Nesting biology of four *Tetrapedia* species in trap-nests (Hymenoptera: Apidae: Tetrapediini)

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Abstract: The nests used in this study were obtained from trap-nests (tubes of cardboard and cut bamboo stems) placed on Santa Carlota Farm (Itaoca Section-IS, Santana Section-SS and Cerrado-Ce), Cajuru, SP, Brazil. The number of nests and corresponding species obtained were as follows: 516 nests of *T. curvitarsis*, 104 of *T. rugulosa*, 399 of *T. diversipes* and 98 of *T. garofaloi*. The most abundant species from SS and Ce was *T. curvitarsis*, and from IS it was *T. diversipes*. In general, most nests were collected during the hot and wet season (September to April). The nests were constructed with sand and an oily substance, and a single female established them. The cells were constructed in a linear series, sometimes followed by a vestibular cell. The number of brood cells ranged from 1 to 10 in *T. curvitarsis* (n=200), and in *T. garofaloi* (n=51), from 1 to 8 (n=30) in *T. rugulosa*, and from 1 to 6 (n=37) in *T. diversipes*. The pollen mass (pollen + oily substance) contained a hollow, sometimes divided by a transverse ridge, on the exposed face of the pollen mass. The egg was vertically positioned in the lower part of the hollow. At times, the closing of a cell was initiated before provisioning was completed, with a construction of a collar at the cell limit. In some nests the final cellular partition also acted as a closure plug. Females began activities at 6:18 a.m. and ended between 3:31 and 6:26 p.m. Some females (*T. curvitarsis*, *T. rugulosa* and *T. garofaloi*) did not spend the nights at their nests, returning to them only the following morning with additional material. In general, the development period (for males and females) was greater in nests collected near the end of the hot and wet season than it was for nests collected in other months. Sex ratios for each species were as follows: *T. curvitarsis*, 1:1; *T. rugulosa*, 1.6:1 female; *T. diversipes*, 1.9:1; *T. garofaloi*, 2.8:1. Males and females of *T. diversipes* exhibited statistically similar sizes and in the other three species the females were larger than the males. The mortality rates were statistically similar: 33.2% for *T. curvitarsis*, 25.8% for *T. rugulosa*, 26.8% for *T. diversipes* and 38.2% for *T. garofaloi*. The parasitoids were: *Coelioxoides exulans*, *Leucospis cayenensis*, *Anthrax* sp., *Coelioxys* sp., *Coelioxoides* sp. and individuals of the family Meloidae. Rev. Biol. Trop. 53(1-2): 175-186. Epub 2005 Jun 24.

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Michener and Moure (1957) divided *Tetrapedia* into subgenera *Tetrapedia* and *Lagobata*. The subgenus *Tetrapedia* occurs from the Neotropical region of Mexico to southern Brazil, and from northern Argentina to Ecuador. The subgenus *Lagobata* is restricted to Brazil. These authors separated this genus from the Exomalopsini (Anthophoridae) and placed it in a new tribe because of the differences in adults. This separation was reinforced when Michener and Lange (1958)

characterized the tribe essentially through the biological data obtained in *T. maura* Cresson, 1878. Roig-Alsina and Michener (1993) placed Tetrapediini in the subfamily Apinae, family Apidae, when the authors extinguished the family Anthophoridae and created the tribe Anthophorini.

The subfamily Apinae has some genera that collect floral oil, including *Centris, Ptilotopus* and *Epicharis* (Centridini), *Paratetrapedia*, *Chalepogenus* and *Tapinotaspis*

(Tapinotaspidini), *Ctenoplectra* (Ctenoplectrini) and *Tetrapedia* (Tetrapediini) (Vogel 1974, 1976b, 1981, Simpson *et al*. 1977, Roberts and Vallespir 1978, Michener and Greenberg 1980, Neff and Simpson 1981, Buchmann 1987). Other species are considered as probable collectors of oily substance, including *Monoeca* (Tapinotaspidini) (Vogel 1974, Roberts and Vallespir 1978) and *Lanthanomelissa* (Tapinotaspidini), *Anthophora* (Anthophorini) and *Exomalopsis* (Exomalopsini) (Neff and Simpson 1981). Only two genera of the family Melittidae were observed collecting floral oil: *Macropis* (Vogel 1976a, 1976b, Michener 1981, Cane *et al*. 1983, Vogel and Michener 1985, Buchmann 1987) and *Rediviva* (Whitehead *et al*. 1984, Whitehead and Steiner 1985, 1992, Buchmann 1987, Steiner and Whitehead 1988, 1990, 1991).

Among the studies carried out on *Tetrapedia* are the works of Michener and Lange (1958), on natural nests of *T. maura*, in Costa Rica, and Roubik (1987), on *Tetrapedia* sp., which nested in trap-nests in Panama.

Although *T. curvitarsis* Friese, 1899, *T. rugulosa* Friese, 1899, *T. diversipes* Friese, 1810 and *T. garofaloi* Moure, 1999 are widely distributed and are common in our region, they remain poorly understood. The purpose of this paper is to present biological data on these species obtained from trap-nests placed in three habitats of São Paulo State in southeastern Brazil.

MATERIAL AND METHODS

Study site: The study was carried out on the Santa Carlota Farm, SP (21°18'–27' S, 47°12'–17' W), Brazil. The farm, drained by several streams, involves an area of 6 300 ha, with altitudes ranging from 540 to 944 m. Approximately 2 200 ha of the total area have native vegetation preserved in isolated patches (semideciduous forests, riparian forests, *cerrados* (*s.l.*) and *cerradões*), surrounded by abandoned orchards, pastures and cultivated land. There are also some areas in several stages of secondary growth. Rhodic Ferralsol and Orthic Ferralsol soils are predominant on the farm.

Trap-nests were placed in three areas of the farm: (1) Santana Section (=SS), characterized by abandoned orchards surrounded by sugar cane plantations, pastures and *cerrado* (*s.l.*) with abandoned houses, stables and sheds. Semideciduous forests and riparian forests were located about 300 m from the orchard; (2) Itaoca Section (=IS), characterized by abandoned houses surrounded by plots planted with sugar cane, corn, rice and sorghum. About 300 m away from the houses there are areas with semideciduous forests and riparian forests; (3) *Cerrado* (*s.l.*) (=Ce), structurally a semideciduous xeromorphic low-arboreal woodland or low forest, or a closed to somewhat open scrub.

Two distinct seasons are recognized in this region: (1) Cold and dry season (May to August) with monthly averages temperatures ranging from 18.2 to 22°C and precipitation from 0 to 116 mm; (2) Hot and wet season (September to April) with monthly average temperatures ranging from 23.2 to 27.9°C and precipitation from 8 to 368 mm.

Trap-nests: Three types of trap-nests (TN) were used. Two of them consisted of tubes made with black cardboard, with one end closed with the same material. The small nests (=SN) measured 5.8 cm in length and 0.6 cm in internal diameter, and the big nests (=BN) measured 8.5 cm and 0.8 cm, respectively. These tubes were inserted into horizontal holes drilled into wooden plates (30 x 11.5 x 5 cm). The other type of trap-nests consisted of bamboo canes (=B) with a nodal septum closing one end; these ranged from 7 to 25 cm in length and from 0.65 to 2.5 cm in internal diameter.

The wooden plates, with tubes and bamboo canes in blundies of 6-8 units were placed along the shelves of a shelter built at the study locations. The types of TN and their number were placed in study locations as follows: SS : 297 SN, 193 BN and 450 B; IS: 300, 120 and 200; Ce: 250, 150 and 200, respectively. The TN were inspected at least once a month during the period January/87 to December/88 in SS, from April/89 to March/91 in IS and from

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November/89 to October/91 in Ce. At each inspection those that contained completed nests were collected and transported to the laboratory. Each nest was replaced with a new TN. In the laboratory all nests were placed in a transparent glass tube and kept at room temperature until the adults emerged. After emergences the nests were opened and their contents analyzed.

Female nesting behavior was observed in six nests of *T. curvitarsis*, two of *T. rugulosa* and six of *T. garofaloi*, from 5th to 9th/ December/88. These observations were made from 06:00 to 20:00 hours. The head width of the emerged individuals (25 females and 25 males) was taken as a measure of body size. Life tables were constructed showing the various causes of mortality at different stages in the life cycle and the relative number of immature individuals dying from each known cause. All specimens were deposited in the Entomology Collection of the Department of Biology, FFCLRP-USP.

RESULTS

Nest numbers and seasonality: A total of 1117 *Tetrapedia* nests were obtained: 516 of *T. curvitarsis*, 104 of *T. rugulosa*, 399 of *T. diversipes* and 98 of *T. garofaloi*. Of these, 366 were from SS, 440 from IS and 311 from Ce. The most frequent species in SS and Ce was *T. curvitarsis* (63.9% and 68.8% of the collected nests, respectively) followed by *T. garofaloi* in SS (15.3%) and by *T. rugulosa* in Ce (20.9%). In IS the most frequent species was *T. diversipes* (79.8%) followed by *T. curvitarsis* (15.4%). The most nesting occurred in the hot and wet season (Fig. 1). The number of nests of *T. curvitarsis* in SN, BN and B was 156, 340 and 20; of *T. diversipes* the numbers were 320, 78 and 1, and of *T. garofaloi* they were 17, 72 and 9, respectively. *T. rugulosa* only nested in SN (n=71) and BN (n=33). In general, SN was the most utilized TN (50.5% of the collected nests), and the most abundant species was *T. curvitarsis* (46.2% of the collected nests).

Nest construction: After finding a suitable trap, the female leaves it returning with the oily substance to line the walls of the TN. During this time there appeared to be considerable confusion in recognition of tubes. After finishing the lining of the TN the female begins to collect sand or the oily substance (transported on her hind legs) for construction of the first cell. It was initiated with construction of the bottom wall of the cell. The thickness of these walls ranged from 0.04 to 0.7 cm (x= 0.15 ± 0.1 cm, n=177) in *T. curvitarsis*, from 0.06 to 0.3 cm (x= 0.12 ± 0.06 cm, n=26) in *T. rugulosa*, from 0.06 to 0.7 cm (x= 0.24 ± 0.17 cm, n=29) in *T. diversipes* and from 0.07 to 0.4 cm (x= 0.17 ± 0.08 cm, n=43) in *T.*
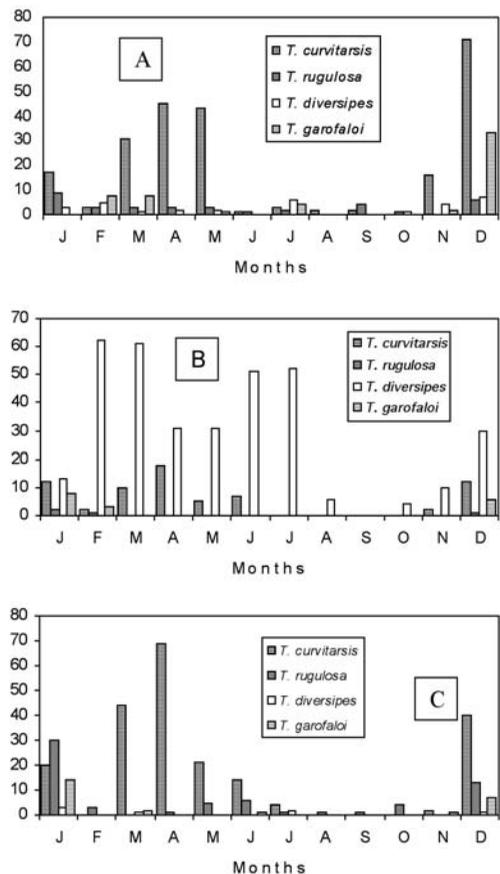

Fig. 1. Monthly number of *Tetrapedia* nests constructed in the three types of trap-nests. A= Santana Section, B= Itaoca Section, C= Cerrado.

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garofaloi. In 15 nests of *T. curvitarsis* and in 6 of *T. diversipes*, these walls were constructed recessed from the bottom.

For construction of one cell the number of flights to collect sand ranged from 12 to 17 (x= 14.3 ± 2.5, n=3) in *T. curvitarsis* and from 5 to 16 (x= 13.3 ± 4.2, n=7) in *T. garofaloi*; those to collect the oily substance ranged from 4 to 8 (x= 6.0 ± 2.0, n=3) and from 1 to 6 (x= 3.1 ± 1.9, n=7), respectively. For provisioning, the number of flights to collect pollen ranged from 8 to 17 (x= 12.5 ± 4.6, n=4) in *T. curvitarsis*, from 13 to 19 (x= 15.3 ± 3.2, n=3) in *T. rugulosa* and from 5 to 9 (x= 7.8 ± 1.8, n=5) in *T. garofaloi*; those flights to collect the oily substance ranged from 2 to 6 (x= 3.5 ± 1.7, n=4) in *T. curvitarsis* and from 1 to 3 (x= 1.6 ± 1.1, n=3). In general, the duration of flights to collect sand ranged from 1.5 to 40 min (x= 9.9 ± 7.6 min, n=117) in *T. curvitarsis*, from 1.5 to 18 min (x= 6.6 ± 5.5 min, n=82) in *T. rugulosa* and from 2 to 62 min (x= 13.2 ± 12.0 min, n=102) in *T. garofaloi*. The duration of flights to collect the oily substance ranged from 6 to 68 min (x= 24.0 ± 15.4 min, n=42) in *T. curvitarsis*, from 5 to 48 min (x= 18.3 ± 9.9 min, n=20) in *T. rugulosa* and from 7 to 51 min (x= 24.0 ± 11.8 min, n=21) in *T. garofaloi*. The duration of flights to collect pollen ranged from 7 to 84 min (x= 37.5 ± 16.4 min, n=89) in *T. curvitarsis*, from 6 to 79 min (x= 28.1 ± 18.5 min, n=34) in *T. rugulosa* and from 13 to 67 min (x= 37.6 ± 11.2 min, n=54) in *T. garofaloi*. One case was observed in which the female lined the internal wall of the cell.

After finishing cell construction the female initiates cell provisioning. Before the female finishes these activities, she oviposits and begins the construction of cell partition, which had a form of a small ring that encircles the entire inner circumference of the nesting tube, thus constricting its diameter. Passing over the cell partition in construction, the female finished the provisioning. The pollen mass has a hollow area, sometimes divided by a transverse ridge, on the exposed face of the pollen mass. The egg was in a vertical position in the lower part of the hollow (Fig. 2).

When returning to her nest with material, the female enters head first but before depositing it, she turns inside the nest. The time spent by the female in the nest for depositing sand ranged from 1.5 to 10 min (x= 3.0 ± 1.8 min, n=51) in *T. curvitarsis*, from 2 to 12 min (x= 5.6 ± 2.3 min, n=50) in *T. rugulosa* and from 1.5 to 6 min (x= 2.7 ± 1.1 min, n=55) in *T. garofaloi*. The time spent for manipulation of this material ranged from 9 to 24 min (x= 13.9 ± 4.8 min, n=9), from 10 to 75 min (x= 29.9 ± 19.2 min, n=10) and from 9 to 49 min (x= 23.2 ± 18.2 min, n=5), respectively. The time spent in the nest after returning with the oily substance ranged from 1 to 12 min (x= 4.3 ± 3.0 min, n=24) in *T. curvitarsis*, from 1 to 8 min (x= 4.8 ± 1.6 min, n=10) in *T. rugulosa* and from 1 to 9 min (x= 4.3 ± 2.2 min, n=20) in *T. garofaloi*. The duration of time spent in the nest for manipulation of the oily substance (the female adds the oily substance to pollen or sand) ranged from 12 to 84 min (x= 34.5 ± 17.7 min, n=23), from 16 to 36 min (x= 27.1 ± 7.3 min, n=8) and from 9 to 22 min (x= 14.3 ± 5.6 min, n=7), respectively.

The durations of time spent in the nest for pollen deposition ranged from 1.5 to 11 min (x= 3.6 ± 2.1 min, n=57) in *T. curvitarsis*,
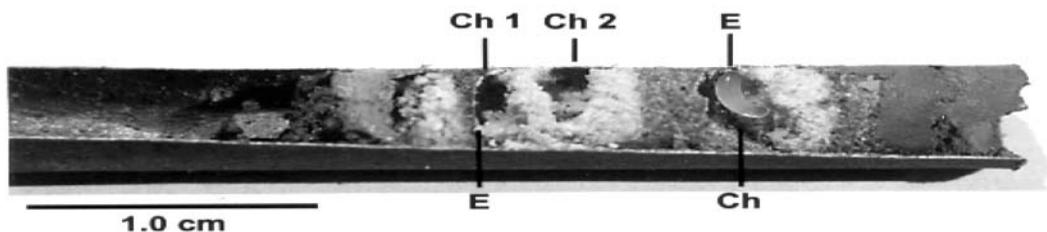

Fig. 2. Nest of *Tetrapedia curvitarsis* in SN, showing a cell with one chamber (Ch) and an egg (E) oriented vertically and another with two chambers.

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from 1.5 to 12 min (x= 3.5 ± 2.3 min, n=53), in *T. rugulosa* and from 1 to 7 min (x= 2.4 ± 1.3 min, n=39) in *T. garofaloi*. The time spent inside the nest for pollen manipulation ranged from 16 to 63 min (x= 34.1 ± 18.9 min, n=7) in *T. curvitarsis* and from 18 to 112 min (x= 47.1 ± 31.4 min, n=7) in *T. rugulosa*. Pollen manipulation was observed once in *T. garofaloi*, lasting 13 min.

After cell provisioning the female sometimes closed the small ring or completed all the closing of the cell. The thickness of cell partitions ranged from 0.08 to 0.45 cm (x= 0.16 ± 0.07 cm, n=150) in *T. curvitarsis*, from 0.06 to 0.47 cm (x= 0.13 ± 0.05 cm, n=110) in *T. rugulosa*, from 0.04 to 0.24 cm (x= 0.10 ± 0.04 cm, n=100) in *T. diversipes* and from 0.06 to 0.34 cm (x= 0.12 ± 0.03 cm, n=125) in *T. garofaloi*. In some nests the females were observed working at night when finishing the cell, partition or nest plug construction.

The cells were constructed in linear series, horizontally oriented. In some nests, between the last brood cell and the nest plug there was a space (vestibular cell), left empty or containing sand (Fig. 3). In 17 nests of *T. curvitarsis*, 3 of *T. rugulosa* and 9 of *T. diversipes* there was no vestibular cell. The lengths of these cells ranged from 0.4 to 9.0 cm (x= 2.4 ± 1.5 cm, n=115) in *T. curvitarsis*, from 0.2 to 4.0 cm (x= 1.9 ± 1.2 cm, n=20) in *T. rugulosa*, from 0.5 to 1.2 cm (x=0.9 ± 0.2 cm, n=7) in *T. diversipes* and from 0.2 to 5.3 cm (x= 1.2 ± 1.3 cm, n=20) in *T. garofaloi*.

In nests without a vestibular cell the last partition was also the nest plug. In these cases the thickness ranged from 0.14 to 0.6 cm (x=

0.3 ± 0.1 cm, n=17) in *T. curvitarsis*, from 0.4 to 0.6 cm (x= 0.5 ± 0.1 cm, n=3) in *T. rugulosa*, from 0.2 to 0.4 cm (x= 0.3 ± 0.08 cm, n=7) in *T. diversipes* and from 0.12 to 0.9 cm (x= 0.3 ± 0.2 cm, n=22) in *T. garofaloi*.

After closing the last brood cell, the female begins collecting material (the same as that for cell partitions) to construct a nest plug. After finishing, the females sometimes line it with an oily substance. To construct the nest plug the females of *T. curvitarsis* completed from 2 to 8 (x= 5.6 ± 3.2, n=3) trips to collect sand and one trip to collect the oily substance. The time spent to construct the nest plug (observed once in each species) was 39 min in *T. curvitarsis*, 28 min in *T. rugulosa* and 19.5 min in *T. garofaloi*. The thickness of the nest plug ranged from 0.1 to 0.9 cm (x= 0.35 ± 0.15 cm, n=115) in *T. curvitarsis*, from 0.15 to 0.5 cm (x= 0.3 ± 0.1 cm, n=20) in *T. rugulosa*, from 0.14 to 0.3 (x= 0.2 ± 0.07 cm, n=7) in *T. diversipes* and from 0.1 to 0.7 cm (x= 0.3 ± 0.2 cm, n=20) in *T. garofaloi*.

The number of brood cells constructed in each nest of *T. curvitarsis* ranged from 1 to 10 (n=200); in *T. rugulosa* from 1 to 8 (n=30); in *T. diversipes* (n=37) from 1 to 6 (n=37) and in *T. garofaloi* from 1 to 10 (n=51). The highest frequencies of cells were from 2 to 5, 3 and 4, 4 and 5 and 4 and 7, respectively.

The time spent for cell construction, provisioning, oviposition and construction of cell partition was 33:39 and 44:04 hs (n=2) in *T. curvitarsis* and from 29:05 to 49:48 hs (n=3) in *T. garofaloi*. In the only case observed in *T. rugulosa* the time spent was 66:06 hs.
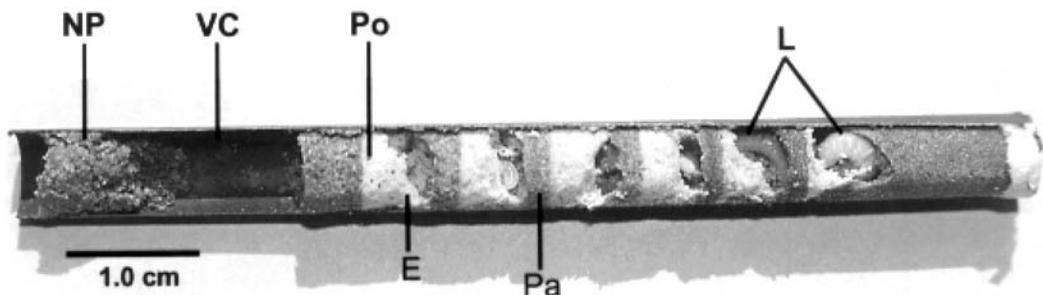

Fig. 3. Nest of *Tetrapedia curvitarsis* in BN, showing a serie of cells. E= egg, L= larva, Po= pollen, Pa= partition, VC= vestibular cell and NP= nest plug.

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The cell lengths of *T. curvitarsis* females ranged from 0.7 to 1.6 cm (x= 1.1 ± 0.2 cm, n=119), of *T. rugulosa* from 0.7 to 1.0 cm (x= 0.9 ± 0.1 cm, n=33), of *T. diversipes* from 0.5 to 1.0 cm (x= 0.7 ± 0.1 cm, n=28) and of *T. garofaloi* from 0.6 to 1.1 cm (x= 0.8 ± 0.1 cm, n=35). Those of males ranged from 0.6 to 1.5 cm (x= 1.1 ± 0.2 cm, n=119), from 0.5 to 1.1 cm (x= 0.8 ± 0.2 cm, n=47), from 0.5 to 1.0 cm (x= 0.8 ± 0.1 cm, n=36) and from 0.6 to 1.0 cm (x= 0.8 ± 0.1 cm, n=72), respectively. The cell diameters of *T. curvitarsis* females ranged from 0.5 to 0.9 cm (x= 0.6 ± 0.07 cm, n=119), of *T. rugulosa* from 0.5 to 0.8 cm (x= 0.6 ± 0.05 cm, n=33) and of *T. garofaloi* from 0.5 to 0.7 cm (x= 0.6 ± 0.04 cm, n=34). Those of males ranged from 0.5 to 0.8 cm (x= 0.6 ± 0.06 cm, n=119), from 0.5 to 0.7 cm (x= 0.6 ± 0.05 cm, n=42) and from 0.45 to 0.7 cm (x= 0.6 ± 0.05 cm, n=72). The cells diameter of females (n=28) and males (n=36) of *T. diversipes* were the same as the TN utilized (0.6 cm).

Females activities: Female of *T. curvitarsis* began activities from 6:18 to 7:17 a.m. (n=16) and for *T. garofaloi*, activity occurred between 6:22 and 7:50 a.m. (n=14). Activity ended between 3:31 and 6:26 p.m. (n=17) and 3:50 and 6:18 p.m. (n=16), respectively. These observations were not made for *T. rugulosa*, because not all females spend the night at their nests. Species of *Tetrapedia* collected sand, the oily substance and pollen practically throughout the entire day. Obviously, this fact was related with stage of nest development. Some females did not spend nights at their nests, returning to them only the following morning with material for construction or provisioning according to the development of the nest. In these cases the last trip for *T. curvitarsis* occurred between 4:52 and 6:25 p.m. (n=4), for *T. rugulosa* between 5:42 and 6:25 p.m. (n=6) and for *T. garofaloi* between 6:10 and 6:19 p.m. (n=2). These females returned to the nests the next morning between 6:53 and 7:27 a.m. (n=6), 7:02 and 8:06 a.m. (n=7), and 7:50 and 8:23 a.m. (n=4), respectively.

In the 84.2% and 61.1% of the last flights, the females of *T. curvitarsis* and *T. garofaloi*, respectively, returned with the oily substance independently of the nest stage. In the other flights (15.8% and 38.9%) the female returned with sand that was utilized for construction of the cellular partition or nest plug. For *T. rugulosa*, in 50% of the flights (those before not spending the night at their nests) the females returned with the oily substance, 37.5% with pollen and 12.5% with sand.

Period of development, sex ratio and size of individuals: The developmental period was determined by the interval between the date of nest collection and the emergence of the adults. For *T. curvitarsis*, in nests collected near the end of the hot and wet season (March, April and part of May), the intervals for males (from 101 to 191 days) and females (from 103 to 211 days) were greater than those observed in nests collected during other months (from 33 to 55 and from 38 to 73 days, respectively). For *T. rugulosa* the same fact was observed for males (from 91 to 189 in hot and wet season and from 25 to 66 days in the cold and dry season) and females (from 95 to 99 and from 28 to 70 days, respectively). For *T. diversipes* this fact was evident only for males (from 92 to 170 and from 27 to 58 days); those for females ranged from 27 to 80 days. The intervals observed for males of *T. garofaloi* ranged from 102 to 290 days, except one case, which lasted 68 days; for females the intervals ranged from 104 to 290 days, independently of the season of the nest foundation.

The sex ratio observed in 894 cells of *T. curvitarsis* was 1.02 males to 1 female, which was significantly similar to a 1:1 (X^2= 0.13; p>0.05). In 116 cells of *T. rugulosa* it was 1.6 males to 1 female, in 108 cells of *T. diversipes* it was 1.9 males to 1 female and in 212 cells of *T. garofaloi* it was 2.8 males to 1 female. These sex ratios were significantly different from 1:1 (X^2= 13.5; X^2= 92.9 and X^2= 50.1; respectively; p<0.05).

The size of males and females were significantly similar only in *T. diversipes* (Mann-Whitney, Z= 0.1; p>0.05). In *T. rugulosa*, *T. curvitarsis* and *T. garofaloi* the females were significantly larger than the males

(Mann-Whitney, $Z= 2.3$; $Z= 2.2$; $Z= 5.5$; respectively; $p<0.05$) (Table 1). No significant differences existed with respect to the sizes of males and females of the four species (Kruskal-Wallis, $H= 59.2$ and $H= 79.1$, respectively; $p<0.05$).

Life tables and mortality factors: Life tables (Tables 2, 3, 4 and 5) were constructed on the basis of 610 cells of *T. curvitarsis*, 116 of *T. rugulosa*, 108 of *T. diversipes* and 212 of *T. garofaloi*. In some cases, the parasitoids died during development, thus they were not identified. Unknown causes were responsible for 144 (70.9%) deaths of the 203 that occurred in *T. curvitarsis*, for 20 (66.6%) of the 30 in *T. rugulosa*, for 12 (41.4%) of the 29 in *T. diversipes* and for 74 (91.3%) of the 81 occurring in *T. garofaloi*.

In the first and second species this factor was followed by unidentified parasitoids (20.7% and 16.6%, respectively), in the third by *Coelioxys* sp. (24.1%) and in the last by *Coelioxoides exulans* (Holmberg, 1887) (2.4%).

Analyzing each stage, it was observed that only in *T. curvitarsis* and *T. diversipes*, the greatest percentage of mortality in the larval stage was not due to unknown causes. In these cases the most common cause was unidentified parasitoid (42 or 53.8% in 78 deaths) and *Coelioxys* sp. (7 or 38.9% in 18 deaths), respectively. In general, the mortality rates occurring in *T. curvitarsis* (33.2%), *T. rugulosa* (25.8%), *T. diversipes* (26.8%) and *T. garofaloi* (38.2%) were significantly similar ($X^2= 3.24$; $p>0.05$).

TABLE 1

Dimensions (head width in mm) of males and females obtained from the four species of Tetrapedia

Species	Males		Females	
	Range	x ± SD (n)	Range	x ± SD (n)
T. curvitarsis	2.32-3.65	2.97 ± 0.25a (25)	2.55-3,48	3.10 ± 0.24b (25)
T. rugulosa	1.97-2.72	2.58 ± 0.15a (25)	2.55-2.84	2.67 ± 0.08b (25)
T. diversipes	2.26-2.66	2.45 ± 0.11a (25)	1.97-2.61	2.43 ± 0.14a (25)
T. garofaloi	2.32-2.95	2.73 ± 0.14a (25)	2.78-3.19	2.99 ± 0.09b (25)

Means followed by the same letter in the same row did not differ statistically (X^2 test, $p>0.05$).

TABLE 2

Life table for Tetrapedia curvitarsis *showing the percentage mortality and its causes at different stages of the life cycle*

Stages of development	Number entering each x (lx)	Mortality factors (dx F)	Number dying in each x (dx)	(dx) as a % of (lx) (100 qx)	1-qx Sx
Eggs	610	Meloidae	1	0.16	0.99
		Unknown cause	84	13.77	0.86
		TOTAL	85	13.93	0.86
Larvae	525	*Anthrax* sp.	4	0.76	0.99
		Coelioxys sp.	5	0.95	0.99
		Coelioxoides exulans	7	1.33	0.98
		Parasitoid	42	8.00	0.92
		Unknown cause	20	3.80	0.96
		TOTAL	78	14.85	0.85
Pupae	447	Unknown cause	22	4.92	0.95
		TOTAL	22	4.92	0.95
Adults in cell	425	Unknown cause	18	4.23	0.95
		TOTAL	18	4.23	0.95
Emerged adults	407				

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TABLE 3
Life table for Tetrapedia rugulosa *showing the percentage mortality and its causes at different stages of the life cycle*

Stages of development	Number entering each x (lx)	Mortality factors (dx F)	Number dying in each x (dx)	(dx) as a % of (lx) (100 qx)	1-qx Sx
Eggs	116	Meloidae	1	0.86	0.99
		Unknown cause	12	10.34	0.89
		TOTAL	13	11.21	0.88
Larvae	103	*Coelioxys* sp.	1	0.97	0.99
		Coelioxoides exulans	3	2.91	0.97
		Parasitoid	5	4.85	0.95
		Unknown cause	7	6.80	0.93
		TOTAL	16	15.53	0.84
Adults in cell	87	Unknown cause	1	1.15	0.98
		TOTAL	1	1.15	0.98
Emerged adults	86				

TABLE 4
Life table for Tetrapedia diversipes *showing the percentage mortality and its causes at different stages of the life cycle*

Stages of development	Number entering each x (lx)	Mortality factors (dx F)	Number dying in each x (dx)	(dx) %como as a % of (lx) (100 qx)	1-qx Sx
Eggs	108	Meloidae	2	1.85	0.98
		Unknown cause	6	5.56	0.94
		TOTAL	8	7.41	0.92
Larvae	100	*Anthrax* sp.	2	2.00	0.98
		Coelioxys sp.	7	7.00	0.93
		Coelioxoides sp.	2	2.00	0.98
		Leucospis cayenensis	1	1.00	0.99
		Parasitoid	3	3.00	0.97
		Unknown cause	3	3.00	0.97
		TOTAL	18	18.00	0.82
Pupae	82	Unknown cause	3	3.66	0.96
		TOTAL	3	3.66	0.96
Emerged adults	79				

DISCUSSION

The occurrence of the highest frequencies of nesting in the hot and wet season, seen in the four *Tetrapedia* species, was also observed in all species of solitary bees studied at same region in nesting in trap-nests (Camillo *et al*. 1994, 1995, Pereira 1997, Jesus and Garofalo 2000).

Lining the tube with the oily substance before beginning the nest construction was also observed by Jesus and Garofalo (2000) in *Centris analis* Fabricius, 1804. Pereira (1997) supposed that the substance utilized by *Centris vittata* Lepeletier, 1841 to line the trap-nests can be produced by the Dufour's gland and this signal will be utilized for identification of the new nest and dissuade other females.

The studied species collected pollen and the oily substance in separate flights. The same fact was observed in *C. analis* in relation to pollen and nectar (Jesus and Garofalo 2000). According to Pereira (1997) females of *C. vittata* collected these two types of food

TABLE 5

Life table for Tetrapedia garofaloi *showing the percentage mortality and its causes at different stages of the life cycle*

Stages of development	Number entering each x (lx)	Mortality factors (dx F)	Number dying in each x (dx)	(dx) como as a % of (lx) (100 qx)	1-qx Sx
Eggs	212	Unknown cause	32	15.09	0.84
		TOTAL	32	15.09	0.84
Larvae	180	*Coelioxys* sp.	4	2.22	0.97
		Coelioxoides exulans	2	1.11	0.98
		Parasitoid	1	0.56	0.99
		Unknown cause	18	10.00	0.90
		TOTAL	25	13.89	0.86
Pupae	155	Unknown cause	2	1.29	0.98
		TOTAL	2	1.29	0.98
Adults in cell	153	Unknown cause	22	14.38	0.85
		TOTAL	22	14.38	0.85
Emerged adults	131				

in separate or in the same flight and floral oils were collected in distinct flights.

The beginning of the construction of cell partitions during the period of provisioning, observed in some nests of the studied species, is a behavior similar to that observed by Pereira (1997) and Jesus and Garofalo (2000) in *C. vittata* and *C. analis*, respectively. According to Pereira (1997) this behavior serves to protect cell contents from predators and parasitoids when the female is absent. The covering of the nest plug with oily material, observed in *Centris* species by Coville *et al.* (1983), Roubik (1989), Pereira *et al*. (1999), Jesus and Garofalo (2000), did not occur in nests of the studied species. The inner wall of the nest plug generally was not smooth and shining, but in some cases it was smoothed by the female.

The occurrence of prepupal diapause is a strategy used by some species of wasps and bees in response to adverse climatic conditions. Prepupal diapause observed in *T. curvitarsis*, *T. rugulosa* and *T. diversipes* occurred in nests collected in March, April and May (cold and dry pre-season). In *T. garofaloi* all immatures presented prepupal diapause.

The nest structure observed in studied *Tetrapedia* species was similar to that described for *T. maura* (Michener and Lange 1958). Contrary to our results, these authors observed that some wood particles occupied a small space at the bottom of the nest, and some had thin transverse layers of wood particles between cells.

Vogel (1974) suggested that *Tetrapedia* could be a floral oil collector because the females have a tarsal brush. According to Neff and Simpson (1981) these floral oil collecting structures in *Tetrapedia* are similar to those of other species such as *Centris* and *Paratetrapedia*. The supposition of Vogel (1974) was confirmed by Neff and Simpson (1981), Buchmann (1987) and Simpson *et al.* (1990).

In this study it was observed that *T. curvitarsis, T. rugulosa* and *T. garofaloi* collected the oily substance for provisioning and nest construction. Utilization of the oily substance in the larval food was also observed in other species of bees by Vogel (1974, 1981, 1984), Neff and Simpson (1981), Cane *et al.* (1983), Kevan and Baker (1983), Simpson and Neff (1983), Gottsberger (1985), Vinson *et al.* (1986), Buchmann (1987), Steiner and Whitehead (1988, 1991), Simpson *et al.* (1990, 1996, 1997), Whitehead and Steiner (1992). Collection of floral oil for nest construction was only observed by Simpson *et al.* (1990).

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One of the more frequent parasitoids in nests of the studied species of *Tetrapedia* was *Coelioxys* sp., which was observed by Michener and Lange (1958) flying near nests of *T. maura*; *Anthrax* sp. was observed parasitizing nests of *C. analis* (Roubik 1989) and *C. vittata* (Pereira *et al*. 1999). Individuals of the family Meloidae were observed by Camillo *et al*. (1994) and Pereira *et al*. (1999) in *C. vittata* and *Leucospis* sp. by Roubik (1989) and Jesus and Garofalo (2000) in *C. analis* and Pereira *et al*. (1999) in *C. vittata*. The occurrence of *Coelioxoides* sp. in nests of the studied species was not observed in species of bees studied in the same region.

Some of the mortality rates of immatures in bees and wasps that constructed nests in trap-nests were near 50% (Krombein 1967, Danks 1971, Raw 1972, Jayasingh and Freeman 1980, Tepedino and Frohlich 1982, Tepedino and Parker 1983, Parker 1986). Some species presented mortality rates higher than 50% (Danks 1971, Jayasingh and Freeman 1980, Jesus and Garofalo 2000) and other species presented rates less than 50% (Camillo *et al*. 1993, 1994, Gathmann *et al*. 1994, Pereira *et al*. 1999) as observed in this study for all studied species.

RESUMEN

Los nidos usados en este estudio fueron obtenidos de nidos de trampa (tubos de cartón y tallos cortados de bambú) localizados en la finca Santa Carlota (Itaoca Sección-IS, Santana Sección-SS y Cerrado-Ce), Cajuru, SP, Brasil. El número de nidos y las especies correpondientes obtenidas fueron: 516 nidos de *T. curvitarsis*, 104 de *T. rugulosa*, 399 de *T. diversipes* y 98 de *T. garofaloi*. La especie más abundante en SS y Ce fue *T. curvitarsis*, y la de IS fue *T. diversipes*. En general, la mayoría de los nidos fueron recolectados durante la estación caliente y húmeda (septiembre a abril). Los nidos fueron construidos con arena y una sustancia aceitosa, y una hembra solitaria se estableció en ellos. Las celdas fueron contruidas en una serie lineal, algunas veces contiguo a una celda vestibular. El número de celdas amplias se distribuyó desde 1 a 10 en *T. curvitarsis* (n=200), y en *T. garofaloi* (n=51), de 1 a 8 (n=30) en *T. rugulosa*, y de 1 a 6 (n=37) en *T. diversipes*. Las masas de polen (polen más sustancia aceitosa) contenían una depresión, algunas veces dividida por una carina transversal, sobre la cara expuesta de la masa de polen. Los huevos fueron puestos en la parte inferior de la depresión. A veces, el cierre de una celda fue iniciada antes de que el aprovicionamiento estuviera completo, con la construcción de un collar en el borde de la celda. En algunos nidos la partición final de las celdas también actuaba como un tapón. Las hembras empiezan sus actividades a las 6:18 a.m. y terminan entre 3:31 y 6:26 p.m. Algunas hembras (*T. curvitarsis*, *T. rugulosa* y *T. garofaloi*) no pasan las noches en sus nidos, regresando a ellos solamente la mañana siguiente con material adicional. En general, el periodo de desarrollo (para machos y hembras) fue mayor en nidos recolectados cerca del fin de la estación cálida y humeda que respecto a los nidos recolectados en otros meses. La proporción de sexos para cada especie fue: *T. curvitarsis*, 1:1; *T. rugulosa*, 1.6:1 hembras; *T. diversipes*, 1.9:1; *T. garofaloi*, 2.8:1. Machos y hembras de *T. diversipes* exhibieron tamaños estadísticamente similares y en las otras especies las hembras fueron más grandes que los machos. Las tasas de mortalidad fueron similares estadísticamente: 33.2% para *T. curvitarsis*, 25.8% para *T. rugulosa*, 26.8% para *T. diversipes* y 38.2% para *T. garofaloi*. Los parasitoides fueron *Coelioxoides exulans*, *Leucospis cayenensis*, *Anthrax* sp., *Coelioxys* sp., *Coelioxoides* sp. e individuos de la familia Meloidae.

Palabras clave: Apidae, *Tetrapedia*, nidos trampa, biología de la anidación, estructura de nido, enemigos naturales, tablas de vida.

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