–10 min. However, they were unable to exclude completely invasion of larger bees.

A. koschevnikovi faced and rushed to others, when >5 honey bees rushed to the same feeding hole. Aggression of honey bees was exhibited when imbibing was interrupted by other conspecific foragers.

Aggressive species, *T. fimbriata*, *T. apicalis* and *T. melina*, did not significantly decrease their visitation rates after encounters with honey bees and unaggressive stingless bees (Table 4; $P > 0.05$; one-sample *t*-test). Visits of *A. koschevnikovi* became significantly fewer after encounters with *T. fimbriata* ($P < 0.01$), but were less affected by encounters with *T. melina* and unaggressive stingless bee species. Unaggressive species, *T. ventralis*, *T. laeviceps* and *T. melanocephala*, reduced their visitation rates after encounters with all the other bee species. Decreases in visitation rates of *T. laeviceps* and *T. melanocephala* were significant ($P < 0.05$) in 8 of 11 cases, but those of *T. ventralis* were not significant ($P > 0.05$) in any of five cases.

Time of the first arrival significantly differed among the seven species (Table 5; $F = 20.2$, $df = 6$, $P = 0.000$). According to the difference between species, four groups: the earliest group (*A. koschevnikovi*, *T. laeviceps* and *T. melanocephala*), earlier group (*T. apicalis* and *T. ventralis*), later *T. fimbriata* and the latest *T. melina* were recognized. Significant interaction between species and experiments indicates that *A. koschevnikovi* was a more constant early-comer than *T. laeviceps* and *T. melanocephala* ($F = 13.7$, $df = 8$, $P = 0.000$).

Height of the visited feeders were significantly differed among the species (Table 6; $F = 22.7$, $df = 6$, $P = 0.000$). *A. koschevnikovi*, *T. fimbriata* and *T. laeviceps* mainly visited canopy feeders (> 20 m), but *T. ventralis* and *T. melanocephala* visited understory feeders (< 15 m). *T. apicalis* and *T. melina* showed intermediate foraging height. An interaction between species and experiments was also significant due to occupation of higher feeders by *T. fimbriata* in experiment 1 ($F = 5.09$, $df = 7$, $P = 0.000$).

Table 2 Mean visitation rate and mean head width of social bee species visited to artificial honey-water feeders

^a Mean visitation rate was less than 0.01 min⁻¹
^b These two species were not discriminated in the field

Species	Code	Mean visitation rate (min ⁻¹)			Head width (mm)
		Exp.1	Exp.2	Exp.3	
<i>Trigona (Trigonula) laeviceps</i>	<i>Lae</i>	1.97	5.36	0.99	1.9
<i>Apis koschevnikovi</i>	<i>Kos</i>	1.67	2.46	3.80	3.7
<i>T. (Lepidotrigona) ventralis</i>	<i>Ven</i>	0.23		2.22	1.9
<i>T. (Tetra) melina</i>	<i>Mli</i>	0.01	0.47	1.12	2.1
<i>T. (Homotrigona) fimbriata</i>	<i>Fim</i>	0.71	0.21		3.1
<i>T. (Tetra) melanocephala</i>	<i>Mla</i>	0.48	0.46	0.11	2.1
<i>T. (Tetrigona) apicalis</i>	<i>Api</i>	0.15			2.6
<i>T. (Tetra) fuscobalteata</i>		0.01	+ ^a	0.14	1.4
<i>Hypotrigona scintillans</i> ^b					1.2
<i>T. (Tetra) collina</i>		0.02			2.3
<i>T. (Tetra) rufibasalis</i>		0.01	0.02	+	2.4
<i>T. (L.) nitidiventris</i>		+	0.01		2.7
<i>T. (L.) terminata</i>				+	2.2

Table 3 Levels of aggressive behavior between pairs of seven bee species (*level 0* no aggressive behavior, *1* threat without body contact, *2* brief body contact, *3* prolonged biting, *4* slaughter). Numbers of observations when the interspecific encounters were found are shown in parentheses. Species codes are shown in Table 2

Actors	Receptors						
	<i>Fim</i>	<i>Api</i>	<i>Mli</i>	<i>Kos</i>	<i>Ven</i>	<i>Lae</i>	<i>Mla</i>
<i>Fim</i>	0 (89)	4 (1)	1 (2)	1,2 (39)	1 (2)	1 (35)	1 (2)
<i>Api</i>	3 (1)	0 (15)	0 (0)	1,2 (7)	0 (0)	1,2 (7)	0 (0)
<i>Mli</i>	0 (2)	0 (0)	0 (111)	0,1,2 (59)	1,2,3 (21)	1,2,3 (60)	1,2,3 (21)
<i>Kos</i>	0 (39)	0 (7)	0 (59)	0,1 (344)	0 (43)	0 (176)	0 (49)
<i>Ven</i>	0 (2)	0 (0)	0 (21)	0 (43)	0 (78)	0 (27)	0 (14)
<i>Lae</i>	0 (35)	0 (7)	0 (60)	0 (176)	0 (27)	0 (381)	0 (76)
<i>Mla</i>	0 (2)	0 (0)	0 (21)	0 (49)	0 (14)	0 (76)	0 (132)

Table 4 Changes in visitation rate (min⁻¹) between two consecutive observations (10 min at 1- to 4-h intervals) after encounter with other species on feeders. Species codes are shown in Table 2. Numbers of observations when the interspecific encounters were found are shown in Table 3

Species code	Encounter with						
	<i>Fim</i>	<i>Api</i>	<i>Mli</i>	<i>Kos</i>	<i>Ven</i>	<i>Lae</i>	<i>Mla</i>
<i>Fim</i>	–	0.00	–0.50	0.67	0.00	0.03	–0.50
<i>Api</i>	1.00	–	. ^a	1.14	.	–0.14	.
<i>Mli</i>	0.00	.	–	0.36	0.33	0.33	0.21
<i>Kos</i>	–1.74**	–2.86	0.00	–	0.05	–0.07	–0.51
<i>Ven</i>	–1.50	.	–0.41	–0.93	–	–1.91	–0.82
<i>Lae</i>	–1.54*	–9.71*	–0.95*	–1.11*	–1.65**	–	–0.93
<i>Mla</i>	–1.00	.	–1.10	–1.85***	–1.54*	–1.30***	–

Significant levels of decrease of visitation rate are shown by *** for $P < 0.001$, ** for $P < 0.01$, and *: $P < 0.05$ (two-tailed one-sample *t*-test)

^a No encounter was observed

Two measures of energetic quality of visited feeders: sucrose concentration of honey-water and size of feeding holes did not significantly differ among the species ($F = 0.37$, $df = 6$, $P = 0.898$; $F = 1.93$, $df = 4$, $P = 0.104$, respectively).

Based on the evidences shown above, we ranked the seven bee species in aggressive dominance and position on the two resource axes partitioned among the species:

arrival time and foraging height (Table 7). The time of the first arrival at feeders had significant negative correlation with the aggressive dominance (Kendall rank correlation coefficient $\tau = -0.67$; $P = 0.035$), but the height of visited feeders did not ($\tau = 0.31$; $P = 0.33$).

Table 5 Time of the first arrival after feeder presentation at feeders visited by seven bee species. No significant ($P > 0.05$) difference between same letters

Species code	No. of feeders visited	Mean \pm SD (h)	Scheffe comparison
<i>Kos</i>	37	5.70 \pm 5.16	ab
<i>Lae</i>	38	7.66 \pm 10.5	ab
<i>Api</i>	5	8.40 \pm 6.58	abc
<i>Mla</i>	27	8.56 \pm 6.89	ab
<i>Ven</i>	17	9.12 \pm 7.59	abc
<i>Fim</i>	21	14.2 \pm 10.8	bc
<i>Mli</i>	20	22.6 \pm 5.98	d

Table 6 Height above the ground of feeders visited by seven bee species. No significant ($P > 0.05$) difference between same letters

Species code	No. of observations	Mean \pm SD (m)	Scheffe comparison
<i>Kos</i>	344	27.9 \pm 15.6	ab d
<i>Fim</i>	89	26.7 \pm 7.27	abcd
<i>Lae</i>	381	24.5 \pm 17.6	abcd
<i>Mli</i>	111	21.7 \pm 19.5	bcde
<i>Api</i>	15	18.9 \pm 8.96	abcdef
<i>Ven</i>	78	14.9 \pm 13.6	cdef
<i>Mla</i>	132	12.2 \pm 16.5	def

Table 7 Rank of species in aggressive dominance, time of the first arrival at visited feeders after feeder presentation, and height above the ground of visited feeders. Rank is descending from dominant to subordinate in aggressive dominance, from earlier to later in time of the first arrival, from higher to lower in height of feeders. Species codes are shown in Table 2

Species code	Rank		
	Aggressive dominance	Time of first arrival at visited feeders	Height above ground of visited feeders
<i>Fim</i>	1	3	2
<i>Api</i>	2	2	4
<i>Mli</i>	2	4	3
<i>Kos</i>	3	1	1
<i>Ven</i>	4	2	5
<i>Lae</i>	5	1	2
<i>Mla</i>	5	1	6

Discussion

Aggressive interference

Numerical observations suggest that aggressiveness of stingless bees on flowers and feeders is species-specific trait (Hubbell and Johnson 1978; Appanah 1981; Khoo 1992). Such specific reactions depend on communication and recruitment systems as well as behavior and morphology of individuals. Mass recruiting to flower patches to defend is prevalent in aggressive species, which are called extirpators by Johnson (1982). Ag-

gressive bees have strongly developed mandibular teeth (Roubik 1989). These species-specific traits produce dominance hierarchy in local bee guilds. *T. fimbriata* is the largest species and won a lethal battle with *T. apicalis*, or threatened *T. melina* by displays on our feeders. Dominance order between *T. apicalis* and *T. melina* were unknown because the encounters between the both were not observed. *T. canifrons* displaced *T. apicalis* by aerial fights on canopy flowers as an observation on feeders by Khoo (1992).

Our results support the occurrence of asymmetric interference competition between aggressive and unaggressive species on the feeders, as shown in previous studies (Johnson and Hubbell 1974; Hubbell and Johnson 1978). The interference at feeding sites may reduce foraging by both attacked bees and their nestmates "informed" by the threatened foragers. Poor recruitment by the attacked scouts may cause a decrease in visitation to the feeding sites. Temporal displacement of bee visitors to *Santiria* flowers also suggests that interference competition occurs at the forest canopy.

The subgenus *Lepidotrigona* was robust to interference by aggressive stingless bees, which may be described by Johnson (1982). Because aggressive species were not observed to behave differently to *Lepidotrigona*, *Lepidotrigona* seems to use resources unavailable for aggressive species to avoid interference competition. Our observations that *Lepidotrigona* can lick up viscous nectar due to its flatter labium support this hypothesis (T. Nagamitsu and T. Inoue, unpublished work).

Resource partitioning

We detected interspecific partitioning of the feeders in time and height but not energetic quality. At canopy flowers, however, temporal replacement of bee species depended on nectar production rate per flower. These conflicting results may be due to the differences between the artificial feeders and the natural flowers, in particular the smaller scale of our feeder presentation (<30 feeding holes on a 25-m² tower) than the observed flowers (>10,000 flowers on 80 m² foliage; Roubik 1993b).

Time of the first arrival at feeding site and energetic quality of foods have been regarded as the main resource axes partitioned among social bee species (Johnson and Hubbell 1975; Hubbell and Johnson 1978; Roubik 1980). In contrast, interspecific partitioning in foraging height in the forest profile may be unique to dipterocarp forests in Sarawak (Roubik 1993a). Understorey foraging of *T. melanocephala* endemic to Borneo is also supported by records of visited flowers in the study site (T. Nagamitsu, K. Momose and T. Inoue, unpublished work). The prediction that aggressive species would forage more in upper strata than unaggressive species was not supported. This result suggests that differences in other traits, the physiology of thermal regulation and the visual system, may cause separation of foraging height (Roubik 1993a).

Honey bees, *A. koschevnikovi*, arrived fastest at the feeders, and foraged at the canopy feeders, in agreement with Roubik et al. (1995). Such high exploitation of floral resources by honey bees may have affected the guild structure of social bees in the Asian tropics where five honey bee species are native (Seely 1985). Understorey foraging and aggressive defense of flowers seem to be favored under the exploitation by honey bees.

Trade-off

Resource partitioning requires both heterogeneity of resources and trade-offs among foraging traits (Brown 1989; Kotler et al. 1993; Brown et al. 1994). If bees sacrifice advantage in any other foraging traits to obtain aggressive dominance, this trade-off may produce resource partitioning between aggressive and unaggressive species.

Such a trade-off was supported by significant correlation between time of the first arrival and aggressive dominance at feeders. A trade-off between aggressive interference and preemptive exploitation has been observed in ant guilds (Fellers 1987; Hölldobler and Wilson 1990). Similar constraints for bees and ants, foraging for ephemeral patches from central places using communication and recruitment systems, may affect such patterns. Though distances between the feeders and colonies affect the arrival time of foragers, we did not examine whether the distances were associated with interspecific variation in arrival time. In our plot, the colonies clumped on large trunks of trees on ridges, which is in contrast to other observations of stingless bees and ants (Fig. 1; Hubbell and Johnson 1977; Cushman et al. 1988). Because such clumped distribution of colonies derives higher variation of distances from feeders to the nearest colonies, more experiments at various sites are necessary to confirm the trade-off.

There are four possible factors that could cause later arrival of aggressive species at the feeders: (1) long foraging distance due to low density of colonies, (2) small population size of colonies, (3) small allocation of foragers for scouting, and (4) low searching efficiency of individual scouts. Among these, (1) is supported but (2) is rejected by a survey of social bee nests in Sumatra (Salmah et al. 1990). In our plot, colonies of aggressive species, *T. fimbriata* and *T. melina*, found to be nearer to towers where feeder experiments were conducted than some colonies of unaggressive species (Fig. 1). Thus factor 1 could not have caused the later arrival of the aggressive species in the study. Factor 3 seems to play a more important role than the factor 4, if aggressive species have communication and recruitment systems which favor occupation of flower patches. Requirement of recruits and guards to the patches already discovered causes scouts searching newly available patches to be fewer. To examine factors 3 and 4, comparative observations of both organization of foragers and behavior of individuals should be conducted (Inoue et al. 1985).

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