
Pollen foraging by *Apis mellifera* and stingless bees *Meliponula bocandei* and *Meliponula nebulata* in Bwindi Impenetrable National Park, Uganda

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Abstract

Pollen foraging of stingless bees *Meliponula bocandei* and *Meliponula nebulata* was compared with that of *Apis mellifera*. Palynological results showed a considerable overlap among the three species. However, *A. mellifera* the larger bee (11 mm) had the highest diversity while *M. nebulata* had the lowest. Among the stingless bees, the larger *M. bocandei* (9 mm) had a wider spectrum than *M. nebulata* (7 mm). The relatively bigger colony and body size of *A. mellifera* were positively correlated to pollen diversity. The recruitment technique to food sources is implicated as one of the factors accounting for the differences in pollen foraging behaviour. Foragers of *M. nebulata* flew out in characteristically distinct bouts, directly leading mates to food sources (piloting). Pollen diversity of *A. mellifera* was lower during the rainy season than in the dry season while for *M. bocandei* and *M. nebulata* there was no seasonal variation. Pollen diets changed over the seasons probably because of the alternating nature of flowering plants. The different pollen foraging strategies could ultimately result in partitioning of food resources.

Key words: Bwindi, diversity, pollen, spectrum, stingless bees, Uganda

Résumé

La récolte du pollen par les abeilles sans dard *Meliponula bocandei* et *M. nebulata* a été comparée avec celle faite par *Apis mellifera*. Les résultats palynologiques ont montré un

recouvrement important de ces trois espèces. Cependant, *A. mellifera*, la plus grande abeille (11 mm.), présentait la plus grande diversité alors que *M. nebulata* avait la plus faible. Parmi les abeilles sans dard, la plus grande, *M. bocandei* (9 mm.), avait un spectre plus large que *M. nebulata* (7 mm.). La colonie et la taille corporelle relativement plus grandes d'*A. mellifera* étaient positivement liées à la diversité du pollen. On implique que le recrutement technique des sources de nourriture a été un des facteurs expliquant les différences dans le comportement de recherche du pollen. Les ouvrières de *M. nebulata* s'envolaient de façon très caractéristique, conduisant directement leurs congénères aux sources de nourriture (piloteage). La diversité du pollen récolté par *A. mellifera* pendant la saison des pluies était plus faible qu'en saison sèche, alors que pour *M. bocandei* et *M. nebulata*, il n'y avait pas de variation saisonnière. Le régime de pollens changeait avec les saisons, probablement en raison de la succession naturelle des plantes en fleurs. Les différentes stratégies de prélèvement des pollens pourraient en fin de compte aboutir à la répartition des sources de nourriture.

Introduction

Pollen resource exploitation by social bees has been widely studied in American and Asian tropics. Several detailed studies and reviews on this subject have been published (Sommeijer *et al.*, 1983; Roubik *et al.*, 1986; Kleinert-Giovannini & Imperatriz-Fonseca, 1987; Imperatriz-Fonseca, Kleinert-Giovannini & Ramalho, 1989; Ramalho, 1990; Nagamitsu *et al.*, 1999; Eltz *et al.*, 2001; Villanueva & Roubik, 2004). The most important characteristic of these studies is that the majority analyse the pollen collected and stored in the pots. Some of these studies deal with pollen diet of a single stingless bee species or honey

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bees, while others compare plants used by different stingless bee species, or by stingless bees and honey bees. A great number of these studies aim at describing competition, which normally leads to resource partitioning by different bee species involved. Most of these inter-specific pollen foraging studies have largely left out the context of afro-tropical bee species, particularly those equatorial. This study is an effort to cover the void. African studies may provide interesting patterns of pollen use and new theories of pollen foraging. This study is aimed at determining the competition for food resources and how the bee species partition their resources.

Among social bees, the possible factors that influence pollen variety foraged include colony size, bee morphology, bee behaviour and availability of pollen. Pollen diet spectrum of a colony normally increases with the number of pollen foragers of that colony unless they all forage for the same pollen. As the number of pollen foragers is related to colony size, bigger colonies will logically have a larger pollen diet spectrum. This was indeed found by Sommeijer *et al.* (1983) for a number of different stingless bee species. In social bees, foraging success is affected by morphological aspects such as proboscis length, body size and colour, as these characteristics greatly affect the ability of the bees to forage in different microclimates and on different flower types (Willmer & Unwin, 1981; Corbet *et al.*, 1995; Biesmeijer *et al.*, 1999). Among the morphological characteristics, body size has the greatest influence because it has a big influence on flight range and with increasing flight range the number of pollen sources available to the bees increases.

One of the important aspects of bee behaviour that has an influence on pollen diet variety is food source communication (Lindauer & Kerr, 1960; Esch, Esch & Kerr, 1965; Esch, 1967; Wille, 1983). When a colony of bees is able to communicate the location of a food source very accurately, a number of foragers will visit this source and thus harvest the same pollen type. When the colony has no or very limited means to communicate the location of a profitable food source to its members, the bees search food sources for themselves which decreases the number of similar pollen loads as the variety of pollen sources is now based on chance. When there are more floral sources available, chance predicts that bees visit more sources and with this the width of the pollen diet spectrum increases. This factor, however, is probably of very little importance as various studies point out that pollen diet spectrum is temporally stable even when the availability of pollen

sources increases (Eltz *et al.*, 2001; Nagamitsu & Inoue, 2002). Making use of the uniqueness of this study where native species of honeybees and stingless bees were studied in the same native afro-tropical forest, a qualitative study focusing on the competition for pollen resources and how the bee species partition their resources is presented.

Material and methods

Study sites and bee species used

The study was conducted in Bwindi Impenetrable National Park located in south-western Uganda. The park is located between latitudes 0°18' and 0°53'S, longitudes 29°35' and 29°50'E. It has 331 km² of natural forest and contains both montane and lowland forest. The park is on the UNESCO's list of world heritage sites for its ecological uniqueness and natural beauty. The altitude of the park ranges from 1160 to 2607 m. The heaviest rains are experienced in March–May and September–November and the two dry season troughs are December–January and June–July (Butynski, 1984). Its annual precipitation is 1130–2390 mm.

Colonies used were located at the Institute of Tropical Forest Conservation (ITFC) in Ruhija. In total, nine colonies were used belonging to three species; two stingless bee species (*Meliponula bocandei* and *Meliponula nebulata*) and *Apis mellifera* (Table 1). The three ground nests of *M. bocandei* were located at about 100 m outside the park border. Nests of *M. nebulata* were located in three different tree cavities. The stingless bees were identified by David W. Roubik at Smithsonian Tropical Research Institute and by consulting Eardley (2004). The colonies of *A. mellifera* kept in boxes were placed outside but close to the park border and near the ground nests of *M. bocandei*. The two most far apart colonies were about 350 m from each other. Therefore, it was taken that all these colonies had widely overlapping foraging ranges.

Pollen samples of stingless bees

Pollen loads for the stingless bees were collected once every two weeks for 12 months (January–December 2003) at 07:00–09:00, 10:00–12:00 and 13:00–15:00 h local time. Returning pollen foragers were caught with a net in front of the nest entrances and loads were taken from the captured foragers. An average of five pellets was collected per sampling hour from each colony. Individual loads of a

Table 1 Colony characteristics of bee species used

Bee species	Initial	Length (mm)	Estimate population	Altitude (m)	Nest site	Nest height (m)
<i>Apis mellifera</i>	AM1	11	10,000	2300	Top bar hive	1
<i>A. mellifera</i>	AM2	11	8000	2300	Top bar hive	1
<i>A. mellifera</i>	AM3	11	10,000	2300	Top bar hive	1
<i>Meliponula bocandei</i>	MB1	9	1200	2320	Ground	0
<i>M. bocandei</i>	MB2	9	1000	2320	Ground	0
<i>M. bocandei</i>	MB3	9	1300	2300	Ground	0
<i>M. nebulata</i>	MN1	7	1800	2330	Tree cavity	1.4
<i>M. nebulata</i>	MN2	7	1800	2290	Tree cavity	2.9
<i>M. nebulata</i>	MN3	7	1600	2330	Tree cavity	3.3

The colony population of the stingless bees was estimated by opening the nests under mosquito nets and counting the bees. For *Apis mellifera*, population was estimated by counting individual bees on the inner faces of the hive and on combs.

particular species on a given day were grouped into a sample. Overall about 780 pellets were collected per colony (five pellets per hour \times six sampling hours in a day \times 26 sampling days in a year). The use of a net to collect pollen loads of the stingless bees did not result in a high number of loads; therefore, all pollen loads collected were acetolysed (Erdtman, 1960) and mounted in glycerin jelly for microscopic examination. From each slide, 200 pollen grains were randomly selected and identified to species level if possible. Pollen slides from the Makerere University herbarium, pollen reference collection and specialized literature (Hamilton, 1972) were used to identify the pollen sources. Some pollen could not be identified to species level and were combined into 'types'.

Pollen samples of *A. mellifera*

To collect pollen loads from *A. mellifera*, a pollen trap was installed at the entrance of each hive. The trap was a single transparent plastic board of 0.5 mm thickness with holes through which bees forced their way. The diameter of the holes was 5.0 mm which is the standard for *A. mellifera*. As with the stingless bees, pollen loads of *A. mellifera* were collected once every 2 weeks for 12 months (January–December 2003) at sampling periods of 07:00–09:00, 10:00–12:00 and 13:00–15:00 h local time. However, the days of collection were different from those for the stingless bees. At each sampling period, pollen loads were collected for 15 min. Loads removed from a colony on each collection day were grouped into a sample. The pollen loads were acetolysed (Erdtman, 1960) and mounted in glycerin jelly for microscopic examination. From each slide, 200 pollen grains were randomly selected and identified to species level if possible. Only pollen types with an occur-

rence of more than 5% of grain number in a given sample were taken into account in the different qualitative analyses (critical value used by Silveira, 1991).

Data analysis

The Shannon–Weiner index of diversity was calculated for each bee species per month: $H_{jk} = -\sum_j \{N_{ijk}/\sum_j(N_{ijk})\} \ln \{N_{ijk}/\sum_j(N_{ijk})\}$ in which H_{ik} is Shannon–Weaver's index of diversity for colony i is species and N_{ijk} is the number of grains of pollen type j sampled from species i in month k . Indices were calculated for each colony per month and thereafter averaged. The overlap in pollen gathered by the colonies was analysed using Schoener's (1968) index, which is based on percentage of similarity; $PS = 1 - \frac{1}{2} \sum_h |ph_i - ph_j|$, where ph_i (ph_j) is the pollen proportion of the h plant species present in the sample of colony i (j) for the month in question. Values for overlap vary from 0 to 1, i.e. from no overlap to complete overlap of the resource utilized. The evenness was analysed using Pielou (1977): evenness, $J = H/H_{\max}$, where H_{\max} is natural logarithm of the total number of species found in the samples for 1 month. The values of evenness vary from 0 to 1, i.e. heterogeneous utilization of resource to homogenous use.

Results

Pollen spectrum of stingless bees and *A. mellifera*

The three colonies of *A. mellifera* visited 71 plant species belonging to 29 families. *Meliponula bocandei* visited 52 plant species belonging to 22 families and *M. nebulata* visited 33 plant species belonging to fourteen families. *Apis mellifera* shared nineteen types with *M. bocandei* and twelve types

with *M. nebulata*. The two stingless bee species shared eleven pollen types. Overall, a total of 72 pollen types could be identified to species level. Some pollen types were prevalent in successive samples of certain bee species but did not

occur, or were only of minor importance, in samples of other species (Table 2). *Bidens pilosa* and *Mimulopsis* sp. formed an important pollen supply for *A. mellifera* and *M. bocandei* but were not important to *M. nebulata*. In contrast *Prunus*

Table 2 Pollen types found in samples of the colonies: x = pollen represented 10–30% of grain number and xxx = pollen represented over 30%. M1-3 = *Apis mellifera* colony 1–3; B1-3 = *Meliponula bocandei* colony 1–3; N1-3 = *Meliponula nebulata* colony 1–3

Family	Species	M1	M2	M3	B1	B2	B3	N1	N2	N3
Acantheaceae	<i>Mimulopsis</i> sp.	x		xxx	x		x			
	<i>Acanthus arboreus</i>	x		x						
Araliaceae	<i>Harungana madagascariensis</i>	x	x							
Asteraceae	<i>Vernonia</i> sp.	xxx	xxx		x	xxx	xxx		xxx	xxx
Bignoniaceae	<i>Markhamia lutea</i>	xxx		x		x	x		xxx	xxx
Convolvulaceae	<i>Ipomea</i> sp.				x	x			x	xxx
Asteraceae	<i>Bidens pilosa</i>	xxx	xxx		xxx	x	xxx			
	Type 1							x	xxx	xxx
Commelinaceae	<i>Commelina</i> sp.	x		x						
Euphorbiaceae	<i>Alchornea hirtella</i>	x		x						
Euphorbiaceae	<i>Croton macrostachyus</i>	x	x			x	x	x	xxx	xxx
	<i>Macaranga</i> sp.				x	x	x			
	Type 2	x		xxx						
	<i>Dryptes</i> sp.		x	x				xxx	xxx	x
Gramineae	<i>Zea mays</i>	x	xxx	xxx						
Leguminosae	<i>Acacia</i> sp.	x		x						
Loganiaceae	<i>Nuxia congesta</i>		x	x				xxx		x
Lobeliaceae	<i>Lobelia gibberoa</i>	x	x							
Meliaceae	<i>Carapa grandifolia</i>	xxx	xxx	x						
Meliaceae	<i>Entandrophragma excelsum</i>	x	x	x						
Moraceae	<i>Myriathus holstii</i>					x	x		x	
Musaceae	<i>Musa</i> sp.	x	x							
Myricaceae	<i>Myrica salicifolia</i>	x	x							
Myrtaceae	<i>Syzygium guineense</i>				xxx	xxx	x		x	x
Papilionaceae	<i>Sebaania sesban</i>	x		x						
Piperaceae	<i>Piper guineensis</i>	x		x						
Proteaceae	<i>Faurea saligna</i>	xxx	xxx			x	x	x		x
Oleaceae	<i>Olea capensis</i>	x	x							
Rosaceae	<i>Hagenia abyssinica</i>	x	x							
	<i>Prunus africana</i>							xxx	xxx	x
Rubiaceae	<i>Coffea</i> sp.		x	x						
Solanaceae	<i>Datura stramonium</i>	x		x		x	x			
Sapotaceae	<i>Chrysophyllum gorungosanum</i>				x	x				
Theaceae	<i>Ficalhoa laurifolia</i>	x	x							
Theaceae	<i>Ficalhoa laurifolia</i>	x	x							
Zigiberaceae	<i>Aframomum</i> sp.	x		x						
Un identified	Type 3		x	x						
	Type 4							xxx	x	x
	Type 5	x	x							
	Type 6				x	x				
	Type 7							xxx	xxx	
	Type 8				x		x			
	Type 9		x							
	Type 10	x		x						

africana and an Asteraceae type 1 were of importance to *M. nebulata*. Pollen types that were shared and of importance to all three bee species included Euphorbiaceae, Myrtaceae, Proteaceae, Asteraceae and Acantheceae.

Major pollen sources used during the seasons

Apis mellifera had fifteen heavily used plant species, *M. bocandei* had twelve heavily used plant species while *M. nebulata* had seven heavily used plants. Some of the major pollen sources such as *Vernonia* sp. and *Eucalyptus* sp. were shared among the three bee species (Fig. 1). There was a seasonal variation among the major pollen sources used. Pollen sources, such as *Vernonia* sp., *Eucalyptus* sp. and *Syzigium guinense*, were in flower for a longer period of time and were therefore used by the bees across the dry and rainy seasons. During the first dry season (December–February), *B. pilosa* and *Eucalyptus* sp. were dominant in the samples of the bee species. In the second dry season (June–July), *Vernonia* sp. and *Eucalyptus* sp. were the most dominant pollen plants. *Vernonia* sp. was the most dominant pollen type collected in the first rainy season (March–May) while *S. guinense* and *Carapa grandifolia* were the most dominant in the second rain season (August–November).

Diversity of pollen diet

The bee species collected pollen from diverse plant sources. *Apis mellifera* had the highest diversity index (diversity index = 1.458, SD = 0.33; evenness = 0.968, SD = 0.1). The two stingless bee species had relatively lower indices (*M. bocandei*: diversity index = 0.9084, SD = 0.47; evenness = 0.973, SD = 0.2; *M. nebulata*: diversity index = 0.6460, SD = 0.62 evenness = 0.71, SD = 0.430; see Fig. 2). The monthly diversity indices were significantly different for the three bee species (Wilcoxon Test: $df = 2$, $n = 12$, $P = 0.003$). There was no significant difference in monthly diversity indices within colonies of the same species: Wilcoxon Test (*A. mellifera*: $df = 2$, $n = 12$, $P = 0.38$; *M. bocandei*: $df = 2$, $n = 12$, $P = 0.259$ and *M. nebulata*: $df = 2$, $n = 12$, $P = 0.536$). The evenness for all the months were not significantly different for the different bee species (Wilcoxon Test: $df = 2$, $n = 12$, $P = 0.477$).

Overlap in pollen diet

Throughout the 12 months of data collection, there was interspecific overlap in pollen types collected by the three

bee species. The highest values of overlap were recorded during the dry seasons (June–July and December–January) and the lowest during the rainy seasons (March–May and September–November; see Fig. 3). The highest values of overlap were recorded among the two stingless bee species and the lowest between *A. mellifera* and *M. bocandei*.

Seasonal variation in pollen diet

The smallest diversity of plant sources utilized by *A. mellifera* was recorded during the rainy seasons and the highest in the dry seasons. For *M. bocandei* and *M. nebulata* there was no clear peak in their indices (Fig. 4a). Data on rainfall in Ruhija where the study was conducted is shown in Fig. 4b and the monthly diversity indices of the three bee species were correlated to their corresponding mean rainfall. The monthly diversity index of *A. mellifera* was negatively correlated with the pooled annual rainfall (Kendall's tau: $r = -0.424$, $n = 12$, $P = 0.027$). There was no significant correlation for the other two bee species (*M. bocandei*: $r = -0.198$, $n = 12$, $P = 0.186$; *M. nebulata*: $r = -0.264$, $n = 12$, $P = 0.120$).

Discussion

Pollen spectrum of *A. mellifera* and stingless bees

The bees collected pollen from a wide range of plant species. This may not be surprising as social bees have year-round colonies which compel them to forage for food year round. They cannot therefore be specialists on one or a few food plants, but rather have to be generalists, using a wide array of food plants (Michener, 1974; Roubik, 1989). In this study, pollen volume was not taken into account hence only qualitative as opposed to quantitative conclusions could be drawn on the relative importance of various plant taxa as pollen sources. Eltz *et al.* (2001) observed that floral resource availability of bees is difficult to quantify in natural forest habitats because of the difficulty of judging the relative importance of certain flowering plant species to the bees in question.

Differences in pollen diets among the bee species

Bee morphology and colony size. The results suggest that the biggest bees (Table 2) took the most resource types. *Apis mellifera* has the largest flight range as it is the biggest among the three species (Roubik & Aluja, 1983; Roubik,

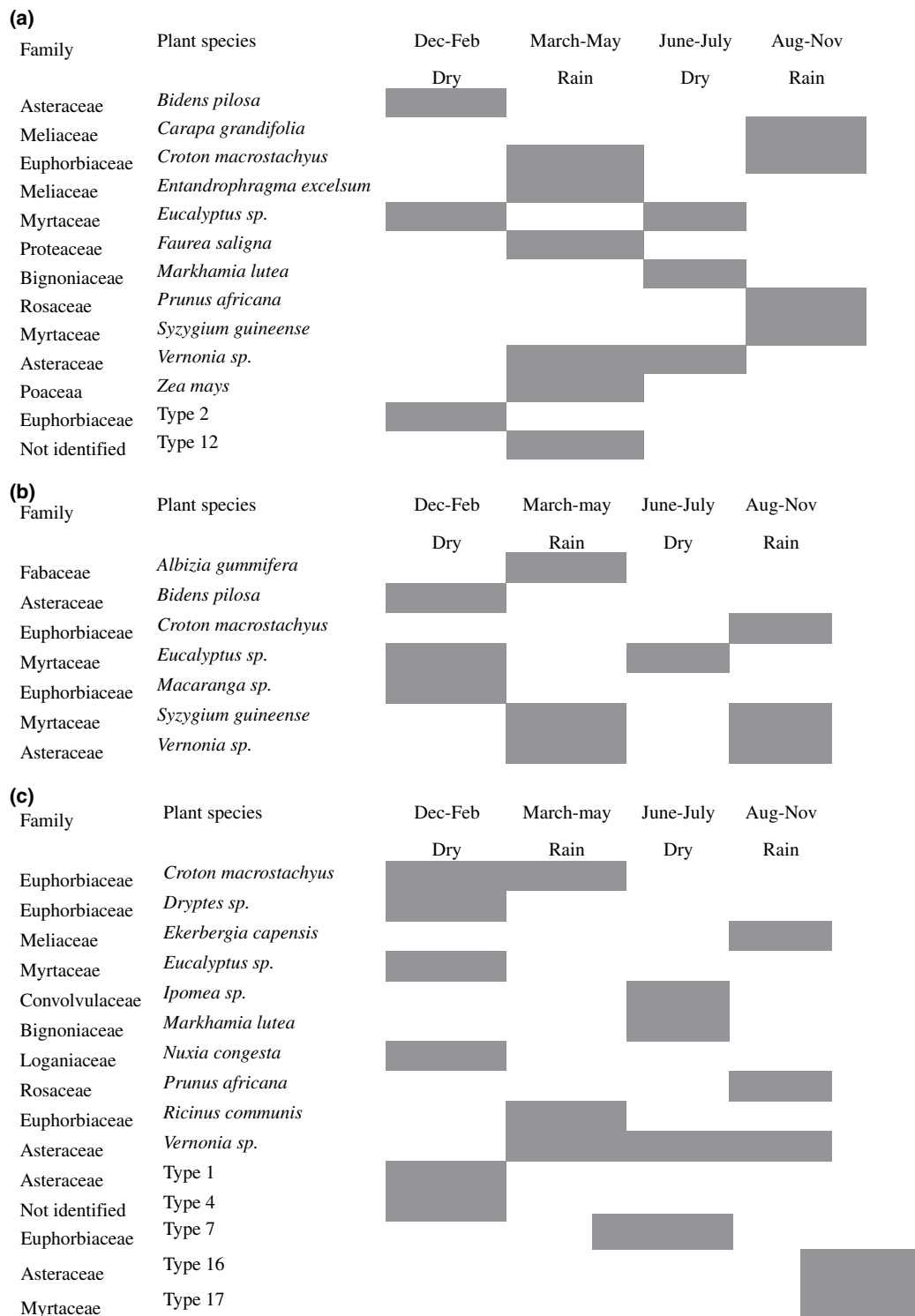


Fig 1 Major pollen sources of *Apis mellifera* (a), *Meliponula bocandei* (b) and *Meliponula nebulata* (c) used during the dry and rainy seasons. Only pollen types that made up more than 30% for two of the three colonies of each species are reported

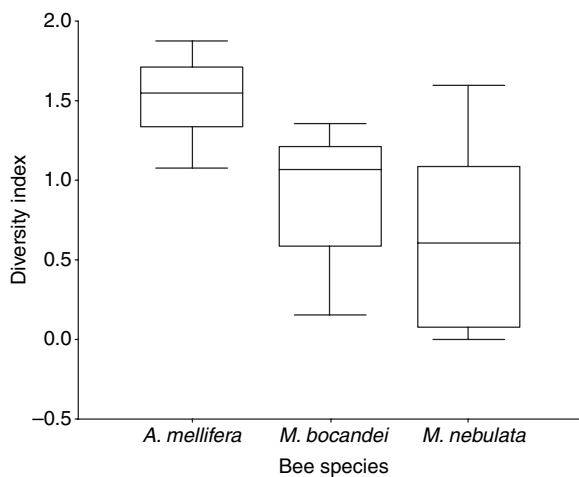


Fig 2 Median range of Shannon-Weiner diversity indices for the three bee species. Data for colonies of each species were pooled

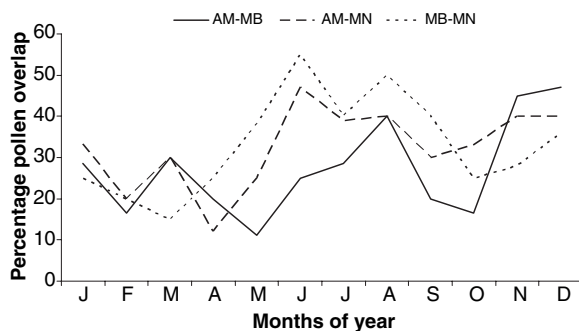


Fig 3 Interspecific monthly overlap between the three bee species. Overlap indices were translated into percentages. AM-MB = overlap between *Apis Mellifera* and *Meliponula bocandei*; AM-MN = overlap between *Apis Mellifera* and *Meliponula nebulata* and MB-MN = overlap between *Meliponula bocandei* and *Meliponula nebulata*

1989). A larger flight range results in a greater number of food sources available to each colony thus increasing the variety of pollen harvested. For the two stingless bee species, the variety of pollen harvested is small as less pollen sources lie within flying distance. However, flight range and foraging range might be quite different (Biesmeijer, 1997) because bees do not use the whole of their flight range for foraging. By having varied flight and foraging ranges, difference in the size and morphology of the bees could facilitate partition of the resources. Koeniger & Vorwohl (1979) showed results opposite to this study. According to their study, *Apis dorsata* showed the narrowest pollen diet, *Trigona iridipennis* the widest. Colony

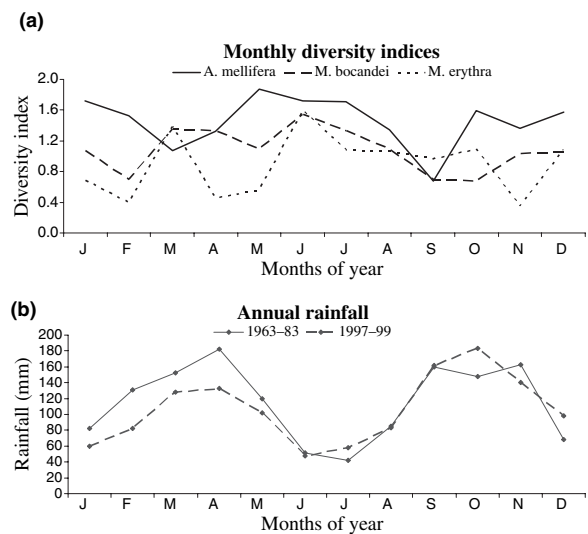


Fig 4 Temporal pollen diet breadth of the three bee species. Depicted in (a) is Monthly Shannon-Weiner diversity indices for the three bee species. Depicted in (b) is the monthly mean rainfall of Ruhija (1963–1983 and 1987–1999). Data source: Butynski (1984) and Bitariho *et al.* (1999) respectively

and body sizes of the former are bigger than those of the latter. They emphasized aggressiveness of *T. iridipennis* at feeding sites as a source of the difference in pollen diet spectrum.

Colony size of *A. mellifera* was the highest (8000–10,000, see Table 1) requiring more pollen while the stingless bees, dependent on the species, have generally fewer individuals per colony requiring less pollen. Similar results were found by Michener, Mcginley & Danforth (1994). For the bees with a smaller number of individuals in a colony, the differences in pollen variety foraged would logically be small, as only a few sources have to be visited to provide enough pollen for the colony. Sommeijer *et al.* (1983) found that bee species with high number of individuals in a colony have a wider width in pollen spectrum. However, from this study, *M. nebulata* had the lowest pollen spectrum and yet it had a higher number of individuals in a colony than *M. bocandei* (Table 1).

Bee behaviour. One of the important aspects of bee behaviour that has an influence on pollen diet variety is food source communication (Lindauer & Kerr, 1960; Esch *et al.*, 1965; Esch, 1967; Wille, 1983). When a colony of bees is able to communicate the location of a food source very

accurately, a number of foragers will visit this source and thus harvest the same pollen type. When the colony has no or very limited means to communicate, the location of a profitable food source to its members the bees search food sources for themselves, which decreases the number of similar pollen loads as the variety of pollen sources is now based on chance. In a study on stingless bee flight and foraging behaviour in the tropical forests of Uganda, Kajobe & Echazarreta (2005) found that workers of *M. nebulata* flew out in characteristically distinct foraging bouts thus directly leading nest mates to food sources (piloting). The low diversity in pollen spectrum of *M. nebulata* may have resulted from this group foraging behaviour. This behaviour of flying in bouts may have been derived as a result of competition with *A. mellifera* which has larger body and colony size.

Kerr (1969) reported that *M. bocandei* uses scent markings as a strategy to guide foragers to food sources. This strategy is a more sophisticated within-nest communication system when compared with that of *M. nebulata*. Such communication and recruitment system makes *M. bocandei* be able to forage as individuals or in small groups probably leading to its wider pollen spectrum. *Apis mellifera* had the widest pollen spectrum. Roubik (1980) explained that this could be as a result of the properties of the *Apis* communication system and of its large worker and colony size. However, although piloting is implicated to have contributed to the narrow diet of *M. nebulata*, it may not always lead to more specialization than scent or dance recruitment. Dance recruitment communicates a single feeding site with a lot of workers in nests, and scent communication recruits a limited number of foragers to a feeding site. If different 'pilots' lead to different feeding sites, a diet of a colony may be wider in piloting than in scent or dance recruitment.

Niche differentiation between sympatric bee species can be effectuated by a number of factors such as body morphology, colony size, food availability and behavioural characteristics like recruitment ability. The recruitment technique to food sources was implicated to be the most important factor accounting for the differences in pollen foraging behaviour. Foragers of *M. nebulata* were directly leading nest mates to food sources (piloting). Despite the competition impact of *A. mellifera* on the stingless bees that could generally lead to only negative effect, these bees are able to coexist in this equatorial afrotropical forest by partitioning their food resources using different foraging strategies.

Pollen diversity and overlap. There was a significantly lower pollen diversity for *A. mellifera* during the rainy season than in the dry season. This suggests that *A. mellifera* collects large amounts of pollen from few species in the rainy season implying that these plant species are truly good pollen sources and are preferred by this bee species. Alternatively, when plant resources become more available, foraging bees are capable of exerting significantly more active choice concerning their pollen diet. According to optimal foraging theory, foragers are expected to consecutively drop nonprofitable food resources from their diet for the more profitable ones (MacArthur & Pianka, 1966). The Shannon index of diversity only gives an idea about the intermediate value abundance of pollen diet but not the pollen sources that are extremely common or rare. As such, this is mainly a qualitative analysis emphasizing the 'important' diet items that were fairly important or very important, and gives little information about diet breadth which includes the many rare items that are taken especially those less than 5% numerically. The palynological results showed a considerable overlap in pollen resources for the three bee species. This overlap may represent the bees' attraction to few sources or lack of attractive alternatives for other pollen sources. It may also be a partial adjustment according to local conditions, including kinds and abundance of competitors and distance to pollen sources (Sommeijer *et al.*, 1983; Roubik *et al.*, 1986; Ramalho, Kleinert-Giovannini & Imperatriz-Fonseca, 1989; Roubik, 1989).

Seasonal variation in pollen diet. The negative correlation found between rainfall and pollen diversity for *A. mellifera* suggests a causal link from rainfall to flowering and then pollen use. The correlation reveals whether the bee species is significantly less likely to specialize on a few pollen types than another species. The pollen diets of the three bee species changed over the seasons probably because the composition of flowering plants offering pollen changed over the seasons (Byarugaba, 1998). The alternating nature of plants as a result of the different seasons in Bwindi Park is an advantage towards continued plant pollination and honey making (Cunningham, 1992). Similar results were reported by Wilms & Wiechers (1997) who found that pollen harvest by *A. mellifera* and *Melipona* colonies depends strongly on flower abundance and therefore may be triggered by seasonal influences.

These sympatric bee species are able to employ different foraging strategies to partition their food resources and

avoid competition. Foragers of *M. nebulata* directly lead nest mates to food sources (piloting) probably leading to the low diversity in pollen spectrum. *Meliponula bocandei* uses scent markings as a strategy to guide foragers to food sources. Such recruitment system enables *M. bocandei* to forage as individuals or in small groups, probably leading to its wider pollen spectrum. *Apis mellifera* had the widest pollen spectrum which could be as a result of using dance language for recruitment. Dance recruitment communicates a single feeding site with a lot of workers in nests.

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