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Foraging Distance of *Melipona subnitida* Ducke (Hymenoptera: Apidae)

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Abstract

The current study aimed at estimating the maximum foraging distance of the stingless bee *Melipona subnitida* Ducke by comparing the efficacy of two methods: training of workers with an artificial feeding source and the capture-recapture technique, which consisted at marking bees that were released at different distances from the nest, after which the number of bees that returned to the colony was recorded. Under the training method, the mean foraging distance of the three colonies studied was 1,120 m and maximum foraging distance of 1,160 m. Yet the number of recruits and reactivated foragers for each colony were quantified, the average maximum distance until recruitment occurred was 886,66 m. In the capture-recapture method, the maximum flight distance of captured foragers ranged from 3,600 to 4,000 m, which was 2,700 m farther than the maximum flight distance recorded using the artificial feeding method. Therefore, we verified that *M. subnitida* is a species that can travel long distances in search for food. Our results also suggest that an abundance of resources near the nest can reduce its foraging area.

Introduction

Bees are primary pollinators in most regions of the world (Bawa, 1990; Silberbauer-Gottsberger & Gottsberger, 1988). Their flight range strongly influences the sexual reproduction of most flowering plants and can further determine the genetic structure of plant populations (Campbell, 1985; Waser et al., 1996). The distance that bees travel in search of a resource can directly affect agricultural crops, given that bee pollination is necessary to generate 30% of the human food supply (Slaa et al., 2006).

To increase the efficiency of collection and exploitation of good resources (Kerr, 1994; Contrera & Nieh, 2007), eusocial bees developed a sophisticated communication system that allows foragers to recruit other bees to profitable food sites (Lindauer & Kerr, 1960; Kerr, 1969; Wille, 1983; Jarau et al., 2000; Nieh, 2004; Aguilar et al., 2005). To save time and energy, bees do not forage over long distances unnecessarily (Frisch, 1967; Seeley, 1994). For example, in the summer, when there is a decrease in the food supply near the nest, bees of the genus *Apis* may use an area 6 to 22-fold larger than the area used during spring or fall (Couvillon et al., 2014).

The methods that have been most commonly used for the study of the maximum flight range of honey bees in general, and stingless bees in particular, include training foragers to feed from artificial feeders, and the marked forager capture-recapture method (Zurbuchen et al., 2010).

The use of artificial feeders to train forager workers makes it possible to train them to the maximum distance that a species may travel in search of food. In this test, the workers that reach the feeder to collect a food sample are marked with a specific color or number combination, usually on the thorax or abdomen (Seeley, 1995). Measuring the maximum foraging distance for each stingless bee species provides information related to the communication and recruitment techniques used by stingless bees to obtain food in response to their environment (Contrera & Nieh, 2007; Kuhn-Neto et al., 2009).

The capture-recapture method involves the release of previously marked workers at a given distance from the mother colony, and then counting the number of marked bees that return to the colony thereafter (Roubik & Aluja, 1983). According to Kuhn-Neto et al. (2009), this method may be less efficient when the workers are released in remote areas that they are not familiar with. Despite a potential loss of foragers that may get lost in unfamiliar release spots, the number of bees that do return to the nest, it is possible to estimate the species' flight radius, which could possibly be greater than obtained with others methods, and provide more reliable information about the distances that bees travel in the community away from their colony to search for resources (van Nieuwstadt & Iraheta, 1996).

The current study aimed to estimate the maximum foraging distance of *Melipona subnitida* Ducke, a species distributed in the Brazilian States of Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe (Camargo & Pedro, 2013), while comparing the efficacy of two experimental methods: (1) training workers to visit an artificial feeder; and (2) capture-recapture (adapted from Roubik & Aluja, 1983). Foraging distance information is critical for understanding the scale at which bee populations respond to the landscape, assessing the role of bee pollinators in affecting plant population structure and planning conservation strategies for plants (Greenleaf et al., 2007).

Materials and Methods

Study area and colony selection

This study was conducted at "Ponta do Mangue" village (2º58'12"S; 42º79'56"W), which is located in the municipality of Barreirinhas along the eastern coast of the state of Maranhão, Brazil. The village is located within the National Park of Lençóis Maranhenses. The park covers a total area of 155,000 ha, of which 453.28 km^2 are covered by vegetation (Brazilian Institute of Environment and Renewable Natural Resources - IBAMA, 2002).

Within the area covered by vegetation, 405.16 km^2 are predominately composed of Restinga, term that represents a set of physiognomically distinct plant communities under marine influence. The species that colonize these areas are mainly from other ecosystems, but with phenotypic variations that differ from those expressed in their original environments (Freire, 1990). The restinga area has shrub species dominance, and herbaceous communities are also present in large areas surrounding lakes (Brazilian Institute of Environment and Renewable Natural Resources - IBAMA, 2002).

To test the efficacy of using artificial feeder and the capture-recapture methods to determine the flight range of *M. subnitida*, four colonies were selected from a meliponary consisting of natural nests and nest boxes kept at Ponta do Mangue village. Two *M. subnitida* colonies were used for both methods (i.e., "colony 1" and "colony 2"), while the other two colonies were used individually for each method (i.e., "colony 3" - artificial feeder and "colony 4" - capture-recapture). Strong colonies with a large number of workers (mean 890 foragers) and sufficient stored food were selected (mean of 115 pots food).

Artificial feeder method – Foraging distance

The experiments were performed in two different months: March 2013 and August 2013. In March, only the workers from colony 1 visited the artificial feeder. After the study with colony 1, which lasted five days, the same methodology was attempted with the other three colonies, though without success. The study continued in August with two other colonies (colony 2 and colony 3), thus totaling three colonies using the artificial feeder method. The weather in the days of study (March and August) did not differ (without rain), thus allowing for a comparison of the replicates.

An artificial feeder consisting of a flat acrylic disc with grooves from the center to the edge was used to evaluate foraging distances. A jar containing food (2.5M, 60%: 40% sugar: water concentration), with the opening facing downwards so that the food would drain, was placed in the center of the disc. Vanilla extract (9 µl/l) was added to the food to simulate floral odor and to increase the attractiveness of workers to the artificial food (Fig 1). The feeder was placed atop a tripod, which allowed for the adjustment of the height and horizontal inclination of the food supply (method described by Frisch, 1967; Nieh et al., 2003).

The first step of the experiment was to train the bees to visit the feeder. The feeder was placed right outside of the hive entrance and then moved a few cm away from the nest (thus, creating a food trail), so that when bees cleared the colony entrance, they tried the food and then followed the trail to reach the tripod with the artificial food source. Each worker that visited the feeder was marked with a dab of acrylic paint on their thorax with one color or a combination of specific

Fig 1. Feeder used to artificially train *Melipona subnitida* to a food source.

colors to differentiate them foragers from each other, as described in Seeley (1995). Foragers were classified as recruits or reactivated foragers. Recruits were those foragers that had never visited the feeder before and found the feeder on their own, while reactivated foragers were those that had fed from the feeder when it was placed in a previous location, for some reason had stopped visiting the feeder temporarily, but found it again later (Kuhn-Neto et al., 2009).

During the training process, when a minimum of 10 bees had visited the feeder and recruitment was in progress (i.e. when new foragers were recruited), the feeder was gradually moved away from the nest. To facilitate the forager's memorization of the new location, the feeder was moved only when workers were feeding. The feeder was always moved only after the first bee recorded at a specific distance left the feeder probably to unload her food sample at the nest, and later returned to the feeder for more food. The number of workers that visited the feeder was recorded every 20 m. If the total number of foragers decreased by 50% from the maximum number recorded previously, the feeder was not moved throughout the rest of the day. The next morning, the feeder was placed at the final location reached on the previous day, and remained at this location until the same number of foragers arrived as was recorded the day before. If the same number of foragers did not arrive within two hours, the feeder was moved to the next distance.

The experiments were performed daily during the period of natural foraging activity for *M. subnitida* (6 am – 5 pm) and ended when the workers stopped visiting the feeder. The experiments with colonies 1, 2, and 3 respectively lasted 56 h over 6 days, 33 h over 3 days, and 32 h over 3 days. Trial duration was determined by the maximum distance to which the colony could be trained.

The full path of the foraging range of each studied colony was classified as three distances: close foraging distance, average foraging distance and maximum foraging distance. The close foraging distance was defined as the distance from the colony's nest to the point where the number of foragers remained above the overall mean of visiting workers along the path during the experiment ($\bar{X}_{VF} = \frac{Tvw}{Ttp}$), where T_{vw} is the total number of visits by workers along the path, and T_{tp} is the total number of points where bees were recorded along the path, dividing these values, we obtain X_{VF} (the mean number of bees that visited the feeder). The average foraging distance was defined as the distance at which the number of workers fell below average to the last distance where workers were recruited. The maximum foraging distance was defined as the last point where occurred the foraging activities at the feeder.

Capture-recapture method – Flight radius

The capture-recapture experiment was performed in August 2013. Three *M. subnitida* colonies were used, two of which were also used for the feeder test (2.2). Workers (n = 150) were captured at the nest entrance and marked on the thorax with nontoxic paint of different colors, totaling 15 groups of 10 workers in each nest. Initially, 10 linear points were marked every 200 m starting at the colony's nest entrance, reaching a total distance of 2,000 m. From the 2,000-meter mark onwards, five more points were marked at a distance of 400 m apart from each other, reaching a total distance of 4,000 m. The distances at which the bees were released were measured from the colony entrance, and the points were located using a GPS device. The bees were released between 9 and 10 am, and the number of bees that returned to the colony was recorded to calculate the percent of successful return.

Workers were recaptured at the colony entrance by observing the bees that arrived. To do this, one researcher released the bees at the established distances away from the nest, while another researcher stood at the nest entrance, observing and quantifying the bees that returned to the nest until 6 pm. The nest was kept closed during the experiments, and was only opened when a new worker approached the nest to prevent the erroneous recounting of bees that had already entered the nest.

Statistical analysis

We performed linear regression between the total distribution of workers visiting the experimental feeders and the distance from the feeder to the colony to evaluate the effect of distance on foraging. We also made a linear regression on the number of recruits and reactivated foragers for each colony and distance (Zar, 1999). In addition, for each colony, the distances at which we measured 75%, 95% and 100% of foraging activity were estimated to reflect the percentage of active workers relative to the total number of workers within a certain distance.

To determine whether the number of workers that returned to the nest (as obtained through the capture-recapture method) differed between colonies, we used the non-parametric Kruskal-Wallis test. The relationship between the percentage of bees that successfully return to the nest and the distance at which they were released was assessed using a simple regression (Zar, 1999). We also used the Mann-Whitney test to assess the significance of the difference between the two methods used in the current study (artificial feeder vs. capture-recapture). All statistical analyses were performed using the Statistica 7.0 software with a critical P-value of 0.05 (Statsoft Inc., 2004).

Results

Foraging distance

Overall, *M. subnitida* foragers achieved a maximum foraging distance of 1,080 - 1,160 m and a maximum recruitment distance of 940 m. The mean foraging distances of the three colonies were as follows: close distance of 653 m, average distance of 863 m and maximum distance of 1,120 m (Table 1). The mean values for 75%, 95% and 100% of foraging activity were 566 m, 833 m and 1,120 m, respectively (Table 2). The number of workers found at each foraging distance is given in Fig 2 for each of the three colonies studied. Overall, the number of foragers trained and recruited to the artificial feeder decreased with distance away from the feeder.

The linear regression analysis of the relationship between the number of bees that visited the feeder and distance showed a strong negative correlation for the three studied colonies ($R = 0.67$; $p < 0.0001$), i.e., the greater the distance, the lower the number of foragers that visited the artificial feeder

Table 1. Foraging distances (m) calculated for the three colonies evaluated by the artificial feeder method. Data shown as averages and ± SD.

	Colony 1	Colony 2	Colony 3	Average/ SD
Close distance	740	600	620	653.33 ± 75.71
Average distance (Maximum recruitment distance)	900	940	820	886.66 ± 61.10
Maximum distance	1,160	1,120	1,080	1,120 ± 40.00

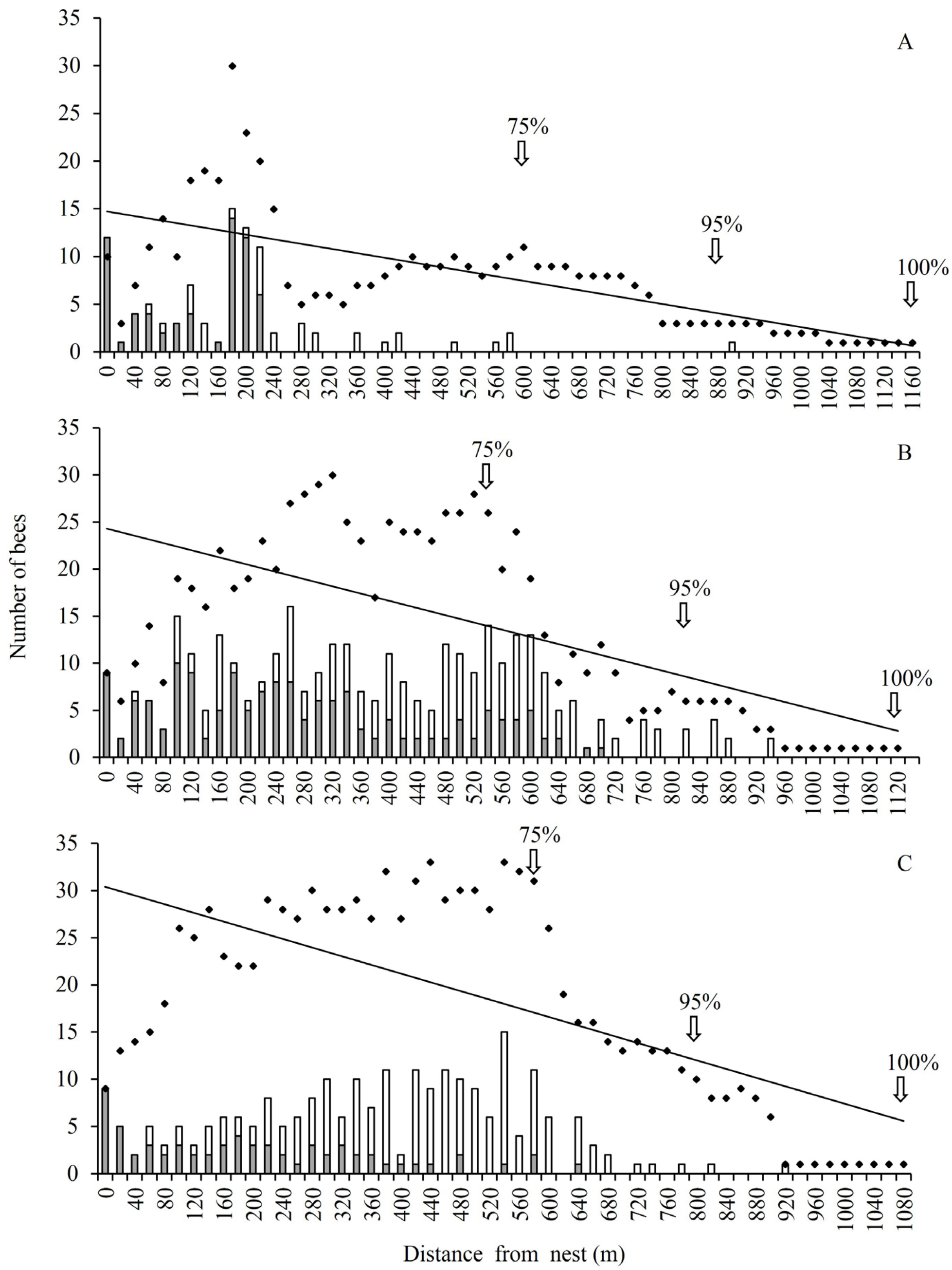

Fig 2. Total distribution of the number of *Melipona subnitida* foragers (black diamonds), recruits (grey bars) and reactivated foragers (white bars) that were observed at artificial feeders to which the bees were trained over time. Arrows indicate the distances defining the areas of 75%, 95% and 100% foraging activity (see Methods for details).

(Table 2). The correlation between the number of recruits and reactivated foragers and distance were also evaluated by linear regression for each colony. In all three colonies, both the number of recruits and the number of reactivated bees were negatively correlated with distance away from the nest (Table 2). Therefore, there was a decline in the number of recruits and reactivated foragers at more distant sites, compared to sites near the nest (Fig 2).

Table 2. Linear relationships between distance (m) and the number of *Melipona subnitida* workers that visited the feeder. In addition, distances that delimited the areas of 75%, 95% and 100% cumulative foraging activity. Data shown as averages and ± SD. A – total number of bees, B – recruits, C – reactivated workers.

	Colony	Linear relationship between distance and the total number of bees that visited the feeder	R	75%	95%	100%
A	1	y = 14.7203 - 0.0121x	0.70*	600	880	1,160
	2	y = 24.3987 - 0.0193x	0.66*	540	820	1,120
	3	y = 30.4169 - 0.023x	0.67*	560	800	1,080
	Avarege/ SD		0.67* ± 0.02	566,66 ± 30.55	833,33 ± 41.66	1,120 ± 40
B	Colony	Linear relationship between distance and the number of recruits	R			
	1	y = 3.5068 - 0.0042x	0.48*			
	2	y = 6.9074 - 0.0074*x	0.80*			
	3	y = 7.0013 - 0.0076*x	0.76*			
C	Colony	Linear relationship between distance and the number of reactivated bees	R			
	1	y = 1.3186 - 0.0013x	0.44*			
	2	y = 4.4289 - 0.0025x	0.27*			
	3	y = 4.3045 - 0.0021x	0.30*			

*p < 0.05 (significant)

Flight radius

The number of workers released by the capture-recapture method and the number of workers that returned to the nest were significantly different in all three colonies studied (Kruskal-Wallis n = 350; p = 0.0175). Thus, the data for the percentage of bees that returned to the nest were analyzed separately. The percentages of released bees that returned from different distances from the nest are shown in Fig 3. The correlation between the percentage of bees that successfully returned to the nest and the distance traveled, as evaluated by linear regression, was highly negative for all three colonies. Therefore, the number of bees that returned to the nest gradually decreased as the distance increased (Table 3). The maximum flight distance of *M. subnitida* measured by the capture-recapture method was 3,600 m for colonies 2 and 3, and colony 1 reached 4,000 m (Fig 3).

Table 3. Linear relationship between the distance (m) at which the *Melipona subnitida* workers were released by the capture-recapture method and the percentage of return to the nest. Data shown as averages and ± SD.

Colony	Linear relationship between distance and % of return	R	Flight radius
1	y = 9.7306 - 0.0022x	0.95*	4,000
2	y = 9.9095 - 0.0024x	0.89*	3,600
3	y = 11.0524 - 0.0022x	0.83*	3,600
Average/ SD		0.89 ± 0.06	373.33 ± 230.94

*p < 0.001 (significant)

Comparison of methods

The results obtained for the foraging distance of *M. subnitida* workers were very different between the two methods used. There was a highly significant difference between the maximum foraging distances obtained by the two methods (U < 0.0001; p = 0.04; Fig 4), with the maximum flight distance recorded in the capture-recapture method being approximately 2,700 m further than that observed in the artificial feeder method.

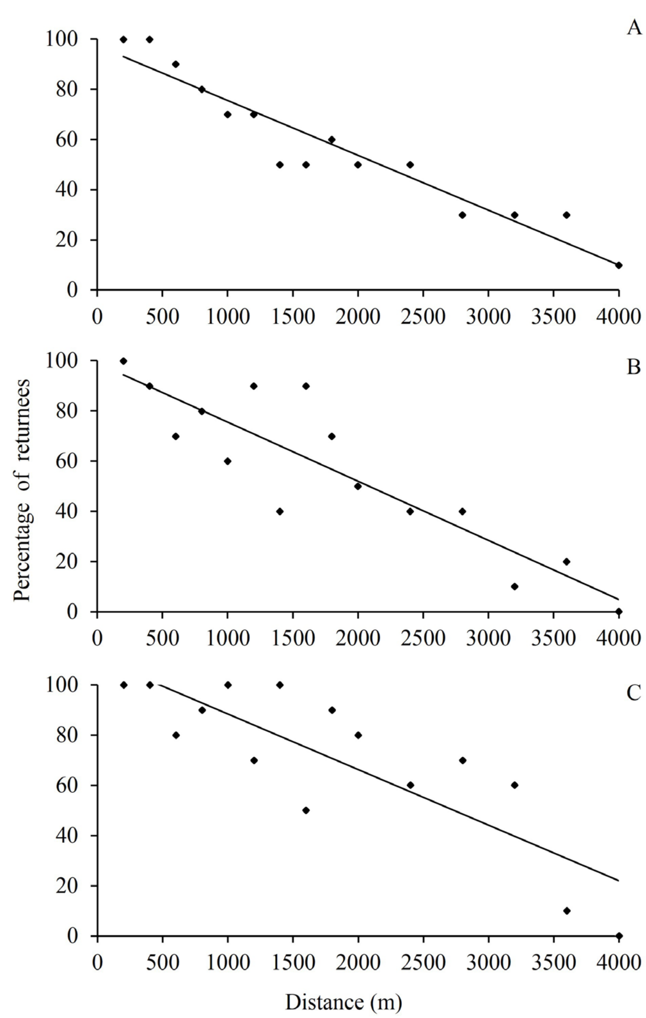

Fig 3. Percentage of returnees for each distance (m) at which the workers were released by the capture-recapture method: A – Colony 1, B – Colony 2, C – Colony 3.

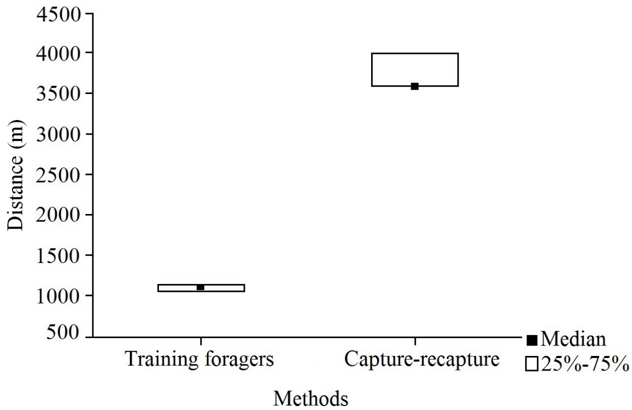

Fig 4. Comparison of the efficacy of two methods to determine the foraging distance of *Melipona subnitida* foragers: (a) training foragers to an artificial feeder, and (b) the capture-recapture method.

Discussion

Our results suggest that the mean foraging distance of *M. subnitida*, as obtained from the artificial feeder experiment, was approximately 1,120 m. This value was lower that reported by Kerr (1987) for *Melipona fasciculata* Smith (approximately 2,470 m) and that reported by Kuhn-Neto et al. (2009) for *Melipona mandacaia* Smith (1,800 m).

Interestingly, the three classifications of *M. subnitida* foraging distances revealed that the close foraging distance was approximately 653 m, indicating that at this distance, *M. subnitida* colonies have a greater ability to maintain a large number of foragers and a facilitated recruitment capacity. The close foraging distance is the distance within which the bees truly dominate a food resource and therefore have a higher probability of pollinating the plants where foragers (van Nieuwstadt & Iraheta, 1996). Considering the distance at which it is possible to recruit workers, which in our study we found to be 863 m on average, it is still likely to establish an effective control of the food source. Beyond this recruitment distance, it seems that it is possible for the foragers to find food, but they would probably have to explore it by themselves and potentially the exploitation of the food resource would be less efficient (Kuhn-Neto et al., 2009).

According to van Nieuwstadt and Iraheta (1996), more than 75% of a stingless bee colony's food-searching activity usually occurs within 40% of the maximum foraging distance. For *M. mandacaia*, 75% of the foraging activity (893.33 ± 11.54 m) occurred within corresponded to 50% of the maximum foraging distance (Kuhn-Neto et al., 2009). This is similar to what we observed for *M. subnitida*, in which 75% of the food-searching activity (566.66 ± 30.55 m) occurred within 51% of the maximum foraging distance in their Restinga environment. Therefore, it can be stated that the farther the colony is from the resource, the lower the number of interested or available foragers is, and consequently, the lower the recruitment of new workers to that food source.

One factor that may have been crucial to the smaller flight radius of *M. subnitida* is the large amount of flowering plants near the colonies. *M. subnitida* workers visit flowers of *Humiria balsamifera* (Aubl.) A. St.-Hil. and *Chrysobalanus icaco* L. to collect nectar. These plant species bloom almost all year round in the studied region; they exhibited high flowering when colony 1 was trained but less flowering during the experiments with colonies 2 and 3. Because other colonies did not follow the feeder in March, the experiment was resumed five months later. The results obtained in March and August were very similar. Therefore, it can be inferred that an abundant supply of a profitable nectar source near the nest decreased foraging and recruitment to an artificial site located at more distant locations.

The large food supply near the experimental colonies in March certainly influenced the number of bees of colony 1 that were recruited to the feeder. However, the foraging distance did not differ among the colonies. Although it was not possible to verify such influence (abundant food sources), workers could potentially be "discouraged" in the search for a farther food source simply because there were other abundant food sources near their nest. A study looking at the foraging ecology of *M. mandacaia*, a native bee from the Caatinga biome (Kuhn-Neto et al. 2009), found a larger foraging distance in that species than what we found in *M. subnitida*. The longer foraging distance of *M. mandacaia* may be in part because there is a marked reduction in the food supply in the Caatinga biome during the prolonged dry season, compared to the constant nectar flow in the Restinga region where our study was conducted.

In the current study, the distances traveled by *M. subnitida* were measured without analyzing other factors. For instance, the distances traveled by bees responsible for foraging activities depend on several factors, including density and seasonality of the food supply, species (Dornhaus et al., 2006), physiology, and body size (Imperatriz-Fonseca et al., 1985). Furthermore, other factors, separately or combined, may also affect flight radius, such as the internal colony conditions and climatic factors (Hilário et al., 2000). However, the days upon which the study was performed did not have any heavy rain and were thus favorable for the experiment because it is known that rain prevents or reduces bee activity (Hilário et al., 2007).

Furthermore, in Apoidea bees, body size may act as a limiting factor to the maximum flight capacity and therefore, maximum foraging distance (Araújo et al., 2004; Greenleaf et al., 2007; Kuhn-Neto et al., 2009; Zurbuchen et al., 2010). However, it is likely that many species actually exercise a lower flight capacity (i.e., occupy a smaller space) depending on other variables such as foraging, specialization in resource searching, navigation, abundance of food resources, and availability of nesting sites.

By using the capture-recapture method, the percentage of bees that returned to the nest was 80% if they were released within 1,000 m of their colonies. Roubik and Aluja (1983), released bees of the genus *Melipona* at different distances from the nest, and found that the mean flight radius of these bees is

2,100 m from the nest. The authors estimated the maximum flight radius for this genus using regression tests and concluded that it could be up to 2,400 m. Taking into account that Roubik and Aluja (1983) used the same method as that used in our study our results in the capture-recapture experiment exceeded the maximum distance conjectured by Roubik and Aluja (1983). This difference could be attributable to the fact that, in the current study, we waited until the end of the day for the return of the workers, while Roubik and Aluja (1983) waited just a few hours.

When comparing the two methodologies used in the current study, we observed that each technique has benefits and limitations. In the artificial feeder test, the foragers' flight range could have been underestimated because some bees got lost in the course of the experiment, or because the artificial food is less attractive than a natural flower, which may discourage the search for a food supply at long distances (van Nieuwstadt & Iraheta, 1996). In the capture-recapture test, by contrast, an overestimation of the actual flight distance could be possible because the released bees only needed to fly back to the nest. Alternatively, there may have been a smaller number of bees that returned to the nest after traveling greater distances, potentially because they became lost due to unfamiliarity with the environment where they were released and because the energy costs associated with orientation are high (van Nieuwstadt & Iraheta, 1996).

The advantage of the artificial feeder method over the capture-recapture method is that it can assess the distance that workers can travel, the number of bees they recruit at each distance as well as the exact gradual reduction in the number of workers along the path, which would be closer to the distance travelled by the bees under natural conditions (Kuhn-Neto et al., 2009). Nevertheless, even with the capture-recapture method, we can determine the distance at which the workers begin to return less successfully.

When an environment is fragmented, numerous aspects of the landscape ecology are affected, as the reduction of dispersion and potential colonization of plant species (Lovejoy et al., 1986; Bierregaard et al., 1992). We can infer that such fragmentation of the landscape may have interfered with our results given that most of the vegetation in the study site is concentrated near the meliponary and the region is surrounded by dunes. According to Roubik (1989), the behavior of bees is likely to be adapted to their environment and will also be determined by the "resource landscape," which includes aspects such as resource quality. Bees require a large area of vegetation to obtain food throughout the whole year and to nest in regions beyond the mother colony. As the Lençóis Maranhenses region is an area in constant flux due to the strong winds and the presence of dunes, the area covered by vegetation tends to decline (Gonçalves et al., 2003), thus resulting in an increase in the distance that *M. subnitida* must fly in search of food. The information related to the foraging distance of *M. subnitida* reported in the current study can thus help to promote strategies for the conservation of this species.

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