
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 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. *Meliponula 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.

Key words: Budongo, Bwindi, communication, foraging, stingless bees

Résumé

Nous avons étudié l'activité de vol de deux espèces d'abeilles sans aiguillon (*Meliponula ferruginea* and *Meliponula nebulata*) et les facteurs environnementaux influençant leur vol. Deux morphes de *M. ferruginea* furent enquêtées: *M. ferruginea* (marron) dans la forêt de Budongo et *M. ferruginea* (noir) dans le parc Bwindi. Les deux espèces d'abeille quittèrent leurs nids par périodes de fourrage typiquement distinctes suggérant que les méthodes de recrutement employées sont peut-être la direction directe, dite «pilottage». Le nombre d'individus revenant fut moins que le nombre qui sortait suggérant que les recrues ne suivent pas les fourrageurs expérimentés pendant tout le trajet jusqu'à la source de nourriture, un phénomène appelé «pilottage partiel». La période de vol de *M. ferruginea* (noir) et de *M. nebulata* en Bwindi fut limitée à quelques heures par jour. *M. nebulata* fourrageait sous la bruine, une stratégie de survie qui pouvait promouvoir son conditionnement reproducteur. Le fourrage pour le nectar et le pollen se produisait pendant la journée tandis que l'enlèvement du débris eut lieu plus souvent en fin de matinée. La température croissante provoquait une croissance majeure dans le nombre d'abeilles sortant du nid. Le nombre d'abeilles sortant augmenta tel que l'humidité diminua jusqu'au niveau optimum de 78%; une croissance dans le taux d'humidité résultait d'un nombre réduit d'abeilles sortant par la suite.

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Introduction

The behavioural flexibility of bees is best characterized 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; De Bruijn *et al.*, 1994; Biesmeijer, 1997). The influences of these factors vary among the different species as 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 *Apis mellifera* 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 co-exist 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 differentiations between sympatric stingless bee species can be determined by the morphology of the bees for example, body size, colour and mouthparts. It can also be determined by the behaviour of the bees for example, timing, ability to recruit, specific collecting behaviour, aggressiveness and food selection. Temporal resource partitioning was described by Frankie, Opler & Bawa (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 afro-tropical 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.

Materials and methods

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 km² of natural forest and contains both montane and lowland forest. The park is on UNESCO's list of world heritage sites because of 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 1160 to 2607 m a.s.l. The annual temperature ranges between 7 and 20°C with a mean of 16.3°C. The heaviest rains are experienced in March to May and September to November and the two dry season troughs are December to January and June to July (Butynski, 1984). Its annual precipitation is 1130–2390 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 km² with the vegetation being semi-deciduous moist tropical rain forest. The mean altitude is 1100 m and the mean temperature range is 14–28°C. The rainfall is 1500 mm and falls mostly in April to May and August to October. The dry season is from December to February.

Bee species

Colonies used in BINP were situated near the Institute of Tropical Forest Conservation (ITFC) in Ruhija. Two morphs of *Meliponula ferruginea* have been identified in Uganda, which previously were called *Meliponula 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 BINP while the brown one exists in Budongo Forest Reserve. Two natural colonies of *M. ferruginea* (black) and three of *Meliponula nebulata* were used (Table 1). The distance between the two most far apart was 15 min 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 (1.5 m 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

Table 1 Nest and colony characteristics of bee species used. The 20 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)	Estimated population	Altitude (M)	Nest site	Nest height (M)
<i>A. mellifera</i>	AM	Budongo	11	10000	1100	Top bar	1
<i>M. ferruginea</i> (brown)	MFbr1	Budongo	6	2500	1100	Log	1
<i>M. ferruginea</i> (brown)	MFbr2	Budongo	6	2300	1100	Tree base	0
<i>M. ferruginea</i> (brown)	MFbr3	Budongo	6	2000	1100	Tree cavity	1.2
<i>M. ferruginea</i> (black)	MFbl1	Bwindi	6	1500	2330	Tree cavity	0.8
<i>M. ferruginea</i> (black)	MFbl2	Bwindi	6	1400	2330	Tree cavity	0.6
<i>M. nebulata</i>	MN1	Bwindi	7	1800	2330	Tree cavity	1.4
<i>M. nebulata</i>	MN2	Bwindi	7	1800	2290	Tree cavity	2.9
<i>M. nebulata</i>	MN3	Bwindi	7	1600	2330	Tree cavity	3.3

other crops. The other two colonies were located in different trees; one at about 50 m and the other 70 m respectively from the farm. Twenty colonies of *Apis mellifera* kept in Top bar hives were located in the middle of the farm.

Bee flight behaviour

We recorded bee flight behaviour in two ways. First, the recorder sat near entrances of colonies (1 m) 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 20.00 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. *Calliandra calothyrsus* is a multi-stemmed shrub that reaches a height of 4–6 m. Its flowers are purplish red and mature over months. *Calliandra calothyrsus* is a primary source of nectar and flowers throughout the year in the farm.

Recording of flight activity and environmental conditions

All bees flying out and into the nest during 15 min every hour were recorded from 06.00 to 20.00 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 2 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 eight 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 eight 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.

Results

Bee flight behaviour at nest entrances

The two stingless bee species exited their nests in characteristically distinct foraging bouts. Early in the mornings, there were a small number of foragers in a bout (five to ten bees for *M. nebulata*). At the peak of foraging (11.00–15.00 hours), a typical bout consisted of 20–60 foragers and lasted between 5 and 30 s. Foragers also returned in bouts however, the returning bouts had a smaller number of bees. For example, *M. nebulata* had an average of five to 20 returning foragers in a bout and lasted for a longer time (20–60 s). 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 number of bouts within which foragers of *M. nebulata* (colony MN1) and *M. ferruginea* (black) colony MFbl1 exited their nests in 15 min during the study period. There was a variation in their frequencies (*M. nebulata*: mean = 42.9; SD = 61.40; n = 26 and *M. ferruginea* (black): mean = 49.7; SD = 54.26; N = 26) as indicated by the large values of standard deviation. For both species, there were relatively a higher number of bouts consisting of smaller number of individuals. Within 15 min of observation, there were two bouts of foragers of *M. nebulata* each consisting of 120–125 individuals exiting their nest. For *M. ferruginea*, three bouts each consisting of 145–150 foragers exited their nest within the same time. These fluctuations suggest that bees exited their nests in bouts.

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 16.00 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 (06.00 hours), *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 08.00–09.00 hours when the nectar was either depleted or dried out because of the hot sun.

Daily flight activity

The daily flight patterns of the bee species were found to be different. *Meliponula ferruginea* (brown) had a longer foraging time, starting at 07.00 hours and stopping at 18.00 hours. *Meliponula nebulata* and *M. ferruginea* (black) had a relatively shorter foraging time, starting to fly at

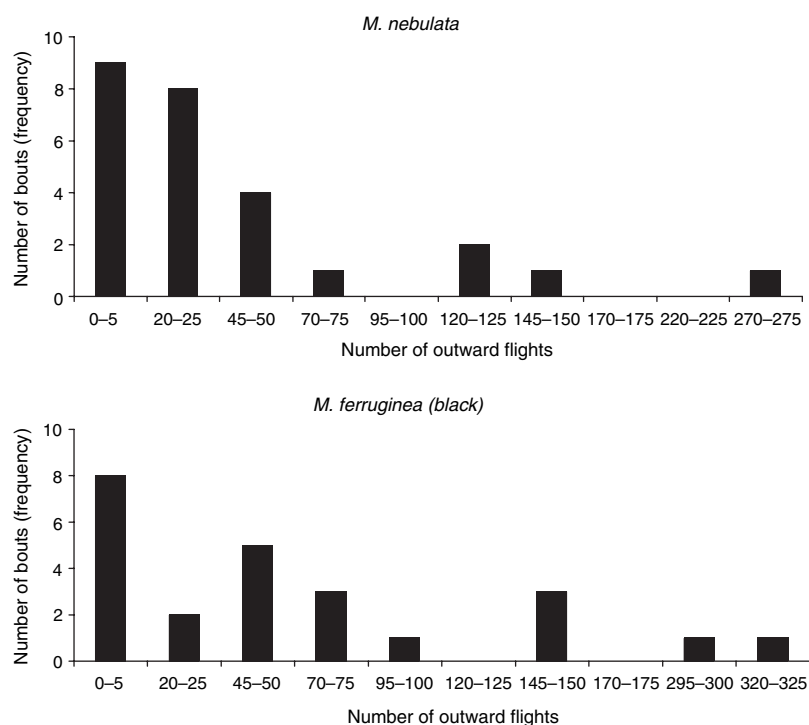


Fig 1 Number of bouts (frequency) within which foragers of *Meliponula nebulata* (colony MN1) and *Meliponula ferruginea* (black) exited their nests in 15 min during the 12 months observation period. The x-axis represents the range of number of outward. The y-axis represents the number of bouts. These fluctuations indicate that bees exit nests in bouts

08.00 hours and stopped at 17.00 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.

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 with *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 to October.

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 10.00 and 14.00 hours (Fig. 4). Nectar foraging took place throughout the day with a peak between 12.00 and 14.00 hours. Pollen foraging took place throughout the day. The peak for pollen collection took place slightly

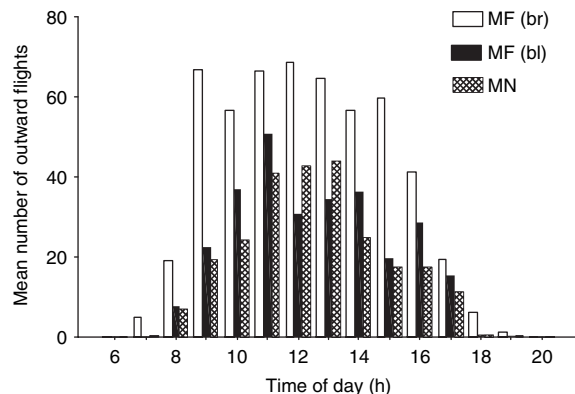


Fig 2 Daily patterns of flight activity related to hours of the day. MF (brown) = *Meliponula ferruginea* (brown), MF (black) = *M. ferruginea* (black) and MN = *Meliponula nebulata*. Bars represent the mean value of all the flights recorded at a particular time of the day in a 15 min period every hour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

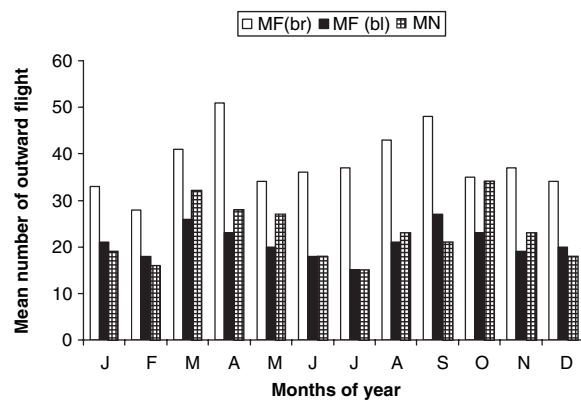


Fig 3 Mean monthly number of exiting bees during 15 min of observation throughout the 12 months of study period. MF (brown) = *Meliponula ferruginea* (brown), MF (black) = *M. ferruginea* (black) and MN = *Meliponula nebulata*

before that of nectar (11.00–14.00 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 07.00 and 19.00 hours with higher rate of collection between 10.00 and 16.00 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.

Environmental 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 as one influences the other. Bees started flying at humidity of about 80%. There was an increase in number of exiting

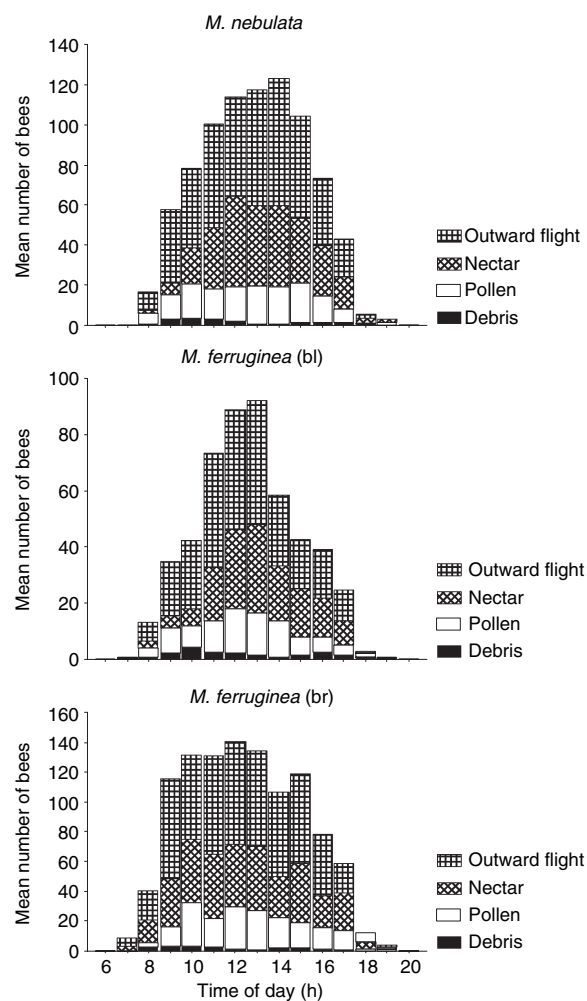


Fig 4 Overall daily foraging activity of the three bee species in the different hours of the day showing the percentages of bees exiting without any material or with debris and those entering the nests with nectar or pollen

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.

Discussion

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

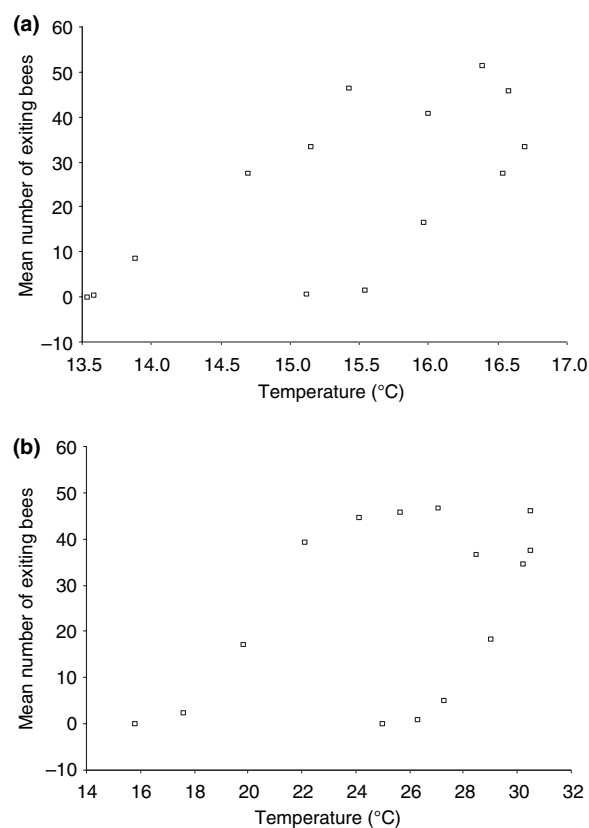


Fig 5 (a) Number of exiting bees at different temperatures and hours of the day for the two bee species studied in Bwindi Park. There were three colonies of *Meliponula nebulata* and two for *Meliponula ferruginea* (black). (b) Number of exiting bees at different temperatures and hours of the day for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

field-based communication (Lindauer & Kerr, 1960; Esch, Esch & Kerr, 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 synchronizing 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). *Meliponula 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 with 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 30–50 m and returned to the nest. On the contrary, 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.

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 co-exist, 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.*, 1999). 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.

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, Kleinert-Giovaninni & Pires (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, De Bruijn & 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 (6–7 mm). Imperatriz-Fonseca *et al.* (1985) attributed the temperature variation to the beginning of flight activity to variation of workers size of *P. 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 (2300 m) and relatively low temperatures (7–20°C) compared with Budongo Forest (altitude 1100 m

and temperature 14–28°C) where *M. ferruginea* (brown) was located. *Meliponula 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 & 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-Giovanini (1982) observed that flight activity decreased when relative humidity reached 70%, even when other factors were in good condition.

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