Nesting biology of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera, Apidae, Centridini)

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ABSTRACT. Nests of *Centris tarsata* Smith, 1874 were obtained from trap-nests in areas of dry semi-deciduous forest (Baixa Grande) and caatinga (Ipirá), in the State of Bahia. Nesting occurred in bamboo canes and in tubes of black cardboard with 5.8 cm (= small tube) and 10.5 cm (= large tube) in length and 0.6 and 0.8 cm in diameter, respectively. In both areas *C. tarsata* nested during the wet season producing four generations in Baixa Grande and three generations in Ipirá. The immatures of one generation underwent diapause at both sites. The bees constructed their nests with a mixture of sand and oil. In general, the cells were elongated and arranged in linear series with its opening pointing towards the nest entrance. Completed nests had two to three cells in small tubes, one to seven cells in large tubes, and two to 13 cells in bamboo canes. The nest plug resembled an uncompleted cell and was externally covered with oil. The cells were provisioned with pollen, oil, and nectar. Nests were parasitized by *Mesocheira bicolor* (Fabricius, 1804) (Hymenoptera: Apidae) and other not identify bee species.
KEY WORDS. Monitoring, nest structure, solitary bees, South American dry forests, trap-nests

RESUMO. Ninhos de *Centris tarsata* Smith, 1874 foram obtidos através da utilização de ninhos-armadilha, em áreas de floresta estacional semi-decídua (Baixa Grande) e de caatinga (Ipirá), no Estado da Bahia. A nidificação ocorreu em gomos de bambus e em tubos de cartolina preta, estes com comprimentos de 5,8 cm (= tubos pequenos) e 10,5 cm (= tubos grandes), e diâmetro de 0,6 e 0,8 cm, respectivamente. Em ambas as áreas *C. tarsata* nidificou durante a estação úmida, produzindo quatro gerações anuais em Baixa Grande e três em Ipirá. Os imaturos de uma das gerações passaram por diapausa em ambos os locais. As abelhas construíram seus ninhos com uma mistura de areia e óleo. Em geral, as células foram alongadas e arranjadas em série linear, com sua abertura dirigida para a entrada do ninho. Os ninhos completados tinham de duas a três células nos tubos pequenos, de uma a sete células nos tubos grandes e de duas a 13 nos gomos de bambu. A parede de fechamento do ninho lembrava uma célula incompleta e era coberta externamente com óleo. As células foram aprovisionadas com pólen, óleo e néctar. Os ninhos foram parasitados por *Mesocheira bicolor* (Fabricius, 1804) (Hymenoptera, Apidae) e por outra espécie de abelha não identificada.
PALAVRAS CHAVE. Monitoramento, ninhos-armadilha, estrutura de ninhos, abelhas solitárias, florestas secas Sul-americanas.

Bees of the genus *Centris* Fabricius, 1804 have widely varying nesting habits. Most species dig nests in the ground, while those belonging to the subgenera *Hemisiella* Moure, 1945, *Heterocentris* Cockerell, 1899, and *Xanthemisia* Moure, 1945 construct their nests in a variety of preexisting cavities, including trap-nests (Coville *et al.* 1983, Frankie *et al.* 1988, 1993, Pereira *et al.* 1999, Jesus & Garófalo 2000).

Centris (*Hemisiella*) *tarsata* Smith, 1804 has only been recorded in Brazil. Information from specimens deposited in entomological collections (J.M.F. Camargo, personal communication) together with data on samples of females and/or males collected on flowers (Camargo & Mazucato 1984, Vogel & Machado 1991, Martins 1994, Silveira & Campos 1995, Albuquerque & Mendonça 1996, Freitas 1997, Schlindwein 1998, Zanella 2000), as well as the localization of nests (Chandler *et al.* 1985, Camilo *et al.* 1995, Viana *et al.* 2001, Silva *et al.* 2001, Aguiar & Martins 2002) indicate the occurrence of *C. tarsata* in the states of Pará, Maranhão, Piauí, Ceará, Paraíba, Pernambuco, Bahia, Minas Gerais, São Paulo, Paraná, Rio Grande do Sul, Mato Grosso do Sul, Mato Grosso, and Goiás.

Little is known about the nesting biology of *C. tarsata*. The only available information consisting of data concerning nesting periods, dimensions of the trap-nests used, nest architecture, and sex ratio, was provided by Viana *et al.* (2001) and Silva *et al.* (2001) from observations made on coastal sand dunes in Salvador (State of Bahia), as well as by Aguiar & Martins (2002), in observations made in the Atlantic rain forest and coastal savannas ("tabuleiros") (State of Paraíba). In this paper data obtained from trap-nests on the nesting biology and seasonal abundance of *C. tarsata* in areas of caatinga (dry savanna) and dry semi-deciduous forests are presented.

MATERIAL AND METHODS

Study Areas

The study was conducted in an area of caatinga of Sempre Verde Farm, Ipirá (12°13'09"S; 39°49'53"W), State of Bahia, and in a dry semi-deciduous forest of Olhos d'Água Farm, Baixa Grande (12°00'29"S; 40°17'21"W), State of Bahia, Brazil The climate in Ipirá is semi-arid, with an average annual temperature of 23.7 °C (average maximum of 28.9°C and average minimum of 19.9°C) and an average annual rainfall of 754 mm (range 157-1560 mm/year) (Bahia 1994). During this study, the dry season extended from February/March to September/October. The rainy season started during October/November and continued until January/February, although it was interrupted by intermittent dry periods. The vegetation in the area is an open arboreal caatinga, often converted to pasture. In B. Grande, the climate ranges from dry to sub-humid. The average annual temperature is 23.6° C (average maximum of 29°C and average minimum of 19.7°C) and the average annual rainfall is 820 mm (range 368-1204 mm/year) (Bahia 1994). During the study period, the rainy season began in September/October and extended until March/April, while the dry season started during April/May and ended in August/ September. The trap-nests were placed in a forest fragment surrounded by bean crop fields.

Methods

As described by Camillo *et al.* (1995), the trap-nests used in this study consisted of hollow bamboo canes, which were cut so that a nodal septum closed one end of the cane, and of tubes of black cardboard, with one end closed with the same material. The bamboo canes varied in internal diameter from 5.0 to 25.0 mm and had variable lengths. The tubes were of two sizes (length x internal diameter): 10.5 x 0.8 cm (= large tubes) and 5.8 x 0.6 cm (= small tubes). These tubes were inserted into horizontal holes drilled into wooden plates (54 holes per plate). The canes and the wooden plates were placed along steel shelves covered with a plastic tarpaulin in order to protect them from the sun and the rain. Two sampling sites were established in each area: one in a forest fragment (P-I) and the other in a farm shed (P-II) in Baixa Grande; and one in a pasture (P-III) and the other in an area of caatinga (P-IV) in Ipirá. A total of 270 cardboard tubes of both sizes plus 100 bamboo canes were set up at each sampling site, except for site P-II where 108 small tubes, 54 large tubes, and 50 bamboo canes were set up.

The trap-nests were inspected once a month from September 1999 to February 2001 in Ipirá, and from November 1998 to February 2001 in Baixa Grande. Each inspection was made with the aid of an otoscope. When traps contained completed nests, they were collected and replaced with empty ones. In the laboratory, each trap-nest was introduced into a transparent glass or plastic tube, 4.0-5.0 cm longer than the trap, with one end closed with a cork. As adult emerged into the glass/plastic tube, the trap was removed and the individuals were collected. The nests were kept at room temperature and observed daily until the adults emerged. A few 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.

Observations of nesting behavior were carried out in Monte Santo (10°19'31"S; 39°13'59"W), State of Bahia. Nesting activities of a female in a bamboo cane were recorded from 5:30 to 17:30 h during two consecutive days. The activities of the female within the nest were observed with the aid of an otoscope. Voucher specimens of bees are deposited in the CUFS collection, Universidade Estadual de Feira de Santana, Bahia.

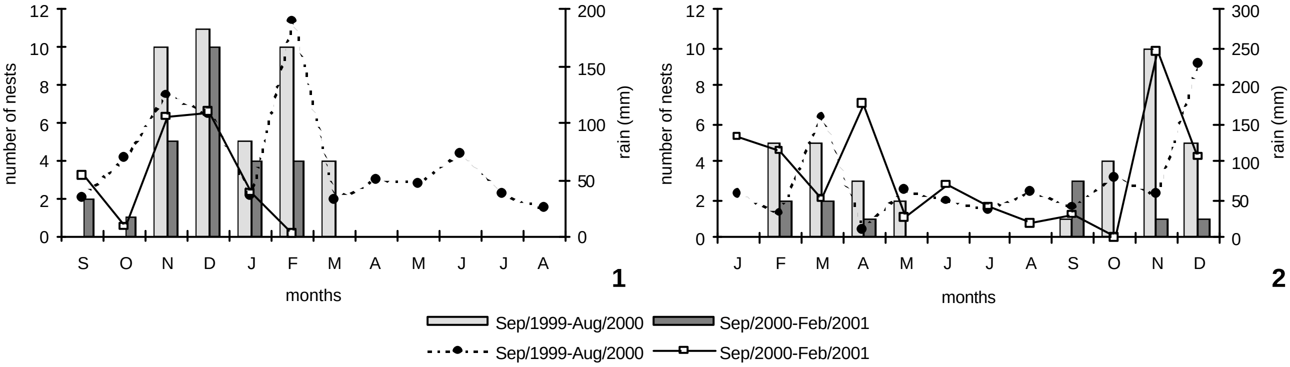
Statistical Analyses

Statistical tests follow Zar (1984) and were performed by using the statistical package SigmaStat for Windows (1994-Jandel Corporation, San Rafael, California). Chi-square tests were used to compare number of nests by area, immature mortality, parasitism rates, and sex ratio. Pearson correlation analysis was performed to verify the intensity of association between frequency of nesting in each area and monthly rainfall. The Mann-Whitney test was used to compare the space occupied by nests in each of the types of trap-nests utilized by bees. Throughout the text all means (x) are given ± SD.

RESULTS

Phenology of nesting

Of the 119 nests obtained, 53 were established in Baixa Grande and 66 in Ipirá. There was no difference between the frequencies of occupation of traps in relation to the number of exposed trap in each area ($\chi^2 = 1.84$; d.f. = 1; p = 0.174). In both areas the nesting activities occurred during the period of greatest rainfall. In Ipirá, *C. tarsata* nested from September to March with the highest frequencies of nesting occurring in November, December and February (Fig. 1), and in B. Grande the nesting occurred from September to May with the highest nesting frequency in November/99 (Fig. 2). In B. Grande no significant correlation was found between the number of nests and the monthly rainfall during both years (r = 0.31; d.f. = 11;



Figures 1-2. Number of nests of *Centris tarsata* (colums) and monthly rainfall (lines): (1) from September 1999 to February 2001, in Ipirá, Bahia; (2) from January 1999 to December 2000, in Baixa Grande, Bahia.

p = 0.319, for 1999 and r = 0.13; d.f. = 11; p = 0.690, for 2000), while in Ipirá the correlation was highly significant (r = 0.71; d.f. = 16; p = 0.001) for the period from September 1999 to February 2001.

Trap-nests used by *C. tarsata* and nest architecture

Centris tarsata utilized all types of trap-nests: 72 % of the nests were built in large tubes, 3 % in small tubes, and 25 % in bamboo canes (Tab. I). Small tubes were utilized only in B. Grande (P-II site) where large tubes were less available and some were occupied by wasps. The bamboo canes utilized by the bees ranged from 51 to 265 mm in length (n = 28) and from 8 to 13 mm in diameter (n = 28), but most nests were established in canes either 9 mm (n = 11) or 10 mm (n = 9) in diameter.

Table I. Frequency of nesting by *Centris tarsata* in each type of trap-nest, in each sampling site in Baixa Grande (BG I and II) and Ipirá (IP III and IV).

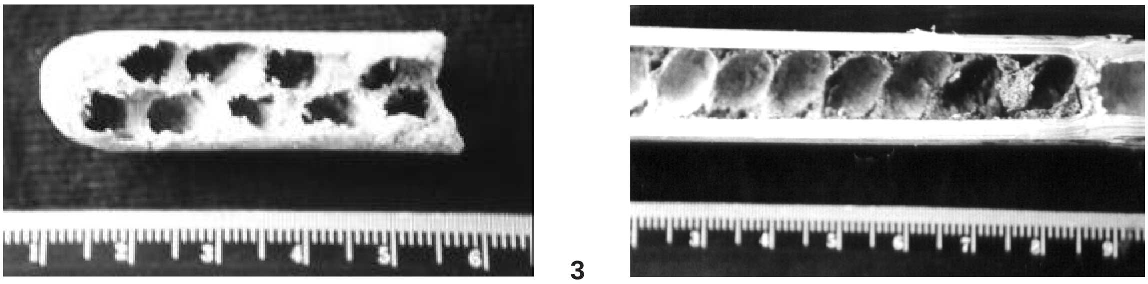
Types of trap-nests	Number of nests per site			
	BG (I)	BG (II)	IP (III)	IP (IV)
Small tubes (5.8 x 0.6 cm)	–	3	–	–
Large tubes (10.5 x 0.8 cm)	31	9	16	30
Bamboo canes	4	6	11	9
Total number of nests	35	18	27	39

The nests were constructed with a mixture of sand and oil. Of the 30 nests analyzed, in 19 the nesting activities had started with the construction of a wall at the bottom of the cavity, followed by the first cell. This wall (missing in 20% of nests) was 0.7 to 2.0 mm thick. In the 5 remaining nests there was a space filled with loose sand ranging from 3.0 to 11.0 mm between the bottom of the cavity and the bottom of the first cell.

Irrespective of the trap-nest utilized, the bees used just part of the available length to construct their nests. The space occupied by the nest (cells and nest plug) ranged from 14.5 to 97 mm (n = 68). In most cases the first cell was built near the end of the trap, or slightly distant from it, and the nest plug was recessed 8 to 111 mm from the trap entrance. No significant difference between the space occupied by nests in bamboo canes (x = 55.6 ± 18.5 mm; n = 25) and that in large tubes (x = 53.4 ± 23.3 mm; n = 43) was observed (Mann-Whitney test, Z = -0.311; p = 0.377).

Cells were elongated, lightly rounded at the bottom, but in nests constructed in bamboo canes the cells tended to be more oval. The cells had a rough and irregular texture (small sand grains) on their outer surface, while the inner surface was smooth and lined with a thin layer of oil. The cell walls did not extend above the cell cap. The cell cap was made of the same material as used for cell construction. This cap resembled a disk without any raised process or prominence on the outer surface but with a small depression in the center or near it on the inner surface. The cell caps had an average diameter of 6.48 ± 0.40 mm (n = 19), being 0.62 ± 0.34 mm thick in the center and 1.39 ± 0.33 mm thick at the edges. The average diameter of the cell opening was 5.26 ± 0.31 mm (n = 56). The outer measurements of the cells ranged from 8 to 17 mm in length (x = 12.3 ± 2.1 mm; n = 66) and from 7 to 11 mm in maximum width (x = 8.5 ± 1.2 mm; n = 66). The lateral cell walls of the same cell were of unequal thickness, ranging from 0.6 to 3 mm (x = 1.6 ± 0.5 mm; n = 59) on the thickest side and from 0.3 to 1 mm (x = 0.51 ± 0.14 mm) on the thinnest side.

Cells were linearly arranged, but two parallel rows of cells were found in one nest (Fig. 3). Cell orientation was generally horizontal (with its opening pointing towards the nest entrance), but in bamboo canes with diameter wider than 0.8 cm, the cells tended be more inclined (Fig. 4). Completed nests had two to three cells in small tubes (n = 3), one to seven cells in large tubes (n = 70), and two to 13 cells in bamboo canes (n = 28) (Fig. 5). Considering all traps together, approximately 10 % of the nests had only one cell, 20 % had 13 cells, and 70 % had three to six cells.



Figures 3-4. Nests of *Centris tarsata*: (3) nest removed from the bamboo with two parallels rows of cells; (4) bamboo cane split in half showing the arrangement of the cells within the cavity.

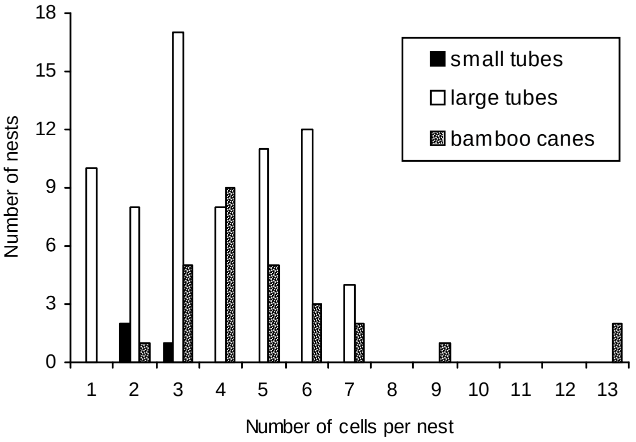
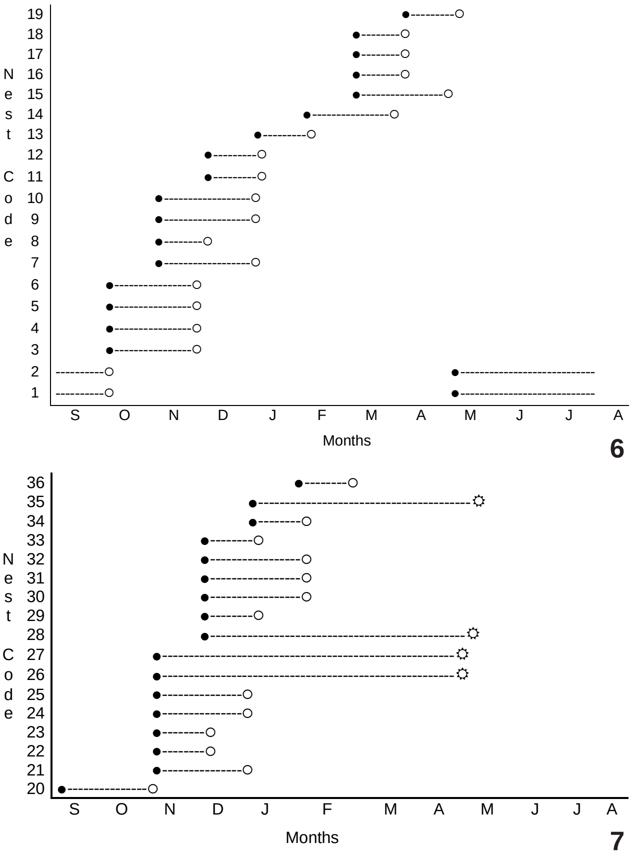


Figure 5. Number of cells per nest according to the type of trap-nest used by *Centris tarsata*.



Figures 6-7. Interval (in days) (——) between the collection (●) of the nest and the emergence (○) of individuals produced in *Centris tarsata* nests established in (6) Baixa Grande and (7) Ipirá, Bahia. (✡) Nests containing prepupae in diapause when they were opened on June 2001.

The cocoon tightly adhered to the inner wall of the cell. The top half of the cocoon was thin (approximately 0.3 mm thick), transparent, beige in color, and composed of a single layer of a cellophane-like material. In its most basal portion, the cocoon was composed of at least two layers, becoming thicker (about 1 mm) and darker (brown) due to the presence of feces deposited between the layers. The top of the cocoon had a slightly raised central area that occupied the central depression of the lower surface of the cell cap.

The nest plug was concave, resembling an uncompleted cell, with the walls ranging in length from 2.9 to 6.5 mm, and extending towards the cavity entrance. The outer surface of the plug was smooth and covered with oil which hardened within a few days.

Cell construction and provisioning

To construct two cells the female made 15 and 18 sand-collecting trips, lasting from 0.3 to 10 min (x = 3.0 ± 2.8 min; n = 39), and gathered at least two loads of oil per cell. The female spent 3,5 hours constructing one cell and seven hours to construct the other. In the first case, cell construction was completed in a single day, whereas for the second one, the construction began in the late afternoon, was interrupted during the night, and was concluded the following day.

A total of 4-5 pollen-collecting trips followed by 3-4 oil-collecting trips were required to provision one cell (n = 3). Pollen-collecting trips had an average duration of 12.6 ± 6.0 min (n = 13), while oil-collecting trips lasted 7.4 ± 2.1 min (n = 11). When returning to her nest with a pollen load, the female entered head first and walked to the cell. On the first two foraging trips, the female stayed from 10 to 49 seconds (x = 22.7 ± 16.0 seconds; n = 6) with her head inserted into the cell; then, she backed out of the cell, turned, and re-entered the cell backwards until reaching its bottom. Thereafter, the female removed the material from her hind legs by scraping alternatively one leg against another. On the third, fourth or fifth foraging trip, before depositing the pollen load, the female stayed from 37 to 270 seconds (x = 115.6 ± 76.9 seconds; n = 7) with her head inserted into the cell and turned clockwise and/or counterclockwise several times. To deposit an oil load, the female followed the same behavioral sequence as described earlier and, before depositing that material she spent 18 to 110 seconds (x = 44.5 ± 30.9 seconds; n = 10) with her head inserted into the cell. The total time spent provisioning (pollen plus oil) each cell (n = 3) ranged from 2,5 to three hours.

Adult emergence and number of generations

In general, adults emerged 5 to 6 weeks after nests were removed from the field, and rarely after more than 47 days. However, individuals from two nests (Fig. 6, nests 1 and 2) established in late May in B. Grande emerged 139 days after the nest have been collected. Moreover, four nests from Ipirá (Fig. 7, nests 26, 27, 28 and 35), constructed between November 2000 and January 2001, were found to contain prepupae when the cells were opened in the laboratory in June 2001.

In B. Grande, four generations per year may occur, with three short life-cycles (October/November to December-January; December to January/February; and February/March to April/May) together with a single long one (May to October) (Fig. 6). During the long life cycle, the immatures spend the dry season in diapause as prepupae. In Ipirá, the data suggest the occurrence of three generations per year (two short life-cycles and one longer one) (Fig. 7) and, in contrast to observations in B. Grande, long life-cycle nests were established at the same time as the short life-cycle nests.

Sex ratio

In addition to the 48 males and 13 females emerged from nests collected in B. Grande, 25 males and 3 females were found dead in the cells. When considering all individuals, emerged and dead in the cells, the sex ratio was significantly males biased (χ^2 = 36.5; d.f. = 1; p = 0.00). In Ipirá, 25 males and 22 females emerged from the nests; these individuals, together with five males and five females found dead in the cells, resulted in a total sex ratio not significantly different from 1:1 (χ^2 = 0.15; d.f. = 1; p = 0.691).

Immature mortality and nest associates

The contents of 266 cells (133 from each area) from 41 nests from B. Grande and 40 nests from Ipirá were analyzed (Tab. II). No significant difference in total mortality was observed between B. Grande (52.6 %) and Ipirá (58.6 %) (χ^2 = 0.97; d.f. = 1; p = 0.323). Similarly, the mortality rate due to unknown causes was not significantly different in the two areas (χ^2 = 0.02; d.f. = 1; p = 0.901), accounting for 41.3 % and 42.1 % of the total mortality in B. Grande and Ipirá, respectively. Pre-emergent adults had the highest mortality rate (26.3 %) in B. Grande, while in Ipirá, eggs, larvae, and pre-emergent adults had similar mortality rates. *Mesocheira bicolor* (Fabricius, 1804) (Apidae, Ericrocidini) and two species of *Coelioxys* (*Cyrtocoelioxys*) (Megachilidae, Megachilini) were the insect parasites associated with the nests of *C. tarsata*. These parasites attacked 15 cells (11.3 %) in eight nests in B. Grande, and 22 cells (16.5%) in 16 nests in Ipirá. There was no difference in parasitism rates between the two sites (χ^2 = 1.54; d.f. = 1; p = 0.214), although the frequencies of attacks by different parasites differed significantly (χ^2 = 4.75; d.f. = 1; p = 0.029): in Baixa Grande, *M. bicolor* was the main enemy, accounting for 73.3 % of all cells parasitized, while in Ipirá, other parasitic bees were the most destructive enemy, accounting for 63.6 % of all cells parasitized (Tab. II).

Table II. Mortality and survival of *Centris tarsata* from a sample of nests established in Baixa Grande (November/1998-February/2001) and Ipirá (September/1999-February/2001).

	Baixa Grande	Ipirá
Number of nests	41	40
Number of brood cells	133	133
Total number of emerged bees	63 (47.4%)	55 (41.4%)
Total number of dead immatures	55 (41.3%)	56 (42.1%)
Dead in Egg stage	9	18
Dead in Larval stage	7	17
Dead in Pupal stage	4	5
Dead in Pre-emergent adults	35	16
Total of cells parasitized	15 (11.3%)	22 (16.5%)
Parasitized by *Mesocheira bicolor*	11	8
Parasitized by other parasitic bees	4	14

DISCUSSION

As suggested for some wasp species (Krombein 1967, Fricke 1991, Garcia & Adis 1995) and reported for two *Megachile* Latreille, 1802 species (Strickler *et al.* 1996), the choice of a nesting burrow of particular diameter by bee species must be also dictated to a considerable extent by the size (head width) of the female. An additional factor in this regard may be the need to fill the cavity with material to make the nest, as occurs in *C. tarsata*. The differential utilization of the three types of trap-nests in this study, together with data reported by Silva *et al.* (2001) and Aguiar & Martins (2002), suggests that *C. tarsata* females nest preferentially in cavities 8-10 mm in diameter.

The utilization of cavities with other diameters may be due to the variability in female size, the low availability of preferential nesting cavities, or perhaps to intra- or inter-specific competition between bees nesting at the same site, as reported by KROMBEIN (1967) for *Trypoxylon* species (Sphecidae).

Studies carried out with trap-nests have shown that *C. tarsata* occurs at higher density in some areas of the northeastern part of the country (VIANA *et al.* 2001, AGUIAR 2002, AGUIAR & MARTINS 2002) than in forest fragments of the southeastern part (CAMILLO *et al.* 1995, GARÓFALO 2000). Its occurrence in sand dunes (VIANA *et al.* 2001, SILVA *et al.* 2001), the dominance in these northeastern areas, and the high and similar nesting frequencies in both areas in this work, indicate that *C. tarsata* is well adapted to nesting in hot, sunny habitats with open vegetation, as sand dunes and caatingas, but also in forested habitats in northeastern Brazil.

The yearly variations in nesting frequency observed in the present study were also reported by VIANA *et al.* (2001) for *C. tarsata* and by other authors (FRANKIE *et al.* 1993, PEREIRA *et al.* 1999, MORATO *et al.* 1999) for other *Centris* species. According to FRANKIE *et al.* (1998), fluctuations in nesting frequency could be a regular characteristic of bees species nesting in preexisting cavities, and may be driven by factors such as differential natural mortality, extreme annual climatic patterns (drought or above normal rainfall), or the disturbance of marginal habitats.

Although *C. tarsata* differed in the duration of the nesting periods in B. Grande and Ipirá, the temporal pattern of activity was similar in both areas with an intensification of nesting activities during the period of greatest rainfall. AGUIAR (2003), in a study on flower visitors in the caatinga of Itatim (State of Bahia), suggested that *C. tarsata* also maintains activity at that site during the rainy season, at least from September to February. This coincides with the nesting period observed in the caatinga in Ipirá. In other habitats there was little coincidence between the nesting activity of *C. tarsata* and either the dry or rainy period. In the Atlantic forest (Mamanguape, State of Paraíba) the highest nesting frequency occurred during the driest period (AGUIAR & MARTINS 2002), while in sand dune areas (Salvador, State of Bahia) a larger number of nests was established in the driest period during the first year of sampling, but in the rainiest period during the second year (VIANA *et al.* 2001). Additional surveys examining fluctuations in floral resource availability in these habitats during both the dry and rainy periods may help to elucidate the nesting patterns observed.

The utilization of sand and oil as nest construction material by *C. tarsata*, as observed in the present study and also reported by SILVA *et al.* (2001), is a characteristic of *Hemisiella* species (COVILLE *et al.* 1983, VINSON *et al.* 1993, 1996, PEREIRA *et al.* 1999, MORATO *et al.* 1999). In general, the shape of C. *tarsata* cells is similar to that described for other species of the genus but the cell cap appears to be unusual since it is not recessed and it does not exhibit any raised process on the outer surface. Also, the cell cap does not show any passageways connecting the cell lumen to the outer environment, as also observed in *Centris pallida* Fox, 1899 (ALCOCK *et al.* 1976, ROZEN & BUCHMANN 1990), *Centris mixta tamarugalis* Toro & Chiappa, 1989 (CHIAPPA & TORO 1994), and *Centris vittata* Lepeletier, 1841 (PEREIRA *et al.* 1999). In most of the *C. tarsata* nests, the cells were oriented horizontally and constructed in a single linear series, as also observed by SILVA *et al.* (2001). However, since the cell arrangement depends on the size and shape of the space in the cavity containing the nest (MICHENER & LANGE 1958), some nests established in bamboo canes showed a cell orientation varying from horizontal to oblique and in at least one of them two parallel rows of cells had been constructed.

Information on the variation in the number of cells per nest of the *Hemisiella* species shows the occurrence of 2 to 8 cells in *Centris lanipes* (Fabricius, 1775) (MICHENER & LANGE 1958), 1 to 5 cells in *Centris transversa* Perez, 1905 (BATRA & SCHUSTER 1977), one to six cells in *C. vittata* (PEREIRA *et al.* 1999), one to seven cells in *Centris dichrootricha* (Moure, 1945) (MORATO *et al.* 1999), and six to eight cells in *C. tarsata* (SILVA *et al.* 2001). These figures are not very different from those observed in the present study since only 2.97% of nests contained more than seven cells. According to PEREIRA *et al.* (1999), the use of preexisting holes for nests may suggest that the number of cells depends upon the spatial limitations of the cavity being utilized. As observed in the present study, the number of cells in a nest tended to increase as increased the length of the trap-nest, corroborating the suggestion made by the cited authors.

The use of floral oils as one of the components of larval food, as observed in the present study, has also been reported for others *Centris* species. The question, however, is to establish whether the floral oils replace the nectar in the larval provisions, as postulated by VOGEL (1974). It has been shown that *Centris trigonoides* Lepeletier, 1841 (SIMPSON *et al.* 1977), *Centris adanae* Cockerell, 1949, *Centris flavifrons* (Fabricius, 1775), *Centris flavofasciata* Friese, 1899 and *Centris aethyctera* Snelling, 1974 use floral oils instead of nectar (VINSON *et al.* 1996, 1997), while *Centris maculifrons* Smith, 1854 (NEFF & SIMPSON 1981) and *C. vittata* (PEREIRA & GARÓFALO 1996) use oil and nectar along with pollen to provision their cells. Although no analysis of the larval provisions of *C. tarsata* has been made, the in-nest behavior of the female before discharging the pollen or oil load into the cell was similar to that exhibited by *C. analis* Fabricius, 1804 females (JESUS & GARÓFALO 2000) when depositing a nectar load on the pollen provision. This behavioral similarity suggests that, in addition to the oil, the larval provision of *C. tarsata* also contains nectar. Therefore, according to information currently available, the *Centris* species may be subdivided into three groups: *Centris bicornuta* Mocsary, 1899 and *C. analis*, which do not utilize oil in the larval provisions (VINSON *et al.* 1996, JESUS & GARÓFALO 2000), *C. trigonoides*, *C. adanae*, *C. flavifrons*, *C. flavofasciata* and *C. aethyctera*, which replace the nectar with oil, and *C. maculifrons*, *C. vittata* and *C. tarsata*, which use oil and nectar.

The covering of the nest plug with oil, as observed in *C. tarsata*, has also been reported by Coville *et al.* (1983), Roubik (1989), Jesus & Garófalo (2000), Gazola & Garófalo (2003) for *C. analis*, Frankie *et al.* (1988) for *C. bicornuta*, Vinson *et al.* (1996) for *Centris nitida* Smith, 1804, and Frankie *et al.* (1988), Vinson *et al.* (1996), Pereira *et al.* (1999) for *C. vittata*. Pereira *et al.* (1999) suggested that the oily covering of the nest plug serves to provide greater protection to the nest, since the plug becomes harder after being covered and may reduce the possibility of nest invasion by natural enemies. This protective function against natural enemies was shown by Gazola & Garófalo (2003) in *C. analis*, while Vinson & Frankie (2000) provided evidence that the oily substance reduces nest usurpation in *C. bicornuta*.

Although the cocoon of *C. tarsata* was similar to those of other *Centris* species in terms of shape which conforms to the inner surface of the cell (Vinson & Frankie 1977, Coville *et al.* 1983, 1986, Vinson *et al.* 1987, Rozen & Buchmann 1990, Camillo *et al.* 1993, Chiappa & Toro 1994, Pereira *et al.* 1999), it differed from these species by the lack of a distinctive nipple on its top. On the other hand, the presence of fecal material compressed at the bottom of the cocoon between the two layers of the cellophane-like material was only observed in *C. flavofasciata* (Vinson *et al.* 1987), *Centris collaris* Lepeletier, 1841 (Camillo *et al.* 1993), and *C. vittata* (Pereira *et al.* 1999).

Although the egg-to-adult period was not determined, the values for the periods between collection of the nests and emergence of adults, besides the observed nesting periods, showed that *C. tarsata* had a smaller number of generations in Ipirá than in B. Grande. This is because the nesting period was larger in B. Grande than Ipirá. On the other hand, irrespectively of the number of generations per year, the immatures of one generation underwent diapause at both areas. In B. Grande, diapause occurred during the most adverse (dry) season. In Ipirá, however, some nests established in the middle of the rainy season had immatures undergoing diapause while others did not. The simultaneous occurrence of nests with and without immatures in diapause was also observed in *Podium denticulatum* Smith, 1856 (Sphecidae)(Camillo *et al.* 1996) and *Ptilothrix plumata* Smith, 1853 (Apidae: Emphorini)(Martins *et al.* 2001). While the role of diapause is similar for all species, acting as a mechanism of protection from the unfavorable season and reducing the risk of extinction (Martins *et al.* 2001), the survival strategies differ among species. Thus, while in *P. plumata* all prepupae of the last generation at the end of the dry season entered diapause, *C. tarsata*, as also observed in *P. denticulatum*, uses two different survival strategies in the presence of adverse conditions, i.e., spending stressful times either as adults or as prepupae in diapause. Our data suggest that the first strategy is used by the largest fraction of the local population in Ipirá and in B. Grande.

Aguiar & Martins (2002) reported sex ratios greatly males biased, similar to those found here in the *C. tarsata* population from B. Grande. On the other hand, the 1:1 sex ratio found in Ipirá was similar to that recorded by Silva *et al.* (2001) for *C. tarsata* and for other *Centris* species such as *C. dichrootricha*, *Centris terminata* Smith, 1804 (Morato *et al.* 1999), *C. vittata* (Pereira *et al.* 1999), and *C. analis* (Jesus & Garófalo 2000, Aguiar & Martins 2002). Several factors can affect solitary bee sex ratios, such as the nesting-cavity diameter (Rust 1998) or length (Stephen & Osgood 1965), seasonal availability of floral resources, female foraging capacity (Torchio & Tepedino 1980), differential losses of outer cells (if those contain predominately one of the sexes), as well as the sex ratio of the parental generation (which influences the mating success of subsequently nesting females) (Vandenberg 1995). Although the reason for the male-biased sex ratio found in B. Grande is unknown, the data suggest that trap-nest dimensions were not involved since similar traps were used in Ipirá, where the sex ratio was 1:1. According to Torchio & Tepedino (1980), the sex ratio can be considered an equilibrium point around which annual variations are expected. If a disproportionate investment is made in the offspring of one sex at any given time, it will be corrected in subsequent generations. Only by accompanying *C. tarsata* populations in B. Grande for a longer period time would it be possible to verify if Torchio & Tepedino's assertion is applicable to this bee species.

Unlike data observed in other studies with cavity-nesting bees (Tepedino & Parker 1983, 1984, Parker 1986), parasites were not the main cause of mortality among immatures of *C. tarsata*. Similar results were observed by Silva *et al.* (2001) also for *C. tarsata*, by Gathmann *et al.* (1994) for several bee and wasp species, by Pereira *et al.* (1999) for *C. vittata*, and by Jesus & Garófalo (2000) and Gazola & Garófalo (2003) for *C. analis*. The different ratios of parasitism found by several workers in *C. tarsata* may be at least partially related to a trap-nest density effect, whereby the dense groupings of nests may facilitate attacks by natural enemies (Cooperband *et al.* 1999). As such, the higher parasitism ratio observed in the present study compared to Silva *et al.* (2001) may be a direct consequence of nest density. Also, as suggested by Parker (1986) for *Osmia sanrafaelae* Parker, 1985, by Frankie *et al.* (1988) for some *Centris* species, and by Jesus & Garófalo (2000) and Gazola & Garófalo (2003) for C. *analis*, high environmental temperatures may be a factor causing the death of immature stages.

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