



RESEARCH ARTICLE - BEES

Nesting Biology of Sympatric Species of Megachilidae Bees in a Conservation Area in Brazilian Atlantic Forest

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Abstract

Megachilidae bees are important pollinators in the Neotropical region, however information on the ecology and behavior of these species is still scarce. The objective of this study was to analyze the nesting biology of sympatric species in the União Biological Reserve, a remnant of Atlantic Forest in the southeastern Brazil. Our results indicated the occurrence of 17 species, representing significant richness compared to other areas in the Atlantic Forest. Five sympatric species built $\frac{3}{4}$ of all nests found and the architecture of their nests was studied including, for the first time, nests of a species of *Megachile* (*Ptilosarus*). The use of petals or leaf fragments in the construction of the nests was observed for species of *Megachile* (*Chrysosarus*), confirming previous data. The nesting activity period in the trap-nests occurred mainly in the rainy season, with different peaks among the species. The results indicate that the distinctive characteristics of the species, such as the type of material used in the nests, the dimensions of cavities, and the asynchronous nesting period, could be important for the niche differentiation of these sympatric species, allowing the maintenance and the survival of the most abundant Megachilidae populations in the area.

Introduction

Megachilidae bees are distributed around the world with more than 4000 species described in 76 genera (Michener, 2000). The New World species occurred from Alaska to southern Chile and Argentina (Raw, 2004) and most of them belong to the genus *Megachile*, the leafcutter bees. One factor that probably contributes to the high species richness of this family is the use of nest building materials not explored by other groups of bees (Litman et al., 2011). The use of leaf or petal fragments in the nest structure of Megachilidae extends the interactions of these bees with plants beyond food sources. Bees of different taxonomic groups use distinct types of material in the nest; species of the tribe Megachilini characteristically use elongated pieces of leaves on the walls

of the nests and leaf discs in the partitions between the cells and in the cell caps; in a different way, Anthidiini bees use plant fibers or resin as the main component in nest construction (Morato, 2001; Alves-dos-Santos, 2004; Camarotti-de-Lima & Martins, 2005; Litman et al., 2011).

Megachilidae females can nest in different places including preexisting cavities in plants or other substrates. This characteristic of life history allows the use of trap-nests as a sampling methodology, since natural nests are difficult to find (Roubik, 1989; Morato & Martins, 2006). The use of trap-nests also makes it possible to obtain more accurate information about nesting biology and the architecture and also about the building materials used in the nests (Garófalo, 2000).

For species distributed in Brazil, some studies deal with the nesting biology of Megachilidae (for example Laroça,



1971; Laroca et al., 1987; Martins & Almeida, 1994; Almeida et al. 1997; Morato, 2001; Morato, 2003; Alves-dos-Santos, 2004; Zillikens & Steiner, 2004; Camarotti-de-Lima & Martins, 2005; Cardoso & Silveira, 2012; Teixeira et al., 2011; Marques & Gaglianone, 2013; Rocha-Filho & Garófalo, 2015; Sabino & Antonini, 2017), in different environments as distinct as forests and open or urban areas. None of them, however, analyzed the factors that would lead to the co-occurrence of species with similar needs of resources.

To understand the ecological processes acting in the co-occurrence of these species, studies are required that address preferences for nesting sites, seasonality, architecture patterns, and the use of floral resources (Blochtein & Marques, 2003; Kambli et al., 2017). These studies will be important to understand the interactions among the bees, including competition or facilitation and this information could help in the conservation of forest fragments, considering the great potential of these bees as pollinators.

The present study aims to answer the following questions: does an ombrophilous forest in the Brazilian Atlantic Forest have expressive richness of Megachilidae species co-occurring? Which factors may be allowing the co-occurrence of these sympatric species?

Material and Methods

Study area

The study was developed in a fragment of dense ombrophilous rain forest in the Atlantic Forest of Brazil, which is an area of protection recently expanded to 7767.80 ha (Reserva Biológica União RJ, 22°25'35" S; 42°2'4" W). The vegetation comprises stretches of lowland forest (up to 50 m altitude) and submontane forest, with regeneration areas in places formerly occupied by eucalyptus plantations (*Corymbia citriodora* (Hook) K.D. Hill & L.A.S. Johnson). The climate is predominantly humid tropical with an average annual temperature of 24 °C, precipitation of approximately 2200 mm/year. In the region, the wet season occurs from October to March and dry season from April to September (MMA/ICMBio, 2008). The vegetation comprises stretches of lowland forest (up to 50 m altitude) and submontane forest, with regeneration areas. The climate is predominantly humid tropical with an average annual temperature of 24 °C and precipitation of approximately 2200 mm/year (MMA/ICMBio, 2008).

Sampling procedure

The bees were attracted to nest in trap-nests made of hollow bamboo canes inserted in P.E.T. bottles attached to wooden stakes 1.5 m from the ground and tubes of black cardboard inserted into wooden plates at the same height in tree branches. Approximately 1440 trap-nests were offered simultaneously and monthly (120 in each sampling point), with diameters ranging from 6 to 20 mm and assorted lengths, from 60 to 215 mm (bamboo canes) and from 50 to 91 mm

(cardboard tubes) distributed equally among the points. Trap-nests were installed at 12 sampling points, located at least 500 m apart between two closest points, and monitored from March 2008 to October 2010. At four of these points, another sampling period was carried out, from March 2012 to March 2013 using 480 trap-nests per month (120 in each point). The trap-nests were monitored monthly, and when the bees finished the activity, trap-nests were replaced by others of the same dimensions (diameter and length), always maintaining the same number of cavities in the sampling points.

Data analysis

Nests of the most abundant species throughout the study periods were analyzed in the laboratory to describe the architecture and material of construction. Characterization of the nest architecture was performed through the types, dimensions, and forms of the elements that constitute the nests. Data obtained were compared with other species of *Megachile* (Zilikens & Steiner, 2004; Aguiar et al., 2005; Torretta et al., 2012; Landry et al., 2014; Torretta et al., 2014; Rocha-Filho & Garófalo, 2015).

The difference between diameters of the trap-nests used by bees of different species was tested by non-parametric Kruskal-Wallis and Tukey test a posteriori (Past 3.20, Hammer et al., 2001). In a similar way, body size of the species was compared using the intertegular distance between the inner borders of the bee tegulae.

The sex ratio was determined by calculating the proportion of the number of males in relation to the number of females considering the total of emergent during the study and differences of the expected (1:1) was tested through X² test using program R (R Development Core Team, 2017).

Results

Richness of bees in the study area

Bees of seventeen species of Megachilidae nested in trap-nests located in dense ombrophilous forest and regenerated areas (Table 1), corresponding to 17.7% of the bee nests found in the area. The five most abundant species (*Megachile (Chrysosarus) pseudanthidioides* Moure, *Megachile (Chrysosarus) sp.*, *Carloticola paraguayensis* (Schrottky), *Megachile (Ptilosarus) sp. 1*, and *Megachile (Pseudocentron) nudiventris* Smith) represented 74.9% of the nests (Table 1).

Period of nesting activity

The nesting occurred mainly in the rainy season, with peaks of activity not overlapped among the most abundant species (Fig 1). *C. paraguayensis* built nests almost exclusively in the rainy season, showing greater activity in February, but they also built one nest in the first and last month of dry season. *Megachile (Chrysosarus) sp.* built nests exclusively in the rainy season, showing greater activity in December-January.

Table 1. Number of nests of Megachilidae constructed in trap-nests in a remnant of the Atlantic Forest in Brazil (União Biological Reserve, RJ, Brazil). The five most abundant species are highlighted. ***cleptoparasites**; **number of nests where respective cleptoparasites emerged.

Species of Megachilidae	Number of Nests	% Nests
ANTHIDIINI		
<i>Carloticola paraguayensis</i> (Schrottky)	14	11.38%
<i>Hoplostelis nigrifula</i> (Friese)*	02**	
<i>Hypanthidium divaricatum</i> (Smith)	02	1.62%
<i>Hypanthidium foveolatum</i> (Alfken)	01	0.81%
<i>Sarantidium marginata</i> Moure & Urban	04	3.30%
MEGACHILINI		
<i>Megachile (Austromegachile) facialis</i> Vachal	01	0.81%
<i>Megachile (Chryosarus) pseudanthidioides</i> Moure	28	22.8%
<i>Megachile (Chryosarus) sp.</i>	20	16.3%
<i>Megachile (Melanosarus) brasiliensis</i> Dalla Torre	03	2.40%
<i>Megachile (Melanosarus) nigripennis</i> Spinola	01	0.81%
<i>Megachile (Moureapis) cf. benigna</i> Mitchell	01	0.81%
<i>Megachile (Moureapis) pleuralis</i> Vachal	02	1.62%
<i>Megachile (Moureapis) pseudopleuralis</i> Schrottky	02	1.62%
<i>Megachile (Pseudocentron) inscita</i> Mitchell	03	2.40%
<i>Megachile (Pseudocentron) nudiventris</i> Smith	14	11.38%
<i>Megachile (Pseudocentron) cf. subcingulata</i> Moure	02	1.62%
<i>Megachile (Ptilosarus) sp. 1</i>	16	13.00%
<i>Megachile (Ptilosarus) sp. 2</i>	09	7.33%
<i>Coelioxys spp*</i>	13**	
Total nests	123	
Species richness (except cleptoparasites)	17	

Megachile (Ptilosarus) sp. 1 presented two periods of activity in the year, with greater peak in March (beginning of the rainy season). *M. nudiventris* constructed nests throughout the year with small peaks in December, May and August. *M. pseudanthidioides* also built nests throughout the year, except in June and July, with periods of greater activity in October–November, periods corresponding to the beginning of the rainy season in the region (Fig 1).

Nest architecture, nest substrate and materials of construction

Among the five most abundant species, *C. paraguayensis* (Anthidiini) differed from the others through the use of resin mixed with sand or clay in the construction of the nests, while the *Megachile* species used leaves and/or petals with or without clay.

The nests of *C. paraguayensis* were constructed in the cardboard trap-nests, and formed a compact clay (n = 10) or sandy (n = 2) tube both bound together with clay (Table 2), and the cells separated by buffers of the same material. The bottom

of the cell was rounded and the wall smooth and aligned with the inner wall of the trap-nest. The female deposited clay and resin at the bottom of the trap-nest before constructing the first cell. The final cell, closest to the opening of the trap-nest, was considered as a vestibular cell, since it contained neither food nor eggs, and was filled with floral buds in 10 of the 12 nests analyzed. These buds were identified as belonging to one or more species of Asteraceae and Malpighiaceae, and a single type filled the vestibular cell of each nest.

The two species of the subgenus *M. (Chryosarus)* used both bamboo and cardboard trap-nests. In the analyzed nests of *M. (Chryosarus) pseudanthidioides* (n = 20) and *M. (Chryosarus) sp.* (n = 19), the cells were constructed externally with leaf fragments and internally with agglutinated petals in a single linear series. These leaf materials were firmly attached to the clay tubes of the nests and were not attached to the trap-nest wall. The petals were deposited so as to form the inner wall of the cells. The cells started at the bottom of the trap-nest without any material deposited prior to construction of the first cell. In the bamboo canes cells of *M. (Chryosarus) spp* never filled completely the trap-nest, but there was a space between the final cell and the opening of the trap-nest.

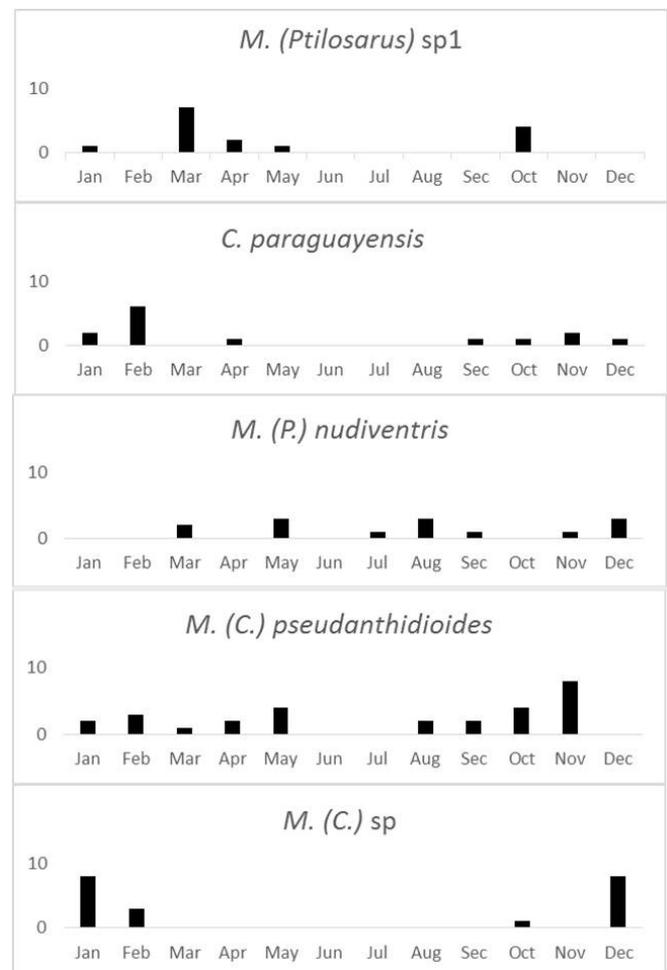


Fig 1. Nesting activity of Megachilidae bees (number of nests constructed in trap-nests) in the União Biological Reserve, RJ, Brazil, from Mar, 2008 to Oct, 210 and from Mar, 2012 to Mar, 2013.

Circular leaf discs formed the closure plugs and the cell partitions and elongated cuts of these materials were on the walls and bases of the cells, resulting in an approximately conical shape of the cell.

M. (Pseudocentron) nudiventris constructed the ten nests analyzed exclusively with leaf fragments, always in bamboo trap-nests. This species also constructed a linear series of cells, and in the majority of nests the female used all the available space of the trap-nest, and the nests length varied as indicated in Table 2. All nests began with the first cell constructed directly on the bottom of the trap-nest through a tube of loosely arranged leaves. The side wall of the cells was formed by elongated pieces of leaf with the base folded inward, aiding closure of the base of the cell; the

partitions consisted of circular discs of leaves. In three nests it was possible to observe the presence of leaves with different patterns of veins, parallel nerved and venation netted, and with different patterns of hairiness, indicating at least two distinct plant species as sources of leaf material for the same nest.

M. (Ptilosarus) sp. 1 used only cardboard trap-nests, and constructed nests with a linear array of cells and a thin layer of clay laterally lining the cells, externally. Cells were constructed with leaf fragments, which were firmly attached to the clay on the outer face. In all nests the construction started at the bottom of the trap-nest. The leaf fragments of the base were disc shaped and on the wall the format was elongated. A single nest presented ring-shaped clay deposited outside the base of each cell on the leaf discs, holding them firmly attached.

Table 2. Most abundant Megachilidae species in União Biological Reserve, RJ, Brazil. Intertegular distance was used to compare body size among bees (M=male and F=female). Evaluated attribute of nests: type (C=cardboard; B=bamboo cane) and diameter of occupied trap-nest, length of constructed nest, number of cells constructed per nest, and cell length (mean \pm standard deviation). All measurements in mm.

Bee species	Intertegular distance M/F	Trap-nest type	Trap-nest diameter	Nest length	Cells per nest	Cell length
<i>Carlaticola paraguayensis</i>	3.15 \pm 0.2/ 3.16 \pm 0.15	C (100%)	6-10 (8 \pm 1.0) n=12	57.9 to 90.1 (73.2 \pm 13.3) n=12	3 to 6 (4.5 \pm 1.0)	8.2 to 23.1 (12.8 \pm 4.2) n=26
<i>Megachile (Chrysosarus) pseudanthidioides</i>	3.17 \pm 0.2/ 3.46 \pm 0.2	C (75%) B (25%)	6-14.2 (8.5 \pm 3.0) n=17	16.1 to 111.6 (70.7 \pm 43.5) n=17	1 to 9 (4.5 \pm 1.7)	12 to 21.4 (15.2 \pm 2) n=62
<i>Megachile (Chrysosarus) sp.</i>	3 \pm 0.1/ 3.51 \pm 0.1	C (60%) B (40%)	8-18.1 (10.8 \pm 3.6) n=19	32.5 to 153.0 (85.1 \pm 39.6) n=19	1 to 10 (4.9 \pm 2.2)	11.5 to 20.6 (15 \pm 1.6) n=89
<i>Megachile (Pseudocentron) nudiventris</i>	3.37 \pm 0.1/ 3.47 \pm 0.2	B (100%)	10.3-16.8 (13.5 \pm 2.2) n=10	62.2 to 214.4 (130.5 \pm 46.5) n=10	4 to 9 (5.7 \pm 1.6)	16.8 to 29.8 (21.7 \pm 3.7) n=33
<i>Megachile (Ptilosarus) sp. 1</i>	2.2 \pm 0.15/ 2.46 \pm 0.15	C (100%)	6 (6 \pm 0.0) n=14	15.4 to 71.1 (53.3 \pm 17.4) n=14	1 to 8 (4.5 \pm 1.8)	7 to 15.3 (10 \pm 1.4) n=49

Trap-nest diameter preferences

The internal dimensions of the occupied trap nests are shown in Table 2. *C. paraguayensis* used 8 mm cavities, on average, while *M. pseudanthidioides* occupied a wide range of diameters, but mainly 6 to 7.9 mm tubes (53% of nests were found in the 6 mm cavities). *M. (Chrysosarus) sp.* used a larger proportion of larger cavities too (from 8 to 11.9 mm), being the only species in the group to occupy cavities larger than 18 mm in diameter. *M. (Pseudocentron) nudiventris* used cavities larger than 10 mm (Table 2, Fig 2) and *M. (Ptilosarus) sp. 1* used only the smallest cavities (of 6 mm).

Body size and sex ratio

The body sizes of the bees inferred by the intertegular distance showed that *M. (Ptilosarus) sp1* was the smallest species and *M. (Chrysosarus) sp* the largest one. Females were,

in general, larger than males (Table 2) and this difference was statistically significant for the two species of *M. (Chrysosarus)* (*M. sp.*: $Q = 8$, $p < 0.05$, and *M. pseudanthidioides*: $Q = 5.5$, $p < 0.05$) and for *M. (Ptilosarus) sp. 1* ($Q = 5.6$, $p < 0.05$). Males of *M. (Ptilosarus) sp. 1* were statistically smaller than the males of the other compared species. Females of this species and of *C. paraguayensis* showed the smallest mean sizes, which differed from the other three species. The species with smaller average size of the females occupied the smaller cavities of trap-nests, whereas *M. (Pseudocentron) nudiventris*, *M. (Chrysosarus) pseudanthidioides*, and *M. (Chrysosarus) sp.* occupied the largest cavities.

All species, with the exception of *M. (Chrysosarus) sp.*, produced more females than males and sex ratios obtained for *M. (Chrysosarus) pseudanthidioides* and *M. (Ptilosarus) sp.1* differed from the expected 1:1 (18♂:34♀, $\chi^2 = 4.92$ $p = 0.02$ and 12♂:27♀, $\chi^2 = 5.77$ $p = 0.01$, respectively).

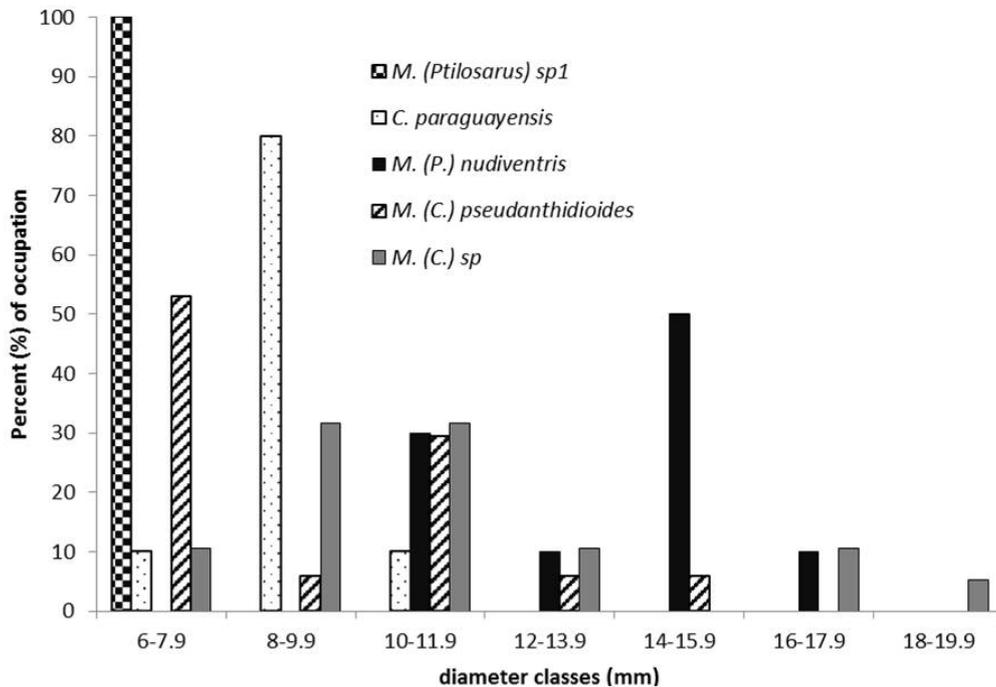


Fig 2. Percent of occupation of the trap-nests used by Megachilidae bees in the ReBio União, presented in diameter classes (mm).

Discussion

Megachilidae species sampled in the Atlantic Forest fragment studied has important representation in the community of bees that nest in cavities when compared to other communities sampled in Brazil (Garófalo et al., 2004), and more specifically in Atlantic Forest (Aguiar et al., 2005; Steiner et al., 2006; Rocha-Filho et al., 2017). The present study indicates that the União Biological Reserve is an important repository of Megachilidae bees, an important group of pollinators in the Neotropical region. This fact is possibly related to some factors such as the large extent of the forest fragment, environmental heterogeneity and well-preserved areas at União Biological Reserve. The great relevance of this forest fragment has been also indicated for orchid bees (Ramalho et al., 2009), vertebrates (Araújo et al., 2008) and plant species (Evaristo et al., 2011).

Five species constructed 3/4 of all Megachilidae nests sampled during the study. Analysis of the nest architecture of these five species showed three main types of materials used: resin mixed with clay or sand, exclusively leaf fragments, or leaf fragments and petals with or without clay.

C. paraguayensis was the only studied species using resin as construction material. This behavior is widely known for Anthidiini (Roubik, 1989; Muller, 1996; Michener, 2000; Camarotti-de-Lima & Martins, 2005), and the antimicrobial and repellent potential of resins is discussed as an advantage against predators or parasites (Ghisalberti, 1979), despite the high energy cost to locate and handle this resource. The limitation of resin availability may be a preponderant factor in the distribution of *C. paraguayensis* nests. The study of the

larval content of the cells (Mello & Gaglianone, unpublished data) indicated the presence of pollen grains of *Dalechampia* sp. (Euphorbiaceae), a species that presents floral resin, a rare feature among angiosperms and essential for these bees. This plant was observed as the most important pollen source for another bee, *Tetrapedia diversipes* Klug, in the same area (Menezes et al., 2012). Further studies are needed to understand the spatial and temporal distribution of nests and their relationship with pollen and resin supplying plants in different environments.

Unlike the use of resins, plant fragments are the most common construction material used by *Megachile* species, the so-called leafcutter bees (Roubik, 1989; Raw, 2004). The use of leaf fragments, exclusively or adhered to the clay, as observed for the species of *Megachile* (*Pseudocentron*) and *Megachile* (*Ptilosarus*), respectively, in the present study, constitutes the behavior most widely performed by species of the genus.

The use of petals, third type of the material used in the nest construction, was observed in this study only for species of *Megachile* (*Chrysosarus*), confirming previous studies with other species of the same subgenus (Zillikens & Steiner, 2004; Laroca et al., 1992; Torreta et al., 2014; Rocha-Filho & Garófalo, 2015). The use of petals for the construction of rearing cells, substituting or together with leaves, was discussed by other authors as being related to the oral apparatus of these bees. Species of *Megachile* (*Chrysosarus*) differ morphologically from species of other subgenus through the complete lack of cutting edges between the mandibular teeth (Mitchell, 1943), which would be related to cutting more delicate material such as finer petals or leaves. The choice

between these different types of materials is probably related to availability in the environment and may vary with the plant phenology in the vicinity of the nests.

The agglutination of vegetal fragments with clay resulted in the formation of a tube of firm walls in the studied nests of *M. (Ptilosarus)* and *Megachile (Chrysosarus)*. This architecture allows a more constant microclimate inside the nest, helping to maintain a favorable environment for the development of the immature bees. Studies carried out for other species of the genus (Zillikens & Steiner, 2004; Torretta et al., 2014) also verified the use of clay among the plant fragments structuring the nest.

Despite this similarity in the agglutination material of the plant fragments, *Megachile (Ptilosarus)* sp. 1 nests analyzed in this study were composed only of leaves, unlike the species of *Megachile (Chrysosarus)*. To our knowledge, this is the first description of the architecture of nests of a species of *Ptilosarus*.

In addition to the building material, other characteristics of nest architecture are very important to understand the ecological role of these bees and their interactions with other bees that also use cavities and with their natural enemies. One of these characteristics can be the linear series of cells, which is related to the disposition of the cavity offered. As the study in natural cavities is hampered by the unpredictability of finding nests and by the camouflage, it is not known how flexible this characteristic is. However, the construction of vestibular cells, commonly observed in this linear structure, would be a strategy against parasite attack. In this case, an

intruder entering the nest would initially reach the vestibular cell and, failing to find a larva or larval food, would possibly abandon it (Morato, 2001; Alves-dos-Santos, 2004). The behavior reported in this paper for *C. paraguayensis*, filling the vestibular cells with floral buds, is apparently unheard of for Megachilidae. This behavior potentially reduces parasitism, hindering the entry of the parasite into the nest or resulting in oviposition in an inappropriate place. Filling the vestibular cell would lead the parasite to mistakenly oviposit on the buds, through the operculum of the cell, keeping the innermost cells safe. This interpretation however needs to be tested. In the study area, the use of floral buds was facilitated by the location of the *C. paraguayensis* nests in open areas, at the edge of the forest, where there are abundant herbs and climbers, with small flowers, flowering all year round and only a few meters from the trap-nests. Other studies at sites with different conditions will allow analysis of whether there are relations between the availability of this resource and the abundance of the nests.

The description of the internal dimensions of the nests of the studied species supplied new information, such as that related to the nests of *C. paraguayensis*, a rarely studied species and for which no descriptions of nests were found in the literature (a compilation of information obtained in the literature for the study taxa is presented in Table 3). The low number of cells seems to be related to the large vestibular cell filled with floral buds, associated with the use of smaller nests, always with cardboard, which decreases the space for the construction of a larger number of rearing cells.

Table 3. Materials used in the construction of Megachilidae nests in União Biological Reserve. The numbers represent the frequency (%) of nests with the respective material; X represents the presence of the material but no information about frequency of use.

Bee species	Reference	Construction materials (% of studied nests)						Number of nests studied
		Leaves	Petals	Clay	Sand	Resin	Others	
<i>Carloticola paraguayensis</i> (Schrottky)	This study			83.4	16.6	100		12
<i>Megachile (Chrysosarus) catamarcensis</i> Schrottky	Torretta et al. 2014	X	X	100				29
<i>Megachile (Chrysosarus) guaranitica</i> Schrottky	Rocha-Filho & Garófalo 2016	100		100				26
<i>Megachile (Chrysosarus) pseudanthidioides</i> Moure	This study	100	100	100				17
<i>Megachile (Chrysosarus) pseudanthidioides</i> Moure	Zilikens & Steiner 2004	100	100	100				14
<i>Megachile (Chrysosarus) sp.</i>	This study	100	100	100				19
<i>Megachile (Pseudocentron) alleni</i> Mitchell	Landry et al. 2014	100			100		3.8	52
<i>Megachile (Pseudocentron) gomphrenoides</i> Vachal	Torretta et al. 2012	100						19
<i>Megachile (Pseudocentron) inscita</i> Mitchell	Aguiar et al. 2005	100						11
<i>Megachile (Pseudocentron) nudiventris</i> Smith	This study	100						10
<i>Megachile (Ptilosarus) sp.</i>	This study	100		100				14

Our data showed that there is overlap in the period of nesting activity of the most abundant sympatric species in Rebio União. However, species activity peaks are not coincident. Among the species that use petals in cell construction, *M. pseudanthidioides* has a much longer nesting period and presents one of the peaks at the end of the rainy season (March), when *M. (Chrysosarus)* sp is not active. Allied to this temporal distinction in nesting activity, the floristic composition of the petal and leaf sources used in the nests of these two species is probably distinct given the high plant diversity and phenological patterns of the plants in the area (Evaristo et al., 2011).

In addition, the two species of *M. (Chrysosarus)* occupy a greater proportion of cavities of different diameters, associated with significantly different body sizes. These characteristics result in non-overlapping ecological niches, a strategy that avoids competition between sympatric species that are closely related and share similar biological characteristics. The species that occupied mainly or exclusively the smallest cavity diameters, *M. pseudanthidioides* and *M. (Ptilosarus)* sp. 1, also overlapped much of the activity period. However, the use of petals in nests of *M. pseudanthidioides* distinguishes the two species in relation to building materials and raises questions regarding the source of possibly distinct leaf fragments related to the different jaw forms observed in the two species. Identification of sources of foliar resources for sympatric species in future studies would be of great relevance to clarify this issue.

Among the species that used the largest cavities, *M. (Pseudocentron) nudiventris* stands out for occupying cavities above 14 mm in 60% of the nests studied. Another distinctive characteristic of this species is the non-use of any binder material between the plant fragments on the cell walls. This species presents activity during most of the year, but with peaks not coincident with any other abundant species in the trap-nests, being the only species to nest in July, peak of the dry season in the region and the lowest temperatures. This fact suggests availability of resources throughout the year in the area, allowing the co-occurrence of different species of the Megachilidae.

M. nudiventris and *M. (Chrysosarus)* sp. are the largest species in the present study. Larger-sized females may have a competitive advantage over smaller species in relation to floral resources, as they could collect a larger volume of nectar and pollen to supply larger cells, in turn generating larger individuals (Klostermeyer, et al., 1973; Pyke, 1978). These species also produced nests with a higher number of cells, in comparison with the other abundant species in the area. Evaluation of the floristic composition used as floral resources by these species could elucidate whether they present greater competitiveness related to the greater body size and greater productivity.

The results indicate that the distinctive characteristics of the species, such as the type of material used in the nests,

dimensions of the chosen cavities, and periods of non-overlapping nesting activity, are important for delimitation of the niches of these sympatric species, enabling maintenance of their populations as the most abundant in the area.

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