

Thomas Eltz · Carsten A. Brühl  
Sander van der Kaars · K. Eduard Linsenmair

## Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia

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**Abstract** We measured the nest density of stingless bees (Apidae, Meliponini) in undisturbed and logged-over dipterocarp forests in Sabah, northern Borneo, and evaluated hypotheses on proximate factors leading to the observed variation: population control mediated by (1) nest predation, (2) limitation of nest trees, or (3) food limitation. Per-area nest density varied twentyfold across 14 forest sites and was significantly affected by locality, but not by the degree and history of disturbance. Nest density was generally high in sites located in the Sepilok Forest fragment (mean 8.4 nests/ha), bordering mangroves or plantations. In contrast, nest densities in continuous forests were all low (between 0 and 2.1 nests/ha, mean 0.5 nests/ha). Yearly nest mortality was low (13.5–15.0%) over 4 years of observation and did not vary between forest localities, thus limiting the potential of nest predation (1) in creating the observed variation in nest density. The presence of potential nest trees (2), though positively correlated with nest density, explained only a minute fraction of the observed variation. Nest density was best explained by differences in the pollen resources (3) available to the bees (quantified by analysis of pollen in bee garbage). Across five selected sites the amount of nonforest pollen (from mangrove or crop plants) included in diets of *Trigona collina* was positively correlated with *T. collina* nest density. External pollen sources are a likely supplement to bee diets at times when little flowering occurs inside the forest, thus in-

creasing overall bee carrying capacity. Pollen limitation was also indicated by direct measurements of pollen import and foraging activity of *T. collina* in three selected sites: Pollen traps installed at nests in high-density Sepilok captured significantly more corbicular pollen than colonies in low-density Deramakot. At the same time, morning foraging activity was also greater in Sepilok, indicating a regulatory increase in foraging in response to high pollen availability. We conclude that the abundance of stingless bees in forests in Sabah is chiefly dependent on the local availability of food resources. Bee populations strongly benefit from edge effects and increased foraging habitat diversity. Electronic supplementary material to this paper can be obtained by using the Springer Link server located at <http://dx.doi.org/10.1007/s00442-001-0848-6>

**Keywords** Pollen foraging · Resource limitation · Nest predation · Population control · Meliponini

### Introduction

A major goal of ecology is to understand what factors determine the abundance of individuals in their habitats. Food supply often has a limiting effect on animals (Power 1984; Butynski 1990; Deslippe and Savolainen 1994), but other factors like climatic conditions or predation may keep local population densities below those at which food shortages occur (Franks and Fletcher 1983; Andrewartha and Birch 1984). In the case of social insects that frequently live in permanent and populous colonies, local colony density may be limited by the availability of suitable sites for nesting. Evidence for nest site limitation has been obtained for some populations of ants (Herbers 1986; Kaspari 1996).

To date only one study has directly addressed ecological factors that are potentially limiting to stingless bee populations (Hubbell and Johnson 1977; see below). Stingless bees are distributed throughout the tropics and live in perennial colonies of a few hundred to several

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T. Eltz (✉) · C.A. Brühl · K.E. Linsenmair  
Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III)  
der Universität Würzburg, Biozentrum,  
Am Hubland, 97074 Würzburg, Germany  
e-mail: eltz@biozentrum.uni-wuerzburg.de  
Tel.: +49-931-8884356, Fax: +49-931-8884352

S. van der Kaars  
Department of Geography and Environmental Science,  
Monash University, Clayton, VIC 3168, Australia

thousand workers (Sakagami 1982; Roubik 1989), with the majority of species nesting in preformed cavities in live trees (Roubik 1979, 1983; Sakagami et al. 1983; Salmah et al. 1990). All are generalist foragers, and some species are known to use floral resources (nectar, pollen) from more than a hundred plant taxa over the course of several seasons in a given habitat (Wilms et al. 1996). Diet overlap between different stingless bee species is often high as determined by studies of flower visitation and pollen foraging (Heithaus 1979; Wilms et al. 1996; Eltz et al. 2001a), indicating high potential for interspecific competition for food. Hubbell and Johnson (1977) intensively studied nest sites and nest dispersion of five species of stingless bees in a tract of dry forest in Costa Rica. Bee species were rather indiscriminant in their choice of nest trees, and suitable cavities seemed not to be in short supply. Instead, two lines of evidence suggested that population densities were primarily limited by food. First, nest density of the different bee species was negatively related to the specific colony weight, suggesting that nest densities were influenced by metabolic requirements. Second, four of five species showed uniform patterns of nest dispersion, indicating that competition for food may set limits to nest densities (Hubbell and Johnson 1977). Meliponine nest dispersion has received less attention in the Paleotropics, but emerging data from Bornean rainforests suggest that patterns are quite different to those found in Central America: nests of the more frequently encountered species are often aggregated in nest trees (Roubik 1996; Nagamitsu and Inoue 1997; Eltz et al. 2001a, in press).

Very little is known about how stingless bees respond to forest disturbance imposed by human activities. Selective logging for timber extraction can drastically reduce the abundance of large trees in residual stands (Cannon et al. 1994) and may thus create a situation in which nest sites become a limiting resource for cavity-nesting bees. Forest management has been shown to severely reduce the availability of tree cavities as well as population densities of hole-nesting birds and marsupials in temperate areas of North America and Australia (Saunders et al. 1982; Lindenmayer et al. 1991; Newton 1994). Hubbell and Johnson (1977) speculated that the colonization of second-growth forest by stingless bees will depend on tree size, and that species depending on large cavities will be excluded from early successional stages. By changing stand structure, light environment and microclimatic conditions, forest disturbance may also affect flowering plants and floral resource availability (Rincon et al. 1999). Salmah et al. (1990) studied the influence of human disturbance on stingless bees in Central Sumatra, covering a wide range of habitats from primary forests to city areas. Stingless bees were censused at flowers and honey baits, and both species diversity and abundance of meliponines decreased along the disturbance gradient.

In the present study, we measured nest density of stingless bees in 14 sites situated in primary and selectively logged dipterocarp forests in lowland Sabah, Malaysia. Logged sites varied in logging history and in-

tensity. To evaluate hypotheses on causal factors involved in creating the observed variation in nest density, we collected large amounts of background data on bee nests, pollen diet, and habitat parameters in the different sites. We focussed on three main hypotheses of population control, potentially interacting to varying degrees with human disturbance:

1. Stingless bees are chiefly limited by nest predation. In contrast to a shortage of food that will mostly reduce colony growth and reproduction, intensive nest predation is predicted to increase mortality of existing colonies. To test whether mortality explains variation in nest density, we monitored colony survival over up to 4 years.
2. Stingless bees are chiefly limited by nest sites. To evaluate nest site limitation, we related stingless bee nest density to an estimate of nest tree availability.
3. Stingless bees are chiefly limited by food resources. Diets of Asian meliponines principally consist of two kinds of substances: nitrogen-rich pollen and sugar-rich nectar, both collected separately or synchronously by foraging workers from floral and nonfloral sources in the habitat. The availability of floral resources is highly variable over time in Bornean forests (Sakai et al. 1999), and food is probably in short supply at least occasionally during the life of an individual colony. To evaluate the importance of food resources in limiting bee populations, we used two different approaches. First, nest density was related to qualitative aspects of pollen diet (composition, diversity, origin) that may be indicative of differences in resource levels. Second, we monitored foraging activity and the amount of pollen harvested by colonies in sites with different nest densities.

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## Materials and methods

### Study sites

Between 1997 and 2000, we studied stingless bees at a total of 14 research sites located in three forest localities in lowland Sabah, Malaysia:

- Danum Valley (4°50–5°00 'N, 117°35–117°45 'E): two sites. The Danum Valley Conservation Area (DVCA) in central Sabah covers 43,800 ha of undisturbed dipterocarp forest (Marsh and Greer 1992). Both sites (L, M) are surrounded by large tracts of continuous forest with distances of more than 5 km to forest clearings in all directions.
- Sepilok (5°54 'N, 118°04 'E): three sites. The Kabil-Sepilok Forest Reserve is a coastal forest fragment of 4,294 ha, with more than one-third of that area consisting of mangrove forest fringing Sandakan Bay. On elevated ground, mangroves are replaced by dipterocarp forest (Fox 1973). To the east, north, and west, the reserve is bordered by plantations. The areas in and around our sites (K, N, Sepilok Laut) have never been logged. Sites K and N are situated in the north of the reserve, approximately 500 m from the forest edge. The cultivated land bordering the forest is highly heterogeneous, and includes old orchards, patches of corn, cassava, and oil palm. The third site, Sepilok Laut [laut=sea, ocean (Malay)], directly borders the mangroves in the south of the reserve.

- Deramakot (5°19–5°20 'N, 117°20–117°42 'E): nine sites. 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 and Amin 1994) and harbors a wide range of logged-over dipterocarp forests with varying degrees and histories of disturbance. The selected sites included (1) old, slightly logged-over forests (logged once with low impact between 1974 and 1976; sites A, B, C), (2) old, heavily logged-over forests (logged once or twice between 1968 and 1970; sites D, E, F), and (3) young, heavily logged-over forests (logged up to three times between 1980 and 1989; sites G, H, I). With the exception of site A, that is close to the Deramakot base camp clearing, all sites were situated within large continuous forest tracts.

In all sites, we established one set of four parallel 600-m transects, each separated by 200 m from neighboring transects. To quantify site characteristics, we measured tree size distribution using angle-count sampling with a Spiegel relaskop (Schreuder et al. 1987) every 100 m along the transects (24 counts per site). Counts were recorded separately for five diameter at breast height (dbh) classes: 5–14, 15–29, 30–59, 60–99, and  $\geq 100$  cm. In addition, we separately recorded trees of the pioneer genus *Macaranga*. We tested for effects of logging history on tree diameter distribution using ANOVA with a nested design [four levels of disturbance (primary and the three levels of logging impact described above) nested within the three localities]. There were significant effects of disturbance on the following measures of stand structure: the degree of skew toward smaller size classes ( $n=14$ ,  $F_{2,9}=5.17$ ,  $P<0.05$ ), the number of large trees above 60 cm dbh ( $F_{2,9}=12.97$ ,  $P<0.01$ ), and the number of *Macaranga* trees ( $F_{2,9}=11.32$ ,  $P<0.01$ ). Thus, the presence of larger trees decreased from primary forests toward more heavily and more recently disturbed sites, whereas the abundance of *Macaranga* increased in the same direction.

#### Nest survey

Stingless bee nests of Southeast Asian forests are found in cavities in tree trunks or underneath the bases of trees (Salmah et al. 1990; Roubik 1996). We searched for bee traffic and nest entrance tubes in bases and trunks of all trees larger than 30 cm dbh situated in 20-m corridors along the established transects. Nest counts were transformed into nest density per hectare by incorporating area searched (length of transect  $\times$  20 m). The total area searched was 4.8 ha per site except in Sepilok Laut where only 2.8 ha were covered. Due to the impressive height of many trees in dipterocarp forests (up to 60 m), we certainly missed bee nests, especially those situated close to or within the canopy. Thus, nest densities can only be considered as relative indices for between-site comparisons.

#### Nest tree availability and nest mortality

In a qualitative analysis of stingless bee nesting trees in Sabah (Eltz et al., in press), we had found that the majority of nests (whole community: 86%; *Trigona collina*: 97%) were situated in or under live canopy trees larger than 60 cm dbh belonging to a large variety of hardwood (non-*Macaranga*) tree taxa encompassing the entire range of timber qualities. Thus, the number of trees above 60 cm dbh present in angle-count samples in a given area was used as a simple index of nest tree availability.

For an analysis of nest predation and mortality, we pooled information on nests located during the quantitative surveys with that of nests found on other occasions in or close to the research sites. The nests were checked repeatedly over up to 4 years for signs of predator attacks. Presence or absence of bees in the entrance tubes of known nests indicated colony survival or death. Mean yearly colony mortality was calculated only for the localities Sepilok and Deramakot. The number of nests in Danum was too small for a meaningful comparison.

#### Pollen diet of a focal bee species

We quantified pollen diets of colonies of *T. collina* in five sites that encompassed the complete range of observed nest densities (see below). *T. collina*, a medium-sized black bee, is the most frequently found stingless bee species in forests in Borneo (Roubik 1996; Eltz et al., in press). Pollen diets were assessed by microscopic analysis of pollen in colony garbage. Workers of *T. collina* and many other stingless bees expel from their nests small pellets of refuse that contain substantial amounts of pollen exines, and these pellets can be collected with the help of special funnel traps that are installed in front of nest entrances (Eltz et al. 2001b). Garbage pollen closely resembles pollen import with a certain time lag, and analyzing garbage at relatively long intervals (up to several months) yields reasonable estimates of long-term colony pollen use (Eltz et al. 2001b). Between April 1999 and November 2000, we collected one to five (mean: 2.6) repeated garbage samples from each of a total of 38 colonies of *T. collina* situated at Sepilok Laut (8 colonies), Sepilok K (8), Danum Valley M (3), Deramakot A (8), and Deramakot G (11). Sampling dates were clustered over time within five distinct sampling periods: April–May 1999, September–October 1999, March–May 2000, July 2000, and November 2000. Total observation time differed between sites (7–19 months; see Fig. 3).

An individual sample consisted of ten garbage pellets. Sample processing, microscopic slide making and the grain volume-based analysis of pollen composition followed the protocol described in Eltz et al. (2001b). The analysis yielded values of the relative representation (in % volume) of different pollen types in a given sample as well as measures of pollen-type richness and evenness (Shannon's *J*; Pielou 1966) per sample. Grain volume is a good indicator of grain mass and protein content across both zoophilous and anemophilous plant taxa (Roulston et al. 2000). Taxonomic identifications of morphotypes to the level of plant family, genus, or species (or taxonomic 'type') were made from original slides by S.v.d.K., partly by comparison with reference pollen collected from flowers in the bees' habitat. Similarity of pollen composition between samples was quantified using the Steinhaus coefficient *S* (Legendre and Legendre 1998), with  $S=2W/(A+B)$ , where *W* is the sum of minimum percentages of the various types, and *A* and *B* are the sums of the percentages of all types in each of two samples. Turnover (dissimilarity) was calculated as  $1-S$ .

#### Foraging activity and pollen foraging of *T. collina*

We obtained estimates of foraging activity for 22 colonies of *T. collina* situated in three sites encompassing part of the observed range of nest densities (sites A, G, K). Foraging activity was estimated by measuring entrance tube traffic with the help of electronic bee counters developed in the Department of Animal Ecology and Tropical Biology in Würzburg (Eltz and Vonend 2001). Infrared-light barriers were attached to the entrance tubes of bee colonies and interceptions were recorded in 5-min intervals by battery-driven controller/data loggers (Tiny Tiger; Wilke Technologies, Germany). A total of nine stations (three per site) were operated between 27 February and 23 July 2000, almost permanently recording tube traffic of 22 colonies (8, 7, and 7 in the respective sites). Manual control counts of bees were done repeatedly in order to detect counter malfunction. Across all nests, there was a tight almost 1:1 linear relationship between electronic and manual counts ( $R^2=0.94$ ,  $P<0.0001$ ), and counter sensitivity did not vary between sites (ANOVA:  $n=67$ ,  $F_{2,64}=1.52$ ,  $P=0.23$ ). Daily sums of interceptions between 7:00 and 10:00 a.m. were used as an index of morning foraging activity.

We used modified garbage traps (Eltz et al. 2001b) to quantify pollen import of the 22 colonies. The modified traps strip off corbicular pollen from a fraction of returning foragers and pollen pellets are collected in sampling buckets. Traps were placed in front of nest entrances between 8:30 a.m. and 2:30 p.m. on 9–12 sampling days per nest between February and July. The total number of pollen pellets collected per colony over the 5 months was used as a measure of colony pollen intake.

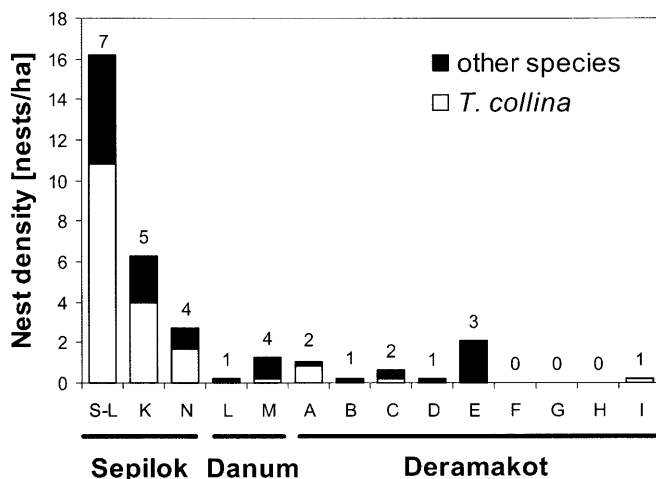
We did not attempt to quantify flowering in our research sites because reasonable quantification would have required immense efforts due to the spatial scale and patchiness of the variation involved. We had the impression that flowering levels were low to intermediate, with no clear increase or decrease over the 5 months at all three sites. On a longer time scale, the study period was part of the nongeneral flowering period following local and regional mass flowering in 1996 and 1998 (Sakai et al. 1999; Eltz et al. 2001a).

## Results

### Nests and nest density

A total of 116 stingless bee nests of 11 species were located during the quantitative nest survey. Among those, *T. collina* was by far the most abundant species (54.7% of nests), followed by *T. melanocephala* (16.2%) and *Hypotrigona pendleburyi* (12.0%). All three are species that predominantly nest in and under tree bases, and we probably found a large proportion of their nests in the searched areas. All but one (*T. melina*) of the other species (see Fig. 1) nest in tree cavities at variable height and are probably underrepresented to varying degrees.

Nest densities (all species pooled) varied drastically between sites and ranged from 0 to 16.2 nests/ha (Fig. 1). Densities varied significantly between localities (Sepilok, Danum, Deramakot; Kruskal-Wallis test:  $n=14$ ,  $H_2=7.04$ ,  $P=0.03$ ), an effect that was almost exclusively based on the elevated nest densities in the Sepilok forest fragment. No clear effects of logging intensity were detectable within Deramakot. On average, 2.0 nests were clustered in a given tree ( $n=57$  nest trees), and the degree of clustering did not vary between the three localities



**Fig. 1** Nest density of stingless bees in 14 forest sites in Sabah. Numbers above columns represent the number of bee species found among the respective nests. Note elevated bee abundance in the Sepilok forest fragment. *Other species* include *Trigona melanocephala*, *Hypotrigona pendleburyi*, *T. terminata*, *T. laeviceps*, *T. haematoptera*, *T. fimbriata*, *T. binghami*, *T. melina*, *T. laeviceps* group, and one unidentified species

(sites with no nests excluded:  $n=11$ ,  $H_2=4.18$ ,  $P=0.12$ ). The number of bee species found nesting also varied between localities ( $n=14$ ,  $H_2=7.30$ ,  $P=0.03$ ; Fig. 1), and was positively correlated with nest density across sites (Spearman  $R_s=0.95$ ,  $P<0.0001$ ). The frequency of *T. collina* in relation to that of other species varied significantly between the three localities (counts pooled for each locality:  $\chi^2=14.9$ ,  $n=116$ ,  $df=2$ ,  $P<0.001$ ) and was highest in Sepilok (Fig. 1).

### Nest predation and survival

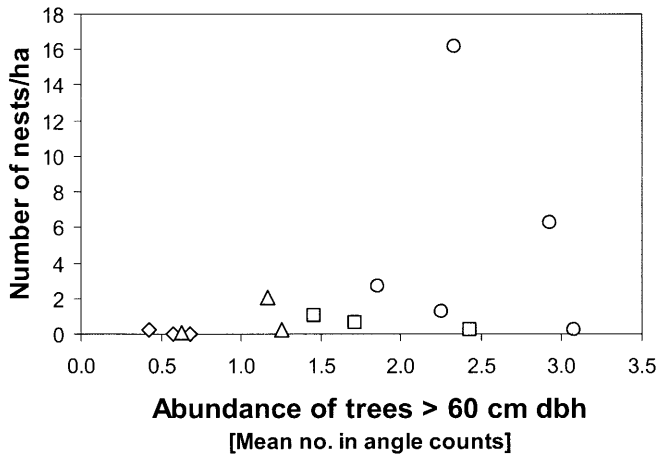
Over 4 years of monitoring the survival of bee colonies, we became aware of only one case of nest mortality clearly attributable to predation. A large animal, presumably a sun bear (*Helarctos malayanus*), had excavated two nests of *T. collina* that were situated in the root system of an emergent tree (dbh 100 cm) in Deramakot. Occasionally, smaller animals superficially damaged the entrances of *T. collina* nests, but the colonies as a whole remained unaffected. Generally, mean yearly nest mortality was equally low in bee-rich Sepilok (0.135,  $n=52$  nests, mean observation time per nest 1.42 years) and in bee-poor Deramakot (0.150,  $n=51$ , 1.3 years). Survival times of nests did not vary between Sepilok and Deramakot in a survival analysis (Gehan's Wilcoxon test, test statistic=-0.013,  $P=0.99$ ). Equally, no differences were observed when only *T. collina* was considered [yearly mortalities of 0.130 in Sepilok ( $n=36$ ) and 0.082 in Deramakot ( $n=27$ )].

### Availability of nest trees

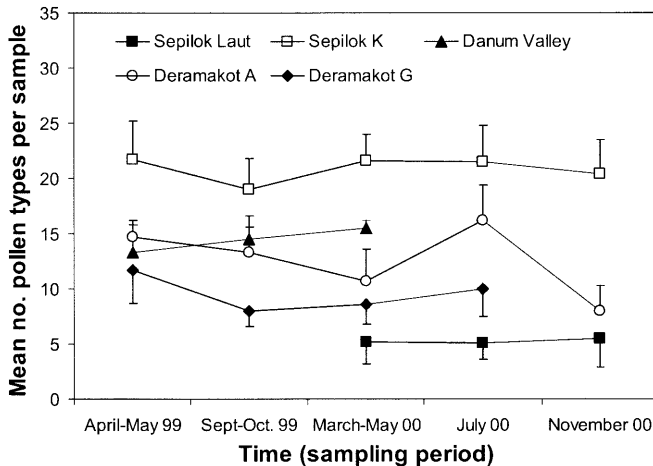
Across sites the presence of trees above 60 cm dbh correlated positively with overall nest density (Spearman  $R_s=0.59$ ,  $n=14$ ,  $P=0.023$ ) as well as nest tree density ( $R_s=0.59$ ,  $n=14$ ,  $P=0.023$ ). No significant correlation was observed for *T. collina* alone ( $R_s=0.357$ ,  $n=14$ ,  $P=0.21$ ). The presence of large trees left much of the observed variation in nest density unexplained, especially the large variation between well-stocked primary sites in Danum and Sepilok (see Fig. 2). The outstanding nest density in Sepilok Laut was not paralleled by an exceptional presence of large trees. We were unaware of any other characteristic of the tree community that could explain the high nest density. Nest tree diversity was similar to other sites and localities (13 different taxa among 19 identified trees), with no pronounced bias in favor of a single tree species.

### Pollen resources of *T. collina*

*T. collina* garbage contained a total of 148 different morphotypes of pollen, belonging to at least 38 plant families. Samples collected from different colonies at the same site at a given point in time were similar in compo-

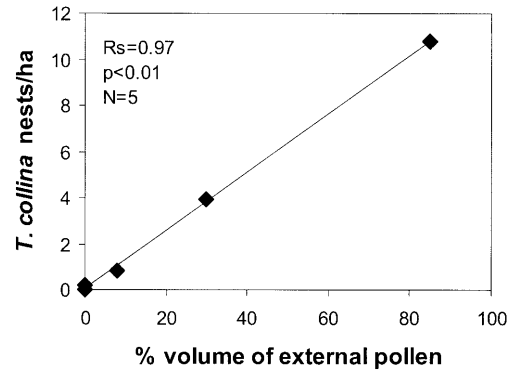


**Fig. 2** Relationship between the presence of large trees and stingless bee nest density in 14 forest sites in Sabah. Different symbols indicate different logging histories: *circles* undisturbed primary forest, *squares* old, slightly logged forest, *triangles* old, heavily logged forests, *diamonds* young, heavily logged forests (see text for details)



**Fig. 3** Pollen-type richness of garbage samples collected from colonies of *T. collina* during five consecutive sampling periods between April 1999 and November 2000. Error bars are either positive or negative standard deviations

sition (Steinhaus coefficient  $\pm$  SD =  $55.8 \pm 24.6\%$  similarity), whereas large differences in pollen diet were evident between localities and sites (see below). A complete list of pollen in the bee diets can be obtained by using the Springer Link server at <http://www.dx.doi.org/10.1007/s00442-001-0848-6> or is available directly from the authors. There were significant differences between sites in grand means of the number of pollen types per nest (ANOVA:  $F_{4,33}=48.2$ ,  $n=38$ ,  $P<0.001$ ) and in the mean evenness (Shannon's  $J$ ) of pollen type representation ( $F_{4,33}=26.7$ ,  $n=38$ ,  $P<0.001$ ). These differences were very stable over time (Fig. 3). Low values in mangrove-bordering Sepilok Laut were mostly based on the fact that samples were heavily dominated by a single pollen type, that of the mangrove tree *Rhizophora apiculata*. In-



**Fig. 4** Relationship between the mean proportion of external non-forest pollen in garbage samples of *T. collina* and *collina* nest density in five different forest sites in Sabah. Nonparametric Spearman  $R$  was calculated to test for correlation. Linear line fitted for better visualization

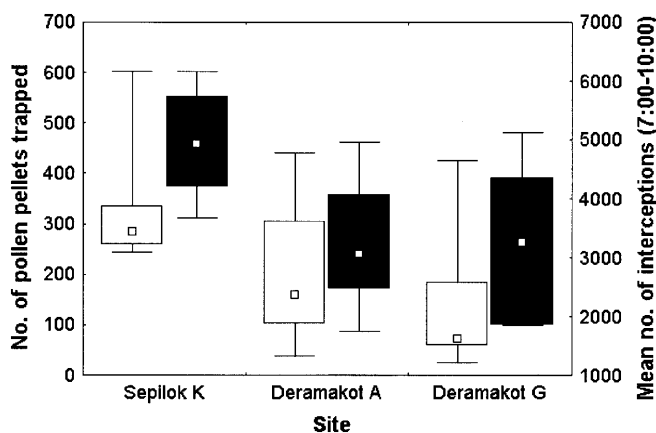
dividual samples collected in May, July, and November 2000 contained relative volumes of *R. apiculata* grains between 59–98% (means across nests of 79.6, 83.5, and 81.3% for each of the three sampling periods). In all other sites, the mean representation of the most dominant grain rarely exceeded 30% of the pollen volume. Sepilok Laut colonies also had very low temporal pollen turnover (7.5% per month) in comparison to the other sites (between 12.7–16.3%). Colonies in plantation-bordering Sepilok K also collected large amounts of nonforest pollen. Their diets were dominated by crop plants like corn (*Zea mays*: mean of 15.6% across sampling periods), manioc (*Manihot esculenta*: 5.7%) and water melon (*Citrullus lanatus*: 5.0%). Nests situated in continuous forest in Danum Valley and Deramakot had either no pollen sources of evidently external origin or (in Deramakot A) were confined to minor sources present among roadside plants (*Mimosa pudica*: 1.8%) and plants grown in the Deramakot Base Camp clearing (manioc: 4.5%; ornamental *Turnera ulmifolia*: 1.6%). Across the five selected sites, there was a positive relationship between the mean proportion of nonforest pollen in garbage (grand means across nests and time) and nest density of *T. collina* ( $R_s=0.97$ ,  $n=5$ ,  $P<0.01$ ; Fig. 4).

#### Pollen use of other meliponine species in Sepilok Laut

To investigate whether the findings on *T. collina* allow more generalized interpretations for stingless bee communities, we repeatedly collected garbage samples from colonies of *T. terminata* (2 colonies), *T. melanocephala* (1), *T. melina* (1), and *T. binghami* (1) in Sepilok Laut. Sampling took place over the same three sampling periods, and treatment and analysis followed the same standards as for *T. collina*. Garbage of all four species contained large quantities of pollen of *R. apiculata* (Table 1), suggesting that the mangrove tree represented an important resource for most if not all meliponine species in the area.

**Table 1** Percent volume of *Rhizophora apiculata* pollen in garbage samples of four additional meliponine species (five colonies) in Sepilok Laut

	March–May 2000	July 2000	November 2000	Mean
<i>Trigona melina</i>	60.0	71.2	27.7	53.0
<i>T. melanocephala</i>	71.7	44.4	51.5	55.9
<i>T. terminata</i> 1	85.4	92.8	70.5	82.9
<i>T. terminata</i> 2	89.7	91.5	26.9	69.4
<i>T. binghami</i>	–	82.6	100.0	91.3



**Fig. 5** Median, quartile range and extremes of indices of pollen import (white boxes) and morning foraging activity (black boxes) of colonies of *T. collina* ( $n=22$ ) situated in three research sites in Sabah. There were significant differences between sites for both variables (see text for details)

#### Foraging activity and pollen foraging of *T. collina*

Morning (7:00–10:00 a.m.) tube traffic of *T. collina* colonies varied significantly between sites (Kruskal-Wallis test:  $n=22$ ,  $H_2=7.79$ ,  $P=0.020$ ; Fig. 5), with traffic in Sepilok K being almost twice as high as in the two Deramakot sites. The difference in tube traffic was restricted to the early morning hours which are known to be the prime time for pollen foraging in meliponines (Inoue et al. 1985; Roubik 1989; T. Eltz, unpublished data). Later in the day (10:00 a.m. to 6:00 p.m.) the number of interceptions no longer varied between sites ( $n=22$ ,  $H_2=3.01$ ,  $P=0.22$ ). The number of pollen pellets trapped per colony over 5 months varied significantly between sites ( $n=22$ ,  $H_2=6.31$ ,  $P=0.043$ ; Fig. 5) and was also highest in Sepilok K.

## Discussion

### Evidence for food limitation

Nest density of stingless bees in dipterocarp forests in Sabah varied more than 20-fold between sites in our study, ranging from a mean of 0.5–0.7 nests/ha in Deramakot and Danum Valley to 16.2 nests/ha in mangrove-bordering forests in Sepilok. Variation in nest density was not explained by differences in nest mortality (indi-

cative of predation), nor was it closely related to logging history and the availability of potential nest trees. Instead, our data suggest that meliponine populations densities in Sabah are chiefly determined by the local availability of food resources.

Generally, stingless bees were particularly abundant in the Sepilok forest fragment where bees had access to floral resources in bordering nonforest habitats. For *T. collina*, a positive relationship was found between nest density and the representation of nonforest species in pollen diets. This suggests that nonforest plants, by providing huge rewards to individual foragers, constituted superior resources for bee colonies and thereby raised stingless bee carrying capacity in edge forests. For example, *R. apiculata*, which heavily dominated bee diets in mangrove-bordering Sepilok Laut, is the most abundant mangrove tree of the area (Fox 1973). It is mainly wind pollinated and produces copious quantities of pollen in easily accessible flowers (Tomlinson et al. 1979; T. Eltz, personal observation). The same is true for corn (*Z. mays*), which was collected in quantities by bees in a plantation-bordering site. Corn has previously been noted to be intensely harvested by bees around the humid tropics (Roubik 1989). In addition to being highly profitable resources at a given time, we hypothesize that nonforest taxa benefit bees by reducing the extent of temporal fluctuations in floral resource availability. Temporal reliability of floral resources may be crucial in Asian dipterocarp forests that are characterized by extreme and partly unpredictable fluctuations in flowering (Sakai et al. 1999). Although data from our research sites are lacking, flowering phenology in plantations, roadsides, and mangroves is likely to differ markedly from that inside the forest. For many mangrove trees, including *Rhizophora*, flowering normally occurs over substantial parts of the year (Christensen and Wium-Andersen 1977; Tomlinson et al. 1979; Wium-Andersen 1981). In mangrove areas in southern Thailand, flowering of *R. apiculata* had distinct seasonal peaks, but some flowers were present at any point in time over 16 months (Christensen and Wium-Andersen 1977). A relatively constant availability of *R. apiculata* pollen probably explains much of its observed predominance in bee diets. Additionally, flowering peaks in mangroves are likely to be out of phase with those in nearby forests, thus enhancing potential benefits to stingless bees. Tomlinson et al. (1979) speculated that *Bruguiera* (Rhizophoraceae) in Queensland, Australia, constitutes a major nectar source during its peak flowering season in May and August, a time when terrestrial plants are generally not flowering.

Evidence from other studies supports the idea of increased nest densities mediated by alternative food sources: Floral resources provided by farmland have been suggested to increase bee abundance due to their availability during times when natural habitats become dry and unproductive (Kremen and Ricketts 2000). In some situations, crop plants with extended flowering seasons may even represent keystone resources for certain bumblebees (Corbet 2000). In this context, it should be emphasized that the positive effect of crop plants on bee populations will depend heavily on the kind of plantation. Diverse agricultural landscapes like those bordering Sepilok K are likely more beneficial to bees than are monocultures. Specifically, the vast and even-aged stands of oil palm (*Elaeis guineensis*), already covering more than 15% of lowland Sabah (Forest Research Centre, Sabah), are not likely to benefit bees. Although oil palm pollen is occasionally collected by certain species of meliponines and honeybees (Kiew and Muid 1991), oil palm is not considered a good forage plant for bees (Roubik 1995). Despite being present in plantations bordering Sepilok K, oil palm pollen was only a minute component of diets of local *T. collina*.

Increased pollen import and morning foraging activity of *T. collina* in our study suggest that the intensity of pollen foraging per colony of *T. collina* was effectively greater in bee-rich Sepilok than in bee-poor Deramakot, indicating differences in pollen availability at the time of the study. One might argue whether an observation period of 5 months is sufficient for a sound comparison of resource levels, and we cannot rule out the possibility that the observed differences would level out over several years. However, the finding does make sense in combination with the data on pollen diets, and strengthens the view that pollen resources are in better supply in areas with a high nest density.

On the whole, our findings in Borneo are in broad agreement with the conclusions of Hubbell and Johnsons (1977) from Costa Rica that stingless bees live in saturated communities that are chiefly limited by food resources. Among food items, our results point to the special importance of pollen. Pollen is the prime source of nitrogen for Asian meliponines and brood production is proximately dependent on pollen availability. Pollen is also the only floral resource that is exclusively provided by flowers. Nectar, in contrast, is also available from extrafloral nectaries (Roubik 1989) and levels of supply are probably less restricted in times of little flowering. In Sepilok Laut, the availability of pollen from mangroves seems to have promoted quite outstanding nest densities. The 16.2 nests/ha found here far exceed meliponine densities reported from other tropical forests, both in Southeast Asia (2.8 nests/ha in Belalong Forest in Brunei; Roubik 1996) and in the Neotropics (~2–4 nests/ha in Costa Rica; Hubbell and Johnson 1977).

## Direct and indirect effects of logging

Our results lack clear indications of a negative influence of selective logging on stingless bee nest density. Although floral resource levels were not directly measured in sites with different degrees of degradation, data on foraging activity and pollen foraging of *T. collina* colonies suggest that resource levels did not vary drastically between slightly logged, old (A) and heavily logged, young (G) forests in Deramakot. This is perhaps surprising because sites were characterized by greatly differing canopy structure. Heavily logged sites had lost large fractions of upper-canopy layers, a finding that is typical for logged-over forests in Borneo (Cannon et al. 1994). However, loss of flowers produced in the forest canopy could be compensated by increased flowering in lower strata that experience increased light levels (Seidler and Bawa 2001). Among Venezuelan forest birds, nectar-feeding guilds were favored by logging in the short term, probably as a result of increased floral resources in the understory (Mason 1996). Generalist flower visitors like social bees may quickly adjust to alterations in forest stratification. In addition, their evident foraging in open habitats like plantations and mangroves suggests that foragers of most species can adjust well to altered microclimatic conditions encountered in heavily disturbed forests.

The availability of potential nest trees varied substantially along the disturbance gradient, but explained only minor fractions of the variation in nest density. This suggests that suitable cavities are not in short supply over a large range of nest densities and forest stand structures. However, the apparent lack of evidence for nest site limitation does not rule out direct negative effects of logging on stingless bees. In a different study (Eltz et al., in press), we analyzed the commercial potential of 142 nest trees of stingless bees in dipterocarp forests in Sabah and concluded that roughly one-third would qualify for harvesting in case of a commercial logging operation. Because absconding of colonies as a response to disturbance is rare in stingless bees (Inoue et al. 1984), felling of the nest tree will very likely kill its associated colonies. Residual effects of logging-induced mortality were possibly weak in our study because logging had taken place more than two decades ago in most Deramakot sites. However, the extremely low nest densities in the most recently logged areas in Deramakot (G, H, I) may still reflect direct logging impact.

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