



RESEARCH ARTICLE - BEES

Pollen Collected and Foraging Activities of *Frieseomelitta varia* (Lepeletier) (Hymenoptera: Apidae) in an Urban Landscape

KP ALEIXO¹, LB DE FARIA^{1,2}, CA GARÓFALO¹, VL IMPERATRIZ FONSECA³, CI DA SILVA^{1,4}

1 - Universidade de São Paulo - Ribeirão Preto, São Paulo - Brazil.

2 - Universidade de São Paulo - São Paulo, São Paulo - Brazil.

3 - Universidade Federal Rural do Semi-Árido - Mossoró, Rio Grande do Norte - Brazil.

4 - Universidade de Santo Amaro (UNISA) - São Paulo, São Paulo - Brazil.

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Corresponding author:

Kátia Paula Aleixo

Faculdade de Filosofia, Ciências e

Letras de Ribeirão Preto.

Universidade de São Paulo

Av. Bandeirantes, 3900, 14040-901

Ribeirão Preto, São Paulo, Brasil.

E-Mail: katialaixo@yahoo.com.br

Abstract

Cities provide resources for animal species that live within them or inhabit their surroundings. This has motivated an increase in ecological studies of urban areas, including the interactions between plants and pollinators. From March 2010 to February 2011, the flowering plants present in the study area, located at the Universidade de São Paulo, Ribeirão Preto, were sampled to evaluate how floral sources were distributed throughout the year. Concurrently, worker bees with pollen loads were collected from four colonies of *Frieseomelitta varia* (Lepeletier, 1836) to identify the sources used by bees. Despite an increase in plant species abundance in July, plants were in bloom year-round and consequently, the production and supply of floral resources were continuous. The workers collected resources from 77 plant species, but only three were extensively exploited. *Delonix regia* (Leguminosae), *Poincianella pluviosa* (Leguminosae) and *Ceiba speciosa* (Malvaceae) accounted for 42% of total pollen grains quantified during the year, showing that *F. varia* intensify pollen collection at few sources at spatiotemporal scale. This study emphasizes the importance of native urban flora to maintain *F. varia* and other bee species. The list of plants presented in this study can be used in the design and planning of urban areas.

Introduction

According to Dearborn and Kark (2009) there are seven possible motivations for urban biodiversity conservation: preserving local biodiversity, creating stepping stones to nonurban habitat, understanding and facilitating responses to environment change, conducting environmental education, providing ecosystem services, fulfilling ethical responsibilities, and improving human well-being.

Although expansion of urban areas are among the human activities that result in the loss of native fauna and flora (McKinney, 2008), there is evidence that cities can provide potential resources for the animal species living within them or in their surroundings, including arthropods such as bees (Nates-Parra et al., 2006; Silva et al., 2007; Wojcik et al., 2008) and butterflies (Bergerot et al., 2010). Indeed, cities can also act as ecological corridors (Owen, 1991).

In cities, communities of bees and wasps are highly diverse (Frankie et al., 2005; Zanette et al., 2005; Matteson et al., 2008) and they are affected by variables that compose the urban landscape such as the availability of resources (Cane et al., 2006; Kearns & Oliveras, 2009). Floral generalist bee species are favored in urban areas (Zanette et al., 2005; Nates-Parra et al., 2006), while specialist bee species are severely affected by urbanization because the plants they usually visit to collect resources are rarely ornamental and therefore, are not often found in urban gardens (Frankie et al., 2009).

In Brazil, studies concerning the use of floral resources by bees in urban areas are uncommon (Knoll et al., 1994; Taura & Laroca, 2001; Agostini & Sazima, 2003; Silva et al., 2007) and do not approach the topic from an urban landscape planning standpoint to promote the conservation of the diversity found within these areas. The social bees known as stingless bees comprise approximately 400 species distributed in the

Neotropical region (Camargo & Pedro, 2007). They live in perennial colonies and the worker bees forage year-round. Although stingless bees are generalists, collecting pollen and nectar from an array of plant species (Roubik, 1989; Ramalho et al., 1990), the workers can intensify collection at certain sources for an amount of time (Eltz et al., 2001; Faria et al., 2012).

While seeking food in flowers, the worker bees play an important ecological role as pollinators of many plant species, which makes them good candidates for commercial pollination, plus the fact that they can easily be kept in hives and are nonaggressive (Slaa et al., 2006).

Frieseomelitta varia (Lepelletier, 1836) is a Neotropical medium-sized species of stingless bee with occurrence in several regions of Brazil (Camargo & Pedro, 2007). Colonies of this species are found not only in areas of natural vegetation (Teixeira et al., 2007), but also in urban areas (Marques-Souza, 2010).

Given stingless bees' ecological importance, the present study aimed (i) to understand the interactions between *F. varia* and urban flora by analyzing the pollen loads from foragers and (ii) to assess the influence of the availability of floral resources and climatic factor in the pollen-foraging workers in an urban landscape.

Materials and Methods

Study area

The present study was conducted in the campus of Universidade de São Paulo (21°10'30" S - 47°48'38" W), located in the city of Ribeirão Preto, in the northeastern part of the State of São Paulo, Brazil, at altitudes ranging from 510 to 800 m.a.s.l.. The campus covers an area of 574.75 ha and the climate of the region is characterized by marked seasonality: cold, dry winters (April to September) and hot, wet summers (October to March). Prior to the advent of coffee production in the region, the vegetation of the campus was predominantly seasonal semideciduous forest. The present day campus represents an urban area that consists of native and exotic plant species used in urban landscaping. There is a forest covering 75 ha of the campus comprised of plant species native of the vegetation of this area (Pais & Varanda, 2010).

Data collection

From March 2010 to February 2011, plant species and individuals in bloom were sampled once a month and during five consecutive days in an area with 500 m radius from the meliponary of Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP), totaling 78 hectares. The radius used to sample the plant species in bloom is according to flight range of the *F. varia* (Lichtenberg et al., 2010). Flower buds of each species were also collected, and the pollen grains

were removed and mounted on slides, which were deposited in the reference pollen collection of FFCLRP.

The plant species were sampled throughout the vertical strata as suggested by Silva et al. (2012), in which trees are considered woody individuals with circumference at breast height (CBH) ≥ 15 cm and more than 2 m high; shrubs are woody individuals with CBH < 15 cm and high between 1 and 2 m; herbaceous are not woody individuals with < 1 m high and lianas are woody individuals that grow laid on other plants without causing damages.

The plant species collected in the study area were classified as ornamental and as native or exotic to Brazil based on literature (Lorenzi, 2008; Souza & Lorenzi, 2008).

Concomitantly to plant species sampling, the pollen-foraging activity of worker bees in four colonies of *F. varia* was studied in relation to climatic factors and the availability of floral resources in the sampled area. These four colonies were kept in the meliponary of FFCLRP and the maximum distance between them was 3 m. They were about the same age and the same size, considering the number of workers and number of storage pots.

Once a month, the number of workers with pollen loads returning to their colonies was quantified for five minutes at a time with the aid of a manual counter at intervals of 30 minutes between 5:30 am and 12:30 pm. From 1:30 pm, the workers were quantified every hour until 5:30 pm because the collection of resources by workers *F. varia* decreases during this time period. Temperature, relative humidity, wind speed and rainfall data were collected at the meteorological station in the Departamento de Biologia, FFCLRP, on the days in which pollen was sampled.

After quantifying the foraging activity of the colonies, three intervals were determined: the beginning, the peak and the end of the foraging activity. On the following day, five workers returning to each colony with pollen in their corbiculae were sampled in each of the three intervals. Thus, fifteen workers with corbiculae loaded with pollen were sampled from each colony ($n = 4$) per day, totaling 60 samples per month. Bees were captured using an aspirator after closing the entries of the colonies, and the pollen loads were removed using a probe. The pollen loads were stored in 70% alcohol, following Silva et al. (2010). After 24 hours, the alcohol was discarded, and the samples were placed in 4 mL of glacial acetic acid for at least 24 hours for subsequent acetolysis according to Erdtman (1960). The pollen grains on the slides were identified by comparison with pollen deposited in the reference pollen collection of FFCLRP. The plant material was deposited at SPFR herbarium (São Paulo Filosofia Ribeirão) of Departamento de Biologia, FFCLRP.

Data analysis

Circular statistics was employed to assess seasonality in resource availability considering the number of plant species

and individuals in bloom from March 2010 to February 2011. To test for the occurrence of seasonality, the Rayleigh's test (Z) was applied to determine the significance of the mean date of flowering event (in months; $\alpha=5\%$) (Zar, 1999). The null hypothesis (H_0) states that when the flowering event is distributed uniformly throughout the year, there is no seasonality. If H_0 is rejected, the mean date is significant and there is a seasonal phenological pattern. The intensity of the concentration around the mean date, denoted by r , can be considered a measure of the degree of seasonality. The vector r has no units and may vary from 0 (when phenological activity is distributed uniformly throughout the year) to 1 (when phenological activity is concentrated around one single date or time of the year) (Morellato et al., 2000). The circular statistics analysis was performed by the Oriana software (Kovach, 2011). The same test was applied to assess the frequency of workers of *F. varia* with pollen loads returning to the colonies throughout the year.

Pearson's correlation coefficient (r) (Zar, 1999) was calculated to test the relationship between the number of species and individuals in bloom and the mean monthly temperature ($^{\circ}\text{C}$) and rainfall (mm) from March 2010 to February 2011. Pearson's correlation coefficient was also calculated to test the relationship between the number of pollen-foraging workers and the climatic factors of the day that they were counted [1. temperature ($^{\circ}\text{C}$); 2. relative humidity (%); 3. wind speed (Km/h)], and the diversity of pollen in the samples of the respective month. The relationship between the latter variable and the number of species that had bloomed throughout the year was also analyzed. The analyses were conducted using R version 2.13.1 (R Development Core Team 2011).

Analysis of the pollen collected by the bees was performed using a binocular microscope with magnifications up to 2560x, which allowed images of pollen grains to be taken with an attached digital camera. The first 400 pollen grains were counted for each sample, as suggested by Montero and Tormo (1990). The percentages were then calculated according to the classification proposed by Maurizio and Louveaux (1965) using the following categories: dominant pollen (> 45% of the total grains on the slide), accessory pollen (from 15 to 45%), important isolated pollen (3 to 15%) and occasionally isolated pollen (< 3%). The plants with pollen classified as dominant and pollen that occurred over a period of at least six months were considered to be key plant species in the maintenance of *F. varia*.

Results

During the study period, 235 plant species and 3285 individuals in bloom were sampled in the meliponary and the surrounding area. The mean flowering date of plant species was significant ($Z = 20.59$, $p < 0.01$) and corresponded to the month of April, revealing a seasonal pattern despite the

low concentration of species around this mean date ($r=0.16$) (Fig. 1A). The mean flowering date of individuals in bloom was also significant ($Z = 167.48$, $p < 0.01$) and corresponded to the month of May, revealing a seasonal pattern despite the low concentration of individuals around the mean date ($r = 0.23$) (Fig. 1B). Considering separately the native and exotic species and individuals in bloom the seasonal pattern was also observed [(native_{species}: $Z = 10.18$, $r = 0.13$; exotic_{species}: $Z = 12.69$, $r = 0.24$) (native_{individuals}: $Z = 115.90$, $r = 0.22$; exotic_{individuals}: $Z = 59.03$, $r = 0.27$); $p < 0.01$] (Fig. 1).

The number of flowering species and individuals were not correlated with temperature and rainfall [(species: $r_{\text{temperature } (^{\circ}\text{C})} = -0.24$, $r_{\text{rainfall}} = -0.31$) (individuals: $r_{\text{temperature } (^{\circ}\text{C})} = -0.54$, $r_{\text{rainfall}} = -0.55$); $p > 0.05$].

The monthly number of pollen foraging workers varied in the four studied colonies, and presented a seasonal distribution throughout the year [($Z_{\text{colony1}} = 403.09$, $r = 0.67$) ($Z_{\text{colony2}} = 477.65$, $r = 0.61$) ($Z_{\text{colony3}} = 214.92$, $r = 0.50$) ($Z_{\text{colony4}} =$

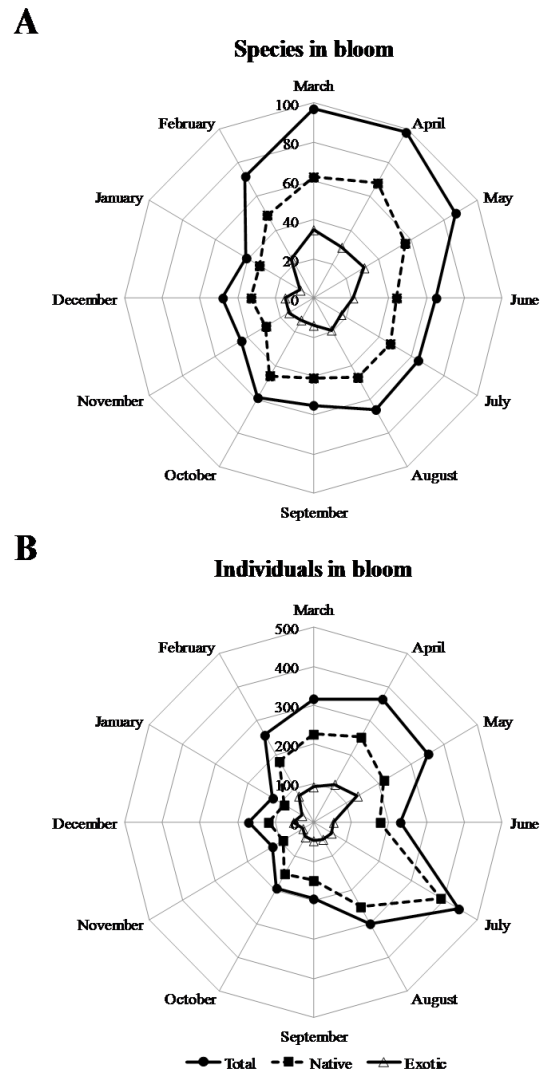


Figure. 1 Distribution of total, native and exotic plant species (A) and individuals (B) that bloomed in the meliponary and its surrounding area from March 2010 to February 2011.

733.75, $r = 0.60$; $p < 0.01$] (Fig. 2). According to the pattern of this event observed in all colonies, the period of highest pollen collection activity by the bees (October) did not coincide with the period with highest availability of floral resources (July) (Fig. 2). The pollen-foraging activity in *F. varia* was not influenced by climatic factors ($r_{\text{temperature } (^\circ\text{C})} = 0.37$, $r_{\text{relative humidity } (\%)} = 0.40$, $r_{\text{wind speed (km/h)}} = 0.40$; $p > 0.05$).

Seventy-seven pollen types distributed in 36 families and 60 genera were identified in the studied samples. Of these, 63 were identified at species level and three remained as undetermined types (Table 1). In general, the workers collected floral resources from a small fraction of the total number of plant species available, corresponding to 32.76% of the sampled plants that bloomed throughout the study period.

More than half of the plant species used by *F. varia* were distributed in seven of the 36 botanical families. The families with the highest number of visited species were Leguminosae and Myrtaceae, which were represented by 11 and 7 species, respectively. However, most of the pollen came from species of Leguminosae and Malvaceae, which were represented by 44.30% and 9.50% of total pollen grains quantified in the samples.

Considering monthly pollen analysis, *Delonix regia* (Leguminosae), *Ceiba speciosa* (Malvaceae) and *Poinciana pluviosa* (Leguminosae) were intensively visited as they showed more than 45% of the pollen grains in the samples (Table 1).

Throughout the year, the three species accounted for

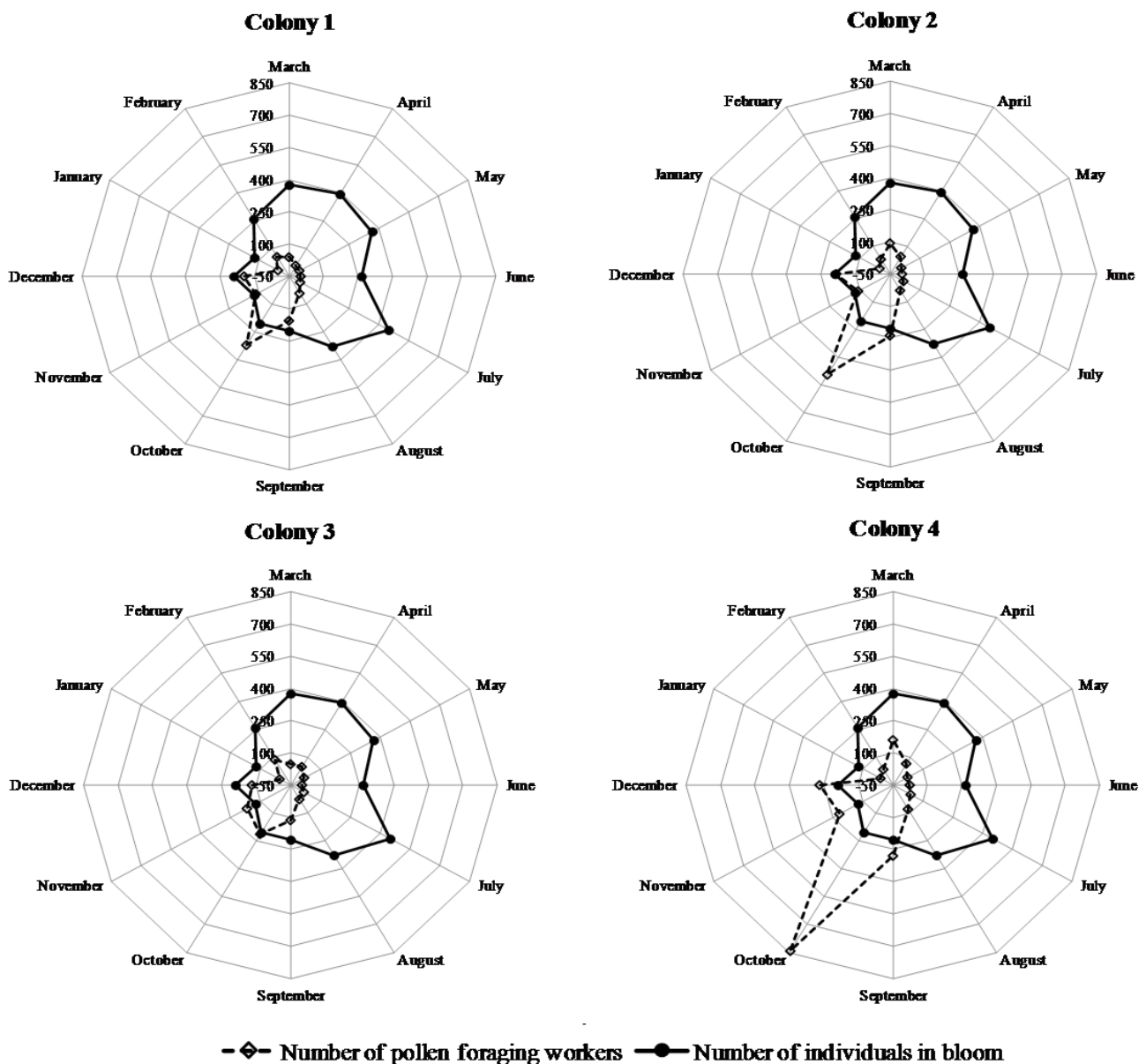


Figure. 2 Distribution of the monthly number of workers of *Frieseomelitta varia* per colony and monthly number of individuals that bloomed in the meliponary and its surrounding area from March 2010 to February 2011.

42% of the total pollen grains. There is almost no overlap in the use of *D. regia*, *C. speciosa* and *P. pluviosa* by *F. varia* (Table 1), which reflects the flowering period of these species in the study area. *Eucalyptus moluccana* (Myrtaceae), *Leucaena leucocephala* (Leguminosae), *Paspalum notatum* (Poaceae) and *Schinus terebinthifolius* (Anacardiaceae) were also important for *F. varia* because they provided food to the colonies for a period of at least six months (Table 1). There was no correlation between mean number of pollen-foraging workers and pollen diversity ($r=0.12$; $p>0.05$), and no correlation between pollen diversity of samples and the number of species bloomed ($r=0.00$; $p>0.05$). Although there was a low richness of plant species in bloom, the highest numbers of pollen types in the samples were found in October and November, with 33.33% and 45.45% of the available sources used, respectively. In contrast, the samples from March and April showed lower numbers of pollen types in relation to the numbers of plant species in bloom, with 16.49% and 13.27% of the available sources used, respectively.

Among the 63 identified species, 59 belong to plants used in urban landscape planning or plants that have a high potential to be used for this purpose. Of these 59 ornamental species that were exploited as food sources, 64.50% species are native to Brazil (Table 1).

Discussion

Despite displaying a seasonal flowering pattern, species were in bloom year-round in the study area, and therefore the production and supply of floral resources was continuous. In a phenological study performed on the campus of the Universidade de Campinas - SP, Brazil (22°46'57" S - 47°04'47" W), which is also an urban area, the species bloomed throughout the year but did not exhibit marked seasonality (Agostini & Sazima, 2003). Those authors argue that species with different flowering periods are used to enhance ornamentation in urban settings, maintaining flowers available for most year-round. In our study, both native and exotic species contributed significantly to the seasonal pattern observed. Besides the revegetated area, the campus also comprises trees species of the seasonal semideciduous forest for the purpose of shading. One of the main factors for the increased species richness of plants in urban habitats is human-aided dispersal of exotic species (McKinney, 2008). However, using native plants in the planning of green areas is important from the conservation point of view, since it favors the maintenance of a vast richness of plant-pollinator interactions.

In the study area, the absence of correlation between the flowering phenology and climatic factors can be explained by the increased irrigation, which is one of the manipulator of floral blooming within the urban landscape. In urban areas, irrigation can influence the continuous production of flowers (Frankie et al., 2005), mainly in shrub and herbaceous strata. In tropical areas, the flowering pattern, and consequently the

resource availability, is associated with seasonal variations in rainfall (van Schaik et al., 1993).

Our study shows that the period of highest food collection activity by *F. varia* is not associated with the period when the resources are more abundant in the field. This result is not in accordance with literature for other species of stingless bees. Although Roubik (1982) and Biesmeijer et al. (1999) have discussed that pollen foraging activity in colonies of *Melipona* species decreased due to reduced pollen availability in the environment, the authors did not evaluate the flowering phenology of plant species.

Although there is no relationship between climatic factors and the mean number of *F. varia* pollen-foraging workers, the flight activity of stingless bees is known to be influenced by such variables, and their pollen-foraging activity reflects the influence of meteorological parameters (Pick & Blochtein, 2002). For example, the flight activity of *Plebeia pugnax* foragers, a small species of stingless bee, may be relatively constant over a wide range of temperatures (Hilário et al., 2001), while the highest intensities of *P. saiqui* worker pollen-foraging activity coincided with the highest temperatures throughout the year (Pick & Blochtein, 2002). Kajobe and Echazarreta (2005) found that the number of worker bees for two medium-sized species of stingless bees decreased in the field when the relative humidity was higher than the optimal value of 78%. The worker bees of *P. pugnax* flew over a wide range of relative humidity, from 30% to 100%, decreasing slowly the number of bees flying after 50% (Hilário et al., 2001). Other factors may affect the flight activity of bees including the population size (Hilário et al., 2000), the reproductive status of the colony (Nunes-Silva et al., 2010) and even the body size of different species, which affects the maximal flight distance and the onset of this activity (Teixeira & Campos, 2005).

Although *F. varia* workers collected resources from 77 plant species, only three species were extensively exploited, showing that the bees intensify pollen collection at few sources at spatiotemporal scale. These results are consistent with the work of Marques-Souza (2010) on *F. varia* in an urban area located in Manaus - AM, Brazil. That author identified pollen of 79 plant species distributed among 60 genera and 37 botanical families, but only four of these species provided 71% of the total pollen collected. This pattern was also found in natural environments by Teixeira et al. (2007) when they analyzed Brazilian studies on the use of floral resources by bees of the *Frieseomelitta* genus in areas with different types of vegetation. Those authors mention that workers visited a large spectrum of plant species but only focused on some of them. Other studies have also shown that stingless bees obtain most of their food from a small number of plant species (Imperatriz-Fonseca et al., 1989; Ramalho, 1990; Pick & Blochtein 2002).

The species intensively visited *D. regia*, *C. speciosa* and *P. pluviosa* have individuals close to the colonies, which

facilitated the access to resources by workers once *F. varia* has a small estimated flight distance compared with estimates for other medium-sized stingless bee species (Lichtenberg et al., 2010). Besides that, those species bloomed in sequence which resulted in a temporal structuration with complementarity in the use of those sources. Factors such as high protein content may also explain the high frequency with which the three plants were exploited (Kleinert et al., 2009). The inflorescences of *E. moluccana*, *L. leucocephala*, *P. notatum* and *S. terebinthifolius* with large numbers of flowers and anthers, plus their long flowering period, provide a large amount of source to stingless bee populations. The eusocial bees, even showing a generalist habit accepted as standard (Ramalho et al., 1990), may exploit the most lucrative sources, being temporarily selective in their food choice (Eltz et al., 2001).

The Leguminosae and Myrtaceae families, which were intensely visited by *F. varia* in the present study, have also been recorded in other surveys of plants used by stingless bees as demonstrated by Ramalho et al. (1990). In a study by Teixeira et al. (2007), bees of the *Frieseomelitta* genus focused their visits on the Caesalpinioideae (Leguminosae), Malpighiaceae, and Anacardiaceae families. Myrtaceae was the second most important family found in samples of *F. varia* by Marques-Souza (2010) and occurred in 11 months of the study period. Of the plants visited by bees in the study by Agostini and Sazima (2003), Leguminosae was one of the two best represented families, with 13 species. Leguminosae is the family with the highest species richness in the area covering the meliponary and its surroundings, which was similar to the study conducted in Campinas.

When considering a monthly analysis, *F. varia* collects a greater diversity of pollen when there are more foragers in the field. Because this species' workers are solitary foragers (Jarau et al., 2003), the interaction with other species of stingless bees would explain this tendency to diversify. The species of stingless bees whose workers forage in large groups through effective recruiting mechanisms dominate the sources of pollen and change the foraging patterns of species such as *F. varia* (Lichtenberg et al., 2010). Consequently, by foraging independently, *F. varia* workers would visit a higher number of different plant species in the same spatiotemporal scale than the group-foraging species, which is reflected in the diversity of resources brought to the colonies. Lichtenberg et al. (2010) experimentally removed the group-foraging workers and found that the solitary foragers, including workers of *F. varia*, had greater access to sucrose solution feeders and collected more of it.

This observation is most evident in the period with the fewest species and plants in bloom (August to January), which overlaps with the highest pollen diversity and number of pollen-foraging workers in the field. Instructing more workers to collect pollen would be a strategy for *F. varia* colonies to ensure their supply of protein even when collecting from low-yield sources. Indeed, when resources are in short

supply, workers of group-foraging stingless bee species visit a wider range of sources. Conversely, in periods of greater resource availability, the workers collect from fewer sources, focusing instead on those that offer more profitable resources (Eltz et al., 2001; Faria et al., 2012).

Another implication of the solitary foraging strategy is the lower importance of mass flowering plant species for the maintenance of colonies of *F. varia* in comparison with other stingless bees species. Although *E. moluccana* was found during nine months of the study period, its relative abundance was low. Furthermore, the other species of *Eucalyptus* and species of *Eugenia*, another mass flowering genus, were included in the occasionally isolated pollen category, with pollen of low visibility, among the species selected to maintain the colonies. The generation of a high number of flowers providing pollen and/or nectar in a short period is a valuable resource for species of stingless bees that recruit nest mates for foraging. It has been noted that the species of the *Eucalyptus* genus are some of the most frequently used species by bees of the *Scaptotrigona* genus (Ramalho, 1990; Faria et al., 2012), which includes the group-foraging species *Scaptotrigona* aff. *depilis* (Jarau et al., 2003).

Our study indicates that ornamental plants can maintain populations of *F. varia*, especially when native flowering species are used to enhance the green areas. This conclusion was also made in other studies about urban ecology (Frankie et al., 2005; Cane et al., 2006). In urban areas exotic flowers generally account for most of the ornamental species, especially in gardens (Acar et al., 2007). Therefore, exotic species are important nutritional resources not only for bees (Agostini & Sazima, 2003; Zanette et al., 2005; Nates-Parra et al., 2006; Frankie et al., 2009) but also for butterflies with generalist habits (Bergerot et al., 2010). Flowers of the exotic species *Tecoma stans* (Bignoniaceae), which is commonly used in landscaping, were visited extensively by bees for collection of nutritional resources; therefore, this species is an important source of resource for maintaining the bee populations in the three Brazilian urban areas studied (Silva et al., 2007). Flowers of *T. stans* are similar to the flowers of *Handroanthus* and *Tabebuia* species, two genera of Bignoniaceae native to Brazil important as sources of nectar for bee populations.

Studies that consider the resource availability for bees usually sample only plants of the tree and shrub strata (Agostini & Sazima, 2003). Nevertheless, some important sources of nectar can be found in herbaceous and liana strata as we could see in this study and in Faria et al. (2012) that was developed in the same area. This result suggests that all the vertical strata are important for the bee's foraging and therefore future studies about bee's trophic niche should consider herbaceous and liana strata on floristic survey.

Urban areas, such as the campus, which nowadays has a beneficial and positive history of land management can act as a refuge for native bees. Urban areas seem to act as a refuge for pollinators, as discussed by McFrederick and LeBuhn (2006)

and López-Urbe et al. (2008), for bees of the Bombini and Euglossini groups, respectively.

The present study has enabled the understanding of resource use by colonies of the eusocial bee species *F. varia*, which is one of the first steps in the management and conservation of this species' populations. The data generated by the present study will be useful for designing and managing green areas in urban environments. Plant species with different flowering periods are recommended, as also planting native species in green areas as gardens and parks. As previously discussed in the literature (Silva et al., 2007; López-Urbe et al., 2008; Wojcik et al., 2008), the designs should aim to increase the number of plants that effectively attract and maintain pollinator populations. This present study emphasizes the importance of plant's diversity to maintain *Frieseomelitta varia* in urban area, as also showed to other species of pollinators (McKinney, 2008).

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References

- Acar, C., Acar, H. & Eroglu, E. (2007). Evaluation of ornamental plant resources to urban biodiversity and cultural changing: A case study of residential landscapes in Trabzon city (Turkey). *Build. Environ.*, 42: 218-229.
- Agostini, K. & Sazima, M. (2003). Plantas ornamentais e seus recursos para abelhas no campus da Universidade Estadual de Campinas, Estado de São Paulo, Brasil. *Bragantia*, 62: 335-343.
- Bergerot, B., Fontaine, B., Renard, M., Cadi, A. & Julliard, R. (2010). Preferences for exotic flowers do not promote urban life in butterflies. *Landscape Urban Plann.*, 96: 98-107.
- Biesmeijer, J.C., Born, M., Lukács, S. & Sommeijer, M.J. (1999). The response of the stingless bee *Melipona beecheii* to experimental pollen stress, worker loss and different levels of information input. *J. Apicult. Res.*, 38(1-2): 33-41.
- Camargo, J.M.F., Pedro, S.R.M. (2007). Meliponini Lepeletier, 1836. In: J.S. Moure, D. Urban & G.A.R. Melo (Eds.), Catalogue of bees (Hymenoptera, Apoidea) in the Neotropical region (pp. 272-578). Curitiba: Sociedade Brasileira de Entomologia.
- Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H. & Williams, N.M. (2006). Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol. Appl.*, 16: 632-644.
- Dearborn, D.C. & Kark, S. (2009). Motivations for conserving urban biodiversity. *Conserv. Biol.* 24 (2): 432-440.
- Eltz, T., Brühl, C.A., van der Kaars, S., Chey, V.K. & Linsenmair, K.E. (2001). Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest. *Insect. Soc.*, 48: 273-279.
- Erdtman, G. (1960) The acetolized method. A revised description. *Sven. Bot. Tidskr.*, 54: 561-564.
- Faria, L.B., Aleixo, K.P., Garófalo, C.A., Imperatriz-Fonseca, V.L. & Silva, C.I. (2012). Foraging of *Scaptotrigona* aff. *depilis* (Hymenoptera, Apidae) in an urbanized area: Seasonality in resource availability and visited plants. *Psyche*, doi: 10.1155/2012/630628.
- Frankie, G.W., Thorp, R.W., Schindler, M., Hernandez, J., Ertter, B. & Rizzardi, M. (2005). Ecological patterns of bees and their host ornamental flowers in two Northern California cities. *J. Kans. Entomol. Soc.*, 78: 227-246.
- Frankie, G.W., Thorp, R.W., Hernandez, H., Rizzardi, M., Ertter, B., Pawelek, J.C., Witt, S.L., Schindler, M., Coville, R. & Wojcik, V.A. (2009). Native bees are a rich natural resource in urban California gardens. *Calif. Agric.* 63, 113-120.
- Hilário, S.D., Imperatriz-Fonseca, V.L. & Kleinert, A.M.P. (2000). Flight activity and colony strength in the stingless bee *Melipona bicolor bicolor* (Apidae, Meliponinae). *Rev. Bras. Biol.*, 60: 299-306.
- Hilário, S.D., Imperatriz-Fonseca, V.L. & Kleinert, A.M.P. (2001). Responses to climatic factors by foragers of *Plebeia pugnax* Moure (*in litt.*) (Apidae, Meliponinae). *Rev. Bras. Biol.*, 61: 191-196.
- Imperatriz-Fonseca, V.L., Kleinert-Giovannini, A. & Ramalho, M. (1989). Pollen harvest by eusocial bees in a non-natural community in Brazil. *J. Trop. Ecol.*, 5: 239-242.
- Jarau, S., Hrncir, M., Schmidt, V.M., Zucchi, R. & Barth, F.G. (2003). Effectiveness of recruitment behavior in stingless bees (Apidae, Meliponini). *Insect. Soc.*, 50: 365-374.
- Kajobe, R. & Echazarreta, C.M. (2005). Temporal resource partitioning and climatological influences on colony flight and foraging of stingless bees (Apidae; Meliponini) in Ugandan tropical forests. *Afr. J. Ecol.*, 43: 267-275.
- Kearns, C.A. & Oliveras, D.M. (2009). Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. *J. Insect Conserv.*, 13: 655-665.

- Kleinert, A.M.P., Ramalho, M., Cortopassi-Laurino, M., Ribeiro, M.F. & Imperatriz-Fonseca, V.L. (2009). Abelhas sociais (Bombini, Apini, Meliponini). In: A.R. Panizzi & P. Parra (Eds.), *Bioecologia e nutrição de insetos - Base para o manejo integrado de pragas* (pp. 373-426). Brasília: Editora Embrapa.
- Knoll, F.R.N., Bego, L.R., Imperatriz-Fonseca, V.L. (1994). As abelhas em áreas urbanas. Um estudo no campus da Universidade de São Paulo. In: J.R. Pirani & M. Cortopassi-Laurino (Eds.), *Flores e abelhas em São Paulo* (pp. 31-42). São Paulo: EDUSP.
- Lichtenberg, E.M., Imperatriz-Fonseca, V.L. & Nieh, J.C. (2010). Behavioral suites mediate group-level foraging dynamics in communities of tropical stingless bees. *Insect Soc.*, 57: 105-113.
- Kovach Computing Services. (2011). Oriana version 4.0 for Windows. Wales: Anglesey.
- López-Urbe, M.M., Oi, C.A. & Del Lama, M.A. (2008). Nectar-foraging behavior of Euglossine bees (Hymenoptera: Apidae) in urban areas. *Apidologie*, 39: 410-418.
- Lorenzi, H. (2008) *Plantas ornamentais no Brasil* (fourth edition). Nova Odessa: Plantarum.
- Marques-Souza, A.C.M. (2010) Ocorrência do pólen de *Podocarpus* sp. (Podocarpaceae) nas coletas de *Friesseomelitta varia* Lepelletier 1836 (Apidae: Meliponinae) em uma área de Manaus, AM, Brasil. *Acta Bot. Bras.*, 24: 558-566.
- Matteson, K.C., Ascher, J.S. & Langellotto, G.A. (2008) Bee richness and abundance in New York city urban gardens. *Ann. Entomol. Soc. Am.*, 101: 140-150.
- Maurizio, A. & Louveaux, J. (1965) *Pollens de plantes mellifères d'Europe*. Union des groupements apicoles français, Paris.
- McFrederick, Q.S. & LeBuhn, G. (2006). Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biol. Conserv.*, 129: 372-382.
- McKinney, M.L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst.*, 11: 161-176.
- Michener, C.D. (2007). *The bees of the world*. The Johns Hopkins University Press, Baltimore.
- Montero, I. & Tormo, R. (1990) Análisis polínico de mieles de cuatro zonas montañosas de Extremadura. *Ann. Asoc. Pal. Leng. Esp.*, 5: 71-78.
- Nates-Parra, G., Parra H, A., Rodríguez, A., Baquero, P. & Vélez, D. (2006). Abejas silvestres (Hymenoptera: Apoidea) en ecosistemas urbanos: Estudio en la ciudad de Bogotá y sus alrededores. *Rev. Colomb. Entomol.*, 32: 77-84.
- Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C. & Zipparro, V.B. (2000). Phenology of Atlantic rain forest trees: A comparative study. *Biotropica*, 32: 811-823.
- Nunes-Silva, P., Hilário, S.D., Santos-Filho, P.S. & Imperatriz-Fonseca, V.L. (2010). Foraging activity in *Plebeia remota*, a stingless bees species, is influenced by the reproductive state of a colony. *Psyche*, doi:10.1155/2010/241204.
- Owen, J. (1991). *The ecology of a garden: the first fifteen years*. Cambridge: University Press.
- Pais, M. & Varanda, E.M. (2010). Arthropod recolonization in the restoration of a semideciduous forest in southeastern Brazil. *Neotrop. Entomol.*, 39: 198-206.
- Pick, R.A. & Blochtein, B. (2002). Atividade de coleta e origem floral do pólen armazenado em colônias de *Plebeia saiqui* (Holmberg) (Hymenoptera, Apidae, Meliponinae) no sul do Brasil. *Rev. Bras. Zool.*, 19: 289-300.
- R Development Core Team. (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Ramalho, M. (1990). Foraging by stingless bees of the genus *Scaptotrigona* (Apidae, Meliponinae). *J. Apicult. Res.*, 29: 61-67.
- Ramalho, M., Kleinert-Giovannini, A. & Imperatriz-Fonseca, V.L. (1990). Important bee plants for stingless bees (*Melipona* and *Trigonini*) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review. *Apidologie*, 21: 469-488.
- Roubik, D.W. (1982). Seasonality in colony food storage, brood production and adult survivorship: studies of *Melipona* in tropical forest (Hymenoptera: Apidae). *J. Kans. Entomol. Soc.*, 55: 789-800.
- Roubik, D.W. (1989). *Ecology and natural history of tropical bees*. Cambridge: University Press.
- Silva, C.I., Araújo, G. & Oliveira, P.E.A.M. (2012). Distribuição vertical dos sistemas de polinização bióticos em áreas de cerrado sentido restrito no Triângulo Mineiro, MG, Brasil. *Acta Bot. Bras.*, 56: 748-760.
- Silva, C.I., Augusto, S.C., Sofia, S.H. & Mosheta, I.S. (2007). Diversidade de abelhas em *Tecoma stans* (L.) Kunth (Bignoniaceae): Importância na polinização e produção de frutos. *Neotrop. Entomol.*, 36: 331-34.
- Silva, C.I., Ballesteros, P.L.O., Palmero, M.A., Bauermann, S.G., Evaldt, A.C.P. & Oliveira, P.E. (2010). Catálogo polínico: Palinologia aplicada em estudos de conservação de abelhas do gênero *Xylocopa* no Triângulo Mineiro. Uberlândia: EDUFU.
- Slaa, E.J., Sánchez Chaves, A., Malagodi-Braga, K.A. & Hofstede, F.E. (2006). Stingless bees in applied pollination:

practice and perspectives. *Apidologie*, 37: 293-315.

Souza, V.C. & Lorenzi, H. (2008). *Botânica sistemática: Guia ilustrado para identificação das famílias de Fanerógamas nativas e exóticas no Brasil em APG II (second edition)*. Nova Odessa: Plantarum.

Taura, H.M & Laroca, S. (2001). A associação de abelhas silvestres de um biótipo urbano de Curitiba (Brasil), com comparações espaço-temporais: abundância relativa, fenologia, diversidade e exploração de recursos (Hymenoptera, Apoidea). *Acta Biol. Parana*, 30: 35-137.

Teixeira, A.F.R., Oliveira, F.F. & Viana, B.F. (2007). Utilization of floral resources by bees of the genus *Frieseomelitta* von Ihering (Hymenoptera: Apidae). *Neotrop. Entomol.*, 36: 675-684.

Teixeira, L.V. & Campos, F.N.M. (2005). Início da atividade de voo em abelhas sem ferrão (Hymenoptera, Apidae): in-

fluência do tamanho da abelha e da temperatura ambiente (Stingless bees (Hymenoptera, Apidae) flight activity beginning: body size and ambient temperature influence). *Rev. Bras. Zool.*, 7: 195-202.

van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.*, 24: 353-377.

Wojcik, V.A., Frankie, G.W., Thorp, R.W. & Hernandez, G.L. (2008). Seasonality in bees and their floral resource plants at a constructed urban bee habitat in Berkeley, California. *J. Kans. Entomol. Soc.*, 81: 15-28.

Zanette, L.R.S., Martins, R.P., Ribeiro, S.P. (2005). Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape Urban Plann.*, 71: 105-121.

Zar, J. H. (1999). *Biostatistical analysis* (fourth edition). New Jersey: Prentice Hall International Editions.

