



Collection of floral resources by bees in *Solanum lycocarpum* A.St.-Hil. (Solanaceae): interference of abiotic factors and need for buzzing behavior

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Abstract. The foraging activity of floral visitors is influenced by habitat conditions and abiotic factors. The aim of this research was to define the faunal composition of the visitor community in *Solanum lycocarpum* A.St.-Hil. (Solanaceae) and to evaluate the influence of abiotic factors on the flight activity of the predominant visitors. The capture of bees was conducted for 15 minutes from the beginning of each hour between 6:00 am and 6:00 pm in a cluster with 15 *S. lycocarpum* individuals during 10 days. Centridini was the predominant tribe of bees, with 83.5% of the total foraging recorded. About 66.5% of foraging was concentrated in the time interval between 8:00 am and 12:59 pm, characterized as an optimal foraging period. At 6:00 am and from 5:00 pm onwards, bees were discouraged from foraging. Only *Epicharis flava* Friese and *Centris scopipes* Friese were classified as predominant species. *Centris scopipes* was the only predominant species whose abiotic conditions interfered in the foraging activities. Since bee foraging records were developed in the summer, environmental conditions did not limit the foraging of most bees during the entire foraging period of the day.

Keywords: Abiotic factors; Behavior; Buzz-pollination; Centridini; Optimal foraging.

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Bees maintain populations of native plants that support biodiversity and ecosystem functioning by promoting pollination (Potts *et al.* 2016). However, floral resources are ephemeral and dispersed, because fluctuate in availability across time and space (KLEINERT *et al.* 2009). Therefore, the foraging efficiency of bees depends on the influence of habitat conditions, such as space and the temporary distribution of food sources (DORNHAUS & CHITTKA 2004; PASQUET *et al.* 2008), as well as, various abiotic factors that can limit flight activity (POLATTO *et al.* 2014; POLATTO & ALVES JUNIOR 2022).

The often unstable natural environment requires bees to make adjustments to their foraging activities to optimize the collection of floral resources. According to optimal foraging, a positive energy balance is expected to occur in the relationship between collection of floral resources and energy expenditure in foraging flight (PYKE 1984). In this context, flight activity tends to be affected by abiotic factors such as temperature, relative humidity, precipitation and wind speed (HILÁRIO *et al.* 2000, 2001; KASPER *et al.* 2008). Among other physiological consequences, these abiotic factors interfere mainly in the energy expenditure for the bee to regulate its body temperature (CARVALHO-ZILSE *et al.* 2007).

Solitary bees species are more vulnerable to interference from abiotic factors than eusocial bees, since the high population density of the colony confined in a hive allows eusocial bees to be in a homeostatic environment in the period immediately before the foraging flight (EICKWORT & GINSEBERG 1980; MORATO & CAMPOS 2000). Therefore, extreme temperature and insolation, from very low or very high, strong winds and low relative humidity can interfere with the flight dynamics of bees (BURRILL & DIETZ 1981; MORATO & CAMPOS 2000), especially solitary species. Indeed, the bees initiate, increase or decrease the foraging rate mainly under the influence of temperature (ROUBIK 1989), since they cannot fly if the temperature is too low (thoracic flight muscles do not reach the minimum threshold temperature that allows flight to be performed) and get dehydrate quickly at high temperature associated with very low relative humidity (KASPER *et al.* 2008).

On the other hand, competitive interactions between bees and their trophic ranges adjust patterns of diversity and abundance, as species share niche space (CANE & SIPES 2009). For example, ROUBIK (1989) reports that there is an advantage for polylectic species, since they are able to meet their needs in times of food shortage due to the use of a greater number of plant species.

In the Cerrado biome, *Solanum lycocarpum* A.St.-Hil. (Solanaceae), a shrubby species, stands out as a source of floral resource available practically throughout the year (CAMPOS 1994), with flowers presenting several attributes related to the melitophily syndrome (TAVARES *et al.* 2017). The fruits of *S. lycocarpum* serve as food for species such as *Chrysocyon*

brachyurus (Maned Wolf), *Tapirus terrestris* (Lowland Tapir), *Cerdocyon thous* (Crab-eating Fox), *Lycalopex vetulus* (Hoary Fox), *Salvator merianae* (Black-and-white Tegu), mainly during the dry season, when other food resources became scarce (MOTTA et al. 2002; OLIVEIRA JUNIOR et al. 2004; PINTO et al. 2007). In addition, its fruits serve as a substrate for the development of the fungus used by the leaf-cutting ant *Atta laevigata* (TAVARES et al. 2016).

Solanum lycocarpum has heterostylic flowers with poricidal anthers, an attribute that restricts pollen collection by visitor, since the release of this resource requires that vibration technique performed by bee species – the buzz-pollination (BEZERRA & MACHADO 2003). Occurrence of heterostyly in *S. lycocarpum*, in which brevistyl flowers are exclusively pollen producers, required an efficient pollination service for the pollen grains to reach the flower stigmas and guarantee the plant's reproduction (TAVARES et al. 2018). Also according to the same authors, *Centris scopipes* Friese and *Epicharis (Epicharis) flava* Friese (Apidae) were the ones that most contributed to the reproductive success of the plant species, since, respectively, 90% and 82.5% of visited flowers only once by them resulted in fruit formation.

Considering the different aspects mentioned and the contribution to the maintenance of the local bee community (TAVARES et al. 2018), *S. lycocarpum* was selected for this study of faunal analysis and the influence of abiotic factors on the foraging activity of bees in their flowers.

The aim of this study was to define the faunal composition of the visitor community in *S. lycocarpum*, as well as to evaluate the influence of abiotic factors on the flight activity of the predominant visitors. Two questions are expected to be answered: (1) What time of day do visitors develop optimal foraging? (2) How do abiotic factors affect the foraging activity of floral visitors?

MATERIAL AND METHODS

Characterization of the selected area. The study was carried out in a semideciduous secondary forest fragment, in the rural area of the municipality of Ivinhema, State of Mato Grosso do Sul, Brazil (22°16'20"S; 53°48'34"W). The fragment was composed of vegetation resulting from regeneration processes, since the primary vegetation was removed for planting eucalyptus. After the removal of eucalyptus, the native species recolonized the area. In this fragment there are patches of vegetation with characteristics of Cerradão and Atlantic Forest. The region's climate is subtropical, ranging from humid to sub-humid (ZAVATTINI 1992). The average annual temperature ranges from 20 to 22 °C, and the average annual precipitation varies from 1,400 to 1,700 mm (ALVARES et al. 2013). The soil type in the region is the Dystrophic Red-Yellow Latosol (EMBRAPA / IBGE 2001).

Sampling method of floral visitors. The sampling of floral visitors was carried out in 10 days, not necessarily consecutive, from January to February 2013 (except rainy days). All samplings were carried out in the same cluster, containing 15 individuals of *S. lycocarpum*. During the sampling of floral visitors, for 15 min from the beginning of each hour, between 6:00 am and 6:00 pm, the entomological net was actively manipulated in search of any animal that landed on the flowers of the cluster. The values of the following abiotic factors were recorded in the period immediately before the beginning of the bee sampling at each hour of the day: temperature, luminosity, relative humidity and wind speed.

Specimens were placed in vials according to the time of capture. The sampled material was sorted and identified according to SILVEIRA et al. (2002). The specimens are deposited

at the Biodiversity Museum (MuBio) of the Faculty of Biological and Environmental Sciences (FCBA) Universidade Federal da Grande Dourados (UFGD).

It is understood that the sampling strategy of floral visitors caused a subsampling during the day, since the captured organisms were prevented from making subsequent visits to the flowers of the cluster. On the other hand, this sampling technique was chosen due to the taxonomic fidelity of having all organisms screened and identified.

Faunistic and statistical analyses. The faunistic characterization of the floral visitors of *S. lycocarpum* was obtained by grouping the species into classes of frequency of visits, constancy and dominance.

Visit frequency classes (total number of visits performed by each species) were established by determining the confidence interval (CI) at 95% probability, resulting in three rankings: (1) very frequent (number of individuals greater than the 95% CI upper limit); (2) frequent (number of individuals located within the CI at 95%); (3) infrequent (number of individuals below the lower limit of the 95% CI).

Based on the occurrence of a particular species on each sampling day, the constancy was calculated using the following formula:

$$\text{Constancy} = \frac{\text{Number of days a particular species was sampled}}{\text{Number of sampling days}} \times 100$$

This classification was obtained: (1) constant ($C \geq 50\%$); (2) accessory ($C \geq 25$ e $< 50\%$) e (3) accidental ($C < 25\%$).

Dominant species were those that exceeded the limit calculated by the formula:

$$\text{Dominant species} = \frac{1}{\text{Total number of species}} \times 100$$

Predominant species were those that were simultaneously within the faunistic indices of very frequent, constant and dominant.

The chi-square test (χ^2) was applied to verify if the foraging activity of bees belonging to the dominant class was homogeneously distributed during the collection times. The same test was applied at the community level of floral visitors. The optimal foraging was established using the number of foragers in each 15 minute period and determining the confidence interval (CI) at 99.9% probability (POLATTO & ALVES JUNIOR 2022). Optimal foraging was characterized when the number of foragers was greater than the upper limit of the 99.9% CI. Inversely, there was a disincentive to foraging by floral visitors when the number of foraging was lower than the 99.9% CI.

To verify if the foraging activity of floral visitors belonging to the dominant class was correlated with abiotic factors, Pearson's correlation test was applied. The test was not applied to species belonging to the non-dominant class, because sporadic foraging of these organisms affects the validation of the correlation coefficient.

BioEstat 5.0 software was used, according to AYRES et al. (2007), to find confidence intervals, and to develop the chi-square test and Pearson's correlation, both with 5% significance levels.

RESULTS

Twelve species of floral visitors were recorded that foraged the flowers of the *S. lycocarpum* cluster, all of which were bees. They exclusively collected pollen from flowers, totaling

322 foraging during the 10 days of sampling. Centridini was the predominant tribe of bees, with 83.5% of the total foraging recorded (Table 1).

The foraging activity of the bee community was heterogeneous throughout the day ($\chi^2 = 321$; $p < 0.0001$). About 66.5% of foraging was concentrated in the time interval between 8:00 am and 12:59 pm, characterized as the optimal foraging period. On the other hand, at 6:00 am and from 5:00 pm onwards, there was a disincentive to bee foraging (Table 1). *E. flava* and *Oxaea flavescens* Klug (Andrenidae) showed optimal foraging activity equivalent to that found for the bees. In turn, *C. scopipes* maintained optimal foraging between 10:00 am and 1:59 pm (Table 1).

Only *E. flava* and *C. scopipes* were classified as predominant species (Table 2). Both species accounted for 77.3% of the total foraging, were present on all sampling days and were dominant in the use of floral resources of *S. lycocarpum*. Conversely, seven species of bees were sporadically found on the flowers of *S. lycocarpum* (3.4% of foragers), being classified as infrequent. The rest of the bees (3 species) constituted 19.3% of the visits and were defined as frequent (Table 2). Regarding foraging constancy, in addition to *E. flava* and *C. scopipes*, three other species were classified in the constant class, namely *O. flavescens*, *Exomalopsis (Exomalopsis) fulvofasciata* Smith (Apidae) and *Centris (Heterocentris) analis* (Fabricius) (Apidae) (Table 2). Finally, three species were defined as dominant – *E. flava*, *C. scopipes* e *O. flavescens* (Table 2).

Table 1. Bee foraging activity on *Solanum lycocarpum* (Solanaceae) flowers during the day. The value entered in each 1-hour period represents the sum of foraging performed by each species during the 10 days of sampling. The numbers followed by the "+" sign represents the optimal foraging of each species, and the "-" sign represents the disincentive to foraging. CI values 99.9%: *Centris (Ptilotopus) scopipes* Friese = between 1.8 and 8.3; *Epicharis (Epicharis) flava* Friese = between 6.3 and 22.3; *Oxaea flavescens klug* = between 0.3 and 4.1; bee community = between 10.9 and 37.8.

Taxa	Time of day													Total
	6	7	8	9	10	11	12	13	14	15	16	17	18	
APINI														
<i>Apis mellifera</i> Linnaeus	0	0	0	1	0	0	0	0	0	0	0	0	0	1
CENTRIDINI														
<i>Centris (Ptilotopus) scopipes</i> Friese	0-	1-	7	3	8+	8+	12+	9+	7	7	6	0-	0-	68
<i>Centris (Heterocentris) analis</i> (Fabricius)	1	0	2	4	0	1	1	2	2	1	1	0	0	15
<i>Epicharis (Epicharis) flava</i> Friese	6-	13	24+	29+	27+	20+	25+	11	7-	6-	6-	5-	2-	181
<i>Epicharis (Epicharoides) maculata</i> Smith	0	0	0	1	0	0	0	0	0	1	0	0	0	2
<i>Epicharis</i> sp.	0	0	1	0	1	0	1	0	0	0	0	0	0	3
EXOMALOPSINI														
<i>Exomalopsis (Exomalopsis) fulvofasciata</i> Smith	0	2	2	1	3	3	6	0	1	0	1	1	0	20
EUGLOSSINI														
<i>Eufriesea nigrescens</i> (Friese)	0	1	0	0	0	0	0	0	0	0	0	0	0	1
XYLOCOPINI														
<i>Xylocopa (Megaxylocopa) frontalis</i> (Olivier)	1	0	0	0	0	0	0	0	0	0	0	0	0	1
TETRAPEDIINI														
<i>Tetrapedia diversipes</i> Klug	0	0	1	0	0	0	0	0	0	0	0	0	0	1
OXAEINI														
<i>Oxaea flavescens</i> Klug	1	3	4+	5+	1	5+	7+	1	0-	0-	0-	0-	0-	27
<i>Oxaea</i> sp.	0	0	0	0	0	0	1	0	0	0	1	0	0	2
Total	9-	20	40+	44+	40+	37+	53+	23	17	15	15	6-	2-	322

The field research was carried out in the summer season. The average temperature during the assessment period was 30.1 ± 3.3 °C (mean \pm standard deviation), relative air humidity was $49.6 \pm 13.4\%$, luminosity of $12,900 \pm 3,100$ and wind speed of 0.8 ± 0.4 m/s. On all sampling days, the weather remained clear or partially cloudy, with no rain.

There was no significant correlation between the foraging activity of *E. flava* and the abiotic factors evaluated (Table 3), although there was a significant reduction in the number of individuals collected throughout the day ($r = -0.367$; $p < 0.0001$). For *C. scopipes*, there was a significant positive correlation between its foraging activity and the abiotic factors luminosity and temperature. Conversely, there was a significant negative correlation between this bee's foraging activity and relative air humidity (Table 3). Finally, the foraging activity of *O. flavescens* showed no significant correlation with abiotic factors and time of day (Table 3).

DISCUSSION

All the floral visitor organisms of *S. lycocarpum* were constituted by solitary bees. Honeybee – the exotic eusocial bee *Apis mellifera* Linnaeus (Apidae) – represented the only exception, although it was collected only once in all sampling days. Sampling only solitary bees does not represent a pattern commonly found in natural vegetation in the Neotropics (e.g., PEDRO & CAMARGO 1991; ANACLETO & MARCHINI 2005; ANDENA *et al.* 2005; SILVA-PEREIRA & SANTOS 2006). The literature cited here recorded low diversity of eusocial bees, but they were predominant in the collection of floral resources.

Poricidal anthers exclude some visitors (pollen eating beetles, flies, and non-buzzing bees, especially honeybee), and act as a mechanism that maximizes pollen collection by legitimate pollinators (HARDER & THOMSON 1989; HARDER & BARCLAY 1994). Therefore, the accommodation of pollen in poricidal anthers was possibly the reason for the absence of intense foraging by honeybee and other eusocial bees (BUCHMANN & HURLEY 1978). On the other hand, according to the same authors, buzzing behavior is well developed in most bees with primitive traits

Table 2. Faunistic characterization of floral visiting bees of *Solanum lycocarpum* (Solanaceae).

Taxa	Foraging		Frequency	Constancy	Dominance
	Number	%			
APINI					
<i>Apis mellifera</i> Linnaeus	1	0.31	Infrequent	Accidental	Not dominant
CENTRIDINI					
<i>Centris (Ptilotopus) scopipes</i> Friese	68	21.12	Very frequent	Constant	Dominant
<i>Centris (Heterocentris) analis</i> (Fabricius)	15	4.66	Frequent	Constant	Not dominant
<i>Epicharis (Epicharis) flava</i> Friese	181	56.21	Very frequent	Constant	Dominant
<i>Epicharis (Epicharoides) maculata</i> Smith	2	0.62	Infrequent	Accidental	Not dominant
<i>Epicharis</i> sp.	3	0.93	Infrequent	Accessory	Not dominant
EXOMALOPSINI					
<i>Exomalopsis (Exomalopsis) fulvofasciata</i> Smith	20	6.21	Frequent	Constant	Not dominant
EUGLOSSINI					
<i>Eufriesea nigrescens</i> (Friese)	1	0.31	Infrequent	Accidental	Not dominant
XYLOCOPINI					
<i>Xylocopa (Megaxylocopa) frontalis</i> (Olivier)	1	0.31	Infrequent	Accidental	Not dominant
TETRAPEDIINI					
<i>Tetrapedia diversipes</i> Klug	1	0.31	Infrequent	Accidental	Not dominant
OXAEINI					
<i>Oxaea flavescens</i> Klug	27	8.39	Frequent	Constant	Dominant
<i>Oxaea</i> sp.	2	0.62	Infrequent	Accidental	Not dominant

Table 3. Correlation between frequency of foraging of the most frequent bees in *Solanum lycocarpum* (Solanaceae) and abiotic factors (r = Pearson correlation test).

Abiotic factors	<i>Epicharis (Epicharis) flava</i>		<i>Centris (Ptilotopus) scopipes</i>		<i>Oxaea flavescens</i>	
	r	p	r	p	r	p
Luminosity	0.169	0.0553	0.219	0.0123	-0.093	0.2938
Relative Humidity	0.127	0.1502	-0.308	0.0004	0.154	0.0794
Temperature	-0.167	0.0584	0.217	0.0133	-0.108	0.2205
Wind speed	-0.025	0.7773	0.127	0.1517	-0.056	0.5258

(Colletidae), but also in Halictidae, Oxaeinae and most species of Apidae, especially in bumblebees and euglossines.

The low diversity of floral visitors sampled (12 species) in *S. lycocarpum* would be expected because it is a plant species with a specialized buzz-pollination system. Two other studies using similar sampling protocols in the same region of this study, found a superior diversity of visitors in plants of another family, Bignoniaceae, whose pollen is housed in anthers with longitudinal dehiscence (POLATTO *et al.* 2007; POLATTO & ALVES JR. 2008).

As for optimal foraging, according to POLATTO *et al.* (2014) and POLATTO & ALVES JUNIOR (2022), two factors potentiated its occurrence in the morning: (1) suitable environmental conditions for foraging flight and (2) floral resources available in large quantity. From 8h00, with adequate environmental conditions, such as an average luminosity of 10,900, temperature of 24 °C, relative humidity of 46% and wind speed of 0.5 m/s, the bees would spend little energy in flight and simultaneously obtain their resources in large quantity and quality. The positive energy balance obtained by maximizing benefits in relation to costs tends to be invested in other activities, such as reproduction (MORSE & FRITZ 1987).

Even considering that the ambient temperature at the beginning of the day could be below values suitable for foraging flights, the buzz-pollination behavior potentiated the ability of bees to promote thermoregulation. In fact, the surface temperature of the bees' thorax is higher than in other parts of the body while they fly and promote the buzzing behavior during pollen collection, as in this region there are

wing movement muscles responsible for internal heating of the body (HARRISON 1987; ROBERTS & HARRISON 1999).

Studies also report that bees with large body sizes – a typical feature of the floral visitor bee community of *S. lycocarpum* – can forage with some independence from ambient temperature (HEINRICH & HEINRICH 1983) and thus can collect more abundant resources in the early hours of the day, even in mild temperatures (HEINRICH & RAVEN 1972). The physiology of each species and the ability to control body temperature may be the main regulating factor of foraging activity (HILÁRIO *et al.* 2001). On the other hand, due to the continuous removal of pollen throughout the day, this resource becomes limited at the end of the day, discouraging bee visits (POLATTO *et al.* 2014; POLATTO & ALVES JUNIOR 2022).

Since bee foraging records were developed in the summer (behavioral descriptions of floral visitors were addressed by TAVARES *et al.* 2018), environmental conditions did not limit the foraging of most bees during the entire foraging period of the day. This fact is explained by the absence of significant correlations between the foraging activity of most bees and the abiotic conditions. TAVARES *et al.* (2015) also reported little influence of abiotic factors on the foraging activity of bees on flowers of *Cucurbita moschata* Poir (Cucurbitaceae) and also related this fact to the environmental conditions found in the collection period (summer).

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