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The light intensity mediates the pollination efficacy of a Caatinga morning glory *Ipomoea bahiensis* (Convolvulaceae)

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Abstract

Pollination is an ecological process that relies on the matching traits of flower visitors and flowers. Morphology, behavior, and temporal patterns play essential roles in mediating the interactions between plants and floral visitors. This study analyzed the temporal aspects of visitors and flowers interaction and the possible adjustment between both organisms. We used *Ipomoea bahiensis* and its flower visitors as a model system. We evaluated the visitor frequency on the flowers throughout the day, flower opening and closing times, pollen availability and stigma receptivity. We also evaluated the highest fruit production time during the flower longevity, and the time of highest pollinator activity, related to climatic factors. Among the floral visitors, bees, especially *Melitoma* spp., *Apis mellifera*, and *Pseudaugochlora pandora* were the most frequent visitors, presenting regular visits synchronized with the flower opening and closing times, which were also regular. This system was influenced mainly by light intensity. Besides, these bees were very active during the times of the highest fruit production. These data indicate the presence of temporal patterns for both the bees and the visited plants, and synchronization between them, being the light intensity as a modulator of the rhythms of bees and plant, confirming the importance of the temporal adjustments for pollination efficiency.

Introduction

The pollination process depends on the adjustment of floral and of visitor traits. Among these traits, morphology and behavior are related to the contact of visitors with the anthers and stigmas of flowers during the resource collection, and this has consequences for the pollination efficiency (Pick & Schlindwein 2011; Paz et al., 2013; Santos & Gimenes 2016; Paz et al., 2018; Araujo et al., 2018). Besides these adjustments, several studies already highlighted the importance of the temporal adjustments between floral visitors and flower and, in particular, associating the daily activity pattern of the pollinators to the temporal aspects of the plant (Gimenes et al., 1993, 1996; Paz et al., 2013). In this context, the time of the day of foraging activity of floral visitors is also an aspect that

may affect the occurrence and quality of pollination (Gimenes et al., 1993, 1996; Paz et al., 2013; Bloch et al., 2017). Several plant reproductive events happen at specific times of the day, which may be the most propitious moment for pollination to occur. Examples of such events include opening and closing times of flowers and anthers, stigma receptivity, production and concentration of nectar and odor (Van Doorn & Van Meeteren, 2003; Terada et al., 2005; Matile, 2006; Silva et al., 2010; Edge et al., 2012; Paz & Pigozzo, 2013; Paz et al., 2013; Van Doorn & Kamdee, 2014).

These patterns observed in organisms throughout the day can be triggered by climatic clues that vary during the day, such as temperature, relative humidity, and light intensity. Van Doorn and Van Meeteren (2003) as well as Van Doorn and Kamdee (2014) demonstrated the influence

of these factors by reporting several examples of how climatic variation (especially light and temperature) can have different outcomes of flower opening and closing for many plant species. In parallel, floral visitors may also change their activity patterns in response to different microclimatic conditions throughout the day (Lutz, 1931; Gimenes et al., 1993, 1996; Torres-Díaz et al., 2007). Therefore, these factors may favor the adjustment of daily activity patterns of visitors and flowers (Gimenes et al., 1993; Gimenes et al., 1996).

Daily activity patterns of plant-pollinator interactions can be of particular interest when plants have ephemeral flowers (e.g., that last less than 12 hours) because the short exposure time of the reproductive structures limits the floral visitor activity time (Terada et al., 2005; Pick & Schlindwein, 2011, Paz et al., 2013, 2018, Santos & Gimenes, 2016; Araujo et al., 2018). Some plants have ephemeral flowers like those of the genus *Ipomoea* (Convolvulaceae) whose most common pollination syndrome is melitophilia. In particular, most pollinators of *Ipomoea* are diurnal bees specialized in pollen harvesting from this genus of morning glories (Wcislo & Cane, 1996; Martins, 2002). Examples of specialized pollinators of *Ipomoea* are the oligolectic bees of the genus *Melitoma* (Terada et al., 2005; Pick & Schlindwein, 2011; Paz & Pigozzo, 2013; Araujo et al., 2018). However, most studies above were based on morphological and behavioral aspects, disregarding the relative importance of daily temporal patterns of the foraging activity of floral visitors.

Given the importance of temporal adjustments between plants and pollinators, this study aims to analyze the daily temporal pattern of the interaction between ephemeral flowers of *Ipomoea bahiensis* (Convolvulaceae) and the most frequent bees. Furthermore, the influence of climatic factors on the flower opening and closing and the forage activities of bees will be verified.

Material and Methods

The study took place at Campus of the Universidade Estadual de Feira de Santana (12º11'S, 38º58'W) in Feira de Santana City, State of Bahia, Brazil. The climate of the region is classified as BSh or semiarid (Köppen & Geiger, 1928). The Campus has a total area of approximately 1.2 km², and the original vegetation was composed of Caatinga, but today most of the area has been converted in anthropic vegetation, with non-native and invasive plants (Santana & Santos, 1999).

The study was performed between July and October/ 2014, period when *Ipomoea* flowering peak occurred in this area. The samplings and observations were performed in four plots (20 x 20 m each) spaced at least 200 m apart. This species presents a vine habit. The flower and visitor were counted in plots and not on individual plants.

Floral Biology

To evaluate the stigma receptivity time throughout the flower duration (from 4:00 to 15:00 h), we immersed ten plant pistils from different plots in Petri dishes containing hydrogen peroxide (H_2O_2) at each hour of the flower duration and observed them in the field with the help of a hand-held magnifier (20 x). Bubble formation occurs when pistils are receptive and enter in contact with H_2O_2; therefore, bubbles represented a positive result for the stigma receptivity (Dafni & Maués, 1998).

We evaluated the opening and closing of flowers by counting the number of flowers at each 15-minute interval while collecting climatic information. First, open flowers were counted from when the first flower opened until when all flowers were open in the sample plot. Second, a similar method was used to determine the numbers of closed flowers, starting when the first flower closed until all the flowers in the sample were closed. Third, the temperature (°C), light intensity, and relative air humidity were recorded simultaneously at each 15 minute interval. This procedure was repeated four times in each observation months (July, August, September, and October/14), each time made upon a different plot.

To determine which climatic predictor was the best explanation for the events of flower opening and closing, we constructed two sets of generalized linear mixed models with Poisson distribution (Zuur et al., 2009). One set of models was built to explain the flower opening while the other was built to explain the flowers closing. Both sets of candidate models consisted of a model with only temperature, relative humidity, or light intensity as predictor variables. Also, we included sampling dates and time of day as random variables. Six models were built using the lme4 package (Bates et al., 2014) for each set of models (flower opening or flower closening). Each set of models were compared among them using the Akaike information criterion with correction for small sample size (Akaike information criterion – AICc) to select the most parsimonious model (Burnham & Anderson, 2002) using the *bbmle* package (Bolker & R Development Core Team, 2014).

To verify the time of most significant fruit production by *I. bahiensis*, we conducted a manipulation experiment where plants' access to pollination was restricted to periods of one hour. We selected and bagged 200 buds before flower openings. Beginning at 04:00 h, we exposed ten flowers to visitation by removing their bags, and after one hour, we bagged the same flowers. We repeated this procedure on another set of ten flowers every hour until 15:00 h. After this exposure, the flowers were bagged and labelled to monitoring fruit development and the fruits formed. This procedure was performed every sampling month, during four days, a day per sampling plot of 20 m², and varied according to the flowers available in the samples.

Daily bee foraging activity

We selected the most frequent floral visitors (species with a frequency greater than 10% during the study), to assess the daily foraging activity in the flowers. These visitors were: *Melitoma* spp. [*Melitoma segmentaria* (Fabricius, 1804),

Melitoma sp. 1, *Melitoma* sp. 2)] (Relative frequency = 25%), *Apis mellifera* Linnaeus, 1758 (23%), *Pseudaugochlora pandora* (Smith, 1853) (12%). Araujo et al. (2018) provide detailed information regarding the number of visits and body size of floral visitors in *I. bahiensis*, in this area.

The number of visits realized by the floral visitors was recorded in the four sampling plots from July to October. All plots were sampled monthly, and the sampling order that each plot was randomly established. Sampling started 30 minutes before the flower opening and ended 30 minutes after the flower closing. During this period, the number of visits was obtained for 15 minutes. Counts were made of the visits of each species that landed on the flower for resource collection (as described in Araujo et al., 2018). Concomitantly, we recorded the microclimatic data of temperature, relative humidity, and light intensity every 15 minutes.

To determine which climatic predictor was the best explanation to the variation on visitor frequency, we constructed generalized linear mixed models with Poisson distribution (Zuur et al., 2009), using the number of visits (abundance) as response variable and temperature, relative humidity, and light intensity as predictor variables. In addition, we included sampling dates and time of day as random variables. These models were developed using the *lme4* package (Bates et al., 2014). The models were compared among them using the Akaike information criterion with correction for small sample size (Akaike information criterion – AICc) to select the most parsimonious model (Burnham & Anderson, 2002) using the *bbmle* package (Bolker & R Development Core Team 2014).

All statistical analyses were performed in the R environment (R Core Team, 2014), and explanatory variables with high correlation (r > 0.7) were not included in the same model to avoid multicollinearity effects.

The specimens of bees sampled were deposited in the entomological collection "Prof. Johann Becker" of the Museu de Zoologia da Universidade Estadual de Feira de Santana (MZFS).

Flower-visitor Interaction

A generalized linear mixed model (GLMM) with a binomial distribution (Zuur et al., 2009) was used to evaluate the time interval of the most massive fruit production, using the time of day as the predictor variable and fruit production (binary) as the response variable, and also include sampling dates as the random variable. In this analysis, each flower was considered a sampling unit. The period between 4:00 and 5:00 h, and between 15:00 and 16:00 h was excluded from the analyses due to the absence of fruit production. This choice could bias the model estimates due to the presence of zeros. This analysis was performed in the *lme4* package (Bates et al., 2014).

After establishing the model, we compared the fruit development at each hour with the control. In a scenario where development time was similar to the control counterpart, it would indicate a crucial time for fruit development. This analysis of comparisons was performed using the *glht* function of the *multcomp* package (Hothorn et al., 2008).

Results

Ipomoea bahiensis flowers had average floral longevity of seven hours and thirty minutes (± 37 minutes). The flowers opened between 04:30 and 07:30 h. It can be observed a difference in the opening hours of the flowers in 3 plots (Plot 1, 2 and 3) and also in two different days in the same plot (Plot 3-A and Plot 3-B, Figure 1). This difference in opening times depends of the area where the plants were located, and also of the day on which the data collection was performed,
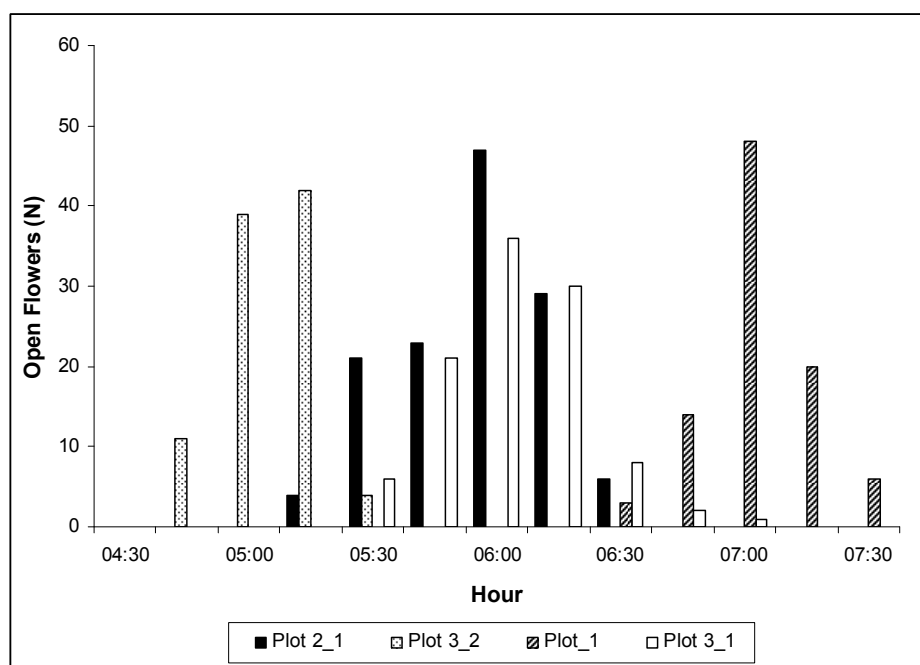

Fig 1. Number of the open flowers in *Ipomoea bahiensis* (Convolvulaceae), per hour interval on the Campus of Universidade Estadual de Feira de Santana, BA, Brazil between July and October 2014.

with flowers opening later in the more shaded area. The microclimate factors of the plots displayed small differences one to the other, even when these were at a distance of just 200 m one from the other, especially concerning light intensity and temperature. Furthermore, the flowers remained closed at temperatures below 18°C, even with an increase in light intensity. The flowers closed between 9:45 and 14:15 h.

Climatic factors played a role both on the flower opening and on the closing processes of *I. bahiensis*. Regarding flower opening, the most parsimonious model included light intensity and temperature as climatic predictors in which the

opening of *I. bahiensis* flowers occurred more frequently with increasing temperature and light intensity ($\chi^2 = 65.85$, gl = 2, p <0.001; β light intensity = 0.40; β temperature = 0.67) (Table 1, Figure 2). On the other hand, the best model for flower closing revealed that the closure of *I. bahiensis* flowers occurred more frequently with increasing air temperature and humidity and decreasing light intensity, simultaneously ($\chi^2 = 69.80$, gl = 3, p <0.001; β light intensity -1.00; β temperature = 0.34; β humidity 0.07) (Table 1). The stigma remained receptive throughout the floral longevity but presented a higher amount of stigmas with bubbles from 8:00 to 12:00 h.

Table 1. Models describing the probability of microclimatic variables that influenced the flower opening (I) and closing (II) processes of *Ipomoea bahiensis* (Convolvulaceae). Comparisons of the different models with sample size correction (AICc), AICc differences (Δ), number of variables (k). The models are classified in the ascending order of AICc.

Response	Model	AICc	Δ	K
(I)	**Log (Light Intensity+1) + Temperature**	712.2	0	5
	Log (Light Intensity+1) + Temperature + Relative humidity	714.6	2.5	6
	Temperature	720.0	7.8	4
	Temperature + Relative humidity	722.4	10.2	5
	Log (Light Intensity+1) + Relative humidity	741.4	29.2	5
	Log (Light Intensity+1)	750.5	38.3	4
	Relative humidity	762.5	50.3	4
	Intercept	773.4	61.2	3
(II)	**Log (Light Intensity+1) + Temperature + Relative humidity**	465.6	0	6
	Temperature + Relative humidity	472.9	7.3	5
	Log (Light Intensity+1) + Temperature	506.3	40.7	5
	Temperature	509.6	44.0	4
	Relative humidity	524.9	59.3	4
	Log (Light Intensity+1) + Relative humidity	525.2	59.6	5
	Log (Light Intensity+1)	527.7	62.1	4
	Intercept	527.8	62.2	3

Daily activity of Potential Pollinators

The most frequent bees (*Melitoma spp.*, and *Pseudaugochlora pandora*, native bees, and *Apis mellifera*, introduced bee) were observed throughout the floral longevity of *I. bahiensis*. Potential pollinators began their activities at 05:00 h, which matched with the opening of the flowers. Solitary native bees concentrated their highest number visits in the interval between 08:00 and 10:00 h (Figure 3) while *Apis mellifera* had their peak of visitation between 09:00 and 11:00 h. The peak of the visitation of both groups of potential pollinators happened when all the flowers were already open. The most parsimonious model for the abundance of potential pollinators on the flowers included the luminous intensity, and this model indicated that the number of visits was more

significant with the increase in light intensity ($\chi^2 = 57.52$; gl = 1, p < 0.001, Table 2).

Table 2. Models describing the probability of microclimatic variables that influenced the abundance of visits of the most frequent bees on the flowers of *Ipomoea bahiensis*. Comparisons of the different models with sample size correction (AICc), AICc differences (Δ), number of variables (k). The models are classified in the ascending order of AICc.

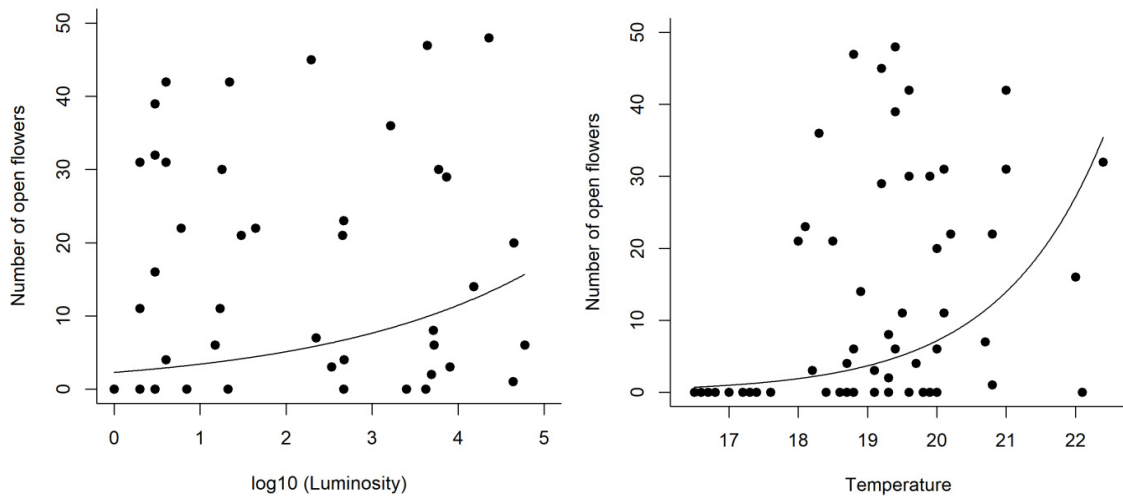| Response	Model	AICc	Δ	K
Bees	**Log (Light Intensity+1)**	2176,4	0	4
	Intercept	2231,9	55,5	3
	Temperature	2232,6	56,2	4
	Relative humidity of air	2233,7	57,3	4

Fig 2. Effect of luminosity (the top) and temperature (the bottom) on the number of *Ipomoea bahiensis* open flowers. The predicted line is based on the best-fitted model using AIC.

Fruit formation was higher between 08:00 and 09:00 h. This interval showed a result similar to that obtained in the control experiment (flowers exposed to visitors throughout the floral longevity) and also presented twice the probability of fruit formation when compared to other times intervals (Figure 4; $\chi2 = 107.78$; gl = 10; p < 0.001). At this time, the bees *A. mellifera*,

Melitoma spp, *P. pandora* and *Ancyloscelis apiformes* and the butterflies *Morys compta compta*, *Nyctelius nyctelius nyctelius*, *Phoebis sennae marcellina* and *Synale hylaspes* were visiting the flower of *I. bahiensis* (Figure 5). Among these bees, *Melitoma* spp., were the most frequent in the flowers and more coincident with the time of greatest fruit production.
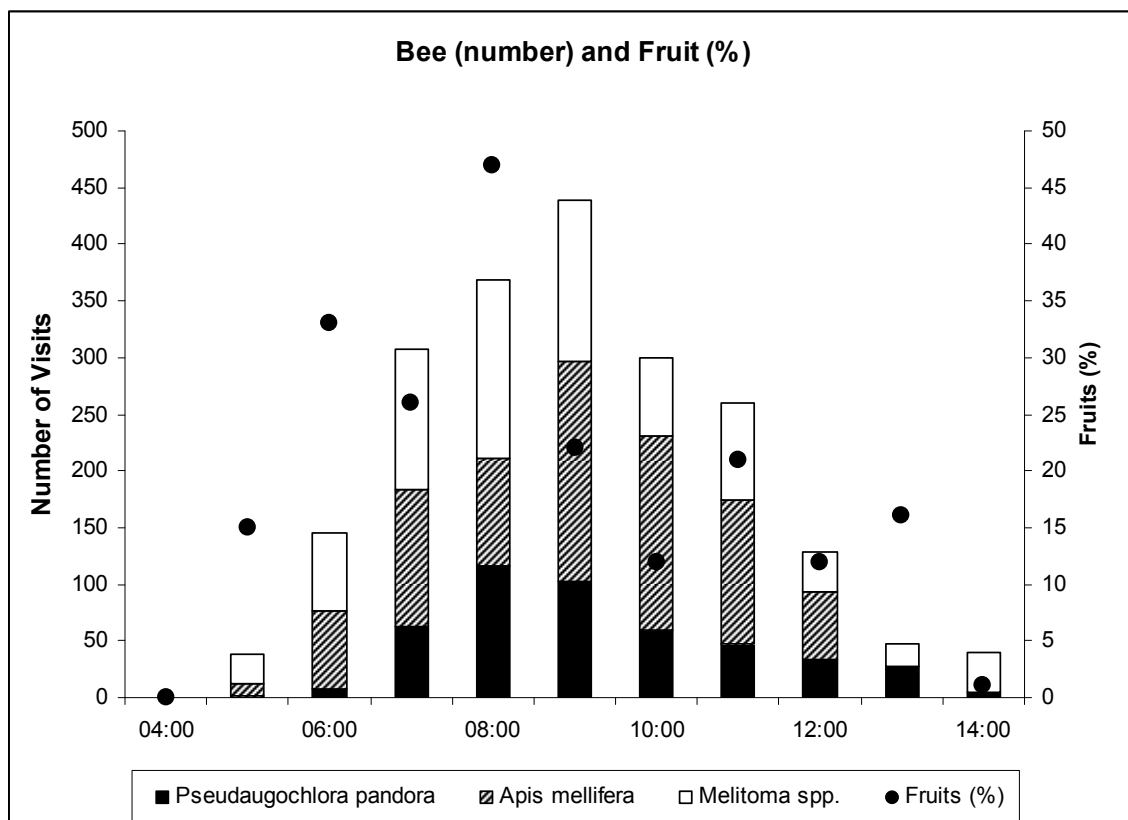

Fig 3. Number of visits of the most frequent bees (*Melitoma* spp, *Apis mellifera,* and *Pseudaugochlora Pandora*) on flowers of *Ipomoea bahiensis* (Convolvulaceae), per hour interval throughout the day, on the Campus of Universidade Estadual de Feira de Santana, BA, Brazil between July and October 2014.
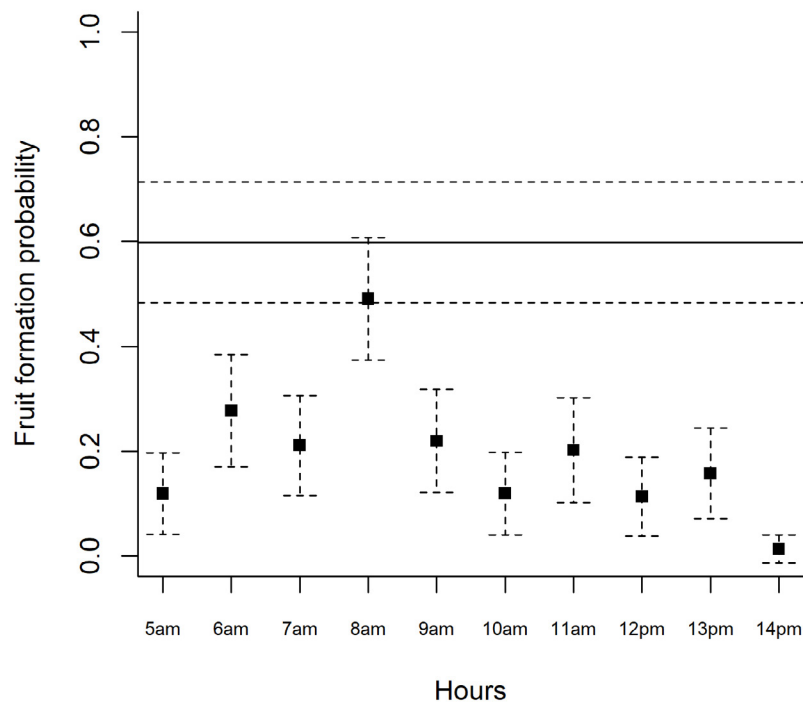
Fig 4. Effect of time of day on fruit formation probability. Squares are mean for each period, and the continuous line is the control mean (treatment exposed all the time). The dashed line is 95% confidence intervals.

Discussion

The flowers of *Ipomoea bahiensis* were studied in an area whose original vegetation was Caatinga, and became anthropized area, where this species occurs frequently. The flowers displayed morphological features that classify them as melitophilous. Among the floral visitor, the bees were more frequent, especially those of the genus *Melitoma.*

These bees are solitary and have already been quoted in the literature as associated with flowers of species of the genus *Ipomoea* (Pick & Schlindwein, 2011). Araujo et al. (2018) studied the same area and observed the bees *Melitoma* spp*., P. pandora*, and *A. mellifera* as the most frequents on the flowers and considered them as potential pollinators. These authors also observed that these bees species had an average size that was compatible with the morphological features of the flowers. The size of the bees, and the proper behavior, allowed the contact between the bee's body and the reproductive features of the plant. Paz et al. (2013) also considered the medium-sized bees as potential pollinators of the *Ipomoea carnea* flowers. Besides, Araujo et al. (2018) claimed that the visits of butterflies and small-sized bees did not produce fruits in the efficiency pollination tests in *I. bahiensis*.

Even the acknowledged relevance of the morphological and behavioral aspects in the pollination activities of these bees, just these adjustments do not guarantee efficient pollination. Besides the aspects mentioned above, also the timing of the interaction is relevant: the flower visitors need to synchronize their activities with those of the flowers (opening and closing times of the flowers, pollen release, stigma receptivity, production of the nectar, and others) so that pollination can occur, and consequently a higher production of fruits (Gimenes et al*.,* 1993; 1996). The literature already described the behavioral and morphological adjustments between visitors and flowers, but few studies have considered the
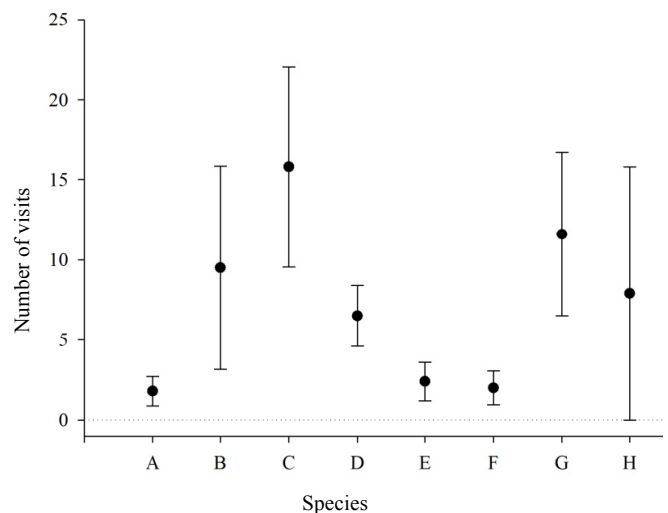

Fig 5. Abundance of visits of species in *Ipomoea bahiensis* (Convolvulaceae) between 8:00 and 9:00 h, in Feira de Santana (BA). Species represented: (A) *Ancyloscelis apiformes*; (B) *Apis mellifera*; (C) *Melitoma* spp.; (D) *Morys compta compta*; (E) *Nyctelius nyctelius nyctelius*; (F) *Phoebis sennae marcellina*; (G) *Pseudaugochlora pandora*; (H) Synale hylaspes. (n > 10 visits) (Complete table with all visitors in Araujo *et al.*, 2018).

timing adjustments until now. If the flowers' timing (most especially as to the opening and closing) does not overlap with the feeding activities of their visitors, pollination may not occur. This timing is crucial, especially in plants with ephemeral flower (lasting less than 12 hours), as observed in the genus *Ipomea*. In this case, the pollinator-flower synchronization must occur during the short flowers' opening.

Ipomoea flowers remain open for about seven hours, and displayed similar hours of opening and closing along the flowering months, suggesting a daily pattern of the flowers' opening and closing. Time patterns of flowers 'opening and closing have already been described in species of the Convolvulaceae (Van Doorn & van Meeteren, 2003, Van Doorn & Kamdee, 2014) and other plants' genera (Kaihara & Takimoto 1980, Tanaka et al., 1989, Ichimura & Suto, 1998). The bees that most frequently visited these flowers must follow these time standards of the flowers' opening (Gimenes et al., 1993; 1996). The most frequent visiting bees probably follow these patterns of opening and closing time of the flowers (Gimenes et al., 1993; 1996). Therefore, these visits should occur at times where there is the greatest condition for the formation of fruit. So, how do we know what those times are? This work adopted a method that allowed to verify that hour interval of the best fruit development, and at this hour interval it was also observed the highest frequency of forage activity of *Melitoma* sp. *P. pandora* and *A. mellifera*. These visiting bees were medium-sized and this characteristic favored contact with the reproductive structures of the flowers.

In the literature, several reports have already been described of the presence of biological rhythm in the daily activities of bees, most especially focusing on the eusocial bees such as *Apis mellifera* (Moore & Rankin, 1985; Moore & Rankin, 1993; Moore, 2001) and sting-less bees (Bellusci & Marques, 2001). Few studies have addressed on the relationship between the forage activities of bees and flowers, with a focus on temporal adaptations. Some studies on this topic were carried out with solitary bee species and the flowers visited (Gimenes et al., 1993, 1996; Gottlieb et al., 2005). Solitary and social bees visited the *I. bahiensis* flowers at similar hours, synchronized with the times of the highest fruit production.

The presence of different bees' species in the *Ipomoea* flowers, displaying similar size, behavior and visiting times, favoring the pollination of the visited plant, can be characterized as functional redundancy. This redundancy can improve the stability of a community (Blüthgen & Klein, 2011). Different visiting species, with similar behavioral and morphological features, may act as potential pollinators of the same plant, as in *I. bahiensis*. Besides the morphological and behavioral features highlighted by Blüthgen and Klein (2011), our study also observed the timing features, where the time of the highest fruit production was coordinated to the activity of the potential pollinators bees of this plant.

The occurrence of temporal events in plants and bees may be influenced by environmental and climatic events,

which may cause the temporal adjustment (synchronization) of both organisms (Koukkari & Sothern, 2006). The luminous intensity and the temperature (as to the opening of the flowers) influenced the interaction between *I. bahiensis* and the visiting bees. Besides this, the opening of the *I. bahiensis* flowers occurred synchronized with the sun rising and, in this period occurred also the most intense modifications of the light intensity and temperature. The relative humidity besides the light intensity and the temperature influenced the closing of the flowers. Studies in controlled experiments highlighted the necessity of the exposition to specific temperatures and light conditions to start the opening process in the flowers of *Ipomea* (Kaihara & Takimoto, 1979), and also in morning flowers of other genera (Tanaka et al., 1989, Ichimura & Suto, 1998, Van Doorn & van Meeteren, 2003, Van Doorn & Kamdee, 2014).

Ichimura and Suto (1998) studied the rhythm of opening and closing of flowers of hybrids of *Portulaca* and pointed out that these rhythms are influenced by the joint action of the high temperature (30-35ºC) and light. Bai and Kawabata (2015) observed that the flowers of *Eustoma grandiflorum* Shinn. (Gentianaceae) opened in the morning and closed at the afternoon's end, and concluded that their rhythms were synchronized by the cycles of light/dark and the direct effects of light intensity.

The climate also influences the daily activities of the bees visiting the *I. bahiensis* flowers. The light intensity is the factor that mostly explained these activities. Lutz (1931) considered the light intensity as the possible signal of the opening time of the nests of eusocial bee and also as an agent of the adjustment of the biological rhythm. Kilkenny and Galloway (2008) observed that the environmental light has a direct and positive influence on the abundance of the visits of the pollinating insects.

According to Polatto et al. (2014), the beginning of the flowers' visitor activity is regulated by light intensity, finishing at the end of the light phase, or with the depletion of the flowers' resources. These factors might have regulated the frequency of the foraging activities of the bees during the day, signalizing the best moment for the foraging on the flower. Prasad and Hodge (2013) studied the bee *Braunsapis puangensis* (Cockerell) that visited the creeping plant *Sphagneticola trilobata* (L.) Pruski in the Fiji Islands. The authors observed the high positive correlation between the daily foraging activities of the bee and light intensity and a strong negative correlation with the relative humidity. As it is well known in the chronobiological concepts, environmental and climatic factors may influence the synchronization and biological rhythms of plants and insects (Koukkari and Sothern, 2006). The time adjustment between the visitors and the flowers may determine the pollinator and its efficiency (Gimenes et al., 1993, 1996; Paz et al., 2013).

In conclusion, this study aimed to understand the different aspects that influence efficient pollination. For a long time, the researches only considered the morphological

and behavioral aspects of the flowers' visitors to explain the efficiency of the plants' pollination. The research observed the influence of both the morphological and behavioral aspects in the bees visiting *I. bahiensis*, but it also highlighted that the timing aspects are crucial for efficient pollination. The interaction between the visiting bees and the flowers highlighted that the flowers' opening displayed a periodicity of about 24 hours, and the highest probability of fruit production at a specific time of the day. These times coincided with the daily activities of the most frequent bees considered potential pollinators of the flowers, mainly influenced by the light intensity. The light intensity is an external factor that would adjust the biological rhythms of the organisms, promoting the encounter between bee and plant, resulting in a higher pollination efficiency.

Acknowledgments

Authors' Contribution

MG: supervision, writing.
LSA: investigation, data curation.
AMM: formal analisys, ilustrations, writing.

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