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Teruyoshi Nagamitsu · Kuniyasu Momose · Tamiji Inoue
David W. Roubik

Preference in flower visits and partitioning in pollen diets of stingless bees in an Asian tropical rain forest

Abstract Floral resource partitioning among stingless bees (*Trigona*, Meliponini, Apidae) in a lowland rain forest in Sarawak, Malaysia, was investigated using tree towers and walkways in a 4-year study that included a general flowering period. We obtained 100 collections of insect visitors to flowers of varying floral location and shape representing 81 plant species. The tendency of 11 species of stingless bees to visit specific flowers with a particular floral location and shape was analyzed by logistic regression analysis. This analysis showed that the proportion of flower visitor collections containing *Trigona fuscobalteata* and *T. melanocephala* differed according to floral location. The former was frequently collected at canopy and gap flowers, whereas the latter was most often collected at understory flowers. The analysis also suggested that *T. erythrogastra* was more rarely collected at shallow flowers than at deep flowers. Analysis of the pollen diets of *T. collina*, *T. fuscobalteata*, *T. melanocephala*, and *T. melina* revealed that similarity of pollen sources differed among the six permutated pairs of the four species. The lowest mean rank of similarity found was between *T. fuscobalteata* and *T. melanocephala*. This result supports the hypothesis that preference in visiting flowers in different locations leads to pollen resource partitioning.

Key words Flower visitation · Foraging · Pollen preference · Resource partitioning · Sarawak · *Trigona*

T. Nagamitsu (✉)
Hokkaido Research Center, Forestry and Forest Products Research Institute, 7 Hitsujigaoka, Toyohira, Sapporo 062-8516, Japan
Tel. +81-11-851-4131 (ext. 246); Fax +81-11-851-4167
e-mail: nagamit@ffpri-hkd.affrc.go.jp

K. Momose
Graduate School for Asian and African Area Studies, Kyoto University, Kyoto, Japan

T. Inoue
Center for Ecological Research, Kyoto University, Otsu, Japan

D.W. Roubik
Smithsonian Tropical Research Institute, Balboa, Republic Panama

Introduction

Stingless bees (Meliponini, Apidae, Hymenoptera) are perennial eusocial insects and the most abundant flower visitors in the tropics (Roubik 1989). Many species of stingless bees often coexist in the same habitat even though they depend on common foods, pollen and nectar. Availability of either foods or nest sites limits the colony density of the bees (Hubbell and Johnson 1977; Inoue et al. 1993). However, interference and exploitation by foragers sharing feeding sites reduces the foraging efficiency of stingless bees (Johnson and Hubbell 1974; Roubik 1980; Roubik et al. 1986). Thus, foragers of cooccurring species may compete with each other for pollen and nectar. As a consequence of the competition, floral resource partitioning is expected to occur.

Results from previous field experiments suggest that coexistence of these competing species is fostered by spatial and temporal variation in floral resource availability of certain plant species (Johnson and Hubbell 1975; Hubbell and Johnson 1978; Johnson 1981; Nagamitsu and Inoue 1997). Species that aggressively monopolize feeding sites tend to use clumped flowers, whereas non-aggressive species excluded from the clumped flowers use scattered flowers (Johnson and Hubbell 1975; Johnson 1981). Species that rapidly discover flowers also coexist with species that discover flowers more slowly, but aggressively monopolize flowers used by the rapid flower-discovering species when they eventually locate them (Hubbell and Johnson 1978; Nagamitsu and Inoue 1997).

Such partitioning of common foods in time and space may be a unique feature of eusocial insects, which can evaluate changing resources by communicating the locations of optimal feeding sites (Seely 1985; Davidson 1998). However, there are also other factors that may enable stingless bees to partition floral resources from plant taxa with differing floral traits. First, tropical rain forests are vertically structured, and thus stingless bees may be specialized in visiting flowers in different types of locations in the forest.

Second, flowers of tropical rain forests are morphologically diverse, and stingless bees may be specialized in feeding on nectar and pollen of flowers with particular morphologies. Previous studies on flower visits and pollen diets of stingless bees have not been well designed to detect floral resource partitioning according to flower location and floral morphology (Heithaus 1979; Roubik et al. 1986; Inoue et al. 1990; Martinez-Hernandes et al. 1994; Wilms and Wiechers 1997). Although Roubik (1993) found that *Trigona fulviventris* was more frequently light-trapped in the understory than in the canopy, it remains uncertain whether this finding reflects specialization in foraging for understory flowers or is attributable to other, unknown, factors.

The purpose of this study was to examine floral resource partitioning of stingless bees according to flower location and morphology. This issue remains open mainly because access to the canopy of tropical rain forests is difficult. To resolve this problem, we built two tree towers (one 50 m tall, and the other 55 m) in a lowland rain forest in Sarawak, Malaysia (Inoue et al. 1995). These towers were connected by a series of aerial walkways that extended 300 m through the forest. Using these towers, we have already shown that six species of stingless bees visited honey-water feeders at different heights (Nagamitsu and Inoue 1997). We showed that 2 of 17 coexisting species had much longer tongues than the other species (Nagamitsu and Inoue 1998).

In the study presented here, we collected flower visitors and analyzed the pollen diets of stingless bees in a 4-year research program. To examine whether preference in visiting flowers with different floral traits leads to pollen resource partitioning, we analyzed our data by the following two methods. First, using logistic regression analysis, we evaluated whether flower location and floral morphology affect the tendency of each stingless bee species to visit specific flowers. Second, we examined whether pollen diet similarity was lowest between pairs of species showing the least similar floral preferences.

Materials and methods

Study site

The study was conducted in the Canopy Biology Plot (8 ha, 200 × 400 m) and a belt transect along the Waterfall Trail (5 ha, 1 km × 50 m) established in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20′ N, 113°50′ E; 150–250 m in altitude). At the center of the Canopy Biology Plot, a canopy access system with two tree towers (one 50 m and the other 55 m in height) and nine aerial walkways (total length, 300 m; 15–35 m above ground) was constructed (Inoue et al. 1995; Fig. 1). The Waterfall Trail was located along a stream from the headquarters of the park to the Operation Raleigh Tower, a structure built in a previous research program. In the study site, the flowering phenology of 576 individually marked plants of 310 species was monitored from August 1992. Results from the monitoring show that general flowering occurred from March to December in 1996, when the proportion of flowering individuals among the marked plants continuously exceeded 10% (Sakai et al., in press).

In the study site, 27 species of stingless bees (*Hypotrigona* and *Trigona*, Meliponini, Apidae) were collected (Inoue et al. 1994). In October 1994, 14 colonies of seven stingless bee species were found in the Canopy Biology Plot. In August 1996, the number of colonies increased to 26. We found 10 colonies at trunk bases, 2 in the cavities of tree trunks, and 14 in wooden nest boxes (10 × 10 × 20 cm) located on the tree towers. These boxes had been set in place for another study on population dynamics.

Flower visits

From June 1993 to October 1996, we surveyed flowers every month from the forest floor in the Canopy Biology Plot and along the Waterfall Trail, and every 2 months we surveyed flowers from the canopy access system and from the

Fig. 1. Canopy access system and colonies of stingless bees for which pollen diets were studied in the Canopy Biology Plot. *Closed circles*, colonies studied in both 1994 and 1996; *open circles*, colonies studied only in 1996
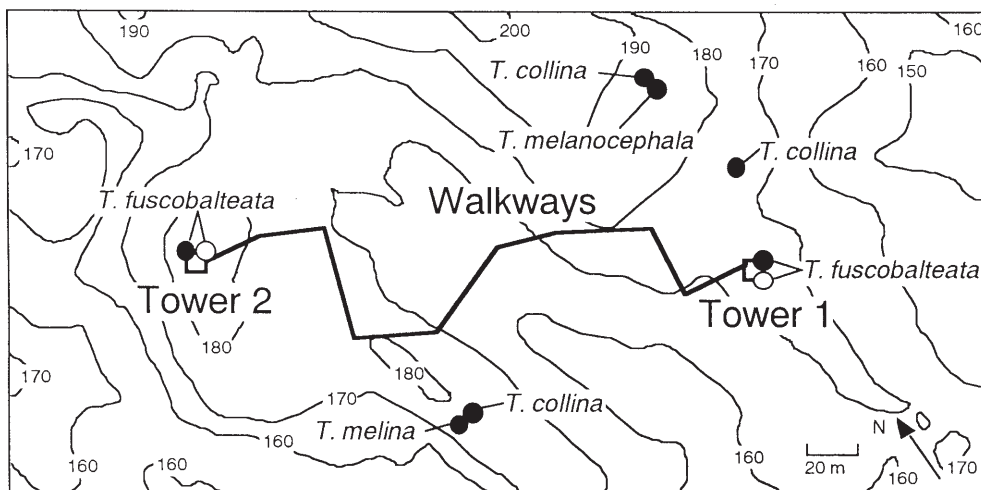
Operation Raleigh Tower. On census days surveys usually started at 0800. When we found flowering plants, we collected flower visitors for at least 10 min at individual flowering plants. At first, we caught visitors flying around and coming to flowers, and later we swept completely visitors on and in flowers. When few flower visitors were collected, we collected additional visitors at various times on following days until the plants finished flowering. Among the collected flower visitors, we examined only stingless bees in the present study. Stingless bee specimens were pinned and identified following the classifications of Schwarz (1939), Sakagami (1975, 1978), and Sakagami et al. (1990). We designated each group of collected individuals of stingless bees visiting flowers of each plant species in each year as 'a collection.'

Specimens of surveyed flowering plants were collected and identified in SAR (Sarawak Herbarium, Forest Department, Sarawak). We recorded the location, shape, and color of flowers of each surveyed plants, following the methods of Momose et al. (1998). The locations of the flowers in the forest structure were divided into three categories: (1) understory (<12.5 m high in the closed forest), (2) canopy (≥ 12.5 m high, above the understory), and (3) gap (outside the closed forest). Flower shape was classified as either shallow (cup, rotate, or brush-shaped), or deep (including papilionaceous, *Caesalpinia*-like, campanulate, bilabiate, urceolate, tubular, and chamber shapes). Floral color was categorized as (1) white and green, (2) yellow, or (3) reddish (including orange, brown, red, pink, and purple).

Logistic regression analysis was performed to examine effects of floral traits on the tendency of each stingless bee species to visit specific flowers (SAS Institute 1994). Effects of flower location, L, and shape, S, on the proportion of collections, P_i, containing at least one individual of stingless bee species, i, was tested. We added effects of flower color, C, and collection year, Y, to models of the analysis as block factors. Collection years were grouped into (1) 1993–1995, before the general flowering and (2) 1996, when the general flowering occurred. A linear model of the analysis is given by

$$\text{logit}(P_i)_{klmn} = \mu_i + Y_k + L_l + S_m + C_n$$
$$(k = 1,2; \; l = 1,2,3; \; m = 1,2; \; n = 1,2,3)$$

where μ_i is mean logit-transformed proportion of collections that contained stingless bee species, i. We tested the null hypotheses that flower location and shape had no effect:

$$H_0: L_1 = L_2 = L_3 = 0, \text{ and}$$
$$H_0: S_1 = S_2 = 0$$

by Wald's χ^2 test. The probabilities of type I error were adjusted by the sequential Bonferoni method for multiple tests for i species (Sokal and Rohlf 1981).

Pollen diets

On June 22–23, August 10–13, and September 17–19, in 1994 before the general flowering, and on May 15–18,

August 4–8, and 19–23 August, in 1996 during the general flowering, we collected pollen loads carried by returning foragers from three colonies of *Trigona collina*, two colonies of *T. fuscobalteata*, one colony of *T. melanocephala*, and one colony of *T. melina* in the Canopy Biology Plot (see Fig. 1). We also studied two additional colonies of *T. fuscobalteata* in 1996. We collected pollen loads of returning foragers with hand nets at 0730, 1030, and 1430 on single days in front of a nest entrance to each colony, which was closed by a cotton cloth for the preceding 20 min.

After the standard procedure of acetolysis (Erdtman 1960), 200 pollen grains from each forager were examined and classified by morphology into taxonomically distinct pollen types (Huang 1972; Roubik and Moreno 1991; Tissot et al. 1994). We regarded the most abundant types of pollen as legitimate pollen sources of the foragers.

We obtained the number of foragers, N_{ijk}, of stingless bee species, i, with pollen type, j, of legitimate pollen source in collection period, k. We then calculated Morishita's similarity index (Morishita 1959), $C_{\lambda kl}$, in period, k, for pair, l, ($l = 1$–6) of species, i and i', as follows:

$$C_{\lambda kl} = 2\sum_j \left(N_{ijk} N_{i'jk}\right) \Big/ (\lambda_i + \lambda_i') \sum_j (N_{ijk}) \sum_j (N_{i'jk})$$
$$\lambda_i = \sum_j \left\{ N_{ijk}(N_{ijk} - 1) \right\} \Big/ \sum_j (N_{ijk}) \left\{ \sum_j (N_{ijk}) - 1 \right\}$$
$$\lambda_i' = \sum_j \left\{ N_{i'jk}(N_{i'jk} - 1) \right\} \Big/ \sum_j (N_{i'jk}) \left\{ \sum_j (N_{i'jk}) - 1 \right\}$$

We tested a null hypothesis that there were no differences in the similarity indices among the species pairs, H_0: $C_{\lambda 1} = C_{\lambda 2} = C_{\lambda 3} = C_{\lambda 4} = C_{\lambda 5} = C_{\lambda 6}$, by Friedmann's test.

Results

Flower visits

From June 1993 to October 1996, we obtained a total of 100 collections of stingless bees visiting flowers (of 81 plant species representing 37 plant families; see Appendix), which were classified according to floral location, shape, and color (Table 1). These collections consisted of 3279 stingless bees of 21 species (Table 2). *Trigona itama* was the most abundant species (comprising 1016 individuals), although *T. fuscobalteata* was most frequently collected, appearing in 34 of the 100 collections. We examined 11 stingless bee species that appeared in more than 10 collections in the following analysis.

The linear model of logistic regression analysis was not rejected for any species, suggesting that there were negligible interactions among year, location, shape, and color (Table 3; Wald's χ^2 test, $P > 0.930$, adjusted by the sequential Bonferoni method for results of tests for the 11 species). The effects of flower location on the proportion of collections containing *T. fuscobalteata* and *T. melanocephala* were significant ($P = 0.045$ and 0.002, respectively, adjusted as above). *T. fuscobalteata* was frequently collected at canopy and gap flowers, whereas *T. melanocephala* often

Table 1. Sample numbers in collections of stingless bees visiting flowers representing three types of location, two types of shape, and three types of color

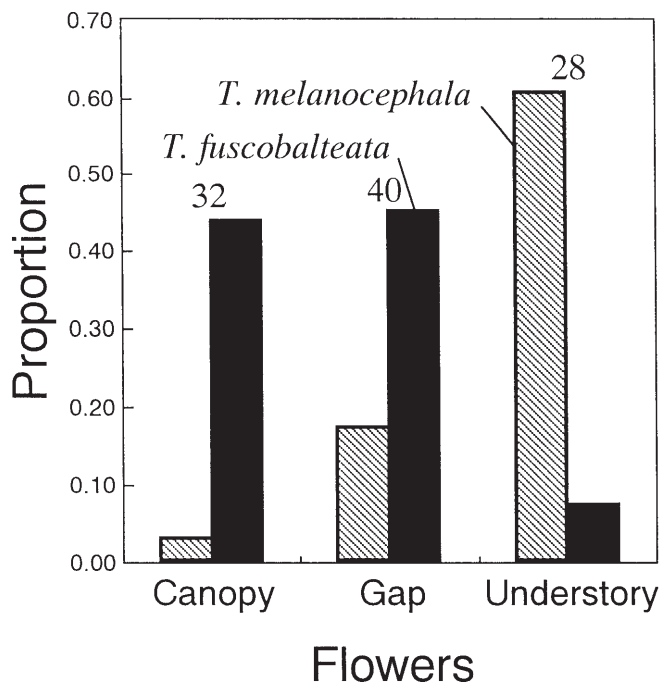| Shape	Color	1993–1995			1996			Subtotal	Total
		Canopy	Gap	Understory	Canopy	Gap	Understory		
Deep	White and green	1	0	4	4	1	2	12	
	Yellow	0	2	1	1	0	0	4	
	Reddish	2	9	5	2	2	1	21	37
Shallow	White and green	3	9	5	6	1	3	27	
	Yellow	3	7	3	8	2	1	24	
	Reddish	0	6	1	2	1	2	12	63
Subtotal		9	33	19	23	7	9		
Total				61			39		100

Table 2. Stingless bee species found in 100 collections of flower visitors, showing the numbers of collected individuals and the number of collections including each stingless bee species

Stingless bees	Code	No. of bees	No. of collections
Species			
Trigona fuscobalteata	fus	380	34
T. itama	ita	1016	32
T. laeviceps	lae	74	26
T. melanocephala	mla	58	25
T. apicalis	api	151	22
T. erythrogastra	ery	113	18
T. ventralis	ven	278	17
T. fimbriata	fim	310	16
T. canifrons	can	405	15
T. collina	col	186	14
T. melina	mli	30	13
T. nitidiventris		45	9
T. rufibasalis		29	7
T. thoracica		28	6
T. reepeni		11	6
T. terminata		46	5
T. haematoptera		46	4
Hypotrigona scintillans		8	4
T. melanoleuca		34	2
T. moorei		29	2
T. geissleri		2	2
Total		3279	

Fig. 2. Proportion (*bars*) of collections containing *Trigona fuscobalteata* and *T. melanocephala* individuals visiting canopy, gap, and understory flowers. The *number* of collections of stingless bees visiting flowers at each type of location is shown

appeared in collections from understory flowers (Fig. 2). An effect of flower shape on the proportion of collections that contained *T. erythrogastra* was marginally significant ($P = 0.079$, adjusted as above). *T. erythrogastra* was more often collected at deep flowers than at shallow flowers (Fig. 3).

Pollen diets

We collected pollen loads from 104, 105, and 65 foragers in three periods in 1994, and from 124, 148, and 147 foragers in three periods in 1996. In pollen loads from the 693 foragers sampled, 102 types of pollen grains were morphologically distinguishable. Among the 102 types of pollen, 55 were identified to the plant family level. The most abundant family was Euphorbiaceae, observed in pollen loads from 198 foragers, followed by Araceae (52), Annonaceae (51), and Leguminosae (38). The main pollen sources differed among the stingless bee species studied. Among 211 foragers of *T.*

fuscobalteata, 132 collected pollen from euphorbiaceous species. Pollen from species of Araceae, Annonaceae, and Leguminosae was collected by 49 of 135 *T. melina* foragers, 41 of 121 *T. melanocephala* foragers, and 37 of 226 *T. collina* foragers, respectively.

The analysis of flower visits (see earlier) suggested that among the four species of which pollen diets were examined, *T. fuscobalteata* and *T. melanocephala* preferred flowers in the most divergent locations. Thus, if differences in flower location preference causes partitioning between plant taxa acting as pollen sources, the pollen diet should be less similar between *T. fuscobalteata* and *T. melanocephala* than those between any of the other five permutated pairs from the four species.

In accordance with this hypothesis, pollen diet similarity significantly differed among the six permutated pairs of the four stingless bee species (Friedmann's test, $P = 0.048$), and

Table 3. Results of logistic regression analysis testing effects of collection year, flower location, flower shape, and flower color on the proportion of collections including each stingless bee species

	Stingless bee species										
	fus	ita	lae	mla	api	ery	ven	fim	can	col	mli
Year	0.737	0.869	0.973	0.361	0.832	0.600	0.849	1.000	0.982	0.991	0.529
Location	0.045	0.152	0.694	0.002	0.833	0.620	0.732	1.000	—	0.641	0.918
Shape	0.978	1.000	0.894	0.755	0.272	0.079	0.974	0.999	1.000	1.000	1.000
Color	0.999	0.632	0.994	1.000	0.631	1.000	—	0.858	1.000	0.999	1.000
Model	0.984	0.930	1.000	1.000	0.998	0.944	1.000	0.986	0.986	1.000	0.993

—, No test was done because no corresponding samples were collected
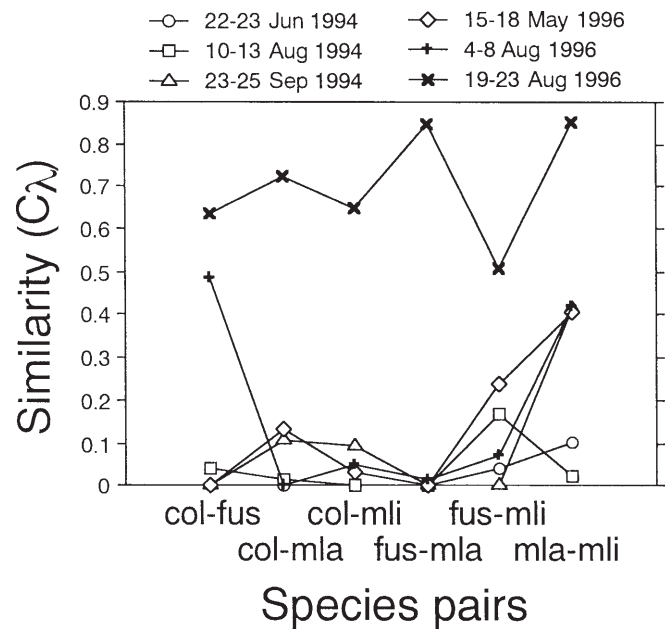Species codes are shown in Table 2. The probabilities of type I errors occurring, adjusted by the sequential Bonferoni method for the four factors and linear models of the analysis, are also shown
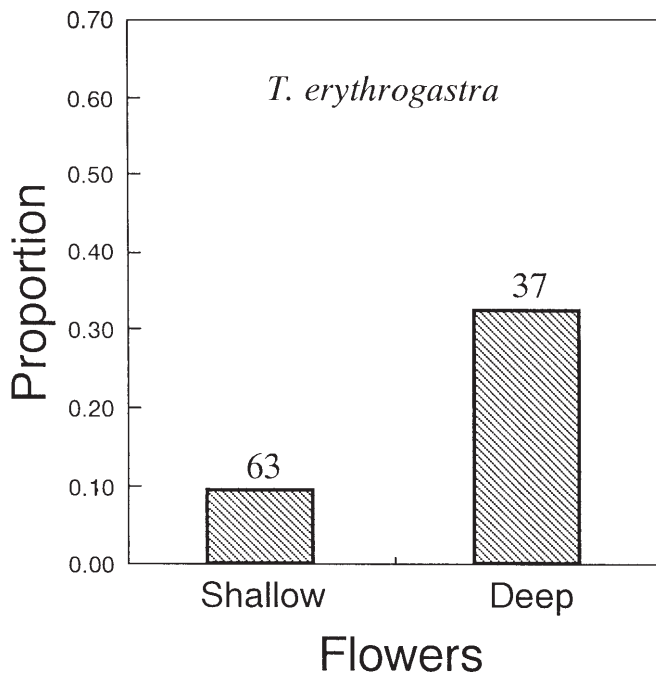
Fig. 3. Proportion (*bars*) of collections containing *Trigona erythrogastra* individuals visiting shallow and deep flowers. The *number* of collections of stingless bees visiting flowers of each type of shape is shown

Fig. 4. Pollen diet similarity measured by Morishita's similarity index, C_λ, between pairs of four stingless bee species. Species codes are as shown in Table 2. Similarities were found in three periods in 1994 and in three periods in 1996

the mean rank of the *T. fuscobalteata* and *T. melanocephala* pairing was lowest in the pollen diet similarity (Fig. 4). However, the range of similarity strongly shifted, from 0.00–0.10 during June 22–23, 1994 to 0.51–0.85 during 19–23, August 1996. In all test periods, except for 19–23, August 1996, when the pollen diet similarity of every pair was extremely high, the similarity between *T. fuscobalteata* and *T. melanocephala* was less than 0.02, indicating almost complete partitioning of pollen sources. Thus, the foregoing prediction was largely supported.

Discussion

Floral resource partitioning has been proposed to occur among stingless bee species, because foragers of these species are likely to compete for pollen and nectar (Johnson and Hubbell 1974; Roubik 1980; Roubik et al. 1986). Available evidence so far accumulated suggests that stingless bee species are able to partition floral resources of the same plant species through temporal and spatial variation in the floral resources (Johnson and Hubbell 1975; Hubbell and Johnson 1978; Johnson 1981; Nagamitsu and Inoue 1997). Pollen and nectar sources of diverse plant species are thus shared among stingless bee species (Heithaus 1979; Roubik et al. 1986; Inoue et al. 1990; Martinez-Hernandes et al. 1994; Wilms and Wiechers 1997).

Stingless bees have also been regarded as generalists in floral resource use that rarely specialize in particular plant taxa with unique floral traits. However, several lines of evidence suggest that floral resource partitioning according to flower location and morphology does occur (Roubik 1993; Nagamitsu and Inoue 1997, 1998). The results presented here show that two stingless bee species visited flowers in different types of locations within the forest structure,

and suggest that these two species did partition pollen according to taxonomic source. Further, one species visited morphologically specialized flowers with enclosed petals, although this result was only marginally significant. These results suggest that floral resource partitioning of stingless bees arises not only from variation in floral resources within plant species, but also from variation in floral traits among plant species.

The observed preference of *Trigona melanocephala* for visiting understory flowers is consistent with our previous observation that this species tended to visit the lowest among honey-water feeders placed at heights ranging from 1 to 50 m above ground level (Nagamitsu and Inoue 1997). However, height above the ground alone cannot explain the different preferences for gap and understory flowers at similar heights. Factors common to both the canopy and gap, but differing in the understory, may affect the observed preference in visiting flowers in different locations.

Possible factors involved include environmental conditions, such as solar radiation, air temperature, and relative humidity, which vary between sunny (canopy and gap) and shaded (understory) places in tropical rain forests. Willmer and Corbet (1981) showed that stingless bee species visiting *Justicia aurea* flowers differed between sunny and shaded places. *T. ferricauda* and *T. jaty* preferred flowers in sunny places, whereas those in shaded places were visited by *T. fulviventris*, which was also more often trapped in the understory than in the canopy in another light trap study (Roubik 1993). This evidence supports the hypothesis that environmental factors that differ between sunny and shaded places affect preference in flower location in the forest structure.

The present results suggest that *T. erythrogastra* preferred complex flowers with enclosed petals to simple flowers with a cup, rotate, or brush shape. The nectar of complex flowers with nectaries concealed by petals is efficiently imbibed only by bees with long tongues (Harder 1983). Our previous analysis of the morphology of 17 stingless bee species, some of which were examined in the present study, showed that *T. erythrogastra* has an extremely long tongue relative to its body size (Nagamitsu and Inoue 1998). This match between the morphology of *T. erythrogastra* and the shape of flowers visited by the species suggests that partitioning of nectar sources arises from variation in floral morphology. However, nectar resource partitioning is difficult to examine, because the taxonomic status of nectar sources is difficult to identify from nectar brought to colonies. In contrast, the taxonomy of pollen sources can be readily distinguished by the morphology of pollen grains brought to colonies.

The results also show that two stingless bee species with different preferences in flower location shared few plant taxa as pollen sources in most periods studied. The quantitative comparison of pollen diet similarity with previous studies is difficult because of the qualitative evaluation of pollen diets used in some previous studies (Appanah et al. 1986; Roubik et al. 1986; Martinez-Hernandes et al. 1994; Wilms and Wiechers 1997). However, this is the first study to find so few pollen sources shared among species. Further,

the results obtained in this study show that pollen diet similarity varied considerably, both seasonally and annually. There was a period when pollen diet similarity was extremely high between all pairs of studied stingless bee species. This result suggests that pollen resource partitioning depends on pollen resource availability, which seemed to fluctuate during this study because of the general flowering that occurred in 1996. However, we did not evaluate temporal changes in floral resource abundance and foraging efficiency in the present study. These issues remain to be addressed in further studies.

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Appendix. Plant species of flowers visited by stingless bees

Plant		Floral trait			Collection code				No. of collection
Family	Species	L	C	S	1993	1994	1995	1996	
Anacardiaceae	*Buchanania sessilifolia*	u	w	d				62	1
Annonaceae	*Enicosanthum coriaceum*	u	w	d				63	1
	Enicosanthum macranthum	u	w	d	1	34			2
	Polyalthia cauliflora	u	y	d	2				1
	Uvaria elmeri	u	w	s		35			1
Ascrepiadaceae	*Gongonema*	g	y	s	3				1
Burseraceae	*Dacriodes laxa*	c	r	s				64	1
	Santiria laevigata	c	w	s	4			65	2
Celastraceae	*Lophopetarum glabrum*	c	r	s				66	1
Compositae	*Eupatrium odoratum*	g	w	s		36			1
	Mikania micrantha	g	w	s	5				1
	Vernonia arborea	g	w	s				67	1
Convolvulaceae	*Ipomoea pes-carpae*	g	r	d	6				1
Cyperaceae	*Carex* sp.	g	w	s	7	37			2
Dilleniaceae	*Dillenia exelsa*	g	y	s				68	1
	Dillenia suffruticosa	g	y	s	8				1
Dipterocarpaceae	*Dryobalanops aromatica*	c	w	d				69	1
	Dryobalanops lanceolata	c	w	s	9				1
	Shorea beccariana	c	y	s				70	1
Elaeocarpaceae	*Elaeocarpus stipula*	g	w	s	10				1
Euphorbiaceae	*Cleistanthus pseudopodocarpus*	c	y	s	11				1
	Cleistanthus sumatranus	c	y	s				73	1
	Dimorphocalyx denticulatum	u	r	s				74	1
	Drypetes longifolia	u	w	s	14	38	51		3
	Drypetes xanthophyloides	u	w	s				75	1
	Homalanthus populneus	g	y	s	15	39			2
	Koilodepas laevigatum	c	y	s	16			76	2
	Macaranga winkleri	g	w	s			52		1
	Mallotus grifithii	u	y	s				77	1
	Mallotus penangensis	c	y	s	12			71	2
	Mallotus wrayi	u	y	s	13				1
	Tapoides sp.	c	w	s				72	1
Fagaceae	*Lithocarpus lucidus*	g	y	s				78	1
Gesneriaceae	*Didisandra* sp.	u	w	d	17	40			2
Guttiferae	*Mesua oblongifolia*	u	w	s				79	1

Appendix. *Continued*

Plant		Floral trait			Collection code				No. of collection
Family	Species	L	C	S	1993	1994	1995	1996	
Hypericaceae	*Cratoxylum sumatranum*	g	r	s		41	53		2
Lauraceae	*Litsea* sp.	u	w	s				80	1
Leguminosae	*Acacia mangium*	g	y	s		54			1
	Callerya nieuwenhuisii	g	r	d	18			81	2
	Cassia sp.	g	y	d	19				1
	Fordia splendissima	u	r	d	20			82	2
	Mimosa pudica	g	r	s		42			1
	Peltophorum pterocarpum	g	y	d		43			1
	Sindora beccariana	c	r	d	21		55		2
	Sindora irpicina	c	r	d				83	1
	Spathorobus ferrugineus	g	r	d				84	1
Melastomataceae	*Melastoma beccarianum*	g	r	d	22	44			2
	Melastoma malabatricum	g	r	d	23	45	56		3
	Memecyron sp.	g	r	s				85	1
	Pternandra multiflora	g	y	s	24		57		2
Meliaceae	*Walsura* sp.	c	w	s				86	1
Musaceae	*Musa campestris*	g	r	d		46			1
Myrtaceae	*Eugenia* sp.	c	w	s		47			1
	Eugenia subrufa	c	w	s				87	1
Olacaceae	*Anacolosa frutescens*	u	r	s	25				1
	Scrodocarpus borneensis	c	w	d			58		1
Palmae	*Calyota* sp.	u	y	s	26				1
Ponteridaceae	*Monochoria* sp.	g	r	s			59		1
Rhamnaceae	*Ventilago malaccensis*	c	y	s				88	1
Rubiaceae	*Ixora woodii*	u	r	d	27	48	60		3
	Uncaria longifolia	g	w	d				89	1
Rutaceae	*Glycosmis* sp.	u	y	s	28				1
Sapindaceae	*Nephelium cuspidatum*	c	w	s				90	1
	Pometia pinnata	c	w	s				91	1
Simaroubaceae	*Quassia borneensis*	c	y	s				92	1
Sterculiaceae	*Heritiera borneensis*	c	w	d				93	1
	Pterocymbium tubulatum	c	w	d				94	1
	Scaphium borneensis	c	w	d				95	1
	Scaphium longipetiolatum	c	r	d				96	1
	Sterculia stipulata	u	r	d	29				1
Theaceae	*Eurya acuminata*	g	w	s		49			1
Tiliaceae	*Grewia latistipula*	c	y	s				97	1
	Grewia stylocarpa	c	y	s				98	1
Ulmaceae	*Trema tomentosa*	g	w	s	30				1
Urticaceae	*Dendrocnide stimulans*	u	w	s	31				1
	Pipturus argentens	g	w	s	32				1
Verbenaceae	*Calicarpa havirandii*	g	r	s		50			1
	Calicarpa pendula	g	r	s			61		1
	Clerodendron megaphyla	u	r	s				99	1
	Stachytapheta indica	g	r	d	33				1
Xanthophyllaceae	*Xanthophyllum velutinum*	c	y	d				100	1
Total					33	17	11	39	100

L, location; c, canopy; g, gap; u, understory; C, color; w, green and white; y, yellow; r, reddish; S, shape; s, shallow; d, deep

Floral traits (L, location; C, color; S, shape) are shown for each plant species. Collections of stingless bees visiting flowers of each plant species are shown for each study year