Honeydew Collecting in Malagasy Stingless Bees (Hymenoptera: Apidae: Meliponini) and Observations on Competition with Invasive Ants

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3 authors, including:

Hauke Koch
University of Texas at Austin

Marlotte Jonker
University of Freiburg

Honeydew collecting in Malagasy stingless bees (Hymenoptera: Apidae: Meliponini) and observations on competition with invasive ants

H. Koch[1*], C. Corcoran[2] & M. Jonker[3]

[1]*Experimental Ecology, Institute for Integrative Biology, ETH Zurich, Universitätsstrasse 16, 8092 Zurich, Switzerland*
[2]*Trinity College Dublin, Dublin 2, Ireland*
[3]*Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708PB Wageningen, Netherlands*

We present the first record of honeydew feeding in Malagasy stingless bees. Two species of stingless bees, *Liotrigona mahafalya* and *L. madecassa,* collected honeydew produced by mealybugs on an *Albizia perrieri* (Fabaceae) tree in the dry deciduous forest of Kirindy, Madagascar. Honeydew might represent an important part of the diet of Malagasy stingless bees, especially in times of scarce floral resources in the highly seasonal environment of western Madagascar. The interaction between the bees and two species of invasive ants, *Monomorium destructor* and *Paratrechina longicornis,* in competition for the honeydew resource, was studied. Numbers of stingless bees and ants on the honeydew source were negatively correlated, with ants decreasing in density distally from the main trunk of the tree and bees showing the opposite trend. Invasive ants could therefore potentially threaten the native bees by displacing them from this resource.

Key words: mealybugs, honeydew, Madagascar, *Liotrigona,* nonfloral resources, displacement.

INTRODUCTION

Honeydew produced by sap-sucking Homoptera is an important resource for a variety of organisms. Ant-homopteran associations are often mutualistic and are especially well documented; in these relationships ants protect their homopteran partners against predators and parasites (Schultz & McGlynn 2000) and often rely on honeydew as their most important food source (Davidson *et al.* 2003).

Bees are also known to collect honeydew, including honey bees (*Apis* spp.), bumble bees (*Bombus* spp.) and several species from the family Andrenidae (Zoebelein 1956a). A few Neotropical species of stingless bees have also been observed to collect honeydew from hemipterans (Roubik 1989), and a species of *Schwarzula* even houses scale insects (Coccidae) inside their nest for this purpose (Camargo & Pedro 2002). Until now, however, there are to our knowledge no reports from the Afrotropical Region, including Madagascar, of stingless bees foraging for honeydew.

Very few accounts exist on the interactions between bees and ants, especially in competition for honeydew. Zoebelein (1956b), for example, notes aggressive behaviour of *Formica* ants against honey bees (*Apis mellifera*) that try to collect honeydew from aphids tended by the ants. Honey bees avoided foraging at honeydew sources occupied by ants (Zoebelein 1956b). Ant colonies often monopolize the honeydew resource on a particular plant and defend it against other inter- or intraspecific competitors, but coexistence of several ant species can also occur (Blüthgen *et al.* 2006). Stingless bees of the genus *Trigona* can chemically deter ants from their nests, presumably with plant-derived terpenes, although it is not known if these deterrents are also used in competition for resources against other ants (Lehmberg *et al.* 2008).

The highly social stingless bees (Meliponini) are represented in Madagascar by eight species in the genus *Liotrigona* (Pauly *et al.* 2001; Koch 2010). While several species inhabit the rainforests of the east (Michener 1990), they are most abundant in the dry regions of the south and west, where the local people also harvest honey from their nests (Brooks & Michener 1988). These bees appear to be polylectic foragers on pollen and nectar and nest in tree cavities or bamboo stems (Pauly *et al.* 2001).

In November 2009, we observed two species of *Liotrigona, L. madecassa* and *L. mahafalya,* collecting honeydew from an unidentified species of mealybug (Pseudococcidae) on a tree, *Albizia perrieri* (Fabaceae), in the dry deciduous forest of Kirindy, Madagascar. The same food source was also used

*To whom correspondence should be addressed.
E-mail: hauke.koch@env.ethz.ch

by two species of invasive ants, *Monomorium destructor* and *Paratrechina longicornis.* Since the tree was standing freely and both ant species were nesting either in the base of the trunk or in the ground nearby, the ants had to travel along the trunk and main branches to reach the honeydew resource. Therefore, we expected the density of ants to decrease with increased pathway length (*i.e.* to honeydew resources distal from the trunk). Bees on the other hand are not constrained in this way, since they can fly to the best available resource site in the tree. We therefore hypothesized that the mealybugs that are further away from the trunk would be visited mainly by bees and less visited by ants. We sampled units of mealybug assemblages across the tree at different distances from the trunk to test this predicted association.

MATERIAL AND METHODS

Ant/stingless bee comparison

Observations were made on four consecutive days at the end of the dry season in November 2009 on a freestanding *Albizia perrieri* on the grounds of the Centre National de Formation, d'Études et de Recherche en Environement et Forestière (CNFEREF) field station (20°03′S 44°39′E), approximately 60 km northeast of the city of Morondava in the Menabe region of west-central Madagascar.

In order to test for different spatial distributions of ants and bees on the study tree we observed 15 cm segments of different randomly selected branches (n = 18), which were evenly distributed along the accessible parts of the tree. The number of ants, stingless bees and mealybugs present in each segment were recorded twice daily, between 8:00–9:00 and 17:00–18:00, coinciding with the peak activity of the bees (H. Koch, C. Corcoran, M. Jonker, pers. obs.), for two days. The numbers of bees, ants and mealybugs were averaged over all four of these observations per segment. The exact number of mealybugs present was difficult to assess, therefore only the number of adult females visible with the aid of a hand lens, was counted as an estimate. The length of the pathway was measured as the shortest distance along branches from the ground to a particular mealybug assemblage. Mealybugs were mostly clustered around the bases of both existing and newly emerging leaves, where they gained access to the phloem with their proboscis. To approximate resource availability for mealybugs, we counted the number of leaves for each branch segment.

To assess the temporal variation of ant activity of the different ant species on the tree, the number of ants crossing a line around the trunk of the tree at 1.5 m height was counted for 5 minutes every hour starting at 4:25 until 19:25 and again at 22:05 on four consecutive days. Since no ants were observed nesting in the tree itself, this provided an estimate of the relative numbers of ants foraging for honeydew at different times during the day. The ambient temperature was recorded using a digital thermometer within a shaded crevice of the tree.

Statistical analysis

Relationships between the different variables were assessed with Spearman rank correlations calculated using Minitab® (Release 13.32) statistical software. A scatter plot of the density of ant and stingless bee individuals against the pathway distance was produced and trendlines were fitted to the data points via a nonlinear regression assuming a logistic population growth model ($b1/1 + \exp(b2 + b3 \times x)$) in IBM SPSS Statistics 19 (2010).

RESULTS

General observations

Liotrigona madecassa and *L. mahafalya* were observed landing on mealybug assemblages on the study tree and ingesting excess honeydew. No specific behaviour by the bees to stimulate honeydew production by mealybugs was observed. Bees were most abundant in the morning and late afternoon with more than one hundred individuals visiting the tree simultaneously during observation times. Bee activity ceased completely towards midday and at night. Two ant species, *Monomorium destructor* and *Paratrechina longicornis,* were observed foraging on honeydew at the same time as the bees. *M. destructor* was the most abundant of these ants on the observed mealybug units with 708 individuals out of 734 ants counted in total (96%). Figure 1 shows the activity of *M. destructor* and *P. longicornis* during the course of the day on the study tree. *P. longicornis* appeared to be crepuscular, with highest activities during dusk and dawn and no activity from 10:00 to 15:00. By contrast, *M. destructor* was more active towards midday and showed reduced activity during the night. Accordingly, the activity of *M. destructor* was

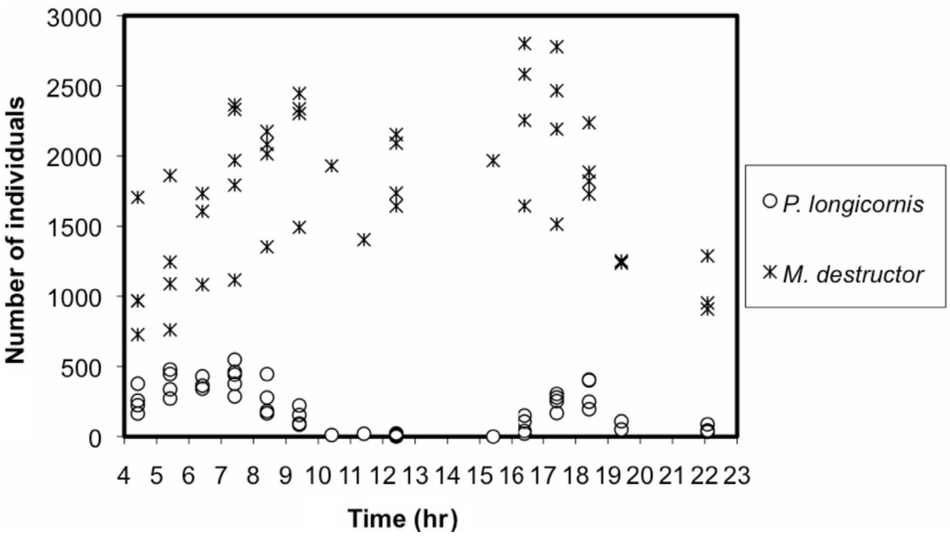

Fig. 1. Diel activity of *Paratrechina longicornis* and *Monomorium destructor* on the studied tree as measured by number of individuals crossing a line around the tree trunk in five-minute intervals, counted on four consecutive days.

positively correlated with temperature (Spearman rank correlation, $r = 0.569$, $P < 0.001$, $n = 44$), while *P. longicornis* exhibited a negative correlation ($r = -0.535$, $P < 0.001$, $n = 44$). The native ant species, *Camponotus gouldi* and *C. maculatus,* were also observed collecting honeydew from the same tree in low numbers, albeit only during the night; no data were collected for these species.

Ant/bee interaction

Results of a Spearman rank correlation analysis for ant, mealybug and bee abundance and the pathway distance are summarized in Table 1. Ant and mealybug abundance were positively correlated and both were highly negatively correlated to pathway distance. Number of leaves however had no effect on mealybug abundance figures ($r = -0.037$, $P = 0.885$, $n = 18$). Bee abundance was negatively correlated with the presence of ants and was not significantly correlated with the presence of mealybugs or pathway distance.

Table 1. Spearman rank correlation of the relationship between the variables measured, *i.e.* ants, mealybugs, bees and the pathway distance ($n = 18$).

	Ants	Mealybugs	Bees
Mealybugs *r*	0.846***		
Bees *r*	–0.494*	–0.18	
Pathway *r*	–0.868***	–0.813***	0.335

*$P < 0.05$; ***$P < 0.001$.

An exponential decrease of ant abundance per mealybug with distance, and a concurrent increase in bee numbers to a plateau was noted (Fig. 2). Bees almost exclusively visited the outermost mealybug assemblages, while ants were only found close to the trunk.

DISCUSSION

We present the first evidence of honeydew collecting by Malagasy stingless bees and suggest that honeydew might be an important part of their diet, especially when floral resources are rare. This might be of particular importance because of the highly seasonal nature of the environment in the western Malagasy dry forests (Sorg & Rohner 1996), where flowers are only available during part of the year. Even in the presence of many flowers, Brooks & Michener (1988) report that *Liotrigona mahafalya* was rarely seen visiting flowers, although being a generally abundant species in their study area. This observation could potentially be explained by a preferential exploration of non-floral resources by *L. mahafalya.*

Unlike previously reported cases of ant-mealybug mutualisms (*e.g.* Way 1963), we did not observe the bees stimulating the release of honeydew in the mealybugs by a specialized behavioural interaction, but rather observed them feeding on excess honeydew around the mealy-

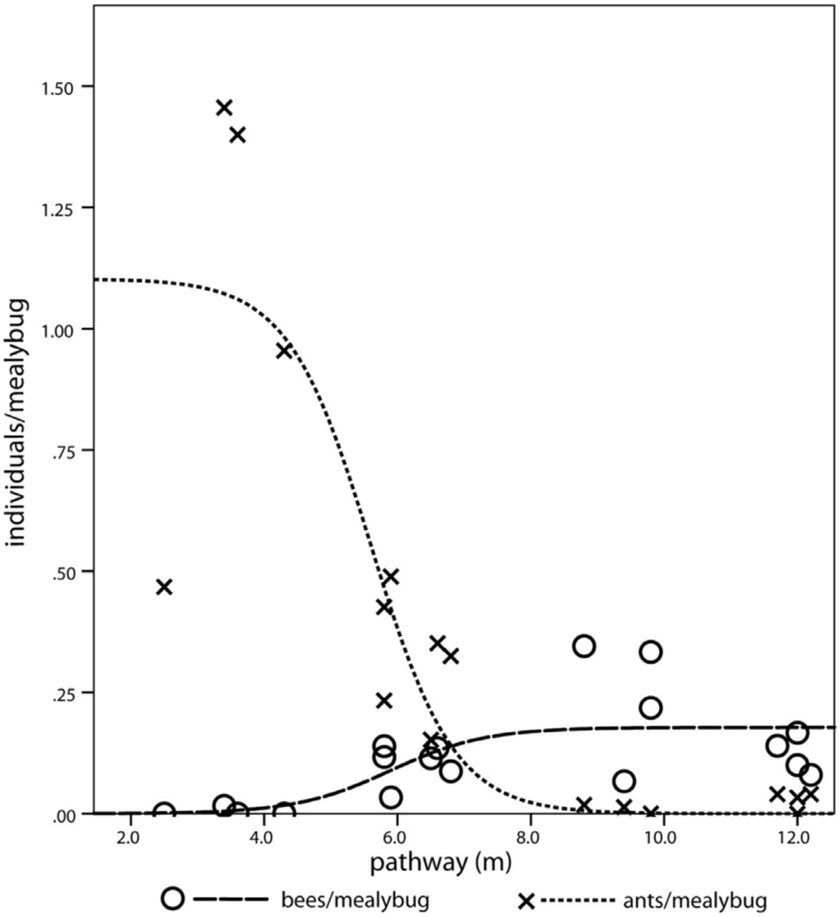

Fig. 2. Relative abundance of bees and ants per mealybug in relation to pathway distance (m); a logistic model was fitted to both sets of data, (bees/mealybug: $y = 0.178/(1 + \exp(8.253 - 1.4 \times x))$, $r^2 = 0.461$; ants/mealybug: $y = 1.103/(1 + \exp(-9.012 + 1.608 \times x))$, $r^2 = 0.785$).

bug colonies; this indicates that the bees may be opportunistic feeders on this resource. Further research is needed to determine the importance of honeydew for the different species of stingless bees in Madagascar.

Optimal foraging theory suggests that individuals try to maximize their net energy intake (MacArthur & Pianka 1966). In order to minimize energy costs related to the distance covered to the honeydew resource, we expected to find more ants congregated at the mealybug assemblages next to the trunk of the tree and closer to their nests, than at distal sites. We indeed observed this negative association between ant abundance and pathway length. The strong correlation of mealybug abundance with ant abundance rather than with potential resources for the mealybugs, as measured by the number of available leaves, also hints at a symbiotic relationship between these two groups of organisms. Such a relationship has been reported before (*e.g.* Schultz & McGlynn 2000) with the ants protecting the mealybugs from predators or parasites in return for food.

The negative association between ants and bees suggests that the ants are potentially outcompeting the bees at the food sources, with the bees only visiting the ephemeral small mealybug colonies that are located distally from the main trunk and visited less regularly by the ants. Both ant species and the two casually observed species of *Camponotus* ants were also collecting honeydew at night (Fig. 1), thereby potentially further depleting the honeydew resources available to the diurnal stingless bees.

Both *M. destructor* and *P. longicornis* are strongly invasive ant species that have spread around the world in the tropics and subtropics and are present throughout Madagascar (Fisher 2003; Wetterer 2008, 2009), with *P. longicornis* having been long-recorded from Kirindy and *M. destructor* probably being a recent invader (Olson & Ward 1996). Invasive ants are known to threaten native ant species by monopolizing exudate-producing food sources (Oliver *et al.* 2008) The invasive Argentine ant, *Linepithema humile,* has also been observed to compete with honey bees for nectar and displace them from flowers in South Africa (Buys 1987; Lach 2008). Similarly, in the light of our findings and because of their widespread occurrence on the island, these invasive ants might present a potential threat to the endemic stingless bees of Madagascar in reducing the honeydew resources available to them. Since we are only reporting an isolated case from a single tree, further studies are needed to assess if this displacement of stingless bees by invasive ants occurs more frequently. Additionally, since we were unable to identify the mealybug species observed in this study, the possibility remains that the mealybug was itself invasive, and therefore the observed interactions between stingless bees and mealybugs might not be part of the natural foraging behaviour of *Liotrigona* spp. To date both species of invasive ants seem to be restricted to disturbed habitats in Madagascar as they are in other parts of their introduced range (Fisher 2003; Wetterer 2008, 2009). The tree used in our study was also not in the undisturbed forest of Kirindy, but in the anthropogenically influenced grounds of the CNFEREF field station. Yet, considering the extremely high degree of destruction of natural habitats in Madagascar (*e.g.* only 3 % of the original dry deciduous forests in Western Madagascar remain (Ganzhorn *et al.* 2001)) and the potential of both invasive ant species to invade even undisturbed habitats in the future (Wetterer 2008, 2009), a threat to native stingless bees appears possible.

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