



RESEARCH ARTICLE - BEES

Climatic Factors and the Extranidal Activities of the Native Bee *Plebeia catamarcensis* (Hymenoptera: Apidae)

GABRIELY N. ARAÚJO^{1,2}, DIEGO M. VICENTE², KAMYLLA B. MICHELUTTI², MICHELE C. PAULA-SILVA³, SIDNEI E. LIMA-JUNIOR³, WILLIAM F. ANTONIALLI-JUNIOR^{1,2,3}

1 - Programa de pós-graduação em Entomologia e Conservação da Biodiversidade, Universidade Federal da Grande Dourados, Dourados-MS, Brazil

2 - Universidade Estadual de Mato Grosso do Sul, Laboratório de Ecologia Comportamental, Dourados-MS, Brazil

3 - Universidade Estadual de Mato Grosso do Sul, Faculdade de Ciências Biológicas, Dourados-MS, Brazil

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Corresponding author

GABRIELY N. ARAÚJO 

Programa de pós-graduação em Entomologia e Conservação da Biodiversidade, Universidade Federal da Grande Dourados, Unidade II

Rodovia Dourados/Itahum, Km 12

Caixa Postal: 364, CEP: 79.804-970

Dourados, Mato Grosso do Sul, Brasil.

E-Mail:

gabriely.araujo055@academico.ufgd.edu.br

Abstract

Stingless bees collect a variety of resources, mostly from plants, for nest construction, hydration, and the feeding of immatures and adults. They also commonly dispose of waste from their colonies. These activities are directly influenced by abiotic factors, which can determine different foraging patterns. Given the current climate change, understanding how physical climatic factors affect bee behavior is extremely relevant. Therefore, this study aimed to investigate how physical climatic factors influence the foraging patterns of the native bee species, *Plebeia catamarcensis* (Holmberg). To achieve this, eight colonies were monitored three times a month from August 2022 to April 2024, with observations conducted from 6:00 to 18:00. The number of foragers entering and leaving the nest was recorded, and the types collected were identified, as well as the conditions of temperature, relative humidity, and light. Temperature and light intensity showed a significant positive correlation with the species' extranidal activity, indicating increased resource collection as these variables rise. Conversely, a negative correlation was observed between relative humidity and activity: as relative humidity increased, activity decreased. The results confirm the hypotheses: the behavior of *P. catamarcensis* foragers is modulated by climatic factors, and a combination of factors acting in concert likely determines the pattern and timing of different extranidal activities.

Introduction

In tropical environments, bees are typically the most abundant floral visitors (Hrncir & Maia-Silva, 2013). For social species, a colony's survival largely hinges on the success of its foragers in collecting resources (Hrncir & Maia-Silva, 2013). Stingless bees, for instance, depend on various plant-derived resources to build their nest structures and feed their brood and adults (Menezes et al., 2023). Foragers leave their colonies to gather essential resources such as food (pollen and nectar), water, and construction materials (like resin and mud), and to remove debris (Hilário et al., 2001).

Foraging activity can vary seasonally throughout the year, and climatic factors such as temperature, light intensity, wind speed, rain, and relative humidity, as well as the availability of plant resources, influence extranidal activities (Aleixo et al., 2017; de Moura et al., 2024).

Intranidal factors, such as colony size and the amount of stored food, also influence these activities and determine different foraging patterns among various bee species (Nunes-Silva et al., 2010). In this regard, a colony's ability to control its internal temperature also affects when its activity begins (Campos et al., 2010; Mota et al., 2023). Species that regulate temperature effectively start their activities earlier



because external temperature is less critical for them. Conversely, species with less efficient temperature control only begin foraging once the nest's interior reaches an appropriate temperature (Campos et al., 2010; Mota et al., 2023). Furthermore, a bee's body size also influences these activity patterns. Relatively larger-bodied bee species start their activities earlier at lower temperatures compared to smaller species, which wait for higher temperatures to begin foraging (Teixeira & Campos, 2005).

Stingless bees, also known as native bees, are part of the family Apidae, tribe Meliponini. These are relatively small bees, with body lengths ranging from 2 to 10 mm, making them among the smallest known bee species (Carrano-Moreira, 2015). Meliponini species exhibit eusocial behavior and are typically found in tropical and subtropical regions. In the Neotropics, approximately 60% of these species inhabit tropical forests, displaying a wide variety of shapes, sizes, and nesting habits (Grüter, 2020). The link between foraging activity in native stingless bees and climatic factors has been documented for several species within the genus *Plebeia* Schwarz, 1938. Examples include studies by Teixeira and Campos (2005) on *Plebeia droryana* (Friese, 1900) and *Plebeia lucii* Moure, 2004; by Silva et al. (2019) on *Plebeia* aff. *flavocincta*, and by Zeballos et al. (2022) on *Plebeia catamarcensis* (Holmberg, 1903).

Bees of the genus *Plebeia* are commonly known as “mirins” and typically build their nests in tree hollows, stone walls, and embankments (Nogueira-Neto, 1997). *P. catamarcensis* is a relatively small bee that nests in highly conductive urban substrates, specifically concrete walls. There are a few studies on the biology of this particular species. Existing research includes a study on the behavior of orphaned colonies (Pinho et al., 2010), on the effect of heat islands on flight and foraging activities (Zeballos et al., 2022), and a more recent study on the effect of neonicotinoids on their colonies (Paula et al., 2023).

Considering the current periods of significant global climate change, it's crucial to understand how abiotic climatic factors influence foraging behavior. Therefore, this study aimed to test the following hypotheses: (i) the extranidal activities of this species are significantly influenced by variations in temperature, relative humidity, and light intensity; (ii) the peak of extranidal activities, especially foraging, will occur during the hottest parts of the day, regardless of the season; (iii) Foragers modify the frequency of resources collected based on climatic conditions during different seasons.

Materials and Methods

Study Area

This research was conducted at the meliponary of the Laboratório de Ecologia Comportamental (LABECO) on the campus of the State University of Mato Grosso do Sul (22°13'18" S, 54° 48' 23" W). This location is in the municipality of Dourados, Mato Grosso do Sul state, Brazil.

The region is considered a transition zone between the Cerrado and Atlantic Forest biomes. According to Zavatini (1992), the climate is classified as humid subtropical, with a hot, wet season from November to April and a cold, dry season from May to October.

Data Collection

The observations were conducted between August 2022 and April 2024, covering nine months of the dry and cold season and nine months of the hot and wet season. Eight *P. catamarcensis* stingless bee colonies were monitored to assess extranidal activity by counting the number of workers leaving and entering the nest. Three observation sessions, each lasting 12 hours (from 6:00 to 18:00), were held monthly, resulting in a total of 54 observation days and 648 accumulated hours of observation.

Each colony was observed for the first 15 minutes of every hour, rotating among them to ensure no single colony was analyzed at the same time slot repeatedly. At the start of each session, the temperature (°C), relative air humidity (%), and light intensity (Lx) were recorded using an HM 6300 multiparameter meter (Highmed). All parameter values were measured at the nest entrance. The resources that foragers either brought to or removed from the colony were identified, classifying them according to the methodology proposed by Carvalho-Zilse et al. (2007): a) waste disposal (hygienic behavior), which was noted when a bee left the colony carrying any material; b) pollen or resin transport, which occurred when a bee returned with a visible load in its corbicula. The specific load was identified following Barbosa et al. (2020), where pollen is recognized by its granular appearance, and resin by its vitreous look; c) nectar or water collection, bees that showed no visible material load but exhibited an apparent abdominal distension, indicating they were collecting nectar or water. For bees without visible abdominal distension, nectar collection was inferred by calculating the difference between the number of bees leaving the nest carrying waste and the number of bees returning with water and nectar (Nunes-Silva et al., 2010).

Statistical Analysis

To evaluate significant differences in the frequency of extranidal activities throughout the day, we applied a Kruskal-Wallis test ($\alpha = 0.05$), followed by Dunn's a posteriori test to compare multiple periods. The results were presented graphically, using different lowercase letters to indicate significant differences among hours. Next, we performed a Spearman's correlation analysis ($\alpha = 0.05$) to check for significant correlations between environmental variables (temperature, light intensity, and relative air humidity) and extranidal activities. We conducted all analyses using Statistica 14 software (Tibco, 2020).

Results

A total of 53,759 extranidal activities were recorded across eight colonies throughout the entire observation period,

spanning both seasons. Specifically, 29,472 activities were logged during the hot and wet season, and 24,287 during the cold and dry season. These activities were categorized into departures from and arrivals at the nest, as detailed in Table 1. Furthermore, they were divided into foraging (resource collection) and waste-disposal activities.

During the cold and dry season, foraging activity began at 8:00 and concluded at 16:00. In contrast, during the hot and wet season, activities started earlier at 6:00 and extended until 18:00 (Fig 1). Climatic factors significantly influenced extranidal activities, showing a significant positive correlation with temperature in both seasons. During the hot and wet season, the correlation was $rs = 0.40$ ($p < 0.05$).

Activity peaked between 11:00 and 13:00 (Fig 1), with median temperatures ranging between 29 and 32 °C (Fig 2). In the cold and dry season, the correlation was $rs = 0.65$ ($p < 0.05$). The peak activity was observed between 13:00 and 14:00 (Fig 1), where the median temperature was around 26 °C. Extranidal activities also showed a significant positive correlation with light intensity in both seasons. During the hot and wet season, the correlation was $rs = 0.11$ ($p < 0.05$). The peak of extranidal activity occurred from 11:00 to 13:00 (Fig 1), with a median light intensity between 1,100 and 1,250 lx (Fig 3). In the cold and dry season, the correlation was $rs = 0.40$ ($p < 0.05$). The peak occurred between 13:00 and 14:00 (Fig 1), with a median light intensity of approximately 1,200 lx (Fig 3).

Table 1. Absolute number of nest entries and exits (extranidal activities) performed by *Plebeia catamarcensis* workers over the two seasons.

Season	Activity Onset ¹	Entries ²	Departures ³	Extranidal Activities ⁴
Hot and wet	6:00	15,681	13,791	29,472
Cold and dry	8:00	12,247	12,040	24,287

¹Activity onset time; ²total number of returning Bees; ³total number of exiting bees; ⁴total extranidal activities per season.

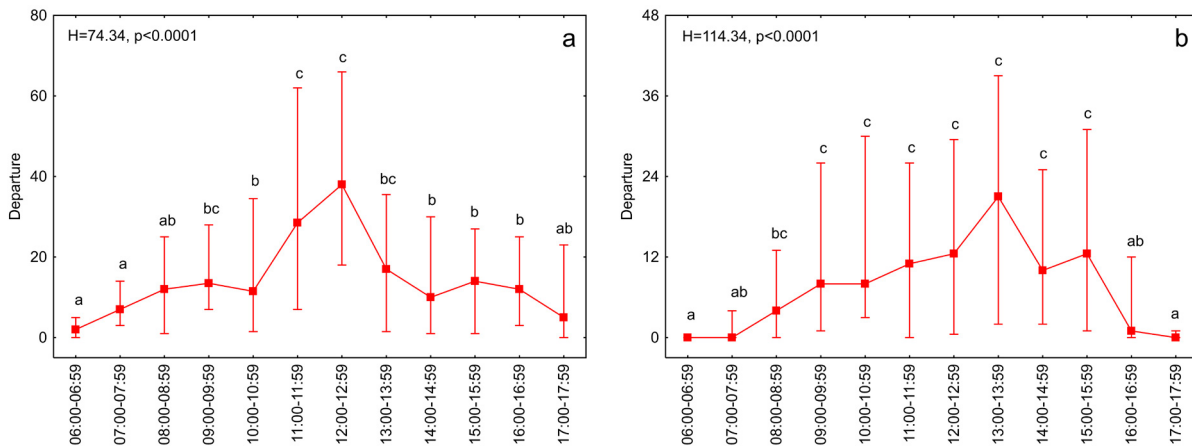


Fig 1. Medians and interquartile ranges of the frequency of nest exits (extranidal activities) of *Plebeia catamarcensis* workers throughout the day, from 6:00 to 18:00, during the: a) hot and wet season; and b) cold and dry season. Different lowercase letters indicate significant differences among hours according to the Kruskal-Wallis test followed by Dunn's post hoc test ($p < 0.05$).

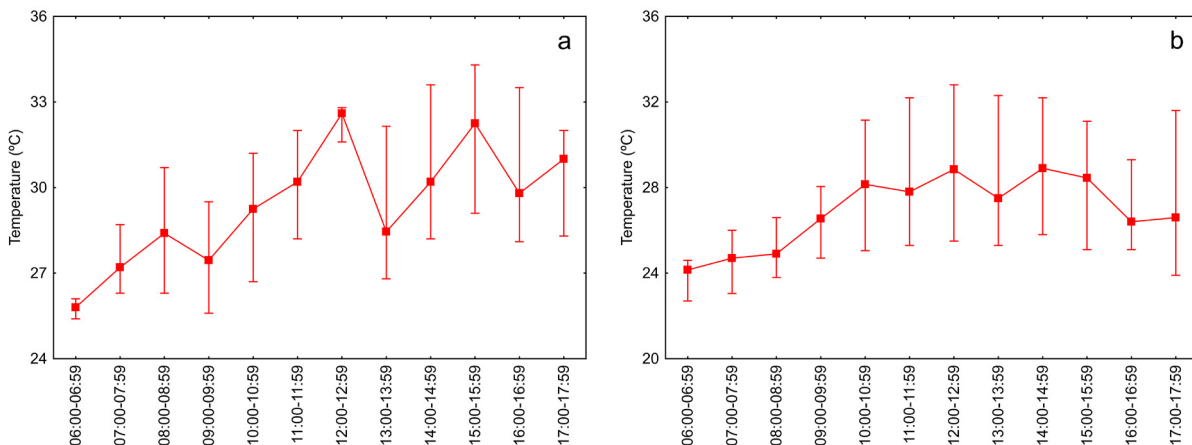


Fig 2. Medians and interquartile ranges of temperature values as a function of hours throughout the day in the two seasons: a) hot and wet; and b) cold and dry.

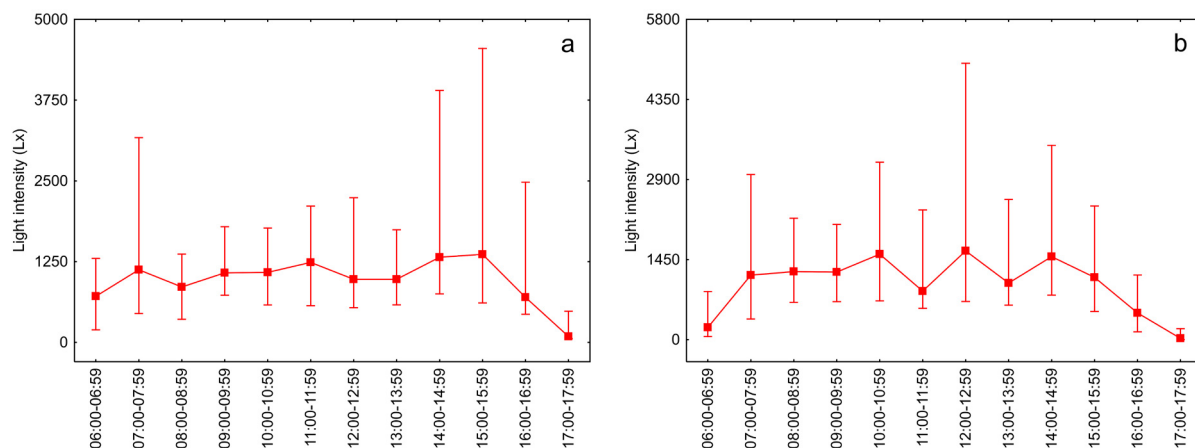


Fig 3. Medians and interquartile ranges of light intensity values as a function of hours throughout the day in the two seasons: a) hot and wet; and b) cold and dry.

On the other hand, despite extranidal activities showing a significant correlation with relative air humidity, this correlation was negative in both the hot and wet season ($r_s = -0.24$; $p < 0.05$) and the cold and dry season ($r_s = -0.49$; $p < 0.05$). The peak of activity occurred from 11:00 to 13:00 (Fig 1), with median humidity values of around 60%-65% (Fig 4) in the hot and wet season and approximately 60% (Fig 4) in the cold and dry season. The median number of items collected or discarded by the colony across seasons is shown in Figs 5 and 6, with water, nectar, and pollen highlighted during these periods. According to Table 2, there is a significant correlation between all climatic parameters and the items collected and discarded during extranidal activities.

Discussion

Our results indicate that climatic factors affect the extranidal activities of *P. catamarcensis* in different ways. Specifically, factors such as temperature and light intensity correlate positively with increases in extranidal activity, whereas relative humidity correlates negatively. In the hot and wet season, extranidal activities begin after 6:00 (Fig 1), when temperatures are above 24 °C (Fig 2), light intensity is approximately 1,000 lx (Fig 3), and relative humidity is below 73% (Fig 4). In the cold and dry season, these activities start later, after 8:00 (Fig 1), under similar temperature conditions (also above 24 °C; Fig 2), with light intensity around 1,300 lx (Fig 3), but with relative humidity below 66% (Fig 4).

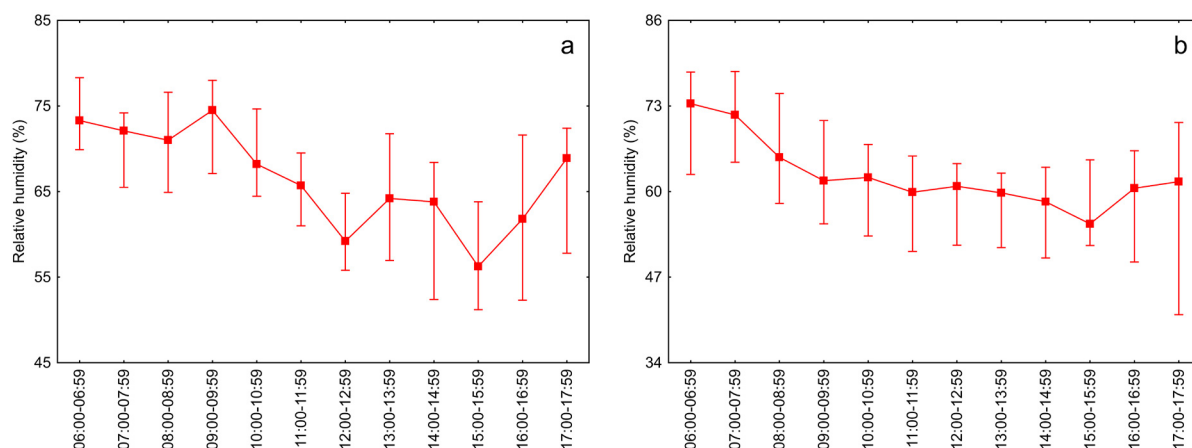


Fig 4. Medians and interquartile ranges of relative air humidity values as a function of hours throughout the day in the two seasons: a) hot and wet; and b) cold and dry.

Table 2. Spearman's Correlation between resources collected throughout the day by *Plebeia catamarcensis* workers and seasonal climatic factors. All calculated coefficients were statistically significant ($p < 0.05$).

Abiotic factors	Hot and wet season				Cold and dry season			
	Water/nectar ⁴	Pollen	Resin	Debris ⁵	Water/nectar ⁴	Pollen	Resin	Debris ⁵
°C ¹	0.43	0.26	0.31	0.38	0.68	0.55	0.42	0.44
UR% ²	-0.26	-0.12	-0.23	-0.26	-0.48	-0.43	-0.31	-0.37
LX ³	0.16	0.17	0.13	0.11	0.40	0.35	0.18	0.16

¹Temperature; ²relative air humidity; ³light intensity; ⁴water or nectar; ⁵waste discard (hygienic behavior).

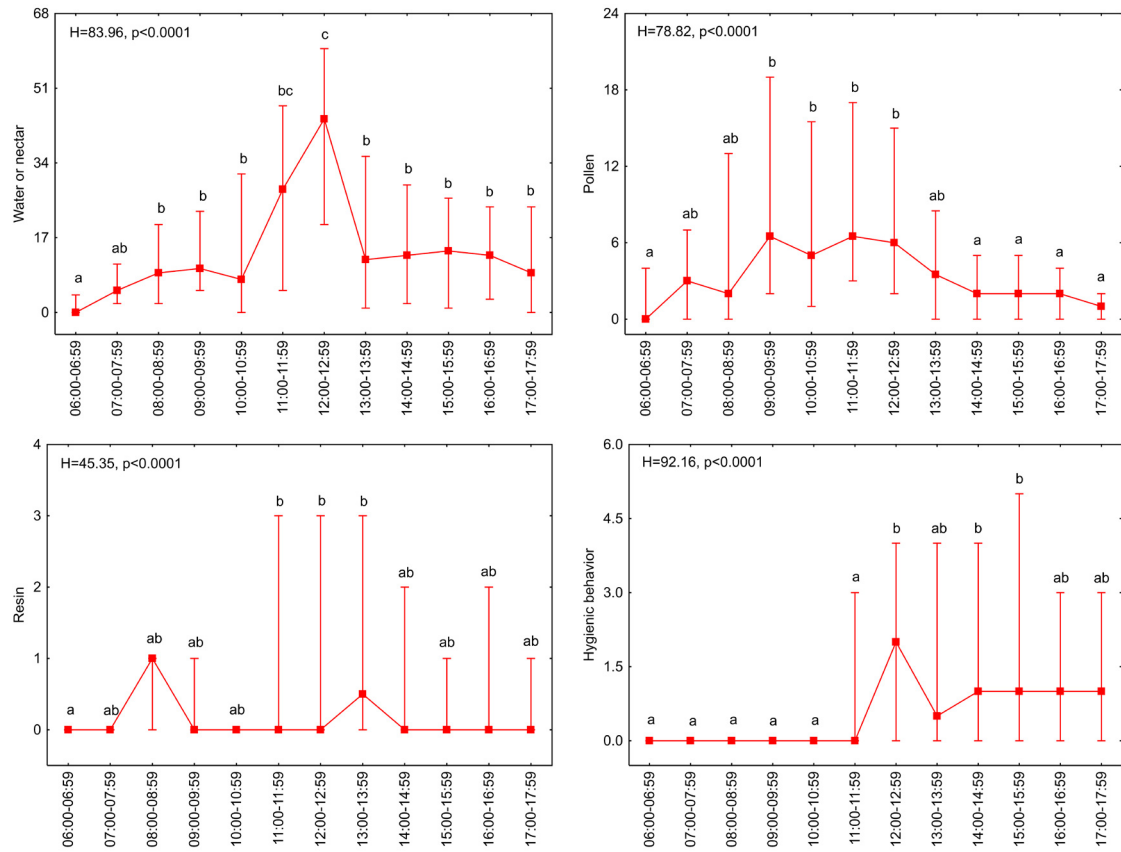


Fig 5. Medians and interquartile ranges of the absolute numbers of items collected and discarded by *Plebeia catamarcensis* workers according to the hours of the day in the hot and wet season. Different lowercase letters indicate significant differences among hours according to the Kruskal-Wallis test followed by Dunn's post hoc test ($p < 0.05$).

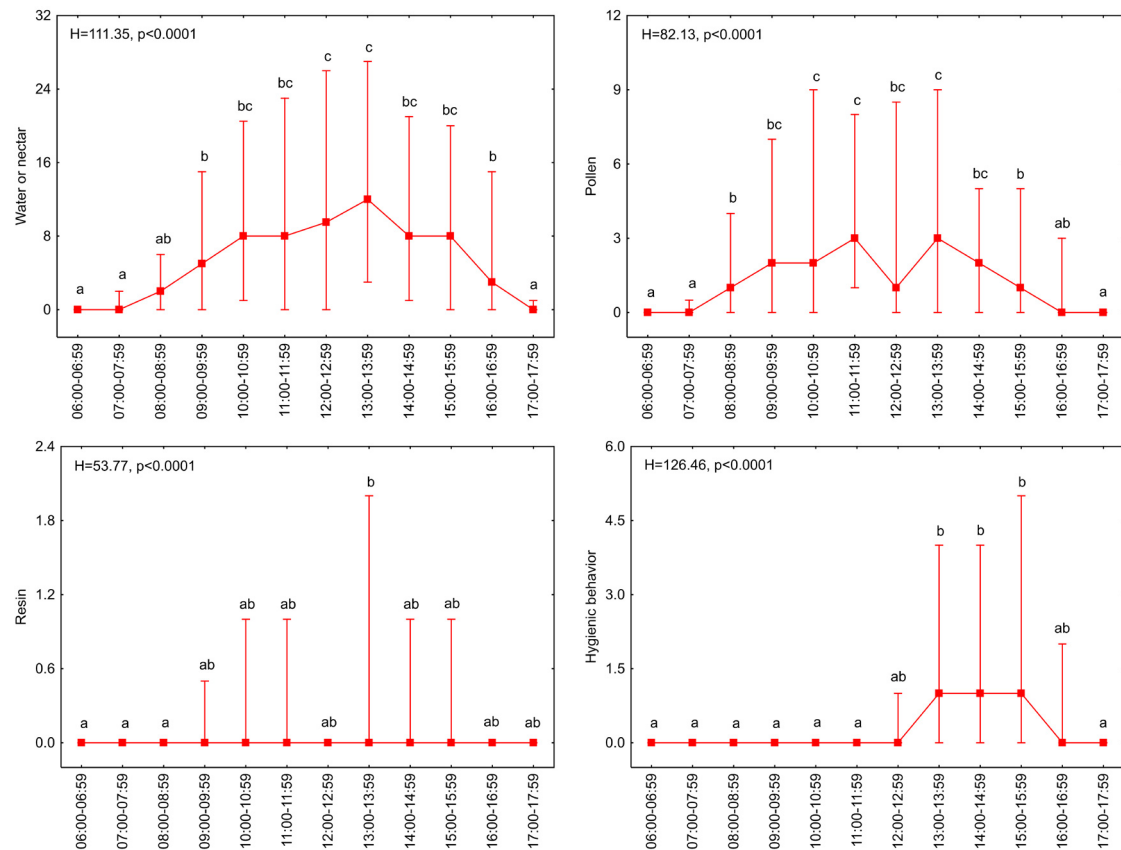


Fig 6. Medians and interquartile ranges of the absolute numbers of items collected and discarded by *Plebeia catamarcensis* workers according to the hours of the day in the cold and dry season. Different lowercase letters indicate significant differences among hours according to the Kruskal-Wallis test followed by Dunn's post hoc test ($p < 0.05$).

Extranidal activities begin earlier in the hot season than in the cold season, even though the ideal temperature conditions for their initiation are the same. This is because in the colder season, the environmental conditions, especially temperature, that are suitable for starting activities occur later in the morning, as temperatures rise more slowly (Aleixo et al., 2017). Extranidal activities showed a greater flow during the hot and wet season (Figs 1, 5, and 6). These results are similar to those found by Hadimani et al. (2024) in their study of *Tetragonula ruficornis* (Smith, 1870). According to Hadimani et al. (2024), this likely occurs due to greater resource availability and more favorable environmental conditions. Conversely, the cold and dry season often presents less favorable environmental conditions and lower resource availability, which accounts for the differing start times and peaks of activity between the seasons.

Temperature and light intensity showed a significant positive correlation with extranidal activities in both seasons (Figs 1, 2, and 3), indicating increased activity as these factors increased. Similar findings were reported by Polatto et al. (2014), who, when investigating the influence of abiotic factors and floral resource availability on the daily foraging activity of bees, observed a positive correlation between temperature, light intensity, and extranidal activity in *Apis mellifera* Linnaeus, 1758. In contrast, Hilário et al. (2001), studying *Plebeia pugnax* Moure (*in litt.*), found a significant correlation only with temperature, whereas light intensity appeared not to affect extranidal activity, as workers performed flights even under low light intensity.

No activities were recorded under 24 °C or above 33 °C in either season. In the hot and wet season, workers began extranidal activities around 6:00, when temperatures were approximately above 24 °C. The peak of these activities occurred between 11:00 and 13:00 (Fig 1), with median temperatures ranging from 29 °C to 32 °C (Fig 2). In the cold and dry season, the first activity records appeared at 8:00 (Fig 1), coinciding with temperatures above 24 °C (Fig 2). The peak activity in this season was observed between 13:00 and 14:00 (Fig 1), with a median temperature of about 26 °C (Fig 2). Teixeira and Campos (2005) observed that *P. droryana* and *P. lucii* foragers typically begin their activities above 20 °C. Similarly, Silva et al. (2019) found that *P. aff. flavocincta* workers do not forage below 24.6 °C. These temperature conditions are consistent with our current study's findings, suggesting that bees of this genus require relatively higher temperatures for extranidal activities. This might vary slightly depending on the specific environment and populations of each species. However, *P. pugnax* workers can forage at relatively low temperatures, starting their activities around 14 °C (Hilário et al., 2001). These observed differences can be attributed to several factors, ranging from intrinsic physiological distinctions between species (Hilário et al., 2001) to variations in the thermoregulatory capabilities of their nests, and even to the environmental conditions where these species are found (Campos et al., 2010; Mota et al., 2023).

The onset of extranidal activities can also be linked to the bee's body size (Carvalho-Zilse et al., 2007). Some bees, particularly native species, have a relatively small body size, leading to significant heat exchange with the environment. This results in higher energy costs, making them more dependent on ambient temperature than larger species (Teixeira & Campos, 2005; Carvalho-Zilse et al., 2007). Consequently, larger bees gain and lose heat more slowly than smaller bees, meaning body size and resource load influence thermoregulation during flight (Pereboom & Biesmeijer, 2003; Naumchik & Youngsteadt, 2023). This pattern may explain why extranidal activities begin later in the day during the cold, dry season compared to the hot and wet season.

The peak activity of colonies likely occurs during times of day when environmental conditions are most favorable for the species. This pattern can vary seasonally, reflecting either greater resource availability in certain hours or a strategy to avoid competition (Aleixo et al., 2017). Light intensity also has a significant positive effect on extranidal activities. This means that as light levels increase, there is a corresponding rise in the number of workers entering and leaving the nest. Extranidal activities were not recorded at median light intensities below 200 lx for the hot and wet season, or below 750 lx for the cold and dry season. Similarly, no activities were observed above 1,500 lx (raw values exceeding 190,500 before median-based transformation) in either season. In the hot and wet season, workers typically start extranidal activities around 6:00, when light intensity is approximately above 1,000 lx. The peak of these activities occurs between 11:00 and 13:00 (Fig 1), with median light intensity ranging from 1,100 to 1,250 lx (Fig 3). During the cold and dry season, the first recorded activities began at 8:00 (Fig 1), when light intensity was above 1,300 lx (Fig 3). The peak in this season is observed between 13:00 and 14:00 (Fig 1), with a median light intensity of around 1,200 lx (Fig 3).

Hilário et al. (2001) observed a similar pattern while studying *P. pugnax*, though that species forages under relatively higher light intensity conditions, around 10,000 to 20,000 lx. However, these differing values can be explained by our methodology: we consistently measured light intensity at the entrances of the nests in the meliponary, where the nests are protected by a roof, resulting in constant shade. Another point is that the values presented in Fig 3 are medians. While light intensity could reach around 30,000 lx at a few moments during the day, the median values are much lower than these extremes, coinciding with the middle hours of the day and gradually decreasing. Studies by Gouw and Gimenes (2013) with *Melipona scutellaris* Latreille, 1811 and *Frieseomelitta doederleini* (Friese, 1900), by de Moura et al. (2022) with *Melipona quadrifasciata* Lepeletier, 1836, and by Streinzer et al. (2016) with *Ptilotrigona occidentalis* (Schulz, 1904) and *Scaura argyria* (Cockerell, 1912), also described similar patterns of positive correlation. Interestingly, this species' peak worker activity doesn't coincide with the highest light

intensity values in either season, despite a significant positive correlation with this variable. Instead, the activity peak in both seasons occurred at light levels just below the highest values. This is likely because environmental variables act not in isolation but in combination (Oliveira et al., 2012). This factor might be related to how bees orient themselves using the sun's position, as light intensity helps them navigate when searching for floral resources during flight (Polatto et al., 2014). Soares et al. (2019) found similar results for *Trigona spinipes* (Fabricius, 1793), also suggesting that increased temperature and light intensity are likely connected to higher solar radiation, making the environment more favorable for activity. Polatto et al. (2014) observed the same pattern when studying *A. mellifera*, *Centris varia* Erichson, 1849, and *Oxaea flavescens* Klug, 1807.

Relative air humidity showed a significant negative correlation with extranidal activities. This means that as humidity levels increased, the intensity of worker extranidal activities decreased. In the hot and wet season, workers engaged in these activities at a humidity level of around 72% at 6:00. The peak of activities occurred between 11:00 and 13:00 (Fig 1), when the median relative humidity was between 60% and 65% (Fig 4). In the cold and dry season, the first records of activity appeared from 8:00 (Fig 1), when relative humidity was above 65% (Fig 4). The peak occurred between 13:00 and 14:00 (Fig 1), with a median of approximately 60% (Fig 4). No behaviors were recorded at values below 50% or above 75% in either season. As humidity rises, the probability of rain increases, which is a limiting factor for these bees. Due to their small size, they are more susceptible to rain, compromising their ability to fly. In such conditions, bees may temporarily suspend foraging until the weather improves (Salatnaya et al., 2023; Vignesh et al., 2024).

Polatto et al. (2014) found a similar correlation between this parameter and the foraging activity of three species: *A. mellifera*, *T. spinipes*, and *O. flavescens*. In contrast, Oliveira et al. (2012), when evaluating the daily rhythm of *Melipona subnitida* Ducke, 1911 during the rainy and dry seasons, observed a significant positive correlation for two extranidal activities in the rainy season and only one in the dry season. This species exhibits high foraging activity in high-humidity environments. Similar results were observed by Silva et al. (2011) with *M. scutellaris*.

Water or nectar was collected throughout the day in both seasons, though predominantly during the morning (Fig 5). Peaks in the collection of these items occurred during the hottest parts of the day: between 11:00 and 13:00 in the hot and wet season, and between 13:00 and 14:00 in the cold and dry season. The collection of water or nectar, in fact, happens during the warmest hours of the day to aid in the colony's thermoregulation or evaporative cooling (Souza-Junior et al., 2020; Maia-Silva et al., 2021).

Oliveira et al. (2012), in their study of *M. subnitida* extranidal activities, also found that water and nectar were the most frequently collected resources by foragers, primarily

gathered during the morning in both seasons. Similar results were observed by Hilário et al. (2001) with *P. pugnax* and Horas et al. (2017) with *Plebeia flavocincta* (Cockerell, 1912). However, Carvalho-Zilse et al. (2007) reported different findings for *Melipona seminigra* Friese, 1903. In their study, nectar was the least-collected resource by its workers.

Pollen was most frequently collected in the morning during the hot and wet season, with peaks between 9:00 and 10:00 and 11:00 and 12:00 (Fig 5), from 17:00 to 18:00. In the cold and dry season, pollen collection also occurred more intensely in the morning, peaking between 11:00 and 12:00 and 13:00 and 14:00, and lasting from 15:00 to 16:00 (Fig 6). The morning preference for pollen collection is a widely described pattern in stingless bees, converging with the results of the present study. This tendency is documented in various species, such as *Melipona fasciata* Latreille, 1811, *M. beecheii* Bennett, 1831, and *Tetragonisca angustula* (Latreille, 1811) (de Bruijn & Sommeijer, 1997), *M. subnitida* (Oliveira et al., 2012), *M. scutellaris* (Silva et al., 2011), *P. droryana* (Friese, 1900), *Scaptotrigona bipunctata* (Lepeletier, 1836), and *M. quadrifasciata* (de Moura et al., 2024), and *M. seminigra* (Carvalho-Zilse et al., 2007). The timing of pollen collection can be attributed to several factors, including competition with other species, energy conservation by switching to nectar collection (for nectar foragers) or synchronization with the pollen release rhythms of plants within the colony's foraging range (Hilário et al., 2001; Borges & Blochtein, 2005; Aleixo et al., 2017).

Resin was the least frequently collected resource by workers during foraging activities. In the hot and wet season, it was gathered throughout both the morning and the afternoon. However, in the cold and dry season, resin collection was predominantly higher in the afternoon (Fig 6). Bees typically collect resin to seal nest crevices, preventing cold drafts (Nogueira-Neto, 1997). Additionally, internal nest temperature is biologically regulated by brood thermogenesis (Roldão-Sbordoni et al., 2024). Jacome-García et al. (2024), studying *Parapatamona zonata* (Smith, 1854), found similar results, observing that less than 1% of workers were dedicated to resin or mud collection. This pattern contrasts with observations by Oliveira et al. (2012) on *M. subnitida*, Hilário et al. (2001) on *P. pugnax*, and Horas et al. (2017) on *P. flavocincta*, all of whom noted a higher frequency of resin collection in the morning.

Bees can use resin to cover their nest entrances and to seal and defend their nests (Nogueira-Neto, 1997; Hilário et al., 2001). For this particular species, they cover the nest entrance at dusk and remove it at dawn. This behavior is modulated by both external environmental conditions and internal colony conditions, as the nest entrance only opens when the temperature is above 24 °C. According to Nogueira-Neto (1997), workers of *Friesella schrottkyi* (Friese, 1900) exhibit similar behavior, using this resource to seal their nest entrance.

Workers of this species primarily discard waste in the afternoon during both seasons. The peak for waste disposal occurs between 12:00 and 13:00 in the hot and wet season.

In the cold and dry season, the peak is observed between 13:00 and 14:00 and again between 15:00 and 16:00. Similarly, *P. pugnax* colonies discard more waste in the afternoon, with this activity peaking around 17:00 (Hilário et al., 2001). Conversely, Oliveira et al. (2012) found that *M. subnitida* discarded more waste in the morning during both the rainy and dry seasons. Horas et al. (2017) observed the same pattern in their study of *P. flavocincta*.

During the hot and wet season, there was a higher frequency of waste disposal compared to the cold and dry season (Figs 5 and 6). There were also differences in peak disposal times between the seasons. These distinctions can likely be attributed to the greater availability of resources for colonies in the hot and wet season, which leads to the production of more waste that needs to be removed.

Overall, our findings support all three hypotheses. The foraging activity of *P. catamarcensis* is indeed influenced by climatic factors, though some exert a different impact than others. Notably, extranidal activities, especially foraging, are more intense during the hottest hours of the day in both seasons. Finally, the frequency with which different resources are collected varies with climatic conditions across the hot and wet and cold and dry seasons, adapting to the colonies' needs. Therefore, we conclude that the behavior of *P. catamarcensis* foragers is modulated by climatic factors. A combination of factors likely acts in concert to determine the pattern and timing of various extranidal activities, ultimately minimizing energy expenditure and exposure to unfavorable environmental conditions.

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Code availability: Not applicable.

Authors' Contributions

G.N.A.: Investigation, data curation, writing-original draft, and writing-review & editing.

D.M.V.: Investigation, data curation, and writing-original draft.

K.B.M.: Conceptualization and methodology.

M.C.P.S.: Conceptualization and methodology.

S.E.L.J.: Formal analysis and visualization.

W.F.A.J.: Conceptualization, methodology, supervision, and writing-review & editing.

References

- Aleixo, K.P., Menezes, C., Imperatriz-Fonseca, V.L. & da Silva, C.I. (2017). Seasonal availability of floral resources and ambient temperature shape stingless bee foraging behavior (*Scaptotrigona* aff. *depilis*). *Apidologie*, 48: 117-127. <https://doi.org/10.1007/s13592-016-0456-4>
- Barbosa, A.B.S., Menezes, H.M., Rosa, F.L. & Freitas, B.M. (2020). Flight activity of the stingless bee *Plebeia* aff. *flavocincta* in tropical conditions as indicator of the general health of the colony. *Sociobiology*, 67: 545-553. <https://doi.org/10.13102/sociobiology.v67i4.4926>
- Borges, V.B. & Blochtein, F.B. (2005). External activities of *Melipona marginata* obscurior Moure (Hymenoptera, Apidae), in distinct times of the year, at São Francisco de Paula, Rio Grande do Sul, Brazil. *Revista Brasileira de Zoologia*, 22: 680-689. <https://doi.org/10.1590/s0101-81752005000300025>
- Campos, F.S., Gois, G.C. & Carneiro, G.G. (2010). Termorre-regulação colonial em abelhas sem ferrão. *Pubvet*, 4: 872.
- Carrano-Moreira, F.A. (2015). Insetos: manual de coleta e identificação (2nd ed.). Rio de Janeiro: Technical Books, 369 p.
- Carvalho-Zilse, G., Porto, E.L., Silva, C.G.N. & Pinto, M.F.C. (2007). Atividade de voo de operárias de *Melipona seminigra* (Hymenoptera: Apidae). *Bioscience Journal*, 23: 94-99.
- de Bruijn, L., & Sommeijer, M. (1997). Colony foraging in different species of stingless bees (Apidae, Meliponinae) and the regulation of individual nectar foraging. *Insectes Sociaux*, 44: 35-47. <https://doi.org/10.1007/s000400050028>
- de Moura, M.E.K., Fanta, M.R., Amandio, D.T.T., Garcia Bertoldo, J., Pereira Lima, V. & Poltronieri, A.S. (2022). Influence of some abiotic factors on the flight activity of stingless bees (Hymenoptera: Meliponini) in Southern Brazil. *Journal of Apicultural Research*, 63: 603-609. <https://doi.org/10.1080/00218839.2022.2028968>
- de Moura, M.E.K., Fanta, M.R., Bertoldo, J.G., Poltronieri, A.S. & Contrera, F.A.L. (2024). Stingless bee foraging activity related to environmental aspects. *Neotropical Entomology*, 53: 1185-1195. <https://doi.org/10.1007/s13744-024-01206-w>
- Gouw, M.S. & Gimenes, M. (2013). Differences of the daily flight activity rhythm in two neotropical stingless bees (Hymenoptera, Apidae). *Sociobiology*, 60: 183-189. <https://doi.org/10.13102/sociobiology.v60i2.183-189>
- Grüter, C. (2020). Stingless Bees: Their Behaviour, Ecology and Evolution. Cham: Springer Nature, 385 p.

- Hadimani, B.N., Kumaranag, K.M. & Dey, D. (2024). First report of nesting habits, nest architecture and foraging behaviour of the stingless bee, *Tetragonula (Tetragonula) ruficornis* (Smith) (Hymenoptera: Apidae: Meliponini) from India. *Sociobiology*, 71: e10114. <https://doi.org/10.13102/sociobiology.v71i2.10114>
- Hilário, S.D., Imperatriz-Fonseca, V.L. & Kleinert, A.M.P. (2001). Responses to climatic factors by foragers of *Plebeia pugnax* Moure (in litt.) (Apidae, Meliponinae). *Revista Brasileira de Biologia*, 61: 191-196. <https://doi.org/10.1590/s0034-71082001000200003>
- Horas, R.M., Silva, L.R., Gomes, M.O., Alves, T.T.L., Holanda-Neto, J.P. & Silva, R.H.D. (2017). Fluxo de entrada e saída da abelha jataí (*Plebeia flavocincta*) em meliponário didático no município de Ouricuri-PE. *Caderno Verde de Agroecologia e Desenvolvimento Sustentável*, 7: 39-42.
- Hrncir, M. & Maia-Silva, C. (2013). On the diversity of foraging-related traits in stingless bees. In P. Vit, S.R.M. Pedro, & D.W. Roubik (Eds.), *Pot-Honey: A legacy of stingless bees* (pp. 201-215). New York: Springer.
- Jacome-García, J.C., Gonzalez, V.H., Riaño-Jimenez, D.A., Herrera-Motta, A.F. & Cure, J.R. (2024). Foraging behavior and the nest architecture of a high-Andean stingless bee (Hym.: Apidae: Meliponini) revealed by X-ray computerized tomography. *Apidologie*, 55: 33. <https://doi.org/10.1007/s13592-024-01074-8>
- Maia-Silva, C., da Silva Pereira, J., Freitas, B.M. & Hrncir, M. (2021). Don't stay out too long! Thermal tolerance of the stingless bee *Melipona subnitida* decreases with increased exposure time to high temperatures. *Apidologie*, 52: 218-229. <https://doi.org/10.1007/s13592-020-00811-z>
- Menezes, C., Alves, D.A., Lucena, D.A.A. & Almeida, E.A.B. (2023). Abelhas sem ferrão relevantes para a meliponicultura no Brasil. São Paulo: Abelha, 97 p.
- Mota, A.V., Trindade, G.N., Toledo, T.S. & Cardinal, K.M. (2023). Termorregulação de abelhas com ênfase em *Apis mellifera*. In B.R. Silva Neto (Ed.), *Zootecnia: tópicos atuais em pesquisa*. Matinhos: Editora Científica Digital. Vol. 2, pp. 229-237. <https://doi.org/10.37885/230211947>
- Naumchik, M. & Youngsteadt, E. (2023). Larger pollen loads increase risk of heat stress in foraging bumblebees. *Biology Letters*, 19: 20220581. <https://doi.org/10.1098/rsbl.2022.0581>
- Nogueira-Neto, P. (1997). Vida e criação de abelhas indígenas sem ferrão. São Paulo: Editora Nogueirapis, 445 p.
- Nunes-Silva, P., Hilário, S.D., Santos Filho, P.S. & Imperatriz-Fonseca, V.L. (2010). Foraging activity in *Plebeia remota*, a stingless bees species, is influenced by the reproductive state of a colony. *Psyche: A Journal of Entomology*, 2010: 1-16. <https://doi.org/10.1155/2010/241204>
- Oliveira, F.L., Dias, V.H.P., Costa, E.M., Filgueira, M.A. & Sobrinho, J.E. (2012). Influência das variações climáticas na atividade de voo das abelhas jandairas *Melipona subnitida* Ducke (Meliponinae). *Revista Ciência Agronômica*, 43: 598-603. <https://doi.org/10.1590/s1806-66902012000300024>
- Paula, M.C., Batista, N.R., Cunha, D.A.D.S., Santos, P.G.D., Antonialli-Junior, W.F., Cardoso, C.A.L. & Simionatto, E. (2023). Impacts of the insecticide thiamethoxam on the native stingless bee *Plebeia catamarcensis* (Hymenoptera, Apidae, Meliponini). *Environmental Pollution*, 339: 122742. <https://doi.org/10.1016/j.envpol.2023.122742>
- Pereboom, J.J.M. & Biesmeijer, J.C. (2003). Thermal constraints for stingless bee foragers: the importance of body size and coloration. *Oecologia*, 137: 42-50. <https://doi.org/10.1007/s00442-003-1324-2>
- Pinho, O.C., Balestieri, J.B.P. & Balestieri, F.C.D.L.M. (2010). Respostas de colônias de *Plebeia catamarcensis* Holmberg (Hymenoptera, Apidae, Meliponina) à orfandade. *Revista Brasileira de Biociências*, 8: 201-207.
- Polatto, L.P., Chaud-Netto, J. & Alves-Junior, V.V. (2014). Influence of abiotic factors and floral resource availability on daily foraging activity of bees. *Journal of Insect Behavior*, 27: 593-612. <https://doi.org/10.1007/s10905-014-9452-6>
- Roldão-Sbordoni, Y.S., Hrncir, M. & Nascimento, F.S. (2024). Brood thermogenesis effects on the thermal dynamics in stingless bee nests (*Melipona scutellaris*). *Insectes Sociaux*, 71: 185-195. <https://doi.org/10.1007/s00040-024-00962-7>
- Salatnaya, H., Kahono, S., Suhri, A.G.M.I., Ismanto, A., Anggraeni, I., Fara, S.B., Hasan, P.A. & Hashifah, F.N. (2023). Diversity, distribution, nesting, and foraging behavior of stingless bees and recent meliponiculture in Indonesia. In M.A. Aziz (Ed.), *Melittology – New Advances* (pp. 1-19). London: IntechOpen. <https://doi.org/10.5772/intechopen.1003758>
- Silva, J.G., Meneses, H.M. & Freitas, B.M. (2019). Foraging behavior of the small-sized stingless bee *Plebeia* aff. *flavocincta*. *Revista Ciência Agronômica*, 50: 484-492. <https://doi.org/10.5935/1806-6690.20190057>
- Silva, M., Ramalho, M. & Rosa, J. (2011). Por que *Melipona scutellaris* (Hymenoptera, Apidae) forrageia sob alta umidade relativa do ar? *Iheringia Série Zoologia*, 101: 131-137. <https://doi.org/10.1590/s0073-47212011000100019>
- Soares, K.O., Lima, M.V., Evangelista-Rodrigues, A., Silva, A.A.F., Silva, F.J. & Da Costa, C.R.G. (2019). Factors influencing the foraging behavior of *Trigona spinipes* (Apidae, Meliponinae). *Biological Rhythm Research*, 52: 1109-1119. <https://doi.org/10.1080/09291016.2019.1616903>
- Souza-Junior, J.B., Teixeira-Souza, V.H.S., Oliveira-Souza, A., Oliveira, P.F., Queiroz, J.P.A.F. & Hrncir, M. (2020). Increasing thermal stress with flight distance in stingless

bees (*Melipona subnitida*) in the Brazilian tropical dry forest: implications for constraint on foraging range. *Journal of Insect Physiology*, 123: 104056.

<https://doi.org/10.1016/j.jinsphys.2020.104056>

Streinzer, M., Huber, W. & Spaethe, J. (2016). Body size limits dim-light foraging activity in stingless bees (Apidae: Meliponini). *Journal of Comparative Physiology A*, 202: 643-655. <https://doi.org/10.1007/s00359-016-1118-8>

Teixeira, L.V. & Campos, F.N.M. (2005). Início da atividade de voo em abelhas sem ferrão (Hymenoptera, Apidae): influência do tamanho da abelha e da temperatura ambiente. *Revista Brasileira de Zoociências*, 7: 195-202.

Tibco Software Inc. (2020). Data Science Workbench, version 14.

Vignesh, B.S., Anujaa, B., & Manickavasagam, S. (2024). Pollination efficiency and foraging activity of stingless bee (*Tetragonula "iridipennis"* sp. group) in open field coriander cropping. *Journal of Applied Horticulture*, 26: 37-40. <https://doi.org/10.37855/jah.2024.v26i01.07>

Zavatini, J.A. (1992). Dinâmica climática no Mato Grosso do Sul. *Geografia*, 17: 65-70.

Zeballos, M., Calviño, A.A. & Zamudio, F. (2022). Is the flight and foraging activity of small-sized stingless bees affected by the urban heat island? The case of *Plebeia catamarcensis* (Meliponini) in Córdoba city (Argentina). *Journal of Apicultural Research*, 61: 632-641.

<https://doi.org/10.1080/00218839.2022.2110431>

