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Plasticity of stingless bee *Melipona fuliginosa* Lepeletier to obtain food resources in Amazonia

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Abstract

The stingless bee *Melipona fuliginosa* Lepeletier is described as being aggressive robber, but there is little information about its raids. Here, we describe two different raids of *M. fuliginosa* on other *Melipona* species: *Melipona paraensis* Ducke and *Melipona fasciculata* Smith. The robbing behavior was observed in the Volta Grande do Xingu region (Pará) and Carajás National Forest (Pará), and the attacks by *M. fuliginosa* occurred at the end of the dry season, shortly before the start of the rainy season, a time of flower scarcity. The raid on *M. paraensis* hive lasted five days and involved no deaths of worker bees of both species; the robbers collected honey and wax. During the pillaging, *M. fuliginosa* workers dedicated themselves exclusively to this task; their flight activity peaked between 8:00 a.m. and 12:00 p.m. but lasted until 6:00 p.m, which is atypical for the species. The raid on *M. fasciculata* differed from the other event because it led to the extermination of all forager workers of five colonies, however, the brood combs as well as the callow workers were preserved; the robbers collected honey and wax. *M. fuliginosa* attack defensive and non-defensive colonies, the events can cause severe damage and may lead to death of the victim colony in natural conditions. Flight activity varies from foraging on flowers during dawn to all day long robbing, showing considerable plasticity to obtain food resources. Robbing behavior could be associated to flower scarcity and artificial feeding.

Introduction

Fights between social insect colonies are common in nature (Sakagami et al., 1993; Gloag et al., 2008; Breed et al., 2012; Cunningham et al., 2014; Grüter et al., 2016), and tend to be motivated by two main reasons: robbing of food from inside the nests and robbing of the entire stock of food, including the nesting site (Cunningham et al., 2014; Grüter et al., 2016). Such fights between colonies vary considerably in terms of mortality; they can generate from few to thousands of victims, and the conflicts can last hours, days or even weeks (Sakagami et al., 1993; Grüter et al., 2016).

Among the approximately 500 species of stingless bees (Meliponini) (Michener, 2013), several have developed robbing or usurpation behavior (Roubik, 1989; Michener, 2007). There are species of exclusive robbers, such as those in the genera *Lestrimelitta* and *Cleptotrigona*, and this behavior is known as cleptobiosis (Nogueira-Neto, 1997; Michener, 2007; Breed et al., 2012). These species do not collect nectar and pollen from flowers but take these resources from the stock inside the nest of other species. There are also facultative robber species (facultative cleptobiotics) that normally forage on flowers but occasionally invade colonies of other species to steal their food storage. This is the case for species such as *Melipona fuliginosa* Lepeletier (Nogueira-Neto, 1997; Camargo & Pedro, 2008), *Trigona spinipes* (Fabricius), *Trigona hyalinata* (Lepeletier) and *Oxytrigona* spp. (Nogueira-Neto, 1997). Finally, there are species whose main objective during attacks is nest usurpation, and these take over all the stock as well as the nest, as in the case of *Tetragonula hockingsi* (Cockerell) (Cunningham et al., 2014) and *Tetragonisca angustula* (Latreille) (Sakagami et al., 1993).

Although fights are common and have serious consequences for bee colonies, little is known about the robbing strategies employed to acquire resources in Meliponini, especially in the case of facultative robber species (Grüter et al., 2016) such as *M. fuliginosa*. *M. fuliginosa* bees are widely distributed through the Neotropics, from the Amazonian region to the Atlantic Rain Forest in Brazil, reaching northern Argentina; they are robust eusocial bees, the largest of the genus *Melipona*, with approximately 15 mm in length (Camargo & Pedro, 2008). They are predominantly black in color and nest inside the trunks or branches of live trees (Roubik, 2006; Camargo & Pedro, 2008).

In the literature, *M. fuliginosa* has been described as an aggressive robber bee (Nates-Parra, 1995; Nogueira-Neto, 1997; Roubik, 2006; Camargo & Pedro, 2008). The formation of mixed colonies with *Melipona fasciata* Latreille has been reported (Roubik, 1981), however, such studies do not provide details of how such events occur.

Here we describe raids by *M. fuliginosa* on two other congeners: *Melipona paraensis* Ducke and *Melipona fasciculata* Smith. *M. fasciculata* is a relatively large and defensive bee, measuring approximately 12 mm. *M. paraensis* is a less defensive species of medium size, approximately 10 mm long. Both species have overlapping distribution with *M. fuliginosa* in the Amazon region (Camargo & Pedro, 2013).

Similar to *M. fuliginosa*, *M. paraensis* and *M. fasciculata* nest in preexisting cavities in the trunks and branches of live trees. In contrast with *M. fuliginosa,* which is not adapted for rearing in rational bee hives (Roubik, 1981; Nogueira-Neto, 1997), *M. paraensis* and *M. fasciculata* are commonly reared for honey production in the Amazon (Cortopassi-Laurino et al., 2006; Venturieri et al., 2012).

Materials and Methods

Study period and site

We observed *M. fuliginosa* raids on *M. paraensis* and *M. fasciculata* colonies in two distinct sites, as follows.

Volta Grande do Xingu region, Pará

The first observation was done in a meliponary located at the margin of the Xingu River, Pará Brazil (3°22’24.3” S, 63°56’25.8” W). This meliponary received wildlife rescue colonies following deforestation for the installation of the Belo Monte hydroelectric plant. The predominant vegetation at the site was a mosaic of “igapó” (blackwater-flooded) forest, dryland forest, “capoeira” (secondary forest) and abandoned pasture (Salomão et al., 2007). According to the Köppen classification, the local climate is equatorial *Am* and *Aw* type, with an average temperature of 26 °C and annual rainfall of approximately 1,680 mm, which is concentrated between December and May (Alvares et al., 2013).

Serra dos Carajás, Pará

The second observation of robbery was done in the meliponary of the Instituto Tecnológico Vale, Desenvolvimento Sustentável – ITVDS, Carajás National Forest, Pará, Brazil (6°2’57.87” S, 50°4’51.46” W), located in a matrix of primary open ombrophilous forest (Zappi, 2017). According to the Köppen classification, the climate of the Carajás National Forest region fits within type *AWi* (Alvares et al., 2013). Temperatures are always above 18 °C with averages between 23 °C and 25 °C. The rains are concentrated between December and April.

Robbery record number 1
M. fuliginosa vs *M. paraensis*

This raid was identified at 2:00 p.m. on November 19, 2015, during the daily inspection of the meliponary, at which point we began to record data on the workers who entered and left the *M. paraensis* colony as well as the *M. fuliginosa* colony. We counted the total number of workers going in and out for five minutes every hour from 6:00 a.m. to 7:00 p.m., that is, from sunrise to sunset. We also observed whether there was aggressive behavior (dead bees inside and in front of the hive, or bees biting and grabbing one another). The observations were carried out for five days until the phenomenon stopped. For each day of observation, we compared the number of *M. fuliginosa* workers entering and leaving the robbed colony as well as entering and leaving their own colony. Because our data did not follow normal distribution (Shapiro-Wilk, $p < 0.05$), we used Kruskal-Wallis test. We used R studio software (RStudio Team, 2016) for statistical analysis.

Colonies observed

M. paraensis: a colony found in a deforested area in a “cajá” (*Spondias mombin*, Anacardiaceae) tree trunk. The trunk containing the colony was transported to the meliponary and was transferred to a beehive one month prior to the attack. At the time of the raid, the colony exhibited three combs of approximately 8 cm in diameter (the pupae had already emerged from the transferred combs). There were approximately 40 food pots, most of them containing honey. There were enough workers to perform the tasks of the new colony, but they had not yet delimited the entrance to the colony, which is typically the width of a worker’s thorax. Thus, the entrance to the beehive was maintained with an opening of approximately 10 mm, although the workers built a six-centimeter-long internal entry tube.

M. fuliginosa: a colony in its original substrate (“acapu” trunk, *Vouacapoua americana*, Fabaceae) that had been rescued from a deforested area four weeks earlier. Through the opening at the top of the hollow trunk, one could see no sign of Phoridae flies (*Pseudohypocera* sp.) and that there were

pollen (most of the pots) and honey pots (three in the upper part). Due to the nest being in a good state and the fact that the species does not adapt well to beehives (Nogueira-Neto, 1997), we chose to keep the colony in the original trunk. This colony was approximately 100 m from the *M. paraensis* colony.

Both colonies (*M. paraensis* and *M. fuliginosa*) as well as the other colonies in the meliponary were given supplemental food (100 ml of 50% sugar syrup) two to three times per week following rescue. The two colonies were new to the place, which already contained other colonies of different species of *Melipona* and other Meliponini genera.

Robbery record number 2
M. fuliginosa vs *M. fasciculata*

We identified this raid a few days after its occurrence during routine inspection of the meliponary on November 4, 2017 (visits were performed every month). In this case, we were able to evaluate the damage caused by *M. fuliginosa* in five colonies of *M. fasciculata.* The attack was inferred based on the observation of dead *M. fasciculata* and *M. fuliginosa* workers on the ground in front of the hives, as well as by comparing the status of the colonies with the previous month's observations from photographic records taken periodically.

Observed colonies

M. fasciculata: five colonies in an intermediate state for the species, all containing five to six brood combs measuring 8–12 cm in diameter and approximately 20 honey and pollen pots in the upper part of the nests (beehive model; Venturieri, 2004) as well as workers foraging, cleaning and guarding as usual. The colonies received approximately 200 ml of 50 % sucrose syrup every two weeks.

M. fuliginosa: wild colony established in a tree in the surrounding forest, so we could not determine the status of the robber colony.

Results

M. fuliginosa vs *M. paraensis*: Description of robbing behavior

From the first day of observation, the number of *M. fuliginosa* workers entering the *M. paraensis* colony increased, reaching a peak on the third day, and then decreased, reaching values close to zero on the fifth day and fully ceasing on the sixth day (Fig 1). On all observation days the robbing occurred from 7:00 a.m. until around 5:00–6:00 p.m., when it ceased altogether. Except for the first and fifth days, the activity peaked between 8:00 a.m. and 12:00 p.m. and decreased after that. The number of workers of *M. fuliginosa* entering and leaving the colony of *M. paraensis,* as well as the number of workers leaving and entering the *M. fuliginosa* colony was statistically equal during all observation days (H(3) = 3.63–0.50, p > 0.30) . Therefore, we conclude that the flow was constant; that is, for each worker entering the colony, another left carrying material from the colony. Likewise, the number of workers leaving and entering the *M. fuliginosa* colony was statistically equal to that of workers entering and leaving the *M. paraensis* colony, indicating that during the days of robbing, all the foragers of the *M. fuliginosa* colony were dedicated to that task.

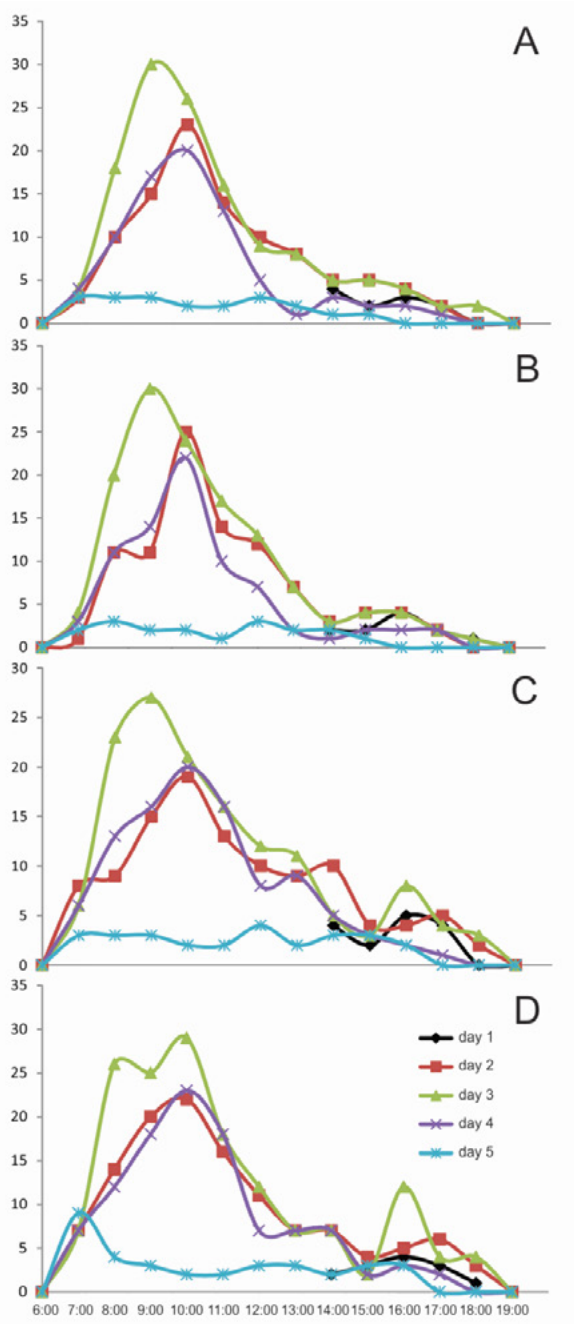

Fig 1. Flight activity of *Melipona fuliginosa* during the robbing of an *Melipona paraensis* colony. (A) *M. fuliginosa* workers entering the *M. paraensis* colony. (B) *M. fuliginosa* workers leaving the *M. paraensis* colony. (C) Workers leaving the *M. fuliginosa* colony. (D) Workers returning to the *M. fuliginosa* colony. There were no statistical differences among A, B, C and D (H(3) = 3.63–0.50, p > 0.30).

From the moment when we realized that the raid was taking place and throughout the observation period, we noticed that the behavior of the *M. paraensis* colony changed. The workers of this species were no longer guarding the entrance, leaving it free for the *M. fuliginosa* workers to access without any kind of reaction. Likewise, there was no internal fighting or reaction on the part of *M. paraensis*, and there were no dead bees or any bees grabbing each other in front of the nest, as is typical in attack situations. During the days of the robbery, most *M. paraensis* workers were concentrated on the walls or at the bottom of the beehive or on the brood combs; the mother queen was not killed. There were also no foraging or flights to remove garbage from the colony, and egg-laying process was also interrupted. It is important to note that although this colony was not very populous (we had found other colonies of the same species that were very populous), the bees foraged and cleaned the nest normally before the robbing, considering what is commonly observed for the species. This led us to hypothesize that the attack by *M. fuliginosa* somehow changed the behavior of the *M. paraensis* workers. The robbing behavior consisted of stealing honey and wax from the food pots, and on the sixth day, after the robbing had ended, the *M. paraensis* workers resumed garbage removal as well as foraging flights and guarding the nest entrance. Feeding and general care enabled the colony to recover.

Fig 2. Upper left: *Melipona fuliginosa* and *Melipona fasciculata* workers dead, grabbing one another. Center left: decapitated *M. fasciculata* worker. Lower left: decapitated *M. fuliginosa* worker. Upper right: *M. fasciculata* colony one month before the robbing. Lower right: the same colony after robbing showing empty pots.

M. fuliginosa vs *M. fasciculata*: Robbery description

On the ground in front of the five *M. fasciculata* colonies, there was evidence of a fight between this species and *M. fuliginosa*. Many headless sets of thoraxes and abdomens of *M. fasciculata* workers were found in front of the hives along with whole and parts of bodies of *M. fuliginosa* in a ratio of 10.5:1. Workers of the two species were also found grabbing each other (Fig 2). After the attack, the *M. fasciculata* colonies predominantly had workers that still could not fly and few forager workers (compared to the previous month). This, together with the bodies of dead bees in front of the hives, indicated that the entire population of adult bees of all colonies had been killed during the attack by *M. fuliginosa*. Internally, all the honey and part of the wax of the pots had been robbed from the *M. fasciculata* colonies, and only the non-flying workers, the brood combs and a portion of the empty pots remained in the colony. Only one colony was infested by Phoridae larvae after the attack. Control of Phoridae with vinegar traps (Nogueira-Neto, 1997), replacement of the bottom of the beehive, and supplementary feeding allowed the colonies to recover.

Discussion

Apparently, the type of attack by *M. fuliginosa* depends on the reaction of the target bee colonies. In the case of *M. paraensis*, the workers did not present defensive behavior, which represented an advantage for the colony because there was no worker mortality, while the defensive behavior of *M. fasciculata* workers resulted in a violent attack, causing the death of the entire population of guards and forager workers of five colonies. This observation demonstrates that the diversity of robbing behaviors varies not only among species (Grüter et al., 2016) but also within the same species when attacking different species, as previously observed on *Lestrimelitta* raids (Sakagami et al., 1993).

In the case of the obligate cleptobiotic bee *Lestrimelitta*, species phylogenetically closer to it are more frequently victims of raids (Sakagami et al., 1993; Quezada-Euán et al., 2013). Moreover, phylogenetically closer species had less aggressive response to the presence of cleptobionts, due to the similarity of cuticular hydrocarbons (Quezada-Euán et al., 2013). That could be also a plausible explanation for the pacific occupation of the *M. paraensis* colony, because *M. fuliginosa* and *M. paraensis* (both in *Michmelia* subgenus) are phylogenetically closer to each other than to *M. fasciculata* (*Melikerria* subgenus) (Ramírez et al., 2010; Camargo & Pedro, 2013). The non-defensive response of *M. paraensis* could be related to the similarity of cuticular hydrocarbon profile of *M. fuliginosa* or to the fact that the attacked colony was already in weakened condition. Pheromones could also be involved, although we did not recognize any smell, such as citral or related substances, known to occur in cleptobiotic *Lestrimelitta* (Sakagami et al., 1993). However, we saw workers of *M. fuliginosa* raising the abdomen and fanning the wings inside the *M. paraensis* nest as well as at the entrance, outside the nest, as described for *Lestrimelitta* raids (Sakagami et al., 1993).

In both observed raids, *M. fuliginosa* bees robbed honey and wax from the pots, differently than *Lestrimelitta*, which takes also stored pollen and larval food (Sakagami et al., 1993). The attacks discussed here occurred in the same period, in the late dry season shortly before the onset of the rainy season, when there is a shortage of flowers. The rainy season is known to be a period of resource scarcity for the stingless bees of the Amazon region (Marques-Souza et al., 1996, 2007). Thus, in both situations, food scarcity could be a possible trigger for the robbing behavior in *M. fuliginosa*. In addition, the artificial feeding and the management of the colonies could have helped to attract the raids.

Flower scarcity has also been associated to violent robberies practiced by *M. fuliginosa* on *Apis mellifera* L. hives (Nates-Parra, 1995). Beekeepers in the region of Santander (Serra Andina) and the Llanos (Amazon lowlands) have reported the decapitation of individuals and robbing of whole colonies of Africanized bees by *M. fuliginosa* (Nates-Parra, 1995). In the present study, we observed the simultaneous attack of five *M. fasciculata* colonies, which certainly required the mobilization of a large number of *M. fuliginosa* workers. As we observed in the attack on the *M. paraensis* colony, all the forager workers of the *M. fuliginosa* colony were involved in the robbing, and this was the only activity carried out by the colony during the pillaging period.

In addition, the flight activity of the *M. fuliginosa* colony changed considerably during the robbery period. Normally, the workers of this species forage in the early hours of the morning, interrupting or considerably reducing their flight activity after 7:00 a.m. (Cortopassi-Laurino et al., 2007). However, as observed here, the flight activity of *M. fuliginosa* extended throughout the day during robbing and was concentrated between 8:00 a.m. and 12:00 p.m., which was different from its normal rhythm.

This change in flight activity due to robbing could explain the sudden change in the flight activity of *M. fuliginosa* observed by Cortopassi-Laurino et al. (2007). They found the peak flight activity of workers to be at 6:00 a.m., but the activity peak changed to 12:00 p.m. during one of the observation days. This change occurred in the last month of the dry season (which is in October in Xapuri, Acre, Brazil), the same environmental conditions recorded for the two raids described hereby.

The raids presented here also help to clarify what Roubik (1981) considered to be a natural mixed colony of *M. fuliginosa* and *M. fasciata*. He wrote that the brood chamber was composed of *M. fasciata* pupae and brood combs containing larvae and eggs laid by a physogastric queen of *M. fuliginosa*. The *M. fasciata* physogastric queen was not found

in the colony. Workers of *M. fasciata* coexisted pacifically with *M. fuliginosa* and kept working normally for the colony. This mixed colony was probably a *M. fasciata* colony invaded by *M. fuliginosa*, not for robbing food and wax but for nest usurpation. It seems clear that a former *M. fasciata* colony was gradually becoming a *M. fuliginosa* colony. However, the author considered it was the opposite.

As well as *M. paraensis*, *M. fasciata* belongs to the *Michmelia* subgenus, indicating again correlation between phylogenetic closeness to *M. fuliginosa* and less defensiveness against its raids. This observation is in accordance with the less defensive behavior of phylogenetically related species to the raids of *Lestrimelitta* (Quezada-Euán et al., 2013).

Comparing the results discussed here as well as the literature reports and the review by Grüter et al. (2016), we can conclude the following: attacks by *M. fuliginosa* are highly organized because the whole colony can be involved in the attack. The species can attack a single sparsely populated colony as well as five sparsely populated colonies simultaneously, the latter case being certainly equivalent to attacking a very populous colony. The attacked colonies did not have high-quality stocks because most of the stocked honey was from sugar syrup. *M. fuliginosa* attacks both non-defensive and defensive colonies and may steal resources or usurp nests. Its attacks cause severe damage to the target colonies and could lead to death in natural conditions. Flight behavior varies from foraging on flowers during dawn to all day long robbing, showing considerable plasticity to obtain food resources. Flower scarcity could be a possible trigger of robbing behavior in *M. fuliginosa*.

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Authors' Contribution

LC, JSGT and UMM were responsibly for fieldwork and data sampling as well as manuscript writing. LC performed Statistical analysis. VLIF revised and improved the manuscript with suggestions.

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