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Bionomic Aspects of the Solitary Bee *Tetrapedia diversipes* Klug, 1810 (Hymenoptera: Apidae: Tetrapediini)

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Abstract

The study aimed to describe bionomic aspects of *Tetrapedia diversipes* Klug, 1810 in order to allow the conservation or breeding of these bees. The nesting biology was studied using trap nests made with cardboard-paper tubes and plastic straws during the period between December 2014 and September 2015, in the Bee Unit of the Federal University of Ceará, Brazil. A total of 135 nests were obtained with 593 brood cells, from which emerged 448 adults and individuals of two parasitic species. The proportion of females (n = 297) was higher than that of males (n = 151) resulting in a sex ratio of 1.97:1. The total mortality in the nests was 24.45% and the majority of deaths recorded occurred at the pupal stage (33.1%). During their reproductive life, females of this bee species were able to construct up to 16 brood cells. The trap-nests removal and transfer to the laboratory shortly after finished by the bees reduced the attack of natural enemies.

Introduction

The solitary bees comprise approximately 85% of the total bee species in the world (Batra, 1984). In the habit of solitary life, females can exhibit complete independence, both in building and provisioning their nests, that is, there is no collaboration or division of labor between females, or between mothers and daughters (Michener, 2007).

Among the bees with a solitary life style, there are those belonging to Tetrapediini, which are restricted to the tropical regions of the Americas and are distributed in two genera: *Tetrapedia* and *Coelioxoides* (Alves-dos-Santos et al., 2002). In Brazil, the genus *Tetrapedia* is represented by 28 species (Moure, 2012), whose biology has been studied through the provision of artificial nests (Trap Nests) in the study areas because females nest in preexisting cavities. This method allows to obtain information about the bionomy of these bees, such as the material used in nest building, nest architecture, sex ratio, natural enemies and pollen resources used in feeding the immature (Alves-dos-Santos, 2002; Camillo, 2005; Alves-dos-Santos et al., 2007; Neves et al., 2014). Studies carried out in Southeastern Brazil using this technique allowed information on the behavior and nesting biology of some bee species belonging to *Tetrapedia* (Camillo, 2005; Menezes et al., 2012; Cordeiro et al., 2011; Rocha-Filho & Garófalo, 2015). However, the way these bees establish themselves in Northeastern Brazil is still poorly described (Aguiar et al., 2005; Neves et al., 2012). In this context, the aim of this work was to study the bionomy of the species *Tetrapedia diversipes* Klug, 1810 by the use of trap nests, considering aspects such as nesting rate; seasonality and nest architecture; development and emergence period; sex ratio (M: F); mortality rate and associated natural enemies. Moreover, the knowledge of the bionomic aspects of this species will provide information for its conservation and the potential development of rational breeding of these bees

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for use in pollination services and for the development of management techniques for the maintenance of these native populations inserted in large urban centers.

Material and Methods

Study area

The study was carried out in the Bee Unit of the Federal University of Ceará, Fortaleza (3°44’33.70 “S and 38°34’45.46” W), Brazil. The climate of the region is warm subhumid tropical, with a rainy season from January to May. The mean annual precipitation is 1,338 mm and the mean temperatures vary between 26°C and 28°C. The study site is surrounded by urban areas and an altered, small fragment of forest with a vegetation characterized as Vegetational Complex of the Coastal Zone and Perennial Forest Paludosa Marítima (IPECE, 2016). In this area it is possible to record the presence of native and exotic plant species.

Trap Nests (TNs)

Trap nests (TNs) for *Tetrapedia diversipes* nesting were made using two types of disposable cylindrical tubes. One type was made of black cardboard, measuring 5.0 mm in diameter, and the other type was made of transparent plastic straw, 4.5 mm in diameter. Both TNs were 12 cm long with one end closed with stingless bee wax. These nests were inserted into each of the 548 pre-existing cavities distributed along nine blocks of wood containing 6 to 10 cavities per line and were located more than 90 cm above the ground, where they were protected from rain and sun. The TNs of cardboard were evaluated from December 2014 to September 2015, while plastic straw TNs were installed in only one of the nine blocks used in the study; for this, 36 TNs of cardboard were replaced by the transparent plastic straws which were evaluated only from June to October 2015, in order to observe the nesting behavior and the time taken in the construction of the brood cells. The TNs were inspected daily and, when finished, they were removed and replaced by new empty ones. Nests founded in cardboard were taken to the laboratory and were kept within a Biochemical Oxygen Demand (B.O.D.) at 27°C until adults emerged. Nests founded on straws were also placed in the B.O.D., but only until the larvae defecated. At this moment, immatures were transferred to artificial cells made of transparent biodegradable capsules to complete their development allowing observations on the development time of males and females. To determine the sex ratio both individuals emerging from cardboard TNs and artificial cells were counted.

One male and one female from each nest were killed and subsequently sent to a taxonomist to confirm the species identification; the other individuals were released in the wild at the nesting site. Bees collected in this study are deposited in the Bee Unit Entomological Collection of the Animal Science Department, at the Federal University of Ceará.

Number of nests built by each female of Tetrapedia diversipes

The number of nests founded by each female during their period of activity was counted through the numerical labeling of 80 bees done after their emergence from the TNs (Fig 1). For this, emerging bees were placed in Falcon tubes and anesthetized by cooling in the freezer. After this procedure tags were fixed in the dorsal part of the thorax, between the wings, using Super Bonder LOCTITE® glue brand. After being tagged, these bees were released near the place where the TNs were installed.

Subsequently, it was observed whether these bees returned to nest in TNs and how many nests were built by them. These observations were made daily in the morning and afternoon shifts for two hours of each monitoring period, totaling 456 hours of observation.

Fig 1. *Tetrapedia diversipes* female labelled with a numerical tag. Bee Unit, Animal Science Department/UFC, Fortaleza-CE, Brazil 2015.

Nest architecture and time of immature development of Tetrapedia diversipes

After the emergence of the adult individuals, the TNs were opened to determine the length, number of built cells, the presence of dead individuals, and the number of empty cells. The same procedure was performed with TNs from which no individuals emerged after four months of incubation.

In order to determine the immature development time, 24 nests built in the transparent plastic straws were opened 17 days after the nest was completed by the female when the larva present in the first cell had already defecated. These older larvae were placed in capsules measuring 24.6 mm in length and 7.7 mm in width (Fig 2), as proposed by Silva et al. (unpublished data). Immatures were transferred according to the order arranged in the nests and deposited in B.O.D. to complete their development. Observations of these capsules were performed daily.

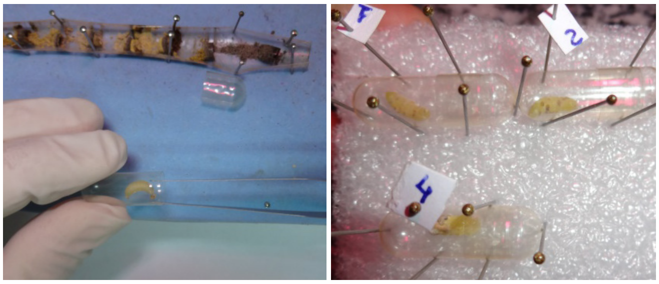

Fig 2. a) Transference of an immature *Tetrapedia diversipes* from a nest built in plastic straw to a rearing capsule. b) Larvae in the capsule identified according to its psoition inside the nest. Bee Unit, Animal Science Department/UFC, Fortaleza-CE, Brazil 2015.

Data analysis

Nesting data were evaluated using descriptive statistics through tables and graphs generated in the Microsoft Excel software version 2010. The sex ratio was obtained dividing the number of females by the number of males and a chi-square test (x^2) was used to analyze whether the proportion of males and females differed from that expected (1:1). In order to analyze the relationship between nesting ratio (%) and environmental variables (temperature, rainfall, and relative air humidity), the Pearson Correlation Test was used in software R. Precipitation had to be log-transformed to reach the normality.

Results

Nesting rate, seasonality and nest architecture

During this study 135 nests of *T. diversipes* were founded, representing approximately 25% of the total number of TNs (n = 548) available. The bee species *Centris analis* and *Epanthidium tigrinum* and two species of wasps, *Trypoxylon* sp. and *Podium* sp., also nested in the trap nests, but were not considered in this study. *Tetrapedia diversipes* females occupied TNs throughout the studied period, but nesting peak occurred from the rainy season to the beginning of the rainy-dry transition period, between March and June 2015 (Fig 3). Although the highest nesting rate occurred in March (5.29%) and June (3.83%), no significant correlations were observed between the monthly nesting rate (%) with temperature (r = -0.1635, P = 0.6517), monthly rainfall (r = 0.4285, p = 0.2166) (Fig 3) and air humidity (r = 0.4954, p = 0.1454).

Brood cell construction was initiated after the *T. diversipes* female selected a cavity. Then, the female began to build the first partition, in what would become the back of the nest, using a mix of sand grains collected near the nesting site, and an oily binder substance, the composition of which has not been determined. The cell partition, which is a structure built between two brood cells organized in a linear series, serves several purposes such as to insure each larva an adequate amount of food, to protect the immature from natural enemies and to indicate to the emerging bee the direction to leave the nest. After building the partition, the female made a series of foraging trips to collect and place a mixture of pollen and oil in the interior of the cell, and after finishing to provisioning all the larval food, she laid a large egg on the food mass and closed the cell with a thin sand wall. This process was repeated in all subsequent cells, always from the furthest to the nearest to the nest entrance (n = 118). The time spent in building the first cell was three days in all observed TNs, while for the other cells the female bee took from two to four days (n = 94). The total construction time in TNs varied from three to fifteen days, according to the number of cells built per nest (n = 24).

The number of nests established by each *T. diversipes* female was variable: out of the 80 tagged females 44 returned to the nests (55%), of which only 11% (n = 5) nested in the TNs available. Each monitored bee built from two to three nests during its reproductive life resulting in the production of 11 to 16 cells per female (Table 1).

Nest architecture was observed in all nests obtained during the study. The nests were linear with brood cells built one after the other. The number of cells per nest ranged from one to eight, with a total of 593 cells for all studied nests. These cells were always arranged in a linear series and their lengths varied from 4.96 to 11.39 mm (= 7.66 ± 1.12). In the analyzed nests, the presence of vestibular cells, which corresponds to the empty space between the nest closure and the last brood cell, was observed in 48.15% of the nests (n = 65) and their length varied from 6.26 to 51.00 mm (= 31.71 ± 12.80).

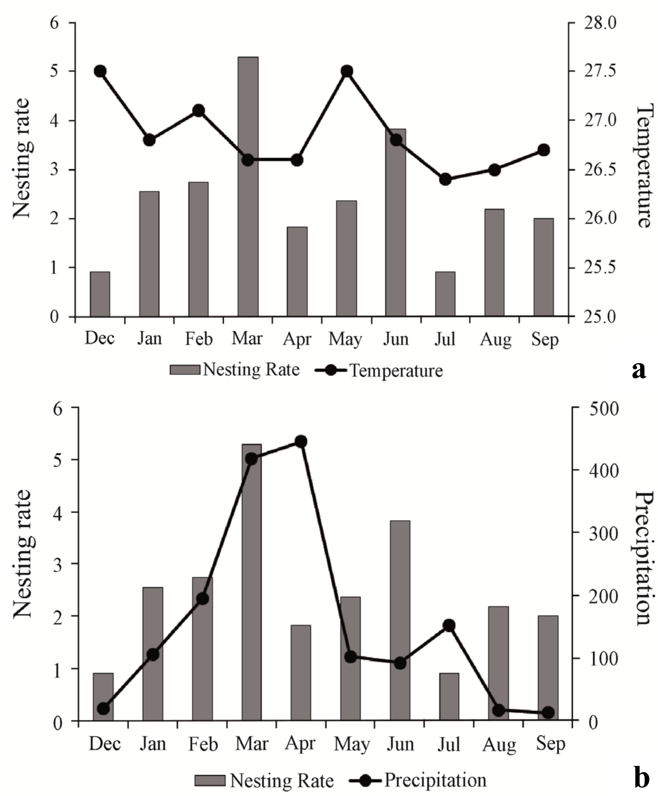

Fig 3. Nesting rate of *Tetrapedia diversipes* and environmental variables: a) mean temperature (°C) e b) monthly rainfall (mm) between December 2014 and September 2015. Bee Unit, Animal Science Department/UFC, Fortaleza-CE, Brazil 2015.

Table 1. Number of nests, brood cells built, and total offspring per female of the solitary bee *Tetrapedia diversipes* between December 2014 and September 2015. Bee Unit, Animal Science Department/UFC, Fortaleza-CE, Brazil 2015.

Tagged females	T.N. founded by females	Total cells by females	Emerged bees ♀	Emerged bees ♂	Total of emerged individuals	Mortality
♀ 20	2	13	7	4	11	2
♀ 33	3	11	5	3	8	3
♀ 54	2	11	6	2	8	3
♀ 56	3	16	6	8	14	2
♀ 77	2	12	5	3	8	4
Mean ± SD			6 ± 0.84	4 ± 2.35	10 ± 2.68	3 ± 0.84

Developmental period, emergency and sex ratio

The time for immature development in *T. diversipes* was obtained from the larvae (n = 113) which were taken from the plastic straw TNs (n = 24) and incubated inside the transparent biodegradable capsules. The immatures transferred to the capsules were in the last larval stage and took 20 to 32 days to become pupae. After becoming pupae, they took another 15 to 20 days to turn into pre-emergent adults, waiting only to complete the sexual dimorphism. The total development time of females varied from 40 to 66 days ($\bar{x}$= 49 ± 5.6, n = 66), while in males this time ranged between 40 and 58 days ($\bar{x}$= 47 ± 4.9, n = 31).

Out of the 593 brood cells built in the two types of TNs studied, 448 adults of *T. diversipes* emerged, of which 151 were males (33.7%) and 297 were females (66.3%), resulting in a sex ratio 1:1.97 (M:F), differing significantly of the proportion 1: 1 (X^2 = 47.58, $p < 0.0001$). The emergence of females was higher than that of males in most of the studied period, with the exception of January, when there was no emergence. In contrast, the highest number of emergences for both sexes was observed in May, counting for 21.2% of registered emergencies (Fig 4).

Mortality and associated natural enemies

Mortality recorded in nests of *T. diversipes* represented 24.45% (n = 145 cells) of the total number of cells constructed (n = 593). In the 145 cells where mortality was observed, immature developmental failure occurred in 67.6% of them (n = 98 cells), and this process was higher at the pupal stage, reaching 33.1% (n = 48 cells), followed by the phase of pre-emergent adults, when 20% (n = 29 cells) died. However, mortality reached only 4.5% (n = 21 cells) in the larval period.

Larvae or immatures that died in the cells due to the attack of natural enemies represented 31% (n = 45 cells) of the built cells, out of which 13.8% (n = 20 cells) were caused by ant attacks and 17.2% (n = 25 cells) due to fungi infection. However, the nests were already with fungi when they were opened and so we can not tell if they caused the death of the immature or if they came later. The mortality caused by cleptoparasites species was only 1.4% (n = 2 cells) caused by a bee species, *Coelioxys* sp. (Hymenoptera: Megachilidae) and a species of Diptera of the family Bombyliidae.

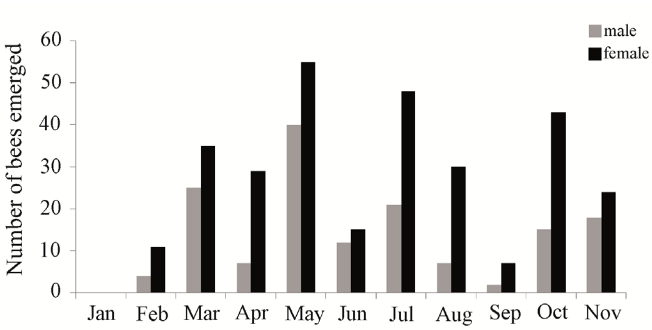

Fig 4. Emergence of females and males of *Tetrapedia diversipes* from January to November 2015. Bee Unit, Animal Science Department/UFC, Fortaleza-CE, Brazil 2015.

Discussion

Data obtained in the present study showed that *T. diversipes* females nested during the whole study period (December to September). The higher percentage of nests was built in March (rainy season) and June (beginning of the dry season), probably due to the greater availability of resources provided by flowering plants in these months, such as *Dalechampia* sp, whose pollen is used in the supply of the breeding cells (Menezes et al., 2012).

No significant relationship was found between the monthly nesting rate and the climate variables. Similar data were recorded with the same bee species in the states of São Paulo, Rio de Janeiro (SE Brazil) and Bahia (NE Brazil) by Aguiar et al. (2005), Camillo (2005), Menezes et al. (2012), and Rocha-Filho and Garófalo (2015). The studies carried out by Alves-dos-Santos et al. (2002) indicate that *T. diversipes* generations often reuse the nests in their birth places. However, these authors did not tag the emergent bees and did not provide data if founders of the new nests were actually bees that emerged from the same nests. Although the nest reuse was confirmed for *T. diversipes* in the present study, it was found that only a fraction of the post-emergent females re-used nests. The low percentage of TNs reused by the females of *T. diversipes* may be related to the interference caused by the handling of females and to the existence of potential nesting sites, represented by natural cavities around the experimental area. However, the availability of these cavities was not investigated during this study.

In respect to the nest architecture, the structure of each brood cell was built with a mixture of sand and oil, similar to that described by Alves-dos-Santos et al. (2002). The nests had one to eight cells, and this same pattern in number of cells per nest was reported by Camillo (2005) and Menezes et al. (2012). However, Aguiar et al. (2005) observed a pattern of two to nine cells per nest of *T. diversipes*. These differences in the number of cells constructed per nest are possibly due to the size of the trap nest available to the bees and the size of the offspring a female bee produces during her reproductive life, as we observed by marking the newly emerged females.

The total time for immature development in *T. diversipes* observed in the present study showed that males and females required a maximum time of 2 months to complete their cycle, suggesting that these individuals did not undergo diapause. This result differs from those obtained by Alves-dos-Santos et al. (2002) and Aguiar et al. (2005), who recorded a longer development time of 6 to 8 months, inferring that in their studies immature specimens of *T. diversipes* presented pre-pupal diapause. It is worth noting that in the work of these authors, the nests of T. *diversipes* were kept at room temperature, and this probably contributed to the difference in the results obtained, since, in the present study, the nests were kept under constant temperature. According to Aguiar and Garófalo (2004), the occurrence of diapause in solitary bees is a protection mechanism to overcome the adverse conditions of a certain period, which does not occur within a controlled environment.

The sex ratio may be influenced by the availability of resources in the environment and a greater proportion of either sex may be directly associated with this factor (Marques & Gaglianone, 2013). In this study, the sex ratio resulting from our TNs showed higher production of females, differing from the results found in other surveys with *T. diversipes*, where males emerged in greater numbers (Menezes et al., 2012; Rocha-Filho & Garófalo, 2015). In other bee genus such as *Centris* (Mendes & Rego, 2007) and *Xylocopa* (Pereira & Garófalo, 2010), a more inclined sex ratio for females was also observed. According to Michener (1974) females have the ability to control the sex of their offspring, but the factors that lead them to decide which egg will be fertilized is still unknown. The difference in the production of males and females observed in several bee species is usually attributed to high rates of parasitism (Aguiar & Martins 2002), a fact not observed in this study, and to several factors such as breeding mortality, seasonality, climate, availability of substrates and floral resources (Michener, 1974; Capaldi et al., 2007). According to Torchio and Tepedino (1980), the sex ratio can be considered an annual balance point, that is, if a greater investment is made in offspring in favor of a specific sex, this proportion must at some point be corrected in the following generations. According to Pereira and Garófalo (2010) this is an important characteristic when aiming at pollination because bee species with female-biased ratio can increase their populations quickly in the places where they are introduced.

Regarding the causes of bee mortality in the nests, they occurred due to failures in the development of the offspring and natural enemy attacks, which are classified according to their behavior in nest parasites, kleptoparasites or parasitoids (Alves-dos-Santos, 2002; Oliveira et al., 2014). In the study of Alves-dos-Santos et al. (2007), the mortality rate among species of *Tetrapedia* ranged from 20 to 40%, ratifying our findings. The highest incidence of mortality recorded for *T. diversipes* in the present study occurred at the pupal stages and at the end of the bee development, in the phase of pre-emergent adults. A higher number of deaths in immature stages was also reported by Camillo (2005) and Rocha-Filho and Garófalo (2015), in studies with the same bee species. According to Aguiar et al. (2013) the mortality of bees' offspring in the early stages of development may be influenced by the manipulation and nest removal when they are transported to the laboratory.

In the present study, the attack by cleptoparasites of T. *diversipes* was not an important mortality factor. Nests parasitized by the bee *Coelioxys* sp. (Hymenoptera: Megachilidae) and the Bombyliidae (Diptera) caused the death of only two individuals (1.4%). Similar results were also found by Aguiar and Martins (2002) and Menezes et al. (2012). Although the kleptoparasitism associated with *T. diversipes* is frequently by *Coelioxoides* (Alves-dos-Santos et al., 2007; Rocha-Filho et al., 2017), the occurrence of kleptoparasites of this genus was not observed in this study. However, the presence of *Coelioxys* sp. (Hymenoptera: Megachilidae) in one of the TNs was probably due to the presence of nests of *Centris analis* (Hymenoptera: Centridine) in the study area. Species of this same parasitoid were observed by Camilo (2005) in T. *diversipes*, T. *garofaloi*, T. *curvitasis* and T. *rugulosa* nests. According to Gerling and Hermann, (1976) and Boesi et al. (2009), females of Bombyliidae most of the time, do not enter the nest of the female founder, they usually hover and oviposit at the entrance of the nest and when their larvae hatch find the host cells and feed in both larva and pupa and pollen.

Brood mortality due to fungi infection was diagnosed in studies carried out on other bee species nesting in trap nests (Morato, 2001; Camarotti-de-Lima & Martins, 2005; Bernardino & Gaglianone, 2008). According to Roubik (1989), fungi can cause high mortality rates in nests of solitary bees, being considered a potential natural enemy of these bees. However, they were not a major problem in the present study, probably due to the controlled environmental conditions in which the nests were incubated.

Predatory ants were responsible for the death of 13.8% of the immature individuals of *T. diversipes*, attacking the trap nests and killing the larvae and plundering the pollen.

Predation of nests by ants was also recorded in studies by Pinto (2005) and Oliveira et al. (2014) using trap nests.

Finally, we can conclude that the use of cardboard trap nests and, in particular, those of plastic straw, made it possible to determine the time required to a *T. diversipes* female builds a brood cell, as well as the number of cells per nest and number of nests throughout its reproductive life. The removal of nests (TNs) from the nesting site as soon as finished by the founder bee may contribute for a reduction in parasitism without compromising the habit of reusing nests by the bees, although in a low proportion. Thus, this study amplifies the knowledge about the nesting biology of *T. diversipes*, but more studies on the bionomy of this species are necessary, aiming at the establishment of more accurate management techniques to this bee species.

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