

Original Article

GEOGRAPHIC RANGE AND NEST ARCHITECTURE OF *CEPHALOTRIGONA CAPITATA* SMITH, 1854 (APIDAE: MELIPONINI) IN THE STATE OF BAHIA, NORTHEASTERN BRAZIL

Rogério M. D. O. Alves^{1,2}Ana M. Waldschmidt³Joana F. Paixão^{1*}Daiane R. Santos⁴Carlos A. L. Carvalho²¹Instituto Federal de Educação, Ciência e Tecnologia Baiano, Catu-Ba, Brazil²Grupo de Pesquisa Insecta, Universidade Federal do Recôncavo da Bahia, Cruz das Almas-BA, Brazil³Departamento de Ciências Biológicas, Universidade Estadual do Sudoeste da Bahia, Jequié-BA, Brazil⁴Universidade Estadual de Feira de Santana, Feira de Santana-BA, Brazil

*corresponding author: jopaixao80@gmail.com

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Abstract

The bees of the genus *Cephalotrigona* (locally known as “mombucas”) play a key role in natural environments but their bioecological features, required to design proper management and conservation strategies, are scarce in most species. Thus, the goal of the present study was to map the occurrence sites of *C. capitata* in the state of Bahia, northeastern Brazil, and to provide useful information about nest architecture to their technical management. This species was recorded in fifteen municipalities in Bahia, totaling forty-one nests. The range of *C. capitata* varied from locations at sea level to seasonal ombrophilous forests at an altitude of 600 m high. The nests were built in trees with a mean diameter of 19.8 ± 3.0 cm. The nest architecture was similar to that reported in other stingless bee species, with a variation in analyzed parameters. The thermoregulation was more efficient in highly populated boxes. The present results can be used for the conservation and management of this species, which represents a potential source of income for local farmers.

Keywords: Apidae, bionomics, meliponiculture, meliponini, stingless bees

INTRODUCTION

The *Cephalotrigona* stingless bees (Apidae: Meliponina), popularly known as “mombucas” in Brazil, are recorded widespread throughout Central and South America, in Mexico, Nicaragua, Costa Rica, Panama and Colombia. They are typically found in such areas of dense vegetation as Atlantic Rainforest, Seasonal Forests and Amazon Rainforest (Roubik, 1983; Quezada-Euán, 2005). In Brazil, two species *C. capitata* Smith, 1874 and *C. femorata* Smith, 1854 have been reported (Schwarz, 1948; Silveira, Melo, & Almeida, 2002). The range of both species include the state of Amapá, Pará (northern region), Ceará (northeastern region),

Mato Grosso (Central Brazil), Espírito Santo, Minas Gerais, São Paulo (southeastern region), Paraná, and Santa Catarina (Southern region) (Silveira, Melo, & Almeida, 2002; Camargo & Pedro, 2017). The occurrence of these species in Bahia has not been recorded so far. The first report about *C. capitata* (cited as *Trigona capitata*) in Brazil was carried out by Ihering (1903) who described their nesting sites and nest traits. Bionomic data about *Cephalotrigona* reported by Zwaal (1992) was based on a species found in Mexico. Authors Sakagami, Beig, & Kyan (1964) analyzed the oviposition process in *C. Capitata femorata*. Even though reports about the occurrence of *Cephalotrigona* spp. in Brazil are available, little is known about the ar-

chitecture of their nests. Therefore, the goal of the present study was to report the occurrence and determine the range of *C. capitata* in the state of Bahia, northeastern Brazil and provide information about the nest architecture to be used in the sustainable management and conservation of this species.

MATERIAL AND METHODS

The records of *C. capitata* were based on interviews, location and rescue of nests, as well as collection of specimens on flowers with the use entomological nets. The analyzed nests were found in trees and rustic boxes, and the coordinates of their locations were obtained through GPS (Global Position System) and SEI (2015) dataset. Dr. J.M.F. Camargo (USP-FFCLRP-1992) as *C. capitata* Smith, 1874, identified the collected bee samples from Canavieiras-BA while Dr. Favizia Freitas de Oliveira (UFBA) identified the specimens from Mundo Novo-BA. The vegetal species herein cited was sampled and sent to identification in the IBGE-RADAM herbarium.

Nest architecture was evaluated based on nesting substrate (diameter and size of trunk cavities and wood thickness), diameter of honey combs, number of food pots and population estimates. The dimensions and internal components of nests were measured with a tape measure, honey amount in pots was estimated with graduate syringes and pollen amounts in pots were estimated with a portable digital scale (Alves, Carvalho, & Souza, 2003; Barbosa et al., 2013). The mean and standard deviation values were calculated for each parameter using the BioEstat v. 5.0 software.

RESULTS

Distribution range

Cephalotrigona capitata was sampled in fifteen municipalities from the state of Bahia (Tab. 1). The estimated range comprises 3.59% of Bahia territory (Fig. 1). Forty-one nests, the largest abundance, were reported in Mundo Novo, Gandu, Igrapiúna, and Wenceslau Guimarães. Eight of those from trees plus two from rustic boxes

were rescued and evaluated in the municipalities of Amargosa, Canavieiras, Gandu, Mundo Novo, Taperoá, and Wenceslau Guimarães (Tab. 1; Fig. 1). The altitude in which the species was sampled ranged from the sea level (Canavieiras) to 600 m high (Mundo Novo) in seasonal forest domains.

Nesting

Nests of *C. capitata* were found in wide hollows of living trees with a large diameter and thick wood (Tab. 2). Only a single colony was observed in openings previously used by *Melipona mondury* in a dead tree of the species *Tapirira guianense* Aubl. Their nests were found in the following tree species characterized by great heights, large trunk diameters and thick wood: *Mimosa* sp. in Cravolândia, *Parkia pendula* and *Sclerolobium* sp. in Taperoá and Igrapiúna, *Tapirira guianense* in Gandu and Wenceslau Guimarães, and *Jacaranda caroba* in Igrapiúna and Camamu.

Nest entrance

The entrance of the evaluated nests were hardly visible, with elongated to dished external structures depending on the colony. Nonetheless, most nests did not present obvious entrances, composed of solid dark resin (Fig. 2). The entrance tube was short and narrow, built from dark cerumen, opening into the nest periphery. In this study, many bees were observed around the tube. Internally, the tube would end in a gallery 21 cm in length and 18 cm in diameter formed by a highly compact and hard material. The entrances of colonies were located between 0.5 to 5.0 m above the ground, with a mean value of 2.83 ± 0.25 m, thus showing the preference of large trees to their nesting. The orifice diameter presented a mean value of 0.88 ± 0.05 cm, usually guarded by a single bee, always located on the internal part.

Defenses

The bees usually defend themselves when disturbed, even in highly populated colonies with large amounts of honey. Some individuals of *C. capitata* were observed on animal feces in Cocos-BA, which usually occurs when there is resources scarcity.

Table 1.
Localities with records of *Cephalotrigona capitata* in the state of Bahia, northeastern Brazil (altitude, latitude, longitude, amount of nests, year, climate, vegetation, mean temperature, and rainfall)

Municipalities	Altitude (m)	Latitude	Longitude	Number of nests (units)	Year	Climate	Main vegetation	Mean temperature (°C)	Rainfall (mm)
Amargosa	400	13°01'09"	39°36'17"	02#/01*	2008	Subhumid to dry	Seasonal forest	21.8	960
Camamu	40	13°56'41"	39°06'14"	02**	2015	Humid to subhumid	Dense ombrophilous forest	24.6	2340
Canavieiras	4	15°40'30"	38°56'50"	02*	1992	Humid to subhumid	Ombrophilous forest	24.1	1739
Cravolândia	477	13°21'31"	39°48'54"	02**	2006	Semiarid/ Subhumid to dry and humid	Seasonal forest / Ombrophilous forest	21.2	753
Cocos	559	14°11' 02"	44°32' 04"	01***	2015	Subhumid to dry and humid	Open Cerrado Park with Gallery forests	23.7	909
Gandu	164	13° 44' 38"	39° 29' 12"	02#/02**01*	2014	Humid to subhumid	Ombrophilous forest	22.8	1449
Igrapiúna	48	13°49'35"	39°08'32"	02*/05**	2015	Humid to subhumid	Dense ombrophilous forest Primary formations Coastal	24.5	2183
Jequié	215	13° 51'27"	40°05'01"	01**	2010	Semiarid and humid	Caatinga/ Seasonal forest	23.2	696
Mundo Novo	604	11° 51' 32"	40°28'21'	02*01**/01#	2002/2006	Semiarid, subhumid to dry	Seasonal forest	22.1	875
Nova Ibiá	292	13°48'36"	39°37'32"	01*	2015	Humid to subhumid	Dense ombrophilous forest	23	1344
Presidente Tancredo Neves	150	13°26'55"	39°25'17"	02**	2014	Humid to subhumid	Ombrophilous forest	23.0	1594
Taperoá	15	13°27'17"	39°05'55"	01#/01*	2006	Humid to subhumid	Ombrophilous forest	23.1	525
Teolândia	192	13°36'06"	39°29'29"	02# 01**	2014	Humid to subhumid	Ombrophilous forest	23.2	1461
Ubaíra	324	13°16'05"	39°39'46"	01#	2006	Subhumid to dry and humid	Ombrophilous forest	22.2	881
Wenceslau Guimarães	178	13°41'13"	39°28'46"	01*/02**/02#	2014	Humid to subhumid	Ombrophilous forest	23.6	1331

Caption: *rescued nests, **located nests, ***records of species presence, # nests in rustic boxes.

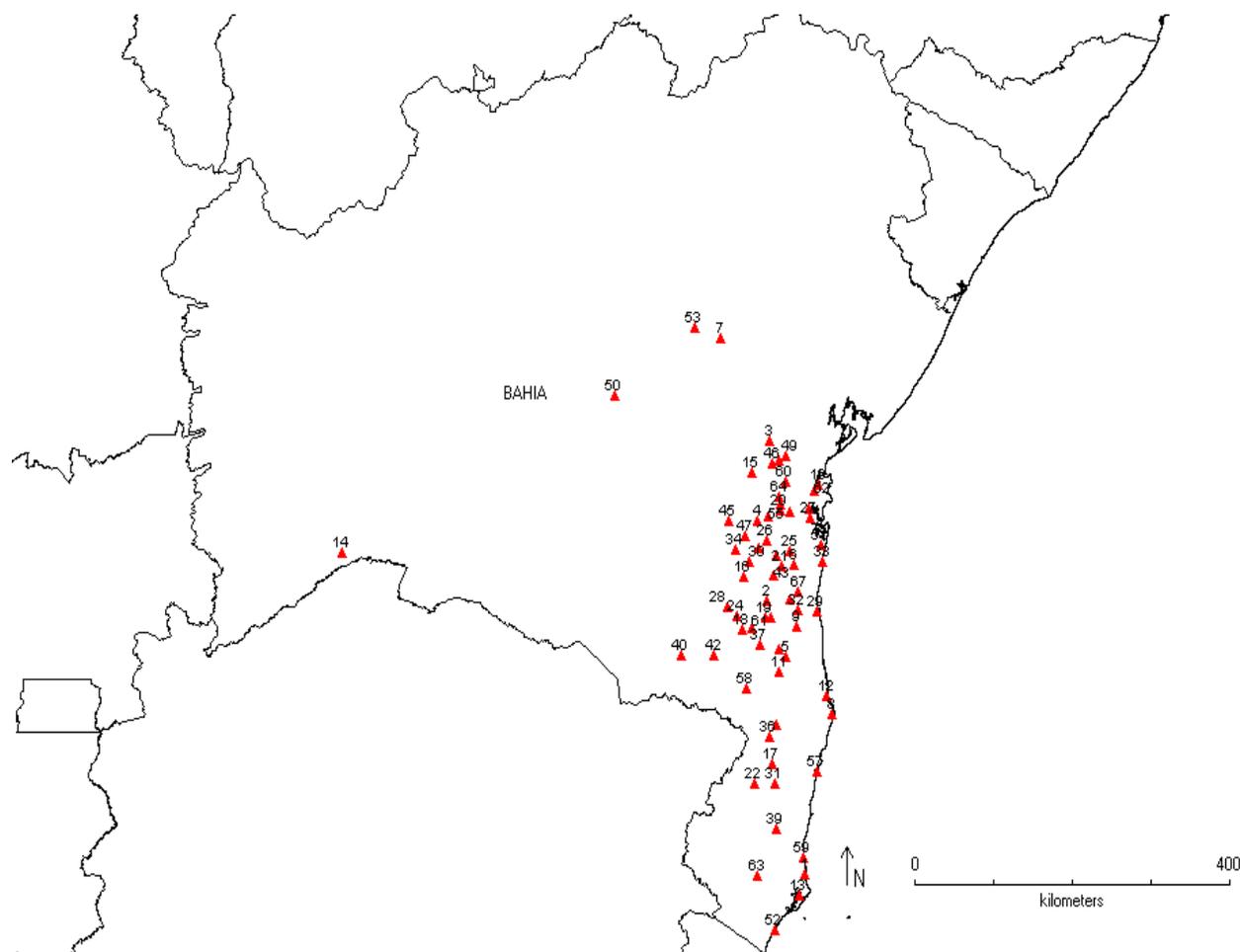


Fig. 1. Spatial distribution of *Cephalotrigona capitata* in the state of Bahia.

Counties: 1 - Alcobaça, 2 - Almadina, 3 - Amargosa, 4- Apuarema, 5- Arataca, 6 - Aurelino Leal, 7 - Baixa Grande, 8 - Belmonte, 9- Buerarema, 10 - Cairu, 11- Camacan, 12 - Canavieiras, 13 - Caravelas, 14 - Cocos, 15 - Cravolândia, 16 - Dário Meiras, 17 - Eunapólis, 18 - Firmino Alves, 19 - Floresta Azul, 20 - Gandu, 21 - Gongogi, 22- Guarantiga, 23 - Ibicaraí, 24 - Ibicuí, 25 - Ibirapitanga, 26 - Ibirataia, 27 - Igrapiúna, 28 - Iguai, 29 - Ilhéus, 30 - Ipiaú, 31 - Itabela, 32 - Itabuna, 33 - Itacaré, 34 - Itagi, 35 - Itagibá, 36 - Itagimirim, 37 - Itaju da Colônia, 38 - Itajuípe, 39 - Itamaraju, 40 - Itambé, 41 - Itapebi, 42- Itapetinga, 43 - Itapitanga, 44- Ituberá, 45 - Jequié, 46 - Jiquiriça, 47 - Jitaúna, 48 - Jussari, 49 - Laje, 50 - Lençóis, 51 - Maraú, 52 - Mucuri, 53 - Mundo Novo, 54 - Mutuípe, 55- Nova Ibiá, 56 - Piraí do Norte, 57 - Porto Seguro, 58 - Potiraguá, 59 - Prado, 60 - Presidente Tancredo Neves, 61- Santa Cruz da Vitória, 62 - Taperoá, 63 - Teixeira de Freitas, 64 - Teolândia, 65- Ubaitaba, 66- Ubatã, 67 - Uruçuca, 68 - Wenceslau Guimarães.

Involucre

The involucre in most analyzed nests contained two to three thin layers of dark cerumen covering the majority of brood combs, even in trees with increased wood thickness. In the rustic boxes, the involucre consisted of a few layers separated by air pockets. Less populated colonies had thicker involucre.

Nest

The *C. capitata* nest contained several brood combs, which varied in diameter and number

according to the hollow dimensions and the stage of colony development (Tab. 2). The food pots are frequently arranged in the ends of combs, with honey pots close to the boundaries of the hollow. The length of the nests ranged from 28 to 98 ± 7.5 cm, while the breeding and feeding areas varied from 18 to 35 cm and from 15 to 50 cm, respectively.

Brood Combs

The horizontal combs were usually rounded, even though the combs of two colonies raised

Table 2.
Evaluated parameters in nests of *Cephalotrigona capitata* from the State of Bahia (n= 10)

Parameters	Unit	Variation	Mean and standard deviation
Length of trunk cavity	cm	50.0-105.0	68.9 ±12
Trunk cavity diameter	cm	15.0-28.0	19.8 ± 3
Wood thickness	cm	8.0 -15.0	11.1 ± 2.5
Length of nest area	cm	28.0-98.0	57.7 ± 7.5
Length of brood area	cm	18.0-35.0	25.2 ± 05
Length of food area	cm	15.0-50.0	32.8 ± 8
Diameter of entrance orifice	cm	0.8-1.1	0.88 ± 0.05
Height of entrance	m	0.5 - 5.0	2.83 ± 0.25
Diameter of brood combs	cm	8.5-20.0	13.15 ± 1
Number of brood combs	Unit	6.0-19.0	12.9 ± 0
Number of honey pots	Unit	13.0-40.0	21.3 ± 9
Diameter of honey pots	cm	2.0-3.5	2.85 ± 0.25
Height of honey pots	cm	2.5-4.5	3.15 ± 0.5
Volume of honey pots	mL	10.0-19.0	14.1 ±1
Estimated honey production	L	1.0-3.5	2.07 ± 0.5
Number of pollen pots	Unit	10.0-37.0	13.4 ± 2.5
Diameter of pollen pots	cm	3.0-3.5	3.25 ± 0.5
Height of pollen pots	cm	3.0-4.5	3.65 ±0
Weight of pollen pots	G	3.5-9.27	5.97 ± 1.37
Population estimates	Unit	6,561.0-20,568.0	13,315.1 ± 3,961.5
Thickness of scutellum	cm	5.0-11.0	8.0 ± 0
Length of scutellum	cm	7.0-18.0	10.9 ± 1.5
Sugar rate	%	65.0-74.0	69.0 ± 1.0

in rustic boxes had a helical shape. The size of brood combs varied from 8.5 to 20.0 cm in diameter, with a mean value of 13.15 ± 1 cm. The number of combs ranged from six to nineteen, with a mean value of 12.9 ± 0 . Larger cells were detected in combs and up to two princesses were observed in the food pots.

Propolis and resin

Resin deposits were observed in the end of involucre in some nests. These egg-shaped deposits store a sticky resin of greenish to dark coloration. The resin is the basis for nest building. When the resin is transferred, for example, to a rational box, the process of nest regeneration is facilitated, because the workers reuse it. After rescue, the transference of the resin to the rustic boxes favored the fast organization

of nests by bees, by using the resin/propolis to caulking the orifices. Cerumen (material used by bees in the production of involucre) when new, is fine and flexible yet rigid, but the cerumen reused by the workers becomes thicker due to the accumulation of layers. The coloration results from the resin compounds and their re-utilization turns the resins darker.

Scutellum

In the boxes, the scutellum could be observed in the inferior and superior parts of nests while this structure was present only in the inferior end of nests in trunks. The mean measurements of the thickest portion of scutellum were 8 cm in thickness and 10.9 cm in length, being smaller in trunks of living trees, since scutellum has the function of thermoregulation, which is not so



Fig. 2. Entrance of *Cephalotrigona capitata* nests found in the state of Bahia.

necessary for nests occupying live trees, which provide natural protection against temperature variations (Fig. 3). In boxes kept in open areas, the scutellum was cudgel-shaped, being located at their upper parts and directed to the main wind flow. No bees were observed leaving the nests with waste.

Food pots

The food pots, large and egg-shaped, formed a compact mass in developed colonies. The pollen pots were located near the nest, as reported in other species, in lower numbers than honey pots depending on the season. However, a greater number of pollen pots than honey pots were observed in some colonies. The mean number of honey pots was 21.3 units/nest. The pots were egg-shaped and built with thick and dark cerumen, and their height ranged from 2.5

to 4.5 cm.

Production of honey and pollen

The honey production in the studied colonies ranged from 1.0 to 3.5 liters, and local people reported from 10 to 15 liters of honey removed from a single colony. The honey coloration ranged from white to pale yellow with a sour to sweet taste. The honey has high humidity, around 60 to 71% (°Bx). The size of pollen pots ranged from 3.0 to 3.5 cm in diameter and 3.5 to 4.5 cm in height. The mean weight of pollen pots was 6.76 g with a variation between 4.25 and 9.27g. The estimated pollen production varied from 67 to 210 g.

Natural enemies

In colonies transferred to wooden boxes without the replacement of scutellum, pollen pots and



Fig. 3. Aspects of scutellum in nests of *Cephalotrigona capitata* from the State of Bahia.

brood combs containing destroyed eggs or larvae, the number of phorids decreased, thus avoiding the loss of colonies.

Population

The number of individuals in ten evaluated colonies ranged from 6,561 to 21,600, with a mean population of $13,315.1 \pm 3,961.5$.

DISCUSSION

Distribution range

Knowledge about the actual distribution range of species is essential for bioecological studies and the design of proper conservation and management strategies since it increases protection of populations from potentially threatened groups (Hey et al., 2003). In the northeastern Brazilian state of Bahia, *C. capitata* was first reported to be found in rainforests or transition zones, characterized by temperatures from 15 to 30°C and thermal amplitude between 3 and 5°C, with cool nights and warm days, high humidity (70 to 90%), and rainfall ranging from 700 to 2300 mm/year (SEI, 2015). Canavieiras, 4 m above sea level, contains mainly vegetation typical of an ombrophilous forest domain with high humidity and narrow thermal amplitude. On the other hand, Cravolândia, Jequié, Mundo Novo, and Amargosa are characterized by lower humidity but the barriers of hills between high altitudes (400 to 600 m) accounts for the increased humidity and the presence of seasonal ombrophilous forests in these localities.

The municipalities of Presidente Tancredo Neves, Gandu, Wenceslau Guimarães, Ubaira, and Taperoá are mostly covered by Atlantic rainforest with a humid climate, ombrophilous vegetation and highly varied altitude from the sea level to 500 m (SEI, 2015). The municipality of Cocos represented the range limit of *C. capitata* in the State of Bahia. It is located in the western portion of Bahia with a dry climate typical of cerrado (Brazilian savannah), gallery forests and mean rainfall of 900 mm/year with a large thermal amplitude. In spite of the presence of forested areas, this region presents low humidity during extremely dry

periods. These features differ from the other localities where *C. capitata* was recorded, which probably hinder their dispersal beyond this point since the environmental conditions are not adequate for their survival.

According to Tab. 1, *C. capitata* nests were found in altitudes ranging from four to 700 metres. Thus, altitude does not seem to limit their distribution. On the other hand, the studied region has a warmer daytime temperature and colder night-time temperature, so daily temperature range seems to be a more relevant factor. This species was found occupying thick tree holes, suggesting this is a species thermoregulatory requirement.

Nesting

The nest analysis indicates that trunk thickness is essential to their nesting, since no nests of *C. capitata* were detected in thin trees. Contrary to Quezada-Euán (2005) from Mexico, colonies with nests in soil were not observed in the present study. Because of their high specificity in relation to nesting conditions and the increased human impacts of the studied region, this species is restricted to the well-preserved humid forest fragments. Apparently, *C. capitata* is not restricted to the height of nests in relation to the ground since Kerr et al. (1967) reported nests 2 m above the ground in living trees from the Amazon forest, while Nogueira-Neto (1970) described nests in trunk hollows close to the tree basis. On the other hand, large trees that provide wide hollows with thick walls are preferred by the studied species. Most likely, these conditions favor the development of high-populated colonies with a large number of brood combs.

Nest entrance

Roubik (1983) reported that aged nests had a protuberance below their entrance in which bees deposited resin. Nogueira-Neto (1970) proposed that the nest entrances represented an orifice built with dark resin mixed with wax, forming an external hardly visible and small projection without an entrance tube. Instead, the entrance is a simple orifice formed of cerumen in the knots or crevices of a trunk

(Wille & Michner, 1973).

Kerr et al. (1967) highlighted that the upper part of the entrance tube in *C. femorata* colonies was rounded (0.8 cm in diameter), while the tube was 2 cm in length, dark brown in coloration, formed from cerumen and resin and guarded by seven docile guards around it. The entrance was an ornamented orifice with dimensions slightly larger than the bee heads. Wille & Michner (1973) reported that the entrance tube in nests could reach up to 65 cm being connected to the food pots.

Although in this study the entrances of evaluated nests were not very visible and although the characteristics of the involucre may differ at different times of the year and in different environments, in general, our observations for *C. capitata* are in agreement with reports by cited authors, for other species.

Defenses

Possibly, the collection of feces by individual *C. capitata* is associated with their nest-protection behavior in dry and low humidity periods. Nogueira-Neto (1970) highlighted that this species is quite docile showing no defense strategies against disturbances. Kerr et al. (1967) reported that the bees bent their abdomen over their thorax assuming a putative defensive.

Involucre

Stingless bees do not thermoregulate their nests as precisely as honeybees do, so active behavioural efforts play a role in this activity (Vollet-Neto et al., 2015). Although meliponini species show an array of nesting and nest thermoregulatory strategies (Viana et al., 2015), their mechanisms are self-organized and arise from simple rules followed by each worker (Jones & Oldroyd, 2006).

Sakagami (1982) stressed that the involucre played a key role in the thermoregulation of colonies, particularly in the breeding areas. Nogueira-Neto (2002), Cortopassi-Laurino (2003) and Viana et al. (2015) observed that the most populous colonies to have involucres with a smaller area than the less populated,

suggesting that thermoregulation is more efficient in high-density populations. The vast majority of the analyzed nests in this study presented involucres with two to three thin layers of dark cerumen covering the brood combs. Similarly, Wille & Michner (1973) reported that the involucre had three thin layers above and a lateral layer below the combs.

In the present study, the involucre structure described for natural nests is similar to that observed in rustic boxes. The involucre is placed below a dark layer composed of cerumen and hard resin. When the boxes are opened and the upper cerumen layer is ruptured, workers come quickly carrying resin in their mandibles to repair the involucres, as reported in other bee species (Zwaal, 1992). Although the involucre characteristics may vary at different times of the year and under different environmental conditions, in general our findings for *C. capitata* are in agreement with those reported by other authors for other meliponini species.

Nest and Captive rearing

Based on the evaluated colonies (Tab. 1), we recommend that the boxes for the captive rearing of *C. capitata* should be 18.0 cm wide x 18.0 cm long with a depth of 10.0 cm per handle or module. With these dimensions and a minimum thickness of 4 cm, the boxes are able to maintain an enhanced temperature balance in the nest area, which favors colony development, reduces scutellum formation and forces the bees to build honey pots. Moreover, it is useful to place another compartment below the box (18.0 x 18.0 x 3.0 cm in height) to serve as waste disposal. This recommendation is based on trunk thickness data presented in Tab. 1, in which nests were found in live trees with trunks thicker than this value. We suggested this thickness for the boxes in order to guarantee adequate conditions for thermoregulation, since live trees allow nests to maintain a constant temperature.

Kerr et al. (1967) observed colonies with a maximum diameter of 28 cm, length of 40 cm, and a storage area of 25 cm x 10 cm. In our study, the nests were built in trees with

a mean trunk cavity diameter of 19.8 ± 3.0 cm and mean length of nest area of 57.7 ± 7.5 . In this way, our study's recordings are in agreement with the findings of these authors, since they suggest that these species require large vertical spaces for their development, while wood thickness is important for colony maintenance. However, not only the thickness of the wood provides adequate thermoregulation, but also technical management which includes feeding and reducing wind and rain incidence to the farming/rearing box.

Brood Combs

In our study, the size of brood combs varied from 8.5 to 20.0 cm in diameter (Tab. 2), which was influenced by nest development and the diameter of hollows ranging between 15.0 and 28.0 cm (Tab. 2). Some nests had from six to nineteen small combs, with an average of 12.9 (Tab. 2) because they had been built in small-diametered hollows, while well-developed nests with a large population built in big/bigger tree hollows had larger combs. These data were in agreement with findings by Kerr et al. (1967), who had analyzed the nests of this species in Amazonas and had found up to seventeen horizontal combs that reached up to 25 cm of diameter. These data are essential to define the proper dimensions of rustic boxes with the intention to rear this bee species in captivity. According to Nogueira-Neto (1970), *C. capitata* build both helical and horizontal brood combs. Similarly, in the present study combs both horizontal (most combs) and helical and real cells were detected. Zwaal (1992) observed the occurrence of royals cells built separately from the brood combs in natural colonies but not in artificial boxes. Ihering (1903) reported no royal cells, even though up to twenty princesses were found in nests, suggesting that the royal cells could have been destroyed after their emergence.

Propolis and resin

According to Kerr et al. (1967), propolis has sticky consistency covering the cerumen and stored in small amounts. Nogueira-Neto (1970)

reported that stored propolis is slightly viscous, while the batumen and caulking are composed of thick layers of dark cerumen. Thus, the observations described in our study, which also identified sticky resin of greenish to dark coloration are in agreement with other studies.

Scutellum

The scutellum is composed by residues accumulated by bees (pollen remnants, bees carcasses, broom residues and debris). This material ferments and assists in thermoregulation, and has been found at various sites within the nest (at the bottom or at the top of the nest, and sometimes close to the breeding combs). The scutellum has yellowish coloration and gives off a strong smell when managed (Zwaal, 1992). Zwaal (1992) observed that the scutellum in natural nests surrounds the breeding area, putatively acting as efficient passive thermoregulators when compared to the active thermoregulation performed by workers (Quezada-Euán, 2005).

In this work, no bees were seen carrying waste away from the nests. On the other hand, we find a lot of scutellum within the nests. This suggests that workers were using the colony residues in the scutellum production, for thermoregulation. *C. capitata* accumulates debris inside the colony in order to form scutellum, because otherwise the workers would discard it. This result is similar to the report by Zwaal (1992), while Roubik (1983) suggested that the scutellum might be involved in the protection and isolation of nests, besides serving as waste disposal.

Food pots

Nogueira-Neto (1970) described egg-shaped pots, and Kerr et al. (1967) observed that this species builds large pots about 4 cm in height, 2 cm in diameter and 3.0 cm in length. Similarly to these authors, we also found honey pots ranging from 2.5 to 4.5 cm in height and from 2.0 to 3.5 cm in diameter and pollen pots ranging from 3.0 to 4.5 cm in height and from 3.0 to 3.5 cm in diameter (Tab. 2).

Production of honey and pollen

Ihering (1903) and Nogueira-Neto (1970) found that *C. capitata* produced high amounts of honey and pollen, and Roubik (1983) reported in Panama a level of honey production ranging from 175 mL to 2,230 mL but poor in taste. In our study, we observed that during the period of data collection, according to the period of the year, the number of pollen pots was superior to those of honey. Thus, the reduced honey production by *C. capitata* colonies coincided with the reduced pasture areas for these bees. In general, the lowest number, diameter, weight, volume and estimated production of the honey pots presented in the Tab. 2 corresponded to the last years of data collection, period coinciding with the increase in deforestation in the studied region as well as the expansion of agriculture and livestock. Deforestation and agricultural expansion also have been cited by Costa et al. (2014) and Brown & Albrecht (2001) as factors that affected the conservation and management of Brazilian native bee species.

Natural enemies

The phorid *Pseudohyocera kerteszi* is considered the main pest of nests of *Cephalotrigona* spp. and other stingless bee species (Sakagami, Beig, & Kyan, 1964). To prevent attacks from these enemies, *Cephalotrigona capitata* build a narrow entrance orifice guarded by one or two bees and a long entrance tube with watchers along it. Some species build cavities that reduce exposure to predators by constructing narrow and long tubes (Roubik, 1983). However, because guard bees move slowly, phorids are able to invade less populous colonies, which do not defend as well as colonies more populous.

The removal of waste would help to avoid attracting parasitic phorids, which can harm a colony. Waste provides a substrate on which potentially harmful microorganisms thrive (Medina, Hart, & Ratnieks, 2014). It contains scutellum stored by the bees, and phorids are attracted by the smell of fermented scutellum. Other species throw the waste but not *C. capitata*. Therefore, the loss of swarms is commonly due to phorid

attacks. In our study, in several colonies were not attacked when waste was removed.

Population

The highly populated colonies in this study was associated with such environmental conditions as natural or slightly disturbed forested areas with a large number of plants producing trophic resources (Zwaal, 1992). Lindauer & Kerr (1960) estimated the nest population from 1,000 to 2,000, and Nogueira-Neto (1970) reported that in strong colonies this number could be much higher. Among the species of meliponines, bees that present larger body size tend to present relatively smaller population size. However, this did not occur with *C. capitata*, which, despite being considered a large body size meliponine, presented populous colonies (Tab. 2) when compared to other meliponines.

Captive rearing

To keep these bees in artificial boxes, the wood thickness and isolation protective mechanisms must be maintained. Roubik (1983) stressed the importance of choosing a hard and thick wood type. Many adaptation issues have been reported in colonies kept in wooden boxes, particularly related to thermoregulation. Zwaal (1992) observed that colonies would disappear shortly when kept in 2 cm thick boxes. If the room temperature remained stable at 21°C the nests did not perish, but when the temperature was below 21°C, the mortality of offspring increased because of their deficiency in maintaining the internal temperature. Therefore, insufficient thermal insulation in boxes is a limiting factor for the captive rearing of this species.

Damasco, Nunes, & Jarduli (2012) reported that in a nest of *C. capitata* captured in Paraná, the swarm was transferred to a wooden box equipped with a waste disposal for residues and formation of scutellum. This adaptation was successful, since the "trash basket" could be replaced by a clean one when it was infested with Phorid larvae, keeping the brood combs safety.

Cephalotrigona capitata were found in wide hollows and thick wood of living trees. Most did

not have obvious entrances and were located between 0.5 and 5.0 m above the ground. This species occupied well preserved stretches of forests that corresponded to the distribution of forested areas of semi-humid to humid climate, characterized by wide thermal variation, with colonies found from sea level to high altitude sites.

The involucre in most analyzed nests had two to three thin layers of dark cerumen covering the majority of brood combs, which were thicker in less populated colonies. The brood combs' diameter and number varied according to the hollow dimensions and the stage of colony development. The food pots were large and egg-shaped and the mean number of individuals in ten evaluated colonies was of $13,315.1 \pm 3,961.5$. From this information, efforts can be made to reproduce in wooden boxes the closest conditions possible to the natural in order to obtain better colony productivity in captive rearing. Based on the plant species most occupied by *C. capitata* and on the aspects related to their bionomics, it will be possible to establish strategies for the conservation of this bee species.

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