

## Research Article

# Environmental Factors Influencing Foraging Activity in the Social Wasp *Polybia paulista* (Hymenoptera: Vespidae: Epiponini)

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Foraging behavior in social wasps is important in the development of the colony and reflects an important ecological interaction between the colony and the environment. Although the social traits of the colony play a role in the foraging activities, the conditions that establish the space and time limits are mainly physical. Here, we evaluate colonies of *Polybia paulista* throughout one year in order to verify the foraging activities and the items collected, as well as the importance of temperature, relative humidity, and solar radiation on motivating foraging. Collection of liquids was always higher than that of solids; preys were collected all year long, and nests showed two annual episodic expansions. The linear mixed effects (LME) model used to analyze which weather factors influence the foraging showed temperature as the most influencing factor on the collection of materials.

## 1. Introduction

*Polybia* is the genus of Neotropical swarm-founding Polistinae (Epiponini) with the highest number of species. The swarm-founding polistines are largely tropical in distribution, and although they comprise a relatively small group in terms of species number, they exceed all other eusocial wasp groups in terms of taxonomic diversity at the generic level, diversity of nest architecture, and range of colony size [1].

Although the Epiponini are highly social bearing complex societies, the morphological caste differentiation is often weak [2]. Bourke [3] suggested that complex societies have complex division of labor, caste differentiation, and a large number of individuals. Conversely, Jeanne [4] suggested that complexity in epiponines is more related to the number of behavioral acts performed by the worker caste than to morphological caste differences.

Sociality extends the possibilities of obtaining resources and provisioning the colony since it shows behaviors such as recruitment and division of labor [5]. Different patterns of social organization among wasps correspond to different possibilities for partitioning location, collecting, transporting, or storing of resources [5].

In Epiponini, workers perform basic tasks related to nest building, foraging, brood feeding, and defense [1]. Such tasks are usually quite complex and highly organized [1]. Division of labor is based on worker's age, and it is very well developed in epiponines even in species with very small colonies [6, 7]. Workers pass through three discrete temporal castes: younger workers perform low-risk activities inside the nest [7]; midage workers perform external nest activities, such as construction, cooling, reception of loads from incoming foragers, and defense against predator and parasites [7]; finally, older workers perform high-risk activities away from the nest, such as foraging [6–10].

Foraging behavior in social wasps is important in the development of the colony and provides a significant understanding on the involvement of the castes in the division of labor [5, 7]. Furthermore, it reflects an important ecological interaction between the colony and the environment, since the colony needs water, plant fibers (pulp), protein, and carbohydrates [11]. The water is required for temperature control [12, 13], nest construction [14], and metabolic processes [5]. Plant fibers are essential for construction and repair of cells, peduncle, and envelope [15]. Animal protein is

used mainly for feeding the larvae [16]. Carbohydrates serve as an important energy source for both adult individuals and brood, so they represent a critical supply for the growth of a wasp colony [5, 13].

Many studies have been done with the purpose of verifying several aspects related to the flight and foraging activity of social wasps, such as daily and seasonal activity of searching for resources, items collected, influence of colony and environment factors on the foraging, and foraging activity behavior patterns [17–33]. The foraging activity of these wasps varies throughout a day and throughout the seasons, but also according to the place where the study is carried out [26].

Although the social behavior of the colony plays an important role in the process of foraging activities, the conditions that establish the limits where and when foraging is feasible are mainly physical, such as light and temperature intensity [34]. Temperature and relative humidity seem to have a great influence on the foraging activity of Neotropical social wasps [19, 20, 24, 26, 30, 31], even luminosity is also recognized as an important factor [18, 23, 30]. Moreover, other factors such as atmospheric pressure and winds may affect foraging rhythm of wasps, with longer days being more favorable for flight [17].

Even though physical conditions are important to determine foraging activity, few authors have tried to access worker behavior throughout a complete colony cycle and to correlate it with ecological aspects that may influence foraging activities. Furthermore, understanding the factors that influence insect activities, such as foraging, is primary for all kinds of posterior studies. So, annual studies such as the presented here bring a valuable contribution to our knowledge on social insect life histories. Here, we show that foraging behavior in *Polybia paulista* is mainly influenced by temperature.

## 2. Material and Methods

**2.1. Study Site.** The study was carried out on Universidade Estadual Paulista “Júlio de Mesquita Filho” campus IBILCE/UNESP (20° 49' 11" W, 49° 22' 46" S), city of São José do Rio Preto, São Paulo State, Brazil, from December 2007 to August 2008 and September 2009 to November 2009.

The study area is characterized by dry winter and wet summer [35] with annual mean temperature of 26.4°C and relative humidity of 68% [36]. The annual distribution of rainfall includes a rainy season with 85% of the total annual precipitation and a dry season with only 15% of the total annual precipitation [36]. The months of the year were divided in two separated seasons, the cold and dry season (CDS, mean temperature: 24.5°C, mean humidity: 63%) from April to September and the hot and humid season (HHS, mean temperature: 26.9°C, mean humidity: 71%) from October to March [36].

**2.2. Data Collection.** Two to four observations were performed monthly, 14 observations were carried out during the HHS, and 12 during the CDS in five different colonies (Table 1). All colonies were in postemergence stage according to the classification proposed by Jeanne [37] and had nearly

the same size, approximately 1,500 wasps. The exact amount of wasps was not censused because our primary goal was to accomplish as much observations as possible in the same nest.

The nests were observed for 15 minutes every interval of two hours, from 10:00 to 16:00 h, totaling one hour of daily observations. We counted the number of wasps returning to the nest and the type of material carried by them (pulp, prey, or liquid material).

In order to identify the material brought by the wasps, the behavior “landing on the nest” was taken into account as described by Prezoto et al. [38] and complemented by Pereira [27]. If she landed with a prey, she had a solid material in her mandibles and walked directly into the nest or, if the prey was very big, she divided this material with another wasp on the nest surface. After that, both entered the nest. When she returned with pulp, she had a dark and rounded solid material in her mandibles, and she passed or divided the material with other wasps. When the wasp returned with liquid (it was not possible to distinguish among wasps bringing nectar or water), she could enter in the nest without any visible material in her mouthparts or she could perform trophallaxis. In this case, one could see the droplets being transferred and her abdomen getting smaller. When she went back and did nothing for about 5 seconds, it was because she returned without any material. In some situations, it was not possible to identify successfully the type of material collected by foragers. In this case, the material was treated as unidentified (un).

We measured the weather conditions right below the nests at the end of each observation. To measure temperature and relative humidity, a thermohygrometer Incoterm was used under the tree where the nests were and light intensity was measured by using a digital luximeter ITLD-240 in an open area 1 m aside the nest.

**2.3. Data Analyses.** Since we are comparing data temporally correlated with one another, statistical methods that assume independence of observations could overstate the significance of any predictive factor. Linear mixed effects (LME) models offer a useful alternative to traditional univariate or multivariate repeated-measures ANOVA models [39]. Therefore, LME models were used to test for statistically significant influence of weather conditions on the number of wasps foraging.

In the first step, the basic model was compared to a model containing the same fixed effects and different random effects for seasonal adjustment (Table 2(a)). In the second step, the seasonally adjusted model without correction for serial correlation was compared to a seasonally adjusted model with serial correlation incorporated as a first-order auto-regressive (AR1) covariance structure (Table 2(b)). Finally, the optimal model in terms of the residual correlation structure was used to test which variables (temperature, humidity, luminosity, season, month, and hour) best explain the number of wasps foraging (Table 2(c)). We applied data dredge statistics (dredge-MuMIn R package, <http://r-forge.r-project.org/>) to automatically generate the best four models combining the fixed terms of the global

TABLE 1: Months in which each nest was sampled and the number of days that each nest was observed, as well as the substrates, growth habit, and height where the nests were found in the social wasp *Polybia paulista*.

Colony	Month(s) sampled	Number of observations	Substrate	Growth habit	Height
N1	Dec (2007), Jan, Feb, Mar, Apr (2008)	8	<i>Caesalpinia echinata</i> (Fabaceae)	Tree	1.5 m
N2	May, Jun (2008)	3	<i>Copernicia</i> sp. (Arecaceae)	Palm-tree	2.0 m
N3	Jul, Aug (2008)	4	<i>Licania tomentosa</i> (Chrysobalanaceae)	Tree	2.0 m
N4	Sep, Oct (2009)	7	<i>Licania tomentosa</i> (Chrysobalanaceae)	Tree	2.5 m
N5	Nov (2009)	4	<i>Copernicia</i> sp. (Arecaceae)	Palm-tree	1.8 m

TABLE 2: Linear mixed effects (LME) models performed between the number of wasps foraging in *Polybia paulista* and six explanatory variables (temperature, humidity, luminosity, season, month, and hour). Tested models comparison:  $k$  = degree of freedom,  $\Delta AIC_C$  = difference in Akaike's Information Criterion for each model from the most parsimonious model, and  $wAIC_C$  =  $AIC_C$  weight.

(a) Random effects			
	$k$	$\Delta AIC_C$	$wAIC_C$
Nest + month	10	0.00	0.779
Nest + month + hour	11	2.5	0.221
Nest	9	21.7	<0.001
(b) Correlation structure			
	$k$	$\Delta AIC_C$	$wAIC_C$
corAR1	11	0.00	0.541
corARMA	11	0.50	0.431
Without correlation	10	6.4	0.022
corCompSymm	11	8.9	0.006
(c) Fixed effects			
	$k$	$\Delta AIC_C$	$wAIC_C$
Season + temp	7	0.00	0.41
Season + temp + humidity	8	1.15	0.23
Temp	6	1.18	0.22
Season + hour + temp	8	2.11	0.14

model. The Akaike information criterion corrected for small sample size ( $AIC_C$ ) was used to select the best fitting LME models [40]. Akaike weights were used to evaluate model-selection uncertainty. A model's Akaike weight ( $wAIC_C$ ) expresses the weight of evidence favoring that model as the best of all those in the model set; the weights of all models together sum to 1 [40]. Data analyses were performed using the program R 2.12.2 [41] (<http://www.r-project.org/>), with the package nlme [42].

### 3. Results

**3.1. Foraging Activity throughout the Year.** Foraging rate was apparently higher in some months along the year. In February, April, June, August, and September, more than 250 wasps were seen foraging in one day, which was sampled only one hour (Figure 1). Collection of liquids (water and

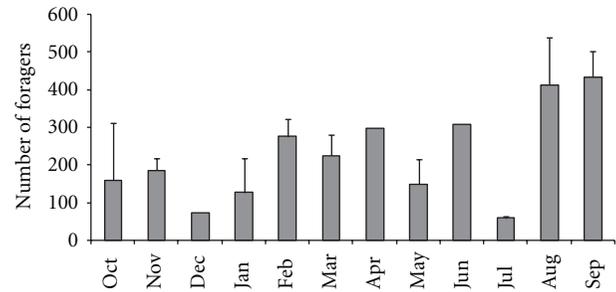


FIGURE 1: Mean number of foragers of *Polybia paulista* observed returning to the nest per day for each month of observation. Each day was sampled four times, during 15 minutes each. Thin bars are standard deviations.

nectar) was always higher than other materials collected (55% to 80% of the collected materials, Figure 2). Collection of solids was small and occurred in all months. In June, we registered the highest prey collection, in which 21% of the foragers returned with this material. In contrast, in July, September, October, November, and December, the lowest rate of prey collection was registered, *ca.* 6.25%. In January, February, March, April, May, and August, prey collection was intermediate (*ca.* 12.2%, Figure 2). Pulp collection occurred in six months, from August to January, and it was made up from 0.2% to 12% of the material collected by the foragers. However, in October and November, only three wasps were recorded collecting pulp. On the other hand, December, January, August, and September presented the highest number of wasps collecting pulp (Figure 2). Construction was observed in three different nests, one in December and January, another in August, and a different one in September.

A small percentage of foragers arrived without any material in almost all months (Figure 2).

**3.2. Environmental Factors.** The maximum temperatures recorded in both seasons were the same; the minimum temperatures and the means differed by about two degrees Celsius (Table 3), which shows a small variation along the year [36]. The amplitude was approximately 10.5°C for the HHS and 12.5°C for the CDS (Table 3). However, the daily amplitude was different for each season, 7.25°C on average for the HHS and 4.6°C on average for the CDS. During the HHS, the maximum humidity recorded was 92% and the minimum was 48%, the mean was 71%, and the median

TABLE 3: Weather conditions recorded throughout the year for the foraging study in the social wasp *Polybia paulista*. Maximum (max) and minimum (min) absolute values and mean values of temperature ( $^{\circ}\text{C}$ ), relative humidity (%), and light intensity ( $\text{lux} \times 100$ ) for each month and the entire season. HHS: hot and humid season. CDS: cold and dry season.

		Temperature ( $^{\circ}\text{C}$ )			Humidity (%)			Light intensity ( $\text{Lux} \times 100$ )		
		Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
HHS	Oct	31.0	22.0	24.4	91	48	69	1248	50	569
	Nov	32.0	24.0	26.1	91	50	70	1487	124	1108
	Dec	26.0	24.0	28.2	79	66	74	498	258	386
	Jan	27.0	21.5	24.6	91	70	80	994	227	494
	Feb	30.0	22.0	24.9	91	65	77	1547	27	888
	Mar	31.5	25.5	26.4	92	52	63	1404	82	910
	Season	32.0	21.5	26.9	92	48	71	1547	27	790
CDS	Apr	32.0	29.0	29.2	67	54	61	1213	64	637
	May	26.5	19.5	30.6	100	59	79	900	16	353
	Jun	27.0	23.0	23.3	83	63	74	933	53	643
	Jul	23.0	20.0	24.8	64	43	51	1031	479	828
	Aug	28.0	23.5	21.6	67	33	52	1087	237	672
	Sep	31.0	20.0	25.8	83	42	67	1253	159	685
	Season	32.0	19.5	24.5	100	33	63	1253	16	644

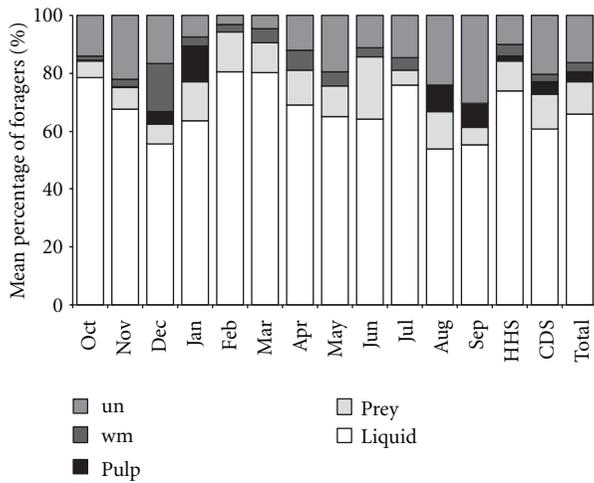


FIGURE 2: Mean percentage of foragers of *Polybia paulista* returning to the nest for each day of observation bringing liquid, prey, pulp, nothing (wm), and unidentified material (un) for each month, season, and the entire year. HHS: hot and humid season. CDS: cold and dry season.

was 71.5% (Table 3). On the other hand, during CDS, the maximum humidity was 100% in a day that was raining, while the minimum was 33%, the mean was 63%, and the median was 62% (Table 3). The amplitudes were large, 49 percentage points throughout HHS and even larger, 67 percentage points during CDS (Table 3). The maximums, minimums, and means of light intensity were very similar in both seasons and varied widely throughout the year (Table 3). According to the climatic data for the last 20 years [36], the period in which our observations were performed

presented a typical weather condition to that geographic region.

Since more than one sampling was done in the same nest and the samplings closer in the time are more likely to be under the same biological effects, the use of LME models is imperative. The model explaining the number of foraging wasps that included only season and temperature was the best supported (Table 2(c), Figure 3).

## 4. Discussion

**4.1. Foraging Activity throughout the Year.** Liquid material was widely collected (Figure 2), and this might be due to its importance in wasps metabolism (water and nectar), maintenance of nest temperature (water), and nest construction (water). Water is a limiting factor for the development of wasps [43]. On the other hand, nectar is extremely important in adults' diet, and several authors pointed out that it is the most collected material in different periods in the year [17, 19, 20, 29, 30, 33, 44].

Pulp collection, used for nest construction and repair, was observed only in six months, two months during the CDS and four months in HHS. However, construction was in fact observed only in four months when the greatest amounts of pulp were collected (August-September and December-January, Figure 2). According to Jeanne [1], as brood reproduction in swarm-founding polistines occurs in pulses, nest expansion is also episodic. Thus, when nest expansion occurs, it is typically a discrete event, lasting several days. In contrast, after a reproductive event, addition of cells to the nest may not occur for months.

Collection of preys occurred all year long (Figure 2). Since preys provide animal protein for brood development, the amount of preys captured by foragers is an indirect

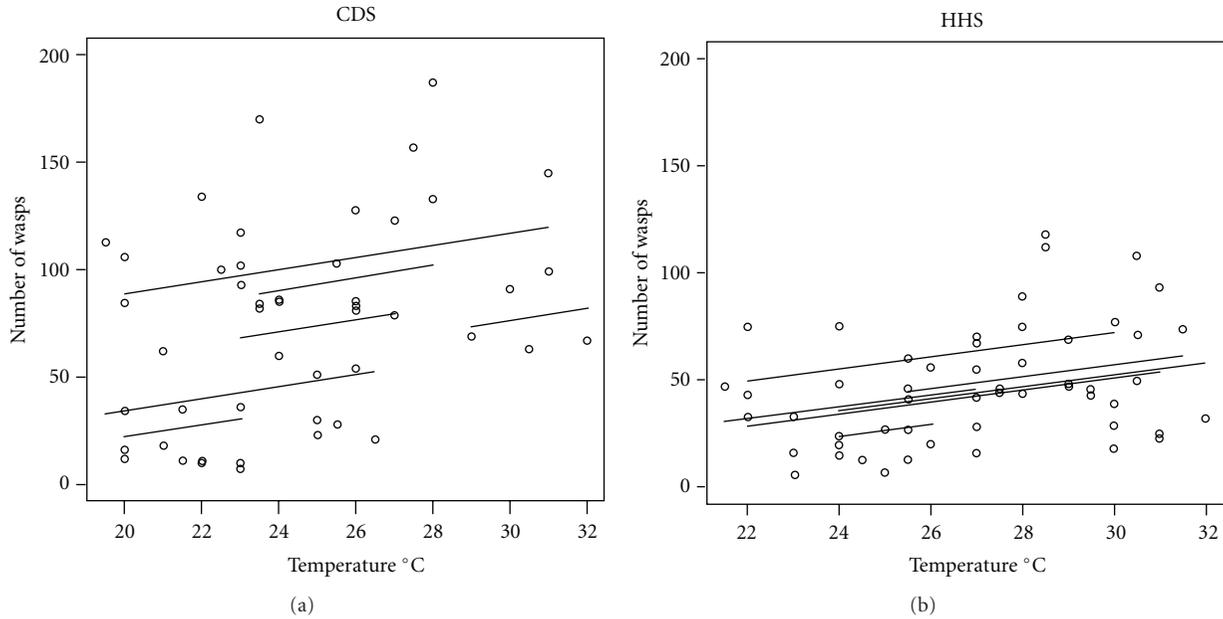


FIGURE 3: Number of foragers that arrived at the nest every 15 minutes in relation to season and temperature. There is a clear influence of temperature on foraging for both. Lines were estimated by linear mixed effect (LME) model, according to the equation: Number of wasps foraging =  $-29.98 + 28.79 \times \text{Season} + 2.82 \times \text{Temperature} + \text{Random effect} + \text{Residual}$ , where Random effect  $\sim N(0, 23.04)$  and Residual  $\sim N(0, 28.06)$ . CDS: cold and dry season. HHS: hot and humid season.

measure of the number of immatures and, consequently, indicates colony reproduction. According to Machado [45], colonies of *Polybia paulista* produce reproductives once a year in the rainy months (HHS) at the ending and beginning of the year. However, the production of workers occurs in the intermediate period. So, a colony can exist for up to three years at the same place, but swarms occur periodically.

The fact that prey was collected all year long suggests that production of workers happens all over the year, depending on the necessity of each nest. It was noted by Jeanne [1] that in regions with unfavorable season (like a harsh wet or dry season), colonies face several reproductive constraints and do not reproduce all the year. The wasps seem to “consider” that both seasons are adequate to raise brood in the place of study.

Moreover, we found some evidences about a greater activity during CDS. It is known that besides an ideal temperature, water is another important requirement for egg development. When it is available in insufficient amounts, the embryogenesis becomes quiescent or the embryo remains in diapauses [46]. However, the ideal humidity quantity necessary for that is not known in any neotropical swarm-founding wasp. So, maybe more activity was recorded in CDS because more water needed to be carried to the nest to increase humidity. Hence, there is probably more to be done to reach the same success reached in HHS for raising brood. Thus, more studies concerning these aspects should be done to improve our understanding in this area. However, it is important to point out that despite of being careful to choose nests with the same size and developmental stage, our data are temporally correlated and the results might have suffered some kind of influence due to the nests chosen.

## 4.2. Environmental Factors

**4.2.1. Temperature.** A variety of studies has demonstrated the influence of weather conditions on social wasp foraging and nearly all of them point to temperature as the key factor influencing foraging [17–33, 38]. We found a great influence of temperature on foraging, since there was an increase in the number of foragers simultaneously to the increase of temperature (Figure 3). This increase in the activities can be partially explained by the wasps’ necessity for water (it is used for nest construction [14], metabolic processes [5], and nest cooling [12, 13]). Generally, when temperature increases also does their water collection once the need for nest cooling is more evident [27]. According to Jeanne [1] when the nest overheats, workers on the envelope fan their wings steadily to ventilate the nest. If that is inadequate, foragers begin to bring water to the nest, where it is spread on the surface of the combs and envelope, bringing about cooling by evaporation [8].

There are lower and upper thresholds of temperature beyond which wasps do not forage. Previous studies suggested a very low limit of 2°C or 5°C for vespine wasps [47, 48]. So, flight will not occur until a certain thoracic temperature is reached [49]. Flying insects can increase their body temperature by producing heat with their flight muscles [50]. Thus, they do this until they reach the ideal temperature for the flight. Concerning higher temperatures, Kasper et al. [28] noted in *Vespula germanica* that foraging activity increased with temperature until 20°C and it was kept practically constant between 20°C, and 35°C. Above 40°C, the foraging activity decreased and virtually ceased, probably because the heating caused by flight can overheat the

wasps [28]. These extreme temperatures were not found in this study, once the minimum was 19.5°C and the maximum was 32°C. Differently of Kasper et al. [28], the foraging increased along with temperature even up to 20°C (Figure 3), probably because these species bear strong biological differences. For example, Resende et al. [20] studying *Polybia occidentalis*, a closer species, noted that foraging increases until 34°C, the maximum temperature recorded.

**4.2.2. Relative Humidity.** Several works on flight activity pointed out that relative humidity can be an important weather factor influencing foraging activity in wasps [18–21, 23, 24, 26, 30–32]. We found no influence of humidity on foraging, possibly because its influence on foraging is smaller than temperature.

For instance, Silva and Noda [18] studying the external activity of *Mischocyttarus cerberus styx* and Resende et al. [20] studying *Polybia occidentalis* noted that foraging increased with temperature and decreased when humidity increased. They affirmed that higher humidity has a major influence on the foraging than moderate or lower humidity, and although humidity has certain influence, it is lower than temperature influence. It is important to say that the most part of such works did not analyze the relative humidity along several months in the year, and depending on the month that is analyzed, an overestimated or underestimated importance of this weather factor may occur. Furthermore, these authors point out that the humidity influence is greater on higher values, and the place of study presents moderate and low humidity during almost all the year. Thus, the lack of influence of this weather factor may be due to its low values recorded.

In addition, other authors such as Kasper et al. [28] did not find any correlation with humidity, and Lima and Prezoto [22], on the other hand, found correlation between these variables on *Polybia platycephala sylvestris* only in hot and humid season. However, even with the separation of the year into HHS and CDS, there are some climatic differences in the localities where our study and those by Lima and Prezoto were performed. Our locality is hotter (23.5°C versus 19.3°C for annual mean [51]) and drier (1,240 mm versus 1,644 mm for annual pluviosity [51]).

**4.2.3. Light Intensity.** The light intensity influence is probably the most controversial factor influencing foraging activity. Some authors found a strong influence of the luminosity while others did not. For instance, Kasper et al. [28] detected strong correlation between these variables. On the other hand, Elisei et al. [23] did not find any correlation in *Synoeca cyanea*.

Osgood [52] and Lerer [53] suggested that the foraging activities of the stingless bee *Trigona hyalinata* begin in the morning by temperature influence, and in the end of the day, there is luminosity influence. It is important to point out that our observations were accomplished until 4 p.m., a period with a great luminosity in the most part of the year, and this might have had an effect on the lack of influence of this variable on the foraging.

As a conclusion, in climates like the one presented here, with a strong wet-dry seasonality and low cold-hot seasonality, the main factor influencing foraging in colonies of *Polybia paulista* in both seasons is temperature. Although there is a great variability in humidity and solar radiation along the year and even along the day, their influence on foraging seems to be small.

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