Sociobiology 60(4): 421-428 (2013) DOI: 10.13102/sociobiology.v60i4.421-428

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - BEES

Nest Entrance Types of Stingless Bees (Hymenoptera: Apidae) in a Tropical Dry Forest of Mid-Western Brazil

FVO Lima[1], R Silvestre[1], JBP Balestieri[2]

1 - Prog. de Pós-graduação em Entomologia e Conservação da Biodiversidade, Universidade Federal da Grande Dourados, Dourados, MS, Brazil
2 - Faculdade de Ciências Biológicas e Ambientais (FCBA - UFGD), Dourados, MS, Brazil

Article History
Edited by:
Candida M L Aguiar, UEFS, Brazil
Received 22 February 2013
Initial acceptance 06 April 2013
Final acceptance 25 September 2013

Keywords
Meliponina, behavior, nest structure, worker defense, nest aggregation

Corresponding author
Felipe Varussa de Oliveira Lima
Laboratório de Ecologia de Hymenoptera (HECOLAB)
Univ. Federal da Grande Dourados
Rodovia Dourados, Itahum, km 12
Cidade Universitária, 79.804-970
Dourados, MS, Brazil.
E-Mail: felipeoliveira@ufgd.edu.br

Abstract

Characteristics of nest structure and nesting habits are useful in taxonomical, phylogenetic, and ecological studies, but for some environments this information is lacking. The external architecture of the nest entrance of native stingless bees (Apidae *sensu lato*: Meliponina) was studied in the Serra da Bodoquena range mountain, Brazil. Our objective was to evaluate the pattern of nesting stingless bees in a tropical dry forest and check if the structure of micro-habitat can modify the default building entrance and the type of substrate used by bees. Colonies were discovered by active search and some workers were collected on the nest entrance with entomological nets. The following characteristics of the nest were described: the substrate used, shape and color of the nest entrance, entrance height aboveground, number of bees guarding the entrance of the colony, worker defense at the nest entrance, and description "*in situ*" of land use in the surroundings of the colony. We assessed a total of 26 nests of six species of Meliponina bees. The observed nest frequency were: *Tetragonisca fiebrigi* (Schwarz, 1938) (n=13), *Scaptotrigona depilis* Moure, 1942 (n=6), *Plebeia* sp.1 (n=4), *Tetragona clavipes* (Fabricius, 1804), *Partamona cupira* (Smith, 1863), and *Oxytrigona tataira* (Smith, 1863) (n=1). The substrates were used in the following order of preference: hollows of living or dead trees, cavities of limestone, termite mounds, and one nest in a wooden box. We detect different patterns of construction of nest entrance in *Plebeia* sp.1; and observed a highest nest aggregation in open areas.

Introduction

Stingless bees are a very crucial group of tropical pollinators and a model system for social insects that has gained increasing attention recently. Stingless bees of the subtribe Meliponina popularly known as 'indigenous bees', are represented by 400 species spread out over all tropical regions of the world, as well as in subtropical regions of the Southern Hemisphere. The Neotropical Meliponina (*sensu* Silveira & Melo, 2002; Melo & Gonçalves, 2005) fauna is one of the most diverse, having high abundance in the Amazon (Michener, 2007; Roubik, 1989; Nogueira-Neto, 1997; Velthuis et al., 2005; Camargo & Pedro, 2007). All species of this tribe are highly social and some are kleptoparasitic (Michener, 2007).

Nesting usually takes place in pre-existing cavities (hollow trees, abandoned nests of termites, ants, birds, etc.), but some species build exposed nests (Wille & Michener, 1973; Wille, 1983; Roubik, 1989). The nest entrance may be composed of a wax or cerumen tube, whose length varies according to the species; other materials, such as geopropolis, feces, and clay may also be used (Roubik, 2006). House's walls, tree branches or rock crevices may be used for exposed or semi-exposed nests (Barreto & Castro, 2007).

Nest characteristics and nesting habits are useful in taxonomic studies (Rasmussen & Camargo, 2008), and ecological studies of Meliponina bees (Michener, 1990; Camargo & Pedro, 2003). The nests of social insects are defended by guard or guardian worker bees (Hölldobler & Wilson, 2009). This behavior helps to protect valuable resources inside the nest; the guards allow worker bees born in the nest to enter, but exclude intruders, and the food stored inside the nest may be stolen by conspecifics or species of intruder bees (Grüter et al. 2011).

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

The availability of food and nesting sites may limit the density of stingless bees (Eltz et al. 2002; Nascimento & Nascimento, 2012; Nunes-Silva et al., 2010). Hence, bee nests may be used as environmental indicators. Human activities, mainly commercial logging, have decreased the availability of nesting sites (Souza et al. 2007). According to Moreno & Cardozo (2002), traditional knowledge makes farmers or residents of rural areas search and harvest products of wild bees.

Kerr *et al.* (2001) appoint that Meliponina bees are threatened by the following factors: a) habitat destruction by deforestation and fires; b) small size of reserves, which may be insufficient to assure genetically viable populations; c) logging of older trees (which have larger hollows); destruction of colonies for honey extraction.

Meliponina species vary the architecture of their nests considerably, using different conformations for their internal and external structure; the nests are built in hollow trees, on the ground, or occasionally in active colonies of other social insects (Wille & Michener, 1973; Roubik, 2006; Rasmussen, 2004). The architecture of the nest entrance is species-specific (Franck et al. 2004). Normandes & Pivello (2009) observed that most of areas in Mid-Western of Brazil are under the risk of losing the connectivity between fragments, and need an urgent strategy to postpone or stop the process of conversion of forests into pasture or agriculture. This scenario compromises biodiversity and the persistence of minimum viable populations.

The aim of this paper was to investigate the building patterns of the nest entrance in Meliponina species from Serra da Bodoquena, Mato Grosso do Sul, Brazil, in order to describe the establishment of colonies in the seasonal deciduous forest by recording the type of entrance, the substrate used and the entrance height aboveground, and correlating guard behavior and aggressiveness with the type of nest entrance. The first approach aims to verify if there are specific adaptations of the bees in relation to micro-habitat and substrate types available in this forest.

Material and Methods

Study area

The nests of stingless bees were observed in four field expeditions held in April 2008, December 2008, May 2009, and October 2011, summing up 40 discontinuous sampling days in areas of seasonal deciduous submontane forest (dry forest) and pastures, located in the Serra da Bodoquena range mountain – central coordinates: 20º52’14”S; 56º35’14”W (Figure 1). In each field excursion we sampled an area of approximately 5 ha, summing up 20 ha in the municipality of Bonito, state of Mato Grosso do Sul, Brazil.

According to the Conservation Plan of the Upper Paraguai Drainage Basin (MMA, 1997), the predominant vegetation in the region is Seasonal Deciduous Submontane Forest, transitional forms in which elements of both Cerrado and Seasonal Semi-deciduous Forest, and floodable fields; both have been markedly altered by human activities.

The Bodoquena Plateau harbors the largest extension of natural forests in the state of the Mato Grosso do Sul. It is considered a watershed, and shelters all headwaters of the rivers of the region, such as Salobra, Prata, Formoso, Perdido, and Sucuri (MMA, 2007).

It is a plateau with the scarp facing the Pantanal, almost entirely composed of carbonate rocks, which originated by deposition on the bottom of an ancient ocean 550 million years ago. Tectonic movements caused intense folding in the limestone layers, forming the mountains that characterize the region (Boggiani et al., 1993).

Nest characteristics and micro-habitat structure

External characteristics of colonies of Meliponina bees in the study region were described and classified in categories

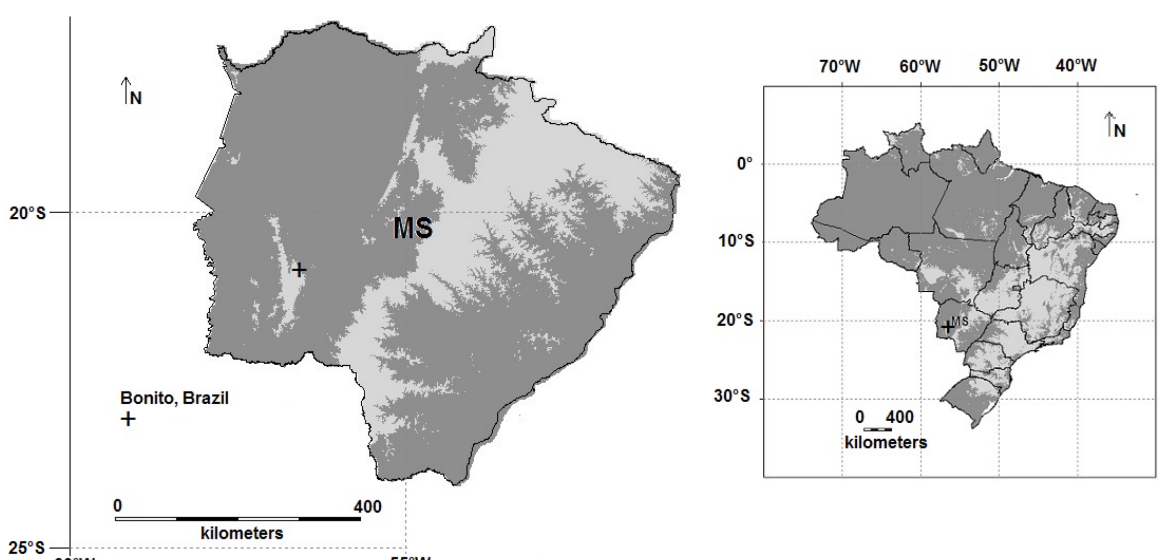

Fig 1. Location of Bodoquena range mountain in the state of Mato Grosso do Sul (MS), Brazil indicating the study site. Light gray indicates altitudes of 300 to 900m.

adjusted as Roubik (1983, 2006) and photographed. The following attributes were measured: 1- Substrate used in nest building. 2- Construction material. 3- Entrance measure and shape. 4- Nest entrance height aboveground (EH). 5- Diameter at breast height (DBH). 6- Nest defensivity. 7- Worker traffic on the entrance. 8- Micro-habitat structure.

The substrate used in nest entrance was classified according to:1.1- Live tree; 1.2- Dead tree;1.3- Limestone;1.4- Termite nest;1.5- Wood box.

The nest entrance material employed in their construction was classified according to:

2.1- Cerumen; 2.2- Propolis; 2.3- Mud; 2.4- Wax.

The entrance to each nest was measured using a centimeter scale, and the diameter of the entry, measured horizontally and vertically. The variety of shapes included:

3.1- Round; 3.2- Elliptical; 3.3- Slot-shaped or irregular; 3.4- Short tube entrance; 3.5- Long tube entrance; 3.6- Camouflage or cryptic entrance; 3.7- Toad mouth.

The measure EH is related to the nest entrance height aboveground: 4.1- < 1m; 4.2- 1m – 3m; 4.3- > 3m.

The measure DBH is related to the trees used as nesting substrate, following the variables: 5.1- < 1 meter; 5.2- 1m - 2m; 5.3- 2m – 3m; 5.4- > 3m; 5.5- not in tree.

To analyze the nest worker defense of the species observed we measured the following variables: 6.1- Presence of multiple entrances; 6.2- Presence of chemical irritants; 6.3- Deposit of balls of propolis on the intruder; 6.4- Workers size (small); 6.5- Workers size (medium).

The worker traffic at the entrance was categorized as follows: 7.1- Low-Flow= up to 10 individuals; 7.2- Moderate-Flow= 10-20 individuals; 7.3- High-Flow= > 20 individuals.

The micro-habitat structure was assessed with a land-use metric that considers a buffer of 50 m radius around the colony, according to the follow categories:

A - Areas with high density of plants, where the vegetation is high (with trees taller than 20 m) and sunlight incidence is low;

B - Areas with intermediate density of plant species (shorter than 20 m), and with a large number of shrubs;

C - Areas with low diversity or low vertical vegetation structure, where one or few plant species predominate; they are open on the edges and receive moderate sunlight;

D - Areas opened by humans with the presence of grasses for pasture and high sunlight incidence .

The statistical clustering analysis based on Bray-Curtis distance was ran using the software PAST (Hammer et al., 2001). We used matrix data with all attributes of the nest characteristics and micro-habitat structure described, to verify the similarity between the nesting patterns presents by the species.

Some workers were collected from each nest and killed in lethal vials with ethyl acetate and then preserved in alcohol 96%. Later, the bees were mounted in the laboratory of Hymenoptera Ecology HECOLAB/UFGD and identified using specialized keys. Vouchers were deposited in the reference collection of the Museu da Biodiversidade (MuBio/UFGD), Dourados, state of Mato Grosso do Sul, Brazil, under numbers Hym00112-A, Hym000115-A, Hym000140-A, Hym000152-A, Hym000187-A, and Hym000526-A.

Results

We assessed the nests of six Meliponina species: *Tetragonisca fiebrigi* Schwarz, 1938 (n=13), *Scaptotrigona depilis* Moure, 1942 (n=6), *Plebeia* sp.1 (n=4), *Partamona cupira* (Smith, 1863), *Oxytrigona tataira* (Smith, 1863), and *Tetragona clavipes* (Fabricius, 1804) (n=1).

Regarding the substrate used, 20 nests were found in hollows of living trees and two in dead trees; two nests of *Tetragonisca fiebrigi* were built in limestone, one nest of *Partamona cupira* was located in a termite nest, and another one in a wooden box (Table 1).

We compared our data with those obtained from other studies on Meliponina nests (Table 2), showing the number of species and the number of nests found in several regions of Brazil and Central America (adapted from Oliveira et al. 1995).

The species with higher number of guard workers at the nest entrance in decreasing order were: *T. clavipes* > *O. tataira* > *S. depilis* > *P. cupira* > *T. fiebrigi* > *Plebeia* sp.1.

We present here a description of the nests of the species sampled in the present study:

Table 1. External nest entrance characteristics of stingless bees sampled in the Bodoquena range mountain, Brazil. DBH - Diameter at breast height; EH - Entrance height aboveground; LF- Low-flow, MF- Moderate-flow, HF- High-flow.

Nests	Species	Substrate	DBH (m)	EH (m)	Worker traffic	Micro-habitat
13	*Tetragonisca fiebrigi* (Schwarz, 1938)	Tree; dead tree; limestone; wooden box	1.70-7.0	0.00-3.07	MF; HF	B, C
6	*Scaptotrigona depilis* (Moure, 1942)	Tree	1.57-3.15	0.3-2.31	MF; HF	A, B
4	*Plebeia* sp. 1	Tree	1.68-2.61	0.00-1.14	LF	B, C
1	*Oxytrigona tataira* (Smith, 1863)	Tree	2.4	6.50	HF	D
1	*Partamona cupira* (Smith, 1863)	Termite nest	0.40	0.70	HF	C
1	*Tetragona clavipes* (Fabricius, 1804)	Tree	1.5	2.10	HF	C

Table 2. Comparison among inventories of Meliponina nests in the Neotropics.

Area (ha)	Number of nests	Nest density/ha	Number of species	Site	Vegetation type	Author
185.5	73	2.6	15	State of Maranhão, Brazil	Savanna (Cerrado)	Serra et al. (2009)
114.0	380	3.3	?	State of Mato Grosso, Brazil	Savanna (Cerrado)	Oliveira et al. (1995)
100.0	15	0.15	9	State of Amazônia, Brazil	Tropical Forest	Oliveira et al. (1995)
64.7	141	2.2	9	Pacific Coast, Panama	Forest, ruins of old Panama (stone walls and buildings)	Michener (1946)
50.4	21	2.4	6	State of Minas Gerais, Brazil	Cerrado, Seazonal Semi-deciduous Forest, Riparian areas, pastures	Siqueira et al. (2007)
38.0	64	1.7	?	State of Goiás, Brazil	Savanna (Cerrado)	Oliveira et al. (1995)
36.7	67	1.8	9	Guanacaste Province, Costa Rica	Tropical Dry Forest	Hubbel & Johnson (1977)
20.0	26	1.3	6	State of Mato Grosso do Sul, Brazil	Tropical Dry Forest, pastures	**(authors datasets)**
5.0	30	5.9	14	Central Panama	Tropical Wet Forest	Roubik et al. (1983)

Tetragonisca fiebrigi

Local names: jataí, jataí-do-sul (Figure 2 A, B, C)

This species always made nest entrances in the shape of a tube, made of soft cerumen, and ranging from light to dark yellow, with thin walls and tiny holes; it was observed in a fallen tree and in a rock crevice on the ground.

The landscape of the colony surroundings was composed of grasses (pasture), rupestrian fields with elements of semi-deciduous forest, and transitional cerrado areas.

Scaptotrigona depilis

Local names: canudo, canudo-torce-cabelos, mandaguari (Figure 2 D).

In the study region nests were observed only in trees. Some trees had also nests of other species, such as *Tetragonisca fiebrigi* and *Oxytrigona tataira* (approximate distance of 3.5 m between entrances), as well as conspecific nests.

S. depilis is slightly aggressive when a person gets too close to the nest entrance; it entangles in the person's hair twisting it and nibbling lightly on the scalp or other parts of the head (personal observation).

We observed an aggregation of males at the nest entrance; some males tried to land on the entrance tube, but were driven out by the guard workers. Males competed for twigs that were close to the entrance. Probably, these males were waiting for a virgin queen to leave the nest so they could fertilize her.

The landscape around the colony was composed of grasses (pasture) and sparse trees, and shrubby vegetation of deciduous forest with limestone outcrops. In general, the nests were found in shaded environments.

Partamona cupira

Local names: Toad mouth "boca-de-sapo", cupira, cú-de-vaca (Figure 2 E, F).

The only nest of this species was found in an abandoned termite mound in April 2008. The landscape around the colony was composed of grasses (pastures), fig trees (*Ficus* sp.) and one Araceae.

Fig. 2. Stingless bees nest entrance in Seasonal Decidual Forest from Bodoquena Range Mountain, Brazil. A-B-C- *Tetragonisca fiebrigi* – in the dead tree (A), in limestone (B), and in live tree (C); D- *Scaptotrigona depilis* in a 'ipê-roxo' tree (*Tabebuia* sp.); E-F- Short entrance tube of *Partamona cupira*, in the shape of a toad mouth, made in an abandoned termite mound "murundu".

Tetragona clavipes

Local names: borá, vorá (Figure 3 A).

Tetragona clavipes exhibited a wide nest entrance, without a tube, made of propolis, and ranging from shades of dark yellow to chestnut. The worker bees were very aggressive, touching the skin of observers and nibbling their faces. We noticed that bees were able to identify intruders at ca. 1-2 m from the nest entrance. They may deposit propolis on the person closest to the nest as a direct defense mechanism or to attract additional workers to defend the colony. On average, 20 to 50 worker bees were recorded performing the attack, depending on how close the person was to the nest.

Oxytrigona tataira

Local names: caga-fogo, mija-fogo (Figure 3 B).

The only nest of *Oxytrigona tataira* recorded was in a tree of *Tabebuia* sp., where there was also a nest of *Scaptotrigona depilis*. The nest of *O. tataira* was about 7 meters aboveground and the nest of *S. depilis* was only 1.5 m aboveground. The landscape surrounding the colony was composed predominantly of grasses (pasture) and sparse trees.

Plebeia sp.1

Local names: mirim, mirim-preguiça (Figure 3 C, D).

Four nests were observed in the area, built in tree trunks. The landscape surrounding the colony was composed of grasses (pasture) and some 'caraguatá' plants (*Bromelia* sp., Bromeliacea) as well as other sparse tree species in a landscape that contains remnants of cerrado enclaves.

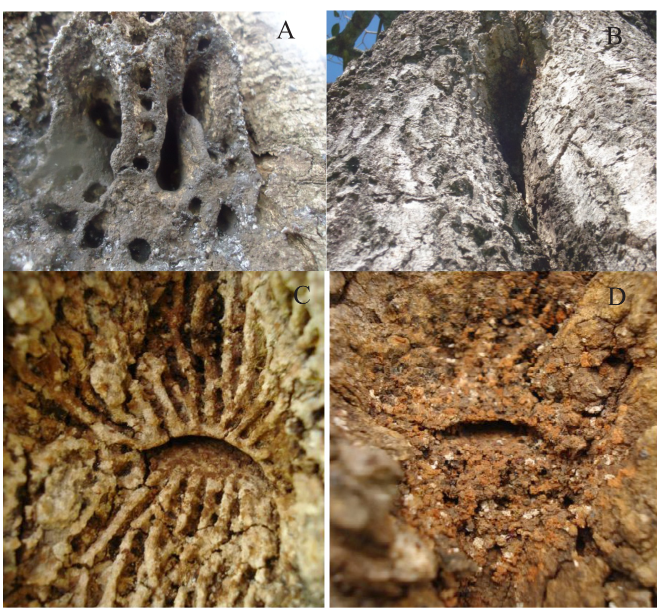

Fig. 3. Types of stingless bees nest entrance in Bodoquena Range Mountain, Brazil. A- *Tetragona clavipes* in a tree; B- *O. tataira* in an 'ipê-roxo' tree (*Tabebuia* sp.); C-D- Two nest entrances types of *Plebeia* sp.1 in live trees, showing a short and striate entrance (C) (which is not characteristic of this species), and an entrance without striae (D)(which is common for this species).

We observed in cluster analisys (Figure 4) that there is a close relation in the strategies of land use between the species *Scaptotrigona depilis* and *Tetragonisca fiebrigi*. This group of species present a similar nesting behavior preferring areas with low diversity or low vertical vegetation structure, where one or few plant species predominate. The high flow of workers and a great defensivity of nest entrance was observed. In some opportunities the species shared the same tree.

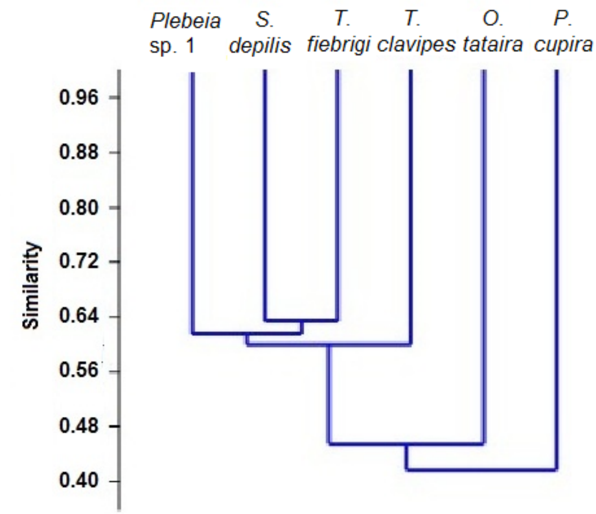

Figure 4- Clustering Analysis with algorithm single linkage and similarity index Bray-Curtis, from six stingless bee species grouped based in matrix data with thirty-six characters (attributes). The *cophenetic correlation coefficient* from this analysis (= 0,8382).

Discussion

A strong correlation between relative entrance area and traffic across the different species strongly suggests a tradeoff between traffic and security, and a significant trend for higher forager traffic to be associated with more guards and for those guards to be more aggressive (Couvillon et al. 2008).

Stingless bees are considered generalist in the selection of nesting sites (Roubik, 1989; Hubbell & Johnson, 1977). According to Roubik (1983) the nests of several species of these bees remain undescribed. Camargo & Pedro (2003) reported the same for the genus *Partamona*.

The nests of *Plebeia* are built in hollow trees, rock walls, fence posts, rock crevices, and walls of old houses, even in urban areas. In general, bees of this genus build an entrance tube made of propolis; in the case of the older entrances, the tube hardens, and remains open at night (Nogueira-Neto, 1997). We observed one different pattern in *Plebeia* sp.1 nest entrance. The external entrance of the nest of *Plebeia* sp.1 exhibited longitudinal striae (similar to those of bees of the genus *Melipona*); this creates a camouflage that prevents predators from finding the nest, especially considering the low flow of bees entering and leaving the nest, and lower aggressiveness. Although, the appearance of the nest entrance with the number of guard workers we noticed that, in general, colonies without an entrance tube have more guards and higher aggressiveness.

The use of determined substrate, and probably the preference for nesting on trees by stingless bees is related to thermal insulation, which helps the colony to retain metabolic heat and provides protection against variations in ambient temperature (Engels et al., 1995). Nests in larger trunks or on the ground are particularly well insulated. Many species, in particular those from the humid tropics, are unable to survive cooling (Michener, 2007). In this Tropical Dry Forest there is a great daily variation in seasonal abiotic conditions.

Regarding nests in trees, DBH was an important criterion in nest selection by some species in the area. Entrance height (EH) of the nests differed among species; it was smaller in *Plebeia* sp.1 (0.49 m) and larger in *Oxytrigona tataira* (6.5 m). Only one nest of the latter species was found.

Three pairs of species shared the same tree: *O. tataira* and *S. depilis; T. fiebrigi* and *S. depilis; T. fiebrigi* and *Plebeia* sp.1. Comparing the observations made in the present study with data published by Kerr *apud* Oliveira et al. (1995) who worked in the states of Mato Grosso and Goiás, we observed that in the Bodoquena range mountain, which is a relatively small area, a larger number of Meliponina colonies were recorded per hectare (nest density), not considering the number of species. The density observed in the present study, approximately 1.3 nests per hectare, is similar to that reported by Roubik (2006) for forest areas, which may harbor up to 150 colonies in 100 hectares, with a density of approximately 1.5 active nests of Meliponina per hectare, varying from 15 to 1,500; depending on the biomass of the colony and on the size of the individuals.

The species *Partamona cupira* e *Oxytrigona tataira* make a distinct pattern in relation to one another. The genus *Partamona* comprises aggressive bees that nest in a wide variety of substrates; most are obligate termitophilous (Camargo & Pedro, 2003). Several species that nest aboveground build their nests in active or abandoned termite nests. Usually, the bee-termite relationship involves other substrates, such as soil (subterranean species) and trees (in the case of a tree termite nest). Nesting by this species has been recorded in a single plant species: *Caryocar brasiliensis* Camb. (Pequi) (Antonini & Martins, 2003). Workers of *Oxytrigona* have mandibular glands that secrete a mixture with formic acid, used for nest defense. This substance is deposited when the bees bite the skin, producing a burn that may last some days (González, 2007).

Pollination carried out by stingless bees allows the production of fruits and seeds by several native plants, many of which are highly important for humans. Without the help of these pollinators, several plant species would be threatened of extinction (Campos, 1983). It is essential for studies to aim not only at sampling species, but also at gathering information on phenology and behavior, morphological adaptations of flowers and bees, and temporal interactions between bee species that explore the same resource (competition) and belong to the same guild, as well as information on nesting behavior, which may support the conservation of forest remnants.

Acknowledgments

CAPES granted us a scholarship for carrying out the present study. ICMBio (Chico Mendes Institute) of Bonito, Mato Grosso do Sul in name of Fernando Villela. Gabriel A. R. Melo helped us to identify bee species. The owners of the farms Pitangueiras, Boqueirão, and Campo Verde provided us with infrastructure for fieldwork. Colleagues from the Laboratory of Hymenoptera Ecology of UFGD-HECOLAB helped us in the field. We also thank Manoel Fernando Demétrio and two anonymous referees for helpful remarks in an early version of this manuscript. This study was carried out under a collection permit from IBAMA (number 10674-11/09/2007). This paper is dedicated to João Maria Franco de Camargo in memorian.

References

Antonini, Y. & Martins, R. P. (2003). The value of a tree species for a stingless bee *Melipona quadrifasciata quadrifasciata.* J. Insect Conserv., 7: 167-174.

Barreto, L. S. & Castro, M. S. (2007). Ecology of nesting of bees of the genus *Partamona* in caatinga, Milagres, Bahia. Biota Neotr., 7(1). doi:10.1590/S1676-06032007000100012

Boggiani, P. C., Fairchild, T. R. & Coimbra, A. M. (1993). O grupo Corumbá (Neoproterozóico-Cambriano) na região central da Serra da Bodoquena (Faixa Paraguai) Mato Grosso do Sul. Rev. Bras. Geoc., 23: 301-305.

Camargo, J. M. F. & Pedro, S. R. M. (2007). Meliponini Lepeletier, 1836. In J. S. Moure, D. Urban, G. A. R. Melo (Eds.), *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical* Region (pp. 272-578). Curitiba: Sociedade Brasileira de Entomologia.

Camargo, J. M. F. & Pedro, S. R. M. (2003). Meliponini neotropicais: o gênero *Partamona* Schwarz, 1939 (Hymenoptera, Apidae, Apinae) - bionomia e biogeografia. Rev. Bras. Entomol., 47: 311-372.

Campos, L. A. O. (1983). Abelhas indígenas sem ferrão. Inf. Agropec., 9(106): 76-80.

Couvillon, M. J., Wenseleers, T., Imperatriz-Fonseca, V. L., Nogueira-Neto, P. & Ratnieks, F. L. W. (2008). Comparative study in stingless bees (Meliponini) demonstrates that nest entrance size predicts traffic and defensivity. J. Evol. Biol., 21: 194–201.

Eltz, T., Bruhl, C. A., Kaars, S. V. D. & Linsenmair, K. E. (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia, 131: 27-34.

Engels, W., Rosenkranz, P. & Engels, E. (1995).Thermoregulation in the nest of the Neotropical stingless bee *Scaptotrigona postica* and a hypothesis on the evolution of temperature homeostasis in highly eusocial bees. Stud. Neotrop. Fauna Environ., 30: 193-205.

Franck, P., Cameron, E., Good, G., Rasplus, J. Y., Oldroyd, B. P. (2004). Nest architecture and genetic differentiation in a species complex of Australian stingless bees. Mol. Ecol. 13, 2317-2331.

González, V. H. (2007). Distribución geográfica de las abejas del fuego en Colombia (Hymenoptera: Apidae, Meliponini, *Oxytrigona*). Rev. Colomb. Entomol., 33(2): 188-189

Grüter, C., Kärcher, M. H. & Ratnieks, F. L. W. (2011). The natural history of nest defence in a stingless bee, *Tetragonisca angustula* (Latreille) (Hymenoptera: Apidae), with two distinct types of entrance guards. Neotrop. Entomol., 40: 55-61.

Hammer, O., Harper, D.A.T. & Ryan, P.D. (2001). PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electr., 4(1), 9pp. Available from <http://palaeo-electronica.org/2001_1/past/issue1_01.htm>. Accessed on 15/12/2012.

Hölldobler, B. & Wilson, E. O. (2009). *The Superorganism: The beauty, elegance, and strangeness of insect societies.* New York: W. W. Norton & Company.

Hubbell, S. P. & Johnson, L. K. (1977). Competition and nest spacing in a tropical stingless bee community, Ecology, 58: 949–963.

Kerr, W. E., Carvalho, G. A., Silva, A. C. & Assis, M. G. P. (2001). Aspectos pouco mencionados da biodiversidade amazônica. Parcerias Estratégicas, 12(2): 20-41.

MMA (1997). PCBAP - Plano de conservação da Bacia do Alto Paraguai. Programa Nacional do Meio ambiente, *Análise integrada e prognóstico da bacia do Alto Paraguai*. Brasília: MMA/SEMAM/PNMA. v.3. 370p.

MMA (2007). "Biodiversidade Brasileira: Avaliação e identificação de ações prioritárias para a conservação, utilização sustentável e repartição dos benefícios da biodiversidade brasileira," Brasília, Secretaria de Biodiversidade e Florestas. Available from <http://www.mma.gov.br>. Accessed on Nov. 2012.

Melo, G. A. R & Gonçalves, R. B. (2005). Higher-level bee classifications (Hymenoptera, Apoidea, Apidae sensu lato). Rev. Bras. Zool., 22(1): 153–159.

Michener, C. D. (2007). *The Bees of the World (2. Ed).* Baltimore, Maryland: The Johns Hopkins University Press.

Michener, C. D. (1990). Classification of the Apidae (Hymenoptera). Univ. Kansas Sci. Bull., 54(4): 75-164.

Michener, C. D. (1946). Notes on the habits of some Panamanian stingless bees (Hymenoptera, Apidae). J. N. Y. Entomol. Soc., 54(3): 179-197.

Moreno, F. A. & Cardozo, A. (2002). Biometric parameters of stingless bee (Meliponinae) colonies on trees cut for lumber in Portuguesa state, Venezuela. Livest. Res. Rural Develop.,14(6). Available from <http://www.lrrd.org/lrrd14/6/more146.htm>. Acessed on Febr. 2013.

Nascimento, D. L. & Nascimento, F. S. (2012). Extreme effects of season on the foraging activities and colony productivity of a stingless bee (*Melipona asilvai* Moure, 1971) in Northeast Brazil. Psyche, 2012. doi:10.1155/2012/267361

Nogueira-Neto, P. (1997). *Vida e Criação de Abelhas indígenas sem Ferrão*. São Paulo: Nogueirapis.

Normandes-Silva, M. & Pivello, V. R. (2009). Conservation of the vegetation remaining of cerrado and land use in Bonito, Mato Grosso do Sul, Brazil. Rev. Bras. Agroecol., 4(3): 86-96.

Nunes-Silva, P., Hilário, S. D., Filho, P. de S. S. & Imperatriz-Fonseca, V. L. (2010). Foraging activity in *Plebeia remota*, a stingless bees species, is influenced by the reproductive state of a colony. Psyche, 2010. doi:10.1155/2010/241204.

Oliveira, M. L., Morato, E. F. & Garcia, M. V. B. (1995). Diversidade de espécies e densidade de ninhos de abelhas sociais sem ferrão (Hymenoptera, Apidae, Meliponinae) em floresta de terra firme na Amazônia Central. Rev. Bras. Zool., 12(1): 14-24.

Rasmussen, C. (2004). A stingless bee nesting with a paper wasp (Hymenoptera: Apidae, Vespidae). J. Kans. Entomol. Soc., 77: 593-601.

Rasmussen, C. & Camargo, J. M. F. (2008). A molecular phylogeny and the evolution of nest architecture and behavior in *Trigona s.s.* (Hymenoptera: Apidae: Meliponini). Apidologie, 9: 102-118.

Roubik, D. W. (1983). Nest and colony characteristics of stingless bees from Panama (Hymenoptera: Apidae). J. Kans. Entomol. Soc., 56: 327-355.

Roubik, D. W. (1989). *Ecology and Natural History of tropical bees*, Cambridge Univ. Press (USA).

Roubik, D. W. (2006). Stingless bee nesting biology. Apidologie, 37: 124-143.

Serra, B. D. V., Drummond, M. S., Lacerda, L. de M. & Akatsu, I. P. (2009). Abundância, distribuição espacial de ninhos de abelhas Meliponina (Hymenoptera, Apidae, Apini) e espécies vegetais utilizadas para nidificação em áreas de cerrado do Maranhão. Iheringia, Ser. Zool., 99(1): 12-17.

Silveira, F. A., Melo, G. A. R. & Almeida E. A. B. (2002). Abelhas Brasileiras, Sistemática e Identificação, Fundação Araucária.

Siqueira, E. L., Martines, R. B., Nogueira-Ferreira, F. H. (2007). Ninhos de Abelhas Sem Ferrão (Hymenoptera, Meliponina) em uma região do rio Araguari, Araguari-MG. Biosci. J., 23(1): 134-140.

Velthuis, H. H. W., Koedam, D. & Imperatriz-Fonseca, V. L. (2005). The male of *Melipona* and other stingless bees, and their mothers. Apidologie, 36: 169-185.

Wille, A. (1983). Biology of the stingless bees. Annu. Rev. Entomol., 28: 41-64.

Wille, A. & Michener, C. D. (1973). The nest architecture of stingless bees with special reference to those Costa Rica (Hymenoptera, Apidae). Rev. Biol. Trop., 219(1): 1-278.

This article has supplementary material that can be downloaded from:

http://periodicos.uefs.br/ojs/index.php/sociobiology/rt/suppFiles/28/0

doi: 10.13102/sociobiology.v60i4.421-428.s28