



Foraging and Drifting Patterns of the Highly Eusocial Neotropical Stingless Bee *Melipona fasciculata* Assessed by Radio-Frequency Identification Tags

OPEN ACCESS

Edited by:

Isabel Marques,
University of Lisbon, Portugal

Reviewed by:

M. N. Kuperman,
Bariloche Atomic Centre (CNEA),
Argentina
Jose Octavio Macias-Macias,
University of Guadalajara, Mexico
William G. Meikle,
Agricultural Research Service,
United States Department
of Agriculture, United States

*Correspondence:

Ricardo Caliri Oliveira
ricardo.oliveira@evobio.eu

†These authors have contributed
equally to this work

Specialty section:

This article was submitted to
Behavioral and Evolutionary Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 11 May 2021

Accepted: 15 July 2021

Published: 04 August 2021

Citation:

Oliveira RC, Contrera FAL,
Arruda H, Jaffé R, Costa L, Pessin G,
Venturieri GC, de Souza P and
Imperatriz-Fonseca VL (2021)
Foraging and Drifting Patterns of the
Highly Eusocial Neotropical Stingless
Bee *Melipona fasciculata* Assessed
by Radio-Frequency Identification
Tags. *Front. Ecol. Evol.* 9:708178.
doi: 10.3389/fevo.2021.708178

Ricardo Caliri Oliveira^{1*†}, Felipe Andrés León Contrera^{2†}, Helder Arruda^{3,4},
Rodolfo Jaffé^{4,5}, Luciano Costa⁴, Gustavo Pessin^{4,6,7,8}, Giorgio Cristino Venturieri^{9,10},
Paulo de Souza¹¹ and Vera Lúcia Imperatriz-Fonseca^{4,12}

¹ Laboratory of Socioecology and Social Evolution, Department of Biology, KU Leuven, Leuven, Belgium, ² Laboratório de Biologia e Ecologia de Abelhas – Instituto de Ciências Biológicas, Universidade Federal do Pará – Rua Augusto Corrêa, Belém, Brazil, ³ Polytechnic School, Universidade do Vale do Rio dos Sinos, São Leopoldo, Brazil, ⁴ Vale Institute of Technology – Sustainable Development, Rua Boaventura de Silva, Belém, Brazil, ⁵ Exponent, Bellevue, WA, United States, ⁶ Vale Institute of Technology – Mining, Ouro Preto, Brazil, ⁷ Institute of Exact and Natural Sciences, Federal University of Pará, Belém, Brazil, ⁸ Computing Department, Universidade Federal de Ouro Preto, Ouro Preto, Brazil, ⁹ Native Bees, Brisbane, QLD, Australia, ¹⁰ Embrapa Amazônia Oriental, Belém, Brazil, ¹¹ School of Information Communication Technology, Griffith University, Gold Coast, QLD, Australia, ¹² Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

Bees play a key role in ecosystem services as the main pollinators of numerous flowering plants. Studying factors influencing their foraging behavior is relevant not only to understand their biology, but also how populations might respond to changes in their habitat and to the climate. Here, we used radio-frequency identification tags to monitor the foraging behavior of the neotropical stingless bee *Melipona fasciculata* with special interest in drifting patterns i.e., when a forager drifts into a foreign nest. In addition, we collected meteorological data to study how abiotic factors affect bees' activity and behavior. Our results show that only 35% of bees never drifted to another hive nearby, and that factors such as temperature, humidity and solar irradiation affected the bees drifting rates and/or foraging activity. Moreover, we tested whether drifting levels would decrease after marking the nest entrances with different patterns. However, contrary to our predictions, there was an increase in the proportion of drifting, which could indicate factors other than orientation mistakes playing a role in this behavior. Overall, our results demonstrate how managed bee populations are affected by both nearby hives and climate factors, offering insights on their biology and potential commercial application as crop pollinators.

Keywords: stingless bee, radio-frequency identification, *Melipona fasciculata*, foraging activity, drifting behavior

INTRODUCTION

Stingless bees are a highly diverse group of social bees comprising more than 500 species native to the tropical and subtropical regions of the world (Grüter, 2020a). They form perennial colonies composed of hundreds to thousands of workers that are common visitors of many flowering plants, including several crop species (Heard, 1999; Michener, 2007). Some species of stingless bees are already successfully managed in small scale, notably those from the genus *Melipona* that have been traditionally used for honey production in the Americas, with several other stingless bee genera used in Africa, Asia and Oceania (Cortopassi-Laurino et al., 2006; Quezada-Euán et al., 2018; Orr et al., 2021). However, despite their great potential to be used as commercial pollinators (Cruz et al., 2005; Del Sarto et al., 2005; Slaa et al., 2006; Bispo dos Santos et al., 2009; Hikawa and Miyanaga, 2009; Nunes-Silva et al., 2013; Caro et al., 2017; Silva-Neto et al., 2019; Giannini et al., 2020; Layek et al., 2021), the large scale application of stingless bee species with this purpose is not yet as developed as for example honeybees and bumblebees (Roubik, 1995; Ramírez et al., 2018; Roubik et al., 2018). This could be a direct consequence of a general lack of knowledge about their biology and natural history. It is therefore important to understand basic aspects of their biology such as foraging activity patterns, as well as their viability to be managed prior to any potential application of stingless bee populations.

Studying the foraging patterns of bees can help to not only increase the knowledge about these important providers of ecosystem services, but also to better formulate beekeeping strategies such as colony density and proximity to both natural areas and crops. Bees tend to forage nearby their hives (Basari et al., 2018), usually ranging from a few meters to about 2 km away from their natal nests (Van Nieuwstadt and Iraheta, 1996; Araujo et al., 2004; Kuhn-Neto et al., 2009; Nunes-Silva et al., 2019). In natural conditions, colonies of a single species are usually located somewhat distant from each other with densities ranging between 0.014–16 hives/ha (Eltz et al., 2002; Silva and Ramalho, 2016). However, there is usually a large number of colonies aggregated next to each other in managed populations, resulting in increased competition for resources and high levels of orientation mistakes or “drifting” when foragers return to their hives. There is a wide variation in the rates of drifting behavior between species and/or the type of environment, being generally higher in managed in contrast to natural populations. For example, in bumblebees, drifting rates vary between 2.7% in natural or semi natural conditions to 28% in greenhouses (Birmingham and Winston, 2004; Takahashi et al., 2010; Zanette et al., 2014), while in honeybees drifting ranges from 1–5% in natural populations up to 42% in apiaries (Pfeiffer and Crailsheim, 1998; Nanork et al., 2005, 2007; Chapman et al., 2009a,b,c). This behavior can have major consequences to colony health since diseases and pathogens may spread across hives via drifted workers (Bordier et al., 2017; Nolan and Delaplane, 2017). Hence, it is a crucial factor to be considered in terms of both honey production and crop pollination.

As yet, many aspects related to foraging patterns and drifting behavior remain poorly understood in stingless bees. In this

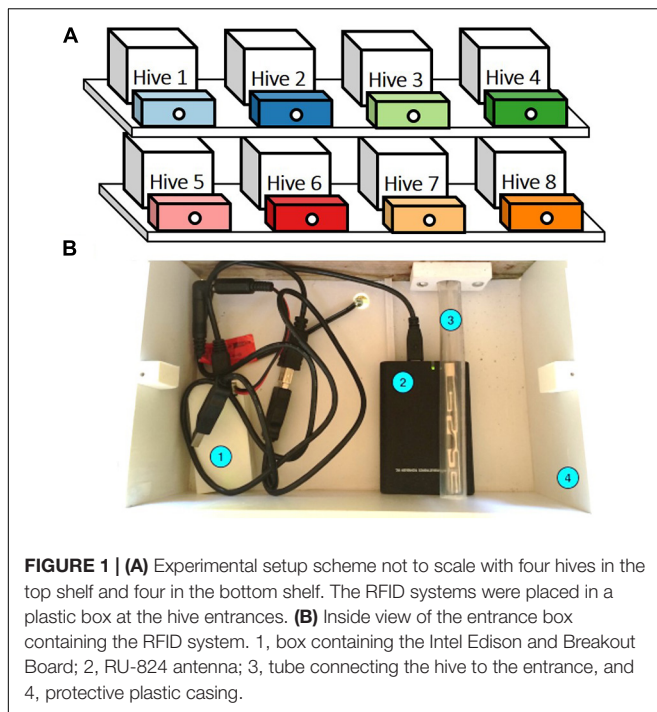
study, we used state-of-the-art radio frequency identification (RFID) tags to monitor the foraging behavior of the stingless bee *Melipona fasciculata* over with special interest in the drifting patterns between colonies. In particular, we tested how marking the colony entrances with different geometric patterns affected the drifting behavior. In addition, we tested if the position of the colonies had an influence in terms of the direction of the drifting rates and, finally, we correlated the data collected with the RFID system with meteorological data to understand how abiotic climatic factors affected both the bees' lifespan and drifting rates.

MATERIALS AND METHODS

Study Species and Experimental Design

This study was performed with the stingless bee *Melipona fasciculata*, which has its natural distribution in the northern region of Brazil (Pedro, 2014). The colonies used in the experiment were located at the meliponary of Eastern Amazon Embrapa, in an environment consisting of a mosaic of agricultural crops, forest remnants, and human habitations, where worker bees could forage freely on their expected range of about 2.5 km (Van Nieuwstadt and Iraheta, 1996; Araujo et al., 2004; Kuhn-Neto et al., 2009; Nunes-Silva et al., 2019). The climate at the site is characterized as tropical with daily mean precipitation of at least 60 mm throughout the year (Alvares et al., 2013).

To analyze the foraging and drifting patterns of *M. fasciculata*, eight experimental colonies were housed in identical hives designed for stingless bees and located in a shed consisting of two parallel rows with four colonies each that were placed 15 cm apart (**Figure 1A**). A plastic tube that extended the colony entrance and allowed the positioning of the antennae and microcomputer of the RFID system was placed in the front of the hive. The entire system was enclosed inside a box that protected entrance tubes from direct light in order to not disturb the forager's behavior (**Figure 1B**). Young worker bees that were not yet foraging were randomly sampled from each hive to receive the RFID tags. Bees were tagged every week for 9 consecutive sessions with 40 workers tagged per week, amounting to 360 bees per colony and 2,880 in total. The process consisted in collecting the young workers in the early morning (8:00–9:00) and placing them in a tube with maximum 5 workers per tube prior to tagging them with the RFIDs. The RFID-tags were then glued with cyanoacrylate adhesive onto the worker thorax (**Figure 2B**) and, after all bees were marked and the glue sufficiently dried, they were returned to their original hive. Workers from *M. fasciculata* tolerated well the RFID-tags glued on their thorax without any apparent disturbance to their flight behavior (Nunes-Silva et al., 2019; Gomes et al., 2020; Costa et al., 2021). Finally, after 42 days of the beginning of the experiment, colonies received simple geometrical individual black and white markings made with electrical tape at their entrances to test whether foragers would then improve recognition of their own hive and drift to fewer foreign hives, i.e., make fewer orientation mistakes. The experiment ran for another 78 days after the marking of the colony entrances until the activity of tagged bees was no longer



observed. Despite the unbalanced number of days before and after marking the colony entrances, the number of worker bees tracked during each period was similar ($n = 1496$ workers during control and $n = 1,203$ during the experimental period).

RFID-System Setup

This study was conducted using the Radio Frequency Identification System Ultra Small Package Tag (USPT) developed by Hitachi Chemical (Endou et al., 2014). The system consisted in a single antenna placed below the colony entrance tube connected to an Intel Edison micro-computer to store data (Figure 1B). Each tag was recorded with an individual ID that included the bee number and her colony of origin prior to being glued onto the bees. Therefore, whenever a tagged bee passed through the entrance tube both worker ID and time of the day were recorded. A caveat of the experimental design was that our system consisted of only one reader per colony, hence the signal sent to the computer did not inform the directionality of the bee's movement (toward or away from the hive) which was then mitigated during data analysis. Moreover, guard bees staying by the colony entrance would have repeated readings over a short period of time. Hence, only signals that were at least 180 s apart were included in the analysis to resolve this issue. Thresholds between 60 s and 5 min are consistently used to filter RFID foraging data in Hymenoptera (Lach et al., 2015; Dosselli et al., 2016; Susanto et al., 2018; Santoro et al., 2019). This threshold was adopted during data filtering in order to reflect only the extranidal flight activity. We opted for this threshold because, while it might misrepresent short patrolling flights, it prevents overestimating their foraging activity.

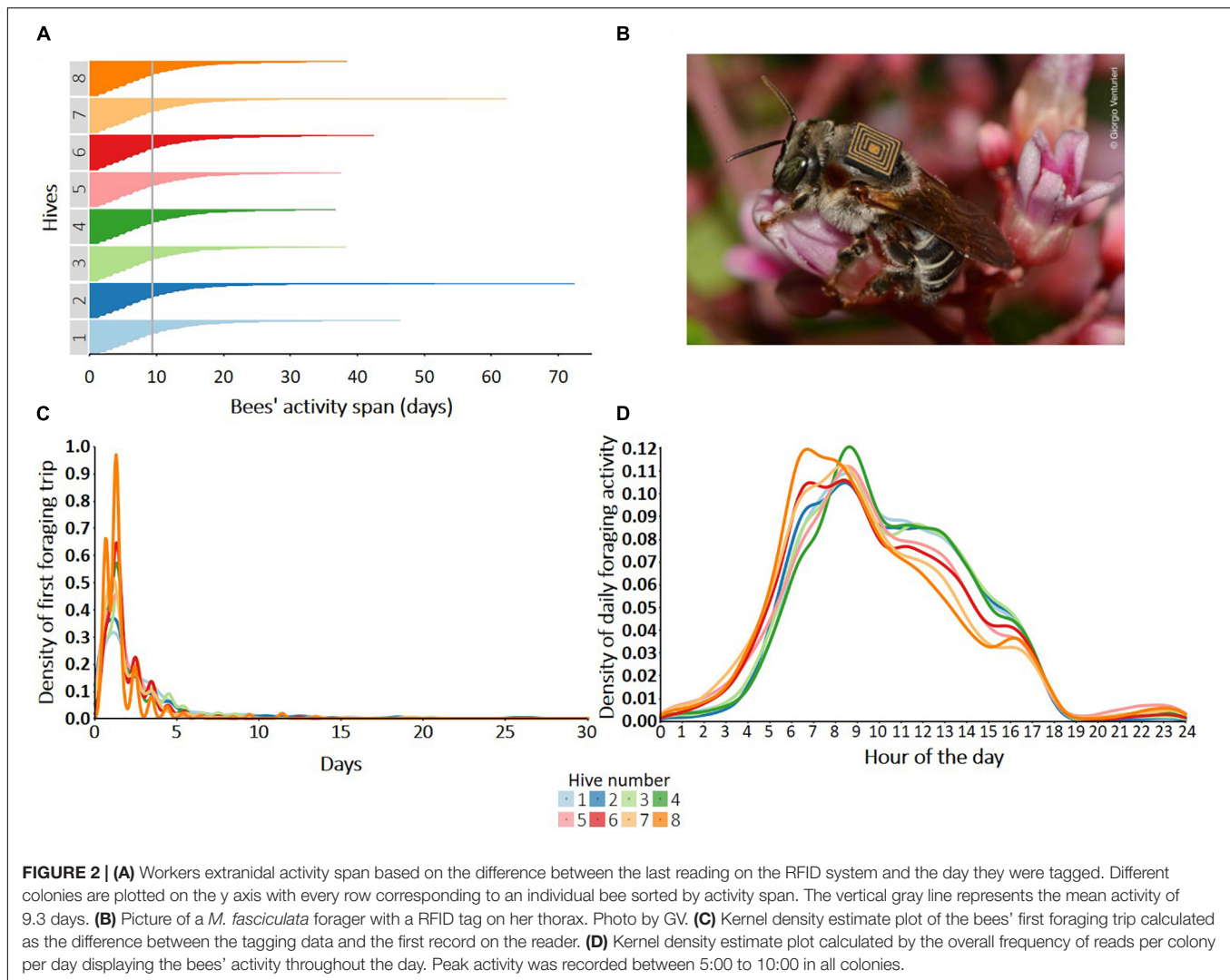
Data Analysis

All statistical analyses were carried out using the R software (R Core Team, 2020). Data filtering and merging RFID and meteorological data was performed using a custom R script (available on data repository). Extranidal activity span of foragers was calculated based on the difference between the last recorded data and the date the bees were tagged (Decourtye et al., 2011; Tenczar et al., 2014; Perry et al., 2015; Dosselli et al., 2016; Santoro et al., 2019). First foraging trip was calculated with the difference between the first trip recorded and the tagging date and the kernel density estimates were calculated based on the smoothed histogram using the “geom_density” function in the R package ggplot2. Likewise, the daily foraging activity were also calculated using the density function in the package ggplot2. To analyze the influence that both biotic and abiotic factors have on the observed drifting rates we used a model selection approach using the package glmulti to select the best set of explanatory variables based on the models Akaike's Information Criterion. The selected best model had drifting numbers coded as the dependent variable with activity span, hive ID, number of days to begin foraging as well as several meteorological factors coded as covariates with a Poisson error distribution. We then used the same approach to select a model with the bees' lifespan coded as the dependent variable but used a *quasipoisson* error distribution to deal with overdispersion detected in this model. In addition, we tested whether the proportion of drifters present on the colonies was different before and after marking the colony entrances by fitting a binomial GLMM with the proportion of foragers that drifted to an unrelated colony as the dependent variable, colony marking (before or after) as a fixed factor and hive ID and an observation-level random effect variable to cope with overdispersion as random factors. Finally, we tested whether drifters had any preference on the direction they would drift. To this end, we ran a binomial GLM with the direction of the drifting event (i.e., horizontal and vertical) as the dependent variable, both the natal hives ID and the host hives ID as cofactors and individual IDs as a random factor. When appropriate, models were tested for temporal autocorrelation, which was not observed in the data. The R script used in the analyses as well as the original datasets are publicly available in the data repository (Oliveira et al., 2021). All models presented in the results section are Poisson GLMs unless otherwise specified. In addition, Wald Z Scores are shortened to Z throughout the text.

RESULTS

Bees Extranidal Activity

Our results show that the tagged workers were active on average for 9.3 days, ranging from a minimum of 1.2 to a maximum of 72.5 days after being tagged (Figure 2A). In addition, bees began foraging on average 2 days after being tagged, with some more extreme cases where workers only started foraging after 25 days and beyond, as registered by the first reading of their tags at the colony entrance (Figure 2C). Foragers were active throughout the day, with most activity being recorded during the early morning hours (between 5:00–10:00), reaching



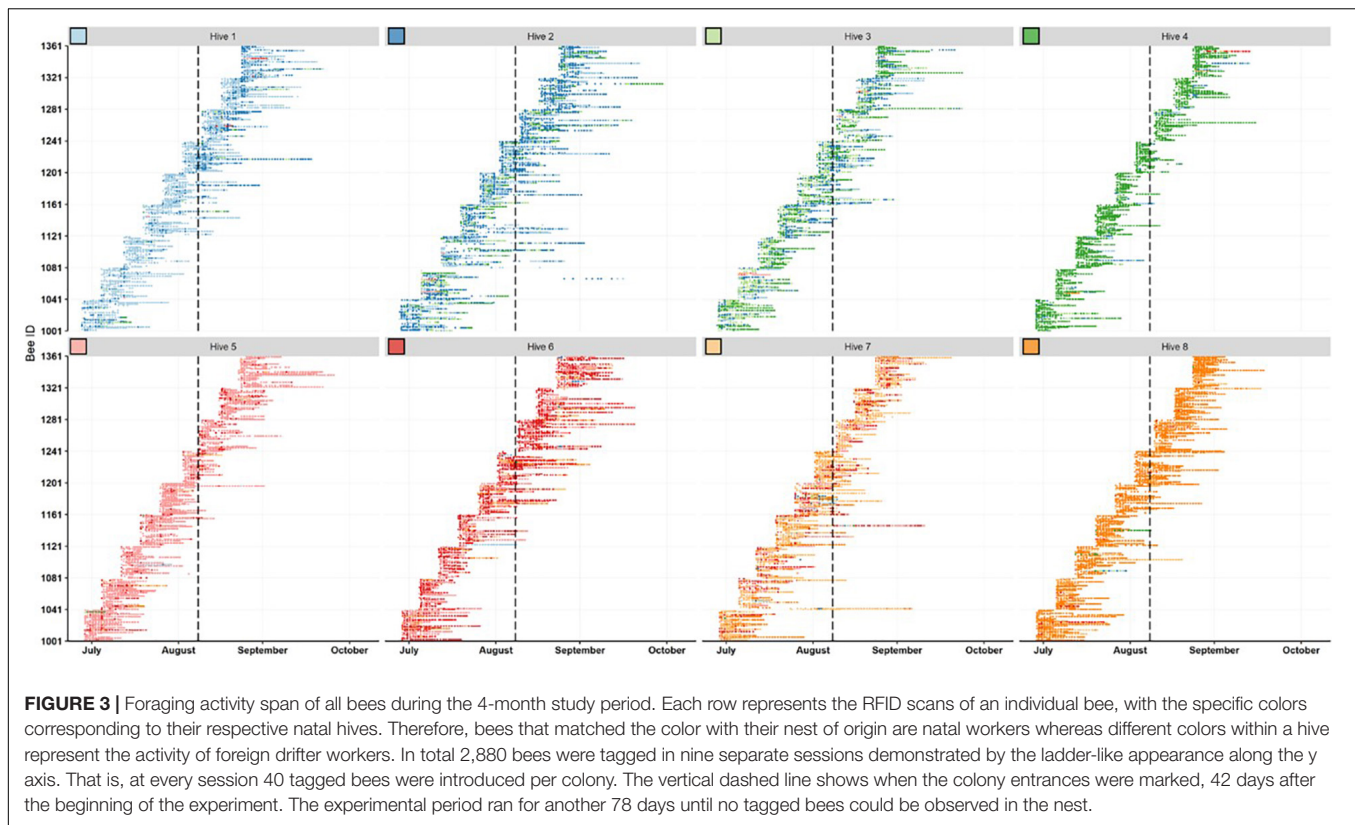
the peak activity at 9:00 and then decreasing until 18:00 (**Figure 2D**). Furthermore, our data show that workers in colony four showed significantly less activity, while in colony one and two significantly more activity than the average was recorded (colony four: $Z = -7.602$, $p < 0.001$; colony one: $Z = 2.373$, $p = 0.047$; colony two: $Z = 5.478$, $p < 0.001$). **Figure 3** illustrates the reconstructed foraging activity of all 2,880 bees during the 4-month study period.

Factors Affecting Drifting Behavior and Foraging Activity

Throughout the study period, 64.1% of all tagged workers drifted to at least one other colony, with 36.6% drifting to only one, 19.1% to two, 7.6% to three foreign colonies, and the percentage decreasing below 1% as the number of foreign colonies increased up to a maximum of seven colonies, i.e., all non-natal experimental colonies (**Figure 4A**). It is interesting to note that the majority of the drifting events was in the horizontal plane, that is, workers mostly drifted to colonies on their left

or right rather than above or below their natal hives (Binomial GLMM, $Z > 8.568$, $p < 0.001$ for all colonies, **Figure 4B**). Moreover, colonies placed on both edges produced fewer drifters than colonies placed between other hives. For instance, foragers in colonies two, three, six and seven showed significantly higher levels of drifting behavior (hive two: $Z = 11.880$, $p < 0.001$; hive three: $Z = 11.499$, $p < 0.001$; hive six: $Z = 4.125$, $p < 0.001$ and hive seven: $Z = 3.514$, $p = 0.001$) while hives four, five and eight had significant fewer drifters (hive four: $Z = -5.746$, $p < 0.001$; hive five: $Z = -5.250$, $p < 0.001$ and hive eight: $Z = -9.716$, $p < 0.001$), with hive one being not significant ($Z = 0.181$, $p = 0.936$). Furthermore, drifting rates were positively correlated with workers' lifespan $Z = 18.113$, $p < 0.001$) and the sooner bees began foraging after being tagged the higher the observed drifting rates ($Z = 7.494$, $p < 0.001$).

In addition to biotic factors, several meteorological factors influenced the levels of drifting behavior, with dew point positively affecting the drifting rates ($Z = 3.205$, $p = 0.001$), while solar irradiation ($Z = -2.804$, $p = 0.005$), maximum relative humidity ($Z = -2.883$, $p = 0.002$) and minimum daily



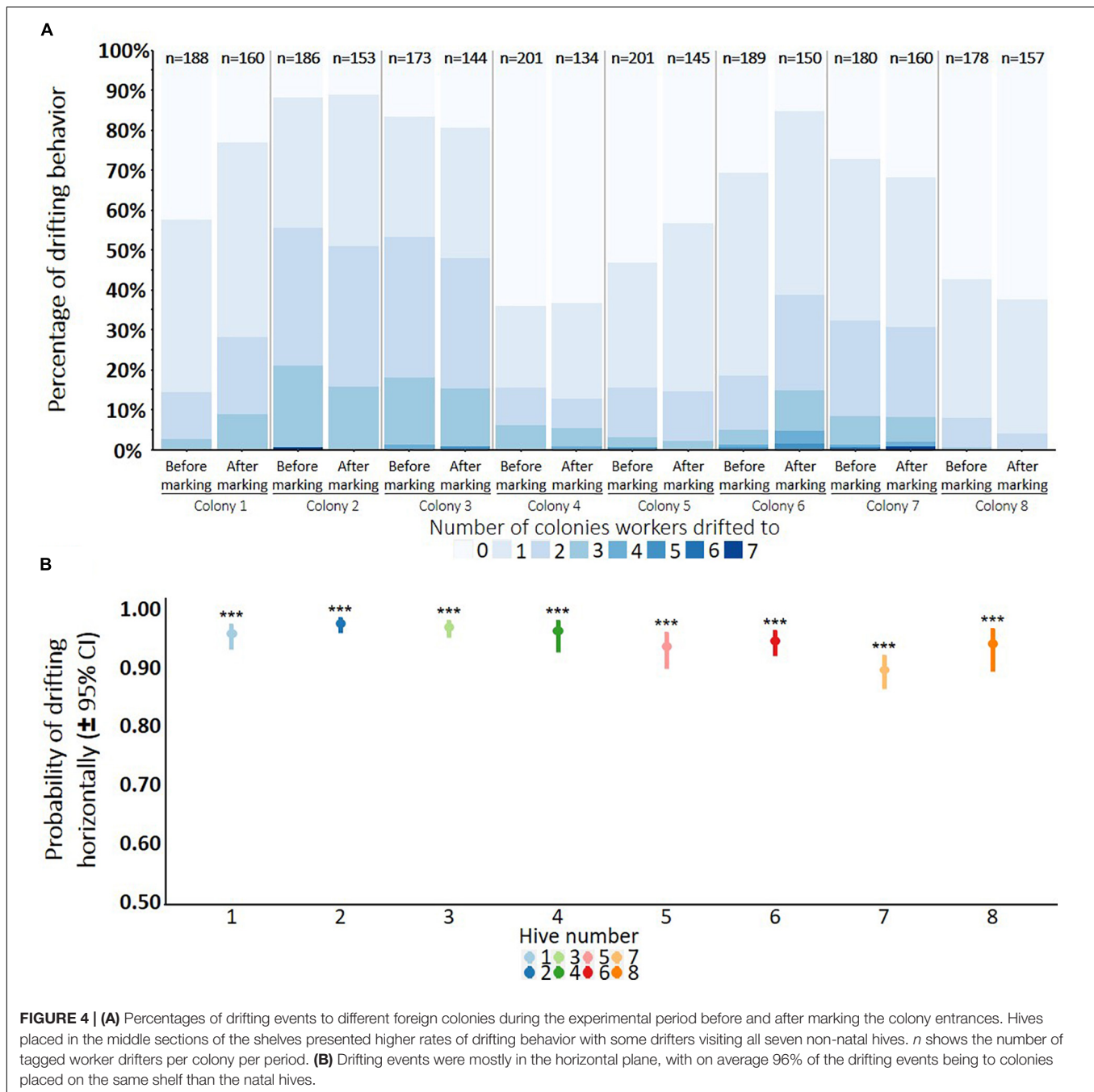
temperature ($Z = -2.722$, $p = 0.006$) were negatively correlated to the drifting rates.

During the experimental period colony entrances received individual markings to test whether foragers would then improve recognition of their own hive and drift to fewer foreign hives, i.e., make fewer orientation mistakes. Intriguingly, we observed an increase in the proportion of drifting events after marking the hive entrances, with 63.9% of tagged bees drifting before and 68.7% after the hive entrances were marked (Binomial GLMM, $Z = 2.508$, $p = 0.012$), which could indicate factors other than mere orientation mistakes playing a role in drifting behavior (Figure 4A).

Finally, it was possible to observe that meteorological factors were also correlated with the workers extranidal activity, whereby maximum daily atmospheric pressure and temperature, precipitation as well as dew point temperature were positively correlated with the bees activity span (max atmospheric pressure: $Z = 6.521$, $p < 0.001$; max temperature, $Z = 5.236$, $p < 0.001$; precipitation, $Z = 3.020$, $p = 0.002$; max dew point: $Z = 2.504$, $p = 0.012$; min dew point: ($Z = 4.710$, $p < 0.001$). Conversely, minimum daily temperature and atmospheric pressure, humidity and wind speed negatively affecting the bees' activity (min temperature: $Z = -8.834$, $p < 0.001$; min atmospheric pressure, $Z = -6.922$, $p < 0.001$; max humidity: $Z = -4.235$, $p < 0.001$; min humidity: $Z = -3.156$, $p = 0.001$; and wind speed: $Z = -9.901$, $p < 0.001$). Table 1 summarizes the relationship of abiotic factors with both drifting behavior and foraging activity.

DISCUSSION

By reconstructing their daily foraging activity of the stingless bee *M. fasciculata*, we could observe that bees forage during the entire day, with the average peak activity per colony at 9:00 in the morning (Figure 2D). In contrast, studies using similar RFID technology show that both honeybees and bumblebees have their peak foraging activity at noon, even during a permanent daylight condition in the arctic circle (Stelzer and Chittka, 2010; Susanto et al., 2018). Similarly to honeybees, stingless bee workers perform different tasks along their lives, from taking care of the young and cleaning the colony soon after emerging, to carrying out more dangerous tasks such as defending the hive and foraging toward the end of their lives with some degree of specialization in certain tasks (Mateus et al., 2019). In the congeneric *M. beecheii* it was shown that some foragers collected mostly pollen whereas some others were specialized in foraging for nectar, with great impact both in their daily activity and lifespan. Nectar foragers were active during the entire day but died approximately 3 days after they began foraging, while pollen foragers were only active for 1–3 h in the early morning but lived on average 9 days after they started foraging (Biesmeijer and Tóth, 1998). These patterns could explain the differences observed in our experiments, where we detected a wide variation in their activity span (1.2–72.5 days). Despite the average extranidal activity span observed in our experiment being seemingly short (9.3 days), it is in line with a similar experiment performed with RFID system in honeybees in which individuals in control colonies lived on average 12.2 days



after being introduced to the hives (Thompson et al., 2016). In addition, even though we did not quantify the precise age of the workers, *Melipona* bees usually start foraging around 25–33 days after emergence (Biesmeijer and Tóth, 1998; Mateus et al., 2019), hence we can estimate the life expectancy of the bees in our experiments approximately between 25 and 105 days, which is consistent with what is found in the literature for *M. fasciculata* and other species of this genus (Grüter, 2020b).

For most social insects, life-threatening challenges increase when workers leave the security of their nests and start their foraging activity. Outside the nest they face an increased

chance of predation, death by the elements (e.g., storms) or by exhaustion (Roubik, 1982; Visscher and Dukas, 1997; Gomes et al., 2015). Indeed, we observed some abiotic factors having strong effects on the bees' activity, notably temperature, atmospheric pressure, and wind speed. An increase in the average daily maximum temperature by one degree during the bee's lifespan corresponded to an increased activity span of 1.7 days. On the other hand, an increase in the minimum daily temperature had the opposite effect, decreasing the bee's activity span by 3.3 days. A possible explanation for this observation is that while bees benefit from higher temperatures

TABLE 1 | Abiotic factors affecting both drifting behavior and foraging activity.

Abiotic factors	Drifting behavior			Foraging activity				
	Log-Mean	z value	p value	Log-Mean	t value	p value		
Temperature max.				1.68	5.24	< 0.001	***	
Temperature min.	−0.85	−2.72	0.006	**	−3.34	−8.83	< 0.001	***
Humidity max.	−0.21	−2.88	0.004	**	−0.42	−4.23	< 0.001	***
Humidity min.				−0.27	−3.16	0.002	**	
Solar irradiation instant.	0.00	−2.80	0.005	**				
Dew Point instant.	0.99	3.20	0.001	**				
Dew Point max.				0.99	2.50	0.012	*	
Dew Point min.				1.71	4.71	< 0.001	***	
Atmospheric Pressure max.				2.73	6.52	< 0.001	***	
Atmospheric Pressure min.				−2.90	−6.92	< 0.001	***	
Precipitation				0.49	3.02	0.003	**	
Wind Speed				−2.03	−9.90	< 0.001	***	
Wind Gust				−0.16	−1.79	0.074		

Estimates are presented in terms of the log mean effect size in which positive values imply a positive relationship with the dependent variable i.e., drifting behavior or foraging activity, while negative values show a negative relationship. Only factors included in the models are shown. Significant effects are shown in bold. Significance levels * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

during daily foraging activity, the same was not true when they were inside their hives during the night, when the minimum temperatures were recorded. A similar pattern was observed for average maximum and minimum atmospheric pressure, where the maximum recorded values had a positive effect whereas minimum values had a negative effect on the bees' foraging activity span. Finally, average recorded wind speed had a negative impact on their survival, likely by impairing the bee's flight ability (Crall et al., 2017). Even though further studies are still needed to fully comprehend how climate factors affect the bees' behavior, our results show that this species is highly susceptible to variations in climate factors with relatively small fluctuations having a significant impact in their lifespan, demonstrating that even small changes in the future climate might cause notable implications in their extranidal activities.

In terms of the drifting behavior, our results show that 64% of the tagged workers drifted to at least one foreign hive, and that some of them were recorded entering all seven foreign hives (Figure 3A). Bees use a combination of landmarks and polarized light to orient themselves in the environment, naturally experiencing some degree of error while returning to their nests (Rossel and Wehner, 1982; Kraft et al., 2011; Kheradmand and Nieh, 2019). The overall low density of nests in natural conditions likely sustain no strong selective pressure for higher accuracy. Nevertheless, high rates of drifting behavior are not uncommonly observed in apiaries (Free, 1958; Free and Spencer-Booth, 1961; Pfeiffer and Crailsheim, 1998), which is likely caused by the high density of hives next to each other, resulting in a larger proportion of orientation mistakes. This happens particularly when resources are abundant and guard bees become more permissive to the infiltration of non-nestmates in their hives (Pfeiffer and Crailsheim, 1998; Downs and Ratnieks, 2000). Although the levels of drifting behavior observed are likely mainly due to orientation mistakes, nest robbing or social parasitism cannot be completely ruled out,

since we observed an increased proportion of drifting behavior after marking the colony entrances which presumably increased the bees ability to recognize their own colony (Plowright et al., 1995). In fact, worker social parasitism is well documented in both honeybees (Nanork et al., 2005, 2007; Chapman et al., 2009a,b,c) and bumblebees (Birmingham and Winston, 2004; Birmingham et al., 2004; Takahashi et al., 2009; Zanette et al., 2014), as well as in other social insect species including wasps (Oliveira et al., 2016). An alternative explanation for the increased proportion of drifting after marking the colony entrances could be linked with bees merely not recognizing their hive entrances. Nevertheless, this is unlikely since about half of the tagged bees ($n = 1203$) began foraging only after the experimental manipulation i.e., they had no prior interaction with the unmarked colony entrances. Whether workers indeed actively drift into foreign colonies and how they manage to avoid being detected as non-nestmates and attacked by guards still deserves further study.

An interesting outcome of our experimental design is the fact the nearly all drifting events took place horizontally, i.e., foragers drifted almost exclusively to colonies placed in the same shelf as their natal hive rather than above or below, and that hives placed in the center of the rows produced more drifters, similarly to what is observed in honeybees (Pfeiffer and Crailsheim, 1998). In contrast, drifting occurred preferentially in the vertical plane in two species of bumblebees, with colonies placed on top significantly receiving more drifter workers (Birmingham and Winston, 2004). These differences in the orientation of the drifting behavior are possibly due to particularities in nesting biology since bumblebees usually nest underground (Kells and Goulson, 2003), while honeybees and most stingless bee species built their nests in tree cavities or branches (Roubik, 2006; Hepburn et al., 2014). Therefore, honeybees and stingless bees would benefit more from higher accuracy in finding their nests in the vertical plane whereas bumblebees would have

a stronger selective pressure toward accuracy in the vertical plane. Our finding demonstrates that the spatial distribution of colonies has important management implications for stingless bee populations. Furthermore, our results also suggest that other factors other than the position of the hives played a role in the rates of drifting behavior. In one hand, the average dew point temperature was observed to be positively correlated to the drifting levels, possible because most foraging activity happens in the early morning hours and a higher temperature overall could be linked with higher metabolic activity. On the other hand, factors like solar irradiation, maximum humidity and minimum daily temperatures were shown to negatively impact drifting rates. These factors are usually linked with lower foraging activity (de Figueiredo-Mecca et al., 2013), which could explain the reduced rates of drifting merely as an outcome of fewer foraging trips.

Stingless bees present great potential to be used in commercial crop pollination (Heard, 1999; Slaa et al., 2006; Giannini et al., 2020; Layek et al., 2021). Indeed, *Melipona* bees have been demonstrated to be efficient pollinators of many economically important fruits and vegetables (Cruz et al., 2005; Bispo dos Santos et al., 2009; Nunes-Silva et al., 2013; Caro et al., 2017; Silva-Neto et al., 2019). A recent study using the RFID technology with the stingless bee *M. fasciculata* showed that workers of this species can return to their nests from distances up to 10 km away from their hives (Nunes-Silva et al., 2019), suggesting that these bees could be well suited for pollination of large scale plantations as well.

Overall, this study presents data on the foraging activity and drifting patterns of the stingless bee *M. fasciculata*, showing the impact of the presence of hives nearby as well as several abiotic factors on both their lifespan and the rates of drifting behavior. This is an important step toward a better understanding of stingless bees' biology, providing insights on how some factors

might affect their application as pollinators in crops as well as in natural areas.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

VI-F, FC, and RJ had the original idea. FC, HA, RJ, LC, GP, and GV performed the experiments. PS provided the RFID system for the experiments. RO analyzed the data and wrote the first draft of the manuscript. All authors revised and approved the final version of the manuscript.

FUNDING

This project was funded by the Brazilian National Council for Scientific and Technological Development CNPq, grant 444384/2018-9; and by individual research grants to VLIF (CNPq 312250/2018-5), RF (CNPq 301616/2017-5) and RCO (Research Foundation Flanders FWO research Grant 1502119N and postdoctoral Grant 12R9619N).

ACKNOWLEDGMENTS

We would like to thank Elisângela Rêgo for helping to tag the bees.

REFERENCES

- Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes Gonçalves, J. L., and Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22, 711–728. doi: 10.1127/0941-2948/2013/0507
- Araujo, E. D., Costa, M., Chaud-Netto, J., and Fowler, H. G. (2004). Body size and flight distance in stingless bees (Hymenoptera: Meliponini): Inference of flight range and possible ecological implications. *Braz. J. Biol.* 64, 563–568. doi: 10.1590/s1519-69842004000400003
- Basari, N., Ramli, S. N., and Mohd Khairi, N. S. (2018). Food reward and distance influence the foraging pattern of stingless bee, *Heterotrigona itama*. *Insects* 9:138. doi: 10.3390/insects9040138
- Biesmeijer, J., and Tóth, E. (1998). Individual foraging, activity level and longevity in the stingless bee *Melipona beecheii* in costa rica (Hymenoptera, apidae, meliponinae). *Ins. soc.* 45, 427–443. doi: 10.1007/s000400050099
- Birmingham, A. L., Hoover, S. E., Winston, M. L., and Ydenberg, R. C. (2004). Drifting bumble bee (Hymenoptera: Apidae) workers in commercial greenhouses may be social parasites. *Can. J. Zool.* 82, 1843–1853. doi: 10.1139/z04-181
- Birmingham, A. L., and Winston, M. L. (2004). Orientation and drifting behaviour of bumblebees (Hymenoptera: Apidae) in commercial tomato greenhouses. *Can. J. Zool.* 82, 52–59. doi: 10.1139/z03-201
- Bispo dos Santos, S. A., Roselino, A. C., Hrnair, M., and Bego, L. R. (2009). Pollination of tomatoes by the stingless bee *Melipona quadrifasciata* and the honey bee *Apis mellifera* (Hymenoptera, Apidae). *Gen. Mol. Res.* 8:751. doi: 10.4238/vol8-2kerr015
- Bordier, C., Pioz, M., Crauser, D., Le Conte, Y., and Alaux, C. (2017). Should I stay or should I go: Honeybee drifting behaviour as a function of parasitism. *Apidologie* 48, 286–297. doi: 10.1007/s13592-016-0475-1
- Caro, A., Moo-Valle, H., Alfaro, R., and Javier, Q. E. (2017). Pollination services of africanized honey bees and native *Melipona beecheii* to buzz-pollinated annatto (*Bixa orellana* L.) in the neotropics. *Agric. For. Entomol.* 19, 274–280. doi: 10.1111/afe.12206
- Chapman, N. C., Beekman, M., and Oldroyd, B. P. (2009c). Worker reproductive parasitism and drift in the western honeybee *Apis mellifera*. *Behav. Ecol. Sociobiol.* 64, 419–427. doi: 10.1007/s00265-009-0858-7
- Chapman, N. C., Higgs, J. S., Wattanachaiyingcharoen, W., Beekman, M., and Oldroyd, B. P. (2009b). Worker reproductive parasitism in naturally orphaned colonies of the asian red dwarf honey bee, *Apis florea*. *Ins. soc.* 57, 163–167. doi: 10.1007/s00040-009-0061-x
- Chapman, N. C., Nanork, P., Gloag, R. S., Wattanachaiyingcharoen, W., Beekman, M., and Oldroyd, B. P. (2009a). Queenless colonies of the asian red dwarf honey bee (*Apis florea*) are infiltrated by workers from other queenless colonies. *Behav. Ecol.* 20, 817–820. doi: 10.1093/beheco/arp065
- Core Team, R. (2020). *R: A Language and Environment for Statistical Computing*. Austria: R Foundation for Statistical Computing.
- Cortopassi-Laurino, M., Imperatriz-Fonseca, V. L., Roubik, D. W., Dollin, A., Heard, T., Aguilar, I., et al. (2006). Global meliponiculture: Challenges and opportunities. *Apidologie* 37, 275–292. doi: 10.1051/apido:2006027

- Costa, L., Nunes-Silva, P., Galaschi-Teixeira, J., Arruda, H., Veiga, J., Pessin, G., et al. (2021). RFID-tagged Amazonian stingless bees confirm that landscape configuration and nest re-establishment time affect homing ability. *Ins. soc.* 68, 1–8. doi: 10.1007/978-3-319-90306-4_147-1
- Crall, J. D., Chang, J. J., Oppenheimer, R. L., and Combes, S. A. (2017). Foraging in an unsteady world: Bumblebee flight performance in field-realistic turbulence. *Interface Focus* 7:20160086. doi: 10.1098/rsfs.2016.0086
- Cruz, D. O., Freitas, B. M., Silva, L. A., Silva, E. M. S., and Bomfim, I. G. A. (2005). Pollination efficiency of the stingless bee *Melipona subnitida* on greenhouse sweet pepper. *Pesqu. Agropecu. Bras.* 40, 1197–1201. doi: 10.1590/s0100-204x2005001200006
- de Figueiredo-Mecca, G., Bego, L. R., and do Nascimento, F. S. (2013). Foraging behavior of *Scaptotrigona depilis* (Hymenoptera, Apidae, Meliponini) and its relationship with temporal and abiotic factors. *Sociobiology* 60, 267–282.
- Decourtye, A., Devillers, J., Aupinel, P., Brun, F., Bagnis, C., Fourrier, J., et al. (2011). Honeybee tracking with microchips: A new methodology to measure the effects of pesticides. *Ecotoxicology* 20, 429–437. doi: 10.1007/s10646-011-0594-4
- Del Sarto, M. C. L., Peruquetti, R. C., and Campos, L. A. O. (2005). Evaluation of the neotropical stingless bee *Melipona quadrifasciata* (Hymenoptera: Apidae) as pollinator of greenhouse tomatoes. *J. Econ. Entomol.* 98, 260–266. doi: 10.1093/jee/98.2.260
- Dosselli, R., Grassl, J., Carson, A., Simmons, L. W., and Baer, B. (2016). Flight behaviour of honey bee (*Apis mellifera*) workers is altered by initial infections of the fungal parasite *Nosema apis*. *Sci. Rep.* 6, 1–11.
- Downs, S. G., and Ratnieks, F. L. W. (2000). Adaptive shifts in honey bee (*Apis mellifera* L.) guarding behavior support predictions of the acceptance threshold model. *Behav. Ecol.* 11, 326–333. doi: 10.1093/beheco/11.3.326
- Eltz, T., Bruhl, C. A., van der Kaars, S., and Linsenmair, E. K. (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of sabah, Malaysia. *Oecologia* 131, 27–34. doi: 10.1007/s00442-001-0848-6
- Endou, T., Ishizaka, Hironori, Oota, Masahiko, Tasaki, Kouji, Hosoi, Hiroyuki, and Company, H. C. (eds) (2014). *RFID Tag and Automatic Recognition System*. United States: WIPO.
- Free, J. (1958). The drifting of honey-bees. *J. Agricult. Sci.* 51, 294–306. doi: 10.1017/s0021859600035103
- Free, J., and Spencer-Booth, Y. (1961). Further experiments on the drifting of honey-bees. *J. Agricult. Sci.* 57, 153–158. doi: 10.1017/s0021859600047626
- Giannini, T. C., Alves, D. A., Alves, R., Cordeiro, G. D., Campbell, A. J., Awade, M., et al. (2020). Unveiling the contribution of bee pollinators to brazilian crops with implications for bee management. *Apidologie* 51, 1–16.
- Gomes, P. A., Suhara, Y., Nunes-Silva, P., Costa, L., Arruda, H., Venturieri, G., et al. (2020). An Amazon stingless bee foraging activity predicted using recurrent artificial neural networks and attribute selection. *Sci. Rep.* 10, 1–12.
- Gomes, R. L. C., Menezes, C., and Contrera, F. A. L. (2015). Worker longevity in an Amazonian *Melipona* (Apidae, Meliponini) species: Effects of season and age at foraging onset. *Apidologie* 46, 133–143. doi: 10.1007/s13592-014-0309-y
- Grüter, C. (2020a). *Stingless Bees: Their Behaviour, Ecology and Evolution*. Berlin: Springer.
- Grüter, C. (ed.) (2020b). *Stingless Bees: An overview*. In: *Stingless Bees*. Berlin: Springer.
- Heard, T. A. (1999). The role of stingless bees in crop pollination. *Annu. Rev. Entomol.* 44, 183–206. doi: 10.1146/annurev.ento.44.1.183
- Hepburn, H., Pirk, C., and Duangphakdee, O. (2014). Honeybee nests Composition, structure, function. *Springer* 978, 642–648.
- Hikawa, M., and Miyayama, R. (2009). Effects of pollination by *Melipona quadrifasciata* (Hymenoptera: Apidae) on tomatoes in protected culture. *Appl. Entomol. Zool.* 44, 301–307. doi: 10.1303/aez.2009.301
- Kells, A. R., and Goulson, D. (2003). Preferred nesting sites of bumblebee queens (hymenoptera: Apidae) in agroecosystems in the UK. *Biol. Conserv.* 109, 165–174. doi: 10.1016/s0006-3207(02)00131-3
- Kheradmand, B., and Nieh, J. C. (2019). The role of landscapes and landmarks in bee navigation: A review. *Insects* 10:342. doi: 10.3390/insects10100342
- Kraft, P., Evangelista, C., Dacke, M., Labhart, T., and Srinivasan, M. (2011). Honeybee navigation: Following routes using polarized-light cues. *Philos. Trans. R. Soc. B Biol. Sci.* 366, 703–708. doi: 10.1098/rstb.2010.0203
- Kuhn-Neto, B., Contrera, F. A., Castro, M. S., and Nieh, J. C. (2009). Long distance foraging and recruitment by a stingless bee, *Melipona mandacaia*. *Apidologie* 40, 472–480. doi: 10.1051/apido/2009007
- Lach, L., Kratz, M., and Baer, B. (2015). Parasitized honey bees are less likely to forage and carry less pollen. *J. Invertebr. Pathol.* 130, 64–71. doi: 10.1016/j.jip.2015.06.003
- Layek, U., Kundu, A., Bisui, S., and Karmakar, P. (2021). Impact of managed stingless bee and western honey bee colonies on native pollinators and yield of watermelon: A comparative study. *Ann. Agricult. Sci.* 66, 38–45. doi: 10.1016/j.aas.2021.02.004
- Mateus, S., Ferreira-Caliman, M., Menezes, C., and Grüter, C. (2019). Beyond temporal-polyethism: Division of labor in the eusocial bee *melipona marginata*. *Ins. soc.* 66, 317–328. doi: 10.1007/s00040-019-00691-2
- Michener, C. D. (2007). *The Bees of the World*. Baltimore: The Johns Hopkins University Press.
- Nanork, P., Chapman, N. C., Wongsiri, S., Lim, J., Gloag, R. S., and Oldroyd, B. P. (2007). Social parasitism by workers in queenless and queenright *Apis cerana* colonies. *Mol. Ecol.* 16, 1107–1114. doi: 10.1111/j.1365-294x.2006.03207.x
- Nanork, P., Paar, J., Chapman, N. C., Wongsiri, S., and Oldroyd, B. P. (2005). Entomology: Asian honeybees parasitize the future dead. *Nature* 437:829. doi: 10.1038/437829a
- Nolan, M. P., and Delaplane, K. S. (2017). Distance between honey bee *Apis mellifera* colonies regulates populations of *Varroa destructor* at a landscape scale. *Apidologie* 48, 8–16. doi: 10.1007/s13592-016-0443-9
- Nunes-Silva, P., Costa, L., Campbell, A. J., Arruda, H., Contrera, F. A. L., Teixeira, J. S. G., et al. (2019). Radiofrequency identification (RFID) reveals long-distance flight and homing abilities of the stingless bee *Melipona fasciculata*. *Apidologie* 51, 240–253. doi: 10.1007/s13592-019-00706-8
- Nunes-Silva, P., Hrnčir, M., da Silva, C. I., Roldão, Y. S., and Imperatriz-Fonseca, V. L. (2013). Stingless bees, *melipona fasciculata*, as efficient pollinators of eggplant (*solanum melongena*) in greenhouses. *Apidologie* 44, 537–546. doi: 10.1007/s13592-013-0204-y
- Oliveira, R. C., Andrés León, Contrera, F., Arruda, H., Jaffé, R., Costa, L., et al. (2021). Foraging and drifting patterns of a highly eusocial neotropical stingless bee assessed by radio-frequency identification tags. *Mendeley Data* [Preprint]. doi: 10.21203/rs.3.rs-162274/v1
- Oliveira, R. C., Oi, C. A., Vollet-Neto, A., and Wenseleers, T. (2016). Intraspecific worker parasitism in the common wasp, *Vespula vulgaris*. *Anim. Behav.* 113, 79–85. doi: 10.1016/j.anbehav.2015.12.025
- Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C. D., and Ascher, J. S. (2021). Global patterns and drivers of bee distribution. *Curr. Biol.* 31:e4.
- Pedro, S. R. M. (2014). The stingless bee fauna in Brazil (Hymenoptera: Apidae). *Sociobiology* 61, 348–354.
- Perry, C. J., Sovik, E., Myerscough, M. R., and Barron, A. B. (2015). Rapid behavioral maturation accelerates failure of stressed honey bee colonies. *Proc. Natl. Acad. Sci. U. S. A.* 112, 3427–3432. doi: 10.1073/pnas.1422089112
- Pfeiffer, K. J., and Crailsheim, K. (1998). Drifting of honeybees. *Ins. soc.* 45, 151–167. doi: 10.1007/s000400050076
- Plowright, C., O'Connell, C. E., Roberts, L. J., and Reid, S. L. (1995). The use of proximal and distal cues in nest entrance recognition by bumble bees. *J. Apic. Res.* 34, 57–64. doi: 10.1080/00218839.1995.11100888
- Quezada-Euán, J. J. G., Nates-Parra, G., Maués, M. M., Roubik, D. W., and Imperatriz-Fonseca, V. L. (2018). The economic and cultural values of stingless bees (Hymenoptera: Meliponini) among ethnic groups of tropical America. *Sociobiology* 65, 534–557. doi: 10.13102/sociobiology.v65i4.3447
- Ramírez, V. M., Ayala, R., and González, H. D. (2018). *Crop Pollination by Stingless Bees*. In: *Pot-Pollen in Stingless Bee Melittology*. Germany: Springer.
- Rossel, S., and Wehner, R. (1982). The bee's map of the e-vector pattern in the sky. *Proc. Natl. Acad. Sci. U. S. A.* 79, 4451–4455. doi: 10.1073/pnas.79.14.4451
- Roubik, D., Heard, T., and Kwapong, P. (2018). "Stingless bee colonies and pollination" in *The Pollination of Cultivated Plants. A Compendium for Practitioners*. (Ed.) D. W. Roubik. (United Nation: Food and Agricultural organization of the United Nations). 2, 39–64.

- Roubik, D. W. (1982). Seasonality in colony food storage, brood production and adult survivorship: Studies of *Melipona* in tropical forest (Hymenoptera: Apidae). *J. Kans. Entomol. Soc.* 55, 789–800.
- Roubik, D. W. (1995). *Pollination of Cultivated Plants in the Tropics. Pollination of Cultivated Plants in the Tropics*. United Nation: Food and Agriculture Organization.
- Roubik, D. W. (2006). Stingless bee nesting biology. *Apidologie* 37, 124–143. doi: 10.1051/apido:2006026
- Santoro, D., Hartley, S., and Lester, P. J. (2019). Behaviourally specialized foragers are less efficient and live shorter lives than generalists in wasp colonies. *Sci. Rep.* 9, 1–10.
- Silva, M. D., and Ramalho, M. (2016). The influence of habitat and species attributes on the density and nest spacing of a stingless bee (Meliponini) in the Atlantic rainforest. *Sociobiology* 63, 991–997. doi: 10.13102/sociobiology.v63i3.1037
- Silva-Neto, C. D. M. E., Ribeiro, A. C. C., Gomes, F. L., Melo, APCd, Oliveira, GMd, Faquinello, P., et al. (2019). The stingless bee mandaçaia (*Melipona quadrifasciata* Lepeletier) increases the quality of greenhouse tomatoes. *J. Apic. Res.* 58, 9–15. doi: 10.1080/00218839.2018.1494913
- Slaa, E. J., Chaves, L. A. S., Malagodi-Braga, K. S., and Hofstede, F. E. (2006). Stingless bees in applied pollination: Practice and perspectives. *Apidologie* 37, 293–315. doi: 10.1051/apido:2006022
- Stelzer, R. J., and Chittka, L. (2010). Bumblebee foraging rhythms under the midnight sun measured with radiofrequency identification. *BMC Biol.* 8:93. doi: 10.1186/1741-7007-8-93
- Susanto, F., Gillard, T., De Souza, P., Vincent, B., Budi, S., Almeida, A., et al. (2018). Addressing RFID misreadings to better infer bee hive activity. *IEEE Access* 6, 31935–31949. doi: 10.1109/access.2018.2844181
- Takahashi, J.-I., Martin, S. J., Ono, M., and Shimizu, I. (2009). Male production by non-natal workers in the bumblebee, *Bombus deuteronymus* (hymenoptera: Apidae). *J. Ethol.* 28, 61–66. doi: 10.1007/s10164-009-0155-y
- Takahashi, J.-I., Martin, S. J., Ono, M., and Shimizu, I. (2010). Male production by non-natal workers in the bumblebee, *Bombus deuteronymus* (hymenoptera: Apidae). *J. Ethol.* 28, 61–66. doi: 10.1007/s10164-009-0155-y
- Tenczar, P., Lutz, C. C., Rao, V. D., Goldenfeld, N., and Robinson, G. E. (2014). Automated monitoring reveals extreme interindividual variation and plasticity in honeybee foraging activity levels. *Anim. Behav.* 95, 41–48. doi: 10.1016/j.anbehav.2014.06.006
- Thompson, H., Coulson, M., Ruddle, N., Wilkins, S., and Harkin, S. (2016). Thiamethoxam: Assessing flight activity of honeybees foraging on treated oilseed rape using radio frequency identification technology. *Environ. Toxicol. Chem.* 35, 385–393. doi: 10.1002/etc.3183
- Van Nieuwstadt, M., and Iraheta, C. R. (1996). Relation between size and foraging range in stingless bees (Apidae, Meliponini). *Apidologie* 27, 219–228. doi: 10.1051/apido:19960404
- Visscher, P., and Dukas, R. (1997). Survivorship of foraging honey bees. *Ins. soc.* 44, 1–5. doi: 10.1007/s000400050017
- Zanette, L. R. S., Miller, S. D. L., Faria, C. M. A., Lopez-Vaamonde, C., and Bourke, A. F. G. (2014). Bumble bee workers drift to conspecific nests at field scales. *Ecol. Entomol.* 39, 347–354. doi: 10.1111/een.12109

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2021 Oliveira, Contrera, Arruda, Jaffé, Costa, Pessin, Venturieri, de Souza and Imperatriz-Fonseca. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.