



RESEARCH ARTICLE - BEES

Cavity Length Affects the Occupation of Trap-Nests by *Centris analis* and *Tetrapedia diversipes* (Hymenoptera: Apidae)

CO SANTOS¹, PEC PEIXOTO², CML AGUIAR³

1 - Pós-Graduação em Ecologia e Evolução, Universidade Estadual de Feira de Santana (UEFS), Bahia, Brazil

2 - Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil

3 - Universidade Estadual de Feira de Santana (UEFS), Feira de Santana, Bahia, Brazil

Article History

Edited by

Astrid Kleinert, USP, Brazil

Received 18 July 2019

Initial acceptance 28 January 2020

Final acceptance 08 April 2020

Publication date 30 June 2020

Keywords

Nesting biology, cavity-nesting bees, crop pollinator.

Corresponding author

Claudia Oliveira dos Santos

Programa de Pós-Graduação em Ecologia e Evolução (PPGEcoEvol/UEFS)

Universidade Estadual de Feira de Santana

Av. Transnordestina s/nº, Novo Horizonte

CEP 44036-900, Feira de Santana-BA, Brasil.

E-Mail: cauoliver2@yahoo.com.br

Abstract

The ideal cavity dimensions for neotropical cavity-nesting bees with the potential to be managed as pollinators have not been getting proper attention. We investigated whether the occupancy of trap-nests by *Centris analis* Fabricius and *Tetrapedia diversipes* Klug, and other nesting aspects, are affected by trap-nest length. The used trap-nests were cardboard tubes measuring 5, 10, 15 and 20 cm in length, and \varnothing 8 mm. The percentage of occupied trap-nests of 10 cm by *C. analis* was higher than that of the 5 cm ones ($\chi^2=11.17$, $gl=1$, $p<0.001$). On the other hand, there was not difference between the occupation of 10 and 15 cm long trap-nests ($\chi^2=0.51$, $gl=1$, $p=0.48$), and between those measuring 15 and 20 cm long ($\chi^2=1.36$, $gl=1$, $p=0.24$). *T. diversipes* occupied a smaller number of 5 cm trap-nests than the 10 cm ($\chi^2=1.52$, $gl=1$, $p=0.22$), as well as that the 15 cm were more occupied than the 10 cm trap-nests ($\chi^2=4.23$, $gl=1$, $p=0.04$); moreover, there was not difference between the occupation of 15 and 20 cm trap-nests ($\chi^2=0.28$, $gl=1$, $p=0.59$). Both species showed higher percentages of dead immatures in nests set in the shortest trap-nests, whereas these mortality percentages were lower in the longest ones. By taking into consideration that there was not significant difference in many of the assessed parameters in comparison to values recorded for 15 and 20 cm long trap-nests, it seems likely to recommend the adoption of 10 cm long trap-nests for *C. analis* reproduction in agricultural sites that depend on the pollination service provided by this bee species.

Introduction

Studies on the nesting biology of wild bee species that have the potential to be managed as crop pollinators are an important step towards the development of management system for these bee species (Bosch & Kemp, 2002). *Centris analis* Fabricius is one of the wild bee species that have risen more interest as manageable pollinator in Brazil, given its abundance and great ability to colonize artificial nesting substrates (Jesus & Garófalo, 2000; Gazola & Garófalo, 2009; Oliveira & Schlindwein, 2009; Pina & Aguiar, 2011; Martins

et al., 2012; Magalhães & Freitas, 2012). Knowledge about the biology of this species has been growing significantly; there are data about the local abundance and time distribution of the nesting activity of populations living in different landscapes, including crop areas (Oliveira & Schlindwein, 2009; Pina & Aguiar, 2011; Martins et al, 2012; Magalhães & Freitas 2012), as well as about nest architecture, nesting behavior (Jesus & Garófalo, 2000) and the attack of natural enemies to brood cells (Gazola & Garófalo, 2003). On the other hand, other nesting aspects, such as the ideal dimensions of nesting cavities, have been poorly investigated (Alonso et al., 2011).



Many aspects of nesting biology can be influenced by the diameter or the length of the used cavities, such as the choice for the cavity (Bosch, 1994a; Bosch, 1994b; Rust, 1998), the number of brood cells produced per nest (Bosch, 1994a; Bosch, 1994b; Alonso et al., 2011), sex ratio (Stephen & Osgood, 1965; Torchio & Tepedino, 1980; Bosch, 1994b; O'Neill et al., 2010; Gruber et al. 2011; Alonso et al., 2011; Seidelmann et al., 2015) and the mortality ratio of immatures (Aguiar & Pina, 2012; Seidelmann et al., 2015). Alonso et al. (2011) have assessed the effect of subtle variations (5.5 to 7.0 cm) in trap-nest length on nesting-cavity selection by *C. analis* females, on the number of brood cells per nest and on sex ratio. Other studies focused on testing longer lengths are necessary in order to produce a more consolidated database capable of subsidizing the management of this crop pollinator.

The relationship between sex ratio and nesting-cavity dimensions is quite important for *Centris* bees, since only females collect floral resources and provide pollination services to oil-flowers and pollen-flowers. *C. analis* females are bigger than males (Jesus & Garófalo, 2000); therefore, their production could be limited in small-diameter cavities, similar to what has been observed in other bee species that show male production bias in narrow cavities (Stephen & Osgood, 1965; Bosch, 1994; O'Neill et al., 2010; Gruber et al. 2011; Seidelmann et al., 2015). Accordingly, it is essential knowing the cavity dimensions capable of producing more females in order to be successful in managing *Centris* populations for crop pollination. The aim of the present study was to investigate whether the occupancy of trap-nests by two oil-bee species, *C. analis* and *Tetrapedia diversipes* Klug, and other nesting biology aspects, such as sex ratio and mortality of the offspring, are affected by different trap-nest lengths.

Materials and Methods

Study site

Sampling was carried out at two agricultural areas, DMQ (Maria Quitéria District) (12°16'00" S/ 38°58'00" W) and DHU (Humildes District) (12°20'08" S/ 38°51'17" W), Feira de Santana Municipality, Bahia State, Brazil. The prevailing soil use in DMQ is the cultivation of temporary crops (beans, *guandu*-beans, maize) and of Acerola trees (*Malpighia emarginata*) in small properties (family farming). The sampling procedure in DHU was carried out in Chácara Bocaiúvas (23.4 ha), which grows organic horticultural products.

Sampling – A sampling point was installed in each site. Each sampling point consisted of 16 wooden blocks measuring varying thickness (from 4 cm to 19 cm); each wooden block had 60 cavities. The used trap-nests were cardboard straws, which were closed with cardboard caps in their rear tips. These straws were inserted into cavities drilled lengthwise in the wooden blocks (Camillo et al., 1995). The cardboard straws had 8-mm internal diameter, following Pina and Aguiar (2011), who reported a high nesting frequency of

C. analis in trap-nests of this diameter, and 4 different lengths (5, 10, 15 and 20 cm). In all cases, the entire cardboard straw was sheltered inside the wooden block, except for 1 cm in the rear tip of it. Each site had four blocks with 240 trap-nests of each of the assessed lengths. The 16 blocks in each location were grouped on steel shelves protected by plastic tarpaulin, based on Aguiar et al. (2005).

The trap-nests were inspected once a month, from October 2011 to September 2012, with an otoscope. Nests presenting concluded closing walls were removed and taken to the Entomology Laboratory of the Universidade Estadual de Feira de Santana (UEFS) to be daily observed until the emergence of adults, who were pinned, dry-mounted, separated by sex and taxonomically identified.

Data analysis

To evaluate if the occupation of trap-nests changed according to trap-nest length, we recorded for each trap-nest available (n=240) if it was occupied. Then, a Chi-square test was applied to assess whether the frequency of occupations (response variable) changed among trap-nests of different lengths (explanatory variable). In case we found a significant difference among the four trap-nests length, we performed subsequent pairwise comparisons (using chi-square tests) between trap-nests of similar lengths (i.e. 5 and 10 cm, 10 and 15 cm and 15 and 20 cm).

A generalized least squares model was performed to assess whether the number of provisioned brood cells changed due to trap-nest length. This model considered the number of brood cells in each trap-nest as the response variable and trap-nest length as explanatory variable. The variance of residues was adjusted according to each trap-nest length category, in order to achieve a better fit the model to the collected data. One analysis was carried out for each bee species. The same model structure described above was repeated to test whether the number of emerged adults changed due to trap-nest length, but we replaced the number of brood cells by the number of emerged adults. For both analyses considering the number of brood cells and emerged adults, only data of *C. analis* collected in DMQ were analyzed, given the low trap-nest occupation recorded in DHM. For *T. diversipes* only data collected in DHU and for traps nests with 10, 15 and 20 cm were analyzed, given the low trap-nest occupation recorded in DMQ and for nests with 5 cm. These analyses were carried out in the nlme package of the R software (R Development Core Team, 2004).

A Chi-square test was applied to verify whether the number of males and females (sex ratio) of the offspring differed from an expected proportion of 1:1. To calculate the expected proportion for each sex, we divided the total number of offspring by two. To evaluate if sex ratio changed according to trap-nest length, we performed a general linear model. For this model we considered the number of males in relation to the total number of individuals in each trap-nest

as the response variable and trap-nest length as the predictor variable. The general linear model was not carried for *T. diversipes* due to the low sample size for trap-nests of 5, 10 and 20 cm length.

A generalized linear model with Poisson error distribution was performed to assess whether the number of brood cells with dead individuals changed due to trap-nest length. The number of dead individuals was considered as the response variable and trap-nest length was considered the explanatory variable. This analysis was only applied to *C. analis* in the DMQ site, given the low nesting frequency observed in the DHM site. Regarding *T. diversipes*, it was not possible to perform this analysis because offspring mortality was very low.

Generalized linear models with Poisson error distribution were used to assess the association between the number of occupied trap-nests on every month of the year and the mean temperature, humidity and rainfall. Weather variables were obtained in the weather station of the Universidade Estadual de Feira de Santana, located in the same municipality as the sampling area. Nine models were built (Tables 4 and 5) and site and species were maintained as predictor variables in most of them (the exception occurred for the null model). We opted to keep site and species in most models because we were interested in evaluate if the number of occupied cells varied in response to climatic variables independent of site and species. The Akaike Information Criterion was used to select the most parsimonious model to explain the relationship between number of occupied cavities and the climatic variables. The significance of the selected model was calculated using a maximum likelihood ratio test. For this, the selected model was compared with a null model that retained only species and site as predictor variables. All analyses were performed in the R software (R Development Core Team, 2004).

Results

1. Occupation of pre-existing cavities

The number of nests established by bees in the DMQ site (Acerola orchard) was almost twice the number recorded for the site used for diversified crops (DHU) (Table 1). *C. analis* was the dominant species in the DMQ site, either when it comes to number of established nests (91% of all bee nests) or number of brood cells (n=460). On the other hand, this species recorded low frequency in the DHU site, whereas *T. diversipes* established 80% of all bee nests (202 brood cells) in it. Other cavity-nesting bee species (*Centris tarsata* Smith and *Megachile* spp) have established few nests in both sites (Table 1).

The percentage of occupied trap-nests by *C. analis* differed between trap-nests of different lengths ($\chi^2=17.85$, $df=3$, $p<0.001$, Table 1). The proportion of occupied trap-nests recorded for the 10 cm trap-nests was higher than that of the 5 cm ones ($\chi^2=11.17$, $df=1$, $p<0.001$), but there was not difference in the proportion of occupied nests between 10 and

15 cm trap-nests ($\chi^2=0.51$, $df=1$, $p=0.48$) and between the 15 and 20 cm ones ($\chi^2=1.36$, $df=1$, $p=0.24$). The percentage of nests established by *C. analis* (n=84) in DMQ for nests with 5, 10, 15 and 20 cm were respectively 7%, 30%, 37% and 26%, indicating that the occupation of 5 cm trap-nests was the smallest, while the occupation was similar among trap-nests of 10, 15 and 20 cm.

Table 1. Number of nests established by solitary bees in trap-nests in two agricultural areas (DMQ and DHU), Feira de Santana, BA, Brazil.

	Bee species	Trap-nest length			
		5cm	10cm	15cm	20cm
Site DMQ	<i>Centris analis</i>	6	25	31	22
	<i>Centris tarsata</i>	-	2	4	-
	<i>Megachile</i> (<i>Acentron</i>) sp. 4	-	-	1	-
	<i>Megachile</i> (<i>Sayapis</i>) sp. 5	-	-	-	1
Total	6	27	36	23	
% cavities occupied	2.5	11.2	15.0	9.5	
Site DHU	<i>Centris analis</i>	-	2	2	-
	<i>Centris tarsata</i>	-	1	-	1
	<i>Tetrapedia diversipes</i>	1	5	15	19
	<i>Megachile</i> (<i>Tylomegachile</i>) sp. 3	-	-	-	2
	<i>Megachile</i> sp. 1	-	-	-	1
	<i>Megachile</i> sp. 2	-	-	-	1
Total	1	8	17	24	
% cavities occupied	0.4	3.3	7.1	10.4	

Most brood cells of *C. analis* in the DMQ site were found in the longest cavities, 15 cm (40%) and 20 cm (30%), whereas the smallest number of brood cells (3%) was observed in the shortest trap-nests (5cm long ones). The number of built brood cells changed according tonest length (Generalized least squares model: $F_{(2,75)}=18.54$, $p<0.001$). The mean number of brood cells varied from 2.6 in 5 cm nests to 6.2 in 20 cm nests (Figure 1). Some cavities were not fully occupied by brood cells in trap-nests at all tested lengths. Variation in the space occupied by brood cells reached 44% of the cavity in 20 cm long trap-nests and 69% in the 5cm long trap-nests.

For *T. diversipes*, the percentage of occupied trap-nests also differed among trap-nests of different lengths ($\chi^2=22.12$, $df=3$, $p<0.001$). There was no difference in occupation between 5 and 10 cm trap-nests ($\chi^2=1.52$, $df=1$, $p=0.22$), but the percentage of occupied trap-nest was higher for 15 cm trap-nests in comparison to the 10 cm ones ($\chi^2=4.23$, $df=1$, $p=0.04$). There was no difference in occupation between the 15 and 20 cm trap-nests ($\chi^2=0.28$, $df=1$, $p=0.59$). Percentage of nests established by *T. diversipes* (n=40) for nests with 5, 10,

15 and 20 cm were respectively 2.5%, 12.5%, 37.5% and 47.5%. Therefore, the smallest occupation in *T. diversipes* occurred for trap-nests with 5 and 10 cm, while the greatest occupation occurred for trap-nests with 15 and 20 cm.

Most brood cells of *T. diversipes* were built in longer cavities, 20 cm (55%) and 15 cm (33%), whereas the shortest trap-nests (5 cm) only sheltered 1.5% of the brood cells built by this bee species. The mean number of cells per nest established in cavities presenting different lengths varied from 3.0 in the only 5 cm nest that was occupied (although not included in the statistical analysis) to 5.8 in 20 cm nests (Figure 1). The occupied space by brood cells varied from 26-27% of the trap-nest (in 20 and 15 cm long straws) to 60% of them (in 5 cm long straws). The mean number of brood cells provisioned by *T. diversipes* did not differ due to trap-nest length (Generalized least squares model: $F_{(2,36)}=2.36$, $p=0.11$).

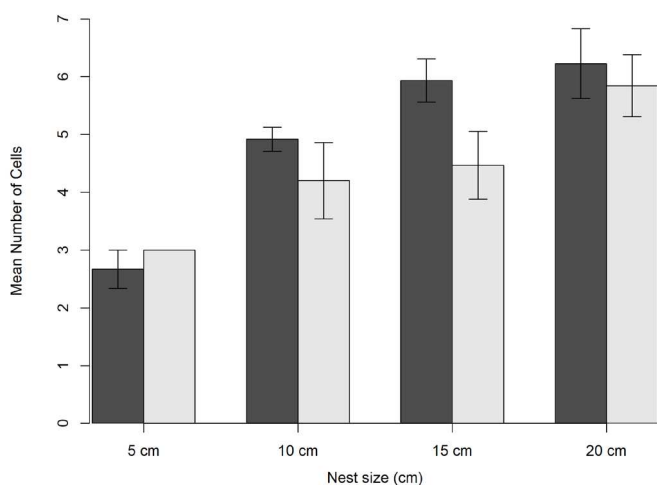


Fig 1. Mean number of brood cells provisioned in trap-nests of different lengths. *Centris analis* (= dark gray bars), *Tetrapedia diversipes* (= light gray bars).

2. Immature mortality, emerged adults and parasitism

The mortality percentage recorded for *C. analis* offspring due to unknown causes reached 17% of the brood cells ($n=460$) assessed in the DMQ site and 29% in DHU ($n=17$). There was immature death in 8% of the brood cells ($n=202$) in *T. diversipes* nests. Mortality percentages were higher at the larval stage in both species (Table 2).

Both species showed higher immature mortality percentage in nests established in the shortest trap-nests (5 cm long), whereas the mortality percentages were lower in the longest trap-nest (20 cm) (Table 2). The number of immature individuals of *C. analis* that died differed among trap-nests with different lengths in the DMQ site ($\chi^2 = 20.64$, $df=3$, $p < 0.001$). The number of dead immatures gradually decreased from the 5 cm to the 20 cm long trap-nests (Figure 2).

The number of emerged adults of *C. analis* was higher in the 15 and 20 cm nests than in the 10 cm ones (Generalized least squares model: $F_{(2,75)}=7.29$, $p=0.001$; Figure 3).

For *T. diversipes*, the number of emerged adults did not differ due to trap-nest length (Generalized least squares model: $F_{(2,36)}=1.93$, $p=0.16$).

The incidence of attacks from natural enemies to the nests was low. Only 0.2% of *C. analis* brood cells in the DMQ site was lost, due to the attack by the cleptoparasitic bee, *Mesocheira bicolor* (Fabricius) (Hymenoptera, Apidae), whereas there was not any attack to *C. analis* nests in the DHU site. It was observed that 7% of *T. diversipes* brood cells were lost because of attack by the cleptoparasitic bee, *Coelioxoides* sp (Hymenoptera, Apidae).

Table 2. Number of immatures of *Centris analis* and *Tetrapedia diversipes* dead in the nests and percentage of brood cells containing dead immatures in cavities of different lengths (5, 10, 15, 20 cm). Sites = DMQ, DHU. E = egg, L = larvae, P = pupae, A = adult

Bee species/ Site	Number of dead immatures				% of brood cells			
	E	L	P	A	5cm	10cm	15cm	20cm
<i>Centris analis</i> / DMQ	17	42	2	17	75	28	13	6
<i>Centris analis</i> / DHU	2	3	0	0	0	11	50	0
<i>Tetrapedia diversipes</i> / DHU	4	12	1	0	100	14	3	8

3. Sex ratio

The sex ratio of *C. analis* offspring in the DMQ site was 0.9M:1F, which was similar to the expected proportion of 1:1 ($\chi^2=0.69$, $df=1$, $p=0.40$). There was no difference in the sex ratio of *C. analis* offspring produced in trap-nests presenting different lengths (General linear model: $F_{(2,47)}=1.35$, $p=0.27$) (Table 3). The sex ratio of *T. diversipes* offspring was 0.4 M:1F, which was significantly different from the expected proportion of 1:1 ($\chi^2=5.45$, $df=1$, $p=0.02$).

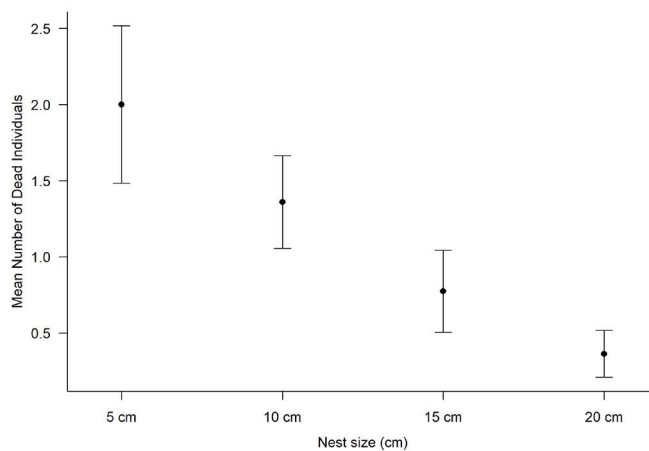


Fig 2. Mean number of dead immatures of *Centris analis* in trap-nests of different lengths.

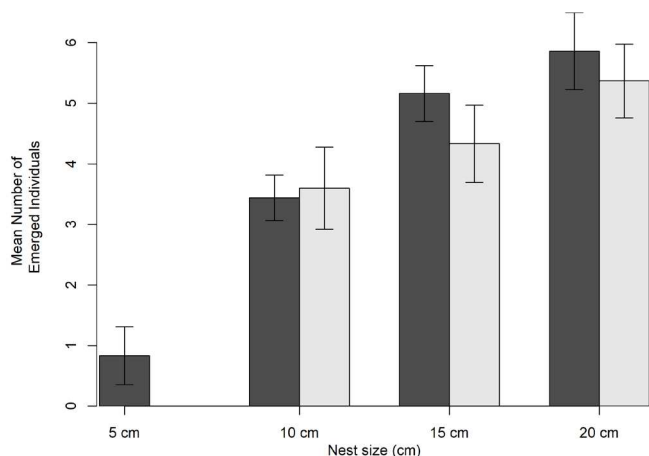


Fig 3. Mean number of emerged adults in trap-nests of different lengths. *Centris analis* (= dark gray bars), *Tetrapedia diversipes* (= light gray bars).

4. Nesting activity and climatic factors

There was nesting activity by solitary bees throughout most the year. *C. analis* mainly nested from September to March and recorded low nesting activity from April to August. *T. diversipes* kept its nesting activity from January to March and from June to September, except for July. Bee nesting activity was associated with climatic factors. According to the Akaike Information Criterion, the model based on temperature and rainfall effects was the most parsimonious (Table 4). According to this model, the number of occupied trap-nests in each month of the year increased as the mean

Table 4. Summary of generalized linear models with Poisson distribution, which describe the relationship between number of occupied nests, temperature and precipitation, using the study site and bee genera as covariates. The models are classified in ascending order of AIC_c values.

Models	AIC _c	df	dAIC _c	w _i
Site + species+ temperature + rainfall	162.7	7	0	0.83
Site + species + air humidity + temperature + rainfall	166.1	8	3.4	0.15
Site + species + air humidity + temperature	171.9	7	9.2	0.008
Site + species+ temperature	172.5	6	9.9	0.006
Site + species + rainfall	176.3	6	13.6	<0.001
Site + species	177.6	5	15.0	<0.001
Site + species +air humidity	179.4	6	16.7	<0.001
Site + species + air humidity + rainfall	179.4	7	16.8	<0.001
Null	233.1	1	70.4	<0.001

(dAIC_c represents the difference between the AIC_c value of model i and the AIC_c value of the most parsimonious model; w_i is the weight of Akaike model i). AIC_c / bias corrected version of the Akaike information criterion.

Table 3. Number of males and females of *Centris analis* and *Tetrapedia diversipes* produced in trap-nests with different lengths. Sites = DMQ, DHU

Bee species/site	Trap-nest Length	Males	Females
<i>Centris analis</i> / DMQ	5cm	02	03
	10cm	22	21
	15cm	48	46
	20cm	24	34
<i>Centris analis</i> / DHU	5cm	0	0
	10cm	3	1
	15cm	2	2
	20cm	0	0
<i>Tetrapedia diversipes</i> / DHU	5cm	0	0
	10cm	4	7
	15cm	13	17
	20cm	13	14

monthly temperature and rainfall also increased ($\chi^2 = 21.22$, df = 2, p = 0.001). This analysis indicated the presence of two outliers with extremely high number of occupied nests. After removing them, the most parsimonious model indicated that the number of occupied nests were related to temperature and air humidity variations ($\chi^2 = 9.5$, df = 2, p = 0.009; Table 5). The number of occupied trap-nests increased as temperature (b = 0.1) and humidity (b = 0.06) also increased.

Table 5. Summary of generalized linear models with Poisson distribution, which describe the relationship between number of occupied nests, temperature and precipitation, using the study site and bee genera as covariates. In this case, two outliers were removed in relation to the results shown in table 4. The models are classified in ascending order of AIC_c values.

Models	AIC _c	df	dAIC _c	w _i
Site + species + air humidity + temperature	113.5	7	0.0	0.33893
Site + species + temperature	114.0	6	0.5	0.26567
Site + species + temperature + rainfall	114.8	7	1.3	0.17358
Site + species + air humidity + temperature + rainfall	116.5	8	3.0	0.07616
Site + species	116.5	5	3.0	0.07443
Site + species + air humidity	117.6	6	4.1	0.04314
Site + species + rainfall	119.2	6	5.7	0.01993
Site + species + air humidity + rainfall	121.0	7	7.5	0.00811
Null	131.6	1	18.1	<0.001

(dAIC_c represents the difference between the AIC_c value of model i and the AIC_c value of the most parsimonious model; w_i is the weight of Akaike model i). AIC_c / bias corrected version of the Akaike information criterion.

Discussion

The oil bee *C. analis* accepted a wide range of cavity lengths (from 5 to 20 cm) as nesting substrate; however, the shortest trap-nests (5 cm) were clearly less attractive than the longest ones (10 cm or longer). The present study did not show any preferential occupancy between the longest trap-nests (10, 15 and 20 cm), and this outcome suggests that they are all appropriate for *C. analis* nesting. Similarly, Alonso et al. (2011) did not find significant differences in occupancy by nesting females of *C. analis* in wooden blocks presenting small length differences (5.5, 6.0, 6.5 and 7.0 cm), although the shortest trap-nests recorded higher occupation in a third study site.

In addition, the number of brood cells produced by *C. analis* was larger in longer cavities. When there is a low incidence of parasitism, as reported in this study, the occupation of longer cavities, where a female can produce a larger number of brood cells, seems to be an advantage, since it would lead to lower costs with the selection and establishment of new nests. On the other hand, in a different scenario, with a higher incidence of parasitism, could be advantageous to spread offspring over several nests, because some cleptoparasites can attack the same nest several times (Gazola & Garófalo, 2003; Aguiar, unpublished data).

The oil bee *T. diversipes* also showed trend of preferring to nest in longer trap-nests. In these straws, females left a considerable portion of the cavity empty. This strategy can play a role, protecting the brood cells against natural enemies. The mortality percentage recorded for *C. analis* offspring due to unknown causes suggests that there are not considerable losses of such offspring in these sites, similar to previous observation in DMQ and in nesting areas close to it (Aguiar & Pina, 2012; Aguiar et al., 2013). On the other hand, Jesus and Garófalo (2000), Gazola and Garófalo (2003), as well as Couto and Camillo (2007) reported great brood cell losses for this species in an urban area. Factors causing the death of immature tropical solitary bees, who nest in trap-nests, remain poorly investigated. Some researchers suggest that high temperatures influence immature mortality (Frankie et al., 1988; Jesus & Garófalo, 2000; Gazola & Garófalo, 2003). However, Couto and Camillo (2007) did not find evidences about the influence of temperature on *C. analis* offspring mortality when they compared mortality percentages in nests established in shady vs. sunny areas. Aguiar et al. (2013) have suggested that nest management during its removal from the field, as well as during nest transportation to the laboratory – which, sometimes means long distances –, could also have some influence on mortality. Bosch and Kemp (2001) previously reported the importance of handling the nests to decrease immature mortality incidence, because the inappropriate handling of *Osmia lignaria* Say (Megachilidae) nests can take larvae away from their provisions and cause death due to starvation.

Results have shown low mortality in the longest trap-nests, although *T. diversipes* and *C. analis* align the brood cells in the trap-nests (Jesus & Garófalo, 2000; Camillo et al., 1995), a fact that could result in difficulty for individuals reared at the bottom of the nest to reach the exit. This outcome suggests that longer cavities would not limit the survival of their offspring. On the other hand, both bee species showed higher mortality percentages in the shortest trap-nests (5 cm).

The sex ratio of *C. analis* offspring produced in trap-nests of different lengths showed no differences; however, it is necessary to consider that the number of nests recorded in 5 cm long trap-nests, as well as the number of emerged adults, was too small, so they were not included in the analysis. On the other hand, Alonso et al. (2011) have concluded that cavity length has influenced offspring sex ratio, since there was male-biased sex ratio in the two shortest trap-nests (5.5 and 6.0 cm), whereas the sex ratio was not significantly different from 1:1 in the two longest ones (6.5 and 7.0 cm).

The nesting activity of *C. analis* was intense in summer and decreased from May to August, as previously reported for DMQ (Pina & Aguiar, 2011). Based on results in the present study, temperature and rainfall have influenced the frequency of nesting in these cavity-nest bees. The low offspring production from mid-fall and throughout the winter must be considered when planning *C. analis* management for crop pollination, as it would result in low availability of female pollinators.

Finally, the present study points out that longer trap-nests (10 cm or longer) are the best options to produce *C. analis* and *T. diversipes* offspring, since they have good acceptance by nesting females, and there is low offspring mortality in nests established in these longer cavities. It seems plausible recommending the adoption of 10 cm trap-nests for *C. analis* breeding in agricultural areas that depend on its pollination service, if one taken into account the higher costs and logistics impairments to produce wooden blocks at the appropriate thickness to shelter the longest trap-nests (longer than 10 cm), as well as the lack of significant difference in many of the assessed parameters in comparison to the parameters recorded for the 15 and 20 cm long cavities.

Acknowledgments

We thank the National Council for Scientific and Technological Development, Brazil (CNPq, proc. no. 475715/2008-0, no. 562518/2010-0), and the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB, TO APP0042/2009) for financial support for this project. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. C.S. Oliveira received MSc scholarship from CAPES.

References

Aguiar, C.M.L., Garófalo, C.A., Almeida, G.F. (2005). Trap-nesting bees (Hymenoptera, Apoidea) in areas of dry

- semideciduous forest and caatinga, Bahia, Brazil. *Revista Brasileira de Zoologia*, 22: 1030-1038. doi: 10.1590/S0101-81752005000400031
- Aguiar, C.M.L. & Pina, W. C. (2012). Mortalidade da prole de abelhas coletoras de óleo (Hymenoptera, Apidae) em áreas cultivadas com aceroleira. *Magistra*, 24: 136-142.
- Aguiar, C.M.L., Medeiros, R.L.S., Almeida, G.F. (2013). Mortalidade da prole em duas espécies de *Centris* (Hymenoptera, Apidae) em uma área urbana. *Magistra*, 25: 37-42.
- Alonso, J.D. S., Silva J.F. & Garofalo, C.A. (2011). The effects of cavity length on nest size, sex ratio and mortality of *Centris (Heterocentris) analis* (Hymenoptera, Apidae, Centridini). *Apidologie*, 43: 436-448. doi: 10.1007/s13592-011-0110-0
- Bosch, J. (1994a). The nesting behaviour of the mason bee *Osmia cornuta* (Latr) with special reference to its pollinating potential (Hymenoptera, Megachilidae). *Apidologie*, 25: 84-93.
- Bosch, J. (1994b). Improvement of field management of *Osmia cornuta* (Latreille) (Hymenoptera, Megachilidae) to pollinate almond. *Apidologie*, 25: 71-83.
- Bosch, J. (1994). *Osmia cornuta* (Latreille) (Hym., Megachilidae) as a potencial pollinator in almond orchards. *Journal of Applied Entomology*, 117: 151-157.
- Bosch, J. & Kemp, W.P. (2001). How do manage the blue orchard bee as on orchard pollinator. Sustainable Agriculture Network. Beltsville, Maryland, 88p.
- Bosh, J. & W. P. Kemp (2002). Developing and establishing bee species as crop pollination: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of Entomological Research*, 92: 3-16. doi: 10.1079/BER2001139
- Camillo, E., Garofalo, C.A., Serrano, J.C. & Muccillo, G. (1995). Diversidade e abundância sazonal de abelhas e vespas solitárias em ninhos armadilhas (Hymenoptera: Apocrita: Aculeata). *Revista Brasileira de Entomologia*, 39: 459-470.
- Couto, R.M. & Camillo, E. (2007). Influência da temperatura na mortalidade de imaturos de *Centris (Heterocentris) analis* (Hymenoptera, Apidae, Centridini). *Iheringia, Série Zoologia*: 97: 51-55. doi: 10.1590/S0073-47212007000100008
- Frankie, G.W., Vinson, S.B., Newstrom, L.E. & Barthell, J.F. (1988). Nest site and habitat preferences of *Centris* bees in the Costa Rican dry forest. *Biotropica*, 20: 301-310.
- Gruber, B., Eckel, K., Everaa, J. & Dormann, C.F. (2011). On managing the red mason bee (*Osmia bicornis*) in Apple orchards. *Apidologie*, 42: 564-576. doi: 10.1007/s13592-011-0059-z
- Gazola, A.L. & Garófalo, C.A. (2003). Parasitic behavior of *Leucospis cayennensis* Westwood (Hymenoptera, Chalcidoidea, Leucospidae) and rates of parasitism in populations of *Centris (Heterocentris) analis* Fabricius (Hymenoptera, Apidae, Centridini). *Journal of the Kansas Entomological Society*, 76: 131-142.
- Gazola, A.L. & Garófalo, C.A. (2009). Trap-nesting bees (Hymenoptera, Apoidea) in forest fragments of the State of São Paulo, Brazil. *Genetics and Molecular Research*, 8: 607-622. doi: 10.4238/vol8-2kerr016
- Jesus, B.M.V. & Garófalo, C.A. (2000). Nesting behaviour of *Centris (Heterocentris) analis* (Fabricius) in southeastern Brazil (Hymenoptera, Apidae, Centridini). *Apidologie*, 31: 503-515. doi: 10.1051/apido:2000142
- Magalhães, C.B. & Freitas, B.M. (2012). Introducing nests of the oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini) for pollination of acerola (*Malpighia emarginata*) increases yield. *Apidologie*, 44: 234-239. doi: 10.1007/s13592-012-0175-4
- Martins, C.F., Ferreira, R.P. & Carneiro, L.T. (2012). Influence of the orientation of nest entrance, shading, and substrate on sampling trap-nesting bees and wasps. *Neotropical Entomology*, 41: 105-111. doi: 10.1007/s13744-012-0020-5
- Oliveira, R. & Schlindwein, C. (2009). Searching for a manageable pollinator for acerola orchards: The solitary oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini). *Journal of Economic Entomology*, 102: 265-273.
- O'Neill, K.M., Pearce, A.M., O'Neill, R.P., Miller, R.S. (2010). Offspring size and sex ratio variation in a feral population of alfalfa leafcutting bees (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America*, 103(5): 775-784. doi.org/10.1603/AN09183
- Pina, W.C. & Aguiar, C.M.L. (2011). Trap-nesting bees (Hymenoptera: Apidae) in orchards of acerola (*Malpighia emarginata* DC) in a semiarid region in Brazil. *Sociobiology*, 58: 379-392.
- Rust, R.W. (1998). The effects of cavity diameter and length on the nesting biology of *Osmia lignaria propinqua* Cresson (Hym.: Megachilidae). *Journal of Hymenoptera Research*, 7: 84-93.
- Seidelmann K, Bienasch A, Pröhl, F. (2015). The impact of nest tube dimensions on reproduction parameters in a cavity nesting solitary bee, *Osmia bicornis* (Hymenoptera: Megachilidae). *Apidologie* 47: 114-122. doi: 10.1007/s13592-015-0380-z
- Stephen, W.P. & Osgood, C.E. (1965). Influence of tunnel size and nesting medium on sex ratios in a leaf-cutter bee, *Megachile rotundata*. *Journal of Economic Entomology*, 58: 965-968
- Torchio, P.F. & Tepedino, V.J. (1980). Sex ratio, body size and seasonality in a solitary bee, *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). *Evolution*, 34: 993-1003.

