Foraging ecology of equatorial Afrotropical stingless bees: habitat selection and competition for resources

PhD thesis

By

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Contents

Preface

This thesis is a result of fieldwork on foraging ecology of Afrotropical stingless bees in Uganda. The focus is on inter-specific foraging ecology of stingless bees and honeybees in their native ecological environment. Most studies on stingless bee ecology are largely based on studies in South America and South-east Asia and have ignored the aspects and context of Afrotropical stingless bee species, particularly to those equatorial. This study makes a primary contribution to filling this void. Inadequate human resource capacity and low infrastructure development have hindered bee research and development in Africa. Very few authors have treated Afrotropical forests, or native honeybees and Meliponini in the same habitat. This study is among the first detailed description of stingless bees in their natural habitat of Afrotropical forests. I experienced problems in the initial stages of designing this study because of lack of background literature about the stingless bees in this region.

In the first place, I am very grateful to Prof. Dr. J.J. Bolhuis for accepting to be my promoter. I thank my co-promoter Dr. Marinus Sommeijer for giving me the opportunity to work with him, first for my MSc and thereafter the PhD. Thank you for supporting me and for giving me advice on work presented in this study. I also thank Prof. Dr. Jan van Hooff for accepting to be my co-promoter especially after his official retirement. I am indebted to Utrecht University especially the dean of Faculty of Biology Prof. Dr. P.J. Weisbeek for allowing me to work in the bee research laboratory. I am very grateful to Dr. David W. Roubik of the Smithsonian Tropical Research Institute (USA) who identified all the stingless bees used in this study. Apart from identifying the bees, Roubik helped in the following ways: reviewing and providing critical comments on my work, providing me with the most recent literature and he was one of my co-authors. Dr. Carlos M. Echazarreta also reviewed and provided critical comments to my work and was also one of my co-authors. Dr. Thomas Eltz gave me his comments on earlier versions of the work. I thank Prof. Joseph Obua of the Faculty of Forestry and Nature Conservation, Makerere under whose Department I carried this study. Frouke Hofstede of the Tropical Bees Research Unit, Faculty of Biology, Utrecht University, gave me critical comments on earlier versions of some of the work. I also thank the staff of centre of biostatistics especially Cas Kruitwagen for his help with some of the statistical analysis.

I acknowledge the support of the institutions that made it possible for me to undertake this study. The study could not have been done without the help of the British Ecological Society (BES) who funded the biggest part of the study. I thank the Faculty of Forestry and Nature Conservation, Makerere University and especially the dean Dr. John R. S. Kaboggoza for providing me with part of the funds for the study. The Utrecht University Scholarship Committee provided me with partial scholarship to visit the university during the stages of proposal writing, analysing and writing up of this thesis. Babette Berrocal and Berthe Schoonman from the International Relations office helped me in this regard. I am grateful to the Royal Museum for Central Africa, Tervuren in Belgium who sponsored me to study their bee collection in 2003. I am also grateful to the Institute of Tropical Forest Conservation (ITFC) in Bwindi Impenetrable National Park (BINP) and Nyabyeya Forest Collage in Budongo Forest Reserve (BFR) for their support during the fieldwork. I thank the Batwa, my resource persons who identified the bee species using folk taxonomy. My gratitude to all the persons who made my stay in Utrecht University Bee Research Department enjoyable and fruitful: my former MSc course coordinator Frans Meeuwsen, Frouke Hofstede, Bert Agterhuis, Tong Xuan Chinh, Cassian Mumbi, Karina Lalama, Desalegn, Victor and all the other MSc bee research students I met at the laboratory.

Lastly, I thank members of my family that include my parents, brothers and sisters for their great support in all aspects of my life. My father Mr. Martin Adrama inspired me to study up to this level.

Chapter One

1.0 Introduction

Studies on habitat selection, bee behaviour, bee-bee competitive interactions and colony events coupled to changing flowering conditions with the passing of seasons are limited in the Afrotropical regions. This study concentrates on two aspects of foraging ecology of stingless bees: habitat selection and competition for resources. The central question is how the native Afrotropical honey-making bees (honey bees and stingless bees) co-exist by partitioning their resources using temporal and spatial foraging strategies.

Stingless bees comprise a highly diverse and abundant group of eusocial bees that inhabit the tropical and subtropical parts of the world. They have attained their greatest diversity in the neotropics (Roubik 1989). Worldwide several hundred species exist, which differ significantly in colour, body and colony size (Roubik 1992, Michener 2000). The taxonomy of stingless bees is sometimes ambiguous as species names have changed over time and different authors have different views on classification and phylogeny (Wille 1983, Roubik 1992, Michener 2000, Eardley 2004). Most genera in most areas have not been adequately analysed for recognition of their forms (Michener 2000). One way of characterising stingless bees is by use of their nests (Michener 1990). Attributes of the nest are useful in taxonomic studies especially in equatorial tropical Africa where little has been studied. Previous studies and reviews on nesting biology of stingless bees have been done by Wille & Michener (1973); Michener (1974); Hubbell & Johnson (1977); Roubik (1979, 1983a, 1989, 1992); Sakagami (1982); Eltz et al. (2002, 2003) and Slaa (2003); Roubik (2006)

Stingless bees are true generalists with regard to selection of nest sites (Hubbell & Johnson 1977, Roubik 1989, Eltz et al. 2002). Most stingless bees build nests in tree hollows, and some species build in abandoned or still occupied nests of ants or termites, either above ground or subterranean (Wilson 1971, Michener 1974, Roubik 1989). Some species like *Dactylurina* and some *Trigona* build fully exposed aerial nests (Sakagami 1982). One of the attributes of most stingless bee nest sites, or in the case of exposed nests, of the nest itself, is excellent insulation (Michener 1974). Nests in large trunks or in the soil are particularly well insulated. Nests in felled trees, in brush that has been burned or that has been trampled or cut by man or other animals, in the earthen banks of road cuts, railways, paths, athletic fields, and in banks made by rushing water have frequently provided the only opportunities to study bee nesting biology (Roubik 1989).

The persistence of endangered species is threatened by three main processes, which may act simultaneously: habitat loss, fragmentation and decrease of habitat quality. Environmental actors that influence density of many *Meliponini* include availability of food, nest sites, and predation (Michener 1974, Hubbell & Johnson 1977, Eltz et al. 2002 and Slaa 2003). Stingless bee colony density is typically 1-3 colonies/ha, causing foraging ranges of the colonies to overlap (Michener 1946, Hubbell & Johnson 1977, Roubik 1983b, Eltz et al. 2003). The biology of tropical moist forests has a close relationship with the agents of pollination, dispersal and regeneration pool. Understanding of nesting ecology, plant-pollinator interactions and reproductive biology of forest plants is essential for the reproductive fitness of the bees. Very little is known about plant-pollinator interactions in afro-tropical equatorial ecosystems. In Bwindi Park, previous records (Cunningham 1992) were made of stingless bees as pollen vectors on the basis of information from the indigenous forest dwellers, the Pygmies, but no scientific studies were made to assess the validity of these observations leading to suggestions that more scientific studies be undertaken to understand the dynamics of forest pollination ecology in tropical equatorial Africa.

1.1 Competition for resources

If two bee species compete for a resource, it must be limiting in such a way that an increase in resource harvest by one species corresponds to diminished harvest by the other. Competition also occurs if resource harvest remains stable but harvest cost increases (Roubik 1978). The honeybee has a large colony and hence more foragers, as well as a more sophisticated communication system, than many of the stingless bee competitors. It is not an overtly aggressive forager and is regularly attacked by few dozen aggressive stingless bees, in the groups *Trigona* and *Tetragona* (Roubik 1980). Its reaction to harassment by these territorial foragers is generally to continue visiting the same inflorescence. Not only the general type of floral resources, but the intensity with which floral resources are used, are similar between honeybees and meliponine bees (Roubik et al. 1986). These authors found that although almost exactly the same pollen and nectar resources were used heavily by stingless bees and honeybees, and although a balance between colony foraging and floral resources exists, most stingless bee colonies escaped competition by the spatial partitioning of resources. The study indicated that competition for flowers was common in neotropical forests, but a reshuffling of foraging sites caused by competition seems slow to affect the reproductive fitness of local species. Competition between species occurs when they interfere with or inhibit each other. Competition for food resources occurs when there is niche overlap and a shortage of resources. Direct competition can occur when aggressive behaviour is used. Several stingless bee species display aggressive behaviour on flowers (Roubik et al. 1986). Some species are better suited for combat and terrifying other species by having strongly developed mandibular teeth, distinct colour, large sized, or by ability to recruit rapidly (Roubik 1989, Johnson 1983).

Ecological factors that can potentially affect population density of many *Meliponini* include availability of and competition for food and nest sites, and predation (Eltz et al. 2002, Hubbell & Johnson 1977 and Slaa 2003). Competition for food not only limits population density, it may also affect nest spacing generating uniform special patterns such as over dispersion which has been found for nest of some species of stingless bees (Hubbell & Johnson 1977). The evidence of inter-species competition for food is usually circumstantial and, despite extensive treatment of the subject, few field studies clearly demonstrate its importance (Roubik 1978). How do the coexisting species utilise these limited resources? Species vary considerably in aggression and in mode and degree of communication between foraging workers. These differences have profound effects on the manner in which a colony finds and harvests resources. Some species can recruit quickly to large numbers: others do not recruit at all. Some species forage in groups: other as solitary workers. Some employ aggression as a competitive technique to sequester resources from rival bees. Other species are rarely seen in agonistic encounters (Johnson & Hubbell 1975), Coexistence on one resource is possible when there is a heterogeneous resource and when a trade-off among foraging traits exists (Roubik 1989). These conditions provide niche separation along space and time.

Foraging strategies are divided into two: group and solitary foraging. In solitary foraging, each bee makes a decision where and when to forage on a resource, whereas in group foraging, groups of workers are directed to a resource by scout bees. Scouts lead the recruits to the resources by pheromone marking at the resource or in a trail from the resource to the hive, or by piloting whereby recruits can follow the scouts either by smell or sight or by making a sound (Lindauer & Kerr 1960). Johnson & Hubbell (1975) and Hubbell & Johnson (1978) found that solitary foragers are quick at discovering new resources and group foragers are good at monopolizing resources but slow in discovering new resources.

The spatial and temporal distribution of resources depends on plant features like phenology and regularity in flowering, and on abiotic (climate) and biotic factors (animals feeding in them). Most tropical plants flower discontinuously with a tendency to flower in particular season (Frankie et al. 1974, Baker & Baker 1983). Many kinds of flowers are open, or secrete nectar, or liberate their pollen at certain times of the day. The length of time during which a flower can provide pollen or nectar varies greatly among plant species.

1.2 The research of this thesis

The focus of this thesis is on the inter-specific foraging relations of honeybees and stingless bees in their native ecological environment of tropical Africa. This is because the knowledge base of the ecology of Afrotropical bees is minute. The general research question showing bee-plant ecological relations is depicted in Figure 1. Aspects of nesting biology of Afrotropical stingless are presented in chapter 3. The chapter discusses stingless bee nest site selection and occurrence. The natural nests made by these bees (trees, shrubs, ground and wall nests) are described. In chapter 4, honeybee and stingless bee colony abundance and predation by apes and humans are discussed. This chapter is part of the efforts to understand nesting ecology of highly social bees (native stingless bee and honeybee populations BINP. Predators are considered in more detail than in previous field studies of honey-making bees. Meliponine nest abundance is analysed relative to availability of nesting sites, food, and the elevation or weather. Temporal resource partitioning and climatological influence on colony flight and foraging of stingless bees is discussed in chapter 5. The study presents the results of observations on flight and foraging of different species studied in a forest habitat. In chapter 6, pollen foraging by *Apis mellifera* and stingless bees *Meliponula bocandei* and *Meliponula nebulata* in BINP is discussed. Making use of the uniqueness of this study where native species of honeybees and stingless bees were studied in the same natural Afrotropical forest, a qualitative study focusing on likely factors causing differences in their pollen foraging behaviour is presented. Botanical sources and sugar concentration of nectar collected by two stingless bee species in BFR is presented in chapter 7. The study describes the important nectar sources of stingless bees and their diversity. It discusses factors influencing sugar concentration of collected nectar and in particular it deals with effect of the bee species on the concentration of the collected nectar. In chapter 8, seasonal availability and preference of honeybees for different forage plants in BFR is described. The important honeybee forage plants in the forest, their flowering and nectar harvesting periods are described. The flowering periods are correlated to climatic factors and brood production to determine if plants in this forest follow similar flowering pattern.

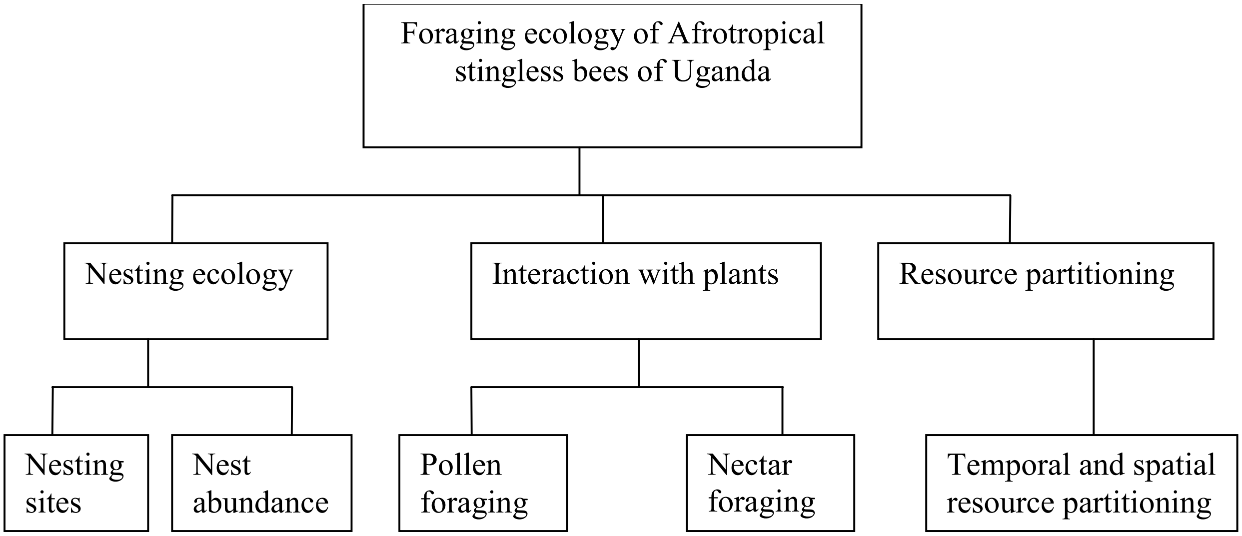

Fig. 1. Overall research question depicting bee-plant ecological relations in the Afrotropical forests

Chapter Two

2.0 Study sites and bee species

2.1 Bwindi Impenetrable National Park (BINP)

Bwindi Impenetrable National Park (BINP) located in south-western Uganda on the edge of the western rift valley lies on the Democratic Republic of Congo (DRC) border. It is located between latitudes 0°18' and 0°53'S, longitudes 29°35' and 29°50'E (Fig. 2). It is one of the largest (331 sq. km) natural forests in East Africa and contains both montane and lowland forest. The Forest Park constitutes an important store of gene pool for tropical bees, which represents a potential for expanding our knowledge and understanding of complex forest biological ecology. The forest park is on UNESCO's list of world heritage sites due to its ecological uniqueness and natural beauty. The park supports a large number of plants and animals endemic to the region, but most notably half of the world's population of Mountain Gorillas (*Gorilla gorilla berengei*). It is also home to another 10 primate species including chimpanzees. The forest underwent rapid exploitation of timber through pit-sawing, extensive gold mining and encroachment for virgin agricultural land in the 1970s and the first half of the 1980s. Population pressures, mining, poaching, grazing of livestock and removal of trees for fuel wood, lumber and poles threatened the conservation of the park (Butynski 1984). The altitude of the park ranges from 1160m from Ishasha gorge to 2607m at the Rwamunyonyi peak. The annual temperature ranges between 7-20 ^{0}C with a mean of 16.3^{0}C. 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 mm-2390 mm.

2.2 Budongo Forest Reserve

Budongo Forest Reserve (BFR), which was part of the study site, is a tropical rain forest. It is situated in Masindi and Hoima districts in Western Uganda between 1°35’ and 1°55’ N, and 31°18’ and 31° 42’ E, (Howard 1991). It is located east of the Western rift valley escarpment and Lake Albert. The forest lies at an average altitude of 1100m (minimum 750 m and maximum 1250 m) above sea level (Eggeling 1947, Howard 1991). The terrain is gently undulating with a gradual slope NNW towards the Albertine escarpment. Budongo forest reserve is an outlier of the great Ituri forest of the Democratic Republic of Congo (Fig 3). These forests resemble in many respects the rain forests of West Africa (Eggeling 1947). Budongo forest covers an area of 825 sq km, making it Uganda's biggest forest reserve (Hamilton 1984), of this 437 sq km (53%) is continuous forest cover, the remaining 47% comprises grassland communities, thought capable of supporting the forest (Howard 1991). The reserve is in part continuous with the Murchison Falls National Park and Bugungu and Karuma game reserves.

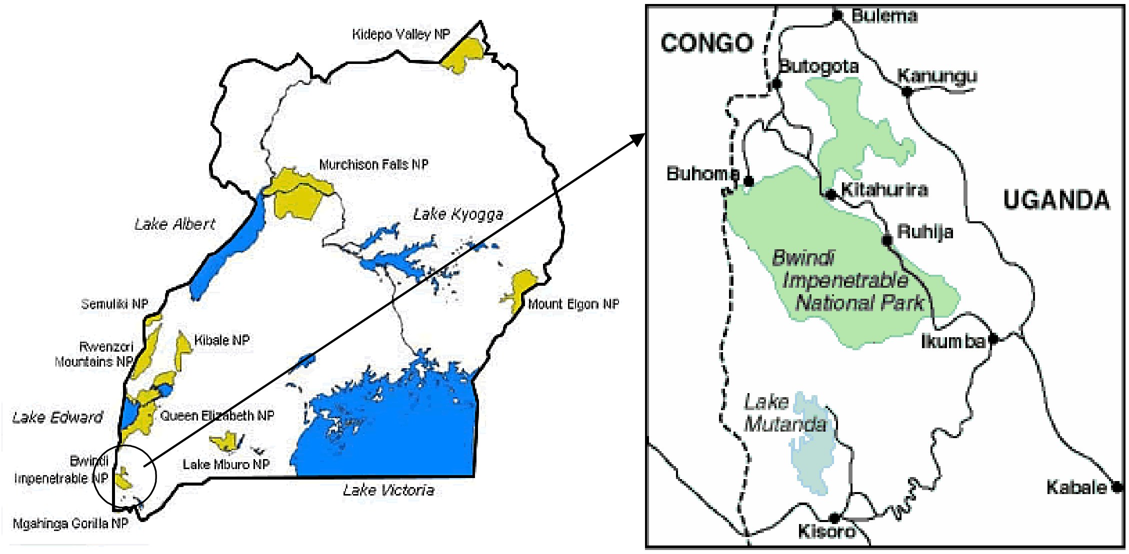

Fig 2. Map of Uganda showing the location of Bwindi Impenetrable National Park (BINP) in south-western Uganda.

Fig. 3. Map of Uganda showing the location of Budongo Forest Reserve in mid-western Uganda.

Nesting biology of equatorial Afrotropical stingless bees (Apidae; Meliponini) in Bwindi Impenetrable National Park, Uganda

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Abstract

An inter-specific nesting biology of highly eusocial stingless bees (meliponini) was studied in Bwindi Impenetrable National Park, south-western Uganda. Fieldwork was guided by Pygmies who are the local indigenous honey-hunters residing around the park. During the fieldwork, stingless bees were identified according to local Pygmy folk taxonomy. A total of 538 natural nests of five stingless bee species belonging to two genera were found: *Meliponula* (four species) and *Hypotrigona* (one). Two morphs of *M. ferruginea* (6 mm) were identified, which previously were called *M. erythra* but now are regarded species synonyms. The bees nested in tree cavities, house wall crevices and underground. There were no exposed nests. Trees harboured nests of the bigger bee species. A broad range of trees (133 trees of 36 species) was used as nesting sites. *H. gribodoi* only nested in house wall crevices. *Meliponula bocandei* and *Meliponula lendiliana* nested both in tree cavities and in the ground thus exhibiting high degree of flexibility which can ultimately lead to better survival of these two species. There was some degree of nest tree height partitioning with bigger bees selecting higher heights. Tree selection by bee species not only depended on tree availability but also on size of the bee. Most bee nests were situated in large trees.

Keywords: Nest sites, Stingless bees, Equatorial, Afrotropical, Hypotrigona, Meliponula, Pygmies, Chimpanzees, Bwindi, Uganda

1.0 Introduction

Stingless bees comprise a highly diverse and abundant group of eusocial bees that inhabit the tropical and subtropical parts of the world. Worldwide several hundred species exist, which differ significantly in colony size (a few dozens to tens of thousands of individuals); in body size (2 to 14 mm) and in body colour (yellow or orange to black, see Roubik 1992, Michener 2000). They represent an important group of pollinators (Heithaus 1979, Momose & Inoue 1994, Nagamitsu & Inoue 1994). The taxonomy of stingless bees is sometimes ambiguous as species names have changed over time and different authors have different views on classification and phylogeny (Wille 1983, Roubik 1992, Michener 2000, Eardley 2004). Most genera in most areas have not been adequately analysed for recognition of their forms (Michener 2000). One way of characterising stingless bees is by use of their nests (Michener 1990). Attributes of the nest are useful in taxonomic studies especially in equatorial tropical Africa where little has been studied. Previous studies on nesting biology of stingless bees have been carried out by Wille & Michener (1973); Michener (1974); Hubbell & Johnson (1977); Roubik (1979, 1983a, 1989, 1992); Sakagami (1982); Eltz et al. (2002, 2003) and Slaa (2003); Kajobe & Roubik (2006)

Stingless bees form perennial colonies, mostly in tree hollows; some species build in abandoned or, occupied nests of ants or termites, either above ground or subterranean (Wilson 1971, Michener 1974, Roubik 1989). Founding of new colonies occurs by colony fission and swarming. The nests of most stingless bee species occupy cavities that the bees find, and may limit by walling off unused areas, but the bees usually do little or no excavating. Other species do not occupy cavities but make exposed nests on tree branches or on cliff faces (Michener 1990). Nests in felled trees, in bush that has been burned or that has been trampled or cut by man or other animals, in the earthen banks of road cuts, paths, fields, and in banks made by rushing water have frequently provided the only opportunities to study bee nesting biology (Roubik 1989). Therefore stingless bees are generalists with regard to selection of nest sites (Hubbell & Johnson 1977, Heithaus 1979, Roubik 1989, Ramalho et al. 1990). One of the attributes of most stingless bee nest sites, or in the case of exposed nests, of the nest itself, is excellent insulation. Nests in large trunks or in the soil are particularly well insulated. Many species, particularly those of the moist tropics, are unable to withstand chilling (Michener 1974).

Roubik (1983a) observed that the nests of many stingless bee species have yet to be described. This observation is especially important in tropical equatorial Africa where little studies have been done on stingless bees. In Bwindi Impenetrable National Park (BINP), previous records (Cunningham 1992) were made of stingless bees nesting in tree hollows on the basis of information from the indigenous honey-hunters, the Pygmies, but no scientific studies were made to assess the validity of these observations. The park constitutes an important store of gene pool for tropical bees which represents a potential for expanding our knowledge and understanding of complex forest biological ecology (Butynski 1984). The biology of tropical moist forests has a close relationship with the agents of pollination, dispersal and regeneration pool. Most studies on stingless bee ecology are largely based on studies in the neoptropics and have ignored the aspects and context of Afrotropical stingless bee species, particularly to those equatorial (but see Darchen 1972, Schneider & Blyther 1988, Kajobe & Echazarreta 2005, Kajobe & Roubik 2006, Kajobe 2006a, Kajobe 2006b). This study therefore, makes a primary contribution to filling this void. This study investigates stingless bee nest site selection and occurrence. The natural nests made by these colonies and their nest selection were documented. Also the trees species, shrubs and ground nesting sites of the stingless bee species were determined.

2.0 Materials and Methods

2.1 Study sites

Bwindi Impenetrable National Park (BINP) located in south-western Uganda on the edge of the western rift valley lies on the Democratic Republic of Congo (DRC) border. It is located between latitudes 0°18' and 0°53'S, longitudes 29°35' and 29°50'E. It is one of the largest (331 sq. km) natural forests in East Africa and contains both montane and lowland forest. The forest park is on UNESCO's list of world heritage sites due to its ecological uniqueness and natural beauty. The park supports a large number of plants and animals endemic to the region, but most notably half of the world's population of Mountain Gorillas (*Gorilla gorilla berengei*). It is also home to another 10 primate species including chimpanzees. The forest underwent rapid exploitation of timber through pit-sawing, extensive gold mining and encroachment for virgin agricultural land in the 1970s and the first half of the 1980s. Population pressures, mining, poaching, grazing of livestock and removal of trees for fuel wood, lumber and poles threatened the conservation of the park (Butynski, 1984). The altitude of the park ranges from 1160 m from Ishasha gorge to 2607 m at the Rwamunyonyi peak. The annual temperature ranges between 7-20 ^{0}C with a mean of 16.3^{0}C. 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 mm-2390 mm.

2.2 Survey of nest sites

Data collection was carried out between March 2002 and February 2004. We incorporated some data from the field assistants of the Institute of Tropical Forest Conservation (ITFC), the research institute based in the park. The study of highly eusocial bees in intact tropical forests can usually be undertaken successfully with the help of local guides and aboriginal peoples, who to some extent depend upon the honey, brood, or resin contained in these nests for their own livelihood (Roubik, 1989). Therefore, this fieldwork was guided by Pygmies who are the local indigenous honey-hunters residing around the park. In some instances, the dwarf honey-guide *Indicator pumilio*, a tiny bird that is endemic to the Albertine Rift Mountains helped us locate nest sites. At first we tried to search for nests once a week however, we could not locate many nests using this method. We located more nests from information supplied by the Pygmies and the field assistants who were tracking chimpanzees and gorillas. Nests were located either by chance during random search or by inspecting trees located along the park trails and by nest located in established plots. Stingless bees from foraging missions were trapped at their nest entrances with a net. They were first identified according to the local Pygmy names. Scientific identification was done by David W. Roubik at the Smithsonian Tropical Research Institute (STRI) and by consulting Eardley (2004).

2.3 Location of nest site

The altitude of each nest located was measured using an altimeter. Nest height was measured using measuring tape for heights less than 2m and Spiegel relascope for nests higher than 2m. Colonies nesting high in the tree trunks could only be identified using binoculars. We might have missed some bee nests situated close to the canopy. Nest entry diameter was measure using a 15cm ruler. The direction in which each nest faced was measured by use of a compass. The distance from each nest to the nearest water source was estimated in metres To determine whether bee species preferred nesting in dead dry wood or live trees and also whether bees preferred nesting under shade the percentage of live wood in a nest trees and tree cover close to each nest were estimated in four categories (0-25, 25-50, 50-75, and 75-100). When a nest was found in a tree cavity, it was identified to species level. Nest trees were either identified by the experienced ITFC field assistants or the leaves of these trees were taken to Makerere University herbarium for identification. Nest tree diameter at breast height (dbh) was measured using a measuring tape. In the case of trees with large buttresses, dbh recordings were taken above those buttresses. When a nest was found in a tree cavity, it was identified to species level. Nest trees were either identified by the experienced ITFC field assistants or the leaves of these trees were taken to Makerere University herbarium for identification. Nest tree diameter at breast height (dbh) was measured using a measuring tape. In the case of trees with large buttresses, dbh recordings were taken above those buttresses.

3. 0 Results

3.1 Stingless bee taxonomy and nest characteristics

A total of 5 stingless bee species belonging to two genera were found to occur in the park: *Meliponula* (four species) and *Hypotrigona* (one). While the other local agricultural communities neighbouring the park generally called all species of stingless bees as "Obuhura", the Pygmies categorised them according to body features like size, colour, and spots on bee body to name them. The Pygmy folk taxonomy was in broad agreement with the scientific classification. Two morphs of *Meliponula ferruginea* were identified. In this study the black one is referred to as *M. ferruginea* (black) and the Pygmies call it "Obugashu". The other is brown, here upon referred to as *M. ferruginea* (brown) and the Pygmies call it "Obuganza" (Table 1). The bees differed significantly in colour from pale (*H. gribodoi*) to black (*M. lendliana*). *M. nebulata* is black with a distinct yellow spot on the head. The biggest species, (*M. bocandei*) was 9 mm long and the smallest, (*H. gribodoi*) 2-3 mm long. The bee nest entrance diameters ranged from 0.3 cm (*H. gribodoi*) to 2 cm (*M. bocandei*). Among the genus *Meliponula*, overlap in cavity entrance diameter was considerable with the minimum being 1cm. Most of the nest entry shapes were circular with that of *H. gribodoi* being the longest (1-5cm). At one incidence, on disturbance by the Pygmies, a nest of *M. ferruginea* (brown) which had originally one entrance developed two entrances with mud ridges that were narrowed. These features were probably used for additional defence.

3.2 Location and number of stingless bee nests

A total of 538 natural nests of the 5 stingless bee species were located in the park. *H. gribodoi* the smallest bee species (2-3 mm) had the highest number (72%) of nests. It was the only bee species that nested in close proximity (as low as 5 cm) from one another. For example, at Kitahurira rangers' camp, a total of 233 nests of *H. gribodoi* were counted on walls of two houses only. This may explain why its total number of nests was high. *M. bocandei* had 9% of total number of nests. Only five nests of *M. lendliana* were located throughout the study period (Table 2). There was more diversity in terms of number of bee species in the northern as compared to the southern sector. All the five bee species were located in the northern sector and only three nested in the southern sector. Though *M. ferruginea* (brown) is a relatively big species (6 mm), it only nested in the northern sector.

3.3 Nesting sites

The bee species nested in tree cavities, house wall crevices and underground (Table 3). There were no exposed nests. Trees harboured more nests as compared to the other nesting substrate. *M. bocandei* and *M. lendliana* nested both in tree cavities and in the ground. It was surprising that *M. bocandei*, the biggest bee species (9 mm) nested only in the ground in the southern sector (2000-2607 m) and only in tree cavities in the northern sector (1160-1700 m). The ground nests for both species were not sheltered from the rain; rather both had entry tubes that diverted surface water around the nests. Some of the ground nests of *M. bocandei* located out side the park were situated in farmlands and not anywhere close to trees or abandoned termite nests. The location of bee nests did not depended on available tree cover (Pearson Chi-Square test: df = 12, n = 125, P > 0.05).

3.4 Nest trees

A broad range of trees (133 trees of 36 species) was used as nesting sites (Table 4). The tree folk taxonomy was in broad agreement with the corresponding scientific classification. None of the bee species had a clear preference for particular tree species. The only high percentage of nests on one tree was observed in *M. feruginea* (brown) in which 58% of its nests were situated on *Parinari exclesia*. But these nests were almost all in one individual tree. This suggests that preference is for this location or the structure of this particular tree and not for the species of the tree. There were only 5 instances encountered were a single tree harboured more than one nest. The most significant was were *Parinari exclesia* a big tree of 112 cm dbh was found habouring 9 nest all of *M. ferruginea* (brown) at various heights and orientation. The bees seemed to nest in any of the living trees or dead wood randomly (Pearson Chi-Square test: df = 12, n = 125, P > 0.05). One might argue that you would need information on the overall abundance of live and dead trees in the habitat to do a proper scientific test. The distance to water source from nests did not influence bee nest site (Pearson Chi-Square test: df = 6, n = 88, P > 0.05). The overall nest orientation was random (Pearson Chi=Square, df = 9, n=129, P > 0.05). However, at Kitahurira rangers' camp, a total of 233 nests of *H. gribodoi* (2-3mm) were counted on two house walls, 69% of which were facing east wards. This may be due to the position of the sun in the mornings which brings about warm temperatures for this small bee species to fly. It is not possible to deduce the degree of selectivity for all the bee species, since there is not enough information on the total range of nest tree cavities available in the forest.

3.5 Diversity of nest trees

The Shannon-Weiner Diversity Index was used to compare the diversity of nest trees in the southern sector to the northern sector. The overall Index was 3.29 with an evenness of 0.9. The indices were almost the same for the two sectors (Table 5)

3.6 Nesting height

Nest heights of the different bee species differed significantly from each other (Kruskal-Wallis test: df = 4, n = 133, p = 0.002). There was some degree of height partitioning with regard to the larger bee species. *M. bocandei* and *M. ferruginea* (black) selected significantly higher heights (Pearson Correlation: r = 0.79, n = 50, P = 0.007). There was no degree of height partitioning for the other bee species (Table 6). *M. bocandei* nested as high as above 45m. Since there were some difficulties in locating higher nests, there could have been some bias in observations towards nests of lower heights.

3.7 Nest tree diameter

Nest trees occupied by cavity nesting species ranged from 18 to 235 cm dbh. This minimum diameter closely corresponds to that found by Slaa (2003, 19 cm). Most bee nests were situated in large trees. A total of 54.9% of nest were in trees between 60 to 99 cm dbh and 79% were in trees above 60 cm dbh (Fig 1). Therefore nest tree diameter was probably the more meaningful indicator of species overlap in nesting site preference. Tree selection by the bee species not only depended on tree availability but also on size of the bee species. The bigger bees (e.g. *M. bocandei* and *M. nebulata*) selected larger trees. The dbh of the different tree species differed significantly from each other (Kruskal-Wallis test: df = 4, n = 133, P = 0.001).

4.0 Discussion

4.1 Taxonomy and distribution of stingless bees

This study may probably be among the first detailed description of stingless bee species, their nests and nesting sites in a natural tropical forest in equatorial Africa. It reinforces the fact that African Meliponines are very poorly known. The study was based on 538 natural nests of five stingless bee species belonging to two genera: *Meliponula* and *Hypotrigona*. We feel that all the stingless bee species occurring in the park were located because our nest surveys were intensive. It should be noted that more than five stingless bee species occur the country however, they have not been studied (Kajobe, pers. comm.). The genus *Hypotrigona* is one of the minute stingless bees, widespread and abundant in tropical Africa although represented by only a few species (Michener 1990, 2000). Other species of this genus not found in this study include *H. araujoi* and *H. braunsi.* There were inter-specific differences in colour, size and nest entrance characteristics among the four species of the genus *Meliponula* (Table 1). This genus ranges from Kenya to eastern Democratic Republic of Congo (DRC), Botswana, northern Transval and Natal (Michener 1990).

Roubik (1992) suggested that there may be about 50 species of stingless bees in Africa belonging to 10 genera. He observed that research on the perennial bee colonies of tropical forests is somewhat impaired by a lack of taxonomic guides and universally accepted nomenclature. This study demonstrates the importance of folk taxonomy in aiding scientific classification of biological flora and fauna. The Pygmy folk taxonomy was in broad agreement with the scientific classification. Posey (1983) also put forward the discovery of nine new species of stingless bees of Meliponinae through the comparison of Kayapo and scientific taxonomic systems. The northern sector contained more diverse number of species as compared to the south with all five stingless bee species being located in the north while only three were found in the south (Table 2). The wide range of elevational gradient seemed to be an important factoring in influencing distribution and abundance of nest sites. Generally, the northern sector is situated in a lower elevational gradient (1160-1900 m), it is therefore warmer and more favourable to all sizes of the bees as compared to the south (1400-2607 m). The larger bees (*M. bocandei*; 9 mm and *M. nebulata*; 7 mm) have smaller surface area to volume ratio and can withstand the lower temperatures in the southern sector.

4.2 Nests and nest sites

The preference for nest sites such as tree cavities, ground and wall crevices was also reported by Michener (1974), Hubbell & Johnson (1977) and Slaa (2003). Roubik (1989) observed that selection of a nest site was determined by availability of resources and protection from natural enemies. He further added that the extent to which nesting bees can perceive and measure this and other pertinent factors will enhance their reproductive fitness. Such features affect the conditions experienced by immature bees, which in turn influence their rate of development and the timing of adult emergence. Nest site specificity only occurred with *H. gribodoi* which built all nests on house wall crevices. The houses probably provided better warmth and protection from both rain and predators. Most nest entrances of this bee faced eastwards probably due to the position of the early morning sun which provides warm temperatures.

Nest location or the building material used may strongly influence the potential for evolutionary divergence (Roubik 1989). The biggest bee (*M. bocandei*, 9 mm) nested only in the ground at relatively higher elevational gradient (1900-2607m) and only in tree cavities at lower gradient (1160-1800m), yet the two populations seem not to be reproductively isolated. This behavioural difference in nest site selection may be ultimately derived from either the differences in elevational gradient or predation pressure. Otherwise one would at least expect some overlap. *M. lendliana* also nested both in tree cavities and in the ground. The criteria used by these two ground nesters to find ideal nesting areas have yet to be elucidated fully. Both use open ground with few or no plant roots. Some of the ground nests of *M. bocandei* located out side the park were situated in farmlands and not anywhere close to trees or abandoned termite nests. It is not clear whether these bees actually “dug” the ground themselves. A firm or hard surface in combination with softer soil in deeper strata with moisture content sufficient to prevent collapse of excavated burrows is the preferred substrate of ground nesting bees (Roubik 1989). More stingless bees seemed to nest in the ground e.g. abandoned 'terrestrial' termite nests in the northern dryer / savanna areas of the country than in the southern wetter areas where more species nested in trees cavities (Kajobe, pers. Comm.). More study should be conducted to validate this broad observation. By nesting both in tree cavities and in the ground, these two species exhibit high degree of flexibility which can ultimately lead to better survival over the others.

H. gribodoi was the only species that exhibited monospecific nesting aggregation. Many of its nests were located in wall crevices in close proximity to each other, suggesting it does not exhibit intra-specific nesting competition. The requirements for nest defense and the utilisation of a suitable nest substrate, which may be the deciding factor in nest location, may combine to produce these aggregating tendencies in *H. gribodoi*. Recently nesting aggregation of *Trigona collina* was reported by Eltz et al. (2003) in Malaysia. The four species of the genus *Meliponula* did not exhibit monospecific nesting aggregation. Nests of each species were scattered all over the park suggesting little or no inter and intra-specific nesting cooperation. Roubik (1989) observed that the amount of inbreeding that can be tolerated by a bee species might influence the dispersal of daughter colonies. There were no cases of exposed nests probably because of the high rate of predation cases (Kajobe & Roubik 2006) or because bee species of the moist tropics are unable to withstand low temperatures (Michener 1974). Slaa (2003) found exposed nests of *Trigona corvina* in a tropical dry forest in Costa Rica.

4.3 Nest trees

In general, the local folk taxonomy of the nest trees was in agreement with the corresponding scientific names. Only few instances were recorded where one local name was given to more than one tree species of the same genus. This may probably be because the local taxonomy is mainly oral, passed from generation to generation without a lot of written document. Five bee species were contained in 36 tree species of relatively large sizes. This implied that tree cavity nesting species were generalists in regard to selectivity in favour of certain tree species. The non specificity resulted to high overlaps in use of nest tree species (Table 4). Hubbell & Johnson (1977) reported similar results in a tropical dry forest in Costa Rica.

The bees in this study nested in both native and introduced tree species suggesting that they are opportunistic in selection of a nest site and use whatever tree species presents a cavity of the correct dimensions and purpose. The only case in which there seemed to be some selectivity was observed in *M. ferruginea* (brown), where 58% of its nests were situated on *Parinari exclesia*. Although almost half of these nests were located in one individual tree, there seemed to be some degree of selectivity because of the structure of this tree. A mature tree of this species is characteristically big, in most cases it has cavities left after its core of living tree is rotten from rainwater entering through the scars left by its fallen branches. The availability of these cavities probably account for the clumping of the stingless bee nests. Only five instances were recorded were more than one nest was located in a single tree. This is in contrast to Eltz et al. (2003) who reported that over 40% of nest trees haboured more than one (maximum: 8) stingless bee nests in an undisturbed forest in Malaysia.

We were unable to detect any difference in the bee species preference for live or dead wood. The bees seemed to nest in any of the living trees or dead wood randomly. The dead trees used were of hardwoods that last for many years with less pressure from termites such as *C. lustanica.* One might argue that you would need information on the overall abundance of live and dead trees in the habitat to come up with a proper conclusion. There was some degree of height partitioning with regard to the larger bee species. In general, the mean height given for a species building nests in tree cavities may be biased towards lower heights, since nests are mostly found near ground level. Roubik (1979, 1983) observed that highly eusocial species rarely make their nest entrances level with the ground or in the tallest branches of forest trees but a height of 30 m seems to be their normal limit. The variations in height may lead to the conclusion that different species are most often active at different strata above the ground however, what we did not determine was whether the reason for height partitioning is more closely related to food, nest site or predation. There was no selectivity in regard to nest tree size. This resulted into high overlap in tree size among cavity nesters. Over 79% of nests of all the five tree cavity nesting species were situated in large trees of dbh above 60cm. These stingless bees are of greatly different worker and colony sizes but have built nests in tree cavities of roughly the same dimensions. This is probably because cavity nesting meliponines can significantly reduce the size of a tree cavity by blocking part of it (Roubik 1989).

Table 1. Local Pygmy folk taxonomy versus the scientific names. Depicted are also the bee and nest entrance characteristics of stingless bee species located in the park

Scientific name	Local Pygmy name	Bee colour	Bee length (mm) N=15	Nest entrance diameter (cm)	Nest entrance shape
Hypotrigona gribodoi (Magretti)	Obuhambamba	Pale	2.0-3.0	0.3-0.5	Tubular, long and tapers
Meliponula (Meliponula) bocandei (Spinola)	Maranga	Brownish	9.0	1.5-2.0	V- Shape/ Funnel
Meliponula (Axestotrigona) ferruginea	Obuganza	Reddish brown	6.0	1.0	Circular and tapers
Meliponula (Axestotrigona) ferruginea	Obugashu	Black	6.0	1.0-1.2	Circular tube
Meliponula (Meliplebeia) lendliana (Friese)	Obuzagali	Black	4.0	1.0-1.2	Circular tube
Meliponula (Meliplebeia) nebulata (Smith)	Obwiza	Black with yellow spot on the head	7.0	1.1-1.4	Circular

Table 2. Number of stingless bee nests located in the park. The large number of nests in the northern sector is due to the number of *H. gribodoi* nests located in wall crevices.

Bee species	Northern sector	Southern sector	Total
Hypotrigona gribodoi	389	0	389
Meliponula bocandei	33	17	50
Meliponula ferruginea (brown)	29	0	29
Meliponula ferruginea (black)	9	19	28
Meliponula lendliana	5	0	5
Meliponula nebulata	6	31	37
Total	471	67	538

Table 3. Type and number of stingless bee nests.

Bee species	Total nests	Tree nests	Ground nests	Wall nests
Hypotrigona gribodoi	389	0	0	389
Meliponula bocandei	50	33	17	0
Meliponula ferruginea (brown)	29	29	0	0
Meliponula ferruginea (black)	28	28	0	0
Meliponula lendliana	5	4	1	0
Meliponula nebulata	37	37	0	0
Total	538	131	18	389

Table 4. List of folk taxonomy versus the scientific classification of nest trees used by stingless bees. Tree scientific names are alphabetically ordered and the bee species are ordered by decreasing abundance. *H. gribodoi* is not included because its nests were only located in house wall crevices.

Nest tree species	Local names	*M. bocandei*	*M. nebulata*	*M. ferruginea* (black)	*M. ferruginea* (brown)	*M. lendiliana*	Total
Agauria salicifolia	ekigwa		5	2			7
Albizia gummifera	omushebeya	1		1	2		4
Alangium chinense	omukofe	1	1	1			3
Bersama abyssinica	omukaka		1				1
Carapa grandiflora	omuruguya	4		2	2		8
Chrysophyllum albidum	omushayu	1	1				2
Chrysophyllum gorungosanur	omushayu		2	3			5
Cupressus lusitanica		2	3	1	1		7
Dichaetanthera corymbosa	omunyinju			1			1
Drypetes gerrardii	omushabarara	1			1		2
Ekerbergia capensis			1	1			2
Entandrophragma cylindricur	omuyovu		1				1
Entandrophragma excelsum	omuyovu	1					1
Eucalyptus sp.	uketusi				1		1
Faurea saligna	omulegyere		2	1			3
Ficalhoa laurifolia	omuvumaga	1	1	1			3
Ficus natalensis	ekyitoma					2	2
Ficus sp.	ekyitoma	3	1		4		8
Glyphaea brevis	omusingati	1					1
Hagenia abyssinica	omujesi		1				1
Maesa lanceolata	omuhanga	1			1	1	3
Maytenus accuminata	omulembwe		3	2			5
Myrica salisfolia	omujeje		2	1			1
Olinia usamberensis			3	2			5
Parinari exclesia	omushamba	6	2		11		19
Podocarpus milanjianus	omufu		1				1
Polyscius fulva	omungo		1				1
Premna angolensis	omuguna		1				1
Prunus Africana	omumba	1	1	1	2		5
Schefflera barteri	omwamira				3		3
Strombosia schefferi	omuhika	4	1	2	2		9
Syzigium guineense	omugote	2	1	3	1		7
Triumphetta macrophylla	omunaba	2					2
Xymalos monospora	omuhotora		1			1	1
Zanthoxylum gilletii	omulemankobe		1	3			4
Zanthoxylum macrophylla	omuchanga				1		1
Total		35	37	28	29	4	133

Table 5. Shannon-Weiner Diversity Index (H'), evenness and total number of nest trees. H'=Shannon-Weiner Diversity Index. It increased with the number of nest tree species J'=Evenness or relative Diversity (H'/Hmax). It indicates how the nest tree species are distributed in the community. Where the evenness is high, the nest trees are many and more diverse. N = Total number of nest trees

	Overall	Southern sector	Northern sector
H'	3.29	2.91	2.76
J'	0.9	0.94	0.91
N	133	52	81

Table 6**.** Nest heights (in metres) of the various bee species. The figures shown are for the lowest, highest and mean heights of the different bee species. The mean standard errors are also included.

Bee species	N	Lowest height (M)	Highest height (M)	Mean height (M)	Std. Error
M. nebulata	37	0.6	45.1	7.5	1.5908
M. ferruginea (black)	28	0.6	41.0	9.4	1.7937
M. bocandei	35	0.8	47.0	16.3	2.2300
M. ferruginea (brown)	29	0.3	39.0	8.3	2.0377
M. lendiliana	4	0.4	5.0	2.7	0.9877
Total	133	2.7	177.1	10.24	0.9850

Fig. 1. Size distribution of nest trees of stingless bees (n = 133). Only 21% of the nest trees had a dbh of less than 60 cm. *H. gribodoi* is not included since its nests only occurred in wall crevices. Error bars represent standard error of the mean.

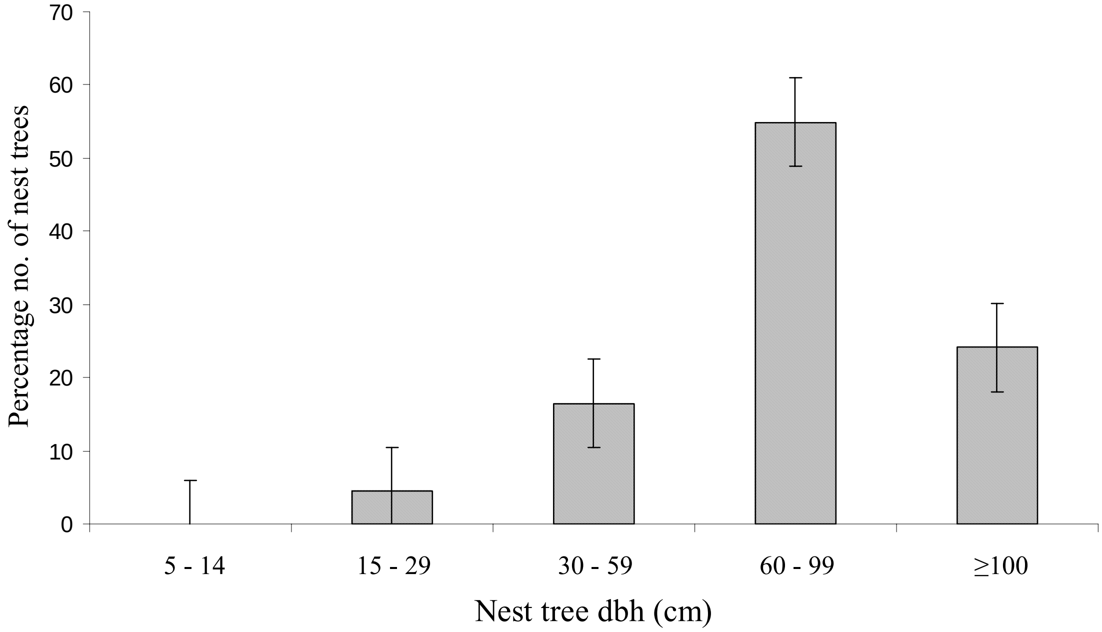
70
60
50
40
30
20
10
0
Percentage no. of nest trees
5 - 14
15 - 29
30 - 59
60 - 99
≥100
Nest tree dbh (cm)

Fig. 1.

Chapter Four

Honey-making bee colony abundance and predation by apes and humans in a Uganda forest reserve

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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.

Keywords: *Apis,* bee nest density, Bwindi–Uganda, chimpanzees, honey, Meliponini, predation, Pygmies

1.0 Introduction

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, 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 honeybee 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.

2.0 Materials and methods

2.1 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 km2) 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 $^{\circ}$C with a mean of 16.3 $^{\circ}$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.

2.2 Survey of nests and nest sites

Fieldwork 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 ($500 \times 20 \times 2 = 20{,}000$ 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 non timber forest products, including nests of *Apis mellifera* for domestication. Because this level of disturbance was not considered natural forest ecology for native honeybees, 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.

2.3 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.

3.0 Results

3.1 Bee species and nest density

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 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).

3.2 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 51with 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.

3.3 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 non-forest 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).

3.4 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 (÷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 (÷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 16m, 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 (÷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 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 as secondary predators, harvesting honey and brood from nests that had recently been opened by humans or chimpanzees.

3.5 Altitude

Fewer bee species nested at higher elevation (data not shown) but no overall change in stingless bee nest abundance occurred, based on $R2 < 0.001$ 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.

3.6 Other causes of mortality

The bees are under threat from forest fires which usually occur during severe drought. In July 1999 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.

4.0 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 1993b), 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 non forest 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 6weeks, 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 wind throws, 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 honeybees and stingless bees compete strongly for food and nesting sites, their populations should display reciprocal trends (Roubik & Wolda 2001), and there has been “arti-ficial” human predation on honeybees in the park (see below). The honeybees, 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-Ara´ujo (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/km2 and varied among species, ranging from 1 nest/km2 (*M. lendliana*) to 12 nests/km2 (*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 honeybee 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 honeybees 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 honeybees 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 honeybees, 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 honeybees. 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.

Table 1. Tropical stingless bee (Meliponini) and honeybee (*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 & Johnson 1977
Panama, moist forest[a]	460, 64.7 ha	–	+	Michener 1946
Panama, moist forest	102, 15.6 ha	–	+	Johnson & Hubbell 1986
Panama, wet forest	375, 8 ha	–	+	Roubik 1983a
Bolivia, moist forest	66, 50 ha 2, 50 ha[b]	+	+	Stierlin & Roubik, unpub.
Bolivia, dry forest	54, 50 ha 2, 50 ha[b]	+	+	Stierlin & 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 & Harrison, unpub.
Thailand, moist forest[a]	1500, 4 ha	+	+	Roubik & Harrison, unpub.
Panama, moist forest	56, 50 ha	+	+	Roubik & 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 & Inoue 1997
Botswana, xeric shrub	7.8, 600 ha[b]	–	+	Schneider & Blyther 1988
Ivory Coast, dry forest	260, 30 ha 10, 30 ha[b]	+	+	R. Darchen, 1972 & 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.*

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

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 purpureum*				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

Fig.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.

Fig. 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).

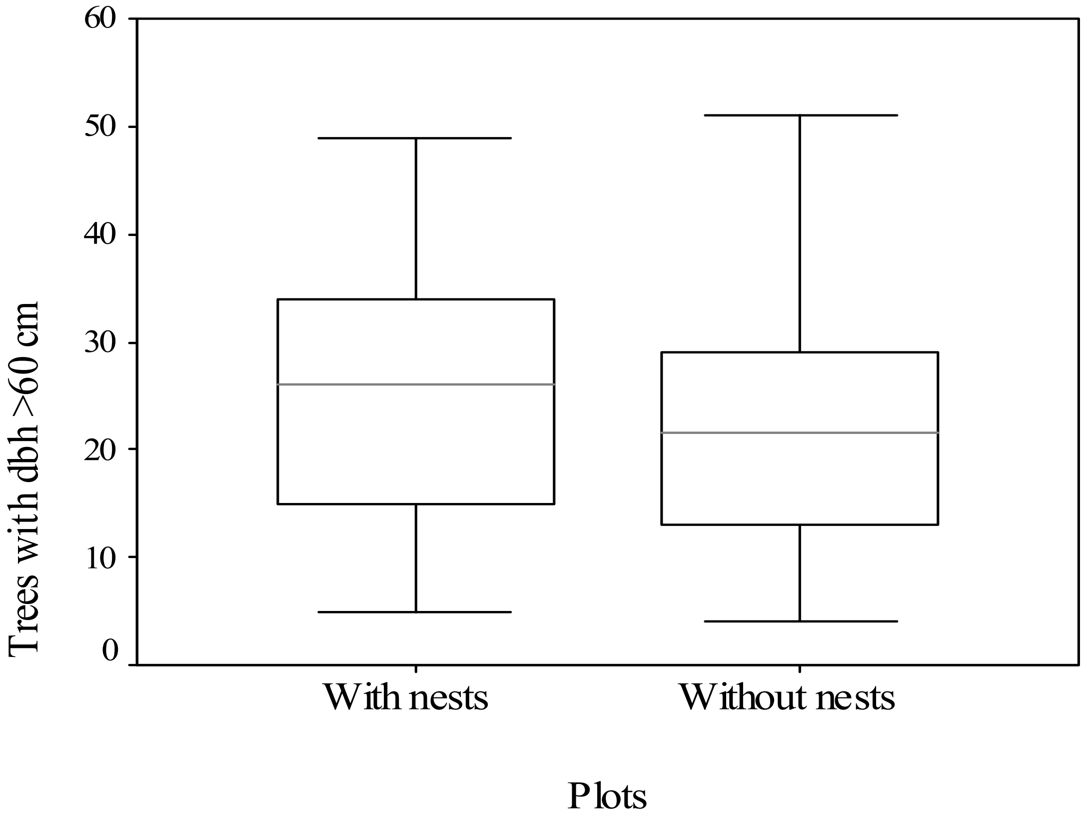
Trees with dbh >60 cm
0
10
20
30
40
50
60
With nests
Without nests
Plots

Fig.1.

Fig.2.

Chapter Five

Temporal resource partitioning and climatological influences on colony flight and foraging of stingless bees (Apidae; Meliponini) in Ugandan tropical forests

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Abstract

We studied the flight activity of two stingless bee species (*Meliponula ferruginea* and *Meliponula nebulata*) and the environmental factors influencing their flight. Two morphs of *M. ferruginea* were studied: *M. ferruginea* (brown) in Budongo forest and *M. ferruginea* (black) in Bwindi Park. The two bee species exited their nests in characteristically distinct foraging bouts suggesting that the recruitment methods used may be direct leading or “piloting”. The number of individuals in a returning bout was less than that in an exiting bout suggesting recruits do not follow experienced foragers the whole distance to the food source, a phenomenon referred to as “partial piloting”. Flight period of *M. ferruginea* (black) and *M. nebulata* in Bwindi was restricted to a few hours each day. *M. nebulata* foraged in the drizzle; a survival strategy which could promote its reproductive fitness. Nectar and pollen foraging took place throughout the day while the removal of debris was greater in the late hours of the morning. Increased temperature resulted in significant increase in number of exiting bees. There was increase in number of exiting bees with decrease in humidity up to an optimal of 78% thereafter, increase in humidity resulted in reduced number of exiting bees.

Keywords: Stingless bees, Foraging, Communication, Bwindi, Budongo

1.0 Introduction

The behavioural flexibility of bees is best characterised by their mobility and flight activity, which determine success in foraging, mating, and reproduction (Roubik 1989). Flight and foraging of bees can be shaped by environmental factors, such as quality and quantity of food, climatic conditions, competition and behaviour of nest mates. Climatic factors such as temperature, light, wind, and humidity sometimes limit foraging activity in some species of stingless bees (Inoue et al. 1985, Willmer 1991, Bruijn et al. 1994, Biesmeijer 1997). The influences of these factors vary among the different species since these species vary in body size, hair and colour. Willmer (1991) observed that in the tropics, bee foraging behaviour may not be constrained by climate and that plants may be the ones that set the pace of foraging behaviour. However, Rinderer (1988) concluded that the chief limiting factor in the spread of *A. m. scutellata* in the neotropics was the variability in rainfall, a primary selective factor in the evolution of this bee species.

Many species of stingless bees are able to coexist in most tropical habitats, resulting in a considerable overlap of plant species used as food resources (Hubbell & Johnson 1978, Roubik 1989). In case of limiting resources, an overlap may cause competition. The competition for food is probably an important force in the evolution of foraging behaviour. Hubbell & Johnson (1978) found aggressiveness on flowers between several species of Trigona stingless bees in Costa Rica. Spatial and temporal niche differentiation between sympatric stingless bee species can be determined by the morphology of the bees for example, body size, colour and mouth parts. It can also be determined by the behaviour of the bees for example, timing, ability to recruit, specific collecting behaviour, aggressiveness, food selection. Temporal resource partitioning was described by Frankie et al. (1976) who found that there was a changing composition of bee species, foraging on a particular flower patch in the course of the day. This suggested that difference in timing of foraging may help to avoid direct competition at flowers. There was a tendency of larger bees to arrive before the smaller species.

Flight and foraging behaviour of equatorial afrotropical stingless bees has been poorly known. This study makes a contribution in filling this gap. Temporal resource partitioning and the effects of environmental conditions on the flight and foraging of these bees were studied. These factors are useful in predicting whether flight and foraging activity of bees correspond to resource availability. The study presents the results of observations on flight and foraging of different species studied at two different forest habitats. Differences in colony foraging were analysed for the different species and were correlated to environmental conditions.

2.0 Materials and Methods

2.1 Study sites

The study was conducted in two forests: Bwindi Impenetrable National Park (BINP) in south-western Uganda. The park is located between latitudes 0°18' and 0°53'S, longitudes 29°35' and 29°50'E. It is 331 km^2 of natural forest and contains both montane and lowland forest. The park is on UNESCO's list of world heritage sites due to its ecological uniqueness and natural beauty. It supports a large number of plants and animals endemic to the region, but most notably half of the world's population of mountain gorillas (*Gorilla gorilla berengei*). The altitude of the park ranges from 1160m to 2607m. The annual temperature ranges between 7-20 ^{0}C with a mean of 16.3^{0}C. 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 mm-2390 mm. The other observations were conducted in Nyabyeya Forestry College. The college is located at the edge of Budongo Forest Reserve in mid-western Uganda between 1° 45' N and 31° 30' E. The forested area is 437 km^2 with the vegetation being semideciduous moist tropical rain forest. The mean altitude is 1100m and the mean temperature range is 14 - 28°C. The rainfall is 1500mm and falls mostly in April – May and August – October. The dry season is from December to February.

2.2 Bee species

Colonies used in BINP were situated near the Institute of Tropical Forest Conservation (ITFC) in Ruhija. Two morphs of *M. ferruginea* have been identified in Uganda, which previously were called *M. erythra* but now are regarded species synonyms (Eardley 2004). The black form is *M. ferruginea* (black) and the other is brown, here called *M. ferruginea* (brown). The black form exists in BIPN while the brown one exist in Budongo Forest Reserve. Two natural colonies of *M. ferruginea* (black) and three of *M. nebulata* were used (Table 1). The distance between the two most far apart was 15 minutes walking. The three colonies of *M. ferruginea* (brown) were situated in Nyabyeya Forest College in Budongo Forest Reserve. One of the colonies was located in a log (I.5m long) in the college's agroforestry demonstration farm. The farm is planted with about 5 ha of *Calliandra calothyrsus* (a good forage plant for bees) among other crops. The other two colonies were located in different trees; one at about 50m and the other 70 m respectively from the farm. Twenty colonies of *A. mellifera* kept in Top bar hives were located in the middle of the farm.

2.3 Bee flight behaviour

We recorded bee flight behaviour in two ways. First, the recorder sat near entrances of colonies (1m) and recorded the number of individual bees in exiting and returning foraging bouts. He also recorded the duration of the exiting and returning bouts. In the second instance, we recorded bee behaviour on flowers during foraging. The foraging behaviour of stingless bees and *A. mellifera* was observed at flowers of *C. calothyrsus* in the agroforestry demonstration farm of Nyabyeya Forest College. The behaviour was recorded from arrival of a bee at a patch of flowers until the observer lost track of the bee. We carried out a simple experiment to determine the blooming time of *C. calothyrsus*. Once a week in the evenings (about 20 hours), we selected a few trees and broke off all flowers that had already opened and only left those that had not bloomed. The next day we monitored these trees. *C. calothyrsus* is a multi-stemmed shrub that reaches a height of 4 – 6 m. Its flowers are purplish red and mature over months. *C. calothyrsus* is a primary source of nectar and flowers throughout the year in the farm.

2.4 Recording of flight activity and environmental conditions

All bees flying out and into the nest during 15 minutes every hour were recorded from 6 till 20 hours. Whenever a bee returned with pollen or nectar, it was recorded. Nectar foragers usually carried no load on the hind tibia and their abdomen was swollen with nectar. Bees flying out to deposit debris were also recorded. Observations were taken once every two weeks. In BINP observations were taken between January and December 2003 while in Budongo Forest Reserve observations were taken between January and December 2002. A total of 390 observations were made at each of the 8 colonies (Table 1). Data for ambient temperature and humidity were taken every hour. The maximum and minimum thermometer was used to measure ambient temperature. An ordinary humidity gauge was used to measure the humidity. The 8 colonies were classified and discussed according to species because colonies within each species were located under the same environment and had almost the same strength.

3.0 Results

3.1 Bee flight behaviour at nest entrances

The two stingless bee species exited their nests in characteristically distinct foraging bouts. Early in the mornings, there was a small number of foragers in a bout (5-10 bees for *M. nebulata*). At the peak of foraging (11-15hours), a typical bout consisted of 20-60 foragers and lasted between 5-30 seconds. Foragers also returned in bouts however, the returning bouts had a smaller number of bees. For example, *M. nebulata* had an average of 5-20 returning foragers in a bout and lasted for a longer time (20-60 seconds). In most cases returning foragers in a single bout brought in the same resources e.g. pollen. Different bouts also returned at the same time with different loads e.g. pollen and resin, suggesting that those bees might have been recruited to harvest different resources. Figure 1 shows the frequency with which a specific number of bees exited the nest of *M. nebulata* (colony MN1) in 15 minutes. There was a variation in their frequencies (x = 42.9; SD = 61.40; N = 26) as indicated by the large value of standard deviation. The frequency with which smaller numbers of bees exited the nest in 15 minutes was higher than that for bigger numbers. However, there was fluctuation in number of foragers exiting the nest in 15 minutes. For example, 125 bees exited with a frequency of 2 and 275 bees exited with a frequency of 1. These fluctuations suggest that bees exited the nest in bouts. These differences showed that there was a fluctuation in number of bouts and / or bees in a bout.

3.2 Bee flight behaviour on flowers of *C. calothyrsus*

The results of our simple experiment showed that flowers of *C. calothyrsus* bloomed and opened at about 16 hours every day. Stingless bees and *A. mellifera* would then forage mainly for nectar. In the evenings, one was able to hear the buzzing sounds of bees from a distance. A large and undetermined number of *A. mellifera* workers foraged mainly in the middle of the farm which contained bigger trees with more flowers. Workers of stingless bees (mainly *M. ferruginea* (brown) and *Hypotrigona gribodoi*) were seen foraging in the smaller and isolated trees of *C. calothyrsus* located at the periphery of the farm. The workers of *A. mellifera* were seen foraging for nectar at night. Probably, the bees would not deplete all the nectar within the day because the flowers opened late in the day. Therefore early next morning (6 hour), *A. mellifera* workers began foraging for the remaining nectar and later on were joined by the stingless bees. Foraging by both *A. mellifera* and stingless bees continued till about 8-9 hours when the nectar was either depleted or dried out because of the hot sun.

3.3 Daily flight activity

The daily flight patterns of the bee species were found to be different. *M. ferruginea* (brown) had a longer foraging time, starting at 7 hours and stopping at 18 hours. *M. nebulata* and *M. ferruginea* (black) had a relatively shorter foraging time, starting to fly at 8 hours and stopped at 17 hours (Fig. 2). The peak foraging time of *M. ferruginea* (brown) had a higher number of outward flights than *M. nebulata* and *M. ferruginea* (black). On clear days, all the bees foraged throughout the day. Occasionally *M. nebulata* was seen foraging on damp, misty days or when there was a drizzle.

3.4 Monthly flight activity

All the colonies were active throughout the year with mean monthly activity having two peaks for all species (Fig. 3). However, the species differed in the mean number of exiting bees and the months in which flight activity was at its peak. Throughout the study *M. ferruginea* (brown) had more number of exiting bees per month in comparison to *M. ferruginea* (black) and *M. nebulata*. The mean monthly activity for *M. ferruginea* (brown) had one peak in April and the other in September. For the other two, their peaks were in March and September-October.

3.5 Overall daily foraging activity for all bee species

The overall daily foraging activity took place throughout the day with peak of exiting bees being between 10-14 hours (Fig. 4). Nectar foraging took place throughout the day with a peak between 12-14 hours. Pollen foraging took place throughout the day. The peak for pollen collection took place slightly before that of nectar (11-14 hours).

Removal of debris was greater in the late hours of the morning and less towards the end of the afternoon.

Nectar was collected throughout the day for all species. However, the time of the day for collection differed among bee species. The collection by *M. ferruginea* (brown) took place between 7-19 hours with higher rate of collection between 10-16 hours (Fig. 4). For *M. nebulata* and *M. ferruginea* (black), collection started later and stopped earlier than for *M. ferruginea* (brown). There was no distinct peak for foragers of *M. ferruginea* (brown) during the day. There was clear peak for *M. nebulata* and *M. ferruginea* (black) in the middle of the day.

3.6 Temperature influence on flight activity

Increase in temperature resulted in a significant increase in the number of exiting bees in both study sites up to a maximum point at which the effect was the opposite. In Bwindi Park, bees started flying at temperatures of about 14°C (Fig. 5a) while in Budongo Forest they started flying at 18°C (Fig. 5b). Later in the day temperature most likely reached limiting heights and suppressed flight activity in both sites. Beyond an optimal temperature of 16.5°C for Bwindi Park and 30°C for Budongo Forest, increase in temperature resulted in a decrease in flight activity. It is impossible to separate the effect of climatological factors such as temperature, light intensity and humidity since one influences the other.

3.7 Humidity influence on flight activity

Bees started flying at humidity of about 80%. There was an increase in number of exiting bees with decrease in humidity up to an optimal humidity of about 78% below which an increase in humidity resulted in drastic reduction in number of exiting bees (Fig. 6).

4.0 Discussion

4.1 Bee flight behaviour at nest entrances

In stingless bees, food source communication consists of a wide range of behaviours and has been reported for many species. Communication seems to be species-specific and ranges from largely within-nest communication to largely field-based communication (Lindauer & Kerr 1960, Esch et al. 1965, Nieh & Roubik 1998). The method of communication used by these two bee species for recruitment to specific food source seems to be direct leading or "piloting". A pilot flight is the direct leading of recruits by experienced foragers to the food source in species without sophisticated within-nest communication about distance or location of food source (Esch et al. 1965, Esch 1967, Johnson 1987). Such group flights in the form of leading by synchronising foraging trips has recently been found in honey bees where recruits use this method under special circumstances, for example unscented food sources (Tautz & Sandeman 2003). *M ferruginea* has been found to use odour of food source and pilot flights where returning foragers and nest mates produce buzzing as a strategy for food collection (Kerr 1969, Michener 1974).

The number of individuals in returning bouts was smaller as compared to that exiting. In several stingless bee genera recruits do not follow experienced foragers the whole distance to the food source, a phenomenon referred to as "partial piloting". Esch (1967) observed piloting in *Melipona quadrifasciata* and *M. merillae.* He observed that foragers guide recruits in a striking zigzag flight into the direction of their feeding place. The recruits regularly lost contact with the forager after 30-50m and returned to the nest. On the other hand, it seems that direct leading can be additional to the deposition of a trail of scent marks (*Scaptotrigona postica*, Lindauer & Kerr 1960, *T. corvine*, Aguilar & den Held 2003). Different bouts also returned at the same time with different loads e.g.

pollen and resin, suggesting that they might have been recruited to harvest different resources.

4.2 Bee flight behaviour on flowers of *C. calothyrsus*

Foragers of *A. mellifera* displaced those of *M. ferruginea* (brown) and *H. gribodoi* from the bigger trees of *C. calothyrsus*. Such displacement can be termed as contest competition (Birch 1957, Milinski & Parker 1991) during which the stingless bees are excluded from the resource as a result of defensive behaviour of *A. mellifera* e.g. threat and aggression. The different species of stingless bees exhibited scramble competition among themselves during which the nectar is not defended and no aggressive interaction takes place. Although the competing individuals generally share the resource *M. ferruginea* (brown) was still competitively stronger and bigger than *H. gribodoi* and exploited the shared resource faster. Species that rely on the same resource, (in this case *A. mellifera* and stingless bees relying mainly on nectar from *C. calothyrsus*) can escape competitive exclusion (Ginsberg 1983, Kephart 1983) and therefore coexist, by differential use of the shared resource. In this case the resources were partitioned by differing in the spatial and temporal uses.

Niche differentiation can be caused by species-specific differences on morphology, physiology and/or behaviour. In bees, morphological aspects such as proboscis length, body size and body colour affect foraging success in different microclimates and on different flower types (Heinrich 1976, Willmer & Unwin 1981, Johnson 1986, Corbet et al. 1995, Biesmeijer et al. 1999a). Foraging by both *A. mellifera* and stingless bees continued till the nectar was either depleted or dried out by the hot sun. The results of pollen foraging deviated from those earlier reported in natural conditions. In our case, pollen was not collected in the early morning hours, as reported. Roubik (1989) explains the early morning pollen peak by arguing that pollen is depleted from dawn onward either by pollinators or by wind, whereas no such considerable decrease occurs with nectar. On the contrary, sugar concentration in nectar increases through the day as a result of evaporation.

4.3 Flight activity patterns

Flight and foraging activity of bees is always influenced by environmental factors with temperature being one of the most important (Heard & Hendrikz 1993, Biesmeijer 1997). Relative humidity also limits flight activity of some species for example, Imperatriz-Fonseca et al. (1985) found that there was a sudden decrease in flight activity of *Plebeia remota* at a relative humidity of 90%. Body size of bees influences flight activity of bees (Biesmeijer 1997) because larger species fly in lower temperatures and light intensities than smaller ones, demonstrating a better heat absorption capacity. All the colonies were active throughout the year with mean monthly activity having two peaks for all species. The mean monthly activity of the bees corresponded to the annual rainfall patterns of the two forest habitats.

There was a temporal divergence when distinguishing between the transportation of the different commodities such as nectar, pollen and debris. Nectar and pollen foraging took place throughout the day while the removal of debris was greater in the late hours of the morning and less towards the end of the afternoon. In a study of colony foraging in different species of stingless bees, Bruijn and Sommeijer (1997) found a temporal division of nectar, pollen and resin collection in *Melipona beecheii* and *M. fasciata*.

Foraging in *M. ferruginea* (brown) generally started earlier in the day and also stopped later than *M. nebulata* and *M. ferruginea* (black). Roubik (1989) explained that the most energetically demanding forager will often arrive first at a foraging patch. However, this may not be the case because the stingless bees have similar sizes (6-7mm). . Imperatriz-Fonseca et al. (1985) attributed the temperature variation to the beginning of flight activity to variation of workers size of *Plebeia remota*. This may be the case in our study. In Bwindi Park where *M. nebulata* and *M. ferruginea* (black) were situated, the flight period was restricted to a few hours each day probably because of the high altitude (2300m) and relatively low temperatures (7-20 ^{0}C) compared to Budongo Forest (altitude 1100m and temperature 14-28°C) where *M. ferruginea* (brown) was located. *M. nebulata* foraged on damp, misty days or when there was a drizzle a survival strategy which can promote its reproductive fitness in the relatively cold conditions in Bwindi Park.

Climatological factors are normally highly intercorrelated and related to the time of the day. This makes an analysis of the separate effects of each factor complicated (Biesmeijer 1997). Heard and Hendrikz (1993) studied the influence of climatic factors on the external activity of *Trigona carbonaria* in Australia. They considered temperature and light intensity as the most important factors determining flight activity of these bees. The minimum temperature for this *Trigona* was 18 °C and relative humidity did not show any significant effect. For *Plebeia emerina*, Kleinert-Giovaninni (1982) observed that flight activity decreased when relative humidity reached 70%, even when other factors were in good condition.

Table 1: Nest and colony characteristics of bee species used. The twenty colonies of *A. mellifera* were not studied individually. Each code represents a single colony for the stingless bee species.

Bee species	Code	Location	Size (mm)	Est. Pop.	Altitude (M)	Nest site	Nest height (M)
A. mellifera	AM	Budongo	11	10000	1100	Top bar	1
M. ferruginea (brown)	MFbr1	Budongo	6	2500	1100	Log	1
M. ferruginea (brown)	MFbr2	Budongo	6	2300	1100	Tree base	0
M. ferruginea (brown)	MFbr3	Budongo	6	2000	1100	Tree cavity	1.2
M. ferruginea (black)	MFbl1	Bwindi	6	1500	2330	Tree cavity	0.8
M. ferruginea (black)	MFbl2	Bwindi	6	1400	2330	Tree cavity	0.6
M. nebulata	MN1	Bwindi	7	1800	2330	Tree cavity	1.4
M. nebulata	MN2	Bwindi	7	1800	2290	Tree cavity	2.9
M. nebulata	MN3	Bwindi	7	1600	2330	Tree cavity	3.3

Fig. 1. Frequency within which bees exited the nest of *M. nebulata* (colony MN1) in 15 minutes during the 12 months observation period. The x-axis represents mid points of number of outward flights within a class range of 25. The y-axis represents the number of outward flights within each class range. These fluctuations indicate that bees exit nests in bouts.

Fig. 2. Daily patterns of flight activity related to hours of the day. MF (brown) = *M. ferruginea* (brown), MF (black) = *M. ferruginea* (black) and MN = *M. nebulata*. Bars represent the mean value of all the flights recorded at a particular time of the day in a 15 minute period every hour over the 12 months of observations.

Fig. 3. Mean monthly number of exiting bees during 15 minutes of observation throughout the 12 months of study period. MF (brown) = *M. ferruginea* (brown), MF (black) = *M. ferruginea* (black) and MN = *M. nebulata*.

Fig. 4. Overall daily foraging activity of the three bee species in the different hours of the day showing the percentages of bees exiting without any material or with debris and those entering the nests with nectar or pollen.

Fig. 5 a. Number of exiting bees at different temperatures and hours of the day for the two bee species studied in Bwindi Park. There were 3 colonies of *M. nebulata* and 2 for *M. ferruginea* (black).

Fig. 5 b. Number of exiting bees at different temperatures and hours of the day for *M. ferruginea* (brown) studied in Budongo Forest.

Fig. 6. Number of exiting bees at different humidity and hours of the day for the two bee species studied in BINP. There were 3 colonies of *M. nebulata* and 2 for *M. ferruginea* (black).

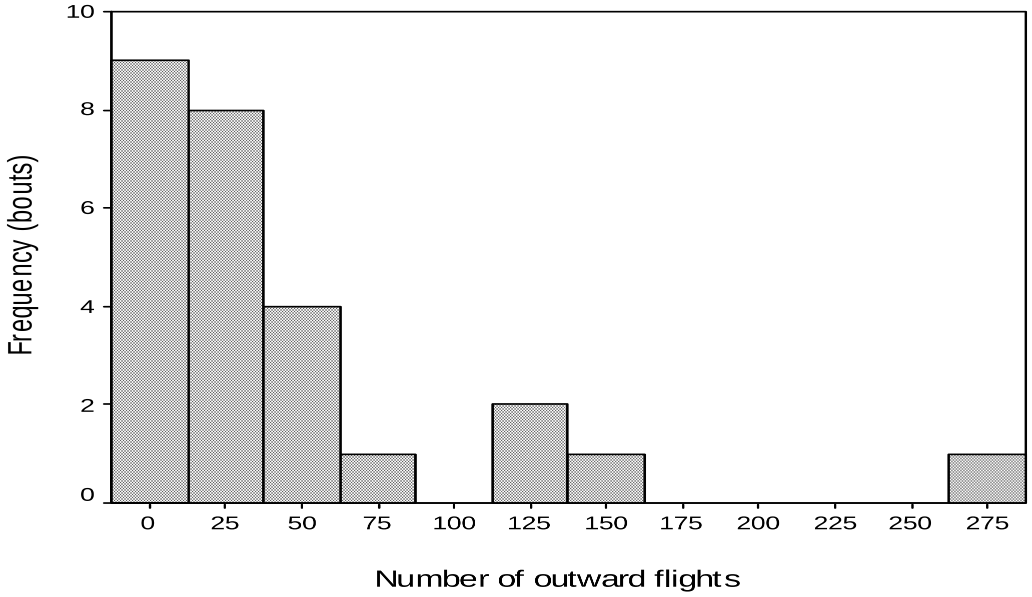
10
8
6
4
2
0
Frequency (bouts)
0
25
50
75
100
125
150
175
200
225
250
275
Number of outward flights

Fig. 1.

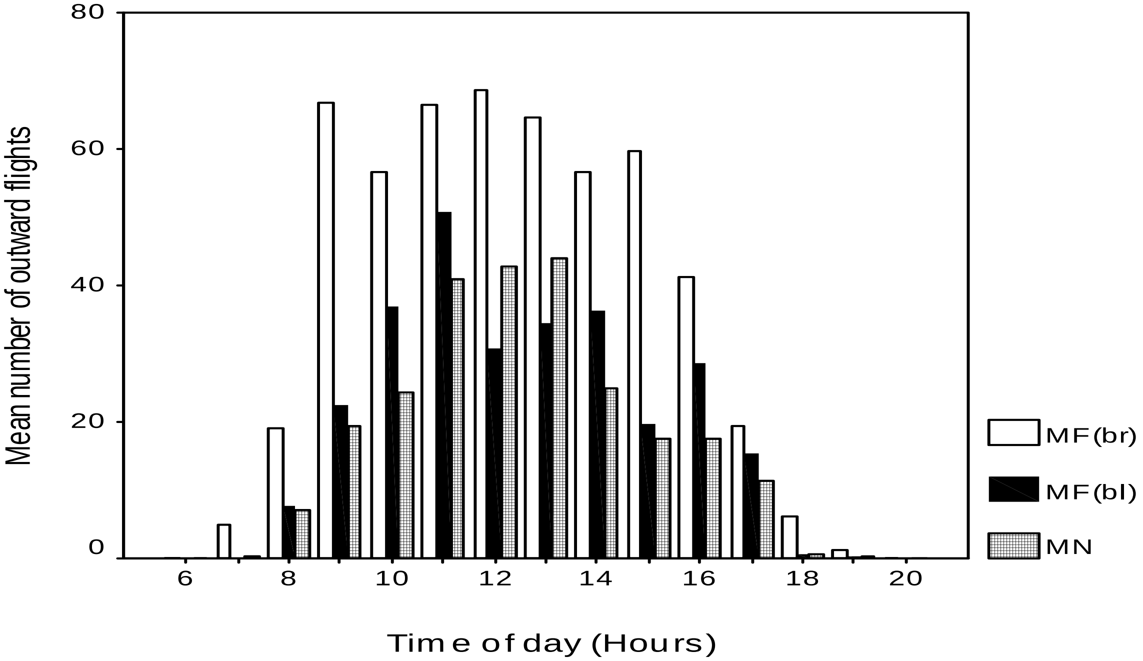
80
60
40
20
0
Mean number of outward flights
6
8
10
12
14
16
18
20
Time of day (Hours)
MF(br)
MF(bl)
MN

Fig. 2.

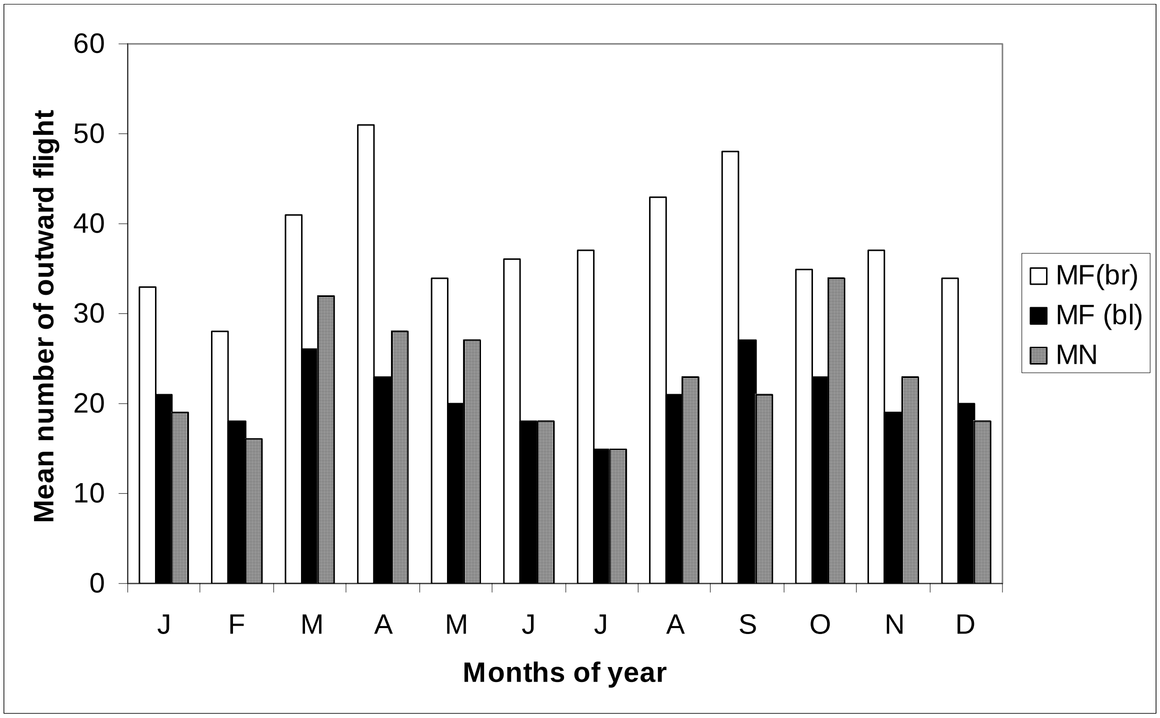
Mean number of outward flight
60
50
40
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D
Months of year
MF(br)
MF (bl)
MN

Fig. 3.

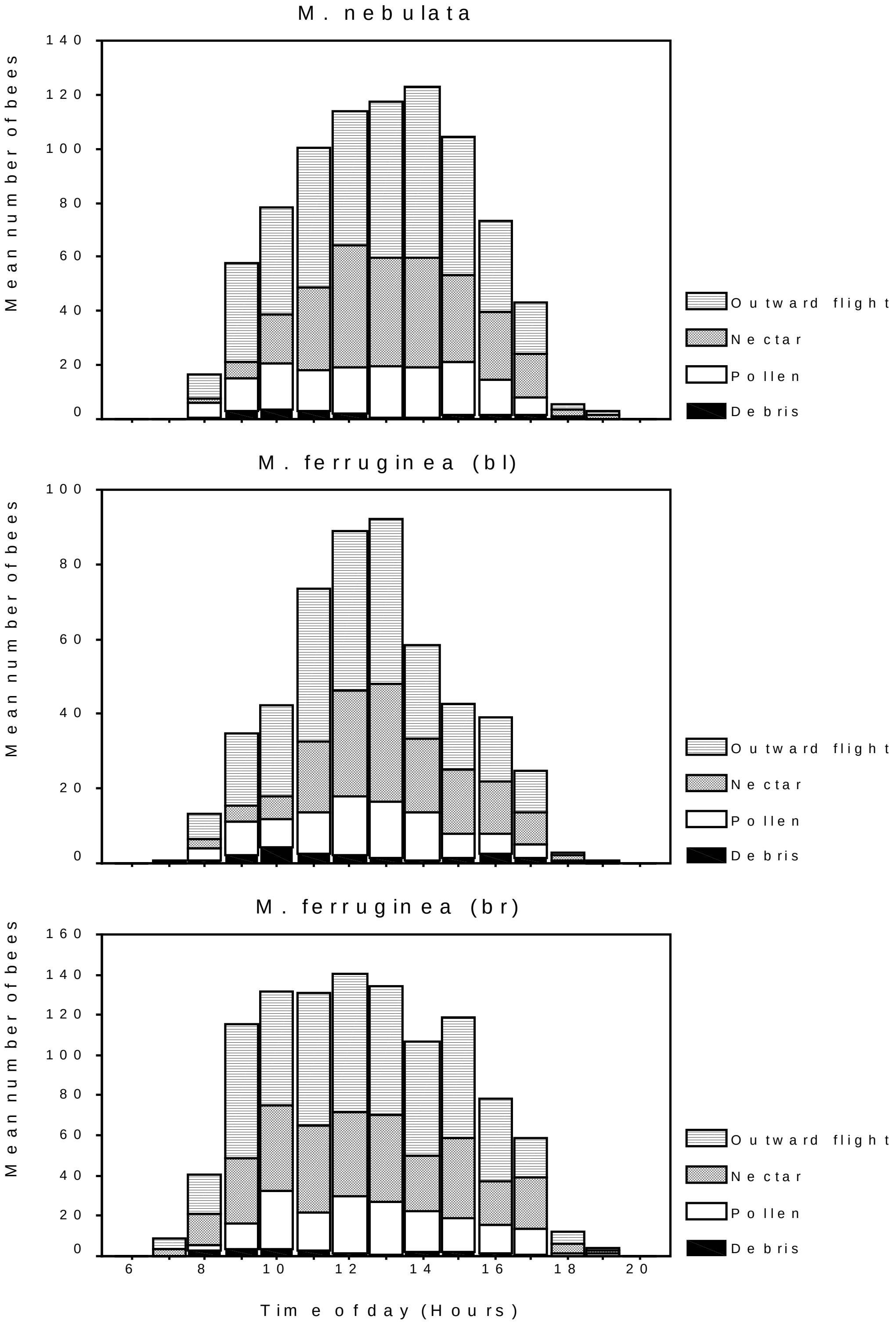
M. nebulata
Mean number of bees
0
20
40
60
80
100
120
140
Outward flight
Nectar
Pollen
Debris
M. ferruginea (bl)
Mean number of bees
0
20
40
60
80
100
Outward flight
Nectar
Pollen
Debris
M. ferruginea (br)
Mean number of bees
0
20
40
60
80
100
120
140
160
Outward flight
Nectar
Pollen
Debris
6
8
10
12
14
16
18
20
Time of day (Hours)

Fig. 4.

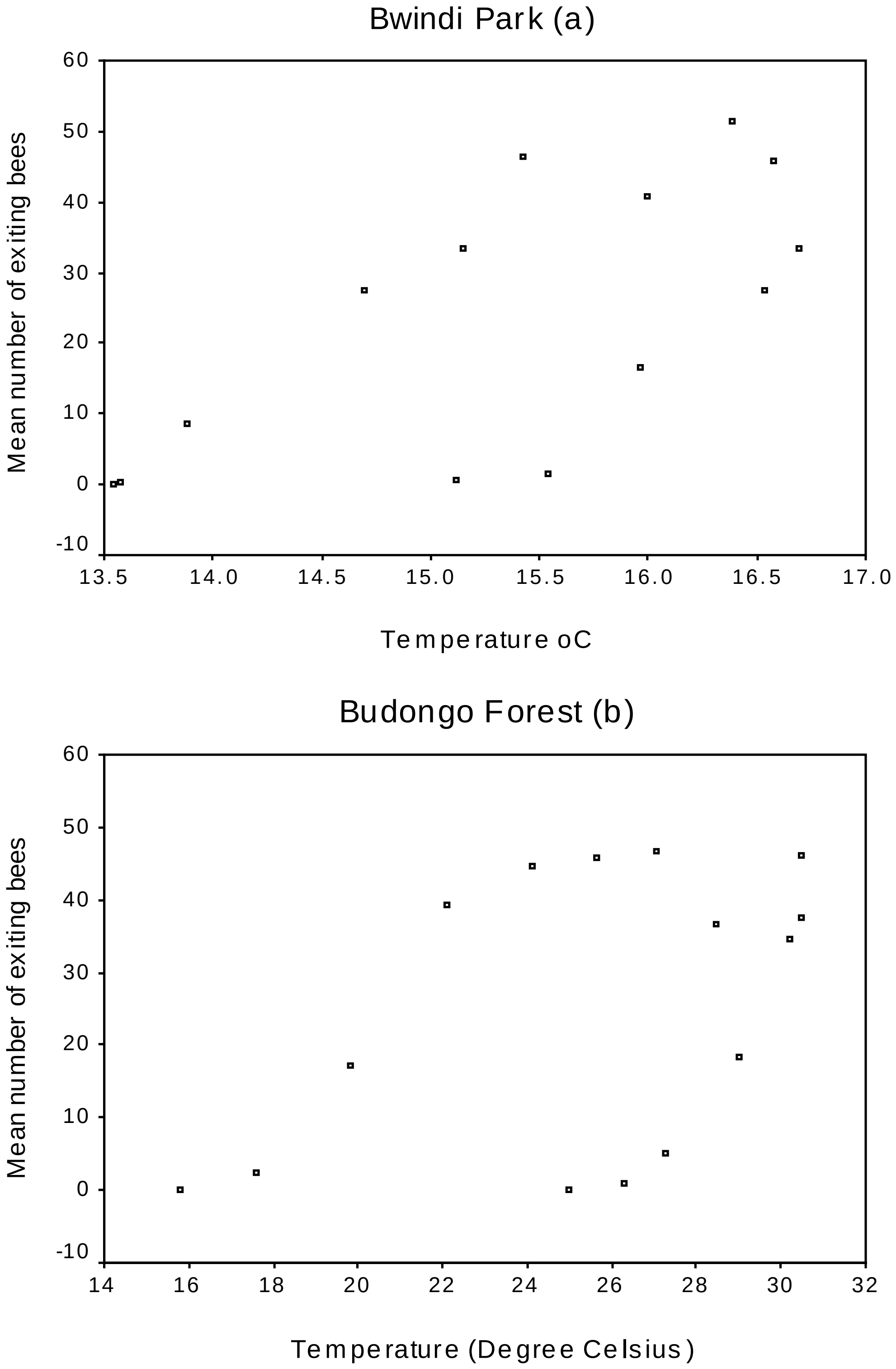
Bwindi Park (a)
Mean number of exiting bees
60
50
40
30
20
10
0
-10
13.5
14.0
14.5
15.0
15.5
16.0
16.5
17.0
Temperature oC
Budongo Forest (b)
Mean number of exiting bees
60
50
40
30
20
10
0
-10
14
16
18
20
22
24
26
28
30
32
Temperature (Degree Celsius)

Fig. 5

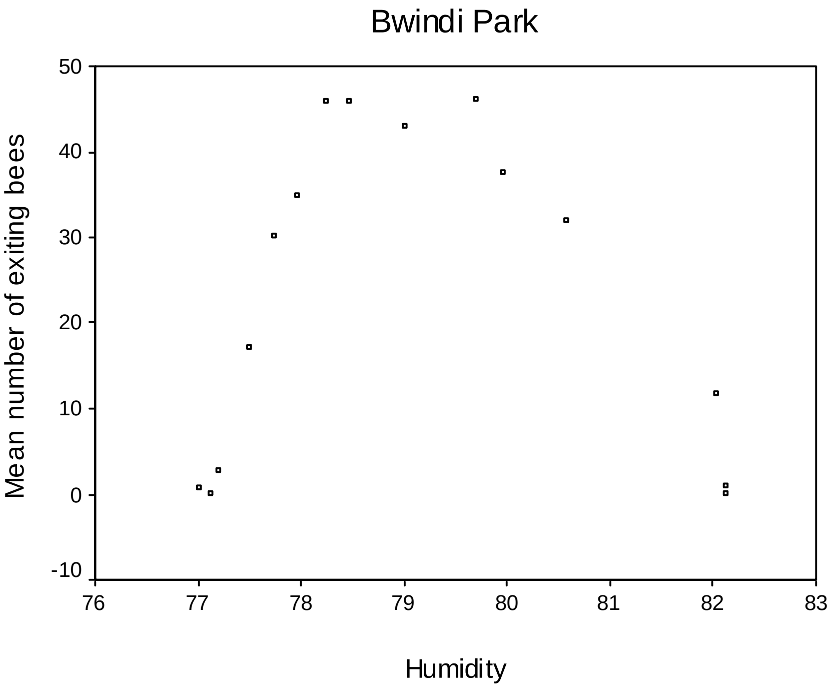
Bwindi Park
Mean number of exiting bees
50
40
30
20
10
0
-10
76
77
78
79
80
81
82
83
Humidity

Fig. 6.

Chapter Six

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

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Running title: Pollen foraging of Afrotropical honey-making bees

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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* was positively correlated to pollen diversity. The recruitment technique to food sources is implicated to have been 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 to partitioning of food resources.

Keywords: Stingless bees, Pollen, Spectrum, Diversity, Bwindi, Uganda

1.0 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-Giovannii & Imperatriz-Fonseca, 1987, Imperatriz-Fonseca, et al. 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 analyses the pollen collected and stored in the pots. Some of these studies deal with pollen diet of a single stingless bee species or honey bees, while others compare plants used by different stingless bee species, or by stingless bees and honeybees. 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 to 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, 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. Since 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, since 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. 1999a). 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 part 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 since 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 since 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 afrotropical forest, a qualitative study focusing on competition of pollen resources and how the bee species partition their resources is presented.

2.0 Material and Methods

2.1 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 is 331 km^2 of natural forest and contains both montane and lowland forest. The park is on UNESCO's list of world heritage sites due to its ecological uniqueness and natural beauty. The altitude of the park ranges from 1160 m 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 mm-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 (*M. bocandei* and *M. nebulata*) and *A. 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 350m from each other. Therefore it was taken that all these colonies had widely overlapping foraging ranges.

2.2 Pollen samples of stingless bees

Pollen loads for the stingless bees were collected once every two week for 12 months (January - December 2003) at 0700-0900 hours, 1000-1200 hours and 1300-1500 hours 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 5 pellets was collected per sampling hour from each colony. Individual loads of a particular species on a given day were grouped into a sample. Overall about 780 pellets were collected per colony (5 pellets per hour x 6 sampling hours in a day x 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 slides, 200 pollen grains were randomly selected and identified to species level if possible. Pollen slides from Makerere University herbarium, pollen reference collection and specialised literature (Hamilton, 1972) were used to identify the pollen sources. Some pollen could not be identified to species level and were combined into ‘types’.

2.3 Pollen samples of *A. mellifera*

In order 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 thick with holes through which bees forced their way. The diameter of the holes was 5.0 mm which is standard for *A. mellifera*. As with the stingless bees, pollen loads of *A. mellifera* were collected once every two week for 12 months (January - December 2003) at sampling periods of 0700-0900 hours, 1000-1200 hours and 1300-1500 hours local time. However, the days for collection were different from those of the stingless bees. At each sampling period, pollen loads were collected for 15 minutes. 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 slides, 200 pollen grains were randomly selected and identified to species level if possible. Only pollen types with an occurrence 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).

2.4 Data analysis

The Shannon-Weiner index of diversity was calculated for each bee species per month: $H_{ik} = -\Sigma_j \, [\{N_{ijk} / \Sigma_j \, (N_{ijk})\} \ln \{N_{ijk} / \Sigma_j \, (N_{ijk})\}]$ in which H_{ik} is Shannon-Weaver’s index of colony i is species and Nijk 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 index

(1968), which is based on percentage of similarity; PS $=1-{}^{1}/_{2}\sum_{h}^{n}|ph_i - ph_j|$. Where ph_i = the pollen proportion of the h plant species present in the sample of colony I for the month in question; and ph_j = idem, for colony j. Values for overlap vary from 0 to 1, i.e. from no overlap to complete overlap of the resource utilised. The evenness was analysed using Pielou (1977): evenness, J = H/Hmax where H max = natural logarithm of the total number of species found in the samples for one month. The values of evenness vary from 0 to 1, i.e. heterogeneous utilisation of resource to homogenous use.

3.0 Results

3.1 Pollen spectrum of stingless bees and *A. mellifera*

The three colonies of *A. mellifera* visited 71 plant species belonging to 29 families. *M. bocandei* visited 52 plant species belonging to 22 families and *M. nebulata* visited 33 plant species belonging to 14 families. *A. mellifera* shared 19 types with *M. bocandei* and 12 types with *M. nebulata.* The two stingless bee species shared 11 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 important pollen supply for *A. mellifera* and *M. bocandei* and were not important to *M. nebulata*. In contrast *Prunus 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.

3.2 Major pollen sources used during the seasons

A. mellifera had 15 heavily used plants, *M. bocandei* had 12 heavily used plants while *M. nebulata* had 7 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 (Dec.-Feb.), *Bidens 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 *Syzigium guinense* and *Carapa grandifolia* were the most dominant in the second rain season (Aug.-Nov.).

3.3 Diversity of pollen diet

The bee species collected pollen from diverse plant sources. *A. 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).

3.4 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 Sep.-Nov.; 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*.

3.5 Seasonal variation in pollen diet

The smallest diversity of *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. 4 a). Data on rainfall in Ruhija where the study was conducted is shown in (Fig. 4 b) 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 = -198, N=12, P = 0.186; *M. nebulata*: r = -0.264, N=12, P = 0.120).

4.0 Discussion

4.1 Pollen spectrum of *A. mellifera* and stingless bees

The bees collected pollen from a wide range of plant species. This may not be surprising since social bees have year round colonies which compels them to forage for food year round. They cannot therefore be specialists on one or 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 leading to the drawing of qualitative as opposed to quantitative conclusions 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 due to the difficulty of judging the relative importance of certain flowering plant species to the bees in question.

4.2 Differences in pollen diets among the bee species

4.2.1 Bee morphology and colony size

The results suggest that the biggest bees (Table 2) took the most resource types. *A. mellifera* has the largest flight range as it is the biggest among the three species (Roubik & Aluja 1983, Roubik 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 since 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 the results opposite to this study. According to their study, *Apis dorsata* showed the narrowest pollen diet, *Trigona iridipennis* the widest. Colony and body sizes of the former are bigger than those of the latter. They emphasised aggressiveness of *T. iridipennis* at feeding sites as a source of the difference in pollen diet spectrum.

Colony size of *A. mellifera* was highest (8,000-10,000, 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, et al. (1994). For the bees with few number of individuals in a colony, the differences in pollen variety foraged would logically be small, since only a few sources have to be visited to provide enough pollen for the colony. 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). Sommeijer et al. (1983) found that bee species with high number of individuals in a colony have a wider width in pollen spectrum.

4.2.2 Bee behaviour

One of the important part 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 since 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 as compared to 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. *A. 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, though piloting is implicated to have contributed to the narrow diet of *M. nebulata*, it may not always lead to more specialisation 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 of 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 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 competitional impact of *A. mellifera* on the stingless bees that could generally lead to negative effect only, these bees are able to coexist in this equatorial afrotropical forest by partitioning their food resources using different foraging strategies.

4.2.3 Pollen diversity and overlap

There was 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 either truly good pollen sources and are preferred by this bee species. Alternatively, when plant resources became 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 non-profitable 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 emphasising the ‘important’ diet items that were fairly 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 of 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, Ramalho et al. 1989, Roubik et al. 1986, Roubik 1989)

4.2.4 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 specialise 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 and 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.

Table 1. Colony characteristics of bee species used. The colony population of the stingless bees was estimated by opening the nests under mosquito nets and counting the bees. For *A. mellifera*, population was estimated by counting individual bees on the inner faces of the hive and on combs.

Bee species	Initial	Length (mm)	Estimate population	Altitude (m)	Nest site	Nest height (m)
A. mellifera	AM1	11	10000	2300	Top bar hive	1
A. mellifera	AM2	11	8000	2300	Top bar hive	1
A. mellifera	AM3	11	10000	2300	Top bar hive	1
M. bocandei	MB1	9	1200	2320	Ground	0
M. bocandei	MB2	9	1000	2320	Ground	0
M. bocandei	MB3	9	1300	2300	Ground	0
M. nebulata	MN1	7	1800	2330	Tree cavity	1.4
M. nebulata	MN2	7	1800	2290	Tree cavity	2.9
M. nebulata	MN3	7	1600	2330	Tree cavity	3.3

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 = *A. mellifera* colony 1-3; B1-3 = *M. bocandei* colony 1-3; N1-3 = *M. nebulata* colony 1-3.

Family	**Species**	**M1**	**M2**	**M3**	**B1**	**B2**	**B3**	**N1**	**N2**	**N3**
Acantheceae	*Mimulopsis* sp.	x		xxx	x		x			
	Acanthus arboreus	x		x						
Araliaceae	*Harungana madagascariens*	x	x							
Asteraceae	*Vernonia* sp.	xxx	xxx		x	xxx	xxx		xxx	xxx
Bignoniaceae	*Markhamia lutea*	xxx		x		x	x		xxx	xxx
Convolvulaceae	*Ipomea* sp.				x	x			x	xxx
Asteraceae	*Bidens pilosa*	xxx	xxx		xxx	x	xxx			
	Type 1							x	xxx	xxx
Commelinaceae	*Commelina sp.*	x		x						
Euphorbiaceae	*Alchornia hirtella*	x		x						
Euphorbiaceae	*Croton macrostachyus*	x	x			x	x	x	xxx	xxx
	Macaranga sp.				x	x	x			
	Type 2	x		xxx						
	Dryptes sp.		x	x				xxx	xxx	x
Gramineae	*Zea mays*	x	xxx	xxx						

Leguminoceae	*Acacia* sp.	x		x						
Loganiaceae	*Nuxia congesta*		x	x				xxx		x
Lobeliaceae	*Lobelia gibberoa*	x	x							
Meliaceae	*Carapa grandifolia*	xxx	xxx	x						
Meliaceae	*Entandrophragma excelsum*	x	x	x						
Moraceae	*Myriathus holstii*					x	x		x	
Musaceae	*Musa* sp.	x	x							
Myricaceae	*Myrica salicifolia*	x	x							
Myrtaceae	*Syzygium guineense*				xxx	xxx	x		x	x
Papilionaceae	*Sebaania sesban*	x		x						
Piperaceae	*Piper guineensis*	x		x						
Proteaceae	*Faurea saligna*	xxx	xxx			x	x	x		x
Oleaceae	*Olea capensis*	x	x							
Rosaceae	*Hagenia abyssinica*	x	x							
	Prunus africana							xxx	xxx	x
Rubiaceae	*Coffea* sp.		x	x						
Solanaceae	*Datura stramonium*	x		x		x	x			
Sapotaceae	*Chysophyllum gorungosanum*				x	x				
Theaceae	*Ficalhoa laurifolia*	x	x							
Theaceae	*Ficalhoa laurifolia*	x	x							
Zigiberaceae	*Aframomum* 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						

Fig. 1. Major pollen sources of *A. mellifera* (A), *M. bocandei* (B) and *M. nebulata* (C) used during the dry and rainy seasons. Only pollen types that made up more than 30% for 2 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 was pooled.

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

Fig. 4. Temporal pollen diet breadth of the three bee species. Depicted in (a) 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 Institute of Forest Conservation (ITFC) Ecological monitoring Programme (1999) respectively.

A

Family	Plant species	Dec-Feb	March-May	June-July	Aug-Nov
		Dry	Rain	Dry	Rain
Asteraceae	*Bidens pilosa*	▨			
Meliaceae	*Carapa grandifolia*				▨
Euphorbiaceae	*Croton macrostachyus*		▨		▨
Meliaceae	*Entandrophragma excelsum*		▨		
Myrtaceae	*Eucalyptus sp.*	▨		▨	
Proteaceae	*Faurea saligna*		▨		
Bignoniaceae	*Markhamia lutea*			▨	
Rosaceae	*Prunus africana*				▨
Myrtaceae	*Syzygium guineense*				▨
Asteraceae	*Vernonia sp.*		▨	▨	
Poaceaa	*Zea mays*		▨		
Euphorbiaceae	Type 2	▨			
Not identified	Type 12		▨		

B

Family	Plant species	Dec-Feb	March-may	June-July	Aug-Nov
		Dry	Rain	Dry	Rain
Fabaceae	*Albizia gummifera*		▨		
Asteraceae	*Bidens pilosa*	▨			
Euphorbiaceae	*Croton macrostachyus*				▨
Myrtaceae	*Eucalyptus sp.*	▨		▨	
Euphorbiaceae	*Macaranga sp.*	▨			
Myrtaceae	*Syzygium guineense*		▨		▨
Asteraceae	*Vernonia sp.*		▨		▨

C

Family	Plant species	Dec-Feb	March-may	June-July	Aug-Nov
		Dry	Rain	Dry	Rain
Euphorbiaceae	*Croton macrostachyus*	▨	▨		
Euphorbiaceae	*Dryptes sp.*	▨			
Meliaceae	*Ekerbergia capensis*				▨
Myrtaceae	*Eucalyptus sp.*	▨			
Convolvulaceae	*Ipomea sp.*			▨	
Bignoniaceae	*Markhamia lutea*			▨	
Loganiaceae	*Nuxia congesta*	▨			
Rosaceae	*Prunus africana*				▨
Euphorbiaceae	*Ricinus communis*		▨		
Asteraceae	*Vernonia sp.*		▨	▨	▨
Asteraceae	Type 1	▨			
Not identified	Type 4	▨			
Euphorbiaceae	Type 7		▨		
Asteraceae	Type 16				▨
Myrtaceae	Type 17				▨

Fig. 1.

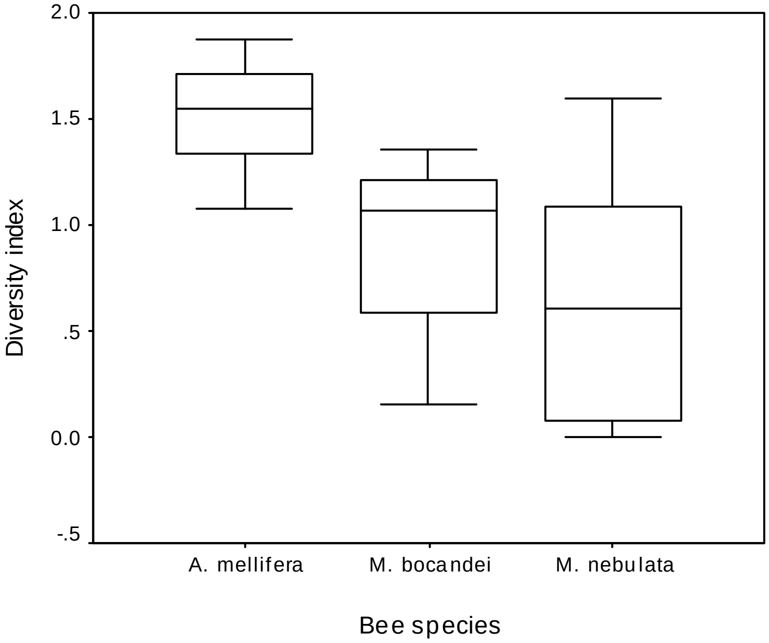
2.0
1.5
1.0
.5
0.0
-.5
Diversity index
A. mellifera
M. bocandei
M. nebulata
Bee species

Fig. 2.

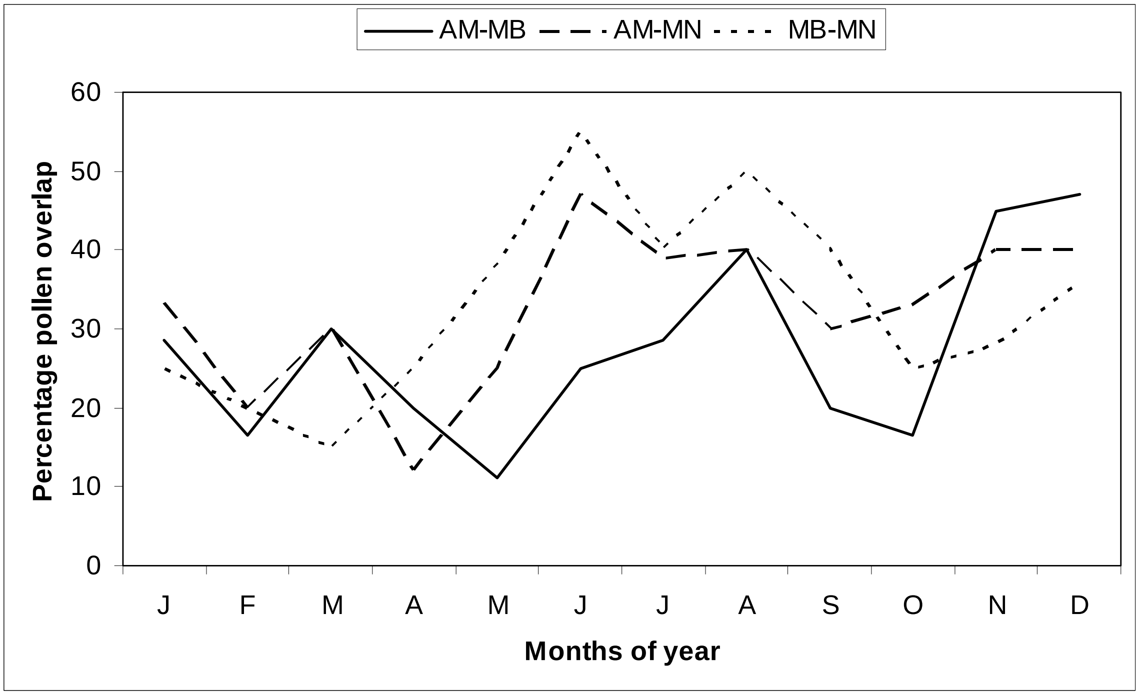
AM-MB
AM-MN
MB-MN
Percentage pollen overlap
0
10
20
30
40
50
60
J
F
M
A
M
J
J
A
S
O
N
D
Months of year

Fig. 3.

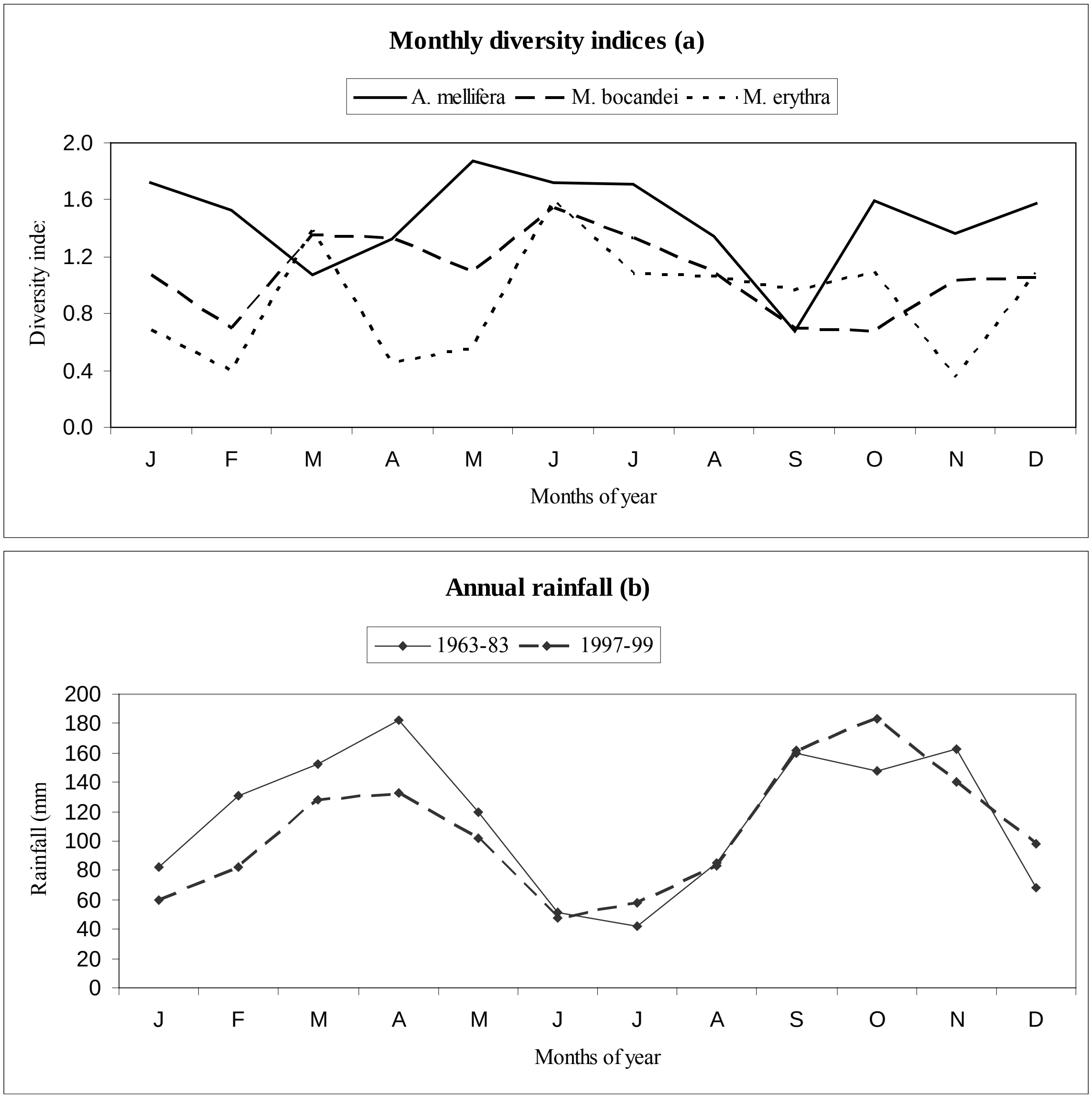
Monthly diversity indices (a)
A. mellifera
M. bocandei
M. erythra
Diversity inde:
2.0
1.6
1.2
0.8
0.4
0.0
J
F
M
A
M
J
J
A
S
O
N
D
Months of year
Annual rainfall (b)
1963-83
1997-99
Rainfall (mm
200
180
160
140
120
100
80
60
40
20
0
J
F
M
A
M
J
J
A
S
O
N
D
Months of year

Fig. 4.

Chapter Seven

Botanical sources and sugar concentration of the nectar collected by two stingless bee species in a tropical African rain forest

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Abstract

Nectar foraging by species of two stingless bees was studied in an African tropical rain forest. Both species *Hypotrigona gribodoi* (2-3 mm) and *Meliponula ferruginea* (6 mm) collected nectar with a wide range of sugar concentration (*H. gribodoi*: 14.2-67.4%; *M. ferruginea*: 9.1-63.4%). *H. gribodoi* collected nectar of higher sugar concentration than *M. ferruginea*. Factors that influenced sugar concentration of collected nectar included botanic origin of the nectar, bee species, bee colonies, month of year, time of day and the local environment. Sugar concentration increased gradually from 0700 h to a peak at 1300 h and declined thereafter. *H. gribodoi* collected nectar from more diverse plant species than *M. ferruginea*. Sugar concentration for both bee species was higher during the dry season than the rainy season. Although the above factors may explain part of the variation in the sugar concentration of nectar, additional explanations lie in the behavioural differences among the bee species.

Keywords: Nectar concentration, nectar sources, *Calliandra calothyrsus,* foraging behaviour, Budongo Forest Reserve

Introduction

Several species of stingless bees can occur sympatrically and their diets partly overlap permitting access to the same resources by many colonies (Sommeijer et al., 1983; Roubik et al., 1986, Kleinert-Giovanini & Imperatriz-Fonseca, 1987; Ramalho et al. 1989, Ramalho 1990, Roubik et al. 1995, Kajobe and Roubik 2006). The overlap in diet can lead to competitive interactions (Hubbel & Johnson 1977, 1978; Roubik & Aluja 1983; Roubik 1989). The competition for nectar can result in the evolution of not only morphological adaptations of both plants and animals but also in a wide range of nectar qualities and quantities presented by plants (Roubik 1989, Biesmeijer et al. 1999b). Flower visitors can differentiate between the amount of nectar in flowers, its sugar concentration, and its composition in sugars, amino acids and lipids (Baker & Baker 1975, 1983; Opler 1983; Roubik & Buchmann 1984; Roubik et al. 1995; Biesmeijer & Ermers 1999).

Honey bees have a preference mainly for those plants that provide a better reward, that is the largest amount of pollen, or nectar, or both, those having more concentrated nectar, and those that have not been foraged on previously by other bees (Roubik 1989). Factors that cause variation in harvested nectar sugar concentration include the botanical origin of nectar, local climate, as well as behavioural differences among bee species and among colonies within the same species (Biesmeijer et al. 1999b). These authors concluded that the variation of climatological conditions between patches might lead to heterogeneous nectar rewards.

Spatial and temporal niche differentiation between sympatric stingless bee species can arise by differences in bee morphology, for example with body size, colour and mouth parts (Biesmeijer et al. 1999a). Resource partitioning can also be the result of behavioural differences among bee foragers, for example the timing of the foraging activity, the ability to recruit, the intrinsic collecting behaviour, aggressiveness, and the food selection (Frankie et al. 1976, Villanueva 1994). Temporal resource partitioning was described by Frankie et al. (1976) who found that the species composition of bee fauna foraging on a particular flower patch changed over the course of a day, thus suggesting that differences in the timing of foraging may help to avoid direct competition among species at flowers. In that study, they noted a tendency for larger bees to forage earlier in the day compared to the smaller species.

Studies are very limited on the floral origin of nectar collected by African stingless bees. There has been no major study to fully explain the nectar foraging ecology of social bees in African tropical rain forests. The patterns and ecological impact of floral choice and foraging behaviour of social bees in this environment are largely unknown. This study was therefore aimed at answering the following questions: what are the important nectar sources of stingless bees in the Budongo forest reserve? What is their diversity? What factors influence the sugar concentration of collected nectar, in particular is there an effect of the bee species on the concentration of the nectar collected? A comparison between honeybees and stingless bees was made in an effort to understand the ecology of their nectar foraging behaviour.

2. Material and Methods

2.1. Study site

The main study was conducted in the Budongo Forest Reserve (BFR), which is a tropical rain forest located in mid-western Uganda. It is an outlier of the great Ituri forest of the Democratic Republic of Congo (Fig. 1). It covers an area of 825 km^2, making it Uganda's biggest forest reserve (Hamilton 1984); 53% of it is continuous forest cover while the remaining comprises grassland communities. It is located east of the Western rift valley escarpment and Lake Albert between 1^{o}35’ and 1^{o}55’ N, and 31^{o}18’ and 31^o 42’ E

(Howard, 1991). The forest lies at an average altitude of 1100 m (minimum 750 m and maximum 1250m) above sea level (Eggeling 1947).

2.2. Bee colonies

We used four natural nests of two stingless bee species, two colonies of *Hypotrigona gribodoi* and two of *Meliponula ferruginea*. These two species were selected because they represent the two genera of stingless bees that have been identified in Uganda. The colonies were located at most 80 m apart in various tree cavities close to the border of the forest. The stingless bees were identified based on Eardley (2004) and their identity was confirmed by David W. Roubik at Smithsonian Tropical Research Institute. Measurement of the bee sizes (dry body length) was recorded in the Royal Museum for Central Africa, Tervuren, Belgium, using an ocular micrometer on a stereoscopic microscope. The smaller bee species, *H. gribodoi* (2-3 mm) is pale in colour. Two morphs of *M. ferruginea* (6 mm), one black and the other brown have been identified in Uganda. They were previously called *Meliponula erythra,* but are now regarded as species synonyms (Eardley, 2004). The brown form is the one that exists in Budongo forest reserve and was therefore used in this study.

2.3. Sampling and analysis of nectar collected by *H. gribodoi* and *M. ferruginea*

From March to August 2002, nectar samples were taken once a week from 10 returning foragers per colony, five times a day at 0600-0700 h, 0900-1000 h, 1100-1200 h, 1300-1400 h and 1500-1600 h local time. The methods used were similar to those used by Biesmeijer et al. (1999b). At the nest entrances, returning nectar foragers were caught with a net. Nectar foragers carried pollen of different colours and on different parts of their bodies (but did not carry pollen loads in their corbiculae). Nectar was collected from foragers by forcing the bees to expel their crop load into a 20 µl capillary tube for the small bee, *H. gribodoi* and 50 µl for *M. ferruginea*. In the case of *H. gribodoi*, samples from 2-3 bees were occasionally combined to obtain more reliable sugar concentration values. Concentration of sugar (actually total dissolved solids) in the nectar was measured with a hand refractometer corrected for ambient temperature (results expressed in g per 100 g of solution). Bees carrying loads with less than 5% in sugar concentration were ignored because they probably consisted mainly of water foragers (Roubik & Buchmann 1984). Data on ambient temperature was taken at each time of nectar collection.

2.4. Identification of nectar and pollen sources

Nectar foragers carried pollen of different colours on different parts of their bodies. These pollen grains adhering to the body of the bees were sampled by trapping the bee with glycerine jelly and we analysed this pollen to identify the nectar sources used by the bees. We obtained a wide variety of samples by selectively sampling foragers from each visually distinguishable pollen colour type. Such a sampling method can cause a slight overestimation of the diversity in nectar diet (Biesmeijer et al. 1999b). Several representatives of each colour of pollen were acetolysed and mounted in glycerine jelly for microscopic examination (Sawyer 1981). The colour and amount of the pollen was recorded. Most slides contained only one type of pollen and slides that contained more than one type were not included in our analysis. The different pollen types were identified by making use of our reference collection and by consulting Hamilton (1972). A nectar source was referred to as a major source if it contributed at least 30% of the samples from one colony during a day of observation. All other sources were referred to as minor sources.

2.5. Nectar collection from *Calliandra calothyrsus* by stingless bees and *Apis mellifera*

This second study was undertaken to provide background data on the possible changes in the concentration of the crop content of the stingless bees between the flowers they foraged upon and their return to the nest. Also we included honeybees in this study to extend our sampling to three species of social bees. Data were taken once a week from June to September 2002 on flower visitation and concentration of collected nectar from *C. calothyrsus* (Mimosaceae) by *A. mellifera, H. gribodoi* and *M. ferruginea* in Nyabyeya Forestry College agroforestry demonstration farm. The farm was planted with about 5 ha of *C. calothyrsus,* a shrub that reached a height of 4-6 m and flowers throughout the year and is a primary source of nectar for bees. Most flowers open at 1600 h for a single night. Foragers were captured immediately after imbibing nectar for an uninterrupted period. Nectar samples were taken once a week from 2-5 foragers of each bee species five times a day at 0600-0700 h, 0700-0800 h, 1600-1700 h, 1700-1800 h and 1800-1900 h. These times were selected in relation to the observed period of anthesis of *C. calothyrsus* in the agro-forestry farm. The same methods, as previously described in 2.3 and 2.4, were used to extract the crop content from the bees and identify the nectar sources respectively. There was little chance the nectar thus sampled came from other flower species or colony stores, since floral constancy of stingless bees is quite high (Slaa et al., 2003). The time taken to visit one flower and five flowers in succession was recorded for some selected individual bees to determine the handling time and foraging speed for the three bee species gathering nectar on *C. calothyrsus*.

2.6. Data analysis

The main dependent variable in this study was the sugar concentration of the crop content expressed as gram (g) of solute per 100 g of solution. These percentages ranged from 9.1 and 67.4 %, and so the data was analyzed as proportion after an Arcsine Square root Transformation (Sokal & Rohlf 1995). To report the means, the results were converted back to percentages. A nested ANOVA was performed to determine the factors influencing sugar concentration of collected nectar. The model used was:

Nectar concentration = Bee species + Colony (bee species) + Month + Time of day + Month*Time of day + Bee species*Month + Bee species*Time of day + Bee species*Month*Time of day Colony (bee species)*Month + Colony (bee species)*Time of day + Colony (bee species)* Month*Time of day + error. Bee species, month and time of day were treated as fixed factors while colony was considered random. Pearson correlation coefficients were calculated to determine the relationship between the temperature and the concentration of collected nectar. The average diversity of pollen types per nest was calculated using a Shannon-Weaver index of diversity: $H'_{ik} = -\Sigma_j [\{N_{ijk} / \Sigma_j (N_{ijk})\} \ln \{N_{ijk} / \Sigma_j (N_{ijk})\}]$ in which H'_{ik} is Shannon-Weaver's index of colony $i_{,}$ over one month k and N is the number of pollen types. Indices were calculated for each colony per month and thereafter averaged. Kruskal-Wallis tests were carried out to compare the nectar handling time and foraging speed on *Calliandra calothyrsus.*

3. Results

3.1. Sugar concentration of collected nectar

The two stingless bee species *H. gribodoi* and *M. ferruginea* collected nectar with a wide range of sugar concentrations (*H. gribodoi*: 14.2-67.4%; *M. ferruginea*: 9.1-63.4%; Table I). Overall, *H. gribodoi* collected nectar with significantly higher sugar concentration compared to *M. ferruginea* (Fig. 2) across each of the daily sampling periods (Fig. 3). Sugar concentration increased gradually from 0700 h in the morning to a peak at 1300 h in the afternoon and there after it declined.

3.2. Main factors influencing sugar concentration of collected nectar

The species of bee, colony within species, month of year and the time of day when the nectar was collected all had a significant effect on the sugar concentration of collected nectar (Tab. II). There was significant difference in monthly sugar concentration for the two bee species (Tab. II). The mean nectar concentration was higher during the dry season (June: 48.9 ± 10.8 and July: 47.8 ± 11.0) compared to the rainy season (March: 40.2 ± 10.0 and April: 32.5 ± 9.9). There was a positive correlation between the concentration of collected nectar and temperature (*M. ferruginea*: 2-tailed, $r = 0.846$, $N = 260$, and *H. gribodoi*: 2 tailed, $r = 0.559$, $N = 313$, $P < 0.0001$ for both species).

3.3. Nectar and pollen sources

By means of palynological analysis, 33 out of the 52 nectar sources could be identified to species level. Overall, more plants were major nectar sources for *H. gribodoi* than for *M. ferruginea*. The two most important families were Fabaceae and Asteraceae. Three of the major species of Fabaceae (*Acacia* sp., *Albizia* sp. and *Calliandra calothyrsus*) were collected by both *H. gribodoi* and *M. ferruginea* (Tab. III). The three species of Asteraceae (*Bidens* sp., *Vernonia* sp and type 14) were exclusively collected by *H. gribodoi*. *Eucalyptus* sp. being one of the two major species of Myrtaceae was collected by both stingless bee species. Combretaceae, Musaceae and Rubiaceae accounted for one major source each. The families of two major types (Type 7 and Type 23) could not be determined. *Calliandra calothyrsus* was used throughout the observation period by both stingless bee species. During the study period, the two stingless bee species collected nectar from 52 different plant species, 13 of which were shared. *M. ferruginea* used 27 plant species (14 exclusively) and *H. gribodoi* used 38 plant species (25 exclusively). *H. gribodoi* collected nectar from a wider range of plants species than *M. ferruginea.* The average Shannon-Weiner index of diversity (H') was higher for *H. gribodoi* than for *M. ferruginea* (Tab. IV).

3.4. Effects of nectar source taxa on sugar concentration

The two stingless bee species shared 13 nectar sources out of which *H. gribodoi* collected 8 of higher sugar concentration than *M. ferruginea* (Tab. V). *H. gribodoi* collected a significantly lower sugar concentration from the plant species it shared with *M. ferruginea* than from sources that it used exclusively (t = 2.69; $P = 0.015$; shared sources: mean = 43; N = 13; exclusive sources: mean = 51; N = 6; Tab. V). Two of the nectar sources exclusively used by *M. ferruginea* had the lowest concentrations (Type 11 with 24.5% and Type 20 with 29.2%).

3.5. Nectar collection from *Calliandra calothyrsus* by stingless bees and *Apis mellifera*

C. calothyrsus was a major source of nectar for the three bee species and was visited by a large variety of other insects. Observations of flower visitation on *C. calothyrsus* showed that *A. mellifera* was the most common visitor while *M. ferruginea* was also quite common and *H. gribodoi* was quite rare. Among the bee species, *A. mellifera* crop content had the lowest mean sugar concentration (40.3 ± 7.9) while *H. gribodoi* had the highest (44.9 ± 9.4; Tab. VI). The concentration of nectar in the crop of foragers of *H. gribodoi* and *M. ferruginea* captured at the nest entrances was similar to that of the crop content from bees captured at flowers immediately after imbibing the nectar for an uninterrupted period (*H. gribodoi*: ANOVA: F = 0.92; df = 1; N = 85; $P > 0.05$; *M. ferruginea*: ANOVA: F = 0.98; df = 1; N = 85; $P > 0.05$). The species of bee had a significant effect on the time taken to visit one flower (handling time) and the foraging speed. It was lowest for *A. mellifera* and highest for *H. gribodoi* (One flower: Kruskal-Wallis test: df = 2, N = 85, $P < = 0.0001$; Five flowers: Kruskal-Wallis test: df = 2, N = 85, $P < 0.0001$; Tab. VI).

4.0 Discussion

4.1. Influence of bee size on sugar concentration of collected nectar

Distinctive preferences for nectar of differing sugar concentrations were found for the species. The smaller bee species *H. gribodoi* (2-3 mm) preferred sugar of significantly higher concentration than *M. ferruginea* (6 mm). If similar volumes are compared, a relatively highly concentrated nectar source is energetically more profitable than or comparable to a nectar source of lower concentration (Roubik 1989). Since we used 20µl capillary tubes to collect crop loads of *H. gribodoi* and 50µl for *M. ferruginea*, it is hypothised that the crop load of the smaller bee, *H. gribodoi* was also smaller. Probably if all factors were kept constant (e.g. weather conditions, distance to food source), the energy saved by taking less concentrated nectar would not compensate foragers of *H. gribodoi* for the calorific loss. By harvesting significantly more concentrated nectar, it is possible that foragers of *H. gribodoi* are able to reduce the energy needed to evaporate the collected nectar to the normal concentration of stingless bee honey which is about 70% (Vit et al. 2004). Roubik and Buchmann (1984) noted that even if greatly rewarding resources are present, less rewarding ones might be preferred if the overall amount of that resource in the patch is high and/or easy to forage. However, a sample size of two stingless bee species with two colonies of each is far too small to enable the drawing of general conclusions as to the importance of the size factor on the nectar selection process of stingless bees.

The two bee species collected nectar with a wide range of sugar concentrations suggesting that the concentrations used partly overlapped between the species. The wide range of sugar concentration can be favourable to both bee species because it can ultimately result in survival of these species in cases of adverse environmental conditions and inadequate nectar resources. Accessibility to nectar sources by the bee species may have limited influence on the concentration of collected nectar because the bee species collected nectar from plant species in the same families and shared some of their major nectar sources.

4.2. Effects of nectar and pollen source on sugar concentration of nectar

Bees must possess a mechanism that can discriminate between nectars of different sweetness to be able to collect the optimal sugar concentration. Other possible mechanisms are distinction by taste or sensitivity to sugar concentration (Biesmeijer et al. 1999b). Variation in plant species used by bee species is one of the factors that explain the variation in sugar concentration of bee collected nectar. The two bee species shared 13 sources, some of which were among their major sources. Of the total range of nectar and pollen sources used by the two species, *H. gribodoi* tended to use plants with higher average nectar concentration. Moreover, the shared nectar sources were those that provided significantly less rich nectar. Thus the botanical origin of the nectar seems to explain only part of the differences in the sugar harvest of the two species.

4.3. Temporal influence on sugar concentration of collected nectar

Another factor that may explain some of the variation in sugar concentration of collected nectar is time of day. This study revealed that the sugar concentration of the bee collected nectar increased from early morning till 1300-1400 h and declined thereafter. This finding is in line with the prediction that higher solar radiation causes evaporation and results in more concentrated nectar in the flowers (Roubik & Buchmann 1984, Roubik 1989). Sugar concentration of collected nectar varied during the months (seasons) of data collection. Monthly changes in flowering phenology are likely to produce differences in nectar richness. With more rain and fewer sunny periods, there will be a low concentration of bee collected nectar. During the dry season, the wind evaporates some of the water in the nectar thereby making it more concentrated.

4.4. Behavioural factors regulating partitioning of nectar resources

The diet diversity of *H. gribodoi* was higher than that of *M. ferruginea.* The recruitment strategies of the bees to food sources may probably explain the differences in diversity. In a related study (Kajobe & Echazarreta 2005) found that workers of *M. ferruginea* exited their nests in characteristically distinct foraging bouts suggesting that the recruitment methods employed may be direct leading or "piloting" (Esch et al. 1965, Esch 1967, Johnson 1987). Such recruitment trait could have led to the reduced diversity in nectar sources for *M. ferruginea.* This hypothesis needs to be tested further because there is little doubt that it is adaptive for a bee to occasionally sample flowers other than those on which it is specialising. Such behaviour may frequently occur in tropical habitats where hundreds of flower species can be presented at one time (Roubik & Buchmann 1984).

4.5 Nectar collection from *Calliandra calothyrsus* by stingless bees and *Apis mellifera*

Despite the fact that bees might have harvested nectar from different flowers, there was no significant difference between the concentration of nectar harvested by foragers of *H. gribodoi* and *M. ferruginea* captured at the hive entrances as compared to nectar from bees captured at flowers. This is in agreement with Roubik et al. (1995) who concluded that nectar recently stored in the crop of bees is not dehydrated. *A. mellifera* was the most common forager on *C. calothyrsus.* Such a situation could have arisen as a result of contest competition (Milinski & Parker 1991) during which the stingless bees are displaced from the resource as a result of aggressive behaviour of *A. mellifera*. Although the competing stingless bees generally shared the resource, *M. ferruginea*, was competitively stronger than *H. gribodoi* and exploited the shared resource faster.

Various sizes and shapes of bee mouthparts may results in differences in rate at which they harvest nectar of differing concentration and from different floral types. Such morphological differences may ultimately lead to nectar resource partitioning. Apart from the differences that floral structure enforces in regulating visitor type, resource partitioning should reflect parameters of foraging success that are dependent upon the physical properties of nectar and upon the bees themselves (Roubik & Buchmann 1984). Comparison of the nectar intake rate of the three bee species shows that the larger bees tended to harvest nectar faster. Fast foragers, which suggest higher nectar intake rate, collected more dilute nectar. By imbibing more dilute nectar at a faster rate, foragers of *A. mellifera* may have reached a balance between foraging energetics and profit.

Based on these results, it is concluded that the botanic origin of the nectar, preference for certain sugar concentration, local environmental conditions, temporal influences and colony recruitment behaviour may be used to explain part of the variation in sugar concentration of the nectar collected. Other factors (not tested in this study) that may influence sugar concentration of the nectar collected include distance of flowers from a bee nest, the number and arrangement of available flowers, floral morphology, and the willingness of nest mates to accept nectar from a returning forager (Roubik and Buchmann 1984, Roubik et al. 1995).

Table 1. Nectar concentration collected by foragers from four colonies of two stingless bee species upon their return to the nest.

Colony number	Number of samples analyzed	Minimum	Maximum	Mean	Standard deviation
		Nectar concentration (g solute/ 100 g solution)			
		Melipona ferruginea			
1	260	9.1	63.4	42.2	1.72
2	260	12.5	63.2	39.8	1.62
		Hypotrigona gribodoi			
1	313	14.2	67.4	43.7	1.56
2	313	15.1	63.4	43.2	1.43

Table 2. Nested ANOVA with the effect of bee species, colonies nested within species, month of year and time of day on the sugar concentration of collected nectar. The blank spaces correspond to non-significant results.

Source of variation	df	SS	MS	F_{cal}	*P values*
Bee species	1	0.1056	0.1056	88.00	**
Colonies (species)	2	0.0223	0.0111	9.25	*
Month	5	4.1933	0.2097	174.00	**
Time of day	4	12.6540	0.1318	109.83	**
Month*Time of day	20				
Bee species*Month	5				
Bee species*Time of day	4				
Bee species* Month*Time of day	20				
Colony(species)*Month	10				
Colony(species)*Time of day	8				
Colony(species)* Month*Time of day	40				
Error	1026	1.2343	0.0012		
Total	1145	18.2095			

Table 3. Important nectar sources for two species of stingless bees in the Budongo forest over six months of observation (March – August 2002). Shading indicates the periods of foraging on the given source.

Plant species	Family	March	April	May	June	July	August
Meliponula ferruginea							
Acacia sp.	Fabaceae	■	■				
Albizia sp.	Fabaceae	■	■				
Calliandra calothyrsus	Fabaceae	■	■	■	■	■	■
Coffea sp.	Rubiaceae		■	■			
Eucalyptus sp.	Myrtaceae	■	■	■			■
Musa sp.	Musaceae				■	■	
Hypotrigona gribodoi							
Acacia sp.	Fabaceae	■	■				
Albizia sp.	Fabaceae	■	■	■			
Bidens sp.	Asteraceae	■	■	■			■
Calliandra calothyrsus	Fabaceae	■	■	■	■	■	■
Combretum sp.	Combretaceae		■	■			
Eucalyptus sp.	Myrtaceae	■	■	■		■	■
Musa sp.	Musaceae				■	■	
Type 7	Unidentified	■	■				
Type 14	Asteraceae					■	■
Type 23	Unidentified	■	■	■			
Syzigium sp.	Myrtaceae		■	■			
Vernonia sp.	Asteraceae	■	■				■

Table 4. Number of nectar sources and Shannon-Weaver's index of diversity for *Hypotrigona gribodoi* and *Melipona ferruginea* given as average over the 6 months of sampling.

Colony	Total number of plant species foraged upon	Diversity index (H')
	Meliponula ferruginea	
1	18	1.78
2	13	1.67
	Hypotrigona gribodoi	
1	24	2.19
2	29	2.23

Table 5. Sugar concentration (g/100 g) of nectar of different botanic origin obtained from the crop of returning foragers of two stingless bee species in the Budongo forest (data collected between March and August 2002).

Plant species	***Hypotrigona gribodoi***		***Melipona ferruginea***		***t*-value**	***P* value**
	Mean	**N**	**Mean**	**N**		
Calliandra calothyrsus	45.4	147	41.2	127	2.24	0.026
Eucalyptus sp.	48.1	129	44.3	98	3.04	0.003
Albizia sp.	44.3	82	40.2	102	2.24	0.026
Acacia sp.	49.1	76	43.2	97	2.44	0.016
Musa sp.	40.4	56	41.3	64	-1.67	0.098
Bidens sp.	46.2	45	38.4	39	3.40	0.001
Type 14 (Asteraceae)	42.1	41	39.4	9	2.45	0.018
Vernonia sp.	52.1	39	49.2	53	3.27	0.002
Syzigium sp.	39.6	28	42.3	25	2.11	0.040
Type 7 (Unidentified)	43.2	22	46.5	42	2.75	0.008
Type 23 (Unidentified)	38.2	19	37.1	8	1.76	0.091
Combretum sp.	37.8	17	32.3	11	3.61	0.001
Coffea sp.	40.3	15	41.2	6	1.44	0.166
Markhamia lutea	56.5	13				
Mangifera indica	48.4	12				
Ipomea sp.	54.4	9				
Senna sp.	47.1	6				
Carica papaya	58.2	5				
Citrus sp.	45.3	3				
Type11 (Unidentified)			24.5	5		
Type 20 (Unidentified)			29.2	4		

Table 6. Sugar concentration of the crop content,handling time and foraging speed for three species of bees gathering nectar on *Calliandra calothyrsus* (N = 85 for all cases; mean ± SD).

Bee species and body length (measured on dry specimens)	**Returning foragers caught at nest entrance**	**Foragers caught at departure from flowers**	**Time to visit 1 flower**	**Time to visit 5 flowers**
	% TDS	% TDS	s	s
A. mellifera (11 mm)		40.3 ± 7.9	4.3 ± 1.6	26.4 ± 5.1
M. ferruginea (6 mm)	41.9 ± 12.4	42.6 ± 6.8	5.2 ± 1.7	28.2 ± 4.5
H. gribodoi (2-3 mm)	44.1 ± 11.8	44.9 ± 9.4	5.5 ± 2.0	31.3 ± 4.0

Fig. 1. Location of the Budongo Forest Reserve (DRC = Democratic Republic of Congo).

Fig. 2. Compared sugar concentration of nectar collected by the foragers of two species of stingless bees over 6 months in the Budongo Forest (March – August 2002).

Fig.. 3. Effect of the time of day (local time) on the sugar concentration of nectar collected by the foragers of two species of stingless bees polled together over 6 months in the Budongo Forest (March – August 2002).


0
100
km
UGANDA
AFRICA
Albert Nile
KENYA
Lake Albert
BUDONGO FOREST
DRC
Lake Kyoga
UGANDA
Kampala
0°
Lake Edward
Lake Victoria
TANZANIA
30°E
35°E

Fig. 1.

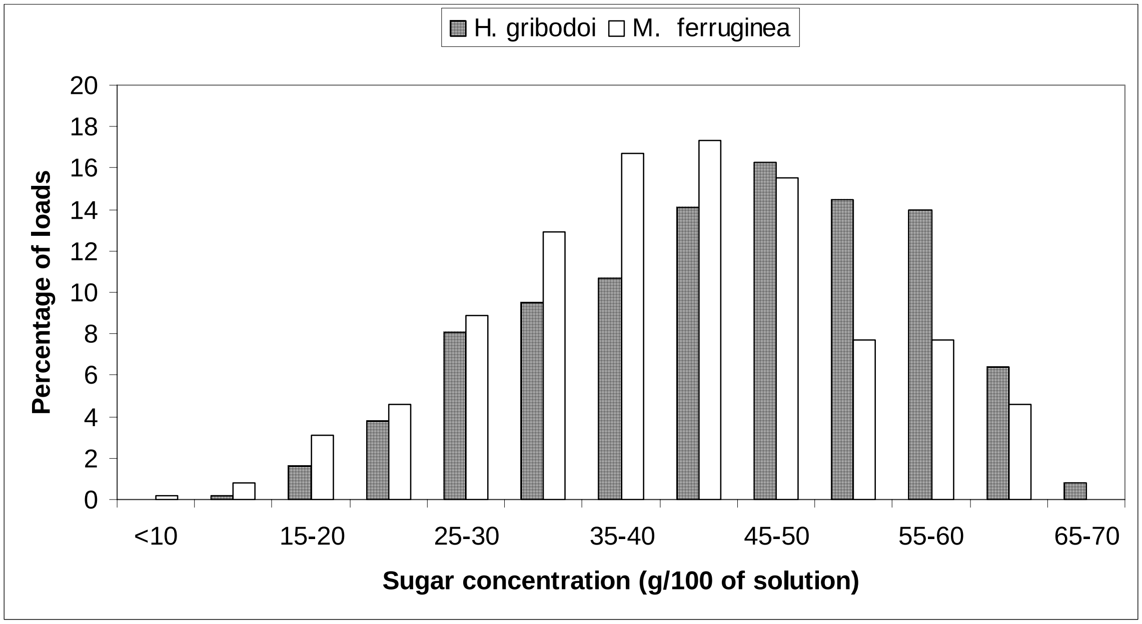
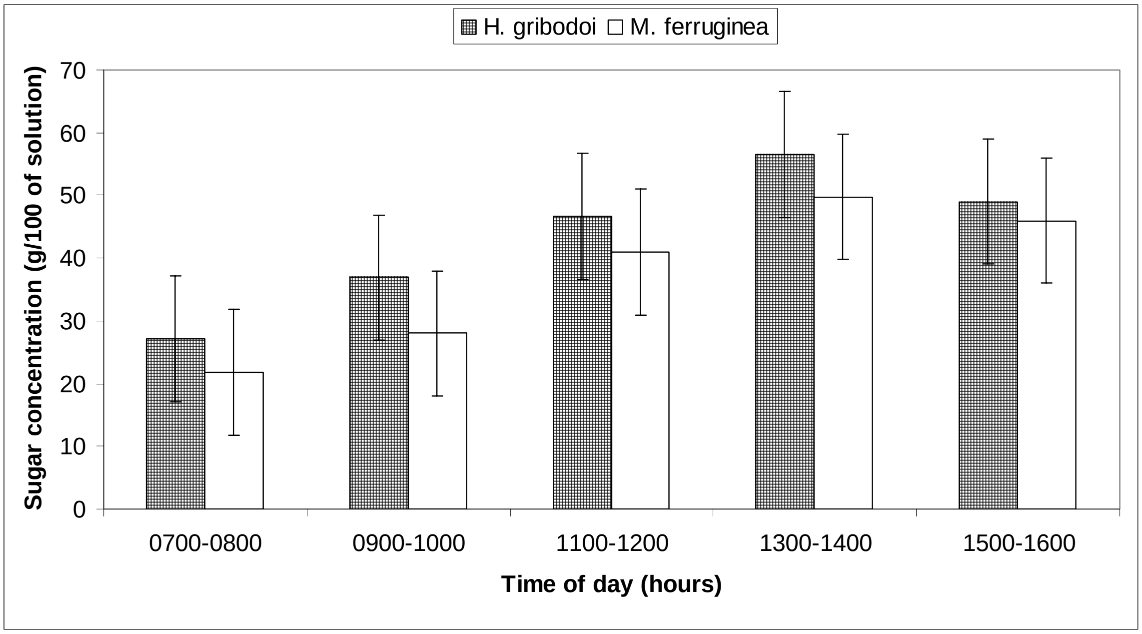

H. gribodoi
M. ferruginea
Percentage of loads
20
18
16
14
12
10
8
6
4
2
0
<10
15-20
25-30
35-40
45-50
55-60
65-70
Sugar concentration (g/100 of solution)

Fig. 2



H. gribodoi
M. ferruginea
Sugar concentration (g/100 of solution)
0
10
20
30
40
50
60
70
0700-0800
0900-1000
1100-1200
1300-1400
1500-1600
Time of day (hours)

Fig. 3

Chapter Eight

Seasonal availability and preference of honeybees for different forage plants in Budongo Forest Reserve, Uganda

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Running head: Seasonal availability of bee forage plants

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Abstract

A study on seasonal availability and preference of honeybees for different forage plants was carried in and around Budongo Forest Reserve, Uganda. Eighty seven plant species belonging to 36 families were recorded to have been used by the bee species with Mimosaceae (10 species) and Caesalphiniceae (7 species) being the most important ones. Other important families included Myrtaceae, Solanaceae and Moraceae. There are two rain seasons (March-May and August-November) and two dry seasons (December-February and June-July. Most bee plants flowered in the rainy seasons. Some of the plants such as *Calliandra calothyrsus* flowered throughout the year. The bee species used trees, shrubs, herbs and climbers for forage. The brood rearing activity was positively correlated with the peak flowering season of major plant species. The brood population was highest during the rainy season and lowest in dry season. The brood population lagged behind flowering seasons which are in turn was induced by rainfall.

Keywords: Bee plants, brood population, flowering season, honeybees, weather, Budongo-Uganda

1.0 Introduction

Flower development in tree species spreads over several months and is dependent upon environmental factors like soil nutrient, light, temperature, moisture and on age of the tree. Tropical trees vary greatly in timing, duration and intensity of flowering (Croat 1969). In spite of the diversity of different periods exhibited by individual tree species, community wide flowering patterns have been found to be remarkably seasonal in many tropical plants (Croat 1969). Flowers from trees, shrubs, herbs, climbers are very important source of pollen and nectar for honeybees. Once most plants have come into bloom, then bee foragers begin to collect nectar. Important honeybee plants should be studied since the amount of nectar they produce is important to the colony (Dandant 1982). A colony will be strong and at its peak strength when the major nectar plants in that area bloom massively. It is necessary to know what plants are available and also when they bloom, whether they supply either nectar, pollen or both and how dependable they are.

Honeybees collect nectar and pollen from different flowering plants but little is known about the species of plants used by honeybees to process nectar into honey in Uganda. Which plants are important sources of forage for honeybees? What is the seasonal availability and preference of honeybees for the different plant taxa? What is the relationship between flowering phenology and the brood rearing activities of honeybees? What is the influence of weather on forage collection and flowering period? Qualitative information about trees species, the flowering period and type of blossom can be used to predict the existence and planning of appropriate intervention to boost honey production. In this study, the important honeybee forage plants in the forest, their flowering and nectar harvesting periods were determined. The flowering periods were correlated to the climatic factors and brood production to check if plants in this forest follow the similar flowering pattern.

2.0 Materials and Methods

2.1 Study site

Budongo Forest Reserve (BFR), which was the study site, is a tropical rain forest situated in mid-western Uganda (fig. 1). It is an outlier of the great Ituri forest of the Democratic Republic of Congo. It covers an area of 825 sq km, making it Uganda's biggest forest reserve (Hamilton 1984), of this 437 sq km (53%) is continuous forest cover, the remaining 47% comprises grassland communities. The reserve is in part continuous with the Murchison Falls National Park and Bugungu and Karuma game reserves. It is located east of the Western rift valley escarpment and Lake Albert between $1^{o}35'$ and $1^{o}55'$ N, and $31^{o}18'$ and 31^{o} 42' E, (Howard 1991). The forest lies at an average altitude of 1100m (minimum 750m and maximum 1250m) above sea level (Eggeling 1947).

2.2 Honeybee plant sampling

Data was collected from March 2001 to April 2004. Ten plots were demarcated for the study. Lists of known bee plants in Uganda obtained from Katende et al. 1995 were sampled in the ten plots. Some of the bee plants were established from observations of bees foraging in the field. The plots were located in three villages (Nyatonzi 3 plots, Biso 3 plots and Nyabyeya 4 plots). These are areas around the Forest Reserve where apiaries were located. Each plot measured 1 x 1 km $=1km^2$. The total area of the plots was therefore 10 km^2. Only plants found within a $1km^2$ of the apiary of the foraging honeybees in an area was sampled because honeybees effectively utilise the plant resource within 1 km radius (Steffan-Dewenter & Tscharntke 1999). A general survey of the plots was first made to cross-check with the lists of known flowering plants, special attention being paid to plants with a high floral population density per unit area or per tree. In each plot, the phenology of the different bee plants was observed and recorded, and samples were taken to Makerere University herbarium for identification. Flowering periods were obtained for each species and correlated with climatic factors. The plant species studied were classified according to their form as trees, shrubs, herbs and climbers.

2.3 Weather and honey harvesting records

Data for ambient temperature and rainfall were obtained from Budongo Forest Project and Nyabyeya Forest College weather stations. The mean minimum temperature ranges from 23-29°C and the mean maximum temperature from 29-32°C. The relative humidity varies between 45-50 % during the dry season and it is about 75 % during the rainy season although it can reach 90 % during very rainy days. The number of beekeepers harvesting honey at different seasons was also recorded.

2.4 Brood population

The total area of honeybee brood (eggs, larvae and pupae) was estimated every 21 days using a wooden frame 7.5 cm x 15 cm in size. This frame was further subdivided. The frame was placed over each side of the brood combs after the honeybees had been shaken from the combs. The area occupied in cm^2 was recorded and the brood populations were calculated from the total area occupied by the brood. Data on brood was correlated to rainfall and flowering.

3.0 Results

3.1 Important honey bee plants and their flowering periods

Eighty seven plant species belonging to 36 families were recorded to have been used by the bee species. The most important plant families in terms of number of species used and their flowering seasons are shown in table 1. Among these Mimosaceae was the largest with 10 species. The second largest family was Caesalpiniaceae with 7 species followed by Myrtaceae, Solanaceae and Moraceae with 5, 5 and 5 species respectively. A number of trees, shrubs, herbs and agricultural crops were used by the bees for both pollen and nectar. The most important plant species used by the bees were trees (above 60%) followed by shrubs (above 20%). Herbs, grasses and lianas were used to a smaller extent (Fig. 2). Most bee plants (providing both pollen and nectar.) were either located in the forest reserve or in the villages surrounding the reserve.

3.2 Rainfall and flowering periods of most important plants

The climate experienced is the tropical climate type, which has 2 rainy seasons, one in March-May and another in August-November (Fig. 3). Budongo Forest Reserve receives rainfall of about 1397 mm annually with 100-150 rainfall days. Rainfall is predominantly with thunderstorm and at times there are hailstorms. Rainfall is most common in the afternoons and evenings.

The flowering period of bee plants varied with the different seasons of the year. Most of the important bee plants flowered during the rainy seasons (March-May and August-November) with exception of plants such as *Hibiscus* sp. and *Calliandra calothyrsus* which flowered throughout the year. Flowering periods of agricultural crops depended on the date when the crops were planted. The number of flowering plants was positively correlated with rainfall (r = 0.46, P = 0.009). A total of 34 % of the bee plant species flowered during the first rain season (March-May), 18% during the first dry season (June-July), 45% during the second rain season (August-November) and 9 % during the second dry season (December-February, Fig. 3). There was some variation among the plant species with respect to length of flowering time. Some of the individual species produced a few flowers for a few days but some plant species bloomed for longer periods, lasting from several weeks to several months. Therefore the flowering periods were immediately followed by increase in brood population.

3.3 Brood population

The brood rearing activity was positively correlated with the peak flowering season of major plant species in the area (r = 0.597; P = 0.041). The brood population of honeybees was highest during the rainy season and lowest in dry season. Brood population declined gradually with the onset of dry season (June-July) rising again in August (table II). There were fluctuations of brood rearing patterns depending on weather conditions.

4.0 Discussion

Budongo Forest Reserve and the surrounding areas support a variety of families and species of trees, shrubs and agricultural crops that provide nectar and pollen to bees for honey production. Observing the behaviour of flowering plants can be very useful in determining when honey can be harvested (Crane 1975). Our results showed that the flowering time of bee plants varied with the different seasons of the year. Most plants bloomed during the rainy season (March-May and August-November) while others like agricultural crops depended on the sowing date. These findings are consistent with those of (Pancel 1993) who found that flower development in tree species spreads over several months and is dependent upon environmental factors like soil nutrient, light, tempersature, moisture and on the age of the tree. The environmental factors stimulate the internal biochemical processes that lead to the initiation of cell differentiation to form flower buds. Reduction in tissue temperature will benefit the phenology and productivity of the understorey plants (herbs and lianas) by minimising exposure to heat stress (Pancel 1993). Most of the plants studies produced both pollen and nectar. According to (Pancel 1993), a high number of plant species in the tropical rainforest and the surrounding areas produce male and female flowers on one tree (diocious) and hence produce both nectar and pollen, while few plants have either male or female flowers (monoecious). The high number of both forest and village depended plants can be attributed to some plant families that are now cultivated by farmers and domesticated to serve for more than two purposes for example *Markamia platycalyx* belonging to family Bignomiaceae is used as fodder for animals, fencing and for bee forage.

In Uganda, some recent study sanctioned by the United Nations Industrial Development Organisation (UNIDO) on honey beekeeping development has been able to describe some of the important bee plants (see Horn 2004). The country is rich in terms of biodiversity and even in a global context it is regarded as one of the important centres of floral biodiversity (Katende et al. 1995). It has a potential for nectar producing plants which can be used by bee colonies during the whole year. There are always enough plants in blossom that the colonies can survive. Even during the non-harvesting time the natural nectar and pollen resources are more than sufficient to keep bees alive (Horn 2004). During the rainy season, the bees collect more nectar and pollen, the young workers eat more pollen, and produce more bee milk. As a result, the queen can lay more eggs, and the nurse bees can feed and rear more brood.

Brood-rearing takes place during the rainfall season, when flowers are in bloom. This stage is characterised by intense activity in the colony. Food is usually abundant. Comb builders work fast to enable the queen to lay; nursing bees feed the young brood; pollen, nectar and propolis are collected (FAO 1990). At the peak of the brood-rearing stage, the population of the hive increases rapidly. Therefore an uninterrupted brood rearing is attributed to the sequential flowering of plants throughout the year, contributing to the availability of pollen throughout the year. Due to these variations, the flowering phenology and biological cycle of honeybees vary from one locality to another, which results in variation of brood rearing and honey flow seasons.

During the dry season (June-July) and December-February), environmental conditions are unfavourable for the bees, and as a result the activity of the colony diminishes. Few worker bees can fly out of the hive. The queen reduces laying, so that the bees rear little brood. In tropical zones (FAO 1990) reported that unfavourable conditions for honeybees occur in different periods and may be caused by different factors such as temperature falling so low that the activity of the colony is reduced. In this case few or no plants are flowering. Only a few bees fly out of the hives, and as a result, very little, if any, nectar is collected. In other areas, drought occurs, and the number of flowers, and therefore the amount of nectar available, is reduced considerably. In these circumstances, the activity of the colony never completely stops. The queen generally does not stop laying as long as stores are available within the hive, although the amount of brood present reflects a much slower rhythm of laying (FAO 1990).

Table 1. Important honey bee plants, their life form, flowering period, pollen and nectar source.

Family	Plant scientific name	Plant form	Flowering period	Pollen source	Nectar source
Mimosaceae	*Acacia* sp.	Tree	March-May	✓	✓
Mimosaceae	*Allbizia* sp.	Tree	March-May, Aug.- Sep	-	✓
Anacardiaceae	*Anacardium occidentale*	Tree	Depending on planting date	✓	✓
Meliaceae	*Azadirachta indica*	Tree	Depending on planting date	✓	✓
Compositae	*Bidens pilosa*	Herb	March-June	-	✓
Sapotaceae	*Butyrospermum paradoxum*	Tree	April-May Aug-Nov	✓	-
Mimosaceae	*Calliandra callothyrsus*	Shrub	Throughout year	✓	✓
Myrtaceae	*Callistemon citrinus*	Tree		✓	✓
Caricaceae	*Carica papaya*	Tree	March-May Aug-Nov	✓	✓
Rulaceae	*Citrus senensis*	Shrub	June, July, Aug.	✓	✓
Combretacaea	*Combretum* sp.	Tree	April-May Aug-Nov	-	✓
Commelinaceae	*Commelina africana*	Herb	June-July	-	✓
Boraginaceae	*Cordia africana*	Tree	April-May Aug-Nov	-	✓
Euphorblaceae	*Croton macrostachyls*	Tree		✓	✓
Caesalpiniaceae	*Cynometra alexandrei*	Tree	March-June	✓	✓
Caesalplniaceae	*Delonix ragia*	Tree	Augt.-Nov.	✓	-
Myrtaceae	*Eucalyptus* sp.	Tree	Throughout year	✓	✓
Moraceae	*Ficus mucuso* sp.	Tree	April-May Aug-Nov	-	✓
Malvaceae	*Hibscus esculentum*	Shrub like	Throughout year	✓	✓
Convolvulaceae	*Ipomea* sp.	Runner	Aug.	✓	✓
Bignomiaceae	*Jacaranda Mimusifolia*	Tree	April-May	-	✓
Mimosaceae	*Leucaena lencocephela*	Shrub	March-June	✓	✓
Anacrdiaceae	*Mangifera indica*		Feb.-April Nov. Dec.	✓	✓
Bignomiaceae	*Markhama* sp.	Tree	April-May	✓	✓
Moraceae	*Milicia exelsa*	Tree	Feb-May	-	✓
Musaceae	*Musa paradisiaca*	Tree like	Throughout year	-	✓
Caesalplniaceae	*Parkinsonia aculenta*	Shrub	March-June	-	✓
Passifloraceae	*Passiflora edulis*	Climber	Throughout year	✓	✓
Rosaceae	*Prunus africana*	Tree	Feb-May	✓	✓
Caesalpilniaceae	*Senna spectabilas*	Tree	Feb-May	✓	✓
Solanaceae	*Solanium* sp.	Shrub	Depending on planting date	✓	✓
Myrtaceae	*Syzigium cuminii*	Tree	Apr-May	-	✓

			Aug-Nov		
Caesalpiniaceae	*Tamarindus lndica*	Tree	Apr-May Aug-Nov	✓	✓
Verbenaceae	*Tectona graandis*	Tree	March-June	✓	-
Oleaceae	*Ulea capensis*	Tree	March-June,	✓	-
Compositae	*Vernonia* sp.	Shrub	April-May Aug-Nov	✓	✓
Poaceae	*Zea mays*	Crop	March-June, Sept,-Dec	✓	✓

Table 2. Relationship between rainfall, temperature and brood area during flowering seasons.

	Dry season			Rainy season			Dry season		Rainy season			
	Dec	Jan	Feb	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.
Rainfall	106	42	38	98	203	172	99	138	126	198	258	184
Temperature	30	31	29	24	25	26	28	30	28	26	25	27
% of flowering bee plants	11	8	15	23	28	36	18	21	29	34	44	23
Brood	82.5	92.1	103.2	137.9	162.17	107.5	81.2	73.5	129.3	183.2	142.3	113.4

Fig. 1. Map of Uganda showing the location of Budongo Forest Reserve.

Fig. 2. Life form composition of bee plants used for pollen and nectar

Fig. 3. Monthly rainfall (a) and percentage of flowering of bee plants (b) in Budongo Forest Reserve


0
100
km
UGANDA
AFRICA
Albert Nile
KENYA
Lake Albert
BUDONGO FOREST
DRC
Lake Kyoga
UGANDA
Kampala
0°
Lake Edward
Lake Victoria
TANZANIA
30°E
35°E

Fig. 1.

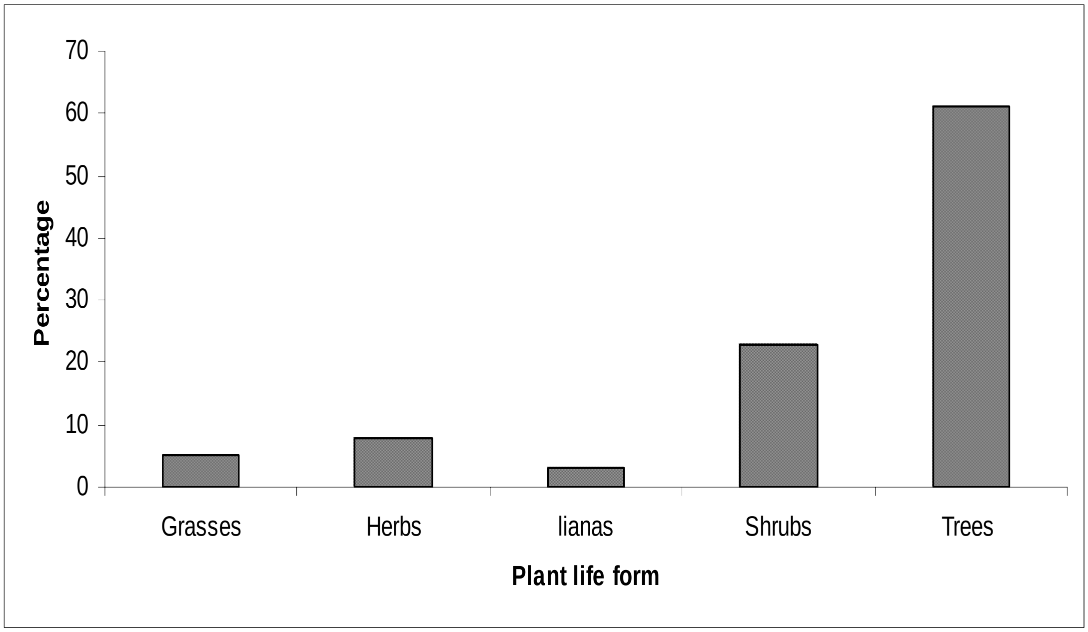
70
60
50
40
30
20
10
0
Percentage
Grasses
Herbs
lianas
Shrubs
Trees
Plant life form

Fig. 2.

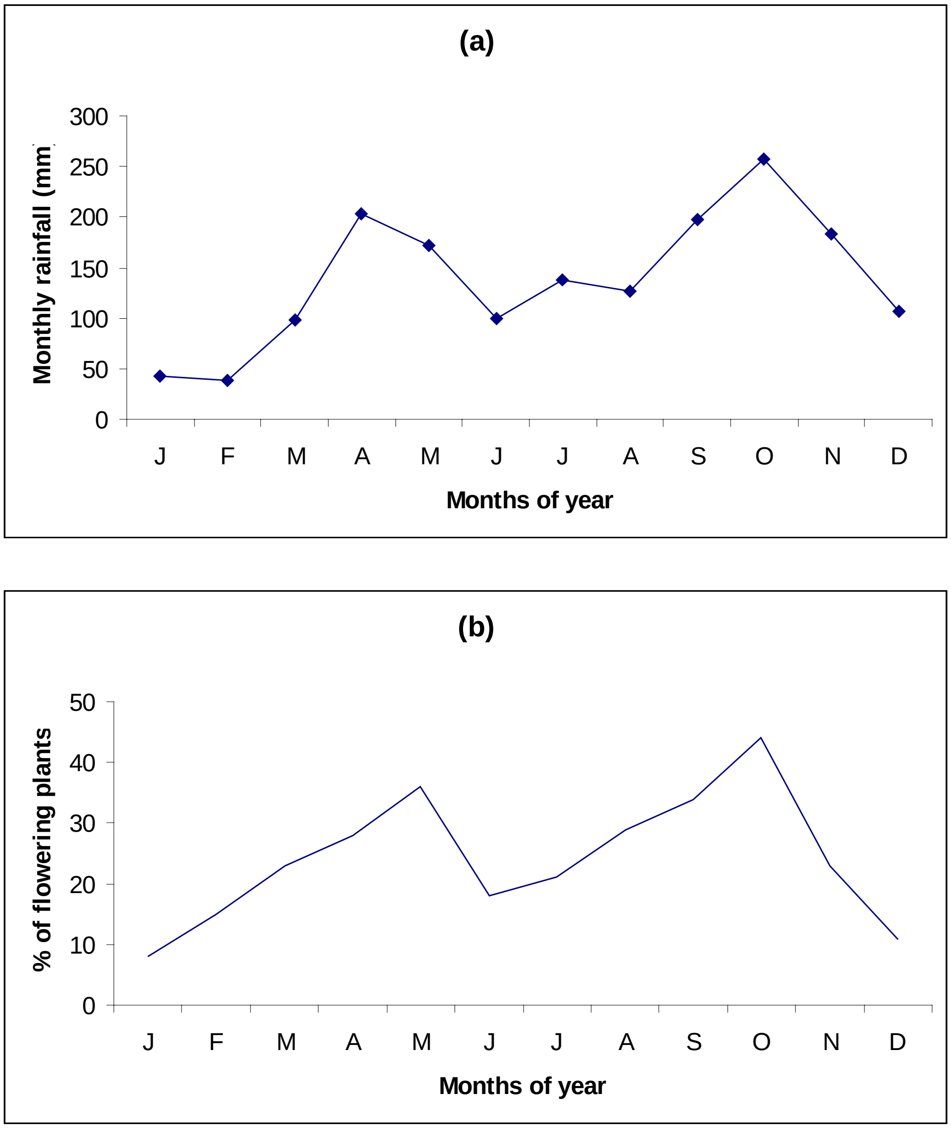
(a)
Monthly rainfall (mm)
300
250
200
150
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D
Months of year
(b)
% of flowering plants
50
40
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D
Months of year

Fig. 3.

Summary and conclusions

This thesis is a result of fieldwork on foraging ecology of Afrotropical stingless bees in Uganda. The focus is on inter-specific foraging ecology of stingless bees and honeybees in their native ecological environment. This is because the knowledge base of the ecology of Afrotropical bees is minute. Aspects of nesting biology of Afrotropical stingless are presented in chapter 3. The chapter discusses stingless bee nest site selection and occurrence. The natural nests made by these bees (trees, shrubs, ground and wall nests) are described. The study was carried out in Bwindi Impenetrable National Park (BINP) south western Uganda (1160-2607m), A total of 538 natural nests of five stingless bee species belonging to two genera were found: *Meliponula* (four species) and *Hypotrigona* (one). *H. gribodoi* aggregated its nests in house walls. *M. bocandei* and *Meliponula lendiliana* nested both in tree cavities and in the ground. There were no exposed nests. Most nests were harboured in large trees and the largest bee species were most often highest from the ground. Nesting included a broad range of tree species (36 species among 133 trees).

In chapter 4, honeybee and stingless bee colony abundance and predation by apes and humans are discussed. This chapter is part of the efforts to understand nesting ecology of highly social bees (native stingless bee and honey bee populations BINP. Predators are considered in more detail than in previous field studies of honey-making bees. Meliponine nest abundance is analysed relative to availability of nesting sites, food, and the elevation or weather. 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). 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.

Temporal resource partitioning and climatological influence on colony flight and foraging of stingless bees is discussed in chapter 5. The study presents the results of observations on flight and foraging of different species studied at two different forest habitats. Results show that the two stingless bee species exited their nests in characteristically distinct foraging bouts suggesting that the recruitment methods used may be direct leading or ‘piloting’. The number of individuals in a returning bout was less than that in an exiting bout suggesting recruits do not follow experienced foragers the whole distance to food source, a phenomenon referred to as ‘partial piloting’. Nectar and pollen foraging took place throughout the day while the removal of debris was greater in the late hours of the morning. Increased temperature resulted in significant increase in number of exiting bees.

In chapter 6, differences in pollen foraging by *Apis mellifera* and stingless bees *Meliponula bocandei* and *Meliponula nebulata* in BINP are discussed. Making use of the uniqueness of this study where native species of honeybees and stingless bees were studied in the same natural Afrotropical forest, a qualitative study focusing on likely factors causing differences in their pollen foraging behaviour is presented. 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. The relatively bigger colony and body size of *A. mellifera* was positively correlated to pollen diet. The recruitment technique to food sources is implicated to have been 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). During the rainy season, pollen diversity of *A. mellifera* was lower as compared to 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 to partitioning of food resources.

Botanical sources and sugar concentration of nectar collected by two stingless bee species in Budongo Forest Reserve (BFR) is presented in chapter 7. The study describes the important nectar sources of stingless bees and their diversity. It discusses factors influencing sugar concentration of collected nectar and in particular it deals with effect of the bee species on the concentration of the collected nectar. Both species *Hypotrigona gribodoi* (2-3 mm) and *Meliponula ferruginea* (6 mm) collected nectar with a wide range of sugar concentration (*H. gribodoi*: 14.2-67.4%; *M. ferruginea*: 9.1-63.4%). *H. gribodoi* collected nectar of higher sugar concentration than *M. ferruginea*. Factors that influenced sugar concentration of collected nectar included botanic origin of the nectar, bee species, bee colonies, month of year, time of day and the local environment. *H. gribodoi* collected nectar from more diverse plant species than *M. ferruginea.* Sugar concentration for both bee species was higher during the dry season than the rainy season. Although the above factors may explain part of the variation in the sugar concentration of nectar, additional explanations lie in the behavioural differences among the bee species.

In chapter 8, seasonal availability and preference of honeybees for different forage plants in Budongo Forest Reserve is described. The important honeybee forage plants in the forest, their flowering and nectar harvesting periods are described. The flowering periods are correlated to climatic factors and brood production to determine if plants in this forest follow similar flowering pattern. Eighty seven plant species belonging to 36 families were recorded to have been used by the bee species with Mimosaceae (10 species) and Caesalphiniceae (7 species) being the most important ones. Other important families included Myrtaceae, Solanaceae and Moraceae. There are two rain seasons (March-May and August-November) and two dry seasons (December-February and June-July. Most bee plants flowered in the rainy seasons. Some of the plants such as *Calliandra calothyrsus* flowered throughout the year. The bee species used trees, shrubs, herbs and climbers for forage. The brood rearing activity was positively correlated with the peak flowering season of major plant species. The brood population was highest during the rainy season and lowest in dry season. The brood population lagged behind flowering seasons which are in turn induced by rainfall.

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Curriculum Vitae

Robert Kajobe was born in 1970 in Koboko, Uganda. From 1992-1996, he studied BSc Forestry in Makerere University, Uganda. In 1998 he went to study an MSc in Tropical Bees in the Faculty of Biology, Utrecht University, The Netherlands where he graduated in 2000. Currently Kajobe is employed as an Apiculturalist in the National Agricultural Research Organisation (NARO). Since 2001 he has been lecturing in the Faculty of Forestry and Nature Conservation, Makerere University. Kajobe is also a visiting lecturer to Gulu University. He is the Technical and Research Officer for The Uganda National Apiculture Development Organisation (TUNADO), an apex body for all beekeepers in the country. He has participated in the provisioning of technical assistance to beekeeping groups in the country. He has traveled and participated in national and international workshops related beekeeping.

In 2002, Kajobe received a Bursary from the British Ecological Society (BES) to conduct bee research in Bwindi Impenetrable National Park (BINP) and Budongo Forest Reserve (BFR) which constituted most of his PhD research. In 2003 he received Pre-Doctoral Biodiversity study visit to Royal Museum for Central Africa (RMCA) in Tervuren, Belgium where he received training in basic taxonomy and specimen data base development. In the same year he received training in basic Pedagogics skills for teachers of higher institutions of learning at the School of Education, Makerere University. In 2006, Kajobe received a Fellowship from the British Ecological Society (BES) to conduct more research in bee ecology in BINP and the agro-ecological zones of Uganda. His research interests include biology and ecology of tropical stingless bees and honey bees. The other interests include honeybee botany, products, health, management and apitherapy.

Publications

Kajobe R. Nesting biology of equatorial Afrotropical stingless bees (Apidae; Meliponini) in Bwindi Impenetrable National Park, Uganda. Manuscript submitted to *Journal of Apiculture Research*

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