Apidologie 31 (2000) 503–515

Original article

Nesting behaviour of *Centris* (*Heterocentris*) *analis* (Fabricius) in southeastern Brazil (Hymenoptera, Apidae, Centridini)

Bartira M. VIEIRA DE JESUS, Carlos A. GARÓFALO*

Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto – USP, 14040-901, Ribeirão Preto, São Paulo, Brazil

(Received 8 August 1999; revised 14 February 2000; accepted 6 March 2000)

Abstract – The nesting behaviour of *Centris analis* was studied on the campus of the University of São Paulo-Ribeirão Preto, SP, Brazil. The bees nested in trap-nests made with black cardboard, measuring 5.8 cm in length and 0.6 cm in internal diameter. The bees constructed their nests with plant material and an oily substance. Completed nests had 1 to 4 cells arranged in a linear series, usually followed by an empty vestibular cell. Cells provisioned with a greater number of pollen trips were more likely to produce females than males. The innermost cells of the nests produced females, and the outermost cells produced males. Nests were parasitized by wasp, *Leucospis cayennensis*, and by bees, *Coelioxys* sp. and *Mesocheira bicolor*. Intraspecific parasitism was observed on 10 occasions. Although the factors inducing *C. analis* females to act parasitically are not known, the nest-site availability and food availability observed in this study apparently did not influence that behaviour.

nesting behaviour / trap-nest / *Centris analis* / Apidae / Brazil

1. INTRODUCTION

Centris is a primarily tropical genus, whose species are separated into 12 subgenera [37, 38]. Species of most subgenera excavate nests in the ground, while those belonging to the subgenera *Hemisiella*, *Heterocentris* and *Xanthemisia* construct their nests in preexisting cavities [6, 7, 14–16]. Although data on nesting biology are available for several nest-excavating species [2, 5–7, 35, 41–44], detailed studies of this aspect for species that nest in preexisting cavities has only been made in *Centris (Hemisiella) vittata* [32].

In this paper we present observations on the nesting behaviour of *Centris (Heterocentris) analis* which ranges from Mexico to

* Correspondence and reprints
E-mail: garofalo@ffclrp.usp.br

Brazil [28]. Previous reports show that, like other species of *Heterocentris*, nesting by *C. analis* occurs on a variety of substrate such as abandoned *Sceliphron* nests [40], old *Melitoma* cells [24, 30] and trap-nests [3, 14, 16, 17, 34]. Frankie et al. [14, 16], studying the preferred nesting habitats of *Hemisiella* and *Heterocentris* species in the Costa Rican dry forest, reported that Oak Riparian forest and Oak Forest were the preferred habitats of *C. analis*. Although those authors have obtained nests of *C. analis*, they provided little detailed information on the nests. Heithaus [19] and Frankie et al. [13, 15] in Costa Rica, and Roubik [34] in Panama, reported information on the seasonal abundance of *C. analis*.

2. MATERIALS AND METHODS

The nesting activities of *C. analis* were observed on the campus of the University of São Paulo-Ribeirão Preto (between 21°05'–21°15' S and 47°50'–47°55' W), State of São Paulo, Brazil, from November 1993 to March 1994. During that period, the mean monthly temperature ranged from 23.6 °C (January/94) to 25.8 °C (November/93) and precipitation from 53 mm (November/93) to 295.3 mm (December/93).

In accordance with Garófalo et al. [17], trap-nests used in this study consisted of tubes made with black cardboard, with one end closed with the same material. The tubes measured 5.8 cm in length and 0.6 cm in internal diameter. A total of 425 tubes were inserted into horizontal holes drilled into five wooden plates ($28.0 \times 24.0 \times 4.0$ cm). Each plate had 85 holes. The plates were placed along two shelves in a shelter built near the laboratory. The shelves were 1.2 and 1.5 m from the ground.

During the study period the traps were inspected daily with an otoscope, and information was recorded from those with active and completed nests. Ten days after being completed, the nests were taken to the laboratory and replaced with similar traps. In the laboratory, each nest was placed in a transparent glass tube, measuring 4.0 cm longer than the trap and with an internal diameter of 0.9 cm. As adults emerged into the glass tube, the trap was removed and the bees were collected. The nests were kept at room temperature (21–29 °C) and observed daily until the adults emerged. After emergence, the bees were released. Before release, females were marked with dots of paint placed on their 4th metasomal segment. Ten to fifteen days after the last emergence from any given nest occurred, the nest was opened and its contents analyzed. Cells and nests from which nothing emerged were also opened, and the cause and stage of mortality were recorded. The head width of individuals was taken as a measure of body size [32]. The individuals utilized were obtained from nests established in trap-nests similar to those used in this work.

Observations on the nesting behaviour were recorded for a total of 250 h. The activities of females within the nests were observed with the aid of an otoscope.

3. RESULTS

3.1. Nest selection

When searching for a nest site the female usually inspects several traps, entering and leaving them rapidly. The female thus makes tens of trap-nest inspections before selecting one for a nest. After finding a suitable trap, the female may remain inactive inside it for up to two hours before leaving it to collect construction material. In other cases, the female walks to the end of the trap, remains there for several seconds, backs up a few centimeters and returns to the end again. These behaviours are repeated several times, and then the female leaves the selected trap to collect construction material.

3.2. Cell construction

When the female returns to her nest with construction material, she enters head first and walks to the end of the nest. After that, she backs out of the nest, turns, and reenters the nest backwards all the way to the end. The female then begins to remove the material on her scopae by scraping her hind legs repeatedly against one another. During this procedure the female moves her entire body around the circumference of the nest and, at the same time, she brushes the material onto the nest walls. The time spent by the female on these activities ranged from 60 to 480 s ($\bar{x}$ = 213.7 ± 105.4 s; median = 208 s; n = 28). The material collected by the female consists of an oily substance of unknown origin. Two (n = 19) or three (n = 9) oily substance-collecting trips were made to line the walls of the constructing cell, and these trips lasted 60 to 820 s ($\bar{x}$ = 317.0 ± 179.9 s; median = 275.0 s; n = 28). After finishing the lining of the cell, the female begins to collect plant material to construct the bottom wall of the cell and the beginning of the first cell partition. The plant material consists essentially of pollen, anther fragments, filaments, and shaving of pollinic sacs and fibers. The female carries those materials primarily on her hind legs, and they are also distributed on the thorax and abdomen. When returning to her nest with plant material, the female enters head first and walks to the end of the nest. Then, she backs out of the nest, turns, and re-enters the nest backwards as far as the bottom of it. Immediately thereafter, the female removes the material from the hind legs by scraping alternatively one against another while the mid legs are used to remove the material on the thorax and abdomen. While removing the material, the female rotates her body and at the same time she presses the material against the bottom of the nest. During this activity, she uses her hind legs and the tip of the abdomen. After finishing that activity, the female initiates the construction of the first cell partition. She then utilizes her fore legs and mandibles to push forward the plant material that fell to the floor of the nest while removing it from her body. In the place where the cell partition will be made, the female presses the material with the fore legs and mandibles against the walls of the nest while rotating her entire body around the circumference of the nest. After that, she backs out of the nest, turns, and backs into the nest. After passing over the cell partition being constructed, the female stops and then rotates inside the cell several times while pressing the plant material placed in the cell partition with her hind legs. The time spent by the female on these activities ranged from 1.0 to 30.0 min ($\bar{x}$ = 7.6 ± 6.3 min; median = 6.0 min; n = 166). Three to ten plant material-collecting trips ($\bar{x}$ = 4.9 ± 1.1 trips; n = 196), ranging from 1.5 to 42.0 min ($\bar{x}$ = 9.4 ± 8.8 min; median = 5.7 min; n = 225) were made to construct the wall of the bottom of the cell and the beginning of the first cell partition. When the female finishes these activities the cell partition has the form of a small ring that encircles the entire inner circumference of the nesting tube, constricting its diameter about 1–2 mm. Before beginning to provision the cell, the female makes an oily substance-collecting trip to line the bottom of the cell; during this activity she repeats the behavioural sequence described for lining the cell wall.

3.3. Provisioning behaviour

When returning to her nest with a pollen load, the female enters head first and walks to the bottom of the cell. Then, she backs out of the nest, turns, and backs into the nest as far as the bottom of the cell. The female removes the pollen from the scopae on her hind legs by scraping the mid legs against the hind legs or scraping the hind legs one against another. The mid legs are also used to remove the pollen from the thorax and abdomen. At the same time while removing the pollen, the female rotates within the

cell several times in both directions and presses the pollen against the bottom of the cell utilizing the hind legs and the tip of her abdomen. The time between pollen-collecting trips ranged from 1.0 to 50.0 min ($\bar{x}$ = 7.5 ± 8.5 min; median = 4.0 min; n = 227). Pollen-collecting trips (n = 258) lasted 2.0 to 92.0 min ($\bar{x}$ = 14.3 ± 11.5 min; median = 12.0 min). Between 4 to 11 pollen-collecting trips were made to provision one cell (n = 250), with five (n = 68), six (n = 60), seven (n = 56) and eight trips (n = 47) being the most frequent number. The number of pollen-collecting trips to provision a female cell ranged from four to 11 ($\bar{x}$ = 7.9 ± 1.5 trips; n = 30), and this was significantly greater than for male cells (range: 5–7 trips; $\bar{x}$ = 5.6 ± 0.7 trips; n = 28) (Mann-Whitney test, Z = –5.53; $P < 0.05$).

After pollen collecting is complete, the female makes a trip to collect plant material that she deposits on the partially constructed cell partition. During the deposition of material the female repeats the behaviours exhibited when constructing the bottom of the cell. After that, she backs out of the nest, turns, and backs into the nest up to the cell partition. The female then adds the material to the edges of the cell partition, pressing the material with the mandibles and fore legs. Once that activity is finished, the female leaves the nest to initiate the collection of nectar. The duration of nectar trips was highly variable, ranging from 0.6 to 76.0 min ($\bar{x}$ = 8.8 ± 10.7 min; median = 5.1 min; n = 166). When returning to her nest with a nectar load, the female enters the nest, depositing her nectar on the pollen provision for 5–190 s ($\bar{x}$ = 61.7 ± 35.2 s; median = 60.0 s; n = 146) while pumping her abdomen. She then backs out of the nest and flies away to collect again. Two to eight nectar-collecting trips were made to provision one cell (n = 195), with four (n = 51) and five (n = 77) trips being the most frequent number. No difference was observed between the number of nectar-collecting trips for provisioning a female (3–8 trips; $\bar{x}$ = 5.77 ± 1.73 trips; n = 31) versus a male cell (4–7 trips; $\bar{x}$ = 5.44 ± 0.69 trips; n = 27) (Mann-Whitney test, Z = –0.60; $P > 0.05$).

3.4. Oviposition and cell closing

After depositing the last nectar load, the female backs out of the nest, turns, and re-enters the nest backwards until inside the cell to oviposit. During the oviposition, the female moves her antennae up and down while making abdominal contractions. The time from body insertion into the cell to body withdrawal ranged from 2.0 to 12.2 min ($\bar{x}$ = 6.2 ± 3.2 min; median = 4.8 min; n = 39). After oviposition, the female withdraws from the cell and immediately begins to turn clockwise and/or counterclockwise several times, until the closing of the cell is complete. During this activity, the female utilizes the hind legs and, probably the tip of the abdomen, to scatter and compact the plant material previously deposited on the cell partition.

The time required for cell construction, provisioning, oviposition, and cell closing ranged from one to five days (n = 200), but 61% and 33% of cells were completed in one and two days, respectively.

3.5. Nest plug

Following the sequence described above, the female makes another cell in front of the first one constructed. After closing the last brood cell, the female initiates new collections of plant material to construct a wall in front of the closure of the last cell and before the nest plug that resembles a cell partition. The nest plug is constructed at the entrance of the trap-nest (Fig. 1) and it is completed after the female finishes the wall in front of the last brood cell. During the completion of the nest plug, the female repeats the behaviours exhibited when constructing the bottom of a cell. The empty space between the nest plug and the last

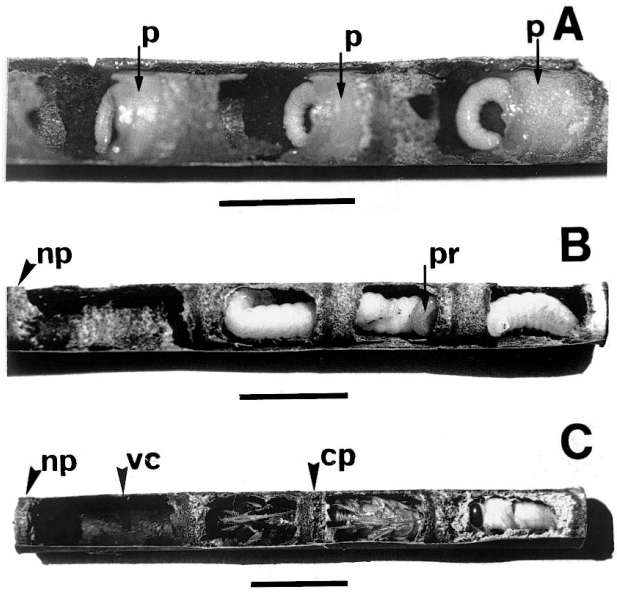

Figure 1. Nests of *C. analis* established in trap-nests with immatures in the larval (**A**), prepupal (**B**) and pupal (**C**) stages. (p = provisions; np = nest plug; vc = vestibular cell; cp = cell partition; pr = parasite (larva of *L. cayennensis* feeding on prepupa of *C. analis*). Scale bars are 1 cm.

brood cell is a vestibular cell (Fig. 1). After finishing the construction of the nest plug, the female covers it with an oily substance. One to five oily substance-collecting trips lasting 0.9–25.8 min ($\bar{x}$ = 9.2 ± 6.8 min; median = 6.8 min; n = 148) were made to cover the nest plug (n = 89), but two (n = 46) and three (n = 30) trips were the most frequent number. The time spent by the female depositing the oily substance on the plug ranged from 0.8 to 10.0 min ($\bar{x}$ = 3.9 ± 2.4 min; median = 3.7 min; n = 89).

Of the 62 marked females, 16 nested in the traps making a total of 25 nests; eight females made only one nest, seven made two nests and one female made three nests. The number of cells constructed by each female ranged from three to nine (Tab. I) and was significantly correlated with her period of activity (r = 0.754; P < 0.01).

A total of 89 nests were made during the study period with the highest frequencies of nesting occurring in January (n = 23 nests) and February (n = 27 nests). The time spent by females completing a nest was significantly correlated with the number of cells built (r = 0.436; P < 0.01; n = 89) (Tab. II).

Table I. Number of nests, cells, and total time (in days) spent by *Centris analis* females in nest construction.

Female No.	Number of completed nests	Number of cells	Period (in days) in activity
1	3	9	30
2	1	3	10
3	1	3	5
4	1	3	3
5	1	3	3
6	1	3	4
7	1	3	3
8	1	4	3
9	1	3	2
10	2	6	4
11	2	6	5
12	2	8	12
13	2	8	10
14	2	6	18
15	2	5	3
16	2	8	22

Table II. Time (in days) spent by *Centris analis* females to complete a nest, according to number of cells constructed.

Number of cell per nest	Number of nests	Time (in days)		
		minimum	maximum	$\bar{x}$ ± s.d.
1	2	1	4	2.5 ± 2.1
2	18	2	5	3.4 ± 1.2
3	60	2	10	4.7 ± 2.1
4	9	3	10	7.0 ± 2.2

3.6. Contents of nests

Cells were constructed in a linear series (Fig. 1), and the number of brood cells per nest ranged from one (n = 2) to four (n = 9), with three (n = 60) being the most frequent number of cells. Of the 89 nests obtained, two nests produced only males, one nest had male and parasite, 11 nests had males and females, two nests had females and parasite, and death of all immatures occurred in 39 nests. Of the 34 remaining nests, dead immatures were found in nests that produced females (n = 10), males (n = 10), both sexes (n = 8), parasite (n = 4), parasite and male (n = 1) and parasite and female (n = 1).

3.7. Sequence of sexes in nests, period of development, sex ratio and size of individuals

Males were reared in cells closest to the nest entrance, and females were reared in cells further away (n = 31). Deviations from this pattern occurred in seven nests. Of these seven nests, males were reared in the innermost cells in two nests, and in the five remaining, dead immatures were contained in the innermost cell, and only females were produced in the other cells. In nests made from early-November to late-February (mid of the wet/hot season) no significant difference was found between the egg-to-adult periods for males (range: 36–62 days; $\bar{x}$ = 53.4 ± 6.7 days; n = 34) as compared to females (range: 37–70 days; $\bar{x}$ = 56.3 ± 6.9 days; n = 19) (Mann-Whitney test, Z = –1.58; $P > 0.05$). A similar result was found for males (range: 61–85 days; $\bar{x}$ = 72.6 ± 8.1 days; n = 10) and females (range: 66–88 days; $\bar{x}$ = 77.3 ± 5.9 days; n = 22) produced in nests made during March (late wet/hot season) (Mann-Whitney test, Z = 1.46; $P > 0.05$). However, the times of development found in each nesting period were significantly different for both sexes (Mann-Whitney tests, Z = –4.69; $P < 0.05$, for males and Z = 5.40; $P < 0.05$, for females). The sex ratio of 85 individuals emerging from 89 nests constructed was 48.2% female to 51.8% male which is not significantly different from a 1:1 sex ratio ($X^2 = 0.04$; $P > 0.05$). The size of females ranged from 2.8 to 4.0 mm ($\bar{x}$ = 3.54 ± 0.15 mm; n = 172), and they were significantly larger than the males (range from 2.9 to 3.5 mm; $\bar{x}$ = 3.21 ± 0.12 mm; n = 172) ($t = 22.94$; df = 342; $P < 0.001$).

3.8. Immature mortality and nest associates

Of the 254 brood cells built in the 89 nests, only 85 (33.5%) produced adult bees. Among the remaining cells, 159 (62.6%) contained dead immatures, from unknown causes, and ten (3.9%) had been parasitized. The immatures died in the egg stage or first instar larva (140 cells), the larval stage (nine cells) and as pre-emergent adults (ten cells). Three species of natural

enemies attacked the nests: the wasp *Leucospis cayennensis* (Hymenoptera, Leucospidae) was the most common, accounting for 60.0% of parasitized cells (Fig. 1). *Coelioxys* sp. (Hymenoptera, Megachilidae) and *Mesocheira bicolor* (Hymenoptera, Apidae) were reared from three and one cells, respectively, corresponding to 30.0 and 10.0% of all parasitized cells. Of the 10 cells parasitized, two were the innermost brood cells of nests, attacked by *Leucospis* and *Coelioxys*. The remaining ones were the outermost brood cell of nests and were attacked by three parasites.

3.9. Intraspecific parasitism

On 10 occasions a female was observed opening a nest recently completed (< 24 h) by another female. The parasite female utilizes her fore legs and mandibles to break the nest plug. After that, she enters the vestibular cell, walks up to the cell partition of the outermost brood cell and breaks it also. After removing some fragments of cell partition, the female enters the brood cell and consumes the existing egg. Once the oophagy is finished, she backs out of the nest, turns, and reenters the nest backwards until inside the cell to oviposit. The female then initiates the closing of the cell, utilizing fragments of the cell partition that had not been removed from the nest. After that, she makes one or two plant material-collecting trips to finish the closing of the cell and initiate the construction of the nest plug. After finishing the closing of the cell, the parasite female makes an oily substance-collecting trip to cover the cell partition, and completes the construction of the nest plug like other females. Of the parasitized cells only one female and three males of *C. analis* and a female of *M. bicolor* emerged. In addition to these individuals, a female was found dead in another cell. The emergence of *M. bicolor* shows that the nest was attacked before being removed to the laboratory.

4. DISCUSSION

The use of sawdust and other plant material for construction of nests, as suggested by Vesey-FitzGerald [40] and reported by Frankie et al. [14, 15], and as observed in this study, is a characteristic of the *Heterocentris* species [6]. But in contrast to the observations of those authors, *C. analis* used plant material to construct the bottom wall of the cells, the cell partitions and the nest plug, while the space between the bottom of the cell and the cell partition was only lined with an oily substance. The presence of cell linings has been reported for *C. inermis* [6], *C. caesalpinae*, *C. pallida* [35], *C. collaris* [2], *C. mixta tamaguralis* [5], all ground nesters, and *C. vittata*, a cavity nester that utilizes a mixture of soil and oily material for nest construction [32]. The cell linings probably serve to protect cell contents from desiccation.

As reported by Coville et al. [6], Roubik [34] and Frankie et al. [16], and as observed in this study, the plug of *C. analis* nests was covered externally with oily material. The covering of the nest plug with such material has also been observed in *C. bicornuta* [14], another *Heterocentris* species, in some nests of *C. nitida* [44], *C. vittata* [14, 32, 44] and *C. tarsata* (Garófalo et al., unpublished data), which are all *Hemisiella* species. As suggested by Pereira et al. [32], the oily covering of the nest plug serves to provide greater protection to the nest, since the plug becomes harder after being covered. This may reduce or, at least, dissuade nest invasion by natural enemies, as reported by Gazola [18].

As in other cavity nesters, the cell arrangement and the number of cells in nests of *Heterocentris*, *Hemisiella* and *Xanthemisia* species depend upon the size of the cavity utilized. Thus, the pattern of cell arrangement in nests of *C. analis* followed the configuration of trap-nests used in this study. A similar pattern was found in the nests of the *Hemisiella* species – *C. lanipes*,

which constructed a nest in an old hole made by wood boring Coleoptera [27], and *C. vittata*, which established itself as well in trap-nests [32]. Concerning the number of cells, Vinson et al. [45] reported that the number of cells in nests of *C. analis* ranged from three to six. This latter value is higher than the maximum number of cells per nest found in this study. This difference may be due in part to trap-nests employed in this study which were shorter than the ones used by other authors. The results obtained in this study showed that *C. analis* females build up to nine cells and that they can live up to 30 days. These values, however, cannot be considered definitive, because the females may move elsewhere and continue producing cells.

Studies on the composition of larval food of some *Centris* species have shown that *C. trigonoides* [36], *C. adanae*, *C. flavifrons*, *C. flavofasciata* and *C. aethyctera* [45] use floral oils instead of nectar, while *C. maculifrons* [29] uses oils in addition to glucose and fructose, these latter presumably from floral nectar sources [45]. On the other hand, Pereira [31], studying the nesting behaviour of *C. vittata*, reported that cell provisioning is made with pollen, nectar and an oily substance which is deposited on the surface of the pollen and nectar loaf. In *C. analis*, similarly to *C. bicornuta* [44, 45] yet unlike other studied species, the cell provisions consisted of pollen and nectar only. Because those two species belong to the subgenus *Heterocentris*, the absence of oil in their larval food may be a characteristic of the subgenus.

The rearing of females from the inner cells and males from the outer cells of *C. analis* nests is a characteristic exhibited by many solitary bee and wasp species also nesting in trap-nests [23]. This was also observed in nests of *C. vittata* established in trap-nests [32]. Deviations from this pattern, as observed in this study, have also been found in some nests of other twig-nesting bees and wasps [20, 23, 26, 33]. While the factors determining the production of out-of-sequence males in nests of *C. analis* are unknown, the occurrence of females in the outermost brood cell of a nest was, in some cases, the result of intraspecific parasitism. This was confirmed by emergence of one female and by the presence of a dead female in parasitized intraspecific cells.

In *C. analis* nests, as also occurs in *C. vittata* [32], the males emerge before females, facilitated by the spatial arrangement of the sexes. This pattern of emergence was also reported for *C. pallida* [1], *C. caesalpinae* [35] and *C. fuscata* [2], all nest-excavating species that construct one cell at the end of each brood tunnel.

Dimorphism in males, as found in *C. pallida* [1], *C. inermis* [6], *C. flavifrons* [38], *C. flavofasciata* [4] and *C. caesalpinae* [35], was not observed in *C. analis*. In this species, like *C. m. tamaguralis* [39] and *C. vittata* [32], the males were significantly smaller than the females, with very little overlap in their respective size ranges. Since body size is associated with the amount of food a larva consumes [8, 9, 21–23], smaller amounts of food are likely deposited in the cells from which the males are produced. Although the amount of food stored in the cells of *C. analis* has not been measured, the smaller number of pollen-collecting trips required to provision the male cells suggests that they receive smaller amounts of food.

The percentage of *C. analis* cells lost to egg and early larval mortality was high. Similar results were reported by Frankie et al. [14] for some *Centris* species nesting in trap-nests. According to those authors, high environmental temperatures would be the cause of mortality and would affect mostly early instar larvae. As during the period of our study the maximum monthly temperatures were relatively high, ranging from 31.5 °C (March/94) to 35.6 °C (November/93), it is probable that this climatic factor has been responsible for the mortality found in *C. analis*. On the other hand, the percentage of parasitized cells was

relatively low. *Leucospis*, *Coelioxys* and *Mesocheira* were the insect parasites associated with the nests of *C. analis*. The first two of those were also observed attacking nests in Panama and, as in this study, the parasitism by *Leucospis* was more frequent than that by *Coelioxys* [34]. On the other hand, Parker [30] and Linsley et al. [24] reported the rearing of one female of *M. bicolor* from cells of *C. analis* constructed in old *Melitoma* cells. As hypothesized by Jayasingh and Taffe [20], in *C. analis* nests the cell built closest to the nest entrance was more heavily parasitized than inner cells. This result, however, must be interpreted cautiously, because the placing of trap-nests in wooden plates protects the innermost cells. Thus, parasites that oviposit through the side wall, usually after the nest is completed, such as *Leucospis*, the most important parasite of *C. analis* nests, do not have access to them. Irrespective of this fact, populations of *C. analis* utilizing trap-nests like those used in this study, will have a disproportionate number of male cells parasitized because the males are normally reared in the outermost brood cell of each nest.

A parasitic female *C. analis* opening a recently completed conspecific's cell, the replacement of the host egg with an egg of her own and the re-closing of the cell, as observed in this study, are all characteristics of brood parasitism. This type of parasitism is one of the six types of intraspecific parasitism that occurs in solitary bees and wasps [12]. Among the bees, brood parasitism was observed in *Osmia tricornis* [11], at least once in *Heriades carinata* [25] and in *Hoplitis anthocopoides* [10]. Intraspecific parasitic behaviour exhibited by *O. tricornis* and *H. anthocopoides* occurred where the bees nested gregariously. This was also observed in *C. analis*, because nesting in trap-nests effectively creates an aggregation. In *H. carinata* and *H. anthocopoides* no bees acted exclusively as parasites because all parasitic individuals were also observed making their own cells. This might also occur in *C. analis*, but definitive evidence is lacking.

Although the factors inducing *C. analis* females to act parasitically are not known, nest-site availability and food availability apparently did not determine that behaviour. As reported by Fabre [11] and Matthews [25] and as observed in this study, the intraspecific parasitism occurred despite an abundance of empty trap-nests. Moreover, the nesting by other females at the same time that parasite females attacked the nests suggests that food availability was not limiting.

As emphasised by Field [12], brood parasitism rarely alters a nest's external appearance, so it can be detected only through direct and constant observation. Thus, the data on intraspecific parasitism rates from the present study come from such observation. However, it is suspected that parasitism in this study did occur in some nests where the behaviour was not directly observed. Intraspecific parasitism is a likely explanation for the fact that females emerged from the outermost cells of some nests, from where males normally emerge.

ACKNOWLEDGEMENTS

This research was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). We are grateful to A.B. Gusman and E. Varanda for identifying the plant material and J.C. Serrano for technical help. We also thank J.C. Brown for the linguistic revision of the manuscript. B.M. Vieira de Jesus received a grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Résumé – Comportement de nidification de *Centris (Heterocentris) analis* (Fabricius) dans le sud-est du Brésil (Hymenoptera, Apidae, Centrini). Le comportement de nidification de *Centris analis* a été étudié sur le campus de l'Université de São Paulo-Ribeirão Preto, SP, Brésil. Les abeilles ont nidifié dans des nichoirs en carton noir

qui mesuraient 5,8 cm de long et 0,6 cm de diamètre intérieur. Ils ont été placés dans des trous percés dans cinq planches en bois ($28 \times 24 \times 4$ cm), posées sur des étagères dans un abri construit sur le site d'étude. Durant la période d'étude (novembre 1993–mars 1994), les pièges ont été inspectés tous les jours à l'aide d'un otoscope. Au laboratoire chaque nichoir a été placé dans un tube de verre transparent, de 4 cm plus long que le piège. Les adultes ont été récoltés et relâchés au fur et à mesure de leur émergence. Après l'émergence, les nids ont été ouverts et leur contenu analysé. Les nids n'ayant donné lieu à aucune émergence ont été ouverts également et le stade auquel l'insecte était mort a été noté. Les abeilles ont construit leur nid avec du matériel végétal et une substance huileuse. Celle-ci a été utilisée pour tapisser le fond et les murs de la cellule et pour recouvrir le bouchon du nid. Le matériel végétal était constitué essentiellement de pollen, de fragments d'anthères, de filaments, des petits morceaux de sacs polliniques et de fibres. Ce matériau a été utilisé pour construire le fond des cellules, les cloisons et le bouchon (Fig. 1). Les cellules ont été approvisionnées de pollen et de nectar. La femelle a démarré la récolte de nectar, une fois la récolte de pollen terminé. Les cellules approvisionnées avec plus de pollen avaient plus de chance de produire des femelles que des mâles. On n'a pas noté de corrélation entre le sexe des adultes ayant émergé et la quantité de nectar dans la cellule. Les nids terminés avaient entre une et quatre cellules disposées de façon linéaire, précédées en général d'une cellule vestibule vide (Fig. 1) ; il a fallu entre un et cinq jours pour constituer une cellule, mais la plupart ont été terminées dans la journée. Une femelle a construit trois nids de neuf cellules et la période la plus longue durant laquelle une femelle est restée au nid a été de 30 jours (Tab. I). Le temps passé par une femelle pour constituer un nid est corrélé avec le nombre de cellules construites (Tab. II). Les cellules les plus internes ont donné des femelles et les plus externes des mâles. Les femelles étaient significativement plus grosses que les mâles et aucun dimorphisme n'a été noté chez les mâles. Les nids ont été parasités par *Leucospis cayennensis* (Fig. 1), *Coelioxys* sp. et *Mesocheira bicolor*. Un parasitisme intraspécifique a été noté à 10 reprises. Dans tous les cas les nids ont été attaqués une fois qu'ils étaient terminés, la femelle parasite remplaçant l'œuf de l'hôte par le sien. Les matériaux utilisés par *C. analis* pour construire son nid sont spécifiques aux espèces d'*Heterocentris*. Comme chez d'autres insectes nidifiant dans des cavités, la disposition des cellules suivait la configuration des nichoirs. La couverture du bouchon avec une substance huileuse a été déjà mentionnée chez d'autres espèces d'*Heterocentris* et d'*Hemisiella*. L'absence d'huile dans la nourriture larvaire de *C. analis* est peut-être une caractéristique des espèces d'*Heterocentris*. On a aussi observé *Leucopsis* et *Coelioxys* attaquer des nids au Panama et, comme dans notre étude, le parasitisme par *Leucopsis* était le plus fréquent. L'élevage de femelles dans la cellule la plus externe du nid a été le résultat, dans certains cas, du parasitisme intraspécifique. Les facteurs induisant la reine de *C. analis* à agir en parasite sont inconnus, mais la disponibilité de sites de nidification et de nourriture ne semble pas avoir influencé ce comportement.

***Centris analis* / Apidae / comportement nidification / nichoir / Brésil**

Zusammenfassung – Nistverhalten von *Centris (Heterocentris) analis* Fabr. in Südost-Brasilien (Hymenoptera, Apidae, Centridini). Das Nistverhalten von *Centris analis* wurde auf dem Gelände der Universität von Sao Paulo in Ribeirao Preto, SP, Brasilien untersucht. Die Bienen nisteten in Kunstnestern aus schwarzer Pappe. Diese Kunstnester waren 5,8 cm lang und hatten einen inneren Durchmesser von 0,6 cm. Die Nisthilfen wurden in Hohlräume gesetzt,

die in 5 Holzplatten gebohrt waren (28,0 × 24,0 × 4,0 cm). Die Platten wurden auf Regale in einer Schutzhütte aufgestellt, die in der Versuchsanlage gebaut war. Während der Versuchszeit (November 1993 bis März 1994) wurden die Nester täglich mit einem Otoskop (Ohrenspiegel) inspiziert. Nach ihrer Fertigstellung wurden die Nester ins Labor überführt und durch ähnliche Kunstnester ersetzt. Im Labor wurde jedes Nest in eine durchsichtige Glasröhre gesetzt, die 4 cm länger als das Nest war. Die geschlüpften adulten Tiere wurden gesammelt und freigelassen.

Die Weibchen wurden vor der Freisetzung markiert. Die nun leeren Nester wurden geöffnet und ihr Inhalt analysiert. Nester, aus denen keine Tiere schlüpften, wurden ebenfalls geöffnet und das Entwicklungsstadium der toten Tiere wurde notiert.

Die Bienen bauten ihr Nest aus Pflanzenmaterial und einer öligen Substanz. Die ölige Substanz überzieht die Boden- und Zellwände und dient der Findung des Verschlusspfropfens. Der Zellboden, die Trennwände und der Pfropfen bestanden hauptsächlich aus Pflanzenmaterial wie Pollen, Antherenfragmenten, Staubfäden, Schnipsel von Staubbeuteln und Fasern (Abb. 1). Die Zellen wurden mit Pollen und Nektar proviantiert. Nach Beendigung des Pollensammelns begannen Weibchen Nektar zu sammeln. In Zellen, die durch mehr Pollenflüge versorgt waren, entwickelten sich mit größerer Wahrscheinlichkeit Weibchen. Die Anzahl der Nektarsammelflüge hatte keinen Einfluss auf das Geschlecht der adulten Tiere.

Fertiggestellte Nester bestanden aus 1 bis 4 linear angelegten Zellen, meist mit einem Abschluss durch eine leere Vorzelle (Abb. 1). Um eine Zelle fertig zu stellen benötigten die Weibchen zwischen 1 und 5 Tage. Die Anzahl der von einem Weibchen gebauten Nester und Zellen lag zwischen 3 bzw. 9. Die längste Zeit, in der ein Weibchen in der Nähe des Nests blieb, betrug 30 Tage (Tab. I). Die Zeit, die ein Weibchen bis zur Fertigstellung des Nestes benötigte, korreliert mit der Anzahl der gebauten Zellen (Tab. II). In den inneren Zellen entwickelten sich Weibchen, in den äußeren Männchen. Die Weibchen waren signifikant größer als Männchen. Es wurde kein Dimorphismus bei Männchen beobachtet. Die Nester wurden von *Leucopsis cayennensis* (Abb. 1), *Coelioxys* sp. und *Mesocheira bicolor* parasitiert. Intraspezifischer Parasitismus wurde in 10 Fällen beobachtet. Dabei wurden die Nester jedesmal erst nach ihrer Fertigstellung angegriffen und das parasitierende Weibchen ersetzte das ursprüngliche Ei durch ein eigenes.

Die von *C. analis* für den Nestbau benutzten Materialien sind charakteristisch für *Heterocentris* Arten. Wie bei anderen Höhlenbrütern folgt die Anordnung der Zellen der Form des Kunstnestes. Das Bedecken des Abschlusspfropfens mit öligen Substanzen kommt auch bei anderen *Heterocentris* und *Hemisiella* Arten vor. *Leucopsis* und *Coelioxys* wurden in Panama ebenfalls beim Angriff auf Nester beobachtet und, wie in dieser Studie, war der Parasitismus bei *Leucopsis* häufiger. Die Aufzucht von Weibchen in der äußersten Nestzelle war in manchen Fällen das Ergebnis intraspezifischer Parasitierung. Obwohl die Faktoren nicht bekannt sind, die eine Parasitierung durch *C. analis* Weibchen bewirken, schien das Angebot an Nistplätzen und Nahrung dieses Verhalten nicht zu beeinflussen.

Nistverhalten / Kunstnester / *Centris analis* / Apidae / Brasilien

REFERENCES

[1] Alcock J., Jones C.E., Buchmann S.L., Location before emergence of the female bee, *Centris pallida*, by its male (Hymenoptera: Anthophoridae), J. Zool. 179 (1976) 189–199.

[2] Camillo E., Garófalo C.A., Serrano J.C., Hábitos de nidificação de *Melitoma segmentaria, Centris collaris, Centris fuscata* e *Paratetrapedia gigantea* (Hymenoptera, Anthophoridae), Rev. Bras. Entomol. 37 (1993) 145–156.

[3] Camillo E., Garófalo C.A., Serrano J.C., Muccillo G., Diversidade e abundância sazonal de abelhas e vespas solitárias em ninhos armadilhas, Rev. Bras. Entomol. 39 (1995) 459–470.

[4] Chemsak J.A., Observations on adult behavior of *Centris flavofasciata* Friese (Hymenoptera: Anthophoridae), Pan-Pac. Entomol. 61 (1985) 265.

[5] Chiappa E., Toro H., Comportamiento reproductivo de *Centris mixta tamarugalis* (Hymenoptera: Anthophoridae). II Parte: Nidificacion y estados inmaduros, Rev. Chilena Entomol. 21 (1994) 99–115.

[6] Coville R.E., Frankie G.W., Vinson S.B., Nests of *Centris segregata* (Hymenoptera: Anthophoridae) with a review of the nesting habits of the genus, J. Kans. Entomol. Soc. 56 (1983) 109–122.

[7] Coville R.E., Frankie G.W., Buchmann S.L., Vinson S.B., Williams H.J., Nesting and male bahavior of *Centris heithausi* in Costa Rica (Hymenoptera: Anthophoridae) with chemical analysis of the hind leg glands of males, J. Kans. Entomol. Soc. 59 (1986) 325–336.

[8] Cowan D.P., Parental investiment in two solitary wasps *Ancistrocerus adiabatus* and *Euodynerus foraminatus* (Eumenidae: Hymenoptera), Behav. Ecol. Sociobiol. 9 (1981) 95–102.

[9] Danforth B.N., Provisioning behavior and the estimation of investiment ratios in a solitary bee, *Calliopsis (Hypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae), Behav. Ecol. Sociobiol. 27 (1990) 159–168.

[10] Eickwort G.C., Gregarious nesting of the mason bee *Hoplitis anthocopoides* and the evolution of parasitism and sociality among megachilid bees, Evolution 29 (1975) 142–150.

[11] Fabre J.H., The mason-bees, Transl. by A.T. de Mattos, Hodder and Stoughton, London, 1914.

[12] Field J., Intraspecific parasitism as an alternative reproductive tactic in nest-building wasps and bees, Biol. Rev. 67 (1992) 79–126.

[13] Frankie G.W., Vinson S.B., Opler P.A., *Centris aethyctera* and *Centris fuscata* in the lowland dry forest of Costa Rica (Hymenoptera: Anthophoridae), in: Janzen D.H. (Ed.), Costa Rica Natural History, Univ. Chicago Press, Chicago, 1983, pp. 707–708.

[14] Frankie G.W., Vinson S.B., Newstrom L.E., Barthell J.F., Nest site and habitat preferences of *Centris* bees in Costa Rican dry forest, Biotropica 20 (1988) 301–310.

[15] Frankie G.W., Vinson S.B., Williams H., Ecological and evolutionary sorting of 12 sympatric species of *Centris* bees in Costa Rican dry forest, in: Bock J.H., Linhart Y.B. (Eds.), The evolutionary ecology of plants, Westview Press, Boulder, 1989, pp. 535–549.

[16] Frankie G.W., Newstrom L.E., Vinson S.B., Nesting-habitat preferences of selected *Centris* bee species in Costa Rican dry forest, Biotropica 25 (1993) 322–333.

[17] Garófalo C.A., Camillo E., Serrano J.C., Espécies de abelhas do gênero *Centris* (Hymenoptera, Anthophoridae) nidificando em ninhos armadilhas, Ciên. Cult. 41 (1989) 799.

[18] Gazola A.L., Parasitismo em populações de *Centris (Heterocentris) analis* (Fabricius, 1804) (Hymenoptera, Apidae, Centridini) com especial referência ao comportamento de *Leucospis cayennensis* Westwood, 1839 (Hymenoptera, Chalcidoidea, Leucospidae), MSc. thesis, FFCLRP-USP, 1999, Ribeirão Preto, Brazil.

[19] Heithaus E.R., Community structure of neotropical flower visiting bees and wasps: diversity and phenology, Ecology 60 (1979) 190–202.

[20] Jayasingh D.B., Taffe C.A., The biology of the eumenid mud-wasp *Pachodynerus nasidens* in trapnests, Ecol. Entomol. 7 (1982) 283–289.

[21] Kim J.Y., Female size and fitness in the leafcutter bee *Megachile apicalis*, Ecol. Entomol. 22 (1997) 275–282.

[22] Klostermeyer E.C., Mech S.J., Rasmussen W.B., Sex and weight of *Megachile rotundata* (Hymenoptera: Megachilidae) progeny associated with provision weights, J. Kans. Entomol. Soc. 46 (1973) 536–548.

[23] Krombein K.V., Trap-nesting wasps and bees. Life histories, nests and associates, Smithsonian Press, Washington, 1967.

[24] Linsley E.G., MacSwain J.W., Michener C.D., Nesting biology and associates of *Melitoma* (Hymenoptera, Anthophoridae), Univ. Calif. Publ. Entomol. 90 (1980) 1–45.

[25] Matthews R.W., The biology of *Heriades carinata* Cresson (Hymenoptera, Megachilidae), Contrib. Amer. Entomol. Inst. 3 (1965) 33 p.

[26] McCorquodale D.B., Owen R.E., Laying sequence, diploid males, and nest usurpation in the leafcutter bee, *Megachile rotundata* (Hymenoptera: Megachilidae), J. Insect Behav. 7 (1994) 731–738.

[27] Michener C.D., Lange R.B., Observations on the ethology of neotropical anthophorine bees (Hymenoptera: Apoidea), Univ. Kans. Sci. Bull. 39 (1958) 69–96.

[28] Moure J.S., Notes on the types of the neotropical bees described by Fabricius (Hymenoptera: Apoidea), Studia Entomol. 3 (1960) 97–160.

[29] Neff J.L., Simpson B.B., Oil-collecting structures in the Anthophoridae (Hymenoptera): morphology, function, and use in systematics, J. Kans. Entomol. Soc. 54 (1981) 95–123.

[30] Parker F.D., Biological notes on some Mexican bees (Hymenoptera: Megachilidae, Anthophoridae), Pan-Pac. Entomol. 53 (1977) 189–192.

[31] Pereira M., Comportamento de nidificação e abundância sazonal de *Centris (Hemisiella) vittata* Lepeletier (Hymenoptera: Apidae: Apinae: Centridini), MSc. thesis, FFCLRP-USP, 1997, Ribeirão Preto, Brazil.

[32] Pereira M., Garófalo C.A., Camillo E., Serrano J.C., Nesting biology of *Centris (Hemisiella) vittata* Lepeletier in southeastern Brazil (Hymenoptera, Apidae, Centridini), Apidologie 30 (1999) 1–12.

[33] Raw A., The biology of the solitary bee *Osmia rufa* (L.) (Megachilidae), Trans. R. Entomol. Soc. London 124 (1972) 213–229.

[34] Roubik D.W., Ecology and natural history of tropical bees, Cambridge Univ. Press, New York, 1989.

[35] Rozen J.G., Buchmann S.L., Nesting biology and immature stages of bees *Centris caesalpinae, C pallida*, and the cleptoparasite *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae), Am. Mus. Novit. 2985 (1990) 1–30.

[36] Simpson B.B., Neff J.L., Seigler D., Krameria, free fatty acids and oil-collecting bees, Nature 267 (1977) 150–151.

[37] Snelling R.R., Notes on the distribution and taxonomy of some North American *Centris* (Hymenoptera: Anthophoridae), Contrib. Science, Los Angeles County Museum Nat. Hist. 259 (1974) 1–41.

[38] Snelling R.R., Studies on the taxonomy and distribution of American Centridine bees (Hymenoptera: Anthophoridae), Contrib. Science, Los Angeles, California Museum Nat. Hist. 347 (1984) 1–69.

[39] Toro H., Chiappa E., Ruz L., Cabezas V., Comportamiento reproductivo de *Centris mixta tamarugalis* (Hymenoptera: Anthophoridae), I Parte, Acta Entomol. Chilena 16 (1991) 97–112.

[40] Vesey-FitzGerald D., Observations on bees (Hymenoptera: Apoidea) in Trinidad, BWI, Proc. R. Entomol. Soc. London A 14 (1939) 107–110.

[41] Vinson S.B., Frankie G.W., A comparative study of the ground nests of *Centris flavifrons* and *Centris aethiocesta* (Hymenoptera: Anthophoridae), Entomol. Exp. Appl. 49 (1988) 181–187.

[42] Vinson S.B., Frankie G.W., Nest variability in *Centris aethyctera* (Hymenoptera: Anthophoridae) in response to nesting conditions, J. Kans. Entomol. Soc. 64 (1991) 156–162.

[43] Vinson S.B., Frankie G.W., Coville R.E., Nesting habits of *Centris flavofasciata* (Hymenoptera: Apoidea: Anthophoridae) in Costa Rica, J. Kans. Entomol. Soc. 60 (1987) 249–263.

[44] Vinson S.B., Frankie G.W., Williams H.J., Chemical ecology of bees of the genus *Centris* (Hymenoptera: Apidae), Fla. Entomol. 79 (1996) 109–129.

[45] Vinson S.B., Williams H.J., Frankie G.W., Shrum G., Floral lipid chemistry of *Byrsonima crassifolia* (Malpighiaceae) and a use of floral lipids by *Centris* bees (Hymenoptera: Apidae), Biotropica 29 (1997) 76–83.