Original Article

Flight radius and climatic conditions affect the external activity of stingless bee *Melipona rufiventris* (Lepeletier, 1836)

Raio de voo e condições climáticas afetam a atividade externa da abelha sem ferrão *Melipona rufiventris* (Lepeletier, 1836)

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Abstract

The objective of this study was to verify the flight radius and the influence of the climatic season and period of the day on the external activity of *Melipona rufiventris* bees. The forager bees were released at different distances to evaluate the flight radius. The following were considered for external activities in the four different seasons of the year (Winter, Autumn, Spring, Summer): the entry with no apparent load was considered as nectar/water, entry with defined and opaque mass in the corbicula was considered as pollen, the entry with undefined and shiny mass in the corbicula was considered as resin/clay or bee exit no load and removal of debris, mass trapped by the jaws. Assessments were performed between 6 am and 6 pm each month. *M. rufiventris* can reach distances of 2 500 meters, however the return decreases as the distance increases. The species performs all activities in and out of the colony during all seasons of the year and periods between 6 am and 6 pm but reduce nectar/water collection and exit from the box without apparent load and with debris between 6:00 am and 10 am in winter. It is concluded that distances greater than 1 500 meters hinder the external activity of bees which is influenced by air temperature, air humidity, time of day, season of the year and food availability.

Keywords: foraging, meliponiculture, behavior, seasonality, extinction.

Resumo

Objetivou-se com esse estudo verificar o raio de voo e a influência da estação climática e período do dia na atividade externa das abelhas *Melipona rufiventris*. As abelhas forrageiras foram soltas em diferentes distâncias para avaliar o raio de voo. Para as atividades externas nas quatro diferentes estações do ano (Inverno, Outono, Primavera, Verão) foram consideradas: a entrada sem carga aparente como néctar/água, a entrada com massa definida e opaca na corbícula caracterizada como pólen, a entrada com massa indefinida e brilhante na corbícula caracterizada como resina/argila ou ainda a saída de abelha sem carga e remoção de detritos, massa presa pelas mandíbulas. As avaliações foram realizadas entre 6h e 18h de cada mês. *M. rufiventris* pode atingir distâncias de 2500 metros, porém o retorno diminui à medida que a distância aumenta. A espécie realiza todas as atividades dentro e fora da colônia durante todas as estações do ano e períodos entre 6h e 18h, mas reduz a coleta de néctar/água e saída caixa sem carga aparente e com detritos entre 6h e 10h no inverno. Conclui-se que distâncias superiores a 1500 metros reduzem a atividade externa das abelhas que é influenciada pela temperatura e umidade do ar, hora do dia, estação do ano e disponibilidade de alimentos.

Palavras-chave: forrageamento, meliponicultura, comportamento, sazonalidade, extinção.

1. Introduction

Bees are pollinators and producers of several products of economic interest (honey, pollen, propolis, wax, resin). Thus, bees perform various activities inside and outside the nest to produce these products, which first need to ensure that they have resources available for feeding and maintaining the colony (Mascena et al., 2018). Are considered as external activity of bees: the search for nectar, water, pollen, resin or leaving the colony with debris.

Knowing how bees prioritize the external activity can help in their breeding/raisin, management and preservation of the species. Climatic conditions vary between seasons (seasonality), and this variation interferes with the foraging

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Received: June 16, 2023 – Accepted: November 30, 2023

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behavior of bees. Knowing the behavior of bees throughout the year helps in establishing the floral calendar and in choosing the times when bees bring less food resources and must be supplemented so as not to drastically reduce the number of individuals in the colony (Freitas et al., 2020).

Many studies on foraging and external activity are currently being conducted with *Apis mellifera*, the most important bee from the standpoint of beekeeping, but the biology and behavior of stingless bees (Apidae, Meliponini) are hardly known, especially in Central and South America (Vit et al., 2013). The comparison between exotic bees, in the case of *A. mellifera*, and native bees has also been poorly studied since certain climatic conditions can benefit native species more, but the opposite can also occur. Studies demonstrating competition between *A. mellifera* and *Trigona spinipes* for resin collection from *Clusia rudae* Planchon & Triana (Clusiaceae) in Minas Gerais, Brazil have already been reported (Carmo and Franceschinelli, 2002).

It is already known that high air temperature limits the foraging activity of stingless bees in tropical environments, including the direct effects of solar radiation and winds. Nevertheless, the activity of this group in situations of elevated temperatures (above 30°C) already suggest they have thermoregulation mechanisms, since this climatic condition is frequent in the tropics (Souza-Junior et al., 2020).

In addition to seasonality issues, few studies on stingless bees have been conducted for the Cerrado biome. So far only our work has been conducted with a focus on feeding and management for *M. rufiventris* (Freitas et al., 2020, 2021). This species, as well as other stingless bees in the Cerrado, have characteristics and particularities that influence their management and consequent production. As a relevant aspect, *M. rufiventris* is today considered by environmental agencies in Brazil as an endangered species and should be protected, since it is a docile and productive species, and very much extracted from nature by responsible beekeepers (people who only extract the nests without concern for their conservation). Thus, understanding the management of this species also contributes to its conservation (Freitas et al., 2020; ICMBIO, 2016).

The effect of climatic conditions on the behavior of external activity of native bees is clear. As there are specificities of bees and local conditions according to each biome, carrying out new studies is of fundamental importance, including in the Cerrado (Freitas et al., 2020). In studies carried out with the Plebeia pugnax Moure (In Litt.) bee in the Atlantic Forest region, the authors highlighted that the external activity intensifies, that is, the number of bees in external activity increases with the increase in temperature up to 22°C, and remains constant between 22° and 34°C (Hilário et al., 2001). Another study with stingless bees performed with Scaptotrigona aff. depilis (Moure, 1942) also showed a temperature reduction effect on its foraging activity. At lower temperatures, there is less external movement, which generates less pollen and honey storage inside the colony (Aleixo et al., 2016).

Seasonality also influences of the behavior of external activity of bees, which consequently influences the development and maintenance of colonies. Understanding this seasonality influence on the behavior of different bee species can help preserve species, especially those that are in danger of extinction, such as *Melipona rufiventris* (Lepeletier, 1836) (ICMBIO, 2016), in addition to native to the Cerrado biome. Thus, the aim of this study was to verify the effect of seasonality on the flight distance and external activity of *M. rufiventris* bees raised in the Cerrado.

2. Materials and Methods

2.1. Study location

The study was divided into two steps (experiment 1 and experiment 2). The first one estimated the possible flight distance of the *M. rufiventris* bee, while the second one verified its foraging activity throughout the year. Both studies were carried out in the meliponary located at the geographic coordinates 15°21'7.5"S latitude and 49°36'0.3"W longitude and at 790 m altitude, close to the GO 154 highway, km 3, Rural Area, in the municipality of Ceres-GO, Brazil, from September 2015 to August 2016.

The study was conducted in the cerrado biome, the second largest biome in Brazil and the only savanna biome in the country. The cerrado is characterized by the presence of dry winter and rainy summer, with vegetation that encompasses forest, savanna, and rural physiognomies (Ribeiro and Walter, 2008). We can report here some melliferous flower species found abundantly in the region to characterize the location: *Inga vera* Willd., *Croton urucurana* Bail., *Didymopanax macrocarpum* (Cham. & Schltdl.) Seem., *Guazuma ulmifolia* Lam., *Cordia sellowiana* Cham, *Terminalia glabrescens* Mart., *Tapirira guianensis* Aubl., *Zanthoxylum rhoifolium* Lam. and *Albizia hasslerii* (Chod.) Burkart, as well as non-arboreal species such as *Vernonanthura polyanthes* (Sprengel) Vega & Dematteis (Pereira et al., 2015; Siqueira et al., 2021).

2.2. Experiment 1

Five *M. rufiventris* colonies already established for more than a year were selected from the Fernando Oliveira – Instituto Nacional de Pesquisas da Amazônia (INPA) rational box model with internal measurements of 18 cm depth X 18 cm width X 7 cm height for each compartment, cm height for each compartment (two compartments), being hive body and upper hive, with floor and roof symmetrical to the area of the box (Figure 1).

Next, 50 forager bees from each colony were captured and marked with non-toxic paint on the thorax (POSCA Permanent Pen, UNI, Marker Pen PC-7M, Bullet Bold Tip, 4.5mm to 5.5mm stroke) (Figure 2) and released at different distances to determine the flight distance, with 10 bees released at 500 m, 10 at 1 000 m, 10 at 1 500 m, 10 at 2 000 m and 10 at 2 500 meters from the meliponary (Figure 3). The bees were released in the northwest direction. The bees were released in the northwest direction, at 6 am.

Colonies were closed at night and opened just before 6am, the time when the foragers that left for outdoor activities were captured. The first bees that came out were captured, and they were only discarded if they had some normality in the wings. The bees were taken to the release site immediately after capture (Figure 2 and 3) according



Figure 1. Box Fernando Oliveira (INPA) of 18 cm depth X 18 cm width X 7 cm height for each compartment (two compartments).



Figure 2. Colored marking on *M. rufiventris* with non-toxic staining for experiment one.

to their color. Then, the return of the bees to the colony was verified within 24 hours and 48 hours after release (Adapted from Roubik and Aluja (1983). By returning to the nest the bees had flown these distances and knew their way back. In the incessant search for food, as we can travel several km per day, they can thus be guided using reference points and use of the sun (Pahl et al., 2011). The entire procedure was repeated four times at 60-day intervals, totaling the release of 200 forager bees per colony (40 individuals per distance).

2.3. Experiment 2

A total of four *M. rufiventris* colonies were selected for the study, which were already established in rational boxes with the same characteristics and dimensions of the boxes used in experiment 1. We opted for a completely randomized design in a 4x3 factorial scheme (seasons x periods of the day). The seasons were winter, spring, summer and autumn, and the periods of the day were considered the intervals from 6 am to 10 am, from 10 am to 2 pm, and from 2 pm to 6 pm, according to a study carried out with *Melipona fascicultata* (Smith) in the Cerrado region (Vit et al., 2013).

The climate data were collected from the INMET in the location of Itapaci, GO, located 40 km from the study site, to define the weather conditions closest climate data to reality. The data are described in the Table 1 (INMET, 2021).

Visual methods were used to count the number of bees that entered and left the colony. The method consists of simultaneous observations of four colonies per hour, 10 minutes for calculating the flow of bees and 5 minutes for checking weather conditions. The evaluator positioned himself next to and 80 cm from the colony entrance hole to record the flow. The entry and exit of bees were considered



Figure 3. Demarcated area for the release of bees at different distances from the meliponary. 500 meters (identified with the white color), 1 000 meters (identified with the yellow color), 1 500 meters (identified with the blue color), 2 000 meters (identified with the red color), 2 500 meters (identified with the green color) the meliponary.

Climate parameters	Winter	Autumn	Spring	Summer
Avg. Temp. (C)	23.78	24.97	26.72	24.83
Max Temp. (C)	24.72	25.72	27.48	25.40
Min Temp. (C)	22.87	24.26	26.00	24.31
Avg. Hum. (%)	55.90	71.43	66.40	80.32
Max. Hum. (%)	59.95	75.01	70.10	83.17
Min. Hum. (%)	52.06	67.80	62.66	77.30
Wind Vel. (m/s)	1.17	0.98	1.51	1.33
Rain (mm)	161.80	248.40	186.20	174.20
Radiation (KJ/m²)	1444.61	1581.34	1601.81	1497.17

Table 1. Mean values per season of climate parameters (except precipitation, which is the sum of the total volume for the period).

external activities. The evaluator or other members of the research team could not pass in front of the colonies, as this could modify behavior or even force the workers to enter other colonies (Carvalho and Marchini, 1999).

The resources transported by worker bees were identified based on the characteristics of each material: resin/clay = undefined and shiny mass loaded in the corbicula; pollen = opaque defined mass charged in the corbicle; debris = removal of debris trapped by the jaws. Nectar/water transport was assigned to individuals who entered the colony without apparent charge.

The climatic factors measured at the site were: ambient temperature (°C) and air humidity (%), measured every 15 minutes with the aid of a thermo-hygrometer of maximum and minimum temperature and relative humidity (%). The instrument was installed in the on-site mediations and data were collected at the observation interval of each colony.

2.4. Statistical analysis

A regression test of the number of bees that returned to the colony in 24 and 48 hours was applied for the flight radius data in relation to the different release distances (500, 1 000, 1 500, 2 000 and 2 500m), with the regression coefficient (R^2) and statistical significance (95%) being observed. The normality of the residuals was verified by the Shapiro-Wilk test for the other variables. We chose to use the non-parametric Kruskal-Wallis test to compare periods and seasons due to the lack of normality found in the results.

The multivariate analysis of canonical components (CCA) was also used to study the relationships between periods, seasons and loads collected by the bees. A 95% significance level was considered. A correlation analysis was subsequently performed between the same attributes, observing the correlation coefficient and statistical significance pair by pair (95%).

3. Results

M. rufiventris can reach at least 2 500 meters away from their nest. Even so, it is noteworthy that the greater the



Figure 4. Return regression for *Melipona rufiventris* 24 and 48 hours after release at different release distances.

distance from the nest, the lower the return of individuals, since distances above 1 000m are already considered distant for this species. Some individuals only returned on the second day (after 48 h), however most returned within the first 24 hours. The return of individuals was not higher than 80% even at short distances (500 m) (Figure 4).

The season of the year and period of the day influenced the bees' search for resources needed to maintain the colony. It is possible to observe that the number of bees involved in the search for nectar/water in all seasons and periods of the day was greater than those involved in the search for pollen. Likewise, the number of bees foraging for pollen was greater than the number of bees seeking resin/clay in all seasons of the year and period of the day (Table 2).

The average number of total bees entering the colony with resin/clay was higher in spring with 638, followed by summer 351, autumn 147 and winter 83, with a spring and summer being the wettest periods in the Cerrado, increasing clay production in the surroundings. Bees followed the same behavior for pollen collection (1162,488 bees in spring, 859 in summer, 431 in autumn and 169 in winter), however the number of bees collecting pollen between 6 am and 2 pm in spring and summer was similar. The mean values and standard deviations of all variables collected by the bees are described in Table S1 of the supplementary material.

The search for nectar/water was influenced by the time of day only in winter, where the number of bees

Entered with resin/clay	Seasons of the year				
Period	Winter	Spring	Summer	Autumn	p-value
6 am-10 am	8Ad	68Aa	396Ab	21Ac	< 0.001
10 am-2 pm	5Ac	46Aa	27ABb	6Bc	< 0.001
4 pm–6 pm	6Ab	44Aa	21Bb	8Bc	< 0.001
p-value	0.899	0.053	0.033	< 0.001	
Entered with pollen					
Period	Winter	Spring	Summer	Autumn	p-value
6 am-10 am	15Ac	125Aa	128Aa	57Ab	< 0.001
10 am-2 pm	18Ab	79Aa	58Ba	25Bb	< 0.001
2 pm–6 pm	8Ac	85Aa	28Cb	24Bb	< 0.001
p-value	0.067	0.244	< 0.001	<0.001	
Entered with nectar/water					
Period	Winter	Spring	Summer	Autumn	p-value
6 am- 0 am	63Bb	180Aa	263Aa	193Aa	< 0.001
10 am-2 pm	240Aa	123Ab	235Aab	156Aab	0.016
2 pm–6 pm	263Aa	139Ab	153Aab	245Aa	< 0.001
p-value	< 0.001	0.379	0.216	0.027	

Table 2. Average number of *Melipona rufiventris* bees collecting (per hour) resin/clay, pollen or entering with nectar/water (no apparent load) at three different times of day in four different seasons.

Different uppercase letters in the column and lowercase letters in the row differ statistically from each other by the Kruskal-Wallis test at the 5% probability level (p<0.05).

performing this type of activity was much lower between 6 am and 10 am. The number of bees collecting nectar/ water in the other periods of the winter day (10 am-2pm, 2 pm-6 pm) was higher among all periods, considering that it was higher in this period than the number of bees collecting nectar/water in spring (Figure 4).

The number of bees leaving the colony without apparent load was greater than the number of bees leaving with debris (Table 2). The average number of total bees leaving the colony without apparent load in spring (3 244) and summer (3 411) was higher than in winter (2 198) and autumn (2 871) (Table 3).

During the experiment data collection, the temperature and humidity were the variables that showed the greatest variance. Regarding bee behavior, resin and clay collection was the behavior that responded to seasonal and environmental variations (Figure 5). Relating the climatic variables with bee activity, temperature was correlated with resin/clay (-0.376), pollen (-0.393) and output without (-0.336) and humidity related to pollen (0.402) (Table 4). Among the activities of the bees, pollen with resin (0.843), with water (0.449), leaving with nothing (0.778) and leaving with nothing with collecting water/ nectar (0.854) were related.

4. Discussion

The period of the day and the season of the year influence the external activity of *M. rufiventris*. Colder, drier days change the bee's behavior, reflecting on the outside activity. Colder days reduce activity during the coldest hours of the day, but dry days mean that *M. rufiventris* must go out more often to get water. Nevertheless, these are some of the variables that influence the behavior of this species. Note that there are other factors that can interfere with this behavior, including food availability in the Cerrado biome, which is linked to seasonality. *M. fasciculata* showed the same behavioral patterns found for *M. rufiventris* in a comparison with the only external and foraging activity study ever conducted in the Cerrado with stingless bees (Freitas et al., 2020).

Few studies also demonstrate the flight and foraging capacity of stingless bees in Brazil, especially for the Cerrado. These characteristics are fundamental for stingless bee breeding in the biome to define the foraging area of each species. In addition, the flight radius also partly defines the potential of the area that influences the bee colony, whether from the influence of an agricultural environment with pesticides, or even for defining priority areas for the conservation of this group (Franceschinelli et al., 2017; Santos et al., 2021).

In this work, we suggest that *M. rufiventris* can reach flights of at least 2.5 km of distance, with its preferential foraging radius of 1 km. These distances are even higher than suggested by (Kuhn-Neto et al., 2009) of 2.1 km of flight distance for *Melipona mandacaia* in the Amazon rainforest. Found that the typical flight distance for *M. fasiculata* is approximately 2 km, also for the Amazon Forest

Leaving without Apparent Load			r		
Period	Winter	Spring	Summer	Autumn	p-value
6 am-10 am	82Bb	384Aa	389Aa	288Aa	< 0.001
10 am-2 pm	246Aa	200Ba	270Ba	169Ba	0.384
2 pm-6 pm	221Aa	226Aba	192Ba	259Aa	0.179
p-value	< 0.001	0.021	< 0.001	0.001	
Leaving with debris					
Period	Winter	Spring	Summer	Autumn	p-value
6 am-10 am	0.5Bb	11Aa	9Aa 5Ba		< 0.001
10 am-2 pm	16Aa	10Aa	10Aa 14Ba		0.768
2 pm–6 pm	19Aa	8Ab	11Aab 19Aab		0.009
p-value	< 0.001	0.792	0.8477	0.005	

Table 3. Average number of *Melipona rufiventris* bees (per hour) leaving the colony with no apparent load or with debris at three different times of day in four different seasons.

Different uppercase letters in the column and lowercase letters in the row differ statistically from each other by the Kruskal-Wallis test at the 5% probability level (p<0.05).

Table 4. Correlation of climate attributes evaluated on site with bee collections.

	Temperature	Humidity	Resin/Clay	Pollen	Water/ Nectar	Output_ without	Exit_with_ debris
Temperature	0	0.00	0.023	0.017	-	0.044	-
Humidity	-0.800	0	-	0.014	-	-	-
Resin/Clay	-0.376	0.302	0	0.00	-	0.00	-
Pollen	-0.393	0.402	0.843	0	0.005	0.00	-
Water/Nectar	-0.144	0.117	0.253	0.449	0	0.00	0.039
Output_without	-0.336	0.303	0.639	0.778	0.854	0	-
Exit_with_debris	-0.100	-0.000	0.042	0.015	0.344	0.241	0



Figure 5. Canonical variables: Different seasons, periods and outdoor activities of the *Melipona rufiventris* bee (E1P1 - winter from 6 am to 10 am, E1P2 - winter from 10 am to 2 pm, E1P3 - winter from 2 pm to 6 pm, E2P1 - spring from 6 pm am to 10 am, E2P2 - spring from 10 am to 2 pm, E2P3 - spring from 2 pm to 6 pm, E3P1 - summer from 6 am to 10 am, E3P2 - summer from 10 am to 2 pm, E3P3 - summer from 2 pm to 6 pm, E4P1 - autumn 6 am to 10 am, E4P2 - autumn 10 am to 2 pm, E4P3 - autumn 2 pm to 6 pm). TEM – Temperature, UR – Humidity, ERES – collection of resin/clay, EPOL – collection of pollen, ESCA – water/nectar ilet, SSCA – output without apparent load, SD – exit with debris.

(Nunes-Silva et al., 2020). We highlight here that both the body size and species habits can interfere with the flight and foraging distance, but also the matrix in which they are found will also greatly affect this dynamic. In view of this, the importance of initiating studies with flight activity and foraging for stingless bees is especially important for the Cerrado biome, as it is a savanna vegetation which is very different from a tropical forest.

In relation to seasonality, herein we suggest that behavior changes in bees occur through both the change in the effect of climate, and from the effect of seasonality on the resources sought by bees. In this case, studies conducted with the *Scaptotrigona depilis* bee showed that the availability of floral resources modifies its foraging behavior, with its main collections being carried out in the rainy season, but for rainforest vegetation (ICMBIO, 2018). There are species flowering throughout the year in the Cerrado; however, the abundance of floral resources is higher during the dry period (autumn and winter) than months with higher rainfall intensity (spring and summer) (Siqueira et al., 2021).

Even so, climate and microclimatic changes alter the behavior and performance of bees. As we found in this study, other studies have also shown that bees reduce their search for nectar in the early hours of the day in winter, but the same does not happen when searching for pollen or resin/clay. Studies conducted with *Trigona carbonaria* Smith, F., 1854 show that bees prefer to absorb nectar at warmer temperatures (up to 30°C), since nectar collected on colder days or periods decreases the chest temperature needed for the flight (Norgate et al., 2010).

Other climatic factors can also contribute to change the behavior of bees. Certain rainy conditions or a lack of moisture may lead bees to stop carrying out outdoor activities. *Plebeia pugnax* perform their outdoor activity in all humidity between 30% and 100%, however the activity tends to decrease when the humidity exceeds 50% (Aleixo et al., 2016). The mobilization of a greater number of bees to search for nectar/water in relation to the search for pollen was already expected, as it is easily observed by meliponiculturists, especially in the dry winter of the Cerrado. This fact has already been evidenced in several studies, for example those conducted with *Trigona collina* Smith, F., 1857. and *Trigona iridipennis* Smith (Smith, 1854) (Nagamitsu and Inoue, 2002).

Other behavioral changes can be related to momentary microclimatic conditions, changing some patterns in the colonies. For example, the number of bees cleaning the box in winter (exiting with debris) is reduced in the early hours of the day in winter, probably due to the low temperature; this pattern occurs in *M. rufiventris*, even though Brazilian Cerrado winters do not have very low temperatures (average minimum of ~22°C, possible minimum of 12°C).

In works with other stingless bees in formations in Brazil, it is noted that the species are adapted to the climatic conditions of each region. The *Melipona subnitida* Ducke, 1910 survive and forage at elevated temperatures in the Tropical Humid Forest (Amazon), and even present high production and foraging activity (Maia-Silva et al., 2015). The *M. asilvai* Moure, 1971 reduces its foraging activity by almost 90% in the rainy season, but without observing a direct relationship with temperature and humidity (Nascimento and Nascimento, 2012). The authors attribute it to other factors such as phenological and even physiological factors of the species (Diapause).

For other Brazilian biomes, *Melipona bicolor* has been studied in an Araucaria Forest area in southern Brazil. The species has its most intense activity during spring and summer, while in autumn and winter they are reduced (Witter et al., 2021). Thus, it is evident that stingless bee species are strongly influenced by seasonality in other Brazilian biomes, whether it is the rains of the Amazon Forest or the cold of the southern region, but each species is adapted to its condition. *M. rufiventris* from the Cerrado region are also affected by seasonal changes, but they change their behavior throughout the day to avoid worse conditions, such as cold or low humidity.

This behavior and alteration in activity peaks can also be observed even in stingless species that nest in the ground such as *Geotrigona subterranea* (Friese, 1901), which has its activity peak between 1 and 2 ap, being considered hot hours of the day (Barbosa et al., 2016). There are still few studies between bees in natural and bred environments, or different nests for the comparisons of behavior and external activity to be deepened.

Another relevant aspect that we draw attention to in this study is the lack of studies on stingless bees from the Brazilian Cerrado. In addition to no studies on external activity except our studies with *M. fasciculata* (Freitas et al., 2021), there are no other studies on any species, nor on flight activity or foraging, and a lack of knowledge about the species that occur here.

5. Conclusions

Variations in air temperature and humidity alter the external activity of *Melipona rufiventris* bees. The entry of bees with resin/clay, pollen and nectar/water in the colony is similar at all times of the day in spring. We also found that the external activity of bees is influenced by weather conditions and food availability.

Acknowledgements

The authors thank CNPq and the Instituto Federal Goiano for financial support. The author Carlos de Melo e Silva Neto thanks CNPq for continuing the productivity grant.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Average number of Melipona rufiventris bees collecting (per hour) resin/clay, pollen, entering with nectar/ water (no apparent load), Output without apparent load and exit with debris at three different times of day in four different seasons. E1P1 - winter from 6 am to 10 am, E1P2 - winter from 10 am to 2 pm, E1P3 - winter from 2 pm to 6 pm, E2P1 - spring from 6 pm am to 10 am, E2P2 - spring from 10 am to 2 pm, E2P3 - spring from 2 pm to 6 pm, E3P1 - summer from 6 am to 10 am, E3P2 - summer from 10 am to 2 pm, E3P3 - summer from 2 pm to 6 pm, E4P1 - autumn 6 am to 10 am, E4P2 - autumn 10 am to 2 pm, E4P3 - autumn 2 pm to 6 pm).

This material is available as part of the online article from https://doi.org/10.1590/1519-6984.275645.