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Nesting and reproductive habits of the solitary bee *Centris analis* in trap nests under a tropical climate[1]

Hábitos de nidificação e reprodutivos da abelha solitária *Centris analis* em ninhos-armadilha sob clima tropical

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ABSTRACT - Pollination is a key factor in global agricultural production, and there is a need to increase the number of bee species that can be bred for pollination in agriculture, such as the oil-collecting solitary bee *Centris* (*Heterocentris*) *analis* (Fabricius, 1804). In this study, the nesting and reproductive behavior of the bee were studied under tropical conditions, with the aim of producing information for breeding and using *C. analis* for crop pollination. The study was conducted from May to October 2017, using trap nests and daily observations from 5.00 a.m. to 6.00 p.m. of nest occupation and building, foraging trips in the field and interactions between individuals and kleptoparasites. The results showed that the bees easily colonize and nest in trap nests for an extended period of the year under tropical conditions, and that the use of this type of nest makes it possible to multiply populations of this species for their potential use in crop pollination. However, sources of floral oil and the availability of nesting sites have both proved to be limiting factors to population growth in this species on bee farms.

Key words: Centridini. Solitary bees. Oil-collecting bee. Bee farming.

RESUMO - A polinização é um fator essencial na produção agrícola mundial e existe a necessidade de aumentar o número de espécies de abelhas que podem ser criadas para a polinização na agricultura, como a abelha solitária coletora de óleo *Centris* (*Heterocentris*) *analis* (Fabricius, 1804). Aqui, os comportamentos de nidificação e reprodutivo dessa abelha sob condições tropicais foram estudados com o objetivo de produzir informações para o criatório e uso de *C. analis* na polinização agrícola. O estudo foi conduzido de maio a outubro de 2017 usando ninhos armadilhas e observações diárias das 5 as 18h sobre a ocupação e construção dos ninhos, viagens de forrageamento ao campo e interações entre os indivíduos e cleptoparistas. Os resultados mostraram que as abelhas colonizam e nidificam facilmente em ninhos-armadilha por um longo período do ano, sob condições tropicais, e a utilização desse tipo de ninho possibilita multiplicar populações dessa espécie visando seu uso potencial na polinização agrícola. No entanto, tanto as fontes de óleos vegetais como a disponibilidade de locais para nidificação se mostraram fatores limitantes ao crescimento populacional dessa espécie em criatórios.

Palavras-chave: Centridini. Abelhas solitárias. Abelha coletora de óleo. Criação de abelhas.

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INTRODUCTION

Pollination is a key factor in global agricultural production and is important in the production of various crops. Among pollinators, bees are the most important, as they visit many flowers to obtain the resources they need to live (FREITAS; IMPERATRIZ-FONSECA, 2005).

However, few bee species are bred for pollination, and such management is basically carried out with bees such as *Apis* (SOUSA *et al*., 2014) and *Bombus* (YANKIT *et al*., 2018), and some solitary species, such as bees of the genus *Osmia* (SEDIVY; DORN, 2014), and the families *Halictidae and Megachilidae* such as, *Nomia melaneri* and *Megachile rotundata* (CANE; DOBSON; BOYER, 2017) in temperate regions.

In tropical climates, the most promising solitary bees for use in pollination are species of the genus *Xylocopa* (FREITAS; OLIVEIRA FILHO, 2003) and oil-collecting bees of the genus *Centris*, such as the species *C. tarsata* (GONÇALVES; SILVA; BUSCHINI, 2012), *C. aenea* (FERREIRA *et al*., 2013) and *C. analis* (OLIVEIRA; SCHLINDWEIN, 2009).

The nesting habits of oil bees that nest in pre-existing cavities have been studied by means of the trap-nest technique, which basically consists of using cardboard tubes of various diameters inserted into holes drilled in blocks of wood for the bees to nest in (AGUIAR; MARTINS, 2002; VIEIRA DE JESUS; GARÓFALO, 2000). Of this group, the species *Centris* (*Heterocentris*) *analis* (Fabricius, 1804) (Apidae: Centridini) has been researched, especially their nesting and reproductive habits. However, these studies have focused on the southeastern region of Brazil (ALONSO; SILVA; GARÓFALO, 2012; GAZOLA; GARÓFALO, 2009; MOURE-OLIVEIRA *et al*., 2017; VIEIRA DE JESUS; GARÓFALO, 2000), with few investigations in the northeast, where the climate is tropical and climate conditions show far less variation throughout the year (OLIVEIRA; SCHLINDWEIN, 2009; PINA; AGUIAR, 2011). Preliminary studies of this bee species show that it has the potential for large-scale breeding, with the aim of using it in the pollination of various agricultural crops (FREITAS *et al*., 2014; MAGALHÃES; FREITAS, 2013; OLIVEIRA; SCHLINDWEIN, 2009). As such, the present study sought to investigate the nesting behavior of *C. analis* under tropical climate conditions, from the search for a nest to the collection of resources for construction and for food supply, in addition to the period the bees are active during the year, with the aim of generating information to make possible the rational breeding and use of this species in crop pollination in the northeast of Brazil.

MATERIAL AND METHODS

Experimental area

The experiment was carried out from May to October 2017 in the Bee Unit of the Department of Animal Science, at the Center for Agricultural Sciences, Federal University of Ceará, Pici Campus, in the municipality of Fortaleza (3°44’33.70” S, 38°34’45.46° W). The experimental area is inserted in a region of warm sub-humid tropical climate, classified as Aw’ according to the Köppen classification (1918). Rainfall predominates from January to May, with an average rainfall of 1338.0 mm and average temperatures of 26 ºC to 28 ºC. The vegetation is characterized as Tabuleiro Forest, belonging to the Vegetation Complex of the Coastal Zone (IPECE, 2016). The study site is surrounded by urban areas with a small fragment of this type of forest, where it is possible to find species of native and exotic plants.

Nests

The experimental design consisted of five blocks of wood, installed 90 cm from the ground and protected from rain and sun by roof tiles. The blocks contained a total of 333 cavities, where 287 trap nests (TN) were distributed, made of black cardboard, 12.0 cm in length and 0.5 cm in diameter.

In order to follow the working routine of the bees, from searching for a nest to collecting resources, the nests were watched continuously from dawn (5.00 a. m.) to dusk (6.00 p. m.) from May to October 2017. During these observations, data were collected on the behavior of the bee while searching for and occupying the nests, the number of nests under construction and nests begun each day, as well as the total number of nests each day, the average number of trips made by the bee to the field during the day to collect each floral resource, and the occurrence of parasitism and nest usurpation.

Throughout the study, after closure of the trap nests and a further period of 15 to 20 days, they were removed from the wooden blocks, labeled with information concerning their original position in the blocks, and packed in tubes of transparent plastic, which were closed with cork stoppers and voile fabric. The tubes with the closed TN were taken to the Bee Analysis Laboratory and placed in a temperature-controlled incubator (27 °C) and inspected daily. Each time a bee emerged from a nest, the sex and number of the individual was noted according to the label, and the insect was then released into an area close to the blocks in the experimental area. The emergence of parasites was also noted. Once all the adults from one nest had emerged, it was opened to obtain data on the number of cells, the size of the brood cells and the size of the vestibule cell (empty space between the last constructed brood cell and the nest closure). Each completed TN was replaced by a new one of the same diameter and length to ensure their continued availability.

Statistical analysis

Data on the number of nests under construction and of nests begun each day, the total number of nests each day (under construction + new cells begun that day), the number of cells, the cell size, size of the vestibule cell, sex ratio, parasitism and nest usurpation were evaluated using descriptive statistics.

For the data on the number of cells, cell size, size of the vestibule cell and sexual ratio, the Pearson correlation test was carried out using the SAS statistical software. The relationship between climate factors (temperature, precipitation and wind speed) and the collection of floral resources (oil, pollen, nectar and plant material) was evaluated by the Pearson correlation test using the SAS statistical software. An analysis of variance was carried out using the Tukey mean-value comparison test at 5% for the mean number of trips to the field made by *C. analis* throughout the day to collect each floral resource.

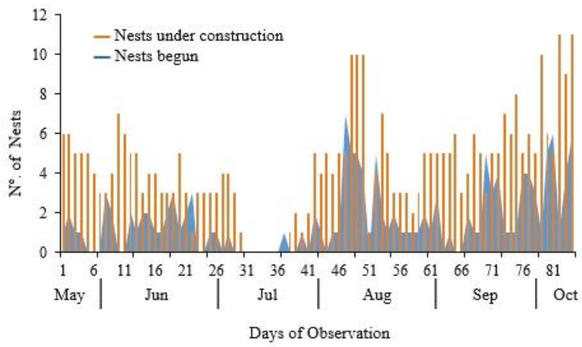
RESULTS AND DISCUSSION

Nesting

The *Centris analis* bee displayed colonization and nesting throughout the period under evaluation, from May to October, except for 6 consecutive days in the middle of July (Figure 1). However, this is not an established pattern for the species, since in the southeast of Brazil, the species does not nest during the cold months of the year (ALONSO; SILVA; GARÓFALO, 2012; MOURE-OLIVEIRA *et al*., 2017; VIEIRA DE JESUS; GARÓFALO, 2000; ALONSO; SILVA; GARÓFALO, 2012; MOURE-OLIVEIRA *et al*., 2017). Even in the northeast of the country, but at a higher Latitude than in the present study, Lima *et al*. (2017), studying this bee for the same period in a fragment of Atlantic forest in Salvador, in the State of Bahia, found nesting during May and October only. Apparently, environmental conditions influence the reproductive activity of *C. analis* throughout the year, with higher temperatures being a determining factor for nesting in this species.

Throughout the experiment, the number of nests under construction each day varied from 0 to 11, with a peak on October 19 and 21. The number of new nests begun each day ranged from 0 to 7, with a peak on August

Figure 1 - Number of trap nests (TN) of the *Centris analis* bee under construction each day and number of nests begun per day, in the Bee Unit, Pici Campus/UFC, from May to October 2017, in Fortaleza, Ceará



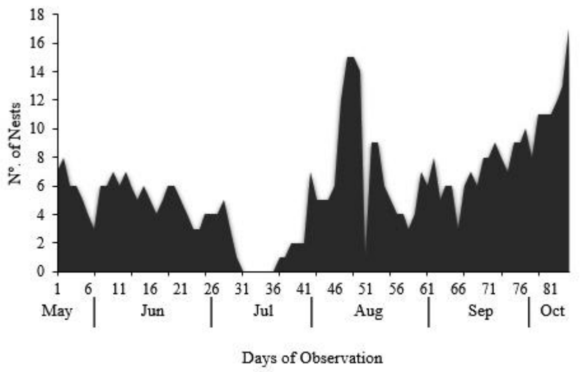
8 (Figure 1). Daily peaks for the total number of nests (under construction + new cells begun that day) occurred in August and at the end of September and October (Figure 2). The maximum number of TN with bee activity was 17 on October 21, followed by August 9 and 10 with 15 TN. The minimum number was 1, on July 6, 13 and 14, days that preceded and followed the short period of six days when there was no activity in the nests, and also on August 12 (Figure 2).

During nest-building, the bees constructed from 1 to 3 cells per day, however, during the period of observation, it was more common for the female to construct only one cell per day. The average time required to build a nest was 3.22 ± 1.27 days.

Once all the brood cells in the nest were finished, a space was left by the bees between the last brood cell and the nest closure, known as the vestibule cell (VIEIRA DE JESUS; GARÓFALO, 2000). It is the last cell of the nest and has no food supply or place to deposit eggs. The size of the vestibule cell ranged from 0.8 cm to 10.5 cm, with a mean of 3.59 ± 1.91 cm, depending on the amount and size of the brood cells constructed by the female. The vestibule cell was found in every nest and is very common in nests of solitary species (ALVES-DOS-SANTOS; MACHADO; GAGLIANONE, 2007; OLIVEIRA, SCHLINDWEIN, 2009; VIEIRA DE JESUS; GARÓFALO, 2000).

Once the nest was closed, the time for the first individual to appear was from 27 to 37 days, with birth being more frequent on the 33 rd or 34 th day. The males were always the first individuals to emerge, due to the female of the species constructing cells that give rise to males in the final portion of the nest, closer to the outside (ALVES-DOS-SANTOS; MACHADO; GAGLIANONE,

Figure 2 - Total number of trap nests (TN) (nests under construction + nests begun) used by the *Centris analis* bee per day, in the Bee Unit, Pici Campus/UFC, from May to October 2017, in Fortaleza, Ceará



2007; MOURE-OLIVEIRA *et at*., 2017). There was a difference of zero to four days between the first offspring to emerge and the birth of the last, the most frequent interval being 1 or 2 days.

The mean number of individuals born was 2.87 ± 1.39 for males and 1.54 ± 0.98 for females. In 26.32% of the nests, only one sex was born, with only 60% being male bees. As an example, there was a maximum ratio of 4 males to no females. In nests with both sexes, a quarter of them had an equal number of male and female individuals. In the remaining nests, 57.14% of the predominant individuals were males, and in 17.86%, more females emerged than males. The sex ratio of the nests was 1.7♂:1♀. However, the sex ratio is not fixed for solitary-bee species, and may vary according to the availability of resources, temperature, parasitism, and the diameter and length of the TN (AGUIAR; MARTINS, 2002; ALONSO; SILVA; GARÓFALO, 2012; MOURE-OLIVEIRA *et al*., 2017).

The number of cells ranged from 1 to 8 in the 38 trap nests evaluated, with a mean length of 4.83 ± 1.57 cm. However, the number of cells per nest seems to vary greatly in *C. analis*, since there are reports of up to 16 cells in a single nest, albeit under different ecological and nesting conditions to the present study (MOURE-OLIVEIRA *et al*., 2017). As such, although more active during most of the year, *C. analis* seems to construct a smaller number of cells per nest under tropical conditions than in milder climates, when its reproductive activity is concentrated over a shorter period.

Cell size varied from 0.8 to 2.5 cm, with a mean of 1.37 ± 0.33. Variations in the size of constructed cells were also found in other studies of this bee, suggesting that there is also no standard cell size (AGUIAR; GARÓFALO; ALMEIDA, 2005; ALONSO; SILVA; GARÓFALO, 2012). The availability of resources and the number of constructed cells seem to influence the size of the cells built in each nest (Table 1).

The number of cells built per nest showed an inverse correlation with the size of the brood cells and the vestibule cell, but a direct correlation with the number of males and females produced. Therefore, the higher the number of cells built per nest, the smaller the size of these cells and the vestibule cell, while the number of bees and of males and females born per nest obviously increased. This increase was higher for males than for females due to the 1.7♂:1♀ ratio mentioned above. However, the size of the brood cells and of the vestibule cell also had a negative correlation with the number of males and females, being larger for the former than for the latter, probably because the males, due to their larger size, are more sensitive to the size of the cell where they develop and need larger cells than do the females. Only the number of emerged males and females showed no degree of correlation (Table 1).

Plant resources

The species *C. analis* are oil-collecting bees and use this resource in both coating and waterproofing the nest, as well as in cell and nest closure. This resource was the first to be collected to begin nest construction. Next, the bee collected plant material, which consisted of pollen,

Table 1 - Correlation of cell number, cell size, vestibule-cell size and number of emerged males and females in trap nests of the *Centris analis* bee, Pici Campus/UFC, from August to October 2017, in Fortaleza, Ceará

	Cell size	Vestibule-cell size	Nº. of males	Nº. of females
Nº. of cells	-0.5011**	-0.7406**	0.8098**	0.3806**
Cell size		0.3529**	-0.3874**	-0.2363*
Vestibule-cell size			-0.7086**	-0.2688*
No. of males				-0.0750

*P<0.05; **P<0.001

anther fragments, filaments, scrapings from pollen sacs and fibers. This material is used to construct the walls of the nest and the closure of the cells and nest (VIEIRA DE JESUS; GARÓFALO, 2000). However, before closing each cell, the bee collected food to supply the young, first pollen and then nectar. Although the number of trips to collect the same resource varied each day, the bees averaged 3.72 ± 1.34 trips to collect oil, 4.37 ± 1.81 trips to collect plant material, 10.36 ± 3.53 trips for pollen and 5.43 ± 1.60 for nectar for every nest constructed. These values are similar to those observed for the same bee species, albeit under the subtropical conditions of São Paulo (VIEIRA DE JESUS; GARÓFALO, 2000).

Correlating the collected resources with the climate factors, there was a direct relationship between the individual resources and the total collected (Table 2). The search for each resource followed a logical order for constructing cells and supplying food, and therefore, over the course of the day, all the resources were collected by the bee.

There was also a direct relationship between these resources and the climate factors. The temperature was directly related to the resources used to feed the offspring (pollen and nectar), as well as to the total of these resources collected, certainly because collecting pollen and nectar requires more trips, and their availability in the plant is usually influenced by the temperature at specific times of day, while the availability of oil and other plant materials is not (Table 2). On the other hand, precipitation showed a negative relation to the collection of plant material only, as it must be difficult to collect such resources when wet. Interestingly, despite the reverse being expected, wind speed had a positive influence on pollen collection, since this is an activity where the bees need to glide frequently over the flowers while packing the pollen into their corbiculae, and stronger winds would hamper this process (DUTRA; MACHADO, 2001) (Table 2). The relationship between climate factors and the abundance of nests, and consequently the collection of floral resources, has been reported in other studies on solitary bees (AGUIAR; MARTINS, 2002; ARAÚJO; LOURENÇO; RAW, 2016); however Gazola and Garófalo (2009) state that climate stability results in population stability.

Foraging activities

The bees always started their activities early, just after sunrise, between 5.00 a. m. and 6.00 a. m. The time of the first recorded departure was at 4.53 a. m. (October 19), but there was one day when the bees only started their activities at 9:07 a. m. (July 25). The end of activities was generally in the late afternoon, between 4.0 p. m. and 5.0 p. m. The latest recorded time was at 5.31 p. m. (August 1 and 9), but on one day, the bee ended its activities near the end of the morning, at 11:41 a. m. (September 27).

The maximum time for the bees to remain in the nest was 360 minutes (October 23). Whereas, the maximum time for remaining in the field was 262 minutes (June 6). For each of these maximum times, pollen was the resource being collected. The minimum time in the nest and in the field for both nests was one minute. It is important to note that as the observations were mainly made during the dry season, there was no influence from rainfall on the bees visiting the flowers. There was no significant difference in either the time in the nest or the time in the field during the months under observation. The time spent in activities both inside and outside the nest was very relative and could be altered by any form of interference during the day, as for example, a variation in climate factors or possible nest invasion (parasitism or usurpation), as also observed by Oliveira and Schlindwein (2009).

It was found that the bees collected all the resources at all the times under study throughout the day. However, they showed a significant preference ($p<0.05$) for collecting certain resources at certain times of the day (Table 3). As such the greatest search for pollen, nectar and plant material took place in the morning, with more foraging between 5.00 a. m. and 7.00 a. m. for pollen, between 6.00 a. m. and 8.00 a. m. for nectar, and

Table 2 - Correlation of the resources collected by the *Centris analis* bee with climate data from May to October 2017, Pici Campus/UFC, in Fortaleza, Ceará

Plant Material	Pollen	Oil	Nectar	Total Collected	Temp. (°C)	Precip. (mm)	Wind (Km/h)
	0.85303**	0.88114**	0.83611**	0.92875**	0.21705	-0.22084*	0.17582
Pollen		0.85361**	0.87120**	0.96598**	0.30525*	-0.19398	0.22031*
Oil			0.89055**	0.93924**	0.18645	-0.20296 -	0.19058
Nectar				0.94551**	0.23853*	0.13959	0.18190
Total Collected					0.26637*	-0.19786	0.20833

*P<0.05; **P<0.001. Temp.: temperature; Precip.: precipitation; Wind: wind speed between 7.00 a. m. and 9.00 a. m. for plant material. On the other hand, oil was mainly collected in the afternoon (Table 3).

There are no studies investigating specific times for resource foraging by *C. analis* or other Centridini. However, the present study seems to confirm that these bees avoid doing most of their foraging during periods of higher temperature. In some studies however, they display peaks of activity in the field between 10.00 a. m. and 12.00 a. m.(SOUZA *et al*., 2016) or 11.00 a. m. and 2.00 p. m. (DUTRA; MACHADO, 2001) when the temperatures are higher, while Siqueira *et al*. (2011) in a study in Petrolina, Pernambuco, a place with much higher average temperatures, saw greater foraging during the early morning, as was found in the present study. During the hottest periods of the day, the bees were seen to remain longer in the nest, resulting in a fall in the search for floral resources in the field. Environmental conditions therefore seem to play an important role in the activities of *C. analis*, not only throughout the year, but also throughout each day.

Parasitism and nest usurpation

Some nests saw parasitism by kleptoparasitic bees of the genus *Coelioxys* sp. (Hymenoptera: Megachilidae). This parasitism was due to the bees laying their eggs in the cells being constructed in the nests of *C. analis* whilst they were out collecting resources. During the period under evaluation, the parasites were seen to act during May, June, September and October, always in the morning, especially during the first three hours of the day. Of the 158 cells from the 38 trap nests in which sex ratio was evaluated, 7.89% of the nests and 2.53% of the cells were found to be parasitized. This kleptoparasite is a natural enemy with a wide geographic distribution and is very common in the nests of solitary bees like *C. analis* (AGUIAR; MARTINS, 2002; GAZOLA; GARÓFALO, 2009; OLIVEIRA; GONÇALVES, 2017). However, their level of infestation is variable, with rates like those found in the present study reported for similar conditions in the State of Paraíba (AGUIAR; MARTINS, 2002), and lower values in the State of São Paulo; although two other parasites were also present, which may have influenced the action of *Coelyoxis* sp (VIEIRA DE JESUS; GARÓFALO, 2000).

In addition to parasitism of the nests, the females of *C. analis* also faced nest usurpation, although it was not frequent for most of the period under study, with the nests only being invaded by other females during October, coinciding with the onset of flowering of the golden spoon (*Byrsonima crassifolia*), a plant that has oil-secreting structures (glands) in the calyx of its flowers and pollen covered in oil (PEREIRA; FREITAS, 2002). Flowering dramatically increased the supply of floral oils in the area, which was immediately reflected in an increase in the number of females in search of nesting sites. Over 10 consecutive days during that month, seven nests were invaded by other females and possibly usurped. Nest usurpation in this species was also reported by Moure-Oliveira *et al*. (2017).

Table 3 - Mean number of trips to the field of the *Centris analis* bee throughout the day to collect each floral resource, Pici Campus/UFC, from May to October 2017, in Fortaleza, Ceará

Time of day	Pollen	Nectar	Plant material	Oil
05:00 – 06:00	8.84 ± 5.50 aA	1.00 ± 1.96 cB	0.44 ± 1.61 cB	0.24 ± 0.52 bB
06:01 – 07:00	6.48 ± 5.05 bA	2.76 ± 3.01 abB	0.93 ± 1.36 bcC	0.38 ± 0.82 bC
07:01 – 08:00	4.41 ± 4.54 cA	3.13 ± 2.92 aB	2.07 ±1.81 abBC	1.13 ± 1.64 abC
08:01 – 09:00	3.78 ± 4.09 cdA	1.93 ± 2.66 bcB	2.21 ± 2.45 aB	1.43 ±1.50 abB
09:01 – 10:00	2.90 ± 3.00 dA	1.30 ± 2.68 cB	1.10 ±1.63 abcB	1.00 ± 1.36 abB
10:01 – 11:00	2.79 ± 2.29 deA	1.69 ± 2.80 bcAB	1.45 ± 2.60 abcB	0.96 ± 1.52 abB
11:01 – 12:00	2.03 ± 2.17 defA	1.43 ± 2.17 cA	1.18 ± 1.94 abcA	1.57 ± 2.38 aA
12:01 – 13:00	1.00 ± 1.11 fA	1.36 ± 1.86 cA	1.56 ± 2.27 abcA	0.68 ± 1.03 abA
13:01 – 14:00	0.82 ± 0.98 fA	1.36 ± 1.87 cA	1.21 ± 2.11 abcA	0.68 ± 0.90 abA
14:01 – 15:00	0.67 ± 1.24 fA	0.96 ± 1.58 cA	0.92 ± 1.14 bcA	1.11 ± 1.34 abA
15:01 – 16:00	0.65 ± 0.84 fA	0.42 ± 0.70 cdA	0.65 ± 1.01 cA	1.35 ± 1.16 abA
16:01 – 18:00	1.46 ± 1.36 fAB	0.88 ± 1.61 cAB	0.38 ± 0.80 cB	1.77 ± 1.48 aA

Means values followed by different lowercase letters in a column differ from each other (P<0.05); Mean values followed by different uppercase letters on a line, differ from each other (P<0.05)

Nest usurpation clearly takes place when there is an increase in the population of nesting females, which leads to a shortage of free nests for colonization. In this situation, females that cannot find unoccupied nests, try to take possession of those already occupied by other females. In the case of bee farms producing large populations of the species, this demonstrates the need to always provide many TN to avoid competition for space between these bees.

Finally, another occurrence seen throughout the evaluation period, was the owner bee no longer returning to its nest, and another bee, on the same or a different day, take that nest for itself and continue to construct the cells normally; this happened repeatedly, and took place during every month of the evaluation.

CONCLUSION

The *Centris analis* bee easily colonizes and nests in trap nests for an extended period of the year under tropical conditions, with the use of this type of nest making it possible to multiply populations of the bee for potential use in crop pollination. However, the rapid response of creating new nests when oil-supplying plants began to flower, and the consequent behavior of nest usurpation, show that both the sources of floral oil and the availability of nesting sites are limiting factors to population growth in this species on bee farms.

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