

Spatio-temporal variation of apine bee attraction to honeybaits in Bornean forests

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Abstract: The abundance and species richness of highly social bees (Apinae: Meliponini, Apini) were studied at 12 dipterocarp forest sites in Sabah, northern Borneo, using standardized honey-water baiting assays. The 12 sites were grouped in five localities varying in the degree and history of disturbance from selective logging. A baiting assay consisted of spraying diluted honey on vegetation along transects and recording bee arrival on the same day. Repeated assays of the same sites were run in two consecutive years, 1998 and 1999. One-way repeated-measures ANOVAs were calculated on bee abundance and species richness, with locality and year as independent factors. There were significant or marginally significant effects of forest locality on all measures of bee abundance and species richness. However, there were also significant interactions between year and locality on these variables, thwarting conclusions on the effects of logging on bee communities. The diverging results of the two years are likely related to spatio-temporal variation of flowering activity prior to and during the assays, with between-year differences being amplified by pronounced differences in climatic conditions (ENSO). Local or regional differences in flowering phenology complicate the application of resource-based baiting techniques for between-site comparisons of bee diversity.

Key Words: Apinae, bee diversity, forest disturbance, Meliponini, survey, *Trigona*

INTRODUCTION

Highly social honeybees (Apidae: Apini) and stingless bees (Meliponini) are the predominant group of flower-visiting insects and likely pollinators in both Old and New World tropical forests (Appanah 1990, Heithaus 1979a, b; Inoue *et al.* 1990, Momose *et al.* 1998, Roubik 1979). In lowland Borneo long-term observations have suggested that approximately one third of all plant species in the forest canopy and understorey are pollinated by apid bees (Momose *et al.* 1998). Forest fragmentation as well as alteration of forest structure after selective logging may potentially reduce social bee populations and disrupt plant-pollinator interactions of forest plants (Ghazoul *et al.* 1998). Thus, measuring disturbance effects on apid bee populations is important with respect to tropical forest conservation.

How to measure apid bee abundance and species richness in a forest? The number of nests per area

(nest density) has been used successfully for between-site comparisons of meliponine population density in Sabah, Malaysia (Eltz *et al.* 2002). However, the value of nest surveys is limited because of the major effort required in finding sufficient numbers of cryptic nests. Also, nest surveys are generally prone to miss nests located in or close to the forest canopy (Eltz *et al.* 2003). Alternative methods involve censusing foraging bees at natural or artificial resources. Flower monitoring has been used to study bee communities in selected locations in the Neotropics (Heithaus 1979a, Wilms *et al.* 1996). In a comparative approach Rincon *et al.* (1999) surveyed understorey bees at flowers in logged and silviculturally treated rain-forest plots in Costa Rica. The results may be symptomatic for problems implicit with the use of flower monitoring: numbers of species and individuals of bees strongly depended on numbers of flowering plants present in plots at the time of the study, but not on plot treatment (Rincon *et al.* 1999). Due to the spatial and temporal variation in flowering, flower monitoring for between-site assessment of bee diversity is bound to require large effort over extensive periods of time. Additional problems arise from restricted access to the forest canopy where most

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flowering is likely to occur (Appanah 1990, Momose *et al.* 1998).

Honey-water baiting, introduced by Wille (1962), may represent a more feasible alternative. The method consists of spraying diluted honey (honey-water) on ground-level vegetation. Bees, mostly highly social species, and other flower-visiting insects arrive after minutes or hours and consume droplets from leaves. In contrast to monitoring bees at natural flowers, honey-water spraying is more easily standardized and equally applicable under a wide range of habitat conditions. A number of studies have used the method for surveying bees (Liow *et al.* 2001, Roubik 1996, Salmah *et al.* 1990). Of those, Roubik's (1996) survey was confined to a single forest site (Belalong, Brunei) at a single point in time. Liow *et al.* (2001) applied honeybaits in different forest and plantation localities in Singapore and found a tendency for higher apine bee abundance in larger primary forests. Salmah *et al.* (1990) used honey-water spraying to study apine bee diversity along altitudinal and disturbance gradients in fragmented landscapes of Sumatra. Combining data from flower monitoring with those of honey-water spraying, the results suggest that high species richness and abundance was associated with the proximity of primary forest habitats (Salmah *et al.* 1990). None of the studies attempted to analyse multiple spatial replicates within forest localities, thus limiting the conclusions that can be drawn with regard to disturbance effects. Equally, no study has so far attempted to quantify the influence of temporal fluctuations of baiting results in relation to the amount of spatial variation found. Here I present the results of a baiting project in Sabah, Malaysia, that surveyed apine bees in a range of primary and logged dipterocarp forests. The assays were repeated in two consecutive years.

METHODS

Stingless bees were studied at a total of 12 research sites that can be grouped according to locality (Figure 1) and, depending on locality, their history and intensity of logging.

Danum Valley: Two sites (L, M). The Danum Valley Conservation Area (DVCA) in central Sabah covers 43 800 ha of undisturbed dipterocarp forest (Marsh & Greer 1992). Both sites are surrounded by large tracts of continuous forest with distances of more than 5 km to forest clearings in all directions.

Sepilok: One site (K). The Kabili–Sepilok Forest Reserve is a coastal forest fragment of 4294 ha, covered by dipterocarp forest on elevated ground (Fox 1973). Site K is situated in the north of the reserve, approximately 500 m distant from the forest edge, and the area in and around it has never been logged.

Deramakot: Deramakot Forest Reserve is a 55 000 ha commercial forest estate in central Sabah (60 km north of Danum Valley). The entire area has been subject to timber extraction since 1956 (Chai & Amin 1994) and harbours a wide range of logged-over dipterocarp forests with varying degree and history of disturbance. I selected three replicate sites in each of three localities within Deramakot that were distinct in residual forest stand structure.

Deramakot-Central: Three sites (A, B, C) covered by old, slightly disturbed forests that were logged once with low impact between 1974 and 1976.

Deramakot-East: Three sites (D, E, F) covered by old, heavily disturbed forests that were intensively logged once or twice between 1968 and 1970.

Deramakot-North: Three sites (G, H, I) covered by young, heavily disturbed forests that were intensively logged up to three times between 1980 and 1989.

Analyses presented elsewhere (Eltz 2001, Eltz *et al.* 2002) have demonstrated significant differences in forest structure between the different forest localities. Generally, the presence of larger trees decreased from primary forests towards more heavily and more recently disturbed sites, whereas the abundance of *Macaranga* pioneer trees increased in the same direction. In all sites one set of four parallel 600-m transects was established, each separated by 200 m from neighbouring transects (Figure 1). Sites were separated from each other by distances of 1 km or more with the exception of G and I, which were separated by only 600 m. An individual baiting assay consisted of spraying 30 marked spray stations positioned along a pair of two neighbouring transects of a given forest site. A 33% (volume) honey-water solution was prepared for spraying, using honey of a single major Australian brand. At each spray station 10 jets (~150 ml) of honey-water from a custom-made insecticide vaporiser were sprayed on a patch of vegetation, adding up to a total of 4.5 l of honey-water per assay. Spraying started between 08h00 and 09h00 and was completed after approximately 90 min, the duration of a walk around one 600 × 200-m rectangle. Bees were recorded at the spray stations during a second circuit that started 150 min after spraying was initiated, and was completed within 240 min. This time schedule had proven to yield maximal numbers of species and individuals of stingless bees during previous tests. Usually bees could be identified directly at the stations. In uncertain cases vouchers were collected and later identified using published keys and descriptions (Rinderer *et al.* 1989, Ruttner *et al.* 1989, Sakagami 1978, Sakagami & Inoue 1985, Sakagami *et al.* 1990, Schwarz 1937, 1939), as well as reference material provided by D. W. Roubik. At each spraying station numbers of individuals of each species were counted or estimated and recorded in five abundance classes: 1, 2–5, 6–20, 21–50, > 50 individuals. Honey-spraying was generally

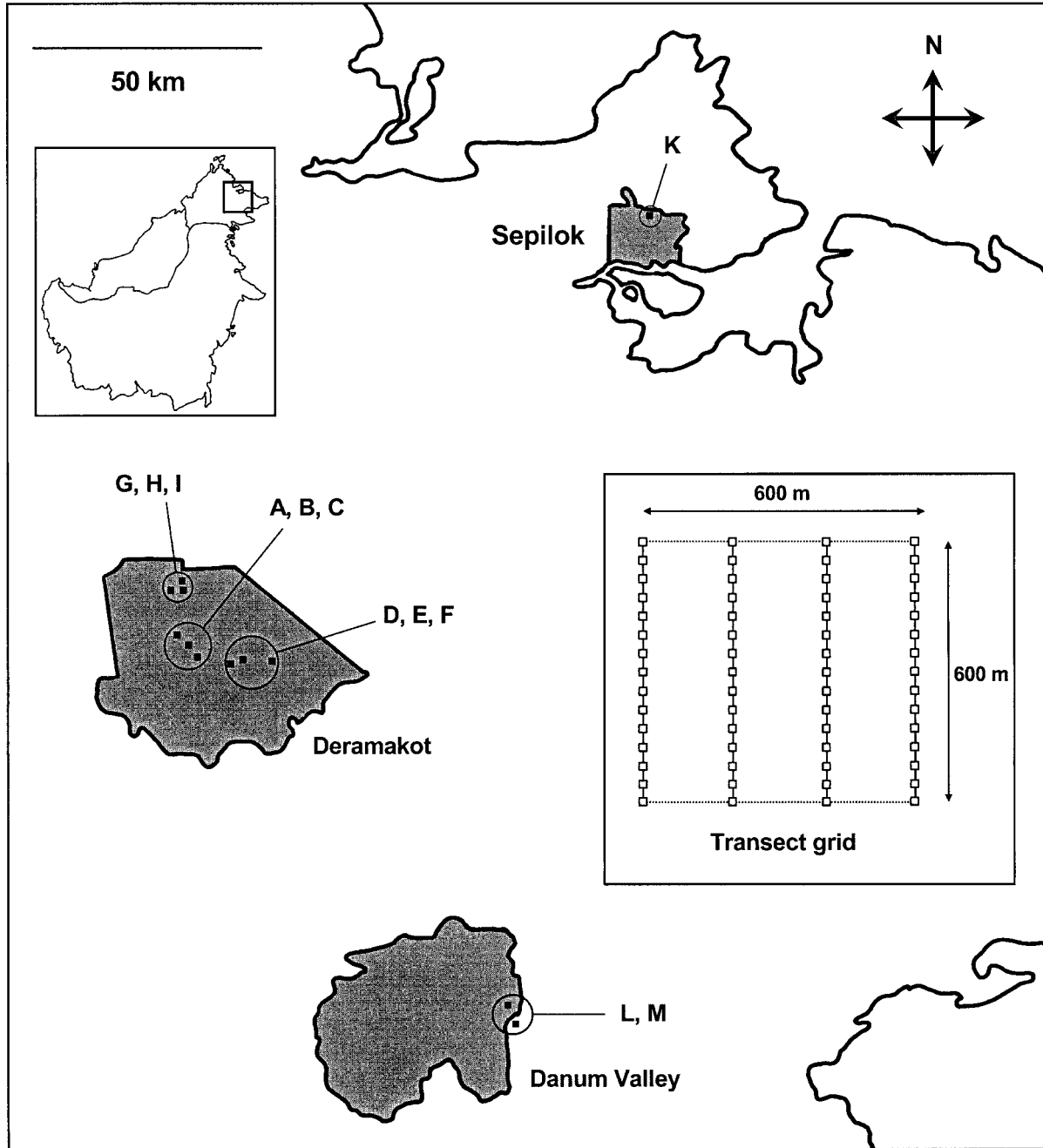


Figure 1. Map of eastern and central Sabah (Malaysia), northern Borneo, showing the 12 forest sites grouped within five localities differing in the degree and history of disturbance from logging (see Methods). Grey areas are the Kabil–Sepilok Forest Reserve, Deramakot Forest Reserve and the Danum Valley Conservation Area. The larger insert shows a schematic view of the transect grids established in each forest site (with small squares representing honey-water spray stations).

restricted to clear or only slightly cloudy days. In case of afternoon rainfall before completion of the assay, the data were discarded and the assay was repeated on a different day.

Using this sampling regime all pairs of transects of all forest sites were sampled once between February and May in 1998. Repeated spraying of a subset (one transect pair per site) was done between February and May in 1999.

In 1999, transect pairs of selected sites (A, C, E, G, M) were sprayed repeatedly over the entire field season. For those, means of measured parameters were calculated across temporal replicates. The following measures of bee diversity and abundance were analysed: the number of bee species per transect pair (species richness), the mean number of bee species per spray station (species incidence), and the mean number of bee individuals per spray station

Table 1. Results of analysis of variance (repeated-measures design) on species richness and abundance of apine bees at honeybaits. See text for details.

Effect	df	F	P
Total number of species per site (species richness)			
Locality	4, 7	3.91	0.056
Year	1, 7	8.68	0.022
Locality × year	4, 7	5.62	0.024
Mean number of species per bait (species incidence)			
Locality	4, 7	6.38	0.017
Year	1, 7	3.26	0.114
Locality × year	4, 7	7.07	0.013
Mean number of individuals per bait (abundance)			
Locality	4, 7	4.97	0.032
Year	1, 7	3.39	0.108
Locality × year	4, 7	4.46	0.042

(abundance; calculated conservatively by averaging the lower bounds of the abundance classes described above). Data of neighbouring pairs of transects (within a given site) were not considered independent samples because they very likely shared bees from overlapping sets of colonies. Therefore, statistical analysis was confined to a single pair per site, specifically the one that was replicated in both years. An ANOVA with a repeated-measures design was used to test for effects of locality (five levels, see above) and year (two levels) on bee diversity and abundance.

RESULTS

Species richness and abundance of social bees

A total of 16 species of stingless bees (including one undescribed form, see Table 2) and four species of honeybee were attracted to honey-water spray stations. Of those, the giant honeybee *Apis dorsata* (Fabricius) was excluded from further analysis because its presence and abundance was probably influenced by patterns of regional migration (Dyer & Seeley 1994). Species richness, species incidence and the abundance of the remaining species in the different sites are presented in Figure 2. Across the two years there were significant or marginally significant effects of forest locality on all three measures of bee richness (Table 1), an effect that was almost exclusively based on the large differences in 1998. There was also significant interaction between the factors 'locality' and 'year' in their effects on the three variables (Table 1). Obviously, the temporal fluctuation of stingless bee numbers was at least as strong as between-

locality effects in 1998. Changes between years were most striking in the primary sites of Danum and Sepilok: whereas honey-spraying produced very large numbers of species and individuals in 1998, corresponding spray stations were almost devoid of bees 1 y later.

Honeybees of the genus *Apis* were generally present at many spray stations (see Table 2), but represented only a small fraction of the individuals and species encountered. Although no separate tests were done, there appeared to be relatively little between-year variation in honeybees as compared with stingless bees.

Community composition

The extreme differences between our findings in 1998 and 1999 suggests that combining information from the two years will not increase the accuracy of how real bee communities are reflected by the data. Therefore, I refrain from further statistical analysis of community composition and total species richness. For comparative purposes a list of species encounter frequencies, pooled for localities and over both years, is given in Table 2.

DISCUSSION

Although there was an overall effect of forest locality on apid bee diversity and abundance in this study, the conclusiveness of the result is clearly reduced by large inconsistencies between years. Whereas the two primary localities were much richer in species and individuals than disturbed forests in 1998, they were comparatively poor in 1999. What are the reasons for these between-year effects? Do the data reflect true shifts in bee diversity and abundance in the respective localities? Two lines of evidence suggest that apid bee numbers at spray stations are not a close correlate of the number of bee colonies present in the habitat. First, stingless bee incidence or abundance of this study is not congruent with data on stingless bee nest density collected in the same sites during a previous study (Eltz *et al.* 2002). Using quantitative nest surveys Eltz *et al.* (2002) found that meliponine population density was very high in edge situations like Sepilok K, but low in all continuous forests including those in primary Danum Valley, a finding that was clearly not paralleled in the honey-baiting study. Second, the drop in the number of baited bees between 1998 and 1999 was not accompanied by extreme rates of nest mortality. On the whole, meliponine bee colonies were relatively stable between 1997 and 2000, showing yearly mortalities below 15% (Eltz *et al.* 2002).

I hypothesize that the observed spatio-temporal variation of bee visits observed in this study is created

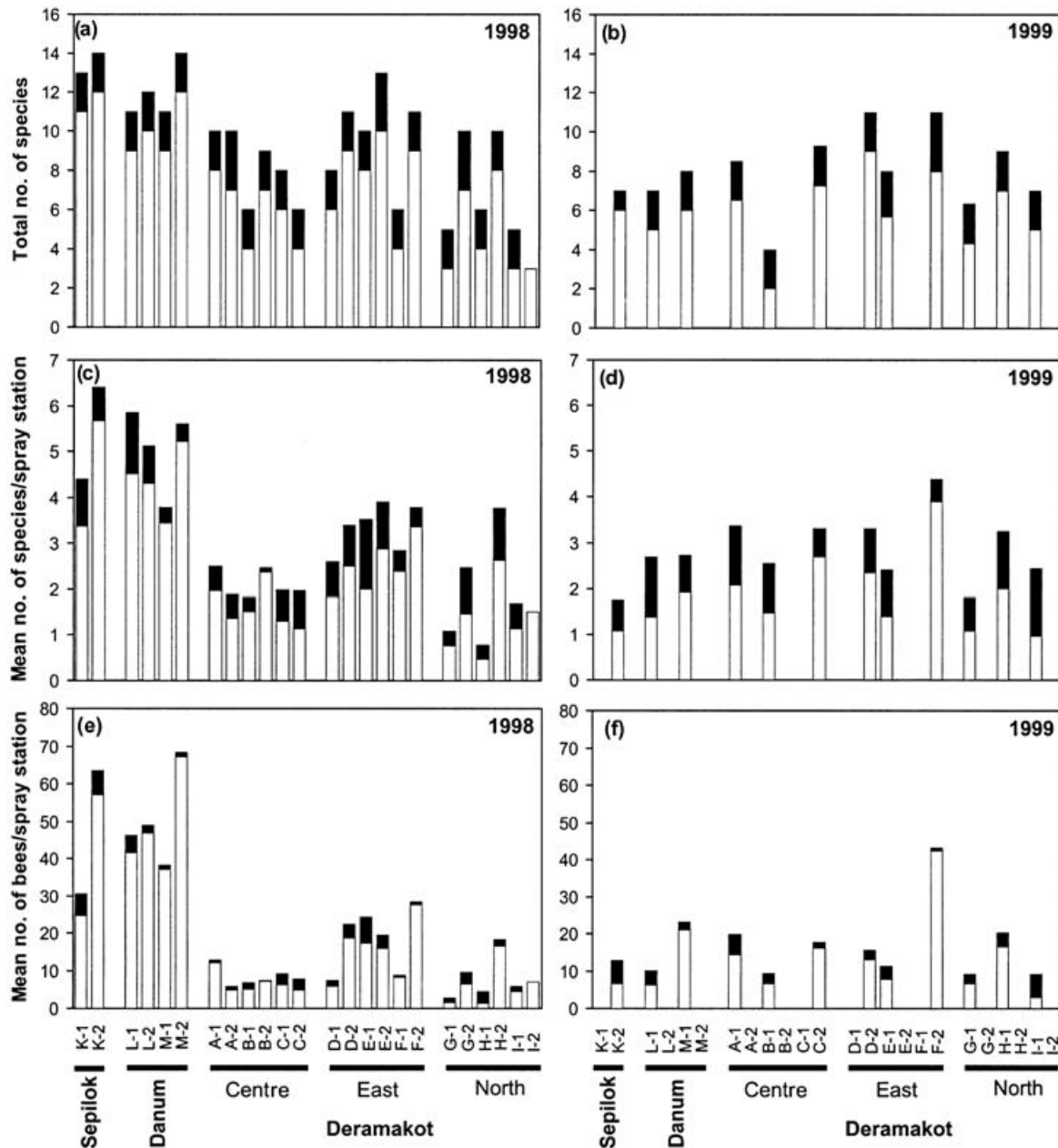


Figure 2. Species richness (a, b), species incidence (c, d), and abundance (e, f) of stingless bees (unshaded) and honeybees (shaded), recorded during individual spraying assays in five forest localities (12 sites: A–M) in 1998 (left) and 1999 (right). Duplicate assays (per site) in 1998 were excluded from statistical analysis.

by the complex interaction of local flowering phenology, bee colony size and bait attractiveness. Flowering could influence baiting results in two opposite ways: first, floral resources available during the months prior to baiting will help build up colonies and increase the number of foraging bees that can be baited (although the number of colonies remains constant). Second, natural flowering that occurs at the time of baiting will reduce bait attractiveness because it increases the availability of alternative food resources. Following this argument, the number of foraging bees at artificial honey-water

baits will be maximal at times when there are strong colonies but few floral resources in the habitat, e.g. at the end of a flowering season. Unfortunately, no complete phenological records are available for the different localities that could be linked to the baiting data. Some indication exists, however, that flowering was very different in the two years, following huge differences in climatic conditions generated by the 1997–1999 El Niño/La Niña cycle (Pacific Southern Oscillation; Kiladis & Diaz 1989). During the first half of 1998 the whole of Borneo experienced a severe dry spell that followed

Table 2. Encounter frequency of species of highly social bees at honey-water spray stations in five forest localities in Sabah (migratory *Apis dorsata* excluded), pooled over years and replicate sites. Numbers represent the mean percentage of spray stations at which the species was observed. Species are ordered by genus and, consecutively, average encounter frequency.

	Sepilok	Danum	Deramakot		
			Centre	East	North
Number of sites	1	2	3	3	3
Sites	K	L, M	A, B, C	D, E, F	G, H, I
<i>Apis cerana</i> (Fabricius)	43.3	24.0	41.9	52.5	48.8
<i>Apis koschevnikovi</i> (Buttel-Reepen)	–	40.1	19.2	29.6	26.8
<i>Apis andreniformis</i> Smith	18.9	–	1.1	1.7	0.4
<i>Trigona laeviceps</i> Smith	74.4	83.2	51.7	82.6	52.1
<i>Trigona melanocephala</i> Gribodo	51.1	53.9	68.3	59.3	35.3
<i>Trigona binghami</i> (Schwarz)	21.1	41.4	11.7	28.1	10.0
<i>Trigona terminata</i> Smith	28.9	30.7	4.2	19.0	11.0
<i>Trigona fuscobalteata</i> Cameron	33.3	12.2	4.0	16.0	9.8
<i>Trigona fimbriata</i> Smith	18.9	40.3	1.4	10.2	3.8
<i>Trigona itama</i> Cockerell	21.1	38.2	8.6	1.9	3.8
<i>Trigona ventralis</i> Smith	15.6	8.9	8.5	8.8	–
<i>Trigona melina</i> Gribodo	41.1	6.3	4.4	0.4	0.4
<i>Trigona collina</i> Smith	11.1	4.0	4.0	4.4	1.1
<i>Trigona laeviceps</i> -group*	4.4	15.0	–	1.9	–
<i>Trigona apicalis</i> Smith	5.6	1.3	2.9	7.3	–
<i>Trigona haematoptera</i> Cockerell	3.3	–	0.5	3.5	0.7
<i>Trigona rufibasalis</i> Cockerell	–	0.1	2.3	2.2	–
<i>Trigona thoracica</i> Smith	1.1	–	0.4	0.4	–
Number of species	16	15	17	18	13

* represents a probably undescribed species that (judging by the workers) can only be distinguished from *T. laeviceps* by its smaller size. Possibly identical with the small variety of *T. laeviceps* mentioned in Sakagami *et al.* (1990).

increasingly dry weather conditions during much of 1997. The outstanding climatic conditions are reflected by rainfall measurements in Danum Valley. Here, 1997–1998 was the driest 2-y period on record (data kindly provided by Nick Chappell, Hydrology project, Royal Society South East Asia Research Programme). In contrast, most of 1999 was very rainy. In Danum Valley, 1999 was the wettest year on record, with rainfall totalling 124% of the normal annual precipitation (same source as above). Generally, increased flowering tends to be associated with dry and sunny periods in tropical areas, and is suspected to coincide with El Niño in eastern Malesia (Ashton *et al.* 1988, van Schaik 1986, Wich & van Schaik 2000). Flowering was indeed pronounced in Sabah during the first half of 1998 (Eltz *et al.* 2001, pers. obs.). Thus, thriving bee colonies may have been partly responsible for the high bee numbers in Danum Valley and Sepilok in 1998. ENSO and related fluctuations in floral resource availability have been suggested to explain dynamics of euglossine bee numbers at fragrance baits in Panama (Roubik 2001).

However, although large-scale climatic phenomena like ENSO have an influence on plant reproductive phenologies, there is also substantial local variation in the exact timing of events. In an analysis of masting in Sumatra and across Malesia, Wich & van Schaik (2000) showed pronounced asynchrony of flowering and fruiting between geographically close areas (e.g. 70 km

between two sites in northern Sumatra). Local patterns seemed equally out of phase in Sabah. Between March and May 1998, Deramakot Forest Reserve experienced a continuous increase of flowering that finally ended in a small mass-flowering event including several species of Dipterocarpaceae (Eltz *et al.* 2001). This particular dynamic of ever-increasing availability of natural flower resources may have led to low bee incidence at the honey-water spray stations in 1998. Although no quantitative data were collected, flowering, although generally high, showed no comparable increase during the same period in Sepilok and Danum Valley (pers. obs.), perhaps rendering baits more attractive to foraging bees. I suspect that it was such local variability of flowering phenology that has led to the observed interactions between year and locality in the bee censuses.

Although the reasons for the observed variation remain speculative, it is obvious that pronounced temporal effects will complicate the application of honey-water baiting for apid bee surveys. Meaningful comparisons of species richness and abundance would clearly require at least 4–6 repeated assays taking place over periods of 2 y, preferably longer. The effort required may be beyond the scope of most applied projects concerned with assessing management impact on biodiversity. Low temporal repeatability of baiting results was also evident in two studies on neotropical meliponines (Baumgartner & Roubik 1989, Breed *et al.* 1999), and fluctuations in bait

attractiveness may be a general problem of phenology-dependent, resource-based methods such as fruit-trapping of nymphalid butterflies or fragrance-baiting of euglossine bees (see Ackerman 1989, Pearson & Dressler 1985, Roubik 2001). In summary, rapid but accurate assessment of stingless bee abundance and diversity seems problematic with available methods. At present, there is little alternative to measuring nest density in studies of population and community ecology of stingless bees.

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