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Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management

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Abstract

Nesting habits of highly social stingless bees (Meliponini) were studied in lowland dipterocarp forests in Sabah, Borneo. A total of 275 nests of 12 species of bees were located. All nests were closely associated with living (91.5%) or dead (8.5%) trees, either within pre-formed cavities in the trunk (cavity nests) or situated in or under the tree base (base nests). Species of bees differed in nesting habit. The majority of species (seven) were cavity nesters, but the majority of nests (81%) were base nests. Nests were often aggregated (mean of 1.94 nests/nest tree), with up to eight colonies and three species in a single tree. Nest trees were mostly large to very large (86.1% above 60 cm dbh) commercial timber trees; 47.3% of nest trees were dipterocarps. According to visual inspection nest trees were of significantly lower expected timber quality then randomly chosen control trees. Taking into account information on tree species, size and expected timber quality, we estimated that 34.0 or 42.6% of nest trees were potential harvest trees, depending on harvesting regulations (reduced impact logging (RIL) versus conventional). Lower percentages under RIL guidelines were mostly due to size restrictions that protect very large trees (>120 cm dbh). Harvesting is likely to kill bee colonies associated with the respective tree. Therefore, and because meliponine colonies are long-lived and have low fecundity, direct impact from logging may have lasting effects on bee populations. Harvesting guidelines that retain high proportions of large and hollow trees should be promoted in order to preserve meliponine pollination in sustainable forest management.

Keywords: Nest site; Cavity-nesting; Hollow trees; Reduced impact logging; Logging impact; Logging-induced mortality

1. Introduction

Cavities in trees are an important structural feature of natural forests, and a wide range of vertebrates and invertebrates depend on them for varying purposes, e.g. nesting and roosting (Lindenmayer et al., 1997; McComb and Noble, 1982; Newton, 1994; Oldroyd et al., 1994). Forest management is expected to pose considerable threat to both cavity-bearing trees as well as the fauna associated with them. Populations of cavity-dwelling animals could be: (i) directly affected by management operations, e.g. through mortality resulting from felling of the tree, or (ii) indirectly, as a result of decreased availability of suitable cavities in managed stands. So far, most research has

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concentrated on measuring or estimating indirect effects on populations of forest birds and marsupials in temperate forests. Forest management has been shown to severely reduce the availability of tree cavities for hole-nesting birds in North America (van Balen et al., 1982; Newton, 1994 and references therein), as well as the availability of tree hollows in southern Australia (Saunders et al., 1982; Bennett et al., 1994; Gibbons and Lindenmayer, 1996). In some cases, reduced availability of cavities was related to reduced population densities of cavity-dependent fauna (Lindenmayer et al., 1991; Newton, 1994; Saunders et al., 1982), suggesting that nest or den sites can become a limiting resource in managed forests. Direct effects of management operations on cavity-dwelling animals have received much less attention, presumably because of difficulties quantifying logging-induced mortality in relatively mobile taxa like birds or other vertebrates. Direct effects, however, could have considerable impact on populations of long-lived organisms with low fecundity.

Stingless bees (Apidae: Meliponini) of Asian dipterocarp forests might be such organisms. Meliponines are eusocial and live in colonies of a few hundred to several thousand workers (Sakagami, 1982). Individual colonies are generally perennial and reported maximum life-spans range from 10 to 26 years (Wille, 1983; Roubik, 1989). Most species found in southeast Asia nest in pre-existing cavities of variable sizes (Sakagami et al., 1983a,b; Salmah et al., 1990), and at least some species are known to nest in association with large canopy trees (Sakagami et al., 1983b; Roubik, 1996) that are likely to be targeted by the timber industry. Furthermore, once established, stingless bee colonies are believed to remain stationary for the rest of the colony cycle because the queen looses the ability to fly (Michener, 1974). Although there have been some exceptions to that rule (Inoue et al., 1984a), absconding of entire colonies as a response to disturbance is extremely rare in stingless bees, suggesting that colonies are heavily dependent on the persistence of their nest trees. Meliponines are among the most predominant flower-visiting insects in the canopy and understory of Asian tropical forests (Inoue et al., 1990; Momose et al., 1998), probably providing important pollinator services during both general and non-general flowering seasons (Momose et al., 1998; Sakai et al., 1999). Their conservation in commercial forests should be of considerable concern to forest managers.

In the present study, we analyzed the nesting habits and characteristics of nest trees of stingless bees in lowland forests in Sabah, Malaysia, in order to estimate the potential direct impact of logging operations on bee populations and communities. Using information on taxonomic composition, size and expected log quality of nest trees, we discuss potential effects of disturbance imposed by different harvesting systems (reduced impact logging (RIL) versus conventional harvesting) and highlight areas of conflict between natural forest management and the conservation of stingless bees and other cavity-dependent fauna.

2. Methods

2.1. Study sites and nest searching

During 20 months of field work between September 1997 and July 2000, we searched for stingless bee nests in three forest reserves in lowland Sabah:

- *Deramakot Forest Reserve*: a 55,000 ha commercial forest reserve in the center of Sabah, north of the Kinabatangan River (5°19′N–5°20′N and 117°20′E–117°42′E). Deramakot is covered by mixed dipterocarp lowland forest of the *Parashorea tomentella–Eusideroxylon zwageri* type and has been subject to timber extraction since 1956 (Chai and Amin, 1994). The searched sites varied in logging history and intensity, including both slightly logged old growth forests with almost intact stratification and heavily and repeatedly logged areas with extremely ragged canopy.
- *Danum Valley Conservation Area*: a 43,800 ha primary forest reserve situated about 60 km southeast of Deramakot (4°50′N–5°00′N and 117°35′E–117°45′E) with largely undisturbed mixed dipterocarp forests of the *Parashorea malaanonan* type A (Marsh and Greer, 1992).
- *Kabili–Sepilok Forest Reserve*: a coastal forest fragment of 4294 ha, with more than one-third of that area consisting of mangrove forest fringing Sandakan Bay (5°54′N and 118°04′E). Lowland mixed dipterocarp forest of the *P. tomentella–E. zwageri*

type is found between 20 and 120 m a.s.l. (Fox, 1973).

Nests were located either by chance during field trips or by inspecting trees located along forest trails (57% of nests), and by standardized nest surveys along transect grids established for quantitative measurements of stingless bee nest density (43% of nests; Eltz et al., 2001). We pooled data sets for the analyses presented below.

2.2. Nests and nest trees

For bee nests (=colonies in the present context) and nest trees we recorded the following data:

1. *Bee species*: Identification of hand-netted vouchers was done using descriptions in Schwarz (1937, 1939), the key for Sumatran species given by Sakagami et al. (1990) and by comparison with reference material. Colonies nesting in more elevated sections of tree trunks could frequently be identified by visual inspection (using binoculars) of bee size and color, as well as the highly characteristic shape of the nest entrance tube. However, colonies nesting at the upper canopy level (30–50 m high) could not be identified and are treated as *Trigona* spp.
2. *Nest type*: We distinguished two general modes of nesting. 'Cavity nests' were situated within hollows in the tree trunks and are characterized by entrance tubes emerging from those hollows via openings in the wood. Cavity nests could be at any height of the tree trunk. 'Base nests', on the other hand, were always situated under or in the bases of trees and are characterized by an entrance tube attached to the outer wall of the tree base, running down the tree until concealed from sight by surrounding soil. Most base nests are probably located within the upper root system of the tree (this was the case in two excavated nests of *Trigona collina*, T. Eltz, pers. obs., and in comparable neotropical *T. cilipes* and *T. fulviventris*, D.W. Roubik, pers. comm.), but in some cases the entrance tube may also curve up into the lower section of the trunk, frequently hollow in large trees (Panzer, 1976).
3. *Diameter of nest trees*: Diameter at breast height was measured (using measuring tape) or estimated by comparison with machetes of known length. In the case of trees with large buttresses dbh recordings were made for the height above the buttresses. Tree diameter is an important criterion for harvesting. Under conventional forestry guidelines in Sabah all timber trees above 60 cm dbh were considered harvestable (Marsh et al., 1996). Recently, an upper cutting limit (120 cm) has been promoted by the Sabah Forestry Department RIL guidelines (Lohuji and Taumas, 1998).
4. *Taxonomy of nest trees*: Trees were either identified in the field by experienced forestry staff, or, in most cases, using dropped leaves originating from the respective trees. Leaf samples were identified by Mr. Leopold Madani (Forest Research Centre, Sepilok), partly by cross-referencing with specimens deposited in the FRC herbarium. Based on these identifications and in accordance to the relevant literature (Burgess, 1966; Hing, 1986; Lemmens et al., 1995; Soerianegara and Lemmens, 1994; Sosef et al., 1998), we classified nest trees as commercial or non-commercial species.
5. *Estimated log quality*: The commercial potential of a subset of nest trees ($N = 47$) as well as that of randomly chosen control trees (no nest, >60 cm dbh, $N = 75$) was estimated by an experienced forest ranger, Mr. Hussin Achmad (Wilaya, Sandakan). In addition to tree size and species, judgements were based on a range of characters including the form and integrity of the trunk, crown shape, presence or absence of epiphytic fungi, and signs of broken branches. Hollowness was also indicated by sound emissions evoked by knocking on buttresses and accessible sections of the trunk using parangs (machetes). Trees were then assigned to one of the three quality classes:
   - Good: no visible flaws, solid and straight log over the entire length, prime quality.
   - Medium: minor flaws, but substantial trunk segments harvestable.
   - Bad: major flaws, no commercially valuable segments of sufficient length to warrant harvesting.

   In combination with other criteria (tree size, tree species) this classification was used to estimate the percentage of nest trees that were likely to be harvested in case of selective logging.

The classification is likely to suffer from inaccuracies and should only be regarded as an approximation of the true harvest potential of nest trees. In particular, the judgement of hollowness could be biased due to the fact that our estimations were based on uninvasive methods. During logging operations, in contrast, tests for hollowness are made by pushing the blade of the chain saw vertically into the stem. If the resistance to the saw abruptly changes, the tree is considered hollow (Trockenbrodt et al., in press). Judgements are somewhat subjective and decisions made by fellers have been shown to be incorrect in many cases (Trockenbrodt et al., in press). Thus, the extent of bias in our own judgements is difficult to estimate. On average, however, our classification in harvest trees (good, medium) and non-harvest trees (bad) is likely to be reasonably close to that made during logging operations.

3. Results

3.1. Nests and nest aggregations

We found a total of 275 natural nests of 12 species of stingless bees in the three different forest reserves. Stingless bees of all but seven nests could be identified to species. Without exception, the nests were associated with living or dead trees (142 trees, see nest tree analysis below) and could easily be classified as cavity nests or base nests. Table 1 summarizes the results of nest type and height for the different species. It was obvious that the different species had distinct preferences in nesting. The majority of species (seven) were cavity nesters, but the majority of detected nests (81%) belonged to predominantly base-nesting species: among those, *Trigona* (*Tetragonula*) *collina*, a medium-sized black bee (~6.5 mm body length), was by far the most common species (52% of all nests), followed by *T.* (*Tetragonula*) *melanocephala* (~5.5 mm; 13.8%) and *Hypotrigona pendleburyi* (~3 mm; 13.4%). The pronounced imbalance in favor of base-nesting species is probably due to difficulties in detecting colonies situated close to or within the canopy. Accordingly, the most common cavity-nesting species, *T.* (*Lepidotrigona*) *terminata* (~6 mm; 7%), has a tendency to nest at relatively low height (Table 1).

Fifty-seven of 142 individual nest trees (40.1%) harbored more than one (maximum: 8) bee nests (mean 1.94 nests/tree), and 64% of the aggregations consisted of more than one (up to three) bee species (mean of 1.3 species/nest tree; Table 2). All species observed in appreciable numbers were sometimes

Table 1
Number, type, and height of nests of stingless bee species

	Number of nests	Number of base nests	Number of cavity nests	Height of cavity nests (m)		
				Mean	Minimum	Maximum
T. (*Tetragonula*) *collina*	143	134	9	2.9	1	15
T. (*Tetragonula*) *geissleri*	1		1	?		
T. (*Tetragonula*) *laeviceps*	7		7	3.1	0.3	10
T. (*Tetragonula*) *laeviceps*-group[a]	2		2	0.8		
T. (*Tetragonula*) *melanocephala*	38	37	1	0.5		
T. (*Tetragonula*) *melina*	6	6				
T. (*Odontotrigona*) *haematoptera*	5		5	4.7	2	10
T. (*Lepidotrigona*) *terminata*	19	1	18	3.1	0.3	15
T. (*Homotrigona*) *fimbriata*	6		6	15	1	35
T. (*Tetrigona*) *binghami*	3		3	9.3	3	20
T. (*Tetrigona*) *apicalis*	1		1	6		
H. (*Pariotrigona*) *pendleburyi*	37	35	2	1.5	1.5	1.5
Trigona spp.	7		7	25.7	10	40
Total	275	213	62			

[a] A probably undescribed species of the subgenus *Tetragonula* that is slightly smaller than *T. laeviceps*. Possibly identical with the small variety of *T. laeviceps* mentioned in Sakagami et al. (1990).

Table 2
Degree of nest clustering and the tendency to form monospecific and/or mixed nest aggregations in individual nest trees of stingless bee species. Species associated in aggregations are indicated by the following abbreviations—b: *T. binghami*; c: *T. collina*; f: *T. fimbriata*; g: *T. geissleri*; h: *T. haematoptera*; l: *T. laeviceps*; l*: *T. cf. laeviceps*-group; mca: *T. melanocephala*; ma: *T. melina*; p: *H. pendleburyi*; t: *T. terminata*

	Nests	Nest trees	Number of nests in aggregations (%)	Nests in aggregations		Associated species
				Monospecific	Mixed	
T. (*Tetragonula*) *collina*	143	72	113 (79.2)	60	53	c, b, f, g, h, ma, mca, p, t
T. (*Tetragonula*) *geissleri*	1	1	1		1	c, f
T. (*Tetragonula*) *laeviceps*	7	5	3 (42.9)		3	l, b, t
T. (*Tetragonula*) *laeviceps*-group[a]	2	2	1 (50.0)		1	t
T. (*Tetragonula*) *melanocephala*	38	36	21 (55.3)	2	19	mca, c, h, ma, p
T. (*Tetragonula*) *melina*	6	6	3 (50.0)		3	c, mca
T. (*Odontotrigona*) *haematoptera*	5	5	2 (40.0)		2	c, mca, t
T. (*Lepidotrigona*) *terminata*	19	19	8 (42.1)		8	b, c, h, l, l*, ?
T. (*Homotrigona*) *fimbriata*	6	6	1 (16.7)		1	c, g
T. (*Tetrigona*) *binghami*	3	3	2 (66.7)		2	c, l, t
T. (*Tetrigona*) *apicalis*	1	1				
H. (*Pariotrigona*) *pendleburyi*	37	20	36 (97.3)	4	32	p, c, mca
Trigona spp.	7	7	1 (14.3)			t

[a] A probably undescribed species of the subgenus *Tetragonula* that is slightly smaller than *T. laeviceps*. Possibly identical with the small variety of *T. laeviceps* mentioned in Sakagami et al. (1990).

found to be part of aggregations, but the likelihood to aggregate and the tendency to form conspecific versus mixed aggregations seemed to vary among species. We tested for differences among the three most abundant base-nesting species, *T. collina*, *T. melanocephala* and *H. pendleburyi*. Frequencies of numbers of nests in a 3 × 3 contingency table (species × type of aggregation) were clearly heterogeneous ($\chi^2 = 49.28; N = 218; \text{d.f.} = 4; p < 0.001$; Fig. 1). Whereas *T. collina* and *T. melanocephala* frequently nested alone, all but one colony of *H. pendleburyi* were found in aggregations with other nests. Interestingly, these were mostly mixed aggregations where up to five colonies of *H. pendleburyi* were associated with one or two of the other base-nesting species. In contrast, the majority of aggregated *T. collina* nests were found in association with conspecifics only, although mixed aggregations were also common. Colonies of *T. melanocephala* either nested alone, or singly in association with other species (Fig. 1).

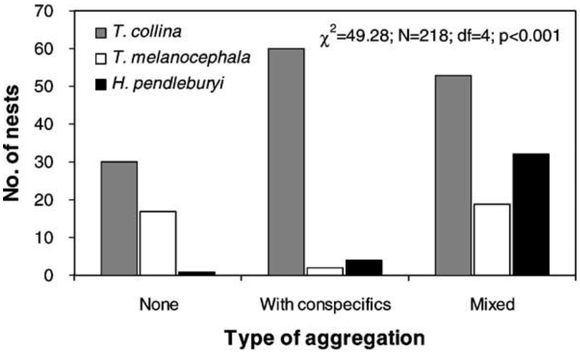

Fig. 1. Frequency of nests of three base-nesting species of stingless bees found singly or in aggregation with other colonies.

3.2. Nest trees: taxonomy

Twelve (8.5%) of the 142 nest trees were dead, the remaining (91.5%) were living trees of which 80 were identified to species or genus (Table 3). The family Dipterocarpaceae was predominant (43.7%), followed by Lauraceae (26.3%), Leguminosae (5.0%), Anacardiaceae, Euphorbiaceae, Olacaceae (each 3.8%) and others. Among Dipterocarpaceae, the genus *Shorea* (Red and Yellow Seraya, Selangan batu) was most common. The vast majority of nest trees belonged to genera and species that are considered commercial timber trees under both conventional (95.0% of trees) and RIL (88.7%) guidelines. The difference between RIL and conventional guidelines is due to the fact that some nest trees belonged to species protected under RIL (*Shorea pinanga*, *Shorea mecistopteryx*; Table 3).

Table 3
Taxonomic composition, local common names and commercial affiliation of nest trees of stingless bees in Sabah

Tree species	Family	Trade name	Number of nest trees	Commercial species	Protected (RIL)
Gluta oba	Anacardiaceae	Rengas	1	x	
Gluta sabahana	Anacardiaceae	Rengas	1	x	
Gluta sp.	Anacardiaceae	Rengas	1	x	
Lophopetalum beccarianum	Celastraceae	Perupok	1	x	
Lophopetalum sp.	Celastraceae	Perupok	1	x	
Dipterocarpus grandiflorus	Dipterocarpaceae	Keruing	1	x	
Dipterocarpus sp.	Dipterocarpaceae	Keruing	1	x	
Shorea acuminatissima	Dipterocarpaceae	Yellow Seraya	2	x	
Shorea atrinervosa	Dipterocarpaceae	Selangan batu	1	x	
Shorea beccariana	Dipterocarpaceae	Red Seraya	1	x	
Shorea exelliptica	Dipterocarpaceae	Selangan batu	1	x	
Shorea falciferoides	Dipterocarpaceae	Selangan batu	2	x	
Shorea fallax	Dipterocarpaceae	Red Seraya	1	x	
Shorea ferruginea	Dipterocarpaceae	Red Seraya	1	x	
Shorea gibbosa	Dipterocarpaceae	Yellow Seraya	1	x	
Shorea johorensis	Dipterocarpaceae	Red Seraya	1	x	
Shorea macroptera	Dipterocarpaceae	Red Seraya	1	x	
Shorea mecistopteryx	Dipterocarpaceae	Kawang	1	x	x
Shorea multiflora	Dipterocarpaceae	Banjutan	3	x	
Shorea parvifolia	Dipterocarpaceae	Red Seraya	2	x	
Shorea pauciflora	Dipterocarpaceae	Oba suluk	2	x	
Shorea pinanga	Dipterocarpaceae	Kawang	3	x	x
Shorea smithiana	Dipterocarpaceae	Red Seraya	1	x	
Shorea waltonii	Dipterocarpaceae	Red Seraya	1	x	
Shorea sp.	Dipterocarpaceae	div.	8	x	
Chaetocarpus castanocarpus	Euphorbiaceae	Kayu dusun	2	x	
Trigonopleura malayana	Euphorbiaceae	Gambir hutan	1		
Lithocarpus, *Quercus* sp.	Fagaceae	Mempening	1	x	
Hydnocarpus woodii	Flacourtiaceae	Karpus wood	1	x	
Callophyllum sp.	Guttiferae	Bitangor	1	x	
Dehassia sp.	Lauraceae	Medang	1	x	
Eusideroxylon zwageri	Lauraceae	Belian	16	x	
Litsea caulocarpa	Lauraceae	Medang	1	x	
Litsea sp.	Lauraceae	Medang	2	x	
Phoebe macrophylla	Lauraceae	Medang	1	x	
Dialium sp.	Leguminosae	Keranji	1	x	
Intsia palembanica	Leguminosae	Merbau	1	x	
Sympetalandra borneensis	Leguminosae	Merbau Lalat	2	x	
Ficus sp.	Moraceae	Kayu Ara	2		
Syzigium sp.	Myrtaceae	Obah	2	x	
Scorodocarpus borneensis	Olacaceae	Bawang hutan	3	x	
Scaphium affine	Sterculiaceae	Kembang semangkok	1	x	
Wikstroemia sp.	Thymelaeaceae	Tindot	1		

Generally, nest tree diversity was high (22 genera with at least 38 species), and many tree species were only represented by a single individual. By far the most common single species (20.0%) was the Bornean Ironwood or Belian (*Eusideroxylon zwageri*, Lauraceae), a tree that is famous for having exceptionally hard and durable wood (Burgess, 1966; MacKinnon et al., 1996). Seventeen of 30 nests associated with *E. zwageri* were cavity nests (57%), a frequency that is significantly different from that found in the whole of the remaining tree community (18%; $\chi^2 = 22.45$; $N = 275$; d.f. $= 1$; $p < 0.001$). Notably, several bee

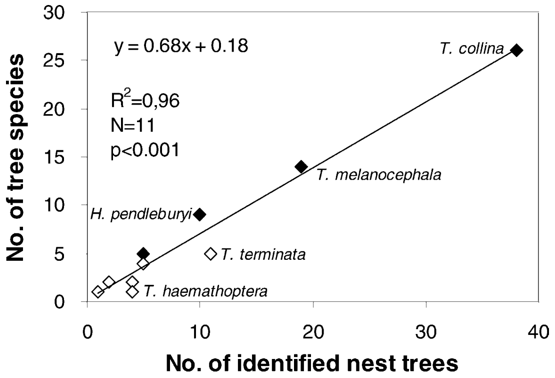

Fig. 2. Relationship between the number of identified nest trees and nest tree species richness for different stingless bee species. Solid diamonds are (predominantly) base-nesting species, open diamonds are cavity-nesting species.

nests were also found in dead Belian trees (five out of the 12 dead nest trees) which, due to the durability of their wood, can escape decay for years or even decades.

Generally, across all species, nest trees tended to harbor either cavity nests or base nests. Only three individual trees were home to both types of bee nests.

All bees species that were recorded in number nested in or under a variety of nest tree taxa, and nest tree diversity per bee species was strongly dependent on the number of identified nest trees ($R^2 = 0.96$; $N = 11$; $p < 0.001$; Fig. 2). The two cavity-nesting species *T. terminata* and *T. haematoptera* had relatively low nest tree diversity, a finding that is due to their apparent preference for *E. zwageri*. In *T. terminata*, six out of 11 identified trees were *E. zwageri*, and in *T. haematoptera* all four identified nest trees belonged to this species.

3.3. Nest trees: size

Most bee nests were situated in or under large to very large canopy trees, with trees harboring base nests being larger on average than trees harboring cavity nests (ANOVA: $F = 8.88$; $N = 120$; d.f. $= 1$; $p < 0.01$; Fig. 3). A total of 86.1% of nest trees were larger than 60 cm dbh, and 73.0% were between 60 and 120 cm dbh, the size range considered fit for harvesting according to official RIL guidelines.

The number of nests associated with a given tree was positively correlated with tree diameter in base-nest trees ($R_s = 0.37$; $N = 81$; $p < 0.0001$), but not among cavity-nest trees ($R_s = 0.01$; $N = 38$; $p = 0.93$). Trees larger than 120 cm dbh (13.1% of all nest trees) were home to 19.1% of all stingless bee colonies (Fig. 4).

3.4. Nest trees: timber quality

One hundred and eight of the 122 nest and control trees inspected were potential timber trees above 60 cm dbh. For these, estimates of log quality were

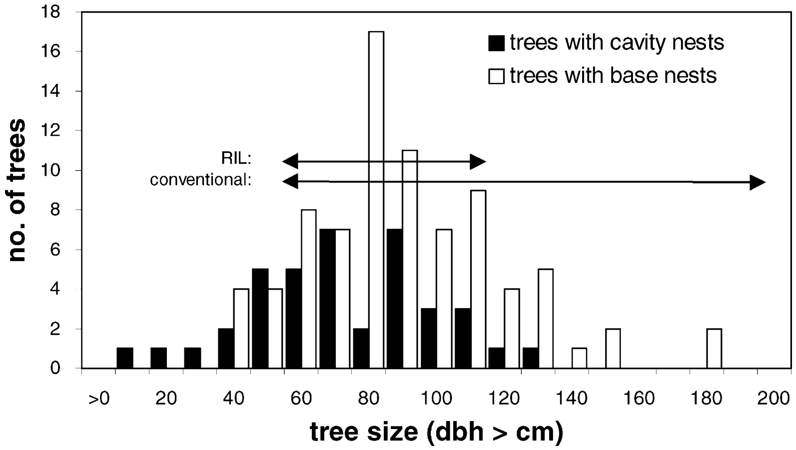

Fig. 3. Size distribution of living nest trees of stingless bees. Note difference in size between trees with cavity nest and trees with base nests. Trees harboring both nest types are not shown ($N = 3$). The arrows indicate harvesting size under conventional and RIL guidelines.

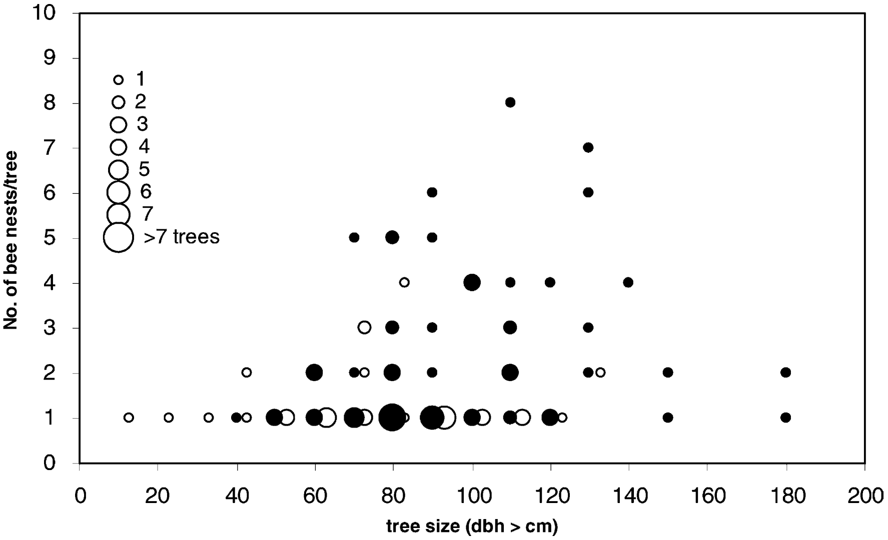

Fig. 4. The number of nests per nest tree as a function of tree size. Data are shown separately for trees with cavity nests (open circles) and trees with base nests (solid circles). Trees harboring both nest types are not shown ($N = 3$).

analyzed. The 51.2% of the nest trees were classified as 'good' or 'medium' timber quality and would qualify for harvesting given they complied with other criteria (harvest size, commercial species). Generally, nest trees were of significantly lower timber quality than control trees ($\chi^2 = 25.59$; $N = 108$; d.f. $= 2$; $p < 0.001$; Fig. 5). In order to test whether this effect was due to the larger size of nest trees, we compared frequencies of a subset of nest and control trees that were matched for size by random sub-sampling. Neither direction nor magnitude of the effect was altered ($\chi^2 = 16.29$; $N = 58$; d.f. $= 2$; $p < 0.001$), suggesting that tree size and timber quality were largely independent in trees above 60 cm dbh. The estimated timber quality did not differ between trees harboring cavity nests and trees with base nests ($\chi^2 = 0.32$; $N = 39$; d.f. $= 2$; NS; Fig. 5).

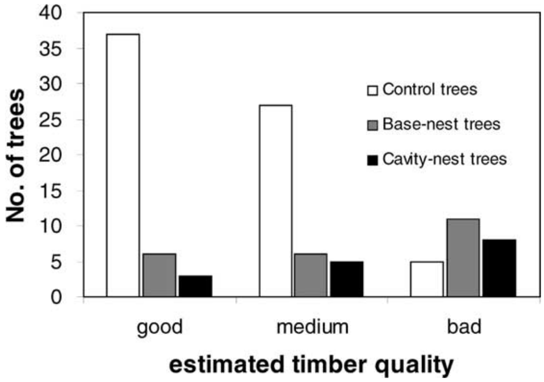

Fig. 5. Wood quality classification of nest and control trees. Frequencies of base-nest trees and cavity-nest trees are shown separately.

3.5. Percentage of potential harvest trees among nest trees

Sixteen of the 47 nest trees (34.0%) inspected by Mr. Hussin Achmad were considered harvest trees under the official RIL guidelines for selective logging published by the Sabah Forestry Department. The remaining trees were either too small (3), too large (4), had been classified as having 'bad' timber quality (21), belonged to non-commercial taxa (3), or showed combinations of these characters (5). When we applied conventional standards the number of potential harvest trees was raised to 20 (42.6%), because four very large nest trees (dbh >120 cm) were now considered fit for harvesting.

These estimates are based on a limited sample of nest trees, but percentages of likely harvest trees are roughly confirmed by results of calculations based on the entire data set. Here, we multiplied the mean likelihood of a nest tree belonging to a harvestable species (see Section 3.2) with the mean probability of having the correct size for harvesting (see Section 3.3) and being of sufficient timber quality (see Section 3.4). Respective percentages of potential harvest trees were 35.5% (RIL) and 41.9% (conventional). This approach assumes that taxonomy, size and timber quality vary independently among nest trees, an assumption that will not strictly apply in reality.

4. Discussion

4.1. Nest surveys and the stingless bee community

The present study provides the first detailed account of stingless bee nests, nest aggregations and nesting resources from natural forest areas in southeast Asia. It is based on a total of 275 nests belonging to 12 species of meliponines. Sakagami et al. (1990) listed 28 species of Meliponini from the whole of Borneo, and data from honey-baiting suggests that up to 22 species can occur sympatrically in a Bornean lowland rain forest locality (Roubik, 1996). Thus, our nest surveys located about one half of the regional stingless bee assemblage. Among the species not located by our surveys, at least six are known to be cavity-nesting species whose nests have been recorded by previous authors from Borneo or Sumatra (Sakagami et al., 1983b; Salmah et al., 1990; Roubik, 1996). Some of these (e.g., *T. canifrons* and *T. thoracica*) are large species that form huge colonies (Salmah et al., 1990) and probably occur in relatively low population densities, but others may have escaped detection because their nests are restricted to the higher canopy. Lack of canopy access and difficulties of detecting canopy colonies may have particularly biased our data for species nesting in small cavities in major branches of canopy trees. Species of the *laeviceps* species group including *T. laeviceps*, *T. fuscobalteata*, and a probably undescribed species (see Sakagami et al., 1990), are particularly likely to exploit this nesting resource. The same species are more frequently found nesting in various artificial structures (house walls, pillars, palm fronds) in close contact with humans (Salmah et al., 1990; Starr and Sakagami, 1987; D.W. Roubik, pers. comm.), but nests found in dropped branches (Eltz, unpublished data) suggest they are present in mature forests as well.

4.2. Aggregated nesting

Generally, stingless bee nests were heavily aggregated within individual nest trees in Bornean forests. Although this trend was apparent in all species that were found in number, aggregated nesting was particularly pronounced in *T. collina*, favoring conspecific aggregations, and in *H. pendleburyi*, showing a tendency to form mixed aggregations with any of the other base-nesting species. Clustering of nests in trees or artificial structures has been reported by several authors (Roubik, 1996; Salmah et al., 1990; Starr and Sakagami, 1987), but the reasons for aggregating are poorly understood. Limited availability of suitable nest sites may be one possible cause, especially in degraded areas that lack sufficient numbers of natural tree cavities. In those situations, presence of cavities and crevices in construction material of farm houses can permit phenomenal concentrations of colonies (Starr and Sakagami, 1987). In undisturbed forests, however, nest cavities are less likely to be limited. Here, clustering may be favored by mechanisms related to how new nest sites are located by bees. In stingless bees colony multiplication is started by scout bees that search for suitable nest sites (Inoue et al., 1984b; Michener, 1974). In forests in Sabah, one can frequently observe single workers of *T. collina* circling the bases of large canopy trees, presumably in search of suitable nest sites (see also Hubbell and Johnson, 1977, for *T. fulviventris* in Costa Rica). It is possible that these scout bees are guided by cues that include (or are enhanced by) the presence of other bee colonies. Specifically, odor of bee brood or nest material (resin) may indicate a particularly suitable nest tree. If no adverse effects are connected to nesting in aggregation bees should favor those nest trees because of reduced searching costs. We hypothesize that scouts of the mixed aggregation specialists *H. pendleburyi* are guided by cues provided by colonies of other species.

The tendency of some Bornean stingless bees to nest in aggregations is markedly different from patterns found in the neotropics. In a dry-forest in Costa Rica, four out of five species of meliponines studied in detail showed a uniform pattern of dispersion, and multiple nests per tree were a notable exception restricted to a single species, *Nannotrigona perilampoides* (Hubbell and Johnson, 1977). Hubbell and

Johnson (1977) argue that aggressive competition for food is the ultimate reason for uniform nest dispersion in group-foraging neotropical meliponines, and that nest spacing is proximately mediated by aggressive encounters between colonies competing for new nest sites. The idea is based on the finding that antagonistic interference between colonies of *Trigona* is strong in neotropical bee communities (Hubbell and Johnson, 1977; Johnson and Hubbell, 1974, 1975). Nest clustering may prevail in Borneo because interspecific aggression between bees is less pronounced. We have spent many weeks observing stingless bees at honey-baits and flowers in Sabah and were rarely aware of antagonistic interactions between individuals or colonies. Instead, our general impression was that of a relatively peaceful coexistence between foragers that were mostly concerned with the exploitation of resources (see Nagamitsu and Inoue, 1997).

4.3. Nest trees

Stingless bee nests were situated in or underneath a large variety of trees. Selectivity in favor of certain species of trees was apparently low as indicated by a proportional increase of nest tree diversity/bee species with nest tree sample size. A similar relationship was found by Hubbell and Johnson (1977) in a Costa Rican dry-forest. Thus, stingless bees seem to be quite opportunistic in their selection of nest sites and are likely to colonize any tree that offers a suitable cavity of the right size. It is likely, however, that tree species differ in their tendency to form suitable cavities due to differences in wood and growth characteristics. Based on our data the only obvious example of an above-average nest tree is the Bornean Ironwood or Belian, *E. zwageri* (20% of identified nest trees). Although, we lack large-scale quantitative tree inventories for our research areas, it is highly likely that *E. zwageri* is over-represented among samples of nest trees (see Fox, 1973). Belian is characterized by exceptionally durable wood that is commercially used for many purposes including heavy construction in marine environments (Burgess, 1966) and, for the bees, may serve as a effective shield against predator attacks. Additionally, Belian has a tendency to form hollows that can be accessed by bees through crevices between living and dead parts of the trunk (T. Eltz, pers. obs.).

Trees may differ in their likelihood of serving as nest trees due to differences in acquiring hollow cores due to stem rot. Panzer (1976) measured core decay of 3586 trees in mixed dipterocarp forests in Sarawak. Across all tree sizes (>30 cm dbh) and species an average of 46% of trees were found to be hollow. Hollowness increased initially with tree size in the smaller size classes, but remained relatively constant (around 54%) in trees above 60 cm dbh. This result is in agreement with our finding that estimated nest tree quality was largely independent of tree size. Notably, the percentage of hollow trees also varied between tree genera. Among dipterocarps Keruing (*Dipterocarpus*) had fewer hollow individuals than expected, perhaps because of specific wood characteristics (e.g. decay inhibitors; Panzer, 1976). Our finding that only two stingless bee nests were associated with the relatively common genus *Dipterocarpus* may be related to its apparent resistance against decay. On the other hand, Kapur (*Dryobalanops*) was relatively prone to core decay according to Panzer (1976), and was not represented among nest trees in this study. Other characters related to tree architecture, e.g. the accessibility of the hollow trunk sections, may influence the quality of different taxa as nest trees.

We have shown that a large fraction of bee nests are situated in commercial timber trees, many of which are members of the principal timber family Dipterocarpaceae. It is of special interest to see how nest frequencies relate to the representation of dipterocarps and other commercial timbers in Sabahan forests. On a coarse taxonomic level quantitative stock data are available for Deramakot forest reserve. During a planning inventory, trees in several hundred temporary plots were classified according to diameter and taxonomic as well as commercial affiliation (Chai and Amin, 1994). Table 4 shows the percentages of trees classified as: (i) dipterocarps, (ii) non-dipterocarp timber trees and (iii) non-commercial trees for trees larger than 60 cm dbh. Frequencies are contrasted with the respective percentages for stingless bee nest trees. The strong affiliation of nest trees with commercial trees roughly reflects general representation in the forest. Within the commercial classes, nest trees seem to be particularly well represented among non-dipterocarps, a finding that is partly based on the fact that *E. zwageri* (20% of all identified nest trees) is part of this class.

Table 4
Percentage of dipterocarps, non-dipterocarp timbers and non-commercial trees among nest trees (this study) and among trees recorded during the medium-term planning inventory in Deramakot forest reserve (Chai and Amin, 1994)

	Percentage of nest trees	Percentage of trees in Deramakot inventory (only >60 cm)
Dipterocarpaceae	43.75	64.42
Commercial non-dipterocarpaceae	51.25	28.85
Non-commercial species	5.00	6.73

4.4. Nest trees, logging, and stingless bee conservation

Harvesting of nest trees is very likely to cause mortality in bee nests, either directly because the nests are destroyed during felling, or indirectly because nests loose protection from predators or adverse effects of the environment (e.g. rain and/or termites). Even nests situated within tree bases that are left in place after harvesting are likely to suffer because predators can gain access to the colony through the hollow base core. This view is supported by the fact that we have very rarely found nests in tree stumps. In case of dead trees with base nests, the trees were still standing (the so-called 'snags'), thus providing structural integrity.

Calculations based on our data on tree taxonomy, size and estimated log quality suggest that at least one-third of the nest trees would be considered potential timber trees for logging. The likelihood of whether a given nest tree will indeed be harvested is influenced by a range of factors including the intensity of timber extraction and the harvesting regulations followed by operators. Extraction intensity in forests in Sabah has varied considerably during past decades, partly depending on management system, but normally resulted in logged-over forests with drastically altered stand structure (Marsh et al., 1996). More recently, efforts have been made to shift practices towards sustainable forest management (SFM) using RIL (Kleine and Heuveldop, 1993; Marsh et al., 1996). Current RIL guidelines published by the Sabah Forestry Department require detailed stock mapping, road and skid trail planning, and restrict harvesting to trees marked for felling by trained foresters (Lohuji and Taumas, 1998). In order to maintain seed sources, commercial trees are supposed to be retained if they are oversized (>120 cm dbh). According to our data this size restriction alone will reduce the proportion of harvested nest trees from 42.6 to 34.0% in comparison to conventional regulations lacking an upper diameter limit. The positive effect on bee populations will be even greater because nests tend to be more heavily aggregated in oversized trees. If RIL guidelines are followed by operators the impact on bees will be further reduced by restricting harvesting to slopes below 25° and by retaining harvestable trees in areas with insufficient regeneration. Furthermore, RIL has been demonstrated to reduce operational damage on non-harvest trees (Marsh et al., 1996), an effect that may be particularly beneficial for bees that nest in dead or low-quality trees with reduced structural stability. In summary, the strict implementation of existing RIL guidelines is highly recommendable in the light of stingless bee conservation and the maintenance of meliponine pollination in managed forests.

Other feasible measures to reduce the direct impact of harvesting on bee colonies, e.g. marking of nest trees for retention, are desirable but probably unrealistic in view of the current situation of the forestry sector in Sabah and southeast Asia in general. The current steep decline of commercially manageable forests in Sabah has led to intensified timber exploitation in the remaining fragments (Putz et al., 2000). In order to meet the planned forest productivity (annual allowable cut, AAC) in sustainably managed forests, Trockenbrodt et al. (in press) suggest to increase the use of timber in intact fractions of hollow trunks as well as large branches. The approach is aimed at: (i) reducing logging waste, and (ii) at increasing the use of timber resources available in poorly stocked management compartments. Whereas the first incentive is clearly recommendable from both economic and ecological points of view, the second implies increased harvesting of hollow trees. This, in turn, may partly offset some of the benefits of SFM and RIL for cavity-dependent wildlife (see above). An obvious trade-off exists between increasing timber productivity and maintaining aspects of ecological integrity in managed forests. More applied studies like that of Trockenbrodt et al. (in press) are needed in order to judge whether the amount of timber volume gained by an increased use of hollow trees justifies the additional damage imposed on the forest ecosystem.

5. Conclusions

We have shown that stingless bees in dipterocarp forests are closely linked to potential harvest trees due to their way of nesting. Selective logging is likely to cause direct mortality to a substantial fraction of residual bee colonies because harvesting of nest trees will destroy or expose bee nests. Due to the fact that meliponine colonies are long-lived and have low fecundity, impact from logging may have lasting effects on bee populations. However, our data also show that potential conflict between timber extraction and bee conservation is reduced when RIL guidelines were applied for estimating logging impact. Harvesting guidelines that retain high proportions of large and hollow trees should be promoted in order to preserve stingless bee pollination in SFM.

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References

Bennett, A.F., Lumsden, L.F., Nicholls, A.O., 1994. Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. Pacific Conserv. Biol. 1, 222–235.

Burgess, P.F., 1966. Timbers of Sabah. Forestry Department, Sabah, Malaysia, Sandakan, 603 pp.

Chai, D.N.P., Amin, T., 1994. Forest Management Unit No. 19—Medium-term Management Plan. Sabah Forestry Department, Sandakan, 88 pp.

Eltz, T., Brühl, C.A., van der Kaars, S., Linsenmair, K.E., 2001. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia, Oecologia D01 10. 1007/s 00442-001-0848-6.

Fox, J.D., 1973. A Handbook to Kabili–Sepilok Forest Reserve. Sabah Forest Department, Sandakan, 102 pp.

Gibbons, P., Lindenmayer, D.B., 1996. Issues associated with the retention of hollow-bearing trees within eucalypt forests managed for wood production. For. Ecol. Manage. 83, 245–279.

Hing, L.W., 1986. 100 Malaysian timbers. Malaysian Timber Industry Board (MTIB), Kuala Lumpur, 226 pp.

Hubbell, S.P., Johnson, L.K., 1977. Competition and nest spacing in a tropical stingless bee community. Ecology 58, 949–963.

Inoue, T., Sakagami, S.F., Salmah, S., Nukmal, N., 1984a. Discovery of successful absconding in the stingless bee *Trigona* (*Tetragonula*) *laeviceps*. J. Apic. Res. 23, 136–142.

Inoue, T., Sakagami, S.F., Salmah, S., Yamane, S., 1984b. The process of colony multiplication in the Sumatran stingless bee *Trigona* (*Tetragonula*) *laeviceps*. Biotropica 16, 100–111.

Inoue, T., Salmah, S., Sakagami, S.F., Yamane, S., Kato, M., 1990. An analysis of anthophilous insects in central Sumatra. In: Ohgushi, R., Sakagami, S.F., Roubik, D.W. (Eds.), Natural History of Social Wasps and Bees in Equatorial Sumatra. Hokkaido University Press, Sapporo, pp. 175–200.

Johnson, L.K., Hubbell, S.P., 1974. Aggression and competition among stingless bees: field studies. Ecology 55, 120–127.

Johnson, L.K., Hubbell, S.P., 1975. Contrasting foraging strategies and coexistence of two bee species on a single resource. Ecology 56, 1398–1406.

Kleine, M., Heuveldop, J., 1993. A management planning concept for sustained yield of tropical forests in Sabah, Malaysia. For. Ecol. Manage. 61, 277–297.

Lemmens, R.H.M.J., Soerianegara, I., Wong, W.C., 1995. Plant resources of southeast Asia. In: Timber Trees: Minor Commercial Timbers, Vol. 5, No. 2. Backhuys Publishers, Leiden, 655 pp.

Lindenmayer, D.B., Cunningham, R.B., Tanton, M.T., Nix, H.A., Smith, A.P., 1991. The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, southeastern Australia. III. The habitat requirements of Leadbeater's Possum *Gymnobelideus leadbeateri* and models of the diversity and abundance of arboreal marsupials. Biol. Conserv. 56, 295–315.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., 1997. Decay and collapse of trees with hollows in eastern Australian forests: impacts on arboreal marsupials. Ecol. Appl. 7, 625–641.

Lohuji, P.L., Taumas, R., 1998. RIL—Operation Guide Book. Sabah Forestry Department, Sandakan, Sabah, 38 pp.

MacKinnon, K., Gusti, H., Hakimah, H., Mangalik, A., 1996. The Ecology of Kalimantan. Periplus Editions, Singapore, 802 pp.

Marsh, C.W., Greer, A.G., 1992. Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. Phil. Trans. R. Soc. London B 335, 331–339.

Marsh, C.W., Tay, J., Pinard, M.A., Putz, F.E., Sullivan, T.E., 1996. Reduced impact logging: a pilot project in Sabah, Malaysia. In: Schulte, A., Schöne, D. (Eds.), Dipterocarp Forest Ecosystems. World Scientific, Singapore, pp. 293–307.

McComb, W.C., Noble, R.E., 1982. Invertebrate use of natural tree cavities and vertebrate nest boxes. Am. Midland Nat. 107, 163–172.

Michener, C.D., 1974. The Social Behavior of the Bees: A Comparative Study. Belknap Press, Cambridge, MA.

Momose, K., Yumoto, T., Nagamitsu, T., Kato, M., Nagamasu, H., Sakai, S., Harrison, R.D., Itioka, T., Hamid, A.A., Inoue, T., 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant pollinator community in a lowland dipterocarp forest. Am. J. Bot. 85, 1477–1501.

Nagamitsu, T., Inoue, T., 1997. Aggressive foraging of social bees as a mechanism of floral research partitioning in an Asian tropical rainforest. Oecologia 110, 432–439.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol. Conserv. 70, 265–276.

Oldroyd, B.P., Lawler, S.H., Crozier, R.H., 1994. Do feral honey bees (*Apis mellifera*) and regent parrots (*Polytelis anthopeplus*) compete for nest sites? Aust. J. Ecol. 19, 444–450.

Panzer, K.F., 1976. Quantifizierung von Stammfäule in hohlen Bäumen des Dipterocarpaceen-Mischwaldes von Sarawak (Borneo). Kommissionsverlag M. Wiedebusch, Hamburg, 178 pp.

Putz, F.E., Dykstra, D.P., Heinrich, R., 2000. Why poor logging practices persist in the tropics. Conserv. Biol. 14, 951–956.

Roubik, D.W., 1989. Ecology and Natural History of Tropical Bees. Cambridge University Press, New York, 514 pp.

Roubik, D.W., 1996. Wild bees of Brunei Darussalam. In: Edwards, D.S., Booth, W.E., Choy, S.C. (Eds.), Tropical Rainforest Research—Current Issues. Kluwer Academic Publishers, London, pp. 56–66.

Sakagami, S.F., 1982. Stingless bees. In: Hermann, H.R. (Eds.), Social Insects, Vol. 3. Academic Press, New York, pp. 361–423.

Sakagami, S.F., Inoue, T., Yamane, S., Salmah, S., 1983a. Nest architecture and colony composition of the Sumatran stingless bee *Trigona* (*Tetragonula*) *laeviceps*. Kontyu 51, 100–111.

Sakagami, S.F., Yamane, S., Hambali, G.G., 1983b. Nests of some southeast Asian stingless bees. Bull. Fac. Educ. Ibaraki Univ. (Nat. Sci.) 32, 1–21.

Sakagami, S.F., Inoue, T., Salmah, S., 1990. Stingless bees of central Sumatra. In: Ohgushi, R., Sakagami, S.F., Roubik, D.W. (Eds.), Natural History of Social Wasps and Bees in Equatorial Sumatra. Hokkaido University Press, Sapporo, pp. 125–137.

Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A.A., Nakashizuka, T., 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. Am. J. Bot. 86, 1414–1436.

Salmah, S., Inoue, T., Sakagami, S.F., 1990. An analysis of apid bee richness (Apidae) in central Sumatra. In: Ohgushi, R., Sakagami, S.F., Roubik, D.W. (Eds.), Natural History of Social Wasps and Bees in Equatorial Sumatra. Hokkaido University Press, Sapporo, pp. 139–174.

Saunders, D.A., Smith, G.T., Rowley, I., 1982. The availability and dimensions of tree hollows that provide nest sites for Cockatoos (Psittaciformes) in Western Australia. Aust. Wildl. Res. 9, 541–556.

Schwarz, H.F., 1937. Results of the Oxford University Sarawak (Borneo) Expedition: Bornean stingless bees of the genus Trigona. Bull. Am. Mus. Nat. Hist. 73, 281–328.

Schwarz, H.F., 1939. The Indo-Malayan species of *Trigona*. Bull. Am. Mus. Nat. Hist. 76, 83–141.

Soerianegara, I., Lemmens, R.H.M.J., 1994. Plant resources of southeast Asia. In: Timber Trees: Major Commercial Timbers, Vol. 5, No. 1. Backhuys Publishers, Leiden, 610 pp.

Sosef, M.S.M., Hong, L.T., Prawirohatmodjo, S., 1998. Plant resources of southeast Asia. In: Timber Trees: Lesser-known Timbers, Vol. 5, No. 3. Backuys Publishers, Leiden, 859 pp.

Starr, C.K., Sakagami, S.F., 1987. An extraordinary concentration of stingless bee colonies in the Philippines, with notes on the nest structure (Hymenoptera: Apidae: *Trigona* spp.). Insects Soc. 34, 96–107.

Trockenbrodt, M., Zamrie, I., James, J., in press. Hollow logs and logging residues from Deramakot Forest Reserve, Sabah, Malaysia. For. Ecol. Manage.

van Balen, J.H., Booy, C.J.H., van Franeker, J.A., Osieck, E.R., 1982. Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest sites. Ardea 70, 1–24.

Wille, A., 1983. Biology of the stingless bees. Ann. Rev. Entomol. 28, 41–64.