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The influence of abiotic factors on the foraging activity of *Cephalotes borgmeieri* (Kempf, 1951)

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Abstract

The foraging activity can be defined as the search for food resources and is an activity of utmost importance for ant colony maintenance. Workers can be exposed to adverse environmental conditions during foraging, and because of it, some species can adjust their foraging behavior to achieve greater success in the search for resources. The foraging behavior has been studied in other ant species; however, studies with the Cephalotini tribe are still scarce in the literature. In this study, we evaluated how *Cephalotes borgmeieri* (Kempf) foragers adjust their foraging activity to variations in abiotic factors. Throughout the day, the flow of foragers is positively influenced by temperature and luminosity and negatively affected by relative air humidity. Wind speed does not affect the flow of foragers. During the day, we can observe four groups of activity intensity: very low, low, medium, and high. The foraging peak occurs at the hottest and least humid times of the day.

Introduction

In the organization of the ant community, there is a crucial relationship between the individual and the group (Burd, 2000). Concerning foraging, this relationship varies widely between ant species, mainly because it is an activity aimed at the search for food resources, which is extremely important for maintaining the colony. Therefore, ant species adopt different strategies for searching for and collecting these resources (Pol & Casenave, 2004; Gordon, 2017).

The foraging strategies can be the most diverse, as pointed out by Lanan (2014). They can be classified into three categories: Without recruitment or solitary, when an individual leaves the nest, forages, and transports the resource alone, without the help of nestmates; With group recruitment, when an individual finds a resource and returns to the nest to recruit nestmates; and Mass recruitment, when the individual finds food, deposits a chemical trail from the resource to the nest, and the nestmates follow this trail to the food.

Among the foraging strategies, the first is considered an ancestral characteristic of Formicidae, adopted by less derived species. The other strategy emerged independently and in more recent species (Reeves and Moreau, 2019). In addition, the foraging task is divided based on the workers' age, whereas the younger ones perform intranidal tasks, such as taking care of the offspring. The older ones perform extranidal tasks, such as foraging and colony defense (Hölldobler & Wilson, 1990) or also by subcastes in which there is the production of individuals with different and specialized body sizes or proportions for different types of work, such as major workers, minor workers, and nurses (West, 2020).

The environment determines the foraging activity of many insects, including ants. Factors such as temperature, humidity, light intensity, wind speed, and availability of food

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resources directly influence their behavior (Heinrich, 1993; Pol & Casenave, 2004; Nguyen et al., 2017). The temperature and relative humidity of the air are some of the main factors that affect the foraging dynamics of several species of ants (Nielsen, 1986), which, for instance, can forage between temperatures of 10 to 45°C (Hölldobler & Wilson, 1990).

Some species, such as *Ectatomma vizzotoi* (Almeida) (Lima & Antonialli-Junior, 2013), *Pheidole oxyops* (Forel) (Assis et al., 2018), and *Anoplolepis gracilipes* (Smith) (Chong & Lee, 2009) tend to forage during the night and early morning as a strategy to avoid high temperatures and low humidity during the day, thus reducing the risk of desiccation. On the other hand, some species have their foraging peak at times with higher temperatures, as is the case of *Formica pallidefulva* (Latreille) and *Crematogaster lineolata* (Say) (Stuble et al., 2013), which present a positive relationship between temperature and their foraging activities, as well as *Pachycondyla sennaarensis* (=*Brachyponera sennaarensis*) (Mayr) (Wheeler & Wheeler, 1971; Mashaly et al., 2013), which has a more intense foraging activity in the summer due to the high temperatures and low humidity in this season.

Within the Formicidae family, the Cephalotini tribe is considered one of the lesser-known groups of ants. This is reflected in the number of species described and that had their behavior and biology further studied, such as *Zacryptocerus varians* (= *Cephalotes varians)* (Smith) (Wilson, 1976; de Andrade & Baroni-Urbani, 1999), *Cephalotes atratus* (Linnaeus) (Corn, 1980; D'avila et al., 2005) and *Cephalotes pusillus* (Klug) (Del-Claro et al., 2002). The genus *Cephalotes* Latreille, 1802, known as turtle ants, belong to the subfamily Myrmycinae and are found in the neotropical region and the southern Nearctic region (de Andrade & Baroni-Urbani, 1999), with an exclusively arboreal habit, using preexisting cavities made in wood by other arthropods (Powell, 2008, 2009; Oliveira et al., 2021). Almost all species have dimorphic workers with the division of labor. Smaller workers are more active during foraging, while larger ones are responsible for defending the nest against invaders, using their heads to block the entrance to the nest (De Andrade & Baroni-Urbani, 1999; Del-Claro et al., 2002; Powell, 2008, 2016, 2020). Their diet is based on pollen, nectar, secretion of hemipterans, bird droppings, and urine of tree mammals (Byk & Del-Claro, 2010; Gordon, 2012; Oliveira et al., 2021).

Cephalotes borgmeieri is a species endemic to Brazil's southeast and central west regions, besides being also found in other countries, such as Paraguay and Argentina. To date, it is noteworthy that this study is a pioneer in the aspects related to its biology and behavior. Thus, the objective was to evaluate, for the first time, how biotic factors affect the foraging behavior of *Cephalotes borgmeieri*. We tested that (i) the species in question would have a higher rate of foraging during the hottest hours of the day, and that (ii) temperature would be the determining variable directly affecting the foraging of this species.

Materials and Methods

Foraging strategy

Study area

This study was carried out on the campus of the University City, in Dourados, Mato Grosso do Sul state, Center-West region of Brazil (22° 13' 18'' South, 54° 48' 23'' West), in a transition area between the Atlantic Forest and Cerrado biomes. The region's climate is transitioning between tropical and subtropical. The average annual temperature ranges from 20 to 22 °C, and the annual rainfall range from 1400 to 1700 mm (de Farias & Berezuk, 2018). Field observations were performed in the rainy season in February, March, December 2021, and January 2022.

The search for colonies of *C. borgmeieri* was carried out actively by looking for the usual entrances of the nests in trees and also using baits rich in nitrogen (cotton soaked in vertebrate urine), two baits per tree, which were fastened with pins based on Powell's method (2009).

Foraging experiment

Preliminary observations showed that *C. borgmeieri* forages only in the daytime. Therefore, the foraging activity of six colonies of *C. borgmeieri* was monitored from early morning to dusk (from 4:00 a.m. to 6:00 p.m.). Observation sessions were performed every hour on two distinct colonies. At the beginning of each observation hour, the values of temperature (°C), humidity (%), wind speed (m/s), and light intensity (Lux) were recorded using a multi-parameter meter HM 6300 (Highmed).

A colony was analyzed in the first 15 minutes of each observation hour, and the foraging flow (number of ants entering and leaving the nest) was recorded. In the next 15 minutes, a second colony was observed.

Statistical analysis

To evaluate whether the foraging flow of workers varies throughout the day, we used a generalized linear mixed model (GLMMs), using the ant flow as the response variable and the time of day as an explanatory variable. The colony was used as a random variable since its size and nutritional status can influence foraging activity (Calheiros et al., 2019). Next, we used a contrast analysis of models to evaluate whether there are distinct groups of foraging activity throughout the hours of the day. The "glmer" function of the *lme4* package (Bates et al., 2015) was used to analyze the GLMMs. We used the Poisson family in the models because the response variable was measured as counting data and the "hnp" function of the *hnp* package (Moral et al., 2017) for visual evaluation of the adjustments.

To assess whether there is a relationship between the flow of workers in foraging activity and the values of temperature, relative humidity, wind speed, and light intensity, we applied individualized GLMMs, in which the flow of workers was the response variable. The values of temperature and relative humidity, wind speed, and light intensity were the explanatory variables in separate models. In these models, the colony was also the random variable. To evaluate which of the environmental variables most influences the foraging activity, we used the R^2 value of the model as the adjustment value (Almeida et al., 2021), using the “rsquared” function of the *piecewisesem* package (Lefcheck, 2016). We used individualized models comparing the adjustment through R^2 instead of a complete model due to the inflation of the model (Zuur et al., 2010; Harrison et al., 2018) since they are known to have two important correlated variables (Online Resource 1).

All statistical analyses were performed using the R software (R Core Team, 2021; version 4.1.0), and the figures were plotted using the *ggplot2* (Wickham, 2016), *gridExtra* (Auguie, 2017), and *ggrepel* (Slowikowski, 2021) packages.

Results

The foraging activity of *C. borgmeieri* workers is predominantly diurnal, with two peaks of activity, one longer between 9:00 a.m. and 1:00 p.m. and the other shorter between 3:00 and 4:00 p.m. The peak activity was 44 ants leaving the colony during the 15 minutes of observation at 9 o’clock (under a temperature of 28.7 °C; humidity of 67.9%; Wind Speed of 0.2 m/s; Light Intensity of 5050 Lux). The highest values for the abiotic factors when workers were observed foraging were: a temperature of 37.2 °C, a relative humidity of 79.2%, a luminosity of 27900 Lux, and a wind speed of 3.4 m/s, while the minimum values were 18.5 °C, 29.1%, 16 Lux and 0.0 m/s, respectively. No foraging activity was detected in four colonies at 4:00 a.m. and 6:00 p.m. In addition, temperature and humidity have more constant patterns (smaller variations), something not found for the variables luminosity and wind speed (Figure 1).

The analysis showed a difference between foraging activity throughout the hours of the day (Figure 2; $\chi^2 = 127.12$; df = 12; p = <0.001), with a separation into three activity intensity groups: low, medium, and high. We considered the activity as low when there were, on average, 3.25 ± 2.41 ants foraging during the 15 minutes of observation. We observed that this low activity occurred at 5:00 a.m. and 6:00 p.m. Foraging was considered to show medium activity when there were, on average, 10.00 ± 6.03 ants foraging during the observation period, occurring between 6:00 a.m. and 7:00 a.m. and 2:00 p.m. and 5:00 p.m. The high foraging activity happened when there were, on average, 17.97 ± 10.96 ants foraging during the observation period of 15 minutes, occurring from 8:00 a.m. to 1:00 p.m. and from 3:00 p.m. to 4:00 p.m. Foraging was considered as “zero” activity when, on average, 0.3 ± 0.51 ants were foraging, which occurred at 4:00 a.m.

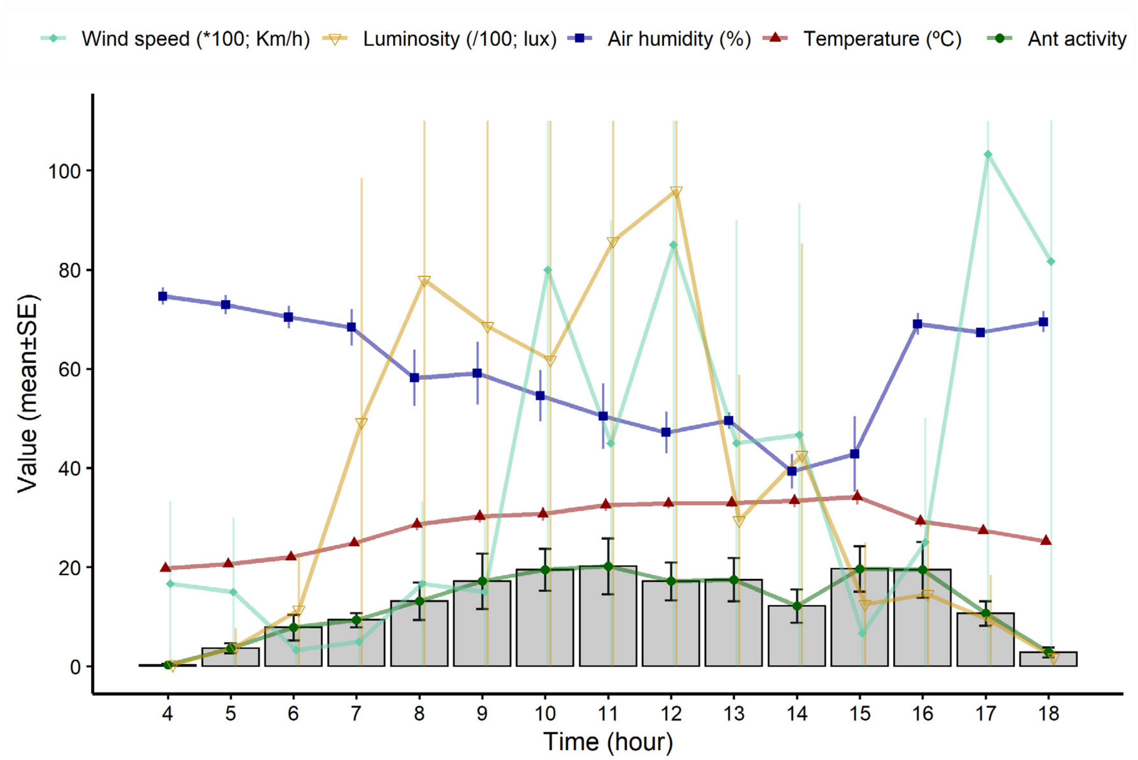

Fig 1. Means of the number of ants from six colonies of *Cephalotes borgmeieri* leaving the nest from 4:00 a.m. to 6:00 p.m. (line with closed circles) and variation of temperature values (closed triangles), air humidity (closed squares), luminosity (open triangles) and wind speed (closed diamonds) recorded on the campus of the University City, Dourados, Mato Grosso do Sul, Brazil. (Symbols indicate the average values and confidence intervals indicate the standard error).

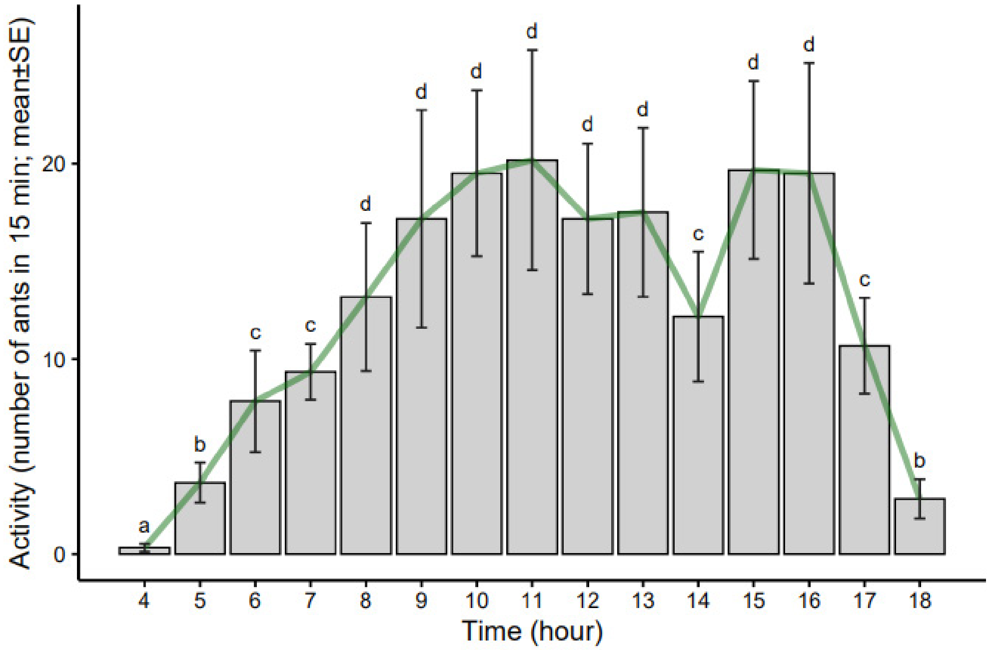

Fig 2. Mean number of foragers in activity every 15 minutes between 4:00 a.m. and 6:00 p.m. of six colonies of *Cephalotes borgmeieri*. The letters were determined by contrast analysis and indicate (a) zero activity, (b) low activity, (c) medium activity and (d) high activity. (Confidence intervals indicate the standard error of the mean found for the six colonies evaluated)

According to Figure 3, there is a significant correlation between foraging flow and temperature values ($\chi^2 = 167.910$; p = <0.001), air humidity ($\chi^2 = 56.804$; p = 0.001), and light intensity ($\chi^2 = 26.890$; p = <0.001) but not wind speed ($\chi^2 = 0.114$; p = 0.736). The variable that best fits the activity of *C. borgmeieri* is the temperature ($R^2 = 0.376$), followed by air humidity ($R^2 = -0.158$) and later by luminosity ($R^2 = 0.099$).

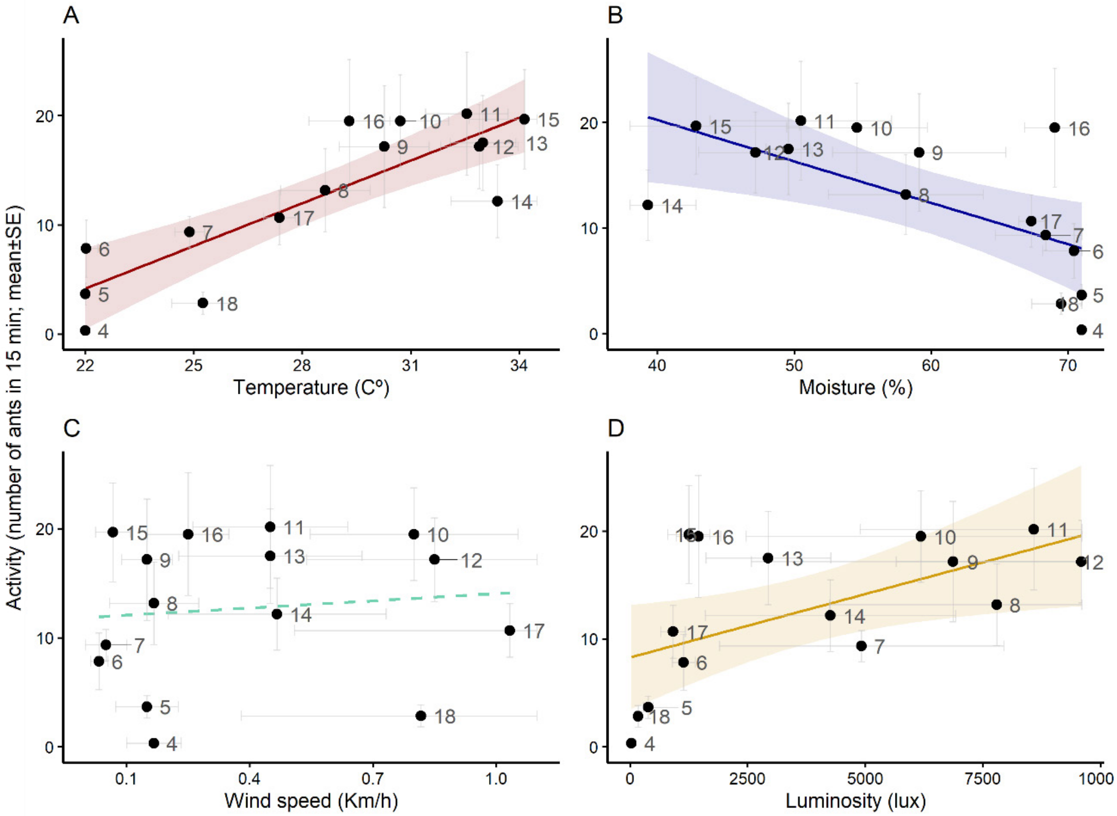

Fig 3. Relationship between abiotic factors and the number of foragers of *Cephalotes borgmeieri* in activity every 15 minutes. (A) Temperature, (B) air humidity, (C) wind speed and (D) luminosity recorded in six colonies on the campus of University City, Dourados, Mato Grosso do Sul, Brazil. (Cloud along the continuous line indicates the regression confidence interval; dotted line indicates non-significant variable; black dots indicate the mean foraging activity and environmental variable in the six colonies at the respective time; confidence intervals indicate the standard error of the mean for foraging activity and environmental variable)

Discussion

Our results show that the foraging activity of *C. borgmeieri* is predominantly diurnal, with its higher flow occurring in the hottest and brightest hours of the day and the lowest relative air humidity. These results are like those described by Del-Claro et al. (2002) for *C. pusillus* and *C. atratus* described by D'avila et al. (2005), which are also diurnal with the highest frequency of foraging occurring in the hottest and driest hours of the day. Creighton (1963) also observed that *Cryptocerus texanus* (=*Cephalotes texanus*) (Santschi) forages during the day, even in laboratory conditions. Gordon (2017) attended that *Cephalotes goniodontus* (de Andrade) also has daytime habits; however, they are inactive during the midday heat, foraging early in the morning and returning in the late afternoon. On the other hand, Wilson (1976) observed that foragers of *C. varians*, in nature, are active at night. Still, they can also forage during the day under constant lighting in the laboratory.

The foraging activity of ants from other subfamilies is also significantly affected by abiotic factors, such as *Formica pallidefulva* and *Crematogaster lineolata* (Stuble et al., 2013), which present results similar to ours: a positive relationship between temperature and foraging; and *Myrmecia croslandi* (Taylor) which is exclusively diurnal, and the beginning of its foraging activity is influenced by surface temperature. However, when the temperature reaches 38 °C, they stop foraging (Jayatilaka et al., 2011). On the other hand, *Linepithema humile* (Mayr), for example, has a negative correlation between its foraging activity and temperature and a positive correlation with humidity (Abril, 2007). Lima and Antonialli-Junior (2013) found similar results for *Ectatomma vizzotoi*. Chong and Lee (2009) also found a positive relationship between foraging and humidity and a negative association with temperature when analyzing the foraging activity of *Anonoplopis gracilipes*.

The foraging activity of *C. borgmeieri* is also positively affected by luminosity since the hottest hours of the day are the ones with the highest solar incidence. A similar result was also seen in *Veromessor pergandei* (Mayr) (Creighton, 1953). However, this species avoids periods close to noon when the surface temperature reaches 48 °C. In nocturnal species, such as *Myrmecia pyriformis* (Smith) (Narendra et al., 2010), the result is the opposite: the intensity of sunlight at sunset determines the onset of foraging, which can be anticipated if the light intensity is lower than normal, or delayed if it is higher. Luminosity may also not influence the outflow of nest workers, as in the species *Pheidole oxyops* (Assis, 2018).

We did not find a significant relationship between wind speed and worker foraging activity in this species. However, it affects the foraging of other ant species, such as the arboreal ant *Cryptocerus texanus* (= *Cephalotes texanus)* (Creighton, 1963), which does not leave the nest on windy days, even if the temperature and luminosity are in adequate condition and *Acromyrmex lobicornis* (Emery) (Alma, 2016) which reduces the number of smaller foragers when it is very windy. An explanation for this result may be related to an adaptive characteristic that ants, especially arboreal ones, have developed, the so-called "adhesive pads" or arolia located in the pretarsa that allow these insects to climb and stick-on surfaces such as trunks and leaves of trees, escaping the force of the wind, which may, eventually, knock them down from the tree (Orivel, 2001; Yanoviak, 2005).

The drop in foraging flow at 2:00 p.m. (Figure 2) under high-temperature conditions (33.4 ± 3.14) and low relative humidity (39.2 ± 8.53) can be a behavioral adaptation or strategy of ants to minimize problems with desiccation since under these conditions the air easily absorbs water from body perspiration, increasing the rate of water loss. Thus, the ants avoid leaving the nest in these conditions (Kleynhans, 2011; Verberk et al., 2015; Bujan et al., 2016; Assis et al., 2018; Ajayi et al., 2020).

On the other hand, they also avoid leaving the colony when the relative humidity is high, probably as a strategy (1) to avoid high atmospheric heat conditions (a combination of high temperature and high humidity), which could increase rates of transpiration and body water loss (Hood & Tschinkel, 1990; Veberk et al., 2015; Bujan et al., 2016) or (2) not to forage when there is a possibility of rain, since, having arboreal habits, workers may face challenges to keep themselves and walk under trunks and leaves when there is much moisture in the substrate (Stark & Yanoviak, 2018) or when they are hit by raindrops (Federle & Endlein, 2003; Bauer et al., 2012).

A probable explanation for these ants to present a positive correlation with temperature and luminosity and a negative correlation with relative humidity may be linked to the physiology and adaptation of some ant species to tolerate water loss. Foraging activity in ants naturally tends to require an ability to tolerate desiccation and dehydration conditions (Ajayi et al., 2020). Arboreal ants are more tolerant to heat (Bujan et al., 2016; Leahy et al., 2022), combining their heat tolerance limits with the hot and dry conditions of the canopy of trees, thus broadening their thermal tolerance ranges (Leahy et al., 2022). This ability to tolerate higher temperatures and low relative humidity may be related to the composition and adaptations in their cuticles.

Because they have a large body surface area, terrestrial insects become susceptible to desiccation, mainly through the cuticle. These insects can conserve water through this waterproof cuticle, which is covered with a layer of epicuticular lipids (hydrocarbons), which is the main mechanism of limiting water loss in the exoskeleton (Ajayi et al., 2020). Therefore, *C. borgmeieri* may, like other arboreal ants, be more resistant to desiccation (Bujan et al., 2016; Leahy et al., 2022), perhaps because they possess the chemical composition of their cuticle efficient compounds to prevent water loss (Bujan et al., 2016). However, we should also consider that arboreal ants could mitigate the effect of high temperatures on their bodies by making trails in the shadows created by the canopy of trees, thus avoiding overheated sunspots (Spicer et al., 2017).

Biotic factors such as predation and competition may also be important factors that will determine the foraging schedule of a species (Assis et al., 2018). Competition is crucial for foraging, which can result in a decrease or interruption of foraging (Traniello, 1989). Some ant species may be forced to forage near limiting temperatures because of competition pressure or predation (Jayatilaka et al., 2011). In the Mediterranean region, for example, subordinate species of ants that are more tolerant to heat are forced to forage near their critical tolerance limit to gain a competitive advantage under the dominant species, which do not tolerate heat (Cerdá, 2001). On the other hand, ants from the Sahara Desert, *Cataglyphis bombycine* (Roger), can expose themselves to temperatures above 53.6 °C to avoid their predators (Wehner, 1992).

These may then be the reasons why *C. borgmeieri* forages under high temperatures, at times of the day when the dominant species that coexist in the same tree avoid, to gain an advantage in food resources or escape from predatory species. This may indicate that *C. borgmeieri* is a subordinate species since, according to Cerdá (2001), subordinate species have a higher temperature tolerance, foraging during the day under high temperatures. On the contrary, dominant species are more limited by temperature, foraging at night.

Cephalotes borgmeieri and other species of the same genus, are active during the day, at warmer times, but with low relative humidity. Thus, higher temperature and luminosity positively influence this species' foraging activity, while higher relative humidity of the air has a negative influence. Wind speed does not influence this activity. Therefore, we confirm, in part, our hypothesis that ants forage in the hottest hours of the day but avoid leaving the nest in high conditions of relative humidity, perhaps as a strategy to avoid high atmospheric heat conditions and desiccation.

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Author's Contribution

CAPR: conceptualization, methodology, investigation, writing-original draft.

JCSL: Investigation, writing-review & editing.

RPSA: Formal analysis and Statistics, writing-review & editing.

FCO: Investigation.

WFA-Jr: supervision, methodology, writing-review & editing.

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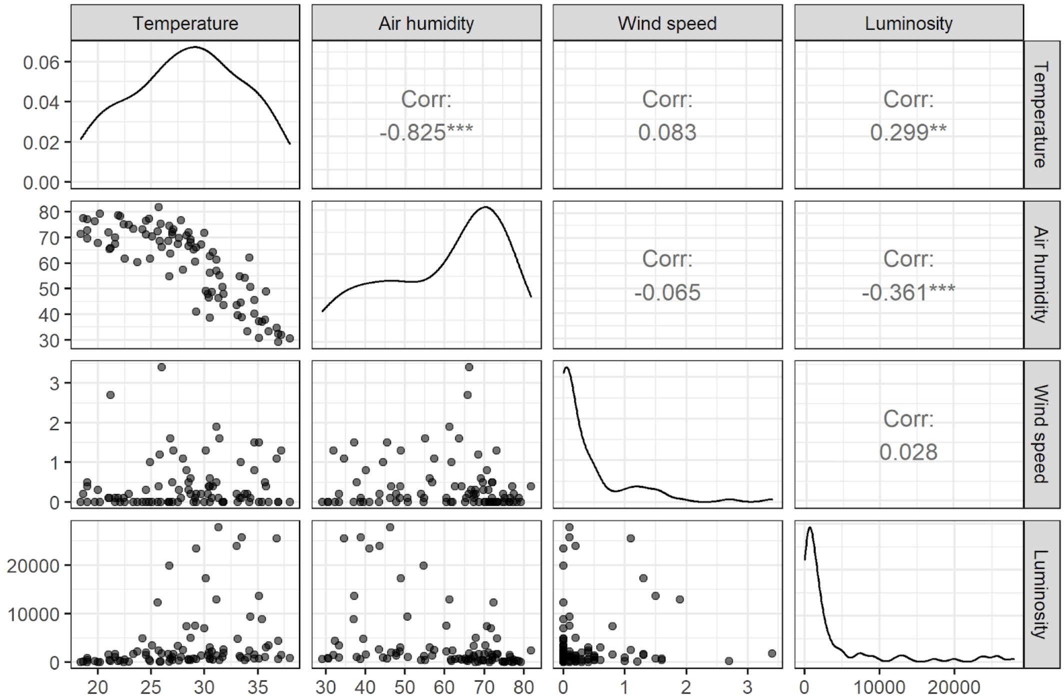
Supplementary Material



Online Resource 1. Correlation between the variables collected (temperature, air humidity, wind speed and luminosity) recorded in six colonies of the ant *Cephalotes borgmeieri* on the campus of Cidade Universitária, Dourados, Mato Grosso do Sul, Brazil.