Honey-Making Bee Colony Abundance and Predation by Apes and Humans in a Uganda Forest Reserve[1]

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ABSTRACT

Honey-making bee colonies in Bwindi Impenetrable National Park were investigated with Batwa Pygmies locating 228 nests of *Apis* and five stingless bees (Meliponini). The relative importance of predation, food supply, nesting site, and elevation affecting abundance were studied for meliponines in particular. Nest predation and overall nest abundance had no correlation with elevation along a 1400 m gradient, nor did flowering phenology or pollen collection. Many suitable, large trees were unoccupied by bee nests. In 174 ha of forest plots, 2 *Meliponula lendliana,* 13 *M. nebulata,* 16 *M. ferruginea,* 16 *M. bocandei,* and 20 *Apis mellifera adansonii* nests occurred, suggesting a habitat-wide density of 39 nests/km^2. Compared to other studies, Ugandan Meliponini were uncommon (0.27 colonies/ha, tropical mean = 1.9/ha), while *Apis mellifera* was numerous (0.12 nests/ha, tropical mean = 0.06/ha), despite park policy allowing humans to exploit *Apis*. Meliponine colony mortality from predators averaged 12 percent/yr and those near ground were most affected. Tool-using humans and chimpanzees caused 82 percent of stingless bee nest predation. Selective factors affecting nest heights and habit may include auditory hunting by predators for buzzing bees, and indirect mutualists such as termites that leave potential nesting cavities. Mobility and free-nesting by honey bee colonies should enable rapid community recovery after mortality, especially in parks where human honey hunting is frequent, compared to sedentary and nest-site-bound Meliponini.

Key words: Apis; bee nest density; Bwindi–Uganda; chimpanzees; honey; Meliponini; predation; Pygmies.

MANY FACTORS DETERMINE ANIMAL POPULATION DENSITY, with the balance between mortality and natality often posing challenges to field ecology and conservation efforts (Andrewartha & Birch 1954, Pimm 1991, Schoener *et al.* 2001, Miskelly & Beauchamp 2004). Recent interest in highly social bee colonies, a preeminent source of concentrated sugar and protein hunted by vertebrates and social insects alike (Roubik 1989) has motivated attempts to link nest distribution and abundance to ecological factors (Hubbell & Johnson 1977, Eltz *et al.* 2002). However, the available data (Table 1) demonstrate that studies are few and most consider small areas or disturbed habitat, thus information on community patterns and nesting ecology are, at best, incomplete.

Almost all Meliponini and Apini are tropical and they constitute the highly social (perennial) honey-making bees. Natural forest nests of meliponines have been studied increasingly, *e.g.*, Hubbell and Johnson (1977), Johnson and Hubbell (1986), Oliveira *et al.* (1995), Roubik (1983a,b; 1996), Eltz *et al.* (2002) and Batista *et al.* (2003), while fewer studies concern natural nesting densities of tropical *Apis*, the "honey bees" (Table 1). Both food and nesting site availability are implicated as determinants of stingless bee nest abundance, but no previous work has treated Afrotropical forests, or even native *Apis* and Meliponini in the same habitat (but see Darchen 1972, Schneider & Blyther 1988, Roubik 1996, Stierlin & Roubik, Table 1). Moreover, if competition and food limit

colony density, such interaction may also determine foraging behavior (Villanueva & Roubik 2004), or colony size, survival, and rate of reproduction. Paradoxically, the persistence of highly social bee colonies is threatened by habitat loss (*e.g.*, Batista *et al.* 2003, Slaa 2003,), yet colonies *in general* often are most abundant, by an order of magnitude, in disturbed habitats (Table 1). Michener (1946), for example, reported that populations of meliponine bee colonies in Old Panama City were high because of the numerous holes and cavities suitable for nesting places in the ruins. Such comparisons, however, obscure the fact that many fewer species are found in such disturbed areas, compared to natural forest (Roubik 1983a). In the forest, unoccupied tree cavities are fairly common (Johnson & Hubbell 1986). However, the size of the tree hole leading to the nest cavity markedly influences acceptability to bees (Roubik 1983a) and whether resident colonies saturate their environment with bees, regardless of nest abundance, is an open question. Besides consideration of nest architecture features, such as placement of decoy brood cells near nest entrances (Camargo 1980, Camargo & Pedro 2003), protective layers of bees on the comb of *Apis* (Seeley 1985), outer nest envelope of *Trigona*, or aggregated colonies in both groups (Roubik 1989), the influence of natural enemies on stingless bee or honey bee nesting ecology has largely been ignored.

Across elevations, differences in weather or vegetation (Andrewartha & Birch 1954) influence animal abundance. For example, in the protected forest considered here, rodents and shrew abundance along an elevational gradient led Kasangaki *et al.* (2003) to conclude that species richness was affected by altitude, weather,

TABLE 1. *Tropical stingless bee (Meliponini) and honey bee* (Apis mellifera) *nest densities estimated from field censuses. The estimate is for 1 km^2 or 100 ha; study area sizes are included.*

Location	Colonies/100 ha, study area	*Apis*	Meliponini	Source
Costa Rica, dry forest	550, 36.7 ha	−	+	Hubbell and Johnson (1977)
Panama, moist forest[a]	460, 64.7 ha	−	+	Michener (1946)
Panama, moist forest	102, 15.6 ha	−	+	Johnson and Hubbell (1986)
Panama, wet forest	375, 8 ha	−	+	Roubik (1983a)
Bolivia, moist forest	66, 50 ha 2, 50 ha[b]	+	+	Stierlin and Roubik (unpub.)
Bolivia, dry forest	54, 50 ha 2, 50 ha[b]	+	+	Stierlin and Roubik (unpub.)
Brazil, moist forest	15, 100 ha	+?	+	Oliveira *et al.* (1995)
Brazil, dry forest	107, unknown[b]	+	−	Kerr, cited by Michener (1975)
Thailand, moist forest	68, 24 ha	+	+	Roubik and Harrison (unpub.)
Thailand, moist forest[a]	1500, 4 ha	+	+	Roubik and Harrison (unpub.)
Panama, moist forest	56, 50 ha	+	+	Roubik and Harrison (unpub.)
Brazil, moist forest[a]	1115, 11.3 ha	+	+	Batista *et al.* (2003)
Mexico, moist forest[a]	6, 400 ha[b]	+	−	Ratnieks *et al.* (1991)
Borneo, moist forest	50, 4.8 ha	−	+	Eltz *et al.* (2002)
Borneo, moist forest[a]	840, 2.8 ha	−	+	Eltz *et al.* (2002)
Borneo, moist forest	274, 12 ha	+	+	Roubik (1996)
Borneo, wet forest	175, 8 ha	+	+	Nagamitsu and Inoue (1997)
Botswana, xeric shrub	7.8, 600 ha[b]	−	+	Schneider and Blyther (1988)
Ivory Coast, dry forest	260, 30 ha 10, 30 ha[b]	+	+	R. Darchen (1972) and pers. comm. (Roubik 1983b)
Uganda, montane forest	27, 174 ha 12, 174[b]	+	+	Present study

[a]Disturbed or secondary growth, mosaic "fragmented" sites.

[b]Estimate for *Apis mellifera*.

and vegetation type. Slaa (2003) observed that reduced sunlight diminished food collection by stingless bees in Costa Rica, and in our Afromontane forest the physical environment varies considerably due to rain and cloud cover, and also temperature. Furthermore, tropical bees are less species-rich at higher elevations, with lower temperatures indicated as the limiting factor (Silveira & Cure 1993, Gonzalez & Engel 2004, Roubik & Hanson 2004).

This study was part of our effort to understand nesting ecology of highly social bees—native stingless bee and honey bee populations—in Bwindi Impenetrable National Park (BINP) across an elevation gradient of 1447 m. Here we consider predators in more detail than do previous field studies of honey-making bees, and analyze meliponine nest abundance relative to availability of nesting sites, food, and the elevation or weather.

METHODS

STUDY SITES.—BINP, located in southwestern Uganda on the western edge of the rift valley, lies between 0°18′ and 0°53′S. latitude, and 29°35′ to 29°50′E. longitude. It is among the largest natural forests in East Africa (331 km^2) and contains both montane and upper elevation lowland forest. The park is a UNESCO World heritage site, which supports a large number of plants and animals endemic to that region, most notably half the world's population of mountain gorillas (*Gorilla gorilla berengei*). It is also home to another ten primate species including chimpanzees. The forest underwent rapid exploitation of timber through pit-sawing and conversion to agricultural land in the 1970s and the first half of the 1980s, which devastated the valleys (Butynski 1984), now in recovery. The altitude of the park is from 1160 m in Ishasha gorge to 2607 m at Rwamunyonyi peak. Temperatures are approximately 7–20°C with a mean of 16.3°C. The heaviest rains occur in March–May and September–November, with two dry seasons in December–January and June–July (Butynski 1984). Annual precipitation varies from 1130–2390 mm.

SURVEY OF NESTS AND SUITABLE NEST SITES.—Field work was conducted between November 2001 and February 2004, using local guides and Batwa Pygmies, the indigenous honey-hunters residing near the park. Methods used to survey nests and suitable nest trees were similar to those of Roubik (1996), Eltz *et al.* (2002), and Hubbell and Johnson (1977). We established 87 plots of 2 ha (500 × 20 × 2 = 20,000 m^2), and two parallel 500 m transects were made in each plot, separated by 100 m. We searched for flying bees and nest entrance tubes on tree trunks of ≥20 cm dbh in 20 m corridors along the transects. We also searched for underground nests and for those in field station house walls and houses near the

park. Because the park is divided into two sectors, northern and southern, which differ by elevation, transects or quadrat counts and surveys along trails were carried out in each sector. At first we tried to search for nests once a week in the plots and elsewhere. Few nests were located using this method. More nests were discovered from information supplied by the Pygmies and field assistants, who were tracking chimpanzees or gorillas. This information was recorded as supplemental. The transect counts were transformed into nest density/ha by incorporating area searched (length of transect × 20 m), or the area encompassed along the trails (Roubik 1996, Roubik & Skelley 2001). The total area searched within transects was thus 174 ha. Stingless bees were readily identified according to the local Pygmy names and then by DWR, consulting Eardley (2004). Colonies nesting high in the trees were found using binoculars, and bees that were not easily identified were collected at up to a height of 56 m. Trees with DBH (diameter at breast height) >60 cm were likely to hold suitable nesting sites for stingless bees (Eltz *et al.* 2002). Therefore, the trees with ≥60 cm DBH were tallied for a simple index of potential nesting sites. In each plot, counts were recorded separately for five DBH classes: 5–14, 15–29, 30–59, 60–99, and ≥100 cm.

The park authorities have instituted a program involving local communities in park management, which allows people to harvest nontimber forest products, including nests of *Apis mellifera* for domestication. Because this level of disturbance was not considered natural forest ecology for native honey bees, the predators of stingless bee nests were of special interest. The larger predators often were identified by our guides using the particular knuckle marks (gorillas and chimpanzees), feces near the nest where the predator had just fed, or its hair. Otherwise, the marks left on the nesting substrate, including scratches and tool marks, and the tools themselves (used by the chimpanzees, see Results) indicated predator identity. Nests that had been predated were recognized to belong to a particular bee species by the nest entrance, placement and architecture, which we discuss elsewhere.

FOOD RESOURCES.—The availability and quantity of floral food used by the forest stingless bees were assessed by comparing pollen types brought to nests by foraging *Meliponula bocandei*, the largest stingless bee species and most abundant, thus expected to have a large foraging range and a broad diet base. Four sites were chosen, two inside the forest at Rungo (five colonies) and Ntendule (five colonies) and two at a border of the park, neighboring the villages Ruhija (four colonies) and Kitahurira (six colonies). These sites represented the complete altitudinal range of observed nests. The methods used were similar to Eltz *et al.* (2002) and Absy and Kerr (1977). Returning pollen foragers were net-trapped at nest entrances. Trappings were done between 1000 and 1500 h, the peak time for pollen foraging in this relatively cool, largely montane park. On average we were able to collect 10–20 bee pollen loads per day from each colony. From June 2002 to January 2004, pollen loads were collected once a week in four sampling periods: two rainfall peaks (March–May and September–November) and two dry season peaks (December–January and June–July). Overall, 150–250 pollen samples were collected per colony. Pollen reference collections and prepared pollen slides from Makerere University herbarium were used to aid in pollen identification. Pollen treatment was made following the methodologies of Sawyer (1988). Pollen collected by *M. bocandei* in four different sites was analyzed for pollen of forest plants or from agricultural plants neighboring the forest. Flowering phenology in the park was recorded throughout the study to document general availability of pollen and nectar.

RESULTS

A total of 47 occupied nests of 5 stingless bees (*Meliponula* and subgenera *Axestotrigona* and *Meliplebeia*) and 20 of *A. mellifera adansonii* were found in the 174 ha plot transects (Tables 1 and 2). Two morphs of *Meliponula ferruginea* were found, one now a taxonomic synonym (Eardley 2004). The black form is *M. ferruginea* (black) and the other is brown, here called *M. ferruginea* (brown), which was absent in the high elevation sector (Table 2). No nests of *M. lendliana* were encountered in the southern sector (Table 2). The walls of park houses at BINP and the lower elevational sector contained nests of *Hypotrigona gribodoi*. Hundreds of nests

TABLE 2.   *Total stingless bee and honey bee nests located in BINP, Uganda. Nests were found along the park trails, on transects or by field researchers. TN = Overall total number of nests. QS = Nests from quantitative plot surveys (transects). Local names are given under the scientific name.* Hypotrigona *(common name Obuhumbwambwa) was only in house walls, thus is omitted in the table.*

Bee species	Northern sector			Southern sector			Overall		
	TN	QS	Nests/ha	TN	QS	Nests/ha	TN	QS	Nests/ha
A. mellifera	41	13	0.08	32	7	0.14	73	20	0.12
M. bocandei (Maranga)	33	12	0.13	17	4	0.05	50	16	0.09
M. ferruginea (brown) (Obuganza)	29	6	0.07	0	0	0	29	6	0.03
M. ferruginea (black) (Obugashu)	9	4	0.04	19	6	0.07	28	10	0.06
M. ferruginea (all)	38	10	0.06	19	6	0.07	57	16	0.09
M. lendliana (Obujagali)	5	2	0.02	0	0	0	5	2	0.01
M. nebulata (Obwiza)	6	3	0.03	31	10	0.12	37	13	0.07

occurred in such houses, yet almost none were located in forest. With six nests of that species included, 228 nests of Meliponini and *Apis* were located in and near plots. In total, the high elevation sector had 68 and the lower elevation sector 87 additional meliponine nests (Table 2). Those considered from outside of the plots were, according to species, from 1.8–2.8 times the number of nests within plots.

The overall stingless bee nest density was 0.27 nests/ha, and including *A. mellifera* there were 0.39 colonies of highly social bees/ha, the equivalent of 39/km^2. Species nest density was lowest for a ground-nesting species (*M. lendliana*: 1 nest/km^2; 4% of nests) and highest for *A. mellifera* in tree cavities (12 nests/km^2; 30% of nests). Nest density for *M. bocandei* was higher in the northern sector (13 nests/km^2) compared to the south (5 nests/km^2). For *M. nebulata*, however, higher density was found in the southern, higher elevation region (12 nests/km^2) compared to the north (3 nests/km^2).

SUITABLE NEST SITES.—Forty-six of the 87 plots surveyed contained at least one honey-making bee nest. Thus 48 percent did not contain any nests. In the 41 plots, the number of potential nest trees, DBH ≥60 cm, ranged from 4 to 51 with a median of 22 (Fig. 1). Occupied and unoccupied trees showed no size difference. All 20 nests of *A. mellifera* were in tree cavities. Soils in which terrestrial nests of stingless bees occurred were found to be mainly humic red loams. Nests of *M. bocandei* were at depths of 20–40 cm and those of *M. lendliana* 10–20 cm, above the water table of this montane forest with steep slopes.

FOOD RESOURCES.—Pollen of 67 species and at least 20 plant families was used by *M. bocandei*. Mean representation of the most dominant pollen was 21 percent (*Vernonia*), a shrub growing in edges and clearings. Colonies in Ruhija and Kitahurira bordering the villages also collected small traces of nonforest pollen during the wet season, including *Zea mays* (2%), *Sorghum nigricans* (2%), *Ipomoea batatas* (1.5%), and *Musa* (1%; Table 3). Thus colony diets were not dominated by agricultural plants. Colonies situated in continuous forest in Rungo and Ntendule used no agricultural pollen. Incoming pollen was sampled readily throughout the year. Herbs, climbers, shrubs, and trees flowered year-long, with peaks at the start of the wet seasons, March–May and September–November (Table 3).

PREDATION AND MORTALITY.—Twenty-eight percent of stingless bee nests were partly or completely destroyed; for the 28 months of field study, yearly nest predation (mean = 12% across species) was 8.6 percent (*M. lendliana*), 10.5 percent (*M. ferruginea*), 12.7 percent (*M. nebulata*), 14.1 percent (*H. gribodoi*), and 16.3 percent (*M. bocandei*). The 28 percent figure includes nests initially found opened and destroyed, thus colonies possibly died before the study, and some may have been killed by invertebrate predators or by multiple predators (Table 4). We did not find unoccupied, intact nests. Of the total stingless bee colonies, 15 percent were destroyed by man (although no one is allowed to enter the park or remove forest products without permission). Chimpanzees (*Pan troglodytes*) destroyed 10 percent. The other predators, civets (*Civettictis civetta*), gorillas (*G. gorilla berengei*), and baboons (*Papio anubis*) destroyed 3 percent of the nests. Humans used special tools such as axes and machetes to cut tree trunks and in the case of the ground-nesting species, used hoes to dig the ground to harvest colonies and food stores.

A comparison of nest heights, simply considering those intact or predated, showed clearly that lower nests were more likely to suffer mortality by predation (χ^2, $P = 0.05$, 2×2 contingency table test, heights >7, compared to others). The mean nest height was 8 m in the upper elevation sector and 10 m in the lower elevation, while the overall mean was 7.3 m for predated nests. Different stingless bee species were not uniformly predated by vertebrates (χ^2, $P = 0.003$), with maximum predation on the largest species, *M. bocandei* (38%) and the lowest on the small *M. lendliana* (20%). The former species had nest heights that averaged 16 m, while those of *M. lendliana* were always in the ground. However, more nests of *M. bocandei* were in the ground ($N = 17$) than any other bee. Elevation had no correlation with the probability of nest predation, nor did the predation intensity of two major predators, humans and chimpanzees, change with elevation (χ^2, contingency table tests, $P = 0.23$ and $P = 0.83$, respectively).

Sticks used by chimpanzees to harvest brood, honey, and pollen were found on the ground near trees with stingless bee nests (Fig. 2). We never observed chimpanzees using the tools, but our Pygmy guides had witnessed such events. All trees with active colonies ($N = 7$) had from one to seven tools scattered near the trunk. Ten tools found at the base of four trees containing nests of *M. nebulata* and *M. ferruginea* (black) had a mean length of 33.8 cm (range 19.2–68.9 cm) and a mean mid-point diameter of approximately 0.7 cm. All sticks had been cleared of attached leaves and twigs. Sticks were missing bark from one or both ends and were peeled as well as chewed; the stems were flexible and believed to be vines or lianas (C. Tutin, personal communication, Fig. 2). The
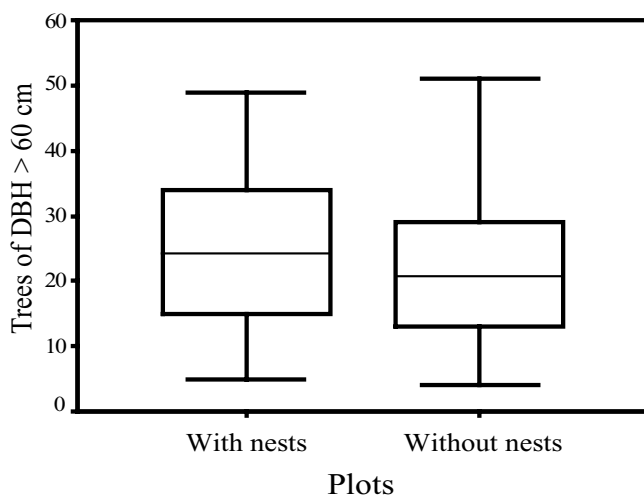

FIGURE 1.   Median range of the number of trees with DBH ≥60 cm found with nests ($N = 46$) or without nests ($N = 41$) in the 87 plots (174 ha) surveyed.

TABLE 3.   *The most abundant pollen types from returning foragers (20/day/colony, biweekly, June 2002–January 2004) of 20 colonies of* Meliponula bocandei *(represented by at least 10% of grain number for the forest plants and at least 1% for agricultural plants) in the high elevation and lower elevation (S. and N., respectively) of BINP, Uganda.*

Family	Species	Southern sector		Northern sector	
		Ruhija	Rungo	Kitahurira	Ntendule
Acanthaeceae	*Mimulopsis*			x	x
Asteraceae	*Bidens pilosa*	x	x		x
Asteraceae	Type 1				
Asteraceae	*Vernonia*	x	x		
Bignoniaceae	*Markhamia lutea*			x	
Commelinaceae	*Commelina*	x			
Convolvulaceae	*Ipomoea*	x		x	
Euphorbiaceae	*Alchornia hirtella*		x		
Euphorbiaceae	*Croton macrostachyus*	x	x		
Euphorbiaceae	*Macaranga*				x
Euphorbiaceae	Type 2			x	
Fabaceae	*Acacia*	x		x	
Fabaceae	Type 3				x
Fabaceae	Type 4				
Loganiaceae	*Nuxia congesta*		x		
Meliaceae	*Carapa grandifolia*	x	x		
Moraceae	*Ficus capensis*			x	
Musaceae	*Musa*	x		x	
Myricaceae	*Myrica salicifolia*		x		
Myrtaceae	*Eucalyptus*		x	x	x
Myrtaceae	*Syzygium guineense*				x
Myrtaceae	Type 5				x
Myrtaceae	Type 6				
Myrtaceae	Type 7		x		
Not identified	Type 8		x		
Not identified	Type 9	x			
Passifloraceae	*Passiflora*	x		x	
Piperaceae	*Piper guineensis*	x			
Poaceae	*Pennisetum purpereum*				x
Poaceae	*Zea mays*	x		x	
Proteaceae	*Faurea saligna*		x		
Proteaceae	*Prunus africana*				
Rubiaceae	*Coffea*	x		x	
Solanaceae	*Datura stramonium*			x	
Zingiberaceae	*Aframomum*			x	

TABLE 4.   *Vertebrate colony predators of stingless bees. Figures indicate number of nests destroyed by each predator, number of nests not predated, and total nests located.*

Bee species	Man	Chimpanzee	Civet	Gorilla	Baboon	Intact	Total
H. gribodoi	2					4	6
M. bocandei	10	9				31	50
M. ferruginea (br)	6	3				20	29
M. ferruginea (bl)	1		3		1	23	28
M. lendliana		1				4	5
M. nebulata	5	3	1	2		26	37
Total	24	16	4	2	1	108	155

as secondary predators, harvesting honey and brood from nests that had recently been opened by humans or chimpanzees.

ALTITUDE.—Fewer bee species nested at higher elevation (data not shown) but no overall change in stingless bee nest abundance occurred, based on $R^2 < 0.001$ from regression of altitude on nests. Larger bee species (*M. bocandei*: 9 mm; *M. nebulata*: 7 mm; *M. ferruginea* black, 7 mm) nested along the entire elevational gradient, as did *A. mellifera*. The smaller species (*M. lendliana*, 4 mm) and *H. gribodoi*, (2–3 mm) were found primarily at 1300–1900 m, while *M. nebulata* was more abundant in the upper montane area.

OTHER CAUSES OF MORTALITY.—The bees are under threat from forest fires which usually occur during severe drought. In July 1999

FIGURE 2.   The tools used by Chimpanzees and humans to remove honey and food from highly social bee nests. Above is a brush made by indigenous people (Bolivia, courtesy of E. Stierlin and H. Szabo), and below are three woody lianas used by Chimpanzees (courtesy C. Tutin, Lope Reserve, Gabon).

bare end was often frayed and smelled strongly of honey, brood, and pollen. The other animals, civets (*Civettictis civetta*), gorillas (*G. gorilla berengei*) and baboons (*Papio anubis*) destroyed stingless bee nests to some degree. They did not use tools but rather, their hands, muzzles, or claws. In most cases they evidently acted

when the area was still extremely dry, a large area in the southern part of the park was destroyed by fire. Local inhabitants tried to extinguish the fire but lacked equipment. At the beginning of August, rain extinguished fires in the few remaining smoldering areas. Other causes of bee mortality, which can contribute to colony death, included generalist predators of insects, such as ants, toads, and lizards, especially when the nests were situated close to the ground.

DISCUSSION

This study provides new information on the nesting density of stingless bees and *A. mellifera*, the native honey sources in Afromontane forest, and evaluates potential factors influencing their abundance. As in all past studies (Roubik 1993), we lack desirable information on production ecology. For instance, we do not know colony size or the amount of stored food, or reproductive rate (a single new nest was seen in the study), but do include information on available nest sites (tree DBH, soil type), food (pollen taxa richness, flowering phenology), colony predators of Meliponini and their relative impact, and elevation or weather. The data on nest locations and predation by different animals indicate that predators strongly influenced nest distribution and abundance. And innovations by intelligent predators have had particular impact in Africa (Brewer & McGrew 1990, Stanford *et al.* 2000). In South Africa, Botha (1970) observed that baboons regularly attack the natural nests of *Apis*, as do macaques (*Langur*). Our study suggests humans had a larger impact than the chimpanzees, with both Pygmies and other local inhabitants using axes or machetes, whereas gorillas had slight impact as bee nest predators, and used no tools.

Predation occurred preferentially on lower nests, <7 m from the ground. At these heights, the large bees are potentially located by sound, made by bees fanning their wings near the nest entrance, in agreement with predatory techniques often used by human honey-hunters in tropical forests (D. W. Roubik, pers. obs.). Although many colonies were attacked and destroyed during the 28 months of the study, some experienced mortality before that time, thus 12 percent average yearly mortality is an overestimate. Stingless bee nest mortality in Sabah, in a Bornean lowland forest, varied from 13 to 15 percent between species (Eltz *et al.* 2002). This figure is comparable to our observations but was presented without data on predation.

Our data suggest that *general* food availability did not influence nest density. First, opposite trends were seen in nest density of two large common species (*M. bocandei* and *M. nebulata*), comparing the northern and southern sector. Second, colonies at the edge of the park and bordering villages had very little pollen from agricultural and nonforest plants. Such a preference for natural diet items within forest suggests that food competition is only mild and transitory, because acute food shortage leads to increased sampling of plant species, outside of forest areas (Eltz *et al.* 2002, Villanueva & Roubik 2004). Third, the richness of major pollen types used by *M. bocandei* was the same across the elevational transect and in forest and border

habitats. These findings are in contrast with Hubbell and Johnson (1977) who found uniform dispersion of some stingless bees, and Eltz *et al.* (2002) who favor competition for food or adequate nesting sites as an explanation of nest dispersion. The alternating nature of mass-flowering by herb, shrub, and climber species in BINP contributed to relatively constant food supplies for bees. In this montane Afrotropical forest, with two wet seasons each year, different plants have different times and rates of flowering. This was illustrated by *Mimulopsis solmsii*, which was a major resource and flowered for 6 wk, contrasting with *Impatiens*, which flowers for a short time but with different species in flower through the year. Inside the forest, gaps and disturbed sites that result from windthrows, pit-sawing or tree death allow pioneers such as *Vernonia* (Asteraceae), the most common pollen type, to occur. Pollen and nectar from the plants in early successional stages are recognized for their importance to stingless bees by indigenous people in Amazonian forests (Posey & Camargo, cited in Roubik 1989, but see Roubik & Moreno 1990). The incoming pollen of *Meliponula bocandei* make us agree with Horn (2004), who stated that Uganda has abundant nectar sources and supplemental feeding is unnecessary for domesticated bees.

Considering 18 other tropical social bee nest surveys, the density of *Apis mellfiera* was higher at BINP or comparable to that found in drier African habitats, but Meliponini were surprisingly uncommon (Table 1). If honey bees and stingless bees compete strongly for food and nesting sites, their populations should display reciprocal trends (Roubik & Wolda 2001), and there has been "artificial" human predation on honey bees in the park (see below). The honey bees, however, being free-nesting, migratory, and readily able to abandon nest sites, may have now approached an equilibrium whereas the sedentary Meliponini are still catching up (see Oliveira *et al.* 1995, Eltz *et al.* 2003), after recent periods of uncontrolled exploitation of all honey-making bees in the park. Nest density might have been greatly reduced when the park underwent continuous exploitation during the 1970s and the first half of the 1980s (Butynski 1984). In addition, Portugal-Araújo (1971) reported that colonies of *M. bocandei* become three or more times their normal size when placed in large box hives. Presence of many available nesting sites markedly increases the numbers of nesting meliponine colonies (Michener 1946, Eltz *et al.* 2002, Batista *et al.* 2003). Such information certainly suggests colony size and number are flexible, and might also imply nesting sites limit colony density and possibly also size, but more information is needed on local population sizes or biomass.

Scaling-up plot information on honey-making bee colonies should be a goal of sustainable harvest strategies or management. Table 1 documents the tendency of small-scale studies to record high abundance of nesting colonies, which are very likely to be clumped in space, as were ours in the transect plots, indicated by approximately half of the plots containing no nests, despite rather uniform presence of large trees. Quite apart from changes in species number and colony size (see Introduction) data from smaller areas may be inapplicable to large-scale nest abundance (Ratnieks *et al.* 1991, Oliveira *et al.* 1995). Studies in

areas >30 ha revealed a mean density of 6.6 nests/100 ha (SD = 4.1), or 1/km^2, for *A. mellifera*. Our data confirm the impression of Darchen (cited by Roubik 1983), for Ivory Coast, and of Schneider and Blyther (Table 1), of approximately 8 to 10 nests/100 ha for African *A. mellifera*. That of stingless bees surveyed in ≥8 ha of forest provide a mean colony density estimate of 181 nests/100 ha (SD = 167, *N* = 11), almost seven times that recorded in BINP (Table 1). The smaller-scale nest surveys, or those in disturbed habitats (Table 1), seem extraordinary and not representative of natural forest habitats. Oliveira *et al.* (1995) found 15 nests in 100 ha of mature Central Amazonian forest, in contrast to higher abundance of nests in disturbed patches, mentioned by Posey and Camargo (1985).

The overall honey-making bee nest density in BINP was 39 nests/km^2 and varied among species, ranging from 1 nest/km^2 (*M. lendliana*) to 12 nests/km^2 (*A. mellifera*), with nest density of two stingless bee species in one elevational sector equal to that of *Apis*. The figures for both the honey bee and the combined stingless bee species may agree with estimates from drier parts of Africa, and from varied habitats in the American and Asian tropics (Table 1, and Slaa 2003). When biomass statistics are considered (Roubik 1989, 1993), we believe that African meliponine nest biomass is larger than the average neotropical species (Roubik 1979, 1983a), while stingless bee and honey bee biomass are similar in Africa. African stingless bees differ from those of other geographic areas, being either relatively large or very small, *e.g.*, *Meliponula* vs. *Hypotrigona* (see Darchen 1972) or *Liotrigona*. The Pygmy guides probably located all of the large species but failed to find one or two of the smallest species. Fewer than 10 species coexist in lowland African forest compared to approximately 20–60 in lowland SE Asia or the Neotropics (see Oliveira *et al.* 1995, Roubik 1996, Nagamitsu & Inoue 1997, Michener 2000, Eardley 2004). An appropriate survey of bees at flowers or baits would need to be undertaken at BINP, to discover possible differences between local species presence and recorded natural nests (Oliveira *et al.* 1995, Roubik & Wolda 2001). The African fauna lacks the many medium–small species characteristic to the Neotropics and Asia, such as *Plebeia*, *Nannotrigona*, *Paratrigona*, *Oxytrigona*, and some *Trigona*. Africa may have few more than 20 meliponine species (Eardley 2004).

The largest biomass of adults, brood, pollen, and nectar of any social bee colony is often that of *Apis*, and in the Asian tropics, large nest aggregations of giant honey bees occur (Dyer 2002, Roubik 2005). Both *A. mellifera* and *A. dorsata* are often migratory, thus, unlike the stingless bees, abandon their nests (Seeley 1985, Roubik 1989, 2005). Moreover, stingless bees do not reproduce by swarming unless a new nesting cavity is prepared beforehand. Only one case of nest initiation by Meliponini (in *M. bocandei*) was seen in 28 months, whereas tropical honey bees tend to reproduce once a year (Roubik 1989). These key differences make ecological and biomass comparisons of Apini and Meliponini difficult. In our study, and summarized in Table 1, stingless bee nests, in aggregate, are approximately 3–20 times the density of honey bee colonies where both occur together. Our data do not establish whether most acceptable nesting sites were occupied, or why some species were rare or absent in the higher elevations at BINP. The vertebrate predators ranged through all areas and were unlikely to eliminate species at certain altitudes (Table 2 and 4). Our study cannot determine the cause of successful nesting by *Meliponula bocandei* in the ground mainly at higher elevations, where it was relatively rare, compared to lower elevations, where its nests were found in trees (Table 2). Tool use or availability to predators may influence such patterns. Our analysis considered only presence of potential nest trees (by DBH class, Fig. 1). Presence or absence of tree hollows was not ascertained. House walls and ground nests were not examined for substrate quality and structure, but it is unlikely that cavities were made, rather, preexisting cavities were used (Roubik 1989).

Because people enter the park to harvest *Apis*, but also do so clandestinely to remove meliponine honey, recent effects of vertebrate predation in BINP were arguably more significant than general food availability or flowering phenology and seasonality, or nesting sites. Both predation pressure from apes and humans, and competition from honey bees, has potentially led to low meliponine densities, 15 percent of that expected from other studies. It may also be true that removal of and predation upon stingless bees, combined with their nest-site limitation and slow reproduction, have allowed the biomass of *Apis* to rise. Despite large size of some *Meliponula* (comparable to a small Neotropical *Melipona*) nest biomass is not large enough in this species so that depressed meliponine nest density would be expected, even if *M. bocandei* were the only meliponine at BINP. The absence of ground-nesting *M. lendliana* in the upper elevation sector of BINP, where ground nests were generally abundant for another species, suggests that incidental or indirect mutualists that leave unoccupied nesting cavities (*e.g.*, termites, Darchen 1972) may also regulate nest populations. The entrance to hypogeous termite nests is not straight and loops in the soil, making nests difficult to reach by humans or chimps using flexible stems as probes (D. W. Roubik, pers. obs.).

In almost all cases, human predation involved destruction of the nest including the brood. Roubik (1989) observed that mammals are the significant large colony predators of honey-making social bees. The Pygmies were the most important predators in BINP. The other agricultural communities (Bafumbira, Bakiga, and Banyankole) neighboring the park mostly kept *A. mellifera* instead of Meliponini. In some instances, the dwarf honey-guide *Indicator pumilio*, a tiny bird that is endemic to the Albertine Rift Mountains, helped direct the Pygmies to stingless bee nests. Crane (1975) reported that baboons and chimps also follow the guiding calls of *Indicator* to locate nests of honey bees. The Pygmies lived for many centuries in BINP forest as hunters of wild animals and gatherers of roots, fruits and honey, and brood or pollen in bee nests for food. In 1991 the government of Uganda evicted them when the reserve was declared a national park. Now obliged to forgo hunting and gathering, the Pygmies are struggling to adapt. Butynski (1984) found similar results in an ecological survey of the park, noting 10–20 people entered the park daily to carry out illegal activities including hunting for wild bee nests.

ACKNOWLEDGMENTS

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