Food niche of *Exomalopsis* (*Exomalopsis*) *fulvofasciata* Smith (Hymenoptera: Apidae) in Brazilian savannah: the importance of oil-producing plant species as pollen sources

Laíce Souza Rabelo\(^a\), Esther Margarida Alves Ferreira Bastos\(^b\) and Solange Cristina Augusto\(^a\)

\(^a\)Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil; \(^b\)Diretoria de Pesquisa e Desenvolvimento, Laboratório de Recursos Vegetais e Opoterápicos, Fundação Ezequiel Dias, Belo Horizonte, Minas Gerais, Brazil

**ABSTRACT**

*Exomalopsis* are ground-nesting species, and their food-niche breadth is little known due to the difficulty in locating the nests and finding efficient bait plants to attract these bees. Some species of *Exomalopsis* were recorded as tomato, hot pepper and eggplant pollinators. Information about the food niche could be useful to increase *Exomalopsis* populations, providing consistent and comparable data for the enrichment of natural and crop areas with adequate plant sources. This study aimed to determine the food niche and the role of pollen size in the diet of *E. fulvofasciata*. We analysed pollen loads of 28 individuals of *E. fulvofasciata* collected from bait plants, in two natural areas of the Brazilian savannah. Only five pollen types belonging to the families Malpighiaceae, Solanaceae, Leguminosae, Myrtaceae and Lythraceae were important for this species. This result indicates that *E. fulvofasciata* is probably a polylectic species. However, we noticed that the *Byrsonima* used as bait plants contribute significantly for its larval provision, indicating that small pollen grains were more frequently collected.

**ARTICLE HISTORY**

Received 12 June 2015
Accepted 13 March 2016
Online 13 April 2016

**KEYWORDS**

Solitary bees; pollen analyses; anther type; pollen size

**Introduction**

*Exomalopsis* is the only genus of Exomalopsini in Brazil (Silveira et al. 2002). Some species of this tribe were reclassified as Teratognathini and Tapinotaspidini (one of the groups specializing in oil collection) (Michener and Moure 1957; Silveira et al. 2002; Alves-Dos-Santos et al. 2007). *Exomalopsis* species build nests in the ground and some species cooperatively provide for each other’s cells, and therefore are considered communal (Rozen 2011).

*Exomalopsis* (*Exomalopsis*) *fulvofasciata* Smith is a species of medium-large bee (≥ 1.2 cm in length), according to the classification proposed by Frankie et al. (1983). This species was recorded in Argentina, Brazil and Paraguay (Silveira 2012). The females build their nests in aggregations in open areas with sandy soil (Aranda and Graciolli 2013).
There are records of females foraging on flowers of Araliaceae, Asteraceae, Bignoniaceae, Bixaceae, Fabaceae, Malpighiaceae, Nyctaginaceae, Sapindaceae, Solanaceae and Sterculiaceae (Gottsberger and Silberbauer-Gottsberger 1988; Guimarães et al. 2008; Imperatriz-Fonseca et al. 2011). Despite these records, most studies do not provide information about the period of activity and floral resources foraged by *E. fulvofasciata*, especially its pollen sources.

In general, bee females present a high degree of floral constancy when foraging for pollen. This behaviour contributes to the pollination efficiency and represents a mechanism used by bees to save energy in trying to find new pollen sources (Thorp 1979; Chittka et al. 1999).

The identification of the food sources used by bees can be performed directly through observation of their visits to flowers or indirectly by pollen analyses (Cane and Sipes 2006). The pollen analysis has been used for determining both the food-niche breadth presented by bee species and the influence of the flower characteristics (e.g. type of anthers) and pollen grains (e.g. grain size) on the use of pollen sources, such as verified for oil-collecting bees (‘Centridini’ and Tetrapediini) (Dórea et al. 2010a, 2010b; Menezes et al. 2012; Rabelo et al. 2012, 2014a, 2014b).

Information on the niche breadth allows the classification of the species into specialization categories. Bees are considered monolectic when they collect pollen only from a single source, oligolectic when collecting from sources belonging to one to three families, and polylectic when collecting from sources belonging to four or more families (Cane and Sipes 2006). Although the use of this classification is controversial, it can be associated with other floral characteristics to elucidate the importance of each pollen source.

The study of *E. fulvofasciata* food niche can contribute data to crop pollination management. Species of *Exomalopsis* were recorded as pollinators of tomato (*Lycopersicon esculentum*) (Santos et al. 2014), hot pepper (*Capsicum annuum*) (Raw 2000) and eggplant (*Solanum melongena*) (Montemor and Souza 2009). Based on information about the food niche, *Exomalopsis* populations could be increased by the enrichment of crop areas with other plant sources, since the management of nests in the soil is difficult.

Considering the difficulty in locating the nests of species that build their breeding place on the ground, an alternative method to obtain information about food niche is the use of bait plants. The choice of bait plants can be made based on previous observations. Thus, during the study of the interactions between *Byrsonima* species and oil-collecting bees in savannah areas, the visits of *E. fulvofasciata* were frequent (Rabelo, pers. obs.). Among Malpighiaceae, the genus *Byrsonima* is one of the most frequently visited by oil-collecting bees to take oil and pollen. However, this flowering plant can also be used by other bee species as a pollen source (Teixeira and Machado 2000; Benezar and Pessoni 2006; Costa et al. 2006; Ribeiro et al. 2008; Bezerra et al. 2009; Mendes et al. 2011; Sazan et al. 2014). These records suggest that these plants can be important food sources and an efficient bait plant for *E. fulvofasciata*.

This study aimed to determine the food-niche breadth and the role of pollen size in the *E. fulvofasciata* diet using *Byrsonima* species as bait plants. We investigated both whether *E. fulvofasciata* is a polylectic species and whether the bait plants contribute significantly to larval provision.
Material and methods

Study areas

This study was conducted in two ecological reserves located in the Brazilian savannah: the Ecological Station of Panga (ESP), Uberlândia, MG, and the State Park of Serra de Caldas Novas (SPSCN), Caldas Novas, GO. These areas comprise a mosaic of savannic-forested phytosociological units. They include woody savannahs, as well as gallery, seasonal deciduous and semi-deciduous forests (Schiavini and Araújo 1989; FEMAGO 2008) and have high similarity in floristic composition (Lopes et al. 2011). The ESP (19°09′20″–19°11′10″S, 48°23′20″–48°24′35″W) has 403.85 ha and SPSCN (17°47′56″S, 48°40′23.7″W), 12,315.36 ha. Both areas extend across a region that has two distinct seasons: warm and wet (October to March) and cold and dry (April to September) (Rosa et al. 1991).

Samplings and records of bee behaviours during foraging activities

We conducted the bee samplings in the warm wet season, due to the higher number of flowering plant species in the Brazilian savannah during this period (Batalha and Matovani 2000). The Exomalopsis bees were collected during their visits to flowers of Byrsonima (Malpighiaceae) used as bait plants. We performed preliminary observations in order to identify plant species that were flowering at the study areas and were attractive to E. fulvofasciata. We chose Byrsonima as bait plant based on frequent observations of floral visits of E. fulvofasciata.

The ESP has five recorded species of Byrsonima: Byrsonima basiloba A. Juss, Byrsonima coccobobifolia Kunth, Byrsonima crassifolia (L.) Kunth, Byrsonima intermedia A. Juss, and Byrsonima verbascifolia (L.) DC. (Costa and Araújo 2001; Silva et al. 2012). Conversely, SPSCN presents four recorded species: B. coccobobifolia, Byrsonima pachyphylla A. Juss, B. verbascifolia and B. intermedia (Lopes et al. 2011).

During the sampling period, only B. intermedia was flowering in the ESP, and B. pachyphylla and B. verbascifolia in the SPSCN (Rabelo LS, per. obs.). Consequently, these Byrsonima species were used as bait plants. The flowering of B. intermedia and B. pachyphylla in Brazilian savannah was registered from September to February (Gaglianone 2001) and July to October (Melo et al. 2014), respectively.

All plants used as baits have yellow flowers with very similar morphologies and offer pollen and oil as floral rewards (Anderson 1979). Like other Byrsonima species, they present anthers with rimosa dehiscence, i.e. anther opening occurs through a longitudinal slot. Their pollen grains are small and powdery and can be directly removed either using the fore leg and mid legs or by vibration (Teixeira and Machado 2000; Benezar and Pessoni 2006; Bezerra et al. 2009; Mendes et al. 2011; Sazan et al. 2014).

We performed three samplings, for three days, from 9 am to 1 pm, totalling 36 h of observations in each area (Table 1). We chose the sampling points that presented at least four individuals of Byrsonima with newly opened flowers. These individuals were located no more than 5 m from each other. During the observation period, a researcher walked among the plant individuals and recorded how the females removed the pollen grains from the flowers, since this bee species does not use oil to nest. After the behavioural record the females were captured using entomological nets, individually wrapped in plastic bottles and immediately sacrificed by freezing.
We captured the bees before they incorporated the grains of *Byrsonima* into the pollen loads. These procedures reduced the potential risk of biases in the evaluation of the importance of bait plant as a food source for *E. fulvofasiata*. We also record the collections of pollen and oil performed by oil-collecting bees, the main floral visitors of *Byrsonima*.

Only the pollen loads presented in the legs were used in the pollen analysis, i.e. the pollen grains that were collected in order to be used as larval provision. In the laboratory, the pollen load was removed and packaged in Falcon tubes containing 2 mL of 70% ethanol. All bees were deposited in the Laboratory of Ecology and Behavior of Bees, Federal University of Uberlândia.

The pollen samples were treated by the acetolysis method (Erdtman 1960). Twenty-eight pollen samples of *E. fulvofasiata* were processed (ESP = 14 samples and SPSCN = 14 samples). For each pollen sample, three voucher slides were prepared and deposited in the collection of the Laboratory of Ecology and Behavior of Bees, Federal University of Uberlândia.

The pollen grains were identified based on the characteristics revealed after acetolysis (Salgado-Labouriau 1973; Roubik and Moreno 1991). Voucher specimens were cross-referenced with a database of pollen grain images (Bastos et al. 2008) and by comparison with the specimens catalogued as reference material in the Laboratory of Plant Morphology, Microscopy and Image, Federal University of Uberlândia. In this study, we used the taxonomic classification proposed by the Angiosperm Phylogeny Group (APG II) (Souza and Lorenzi 2005).

After the identification, the morphologically similar pollen grains were grouped into pollen types according to the methods proposed in the literature (Salgado-Labouriau 1973; Vilhena et al. 2012). In some cases, it was possible to determine the species that composed the pollen type.

**Pollen analysis: breadth and uniformity of the food niche and classification of pollen types**

After the pollen identification, quantitative analysis was accomplished by dividing each slide into four quadrants, in which approximately 100 pollen grains were counted, totalling 400 for each slide and, therefore, 1200 pollen grains per sample. If the quadrant contained less than 100 pollen grains, all of them were counted and expressed as percentages of the pollen sum (Vilhena et al. 2012). Pollen types with proportion lower than 3% in each sample were discarded, as they were considered either contaminants or only sources of nectar. Quantitative analysis was performed using a magnification of 200×.

| Sample | Dates | Intervals | Total of days and hours |
|--------|-------|-----------|------------------------|
| Sample 1 | 22, 23, 26 November 2012 | 9 am to 1 pm | 3 and 12 |
| Sample 2 | 30, 31 March/1 April 2013 | 9 am to 1 pm | 3 and 12 |
| Sample 3 | 6, 9, 13 December 2013 | 9 am to 1 pm | 3 and 12 |
We calculated the niche breadth using the Shannon–Wiener index \((H')\): \(H' = - \sum (pk \times \ln of pk)\), where \(pk\) represents the proportion of pollen types present in the pollen load as proposed by Camillo and Garófalo (1989). The uniformity of pollen types in the samples was determined according to the Pielou evenness index \((J')\): \(J' = H'/H'_{\text{max}}\), where \(H'_{\text{max}}\) represents the logarithm of the total number of pollen types present in the each area. This evenness index ranges between 0 and 1, and values near 1 represent high uniformity in the pollen collection, i.e. the pollen types were collected at similar proportions. Both analyses were performed for each area separately using PAST 2:13 software (Hammer et al. 2001).

According to type of anther, the pollen types were classified into poricidal and non-poricidal based on literature information. The flowers that present pollen inside a tube-like anther with a small apical pore were classified as poricidal sources, while non-poricidal flowers present anthers with longitudinal or valvular opening (Souza and Lorenzi 2005). These categories were determined due to behavioural differences to explore each of these types of resources (Buchmann 1978). They were also classified according to the size of the grains: small \((s) = 10–25 \mu\text{m}\) and medium \((m) = 25–50 \mu\text{m}\), as proposed in the literature (Barth and Melhem 1988; Bastos et al. 2008).

**Data analysis**

To compare the richness of pollen sources between the areas and to verify if our sampling effort was enough to record most of the pollen sources expected to be used in each area we constructed extrapolation curves based on the samples using the program EstimateS 9.1.0 (Colwell 2013). This analysis allows the estimation of the total number of expected pollen types present at the samples if the sampling effort reaches the asymptote (Colwell 2013).

The similarity in the utilization of pollen sources by *E. fulvofasciata* between the two study areas was determined by \(PS = \Sigma\) (lowest percentage for each pollen type) (Brower et al. 1997). This index is also known as the Renkonen index and is based on the relative abundance of the pollen types presented at each area. It ranges from 0 (the females used a completely different group of pollen sources for larval provision) to 100% (the females used exactly the same pollen source and at the same percentages).

The possible difference in the food-niche breadth between the two assessed areas was evaluated by the one-sample \(t\) test of Hutcheson, using the PAST 2:13 program (Hammer et al. 2001).

We verified the possible differences in the relative abundance of pollen sources, according to the type of anthers and size of pollen grains, using chi-square tests for each area separately (Zar 2010).

To establish the influence of the use of *Byrsonima* as bait plant in each evaluated parameter, all the analyses were repeated excluding this pollen type.

**Results**

We collected 420 bees, 206 at ESP and 214 at SPSCN. *Exomalopsis fulvofasciata* represented 10.48% of the records, being the second most abundant species. This species occurred in 77.78% and 44.44% of the samplings, at ESP and SPSCN, respectively.
We collected 44 females of *E. fulvofasciata* during their visits to flowers of *Byrsonima*, 23 of them to *B. intermedia*, at the ESP, and 21 to *B. pachyphylla*, at SPSCN (Figure 1). Visits to flowers of *B. verbascifolia* were not observed.

In order to collect pollen, *E. fulvofasciata* approached the flower by the front and fixed itself using the jaws. The female curved its body over the anthers and vibrated the structure. These procedures removed the pollen grains from the anthers and they remained attached to the ventral surface of the female’s body.

Sixteen females exhibited pollen collected by vibration from the flowers of *Byrsonima* only on the surface of the ventral region of their bodies (ESP = 9 and SPSCN = 7). The absence of pollen in their scopa indicates that these bees did not visit other plants before their capture. Twenty-eight females presented pollen in their scopa (ESP = 14 and SPSCN = 14) before their behaviours were recorded. In both cases, the pollen grains from bait plants were not added to their scopa after the visits.

Pollen analyses showed that only five pollen types, belonging to five botanical families, were quantitatively important for *E. fulvofasciata* (ESP = five types and SPSCN = three types) (Table 2). Eleven pollen types presented an abundance of less than 3% in each sample and were excluded from the analyses. The extrapolation analysis showed that 87.11% and 100% of the pollen types estimated for ESP (x = 5.69 ± 1.23) and SPSCN (x = 3.00 ± 0.00), respectively, were sampled (Figure 2). Therefore, these analyses showed that our sample effort was representative considering that we sampled most of the pollen types that should be present in the pollen loads.

The similarity in the use of pollen types between the areas was high (PS = 89.30%), and we observed few pollen types per sample. At the ESP, we recorded one to four

---

**Figure 1.** Number of *Exomalopsis fulvofasciata* recorded on *Byrsonima* flowers in the two savannah areas. Ecological Station of Panga, MG (ESP) – 1 to 9 and State Park of Serra de Caldas Novas, GO (SPSCN) – 10 to 18.
pollen types per sample \( (x = 1.57 \pm 0.82) \), while at SPSCN, one to two pollen types \( (x = 1.57 \pm 0.49) \) (Figure 3). The *Byrsonima* type has been the main source of pollen for *E. fluvofasciata*, 84.55% and 90.72% at the ESP and SPSCN, respectively. This pollen type was present in all samples of both areas and 14 samples presented only *Byrsonima* type after the exclusion of those with abundance less than 3% (ESP = eight samples and SPSCN = six samples) (Table 2, Figure 3).

### Table 2. Pollen types identified in pollen loads of *Exomalopsis fluvofasciata* in the two savannah areas [Ecological Station of Panga, MG (ESP) and State Park of Serra de Caldas Novas, GO (SPSCN)].

| Pollen type | FR | PS | FO | RA | FO | RA |
|-------------|----|----|----|----|----|----|
| LYTHRACEAE |    |    |    |    |    |    |
| Cuphea type | P/N | M | 21.43 | 8.51 | — | — |
| LEGUMINOSAE |    |    |    |    |    |    |
| Acosmium type | P/N | S | 21.43 | 4.44 | 49.98 | 8.56 |
| MALPIGHIACEAE |    |    |    |    |    |    |
| *Byrsonima* type | P/O | S | 100.00 | 84.55 | 100.00 | 90.72 |
| MYRTACEAE |    |    |    |    |    |    |
| *Eugenia* type | P | M | 7.14 | 2.19 | — | — |
| SOLANACEAE |    |    |    |    |    |    |
| *Solanum* type | P | M | 7.14 | 0.31 | 7.14 | 0.73 |
| Richness | — | — | 5 | 3 | — | — |
| \( H' \) | — | — | 0.59 | 0.33 | — | — |
| \( J' \) | — | — | 0.37 | 0.30 | — | — |

Abbreviations: FR, floral resources offered (P, pollen; O, oil; N, nectar); PS, class of pollen size grains (S, small; M, medium); FO, frequency of occurrence; RA, relative abundance; \( H' \), food-niche breadth given by the Shannon–Wiener index; \( J' \), uniformity in the collection of resources given by the Pielou index.

*The *Byrsonima* type is comprises the species *Byrsonima intermedia* in ESP and *Byrsonima pachyphylla* in SPSCN.*

**Figure 2.** Estimated number of pollen types in each study area using extrapolation curves. ESP: Ecological Station of Panga, MG and SPSCN: State Park of Serra de Caldas Novas, GO.
The *Acosmium* and *Solanum* types were also present in both areas (Table 2), but in low abundance. The *Cuphea* and *Eugenia* types occurred only in samples obtained in the ESP. In both areas, there was predominance of the use of plants with non-poricidal anther ($\chi^2_{ESP} = 17,585.70; \text{df} = 1; p < 0.001$ and $\chi^2_{SPSCN} = 13,620.97; \text{df} = 1; p < 0.001$) (Figure 4). Furthermore, most samples presented only pollen types belonging to non-poricidal anthers, 92.86% in the ESP and 92.86% in the SPSCN.

Figure 3. Absolute abundance of pollen types and the number of types observed in each sample. (A) Ecological Station of Panga, MG (ESP), and (B) State Park of Serra de Caldas Novas, GO (SPSCN).
The food-niche breadth of *E. flulvofasciata* in ESP (*H'*= 0.59) was significantly higher than in SPSCN (*H'*= 0.35) (*t* = 25.61, *df* = 31,767.00; *p* < 0.001), and, in both areas, the uniformity of pollen types was low (*J'_{ESP}*= 0.37 and *J'_{SPSCN}*= 0.30).

The pollen types fell into two categories according to the size: small (*Byrsonima* and *Acosmium* types) and medium (*Cuphea*, *Eugenia* and *Solanum* types) (*Table 2*). There was a predominance of the use of small pollen grains in both areas (*χ^2^_{ESP}*= 10,828.73; *df* = 1, *p* < 0.001 and *χ^2^_{SPSCN}*= 13,620.97; *df* = 1; *p* < 0.001) (*Figure 5*). Most of the samples presented exclusively small grains (ESP: 78.57% and SPSCN: 92.86%).

Figure 4. Abundance of pollen types according to the anther type: poricidals (P) and non-poricidals (NP). (A) Ecological Station of Panga, MG (ESP), and (B) State Park of Serra de Caldas Novas, GO (SPSCN).

Figure 5. Abundance of pollen types according to grain size categories: small (S) and medium (M) in two natural areas. (A) Ecological Station of Panga, MG (ESP), and (B) State Park of Serra de Caldas Novas, GO (SPSCN).
After removing the *Byrsonima* type of analyses, we observed the same pattern regarding the utilization of sources with non-poricidal anthers ($\chi^2_{\text{ESP}} = 497.42$, df = 1, $p < 0.001$, $\chi^2_{\text{SPSCN}} = 925.96$; df = 1; $p < 0.001$) and an increase in the difference between the diversity indices ($H'_{\text{ESP}} = 1.04$ and $H'_{\text{SPSCN}} = 0.27$; $t = 34.90$, df = 2,464.40, $p < 0.001$), as well as in the uniformity, especially in the ESP ($J'_{\text{ESP}} = 0.75$ and $J'_{\text{SPSCN}} = 0.40$). However, there was a predominance of medium grains in both areas ($\chi^2_{\text{ESP}} = 2,532.56$, df = 1, $p < 0.001$, $\chi^2_{\text{SPSCN}} = 925.96$, df = 1, $p < 0.001$). Furthermore, there was a reduction of 23.30% in this similarity index (PS = 68.48%).

**Discussion**

We observed few pollen types that were quantitatively important for *E. fulvofasciata*, among which the *Byrsonima* type was the main pollen source. Considering the spatial and temporal differences in the samples analysed, we can conclude that the use of *Byrsonima* species as floral resources is a frequent choice of *E. fulvofasciata*, at least during the wet season and flowering period of these Malpighiaceae species.

Although *Byrsonima* flowers are non-poricidal, *E. fulvofasciata* used vibration to collect pollen. The use of vibration on flowers with non-poricidal anthers allows the collection of a larger amount of pollen grains per unit time of handling compared to other behaviours (Buchmann 1985). Thus, it may represent a more economical mechanism of collecting pollen. This strategy has been observed in bees of the genera *Centris* and *Epicharis*, considered efficient pollinators of *Byrsonima* species (Gaglianone 2003; Teixeira and Machado 2000; Bezerra et al. 2009). Taking into account the frequency of visits to flowers and behaviour of by this species of bees, we concluded that *E. fulvofasciata* probably contributes to the reproduction of *B. intermedia* and *B. pachyphylla*.

The high abundance and frequency of the *Byrsonima* pollen type in the samples, as well as its features, may also influence the predominant use of small pollen grains. Each bee species requires a specific pollen volume for larval provision according to its body size (Müller et al. 2006). Hence, the variation in pollen size (Barth and Melhem 1988) can favour the establishment of a trade-off between the number and the size of pollen grains. Thus, the bees can invest in gathering either many small grains or a smaller number of larger grains. In this context, the small size of pollen can facilitate the collection of a greater number of grains in a few visits to *Byrsonima*, minimizing the energy expenditure of female bees. This pattern of predominant use of pollen grains with specific size has also been observed for other solitary bee species, such as *Centris* (*Heterocentris*) *analis* (Fabricius) and *Centris* (*Hemisiella*) *tarsata* Smith, which use medium grain sizes (Rabelo et al. 2014a), and *Tetrapedia diversipes* Klug and *Diadasia* spp., which use large grain sizes (Sipes and Tepedino 2005; Menezes et al. 2012).

Other pollen sources were also identified. Plants offering only pollen as floral resource, such as *Solanum* and *Eugenia* (Souza and Lorenzi 2005), were used as pollen sources and their importance for *E. fulvofasciata* can be determined based on pollen abundance. On the other hand, flowers that offer pollen and nectar as floral rewards, for example, *Cuphea* and *Acosmium*, can be exploited for the collection of both. There are records of nectar exploitation of Cuphea’s flowers by *Xylocopa* and *Centris* (Ribeiro et al. 2008; Ramalho and Rosa 2010). There are reports on other species that forage on
Acosmium’s flowers for nectar (Viana and Kleiner 2006), and the high abundance in some samples also suggests their use as a pollen source.

These native plant species used as provision sources for E. fulvofasciata could be used in order to maintain this bee in crop areas, since it is still not possible to manage the nests of this ground-nesting species. The presence of natural areas around the crop could ensure important pollen sources, e.g. Byrsonima, and suitable nesting sites, since this species nests on the ground and some agricultural practices can destroy its nest. Exomalopsis fulvofasciata is considered a pollinator of hot peppers (Raw 2000) and has the potential to pollinate plants that require buzz pollination, since it is able to vibrate in order to collect pollen, as observed in this study.

We also found few pollen types per sample. This pattern may be ascribable to floral constancy. Bees may forage on several flowers of the same species to collect resources (Cane and Sipes 2006). This behaviour results in energy savings by reducing their energy expenditure to locate and handle various floral types (Thorp 1979). As regards to the plants, their floral constancy may favour the process of pollen transport between individuals of the same species promoting pollination and act as a mechanism of speciation (Chittka et al. 1999).

The floristics of the areas (Lopes et al. 2011) and the predominant use of the Byrsonima type may have promoted the high similarity in the use of pollen sources between the study areas. The greatest contribution of the Byrsonima type consisted in providing a low uniformity index in the collection of resources. These results, associated with the great proportion of pollen grains from Byrsonima in all the samples, reinforce the choice of this species during the period of increased availability of floral sources.

Based on the number of plant families used as pollen sources, E. fulvofasciata could be considered a polylectic species (Cane and Sipes 2006). However, considering that our records are restricted to the warm and wet season, additional studies on the dry and cold season are useful to verify if E. fulvofasciata is active in this period and to obtain new information about its food niche.

Our results indicate that E. fulvofasciata is probably a polylectic species. However, we noticed that the Byrsonima type contributes significantly to its larval provision, indicating that small pollen grains were more frequently collected. Taking into account the frequency of visits to flowers and the behaviour during the visits, we also considered that E. fulvofasciata is probably a pollinator of B. intermedia and B. pachyphylla.

**Acknowledgements**

The authors are grateful to Dr Paulo Eugenio Oliveira (LAMOVI-IB/UFU) for the conditions offered by the laboratory and access to reference slide collections of the study areas; to Dr Ivan Schiavini for the identification of the bait plants; to the officers and employees of the State Park of Serra de Caldas for the collection conditions in the study area; to the project Biodiversity Patterns and Ecological Processes in the Cerrado Ecosystems in the region of the Triângulo Mineiro and Southeast of Goiás (sub-basin of the Paranalba River).
Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Thanks to Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (PELD - 403733/2012-0) and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for funding this study. S.C. Augusto received research fellowships from CNPq [307222/2012-8], and L. S. Rabelo received a grant from CAPES.

References

Alves-Dos-Santos I, Machado IC, Gaglianone MC. 2007. História natural das abelhas coletoras de óleo [Natural history of oil collecting bees]. Oecol Bras. 11:544–557.

Anderson WR. 1979. Floral Conservatism in Neotropical Malpighiaceae. Biotropica. 11:219–223.

Aranda R, Graciolli G. 2013. First report of Exomalopsis fulvofasciata (Hymenoptera: anthophoridae) as host of two Timulla species (Hymenoptera: Mutillidae). Biota Neotrop. 13:382–384.

Barth OM, Melhem TSA. 1988. Glossário ilustrado de palinologia [Illustrated glossary of palynology]. Campinas: Editora da Unicamp.

Bastos EMAF, Thiago PSS, Santana RM, Travassos A [CD-ROM]. 2008. Banco de imagens de grãos de pólen: mais de 130 espécies de plantas apícolas [Database of images of pollen grains: over 130 species of honey plants].

Batalha MA, Matovani W. 2000. Reproductive phenological patterns of Cerrado plant species at the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and woody floras. Rev. Bras. Biol. 60:129–145.

Benezar RMC, Pessoni LA. 2006. Biologia floral e sistema reprodutivo de Byrsonima coccolobifolia (Kunth) em uma savana amazônica [Floral biology and reproductive system of Byrsonima coccolobifolia (Kunth) in an Amazonian savanna]. Acta Amaz. 36:159–168.

Bezerra ES, Lopes AV, Machado IC. 2009. Biologia reprodutiva de Byrsonima gardnerana A. Juss. (Malpighiaceae) e interações com abelhas Centris (Centridini) no Nordeste do Brasil [Reproductive biology Byrsonima gardnerana A. Juss. (Malpighiaceae) and interactions with Centris bees (Centridini) in Northeastern Brazil]. Revista Brasil. Bot. 32:71–84.

Brower JE, Zar JH, von Ende CN. 1997. Field and laboratory methods for general ecology. 4th ed. EUA: Wm. C. Brown Publishers.

Buchmann SL. 1978. A biophysical model for buzz pollination in angiosperms. J. Theor. Biol. 72:639–657.

Buchmann SL. 1985. Bees use vibration to aid pollen collection from non-poricidal flowers. J Kansas Entomol Soc. 58:517–525.

Camillo E, Garófalo CA. 1989. Analysis of the niche of two sympatric species of Bombus (Hymenoptera, Apidae) in southeastern Brazil. J. Trop. Ecol. 5:81–92.

Cane JH, Sipes S. 2006. Characterizing floral specialization by bees: analytical methods and revised lexicon for oligolectic. In: Waser NM, Ollerton J, editors. Plant-pollinator interactions: from specialization to generalization. Chicago: University of Chicago Press; p. 99–122.

Chittka L, Thomson JD, Waser NM. 1999. Flower constancy, insect psychology, and plant evolution. Naturwissenschaften. 86:361–377.

Colwell RK 2013. EstimateS: Statistical estimation of species richness and shared species from samples, version 9. http://purl.oclc.org/estimates

Costa AA, Araújo GM. 2001. Comparação da vegetação arbórea de cerradão e de cerrado na Reserva do Panga, Uberlândia, Minas Gerais [Comparison of woody vegetation of cerradão and cerrado in the Panga Reserve, Uberlândia, Minas Gerais]. Acta Bot. Bras. 15:63–72.
Costa CBN, Costa JAS, Ramalho M. 2006. Biologia reprodutiva de espécies simpátricas de Malpighiaceae em dunas costeiras da Bahia, Brasil [Reproductive biology of sympatric species of Malpighiaceae in coastal dunes of Bahia, Brazil]. Revista Brasil. Bot. 29:103–114.

Dórea MC, Aguiar CML, Figueroa LER, Lima LC, Santos FAR. 2010a. Residual pollen in nests of Centris analis (Hymenoptera, Apidae, Centridini) in an area of Caatinga vegetation from Brazil. Oecol. Aust. 14:232–237.

Dórea MC, Aguiar CML, Figueroa LER, Lima LCLE, Santos FAR. 2010b. Pollen residues in nests of Centris tarsata Smith (Hymenoptera, Apidae, Centridini) in a tropical semiarid area in NE Brazil. Apidologie. 41:557–567.

Erdtman G. 1960. The acetolized method. A revised description, Svensk Bot. Tidskr. 54:561–564.

FEMAGO. 2008. Parque Estadual da Serra de Caldas Novas [State Park of Serra de Caldas Novas] [internet]. Available from http://www.semarhtemplate.go.gov.br/uploads/files/plano_de_manejo_do_parque_estadual_da_serra_de_caldas_novas.pdf

Frankie GW, Haber WA, Opler PA, Bawa KS. 1983. Characteristics and organization of the large bee pollination system in the Costa Rican dry forest. In: Jones and CE, Little RJ, editors. Handbook of Experimental Pollination Biology. New York: Van Nostrand Reinhold Co; p. 411–447.

Gaglianone MC. 2001. Nidificação e forrageamento de Centris (Ptilotopus) scopipes Friese (Hymenoptera, Apidae). Rev. Bras. Zool. 18:107-117.

Gaglianone MC. 2003. Abelhas do tribo Centridini na Estação Ecológica de Jataí (Luiz Antonio, SP): composição de espécies e interações com flores de Malpighiaceae [Bees of Centridini tribe in the Ecological Station of Jataí (Luiz Antonio, SP): species composition and interactions with flowers of Malpighiaceae]. In: Melo GAR, Alves-dos-Santos IC, Editors. Homenagem aos 90 anos de Jesus Santiago Moure [Tribute to the 90 years of Jesus Santiago Moure]. Criciúma: UNESC; p. 279–284. Apoidea Neotropica: UNESC.

Gottsberger G, Silberbauer-Gottsberger I. 1988. Evolution of flower structures and pollination in Neotropical Cassiinae (Caesalpiniaceae) species. Phyton (Austria). 28:293–320.

Guimarães E, Stasi LC, Maimoni-Rodella RCS. 2008. Pollination biology of Jacaranda oxyphylla with an emphasison staminode function. Ann Botany. 102:699–711.

Hammer Ø, Haper DAT, Ryan PD. 2001. PAST: paleontological Statistics software package for education and data analysis. Palaeontol. Electron. 4:1–9.

Imperatriz-Fonseca VL, Alves-dos-Santos I, Santos-Filho PS, Engels W, Ramalho M, Wilms W, Aguilar JBV, Pinheiro-Machado CA, Alves DA, Kleinhert AMP. 2011. Checklist das abelhas e plantas melítófilas no Estado de São Paulo, Brasil [Checklist of bees and melittophilous plants in São Paulo State, Brazil]. Biota Neotrop. 11:1–25.

Lopes SF, Vale VS, Oliveira AP, Schiavini I. 2011. Análise comparativa da estrutura e composição florística de Cerrado no Brasil Central [Comparative analysis of the structure and composition of Cerrado in Central of Brazil]. Interciência. 36:8–15.

Melo MS, Oliveira DE, Franceschinelli EV. 2014. Density and fertility of Byrsonima pachyphylla A. Juss. (Malpighiaceae) in small fragments of the Brazilian Cerrado. Acta Bot. Bras. 28:259–265.

Mendes FN, Rêgo MMC, Albuquerque PMC. 2011. Fenologia e biologia reprodutiva de duas espécies de Byrsonima Rich (Malpighiaceae) em área de Cerrado no Nordeste do Brasil [Phenology and reproductive biology of two species of Byrsonima Rich (Malpighiaceae) in Cerrado area in northeastern of Brazil]. Biota Neotrop. 11:103–115.

Menezes GB, Gonçalves-Esteves V, Bastos EMAF, Augusto SC, Gaglianone MC. 2012. Nesting and use of pollen resources by Tetrapedia diversipes Klug (Apidae) in Atlantic Forest areas (Rio de Janeiro, Brazil) in different stages of regeneration. Rev Bras Entomol. 56:86–94.

Michener CD, Moure JS. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). Bull. Am. Mus. Nat. Hist. 112:395–412.

Montemor KA, Souza DTM. 2009. Biodiversidade de polinizadores e biologia floral em cultura de berinjela (Solanum melongena) [Biodiversity of pollinators and floral biology of eggplant (Solanum melongena)]. Zootecnia Trop. 27:97–103.

Müller A, Diener S, Schnyder S, Stutz K, Sedivy C, Dorn S. 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee–flower relationships. Biol Conserv. 130:604–615.
Larval food sources of *Centris (Heterocentris) analis* (Fabricius, 1804) (Hymenoptera: apidae), an oil-collecting bee. Journal of Natural History. 46:1129–1140.

Oil-collecting bee–flower interaction network: do bee size and anther type influence the use of pollen sources? Apidologie. doi:10.1007/s13592-014-0336-8.

Differentiated use of pollen sources by two sympatric species of oil-collecting bees (Hymenoptera: apidae). Journal of Natural History 48:1595–1609.

Ecology of the interaction between small keel flowers of *Stylosanthes viscosa* Sw. (Faboeidae) and large bees *Xylocopa (Neoxylocopa) cearensis* Ducke, 1910 (Apoidea, Hymenoptera) in tropical dune. Biota Neotrop. 10:93–100.

Foraging behaviour of wild bees at hot pepper flowers (*Capsicum annuum*) and its possible influence on cross pollination. Ann. Bot. 85:487–492.

Pollen loads of pollinating bees of *Byrsonima chrysophylla* Kunth. (Malpighiaceae): fidelidade e fontes alternativas de recursos florais [Pollen loads of pollinating bees of *Byrsonima chrysophylla* Kunth. (Malpighiaceae): loyalty and alternative sources of floral resources]. Acta Bot. Bras. 22:165–171.

Potential pollinators of tomato, *Lycopersicon esculentum* (Solanaceae), in open crops and the effect of a solitary bee in fruit set and quality. J. Econ. Entomol. 107:987–994.

Potential pollinators of tomato, *Lycopersicon esculentum* (Solanaceae), in open crops and the effect of a solitary bee in fruit set and quality. J. Econ. Entomol. 107:987–994.

Considerações sobre a vegetação da Reserva Ecológica do Panga (Uberlândia) [Considerations on the vegetation of Ecological Reserve of Panga (Uberlândia)]. Soc Nat (Online). 1:61–66.

Distribuição vertical dos sistemas de polinização biótico em áreas de cerrado sentido restrito no Triângulo Mineiro, MG, Brasil. [Vertical distribution of biotic pollination systems in cerrado strict sense in the Triangular Mineiro, Minas Gerais, Brazil]. Acta Bot. Bras. 26:748–760.

Abordagem preliminar das condições climáticas de Uberlândia [Preliminary addressing of climate conditions Uberlândia]. Sociedade E Natureza. 5:98–101.

The pollen and spores of Barro Colorado Island. St Louis (Missouri): Missouri Botanical Garden.
identification of families of Angiosperm from Brazilian flora based on APG II]. Imprenta Nova Odessa: Instituto Plantarum de Estudos da Flora.

Teixeira LAG, Machado IC. 2000. Sistema de polinização e reprodução de *Byrsonima sericea* DC (Malpighiaceae). Acta Bot. Bras. 15:1–12.

Thorp RW. 1979. Structural, behavioural, and physiological adaptations of bees (Apoidea) for collecting pollen. Ann MO Bot Gard. 66:788–812.

Viana BF, Kleiner AMP. 2006. Structure of bee-flower system in the coastal sand dune of Abaeté, northeastern Brazil. Rev. Bras. Entomol. 50:53–63.

Vilhena AMGF, Rabelo LS, Bastos EMAF, Augusto SC. 2012. Acerola pollinators in the savanna of Central Brazil: temporal variations in oil-collecting bee richness and a mutualistic network. Apidologie. 43:51–62.

Zar JH. 2010. Biostatistical analysis. 5th ed. Upper Saddle River (NJ): Imprenta Upper Saddle River, Prentice Hall.