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Nesting biology of two species of *Megachile* (*Moureapis*) (Hymenoptera: Megachilidae) in a semideciduous forest reserve in southeastern Brazil

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Abstract – Nests of *Megachile* (*Moureapis*) *benigna* and *Megachile* (*Moureapis*) *maculata* were obtained during a 12-month trap-nesting program in a semideciduous forest reserve in southeastern Brazil. Trap nests were bamboo culms wider than those usually used in trap-nesting studies and it is suggested that species of *Moureapis* may prefer to nest in wide cavities. Nest construction was concentrated in the warm rainy season, but *M. benigna* had a secondary peak of nesting activity in the mid dry season, suggesting it is a bivoltine species. No species occupied the entire length of trap nests, but several linear series of cells were frequently packed inside a single culm. Nests of *M. benigna* were parasitized by one unidentified species of *Coelioxys*. Unidentified chalcidoid wasps emerged from some nests and phorid flies emerged from another one. In both cases, the developing host bees were killed. An unidentified conopid fly emerged from an adult female *M. maculata* found dead inside an incomplete nest.

Atlantic forest / wild bees / bionomy / nest materials / trap nests

1. INTRODUCTION

Species of *Megachile* (Megachilidae) occur practically all over the world and are widespread in Brazil where the genus is represented by 161 species (Silveira et al. 2002). Females of most species in the genus use leaf pieces (sometimes flower petals) to build their nests (e.g., Michener 1953, 2007; Krombein 1967) in pre-existing cavities, such as slits in rocks or burrows in the ground, dead wood, or man-made objects (Michener 2007). However, Eickwort et al. (1981) suggested that excavation of nests in the soil by female *Megachile* may be much more common than once supposed.

Although their nests are usually inconspicuous in the wild, studying *Megachile* nesting biology is facilitated because females of many of their species readily accept trap nests made of drilled wooden blocks or bamboo culms (e.g., Krombein 1967; Laroca 1971; Strickler et al. 1996; Pitts-Singer and Cane 2011). Although *Megachile* nesting ecology has been reasonably well studied in Europe and North America (e.g., Michener 1953; Hobbs and Lilly 1954; Krombein 1967; Richards 1978; Eickwort et al. 1981; Raw 1984, 1988; Williams et al. 1986; Cane et al. 1996; Barthell et al. 1998; Kemp and Bosch 2000; Armbrust 2004; Jenkins and Matthews 2004; Pitts-Singer and Cane 2011), it has been poorly investigated in Brazil with few works published, frequently with only incomplete information (von Ihering 1904; Laroca 1971, 1987; Blochtein and Wittmann 1988; Martins and Almeida 1994;

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Almeida et al. 1997; Zillikens and Steiner 2004). For the subgenus *Moureapis*, only fragmentary information is available on nests of a single species (*Megachile apicipennis* Schrottky, 1902) (von Ihering 1904; Laroca 1991). Moreover, Buschini et al. (2009) made a study of the pollen deposited in 16 nests of an unidentified species of this subgenus.

Although countless parasites attack nests of bees (e.g., Krombein 1967), knowledge on the infestation of neotropical species is scarce (Genaro 1996). Several insect groups have been recorded in association with nests of *Megachile*. Among the most common are the cleptoparasitic bees of the genus *Coelioxys* (Megachilidae, Megachilini; e.g., Michener 1953; Krombein 1967; Blochtein and Wittmann 1988; Yanega 1994; Krombein and Norden 1995; Scott et al. 2000; Morato 2003; Zillikens and Steiner 2004) and chalcidoid wasps (Chalcidoidea; Peck 1969). Moreover, some species of Diptera (e.g., Conopidae) have been recorded as parasitoids of adults (e.g., Krombein 1967; Doroshina 1991).

Nests and some aspects of the nesting biology of two species of *Megachile* (*Moureapis*) Raw, 2002 obtained in trap nests are described here as a contribution to the knowledge of the neotropical species of this subgenus.

2. MATERIALS AND METHODS

Data were collected at the Reserva Particular do Patrimônio Natural “Estação Ambiental de Peti” (Private Reserve of Natural Heritage “Peti Environmental Station”; from now on, “Peti”), which is a semideciduous forest reserve owned by the Minas Gerais State Energy Company (CEMIG). The 605-ha reserve is at 19°53'57"S, 43°22' 07"W, between 630 and 806 m elevation, in the municipalities of Santa Bárbara and São Gonçalo do Rio Abaixo in the state of Minas Gerais, Brazil. Regional climate according to Köppen's classification is the subtropical moderately humid with an annual average temperature of 21.7°C (Köppen in Peel et al. 2007). Local vegetation is mostly composed of secondary forest in various regeneration stages. Otherwise, there are small tracts of cerrado (Brazilian savanna), rocky fields (on mountain tops), and gardens with exotic species.

Trap nests were hollow bamboo culms with one open end. Originally intended to collect euglossine nests (Hymenoptera: Apidae: Euglossina), they were about 21 cm long, with diameters varying between 1.5 and 3.5 cm, wider than generally used in trap-nesting studies. Bundles with six culms situated horizontally were tied to tree trunks, about 1.5 m above the soil surface, three facing one arbitrarily chosen direction and three facing the opposite direction. These bundles were set at 10-m intervals along three trails inside the forest.

Because no direct observation could be made to verify that cells within a single bamboo culm were constructed by the same females, from here on, a single row of cells will be called a “cell series”, and “trap nest” will refer to a single bamboo culm, which thus may contain several cell series of a single female or represent a multiple nest used by different females.

A total of 276 trap nests were kept in the field between May 2002 and May 2003. They were inspected monthly starting in June 2002. Culms occupied by bee nests were collected and taken to the laboratory. New empty culms were used to replace those collected. Culms occupied by termite or ant nests were cleaned and left in the bundles. When a female bee was observed actively nesting, the culm she was using was left in the field until the next inspection in the following month. In November, the trap nests were not inspected.

In the laboratory, culms brought from the field were open longitudinally and each cell series found inside was kept in a glass assay tube plugged with a cotton wad. The nests were examined daily for emergence, except on weekends. All insects emerging from the nests were killed with acetyl acetate and pinned. They were identified and deposited with their nest material in the Entomological Collection of the Taxonomic Collections of the Universidade Federal de Minas Gerais.

After emergence of the bees, the cell series were dissected. The material employed in the construction of the outer leaf layer (see below) of a sample of 10 cell series for *Megachile benigna* and three cell series for *Megachile maculata* was analyzed and classified as: (1) an entire leaf or leaflet, which had a central vein and only its basis cut by the bee; or (2) a leaf

piece, which had no central vein and usually had all borders cut. Anatomical characteristics of the nesting material were evaluated to distinguish between leaf and petal fragments. The material used by each species in constructing the inner layer of the cells (see below) could not be verified.

The number of cell series per trap nest and the number of cells per cell series were counted and the internal diameter of the trap nests was measured to the nearest millimeter. Sex ratios were estimated for each species as the number of emerged females per emerged male. The χ^2 test was applied to test whether those ratios differed from 1:1. Statistical analyses were made using BioEstat 4.0 (Ayres et al. 2005).

Two mortality types were considered in this study, according to Bosch and Kemp (2001)—(a) mortality due to other organisms (e.g., parasites, predators, and pathogens) and (b) other mortality events related, for example, to mechanical damage, inadequate temperature, and/or humidity conditions and inadequate food supply. This may be difficult to differentiate from mortality caused by microorganisms (e.g., bacteria and fungi). Mortality rates (%) were calculated in relation to the total number of finished cells for each *Megachile* species.

3. RESULTS

Nests of four species of *Megachile* were obtained during the 12-month sampling period. Here, the nests and some bionomic aspects of two of them, *M. benigna* Mitchell, 1930 and *M. maculata* Smith, 1853 are presented. Both species belong in the subgenus *Moureapis* Raw, 2002, the latter one being frequently referred to in the literature as *Megachile anthidioides* Radoszkowski, 1874. A total of 95 specimens of these two species were obtained from 33 nests. The total number of specimens, of females and males that emerged, and the sex ratios are presented in Table I. The most abundant of the species was *M. benigna* with almost 95% of the bees emerged. All five specimens obtained of *M. maculata* were females but for *M. benigna*, the sex ratio obtained (1.2 females per male) did not differ significantly from 1:1 (Table I).

Table I. Number of emerged specimens of the two species of *Megachile (Moureapis)* obtained in trap nests in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil).

Species	<i>n</i>	♀	♂	sr
<i>M. (Moureapis) benigna</i>	90	49	41	1.20
<i>M. (Moureapis) maculata</i>	5	5	0	–

n total, ♀ number of females, and ♂ number of males obtained in all cell series, *sr* sex ratio

3.1. Nest architecture and nesting activity

The cells of both species were always located at the inner end of the culms, leaving a long empty space between the last cell constructed and the entrance of the trap nests. However, two or more cell series were frequently packed inside a single culm (Figure 1). In almost all cases, only bees from the same species emerged from these multiple cell series. Only in two instances, individuals of different species emerged from the same trap nest. One case involved *M. benigna* and *M. maculata* and the other, *M. benigna* and *M. (Chrysosarus)* sp.

Females of *M. benigna* occupied 13 trap nests, constructing an average of 8.3 cell series per trap nest and 3.6 cells per cell series, while females of *M. maculata* occupied two trap nests, constructing an average of four cell series per trap nests and 2.7 cells per cell series (Table II).

The cell series obtained were structured as commonly described for *Megachile* and included two-layered cells positioned head to tail. The inner layer of the cells of both species was constructed with leaf pieces tightly stuck together (il in Figure 2). The outer layer is a cup of leaf pieces or, sometimes, entire leaves or leaflets (Table III) loosely arranged, one partially inserted into the one behind it (ol in Figure 2). Anatomical characteristics revealed that all cell series examined (of both species) were constructed only with leaves and had no flower petal fragments.

The numbers of finished, unfinished, and empty cells in the nests of the two species are shown in Table IV. An empty cell, with remains



Figure 1. Bottom of a trap nest containing several cell series of *Megachile (Moureapis) benigna*. Smallest unit on the scale is equal to 1 mm.

of a cap but with no vestige of provision, was found in a cell series of *M. maculata*. This series contained four cells, but bees emerged from only three of them. It is assumed that the empty cell, which was the last one and nearest to the trap nest entrance, was capped without food provision and that it was opened by the first bee to emerge from a cell behind it.

The nesting activity was mostly concentrated in the rainy season (Figure 3) but the nesting of *M. benigna* was extended, presenting two activity peaks—the main one (53.3% of the cell series) in December and January (coinciding with the activity of *M. maculata*) and a secondary one in mid-August (26.7% of the cell series). It should be remembered that part of the cell series recorded in December might have actually been constructed in November when no nest inspection was done in the field.

3.2. Nest associates and bee mortality

Several nest associates were found in the nests of *M. benigna*. Two male specimens of an unidentified species of *Coelioxys* (Megachilidae) emerged from one cell series (Table V). Also, many specimens of an unidentified phorid fly emerged from another cell series, apparently causing the death of one host bee. Two other fly species (Mycetophilidae) and one Psocoptera emerged from another *M. benigna* cell series. All host cells produced adult bees in this cell series. A large number of unidentified chalcidoid wasps (Hymenoptera) emerged from another cell series, apparently causing the death of one of the three host bees. The only nest associate found in a nest of *M. maculata* was a conopid fly that emerged from a nest containing a single unfinished cell and a dead adult female.

Table II. Cell series of two species of *Megachile (Moureapis)* collected in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil).

Species	Ntn	0 (cm)	Nc	Ctn	Ncs	Ccs
<i>M. (Moureapis) benigna</i>	13	2.3±0.4	108	8.4±5.7	30	3.6±1.3
<i>M. (Moureapis) maculata</i>	2	±0.3	8	4.0±1.4	3	2.7±1.5

Ntn number of trap nests occupied, *0* mean internal diameter of trap nests (±standard deviation), *Nc* total number of cells, *Ctn* mean number of cells per trap nest (±standard deviation), *Ncs* total number of cell series (see text for details), *Ccs* mean number of cells per cell series (±standard deviation). Values of *Ccs* did not differ ($\alpha=0.05$; Dunn's test)



Figure 2. Part of a series of cells of *Megachile (Moureapis) benigna* from which the oldest one was detached. The loose outer layer (*ol*) of this cell was removed, exposing the tight inner layer (*il*). Note the circular leaf cap enclosing the exposed cell. The smallest unit on the scale is equal to 1 mm.

The percentages of cells and cell series parasitized for each species are shown in Table VI. Causes of mortality were not always obvious (Table VII). Only cases of mortality due to the attack by other organisms could be verified. Nine *M. benigna* did not emerge from their cells for unknown reasons. Two of these nine cells were infested by a saprophytic fungus (*Apiocarpella* sp.—Sphaeropsidales), which may have grown on the dead bees and/or food

provision but which probably did not kill the bees directly.

4. DISCUSSION

Nests of the two species of *Megachile (Moureapis)* obtained in the trap nests in Peti had not been previously described and only two nests of another species in the subgenus, *M. apicipennis* Schrottky, 1902, were already known (von Ihering 1904; Laroca 1991). These two *M. apicipennis* nests, however, were so different from each other that they certainly did not belong to the same species and subgenus. In the nest described by von Ihering (1904), the cells were constructed with mud, by a bee belonging in other subgenus, such as *Chrysosarus* (e.g., Laroca 1971; Zillikens and Steiner 2004, Cardoso and Silveira, unpublished data). The nest illustrated and briefly described by Laroca (1991), however, conforms to the ones collected in Peti, including the fact that more than one cell series were packed side-by-side inside a bamboo culm.

The general structure of nests of *Moureapis*, considering those of *M. benigna* and *M. maculata* studied here and that of *M. apicipennis* presented by Laroca (1991), is the same as those described for most other *Megachile* (e.g., Michener 1953; Medler 1958; Krombein 1967; Laroca 1971;

Table III. Types of leaf material used by species of *Megachile (Moureapis)* in the construction of the outer layer of the cell series obtained in trap nests in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil).

Species	<i>T</i>	Employed material (%)	
		EL	LP
<i>M. (Moureapis) benigna</i>	10	26.4 (210)	73.6 (408)
<i>M. (Moureapis) maculata</i>	3	38.8 (68)	61.2 (77)
Totals	13	278	485

T total number of cell series for which leaf material was analyzed. mean percentage of entire leaf or leaflets (EL) and of pieces of leaf or of leaflets (LP). The total numbers of each kind of material for each species of *Megachile* are between parentheses

Table IV. Cell status in the nests of the species of *Megachile (Moureapis)* obtained in trap nests in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil).

Species	Cell status			Total number of cells
	Finished	Unfinished	Empty	
<i>M. (Moureapis) benigna</i>	104	4	0	108
<i>M. (Moureapis) maculata</i>	6	2	1	8

A finished cell is one closed and provisioned or one from which a bee has emerged, an unfinished cell is an open cell with a thin “leaf wall” (just one or a few layers of leaf peaces not tightly stick together), an empty cell is a cell with no food provision (see text for explanation)

Laroca et al. 1987). The two species of *M. (Moureapis)* studied at Peti regularly used entire leaves and/or leaflets to construct their cells, as documented for some other species of *Megachile* (e.g., Yanega 1994; Zillikens and Steiner 2004; Raw 2007). However, these materials were used irregularly, probably due to spatial and temporal variation in the availability of convenient-sized leaves or leaflets needed by these bees. For example, *M. benigna* regularly used leaf fragments or leaflets to construct their brood cells in one site in April. These materials were employed by both *M. maculata* and *M. benigna* in December in another site along another trail. However, entire leaves or leaflets were not employed in the construction of cell series of *M. benigna* collected in the same period but approximately 40 m away from the previous ones.

The concentration of nesting activity by *Megachile* in the warm, rainy season as observed in Peti was also described for other bees in other areas of Brazil (Becker et al. 1991; Camillo et al. 1995; Oliveira 1999; Alves-dos-Santos 2003; Martins et al. 2002). Some authors (e.g., Viana et al. 2001) considered that such activity peaks are associated with food availability. No measure of seasonal fluctuation of floral resources was done in Peti. However, the period between October and March is when bees are most abundant and diverse at flowers in the region (Silveira et al., unpublished data). A comparison between the distributions of the nesting activities of the species studied here is hindered by the very small number of nests obtained of *M. maculata*. This may be the result of *M. maculata* being rarer than *M. benigna* in the Peti area or in the specific environment

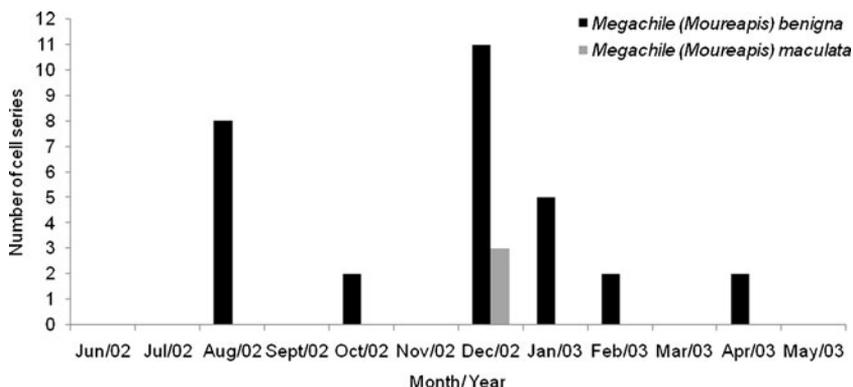


Figure 3. Nesting activity of the two species of *Megachile (Moureapis)* Raw obtained in trap nests in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil) along a year.

Table V. Insects associated with cells of *Megachile (Moureapis)* obtained from trap nests in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil).

Host species	NC	H	P
<i>M. (Moureapis) maculata</i>	1	–	1 Conopidae (Diptera) ^a
	4	2 ♂; 2 ♂	<i>Coelioxys</i> sp.
	5	4 ♀	Phoridae (Diptera) ^b
	3	1 ♀; 1 ♂	Chalcidoidea ^b
<i>M. (Moureapis) benigna</i>			1 Psocoptera ^c
	3	3	1 <i>Mycetophilidae</i> sp. 1 (Diptera) ^c
			1 <i>Mycetophilidae</i> sp. 2 (Diptera) ^c

Each line in front of a species name represents a different cell series constructed by females of that species. NC number of cells in the cell series, H and P the number and sex of host bees and of parasites emerged from the series, respectively

^a This fly is a parasitoid of adult bees and probably emerged from the nesting female (see text)

^b Many specimens

^c Probably commensals because all host individuals emerged from the nests

sampled. Another reason that *M. maculata* may not have been found very often is that this species did not prefer the size, texture, or placement of the bamboo culms. They may have been incidental in the culms, but common in other types of nesting materials.

The number of generations produced by tropical bees has been less studied than voltinism in bees from temperate zones. It seems, however, that production of one to two broods each year is common in the tropics (Roubik 1989). Sakagami and Laroca (1971), reviewing the literature on the reproduction of species of *Xylocopa* and *Ceratina*, suggested that bivoltinism is expected where there is a single pronounced dry season, such as in Peti. However,

only two studies on Brazilian *Megachile* were found to contain data on the number of yearly generations. In one of them, the species, *Megachile (Chrysosarus) pseudanthidioides* was bivoltine and it was suggested (Zillikens and Steiner 2004) that this could be an adaptation to escape the cool winter when less food is available. Another study (Martins and Almeida 1994) on *Megachile (Schrotkyapis) assumptionis* was conducted in Belo Horizonte located about 60 km from Peti and under the same climatic conditions. This species seems to be univoltine, diapausing during the regional warm, rainy season. *M. assumptionis* was suggested to be a specialist in occupying abandoned nests of *Ptilothrix plumata*, and its

Table VI. Number (*n*) of cell series, finished cells, and parasite infestation rates (%) recorded for two species of *Megachile (Moureapis)* Raw obtained in trap nests in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil).

Host species	Cell series		Finished cells	
	<i>n</i>	% infested	<i>n</i>	% infested
<i>M. (Moureapis) benigna</i>	30	10	104	3.8
<i>M. (Moureapis) maculata</i>	3	0.0	6	0.0
All species	33	9.1	110	3.6

Table VII. Numbers of *Megachile* bees killed by different mortality agents and by unknown causes in trap nests in the RPPN Estação Ambiental de Peti (Minas Gerais, Brazil).

Species	Mortality agents			TM (%)	Unknown mortality cause (%)
	Chalcidoidea	Phoridae (Diptera)	<i>Coelioxys</i> spp.		
<i>M. (Moureapis) benigna</i>	1	1	2	3.8	9 (8.7)
<i>M. (Moureapis) maculata</i>	0	0	0	0	0 (0.0)

TM total ratio of mortality caused by known agents

nesting activity was correlated with availability of such nests. It also may be related to specialization on some food resources, but no information is available on this.

With only these examples, it is impossible to make any generalization on the determination of voltinism in Brazilian *Megachile*. Thus, explanation on why *M. benigna* is bivoltine in Peti is speculative. Although the regional cool dry season is considered to be a season of food scarcity, there are many plants, especially tree species, which flower abundantly in August–September just before the beginning of the rainy season. Thus, the second adult population of *M. benigna* in Peti may emerge in synchrony to this resource boom.

Despite the large space available in the trap nests used in Peti, the numbers of cells per cell series were relatively small (between one and six), as compared, for example, with up to 17 cells found by Stephen and Torchio (1961) in cell series of *Megachile rotundata*. Of course, in Peti, an unknown portion of the smallest cell series were collected before the nesting female had finished them. On the other hand, leaving the occupied trap nests an additional month in the field would certainly allow for many bees to emerge and leave the nests before being collected.

The sex ratio observed for *M. benigna* in Peti is compatible with values reported for other species in the genus (e.g., Krombein 1967). However, the small sample sizes do not allow for many conclusions to be taken from the data, especially in relation to *M. maculata* from which only five specimens were obtained. Moreover, it could be argued that the sex ratios obtained in this study might be biased if a

relatively large proportion of incomplete cell series were collected. If this was the case, and if male cells of *M. benigna* tend to be the last to be constructed in each cell series, as is common among other species in the genus (Krombein 1967; Scott et al. 2000), then, sex ratio for this species may actually be more male biased than recorded here. However, considering the small number of unfinished cells in *M. benigna* cell series (four unfinished cells in a total of 104, Table IV), it is reasonable to consider that most of the nests were actually concluded by the bees and, thus, that the sex ratio calculated here are fair estimates of the real sex ratio of these bees in Peti.

Another issue worth rising is the potential influence of hole width on the sex ratio of progenies produced by females. It has been shown for other *Megachile* species that nests built in the narrowest cavities usually contain a highly male-biased progeny (e.g., Krombein 1967; Bosch and Kemp 2001). This also seems to be confirmed by the highly female-biased progeny produced by *M. (Chrysosarus) pseudanthidioides* nesting in wooden boxes, which did not limit the space for cell construction (Zillikens and Steiner 2004). However, the data obtained in Peti seem to contradict this relationship because progenies of *M. benigna* with balanced sex ratios were produced in the wide trap nests. Thus, culm diameter alone does not seem to determine the sex ratio of the progenies of *M. benigna* and nesting females seem to be able to define the diameter of their cells independently of the culm walls. This suggests adaptation by these bees to nest in relatively wide cavities. The idea that *Moureapis* actually may prefer to use such wide cavities is reinforced by the fact that all nests

now known of species in this subgenus, *M. apicipennis* (Laroca 1991), *M. benigna*, and *M. maculata* (this study) were constructed in similar nesting substrates. This is an interesting issue, which deserves more studies.

Many of the mortality agents known to act on *Megachile* were recorded in the nests obtained in Peti. Of the organisms emerging from the cell series, *Coelioxys* spp. are known to parasitize nests of *Megachile* and other bee species, and chalcidoid wasps and conopid flies are known to be parasitoids of *Megachile* (e.g., Michener 1953; Krombein 1967; Peck 1969; Blochtein and Wittmann 1988; Woodward 1994; Morato 2003; Pitts-Singer and Cane 2011). Phorid flies are known to be both cleptoparasite and parasitoid of bees (Krombein 1967; Brown 1997; Gonzalez et al. 2002; Otterstatter et al. 2002; Wcislo et al. 2004; Brosi et al. 2006; Smith and Brown 2008) and, in the case of Peti, it is not clear if these flies fed on the brood provision or on the bee larvae themselves. The conopid fly emerged from a nest of *M. maculata* was probably responsible for the death of the adult female found in the nest, since these flies are known parasitoids of *Megachile* (e.g., Krombein 1967; Doroshina 1991).

Mycetophilid flies, as those emerged from a cell series of *M. (Moureapis) benigna*, are known to feed on fungi (Borror and DeLong 1988) and, thus, can probably be discarded as a threat to the bees. The same can be said of the Psocoptera, which also emerged from the same cell series and should not be a death agent for bees.

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Biologie de la nidification chez deux espèces de *Megachile* (*Moureapis*) (Hymenoptera: Megachilidae) dans une réserve de forêt semi-caducifoliée du sud-est du Brésil

Forêt atlantique / abeilles sauvages / nid / matériau / nid-trappe / bionomie

Zur Nestbiologie von zwei *Megachile* (*Moureapis*)-Arten (Hymenoptera: Megachilidae) in einem Halbtrockenwald-Schutzgebiet in Südostbrasilien.

Atlantischer Regenwald / Wildbienen / Bionomie / Nestmaterial / Nistfallen

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