



RESEARCH ARTICLE - BEES

Exploitation of Floral Resources and Niche Overlap within an Oil-collecting Bee Guild (Hymenoptera: Apidae) in a Neotropical Savannah

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Abstract

Oil bees exploit host plants for resources to feed the adults and offspring, as well as for the construction of their nests. The aim of the current study is to investigate how the species in this guild distribute their foraging effort, and the range in their niche overlap levels. Our hypothesis is that niche overlap levels are strongly affected by the exploitation of some key plants, those profitable and locally abundant oil-plants. The bees were sampled for six months, during their visits to the flowers in a savannah (Cerrado). These oil-bee species explored the floral resources provided by 13 plant species. The trophic niche of the most abundant species, *Centris aenea* Lepeletier, was relatively narrow, similarly to those of *Epicharis* species. Low overlap of trophic niches ($TrNO \leq 30\%$) was most commonly found. The distribution of bee visits to the host plants revealed redundancy in the floral resource exploitation. However, the foraging concentration levels in some key plants were different for distinct oil-bee species, and it contributed to the low overlap of niches between many pairs of species.

Introduction

Bee populations usually share food items of adults and larvae diets (Quiroz-Garcia et al., 2001; Müller et al., 2006; Roubik & Villanueva, 2009; Vilhena et al., 2012; Andena et al., 2012). They may also use the same nest-building materials, as well as the substrates for nesting (Frankie et al., 1993; Thiele, 2005; Aguiar et al., 2005; Martins et al., 2012), among other resources. Additionally, these populations also overlap each other to some level in the exploitation of these resources throughout the day and/or year (Santos et al., 2013). Therefore, bee populations face varying levels of overlap in several dimensions of their niches. Research on the dynamics of niches overlap is a promising approach for understanding the organization of bees communities, the local patterns of populations abundance, and its temporal fluctuations. However, the effects of trophic niches overlap among bee species have been little discussed (Wilms et al., 1996; Roubik & Villanueva, 2009).

Studies on niche overlap among bee species have mostly addressed the trophic dimension, while few have investigated the overlap in the temporal dimension of the niches (Santos et al., 2013; Barônio & Torezan-Silingardi, 2016). These studies have focused on a small portion of bee communities, the eusocial species (e.g. Camillo & Garófalo, 1989; Wilms et al., 1996; Wilms & Wieschers, 1997). In spite of non-eusocial bee species being the largest portion of the neotropical communities, they are rarely included in niches overlap studies (Steffan-Dewenter & Tschamtker, 2000; Aguiar, 2003b; Aguiar et al., 2013; Andena et al., 2012; Carvalho et al., 2013; Rabêlo et al. 2014).

The guild of oil-collecting bees is composed of species showing specialized morphology and behavior concerning floral oil gathering (Neff & Simpson, 1981; Vogel & Machado, 1991; Coccuci et al., 2000), which is a fundamental resource for the establishment of these bee populations in the habitat, since the floral oils are essential for nest construction, as well



as larval food in several species (Jesus & Garofalo, 2000; Vinson et al., 1996; Pereira et al., 1999; Aguiar & Garofalo, 2004). Therefore, progeny production by these bees strongly depends on the exploitation of oil-producing plants as well as of pollen-source plants.

The oil-bee/oil-plant ecological relationships are generally not species-specific (Sigrist & Sazima, 2004; Rosa & Ramalho, 2011; Mello et al., 2013). Thus, some of the oil-producing plants are visited by most oil-bee species in each habitat (Gaglianone, 2003; Mello et al., 2013). In the current study we investigated how the species belonging to a guild of oil-collecting bees distribute their foraging efforts in the floral resource sources – including oil-producing and non-oil-producing plants - and how the overlap levels of trophic and temporal niches vary. Since oil-collecting bees have a strong dependence on floral oils, we hypothesized that this guild has a structure that is driven by the bottom-up principle. Our hypothesis is that niche overlap levels are strongly affected by the exploitation of some key plants, those profitable and locally abundant oil-plants.

Materials and Methods

Study Area

The field work was carried out in an area located in Chapada Diamantina region, where a Long-term Ecological Research has been developed. The sampled vegetation is of Cerrado type, and it is located in Palmeiras municipality (12°25'S /41°29'W), Bahia State, Brazil. The mean annual temperature is 22° C and the annual rainfall ranges from 600 to 1,000 mm (Centro de Estatística e Informações, 1994).

Sampling

Three sampling sites 900-1,500m distant from each other were sampled in this area, and three transects (1,000 m length and 20 m width) were chosen in each site. Sampling was monthly carried out for three consecutive days, from October 2013 to March 2014 - period that includes the end of the dry season and all the rainy season, which began in November. A transect of each site was randomly selected for sampling every collection day. The daily sampling effort was of 8 hours (from 08:00 a.m. to 04:00 p.m.), thus totaling a sampling effort of 144 hours distributed in 18 sampling days. Bees were captured on the flowers using entomological nets, without choosing bee or plant species (adapted from Sakagami et al., 1967). Fertile botanical material was collected for exsiccates.

We collected data on the two locally most abundant oil-plants *Byrsonima sericea* and *Byrsonima cydoniifolia*. We used data from 30 individuals of *B. sericea* and *B. cydoniifolia* (10 individual plants of each species from each site) to determine the flower production period and to estimate their flowering intensity. Regarding each individual plant, a 25 x 25 cm “square box” (height ranging from 1.40 m to 1.70 m) was placed on the canopy and the inflorescences

found in the canopy volume delimited by the “square box” were counted. Flower buds and open flowers were counted in at least 10 inflorescences in order to calculate the mean number of flowers per inflorescence. The radius and height of each individual plant were measured to calculate the volume of the flowering canopy. These measurements were used to estimate the inflorescence density of each plant by multiplying the number of inflorescences by the flowering canopy volume/“square box” volume ratio. After estimating the inflorescence density per individual plant and obtaining the mean number of flowers per inflorescence, we estimated the amount of flowers monthly produced by each *Byrsonima* plant.

Data analysis

We used the Shannon diversity index ($H' = - \sum p_k \times \ln p_k$) (Shannon, 1948) to calculate the niche breadth of bee species, where p_k is the proportion of individuals of the bee species collected in the plant species “k” and, $\ln p_k$ is the neperian logarithm of p_k . We used the Schoener index ($NO = 1 - \frac{1}{2} \sum_k |p_{ik} - p_{hk}|$) (Schoener, 1968) to measure the niche overlap between each pair of oil-bee species, where p_{ik} and p_{hk} are the proportions of individuals of the bee species “i” and “h” collected in each species of plant (“k”) (to calculate the trophic niche overlap) or in each month (“k”) (to calculate the temporal niche overlap). This overlap index varies from 0 to 1.

Bee species represented by five or more individuals were selected to analyze the width and the overlap of trophic and temporal niches. This abundance threshold is lower than that used in previous studies (e.g. Aguiar, 2003b; Aguiar et al., 2013; Santos et al., 2013). However, it has already been adopted in other niche overlap analyses (e.g. Andena et al., 2012; Carvalho et al., 2013). The main reason for using this lower threshold lies on the fact that most oil-collecting bee species occur on flowers in low frequency in natural habitats (Aguiar 2003a; 2003b; Aguiar & Zanella, 2005; Andena et al., 2005; 2012; Santos et al., 2013; Silva et al., 2015). Consequently, oil-collecting bees are rarely included in niche analyses. Abundance influences the species ability to occupy the niches, and is influenced by the multiple dimensions of the niche, which regulate the size of the population (Begon et al., 2006). Thus, it is worth analyzing the niche of infrequent species to look for evidences of how the interactions among them and other species in the guild during resource exploitation may affect their local abundance.

Results

Twenty species were recorded in this guild of oil-collecting bees (Table 1). These bee species explored floral resources provided by 13 plant species. Among them, only three species were oil-producing plants (*B. sericea*, *B. cydoniifolia* and *Stigmaphyllon paralias*, Malpighiaceae). *B. sericea* and *Pityrocarpa moniliformis* (Fabaceae) were the most important food resources to these bees (Table 1). During the late dry

season and the early rainy season (Oct/ Nov), these bees explored food resources on few plant species (1 and 4) (Fig. 1). In this period, bee frequencies on flowers were lower than in the rainiest months (Table 1). Two *Byrsonima* species produced flowers during the rainy season, from December on (Fig. 2A, B), resulting in increased floral oil and pollen supply in the habitat, since these plants show high local abundance. A bee abundance peak was recorded in February, and it was strongly influenced by the high abundance of *Centris aenea* Lepeletier (Table 1).

These bees explored floral resources from 1 to 7 plant species. The two most abundant species of *Centris* (*C. aenea* and *C. fuscata*) differed sharply in their trophic niche width. *Centris fuscata* Lepeletier showed the widest trophic niche ($H'1=1.58$). In contrast, *C. aenea*, the most abundant species, had a trophic niche ($H'1 = 0.60$) narrower than *C. fuscata* and other species of *Centris* (Table 1). Although *C. aenea* explored more

plant species than the other oil-collecting bees, its preferential foraging on *B. sericea* strongly influenced the trophic niche width decrease. This trend to a narrow trophic niche became even more pronounced when this species was abundant on flowers ($H'1_{\text{February}} = 0.13$ in; $H'1_{\text{March}} = 0.32$). The very different levels of foraging on *B. sericea* flowers by the two most abundant *Epicharis* species also resulted in a strong difference in the width of their trophic niches, with moderate overlap (Table 1).

C. aenea, *Epicharis analis* Lepeletier and *C. fuscata* showed the longest activity period (Table 1). Among the most abundant species, *C. fuscata* and *E. analis* showed the highest temporal niches width ($H'2 = 1.27$; $H'2 = 1.07$, respectively) (Table 1). Although *C. aenea* showed the longest activity period among the bees in this guild, its temporal niche was not so wide ($H'2=0.51$), because the H' index suffered strong influence from a peak of abundance concentrated in February (Table 1).

Table 1. Abundance of oil-collecting bee species (n), trophic niche width ($H'1$) (Shannon index), temporal niche width ($H'2$), and plant species visited for floral resources in a savannah area in the Chapada Diamantina, Brazil. Number of flower-visiting bees captured in each plant species in brackets. * Bee species collected in a single plant or month. Bv: *Bowdichia virgilioides*, Cc: *Centrosema coriaceum*, Pm: *Periandra mediterranea*, Pi: *Pityrocarpa moniliformis* (Fabaceae)/ Bc: *Byrsonima cydoniifolia*, Bs: *Byrsonima sericea*, Sp: *Stigmaphyllon paralias* (Malpighiaceae)/ Ep: *Eugenia cf. puniceifolia* (Myrtaceae), My: Myrtaceae sp.1/ Pe: *Passiflora edulis* (Passifloraceae)/ Sf: *Serjania faeolata* (Sapindaceae)/ Sa: *Simarouba amara* (Simaroubaceae)/ Sc: *Stachytarpheta crassifolia* (Verbenaceae).

Bee species	n	H'1	Plants visited	H'2	Oct	Nov	Dec	Jan	Feb	Mar
Centridini										
<i>Centris aenea</i> Lepeletier	94	0.60	Bv (1)/Pe (1)/Bc (1)/Bs (80)/Ep(1)/ Pi (9)/ Sa (1)	0.51	1	1	1	-	81	10
<i>Centris moerens</i> Perty	3	1.09	Bs (1)/Pe (1)/Sc (1)	0.63	1	2	-	-	-	-
<i>Centris sponsa</i> Smith	5	1.33	Pe (2)/Bs (1)/ Pi (1)/Sa (1)	0.10	-	1	-	-	3	1
<i>Centris caxienseis</i> Ducke	6	1.32	Bc (2)/ Bs (1)/ My (1)/Sp (2)	1.01	-	-	2	3	2	-
<i>Centris leprieuri</i> Spinola	2	0.69	Pe (1)/Bs (1)	*	-	-	-	-	2	-
<i>Centris nitens</i> Lepeletier	1	*	Bs (1)	*	-	-	-	-	1	-
<i>Centris fuscata</i> Lepeletier	9	1.58	Bv (2)/Pe (1)/Sf (2)/Cc (2)/ Pi (2)	1.27	4	-	2	-	1	2
<i>Centris</i> sp.1	4	0.56	Bc (1)/Bs (3)	0.56	-	-	1	-	3	-
<i>Centris</i> sp.3	1	*	Bs (1)	*	-	-	-	-	1	-
<i>Centris</i> sp. 6	1	*	Pi (1)	*	-	-	-	-	-	1
<i>Epicharis analis</i> Lepeletier	24	0.64	Bs (9)/Pi (15)	1.07	-	-	1	4	5	14
<i>Epicharis bicolor</i> Smith	33	0.36	Bs (30)/Pi (1)/ Sp (2)	0.80	-	-	-	18	14	1
<i>Epicharis cockerelli</i> Friese	4	*	Bs (4)	1.03	-	-	1	1	2	-
Tapinotaspidini										
<i>Lophopedia nigrispinis</i> Vachal	2	0.69	Sf (1)/ Pi (1)	0.69	-	-	1	-	-	1
<i>Monoeca</i> affs. <i>mourei</i> Aguiar	1	*	Sp (1)	*	-	-	-	1	-	-
<i>Tropidopedia nigrocarinata</i> Aguiar & Melo	9	1.14	Sf (5)/ Bs (2)/ Pm (1)/ Sp (1)	0.32	-	-	8	1	-	-
<i>Xanthopedia</i> sp.1	5	0.50	Sf (1)/ Bs (4)	0.50	-	-	1	-	4	-
<i>Urbanapsis diamantina</i> Aguiar & Melo	7	0.79	Bs (4)/ Sf (1)/ Sp(2)	0.79	-	-	1	5	-	1
Tetrapediini										
<i>Tetrapedia amplatarsis</i> Friese	3	*	Bs (3)	*	-	-	-	3	-	-
<i>Tetrapedia diversipes</i> Klug	3	0.63	Pm (1)/ Sf (2)	*	3	-	-	-	-	-
Total	217				9	4	19	36	119	31

were affected mainly by the intensity of exploitation of *B. sericea*. This oil-plant is locally abundant and produces a high amount of floral oil (Aguiar et al, accepted for publication on Sociobiology). Additionally, it also supplies many bee species with pollen (Teixeira & Machado, 2000). Thus, *B. sericea* is a key resource to the maintenance of oil bee populations in this savannah.

Several oil-collecting bee showed relatively narrow trophic niches ($H' < 0.8$), compared to other bee species in other phytophysiognomies (Aguiar, 2003b; Aguiar et al., 2013). Similarly, narrow trophic niches were recorded for *Centris* and *Epicharis* species ($H' < 0.9$) in another Brazilian Cerrado site, where these species also used a small set of host plants, and mainly explored *Byrsonima intermedia*, another Malpighiaceae oil-plant (Andena et al., 2012). On the other hand, it is known that some *Centris* and *Epicharis* species use many plant species in their diet (Gaglianone, 2003; Aguiar et al., 2003; Vilhena et al., 2012; Santos et al., 2013). It means that some of them can replace the sources of floral resources in different habitats.

The number of plant species exploited by *C. fuscata* and *C. aenea* suggested that these bee species probably exploit a diverse set of food sources. This finding agrees with previous records of the *C. fuscata* and *C. aenea* host plants (> 30 species), which were compiled in a number of areas covered by xerophilous vegetation (Caatinga) (Aguiar et al., 2003). In the studied savannah, *C. aenea* showed a trophic niche narrower than that recorded in the xerophilous vegetation (Caatinga), where its niche width was approximately two times wider ($H' = 1.59$) (Aguiar & Santos, 2007). Previous studies have indicated that this species exploits many host plants (Aguiar et al., 2003; Aguiar & Gaglianone, 2003), but we found that females can show floral fidelity to abundant resources, such as *Byrsonima*. This *C. aenea* population seems to be particularly favored in periods of high availability of the floral resources provided by *B. sericea* and it shows high dominance in the guild of oil-collecting bees. This bee species may form large nesting aggregations in places showing high density of *Byrsonima* trees (Aguiar & Gaglianone, 2003), and this strategy leads to reduction in the costs and time required to collect resources for brood cell building and provisioning.

C. aenea and *C. fuscata* showed very low trophic niche overlap, mainly due to the non-use of the host plant *B. sericea* by *C. fuscata*. The overlap was also low in the time axis, because the highest abundance of each occurred in different months. Thus, we found a niche-separation trend in both analyzed axes (diet and time). Large differences in these two populations size may influence the distribution of individuals in the host plants. Consequently, these differences may affect the observed overlap, since *C. aenea* was approximately 10 times more abundant than *C. fuscata*.

Apparently, neither the differences between body size (robust vs. small bees) nor differences in abundance explain the overlap levels in the trophic niches. These findings suggest that, in the studied community, the foraging effort allocation

of each oil-bee species to explore *B. sericea* resources is a more important factor to determine the niche overlap levels than the phylogenetic proximity among the species. Similarly, Andena et al. (2012) found that bee species of the same genus, including *Centris*, use different food resources, thus they show trophic niches more similar to those of species from other genera than to those of congeneric species.

Although bee visits to the host plants revealed redundancy in the exploitation of floral resources, the foraging concentration on some key plants were different among oil-bee species, that contributed to the low niche overlap in many of the comparisons made between each set of two species (each pair of species). In addition, interspecific differences in the length of nesting periods and/or in the number of generations per breeding season may have some effect on the lowering of both temporal and trophic niche overlap, since individuals of different generations can forage on different host plants blooming at different periods throughout the nesting season of each bee species.

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