Nesting biology and immature stages of the oil-collecting bee *Epicharis dejeanii* (Apidae: Centridini)

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Abstract – An aggregation of the oil-collecting bee *Epicharis dejeanii* Lepeletier was studied at Ilha das Flores, southern Brazil. Data on seasonality, types of floral resources collected, and nesting biology were registered. The nesting area occupied 120 m² with density of up to 8 nests/m². The tunnel entrances remained always open and surrounded by a tumulus. Adult activity lasted approximately 70 days. The females built the nest, provisioned food, and laid the egg in 4 days. The nest's architecture was very diverse, and they were between 40 and 140 cm in depth with one or two brood cells at the end of the tunnel. Diapause occurred in the postdefecating larval stage, and there was no cocoon. Immature stages and nest architecture are described and illustrated.

Solitary bee / Larval development / Nesting architecture / Baía da Babitonga

1. INTRODUCTION

The Centridini tribe (Hymenoptera: Apidae) is the largest group of noncorbiculate bees of the Neotropical Region (Michener 2007). In this select group of oil-collecting bees, females of this lineage collect this resource from several botanical families (Vogel 1976) to use it, along with other elements, to construct the brood cells and as food for their progeny (Neff and Simpson 1981; Buchmann 1987).

The nesting habits in centridine bees are diverse. However, the substrate used for many of the species of *Centris* Fabricius and *Epicharis* Klug, both genera that conform the tribe, yet is unknown. According to the data available, all species already

studied of *Epicharis* construct their nest in soil (Gaglianone 2002).

In general terms, *Epicharis* species are widely distributed in the Amazon basin with only a few species occurring in other areas on the Neotropics. Despite their wide distribution range, there are only available data on the bionomy of nine of the 35 known species: *E. albofasciata* Smith, *E. analis* Lepeletier, *E. flava* Friese, *E. metatarsalis* Friese, *E. nigrita* Friese, *E. obscura* Friese, *E. picta* Smith, *E. zonata* Mocsáry, and *E. dejeanii* (Camargo et al. 1975; Roubik and Michener 1980; Raw 1992; Laroca et al. 1993; Hiller and Wittmann 1994; Inouye 2000; Thiele and Inouye 2007; Werneck 2012; Gaglianone et al. 2015; Rozen 2016).

E. dejeanii is the only member of the subgenus *E. (Anepicharis)* Moure and is widely distributed in Brazil (Moure et al. 2007). Preliminary observations on its bionomy were published by Hiller and Wittmann (1994), but still important data on its life cycle remains unknown. In this study, new information on the nesting habits and life cycle of

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E. dejeanii are presented. These data are complementary with those previously known for this species, increasing the knowledge on the bionomy of this solitary oil-collecting bee.

2. MATERIAL AND METHODS

A population of *E. dejeanii* was studied between November 2017 and January 2018 at Ilha das Flores, Babitonga's Bay, north coast of Santa Catarina state, southern Brazil. The aggregation was located in an uncovered area with sandy and flat soil (Fig. 1). This island contains approximately 9 ha and is formed mainly by arboreal vegetation of dense ombrophilous forest. The climate of the region, according to Köppen (1948) is classified as "Cfa" (warm and humid subtropical) with well-defined seasons and without periods of drought throughout the year.

The nesting habits of the species were directly observed and digitally recorded. To guide the excavations and to obtain the size of tunnels was followed the methodology proposed by Marinho et al. (2018) which consists in to use a flexible rubber tube marked with centimeters. We used a tube with 0.6 cm of diameter and 150 cm in length. The brood cells collected were conditioned separately in plastic bags-containing substrate (sand) from the nesting site to accompany the immature development in the laboratory. The nests' architectures were registered, and the cells were dimensioned.

The hours of external activities of females and males were registered, as well as the frequency of types of floral resources collected by females (pollen or oil) throughout the days. Larvae in predefecating and postdefecating stages are morphologically described and illustrated.

Figure 1. Nesting area of *E. dejeanii* at Ilha das Flores, Babitonga's Bay, Santa Catarina State, Brazil.

3. RESULTS

3.1. Sazonality, aggregation, and building new nests

The nests were aggregated in an area of 120 m² whose density varied between 1 and 8/m² ($\bar{X} = 3.43 \pm 1.87$). More than 100 openings were observed, including new nests and those where occurred only emergencies. The entrances remained always opened. Externally, the newly founded nests ($N=25$) had a small mound of sand (tumulus) resulting from the excavation, with averages of 5 cm in height and 11 cm in diameter. The entrances had a circular format with 1.5 cm in diameter ($\bar{X} = 1.51 \pm 0.6$ cm; $N = 25$), and almost all were facing upwards. Eventually, some nests had double entrances (Fig. 2a) or had a small lateral slope on the tumulus (Fig. 2b).

Some female's activity was observed in some nests without tumuli, which would indicate that they were reusing some pre-existing nests. The population studied was univoltinuous, with only one

generation per year. The adult period of the specimens, as well as the nesting activity, lasted approximately 70 days. The immature stages, between egg and pre-pupa, occurred in less than 60 days. The diapause occurred in the postdefecating larval stage.

For the choice of nesting site, females made short zig-zag flights very close to the ground (3–5 cm height). After landing, the excavation began immediately and the activity was maintained uninterruptedly throughout the day. Females began the excavation with the use of fore and middle legs, with fast movements to push back the sand, under the body. The head was face down, making short movements with the mandibles from front to back. The females pushed the excavated sand sideways, making fast and coordinated movements with the hind legs. The first few centimeters of the tunnel were started downwards, vertically. Short vibrations could be heard during this step.

Once the bee was fully inserted into the tunnel, the female used the distal terga to push the sand outward, from bottom to up. When the metasoma reached the surface, the bee made semicircular movements by spreading the sand on the outer

Figure 2. Schematic drawing showing nest architectures found in *E. dejeanii*, with double entrance (a); small curve in the tumulus (b); location of the brood cells (c).

side homogeneously forming the tumulus. Newly built nests were observed ($N = 15$), and their depths were registered after 24, 48, 72, and 96 h. However, no depth variations were detected after 24 h.

During the night, the females rested in the nests, and they started to fly daily around 6:30 pm (daylight saving time-DST). In the first day, after emergence and mating, females searched for a place to build their nests and started the excavations. In the second day, the females performed the first flights returning without resources in their scopes. The collection of floral oil started later in the morning and lasted until the late of the afternoon. Eventually, the collection of oils extended until the morning of the next day. Pollen collections began at the third day or the beginning of the fourth day. To collect pollen, the trips lasted from 6 to 31 min ($\bar{X} = 14 \pm 6.6$; $N = 25$); while to collect oil, the females lasted from 11 to 18 min ($\bar{X} = 12 \pm 2.35$; $N = 8$). The females which arrived with pollen + oil in their scopae lasted, on average, 13 min (± 2.2 ; $N = 8$). Inside the nests, the females stayed between 8 and 55 min ($\bar{X} = 23 \pm 3.55$; $N = 20$). The complete period between the excavation and the

abandonment of the nests occurred in 3 to, rarely, 4 days (Fig. 3).

3.2. Nesting architecture and brood cell

The nests excavated ($N = 15$) presented heterogeneity in their architecture. Some of them began with a small descending tunnel (20–30 cm), followed by a slope of 30–45° from the ground level by a further 20–30 cm, becoming after, horizontal. Others presented a vertical tunnel with more than 30 cm in depth until slope occurs. In the end, the tunnels became horizontal, eventually curved to the right or to the left. In the inclined route, short branches could be found with or without brood cells. Vertical tunnels with a small-inclined stretches were also found, becoming briefly horizontal at the end. The depths ranged from 40 to 140 cm ($\bar{X} = 77 \text{ cm} \pm 26.14$; $N = 25$). There were found only one or two brood cells per nest, located at the end of the tunnel and/or in short branches (Fig. 2c). The cell position was always horizontally or slightly inclined.

The brood cells size ranged between 35 and 36 mm in length ($\bar{X} = 35.2 \text{ mm} \pm 0.45$; $N = 5$), 19–20 mm in maximum diameter ($\bar{X} =$

Figure 3. Sequence of flights performed by a female of *E. dejeanii* during the 2 days that the nest was active. On the first day, the female dug the nest. The red arrow suggests the moment of oviposition.

19.6 mm $\pm$ 0.55; $N = 5$) and 10–11 mm in the operculum diameter ($\bar{X} = 10.4$ mm $\pm$ 0.55; $N = 5$). The volume of the cells had, on average, 3.8 mL ($\pm$ 0.04; $N = 5$). Inside, a food composed with a whitish, dry, and compressed mass of pollen was found occupying approximately 30% of the cell. The inner wall of the cell was finely coated by a polished, bright slightly streaking layer. The operculum is flat, retracted into the edge of the cell, and completely sealed. Its inner wall does not have a polished and glossy layer. However, the sand is strongly compacted, since it seems that some substance has been added to stick the grains. The total wall thickness of the cell is approximately 1 mm, twice the thickness of the operculum. No cocoons were observed inside the cells that contained pre-pupa stage.

In one nest, a brood cell was found with a quite brittle dead adult covered by several collembolans of the genus *Folsomia* Willem

(Isotomidae: Proisotominae). Three specimens of *Tetracha brasiliensis* (Kirky) (Coleoptera: Cicindelidae) were found in different nests during the excavations, however, were not inside the cells. This is the first record of this species interacting with nests of *Epicharis* bees.

3.3. Immature stages

Five cells were laterally opened to observe the activity of the immatures (Fig. 4e). The larva intercalates periods of feeding and resting during several times a day until the pollen mass ends at around 25–30 days. During this period, its size changes from approximately 5 to 22 mm when it reaches the stage of postdefecating larva. Throughout the feeding period, the larva maintains a whitish coloration and a turgid appearance. In the postdefecating stage, the larva becomes yellowish and more flaccid.

Figure 4. Predefecting larva of *E. dejeanii* (lateral view) (a); postdefecating larva of *E. dejeanii*: lateral view (b), dorsal view (c), ventral view (d); Larva feeding in brood cell (e). Scales a–d = 3 mm; e = 5 mm.

3.3.1. Predefecating larva (Figure 4a)

The larva's body has whitish/light yellow coloration, length of 12 mm, and diameter of 2 mm. It also has glabrous, thin, and slightly sclerotized integument. Ten pairs of brown spiracles measure equally 0.13 mm of diameter, with their edges spare and more sclerotized than the body. The first two pairs positioned near the posterior edge of the thoracic segments I–II, absent in segment III; the other pairs are positioned near the anterior edge of the abdominal segments I–VIII. The anal opening is not visible. The cephalic capsule is rounded, with similar coloration than the rest of the body, 1.4 mm width and 1.25 mm in length (from vertex to labrum). The clypeus and labrum are distinguished by a subtle suture. The mandible is well-developed, with 0.6 mm in length, directed anteroventrally; its base measures 2/3 of its total length. The mandibular integument has darkened band and serrated margin and apical tooth present. The maxilla is well-developed with maxillary palpus absent/not visible. The antennae are absent; the antennal alveolus is weakly developed. The longitudinal sulcus is not well-defined, from the supraclypeal area to the apex.

3.3.2. Postdefecating larva (Figure 4b–d)

The larva's body has dark yellow integument, lighter and less sclerotized than the cephalic capsule, length of 22 mm, and diameter of 9 mm. Ten pairs of dark brown spiracles are more sclerotized and spare (diameter 0.28 mm). The first two pairs are positioned near the posterior edge of the thoracic segments I–II, absent in segment III; the others are positioned near the anterior edge of the abdominal segments I–VIII, as in predefecating stages. The peritreme is weakly developed; below it, there are several white short bristles directed towards the opening at the center of the spiracle. The anal opening's transversal length is 1.2 mm. The ventral surface of the body has no tubercles or other projections; the dorsal surface has two distinct bands of spicules (0.08 mm in length) in the II–III thoracic segments, and the I–VI abdominal segments are separated by a medial region. The thoracic and abdominal segments have 4–11 spicules on each

band. The number of spicules per band varies between the right and left sides. Dorsal and ventral surfaces of the body are weakly transversely striated.

The cephalic capsule is round, dark yellow, more sclerotized than the rest of the body, 2.0 mm of width and length (from vertex to the labrum). The epistomal sulcus is unformed. The clypeus and labrum are light brown, striated, and distinctly separated by a strong sulcus; labrum bilobed. The supraclypeal area has two depressions located in the frontal region. The mandibles are directed anteroventrally and are darker than the cephalic capsule, with rounded anterior margin, not serrated and without apical tooth (mandibular length 1.3 mm). The maxilla is cylindrical with maxillary palpus slightly evident. Prementum and postmentum are separated by a suture. Antennal alveolus is weakly evident. Antenna is absent. Salivary opening is located transversally to the front of the labiomaxillary region.

4. DISCUSSION

The only information available on some biological aspects of *E. dejeanii* was published by Hiller and Wittmann (1994) who studied a population in Rio Grande do Sul state, Brazil. Although this study also occurred in the southern region of that country, some behavioral variations were observed among both populations, such as periods of activity, density of aggregations, number of cells per nest, and depths.

The southern region of Brazil has a subtropical climate, with winters well marked by low temperatures. Due to this, in several solitary bees, during the mild seasons (autumn and winter), adults are not present, and the immatures are in diapause (Michener 2007). In this period, there is a reduction of metabolic activity (Belozarov 2009), a strategy that allows the individuals to remain safe until the return of favorable climatic conditions for their complete development (Danks 2007; Michener 2007).

The period of adult activities was longer in the present study, and the emergence at Ilha das Flores began 1 month earlier than that observed by Hiller and Wittmann (1994). The begin of the diary

activities was later in Ilha das Flores, since those authors observed the first flights of the day at 5:30 am, therefore, an hour earlier.

The construction of the main tunnel occurred before the first 24 h, corroborating the observations of Hiller and Wittmann (1994) that affirmed to be 18 h the necessary time to finish it. However, the authors suggested that the construction of the first brood cell should also be included at this time. In this study, the females were only observed returning with floral oil from the second day after nest establishment, therefore, the cell should be started only from this moment. Some females reused pre-existing nests, and this behavior was also observed in *E. nigrita* by Martins et al. (2019). These authors registered females that excavated their nests behaving very similarly to *E. dejeanii*.

The greater daily energy investment in the population studied by Hiller and Wittmann (1994) may be one reason why the aggregation of adults had a period of approximately 30 days less than in Ilha das Flores. Other factors may be linked to the availability of the necessary floral resources as well as the temperature, besides the locality has a temperate climate and summer with lower temperatures.

The sandy and uncompacted soil facilitates the excavations, which may justify the great depth found in some nests. Tunnels containing more than 1 m in length were recorded only in *E. flava* (Camargo et al. 1975), *E. metatarsalis* (Inouye 2000; Thiele and Inouye 2007) and *E. picta* (Werneck 2012). However, none of them reached the maximum depth found in the present study.

The shallowest tunnel found at Ilha das Flores was 40 cm, while Hiller and Wittmann (1994) recorded nests from 25 cm. Significant differences are in the density of aggregation and in the high number of brood cells that the same authors found, reaching 25 entrances/m² and 52 brood cells in five excavated nests (average of 10 brood cells per nest). These numbers are much higher than those found in the present study (maximum of 8 entrances/m², 1 or 2 cells per nest).

The plasticity in the quantity of brood cells was already observed in *Centris flavifrons* (Fabricius) (Martins et al. 2014) and in *E. nigrita* (Martins et al. 2019), whose variation was between 1 and 12 and 1–5 cells per nest, respectively. The same authors discussed this plasticity when compared

the data presented by other studies (see Vinson and Frankie 1988; Vinson et al. 1996, 1997; Gaglianone 2005; Rêgo et al. 2006; Gonzalez et al. 2007). This could be the reason to explain the high difference between our data and those presented by Hiller and Wittmann (1994).

Nesting on sandy substrates, as well as low numbers of the brood cells, are characteristics of the *Epicharis* species studied (Roubik and Michener 1980; Coville et al. 1983; Raw 1992; Gaglianone 2001, 2002; Rocha-Filho et al. 2008; Gaglianone et al. 2015). Thus, when contrasted with the data presented by Hiller and Wittmann (1994), the number of the brood cells in each nest is very low. However, it is in conformity with the information known for the genus, since other studies showed, for the most part, one or two cells per nest excavated, except those found by Rozen (2016) for *E. albofasciata* and Martins et al. (2019) for *E. nigrita*.

Hiller and Wittmann (1994) also found brood cells in an irregular arrangement, ranging from horizontal to vertical and with different angulations, always close to each other. In the present study, the cells found were arranged horizontally or slightly inclined in relation to the horizontal level. In *E. zonata*, the cells found were almost always vertical, in ramifications that isolated one cell from the other, and the nests did not present great depths (15–52 cm) (Roubik and Michener 1980). Rozen (2016) also verified that the positioning of the *E. albofasciata* cells is vertical, and the density varied between 2 and 7 per nest, adhered one to each other; the depth of the tunnels also being shallow (16–30 cm). Rocha-Filho et al. (2008) studying nests of *E. bicolor* Smith, 1854, verified that the nests of that species had short extensions (10–25 cm) and vertical architectures varying between one and two cells per nest. The arrangement of the cells found by those authors varied between horizontal, transversal, and vertical. Considering this, both the arrangement of the cells and the depths of nests do not seem to have a pattern within the genus.

The brood cells found in the excavations were taken to the laboratory and opened to monitor the development of the immatures. However, they were attacked by fungi. Problems related to fungi have also been reported by Gaglianone (2001),

Werneck (2012), Martins et al. (2014) and Gaglianone et al. (2015). Gaglianone (2001) reported the difficulty in keeping the cells in the laboratory without suffering fungi attacks. This author also noted fungi attack in cells of *Centris scopipes* Friese at its nesting site.

According to our results, postdefecating larvae do not form a cocoon, as already mentioned by Hiller and Wittmann (1994). The absence of cocoon was also observed in all other species of *Epicharis* (Rozen 1965; Roubik and Michener 1980; Gaglianone 2005; Gaglianone et al. 2015). The development between egg and pre-pupa stages occurred in less than 2 months in the present study. This rapid growth of immatures was also reported by Roubik and Michener (1980), Rocha-Filho et al. (2008) and Gaglianone et al. (2015) in other species of the genus.

Reports of cleptoparasitism in Centridini by bees of the genus *Mesoplia* Lepeletier (Apidae: Ericrocidini) and *Rhathymus* Lepeletier and Serville (Apidae: Rhathymini), as well as beetles of the family Meloidae, especially those of the genus *Tetraonyx* Latreille (Coleoptera: Meloidae), are abundant in the literature (see Camargo et al. 1975; Raw 1992; Hiller and Wittmann 1994; Morato et al. 1999; Gaglianone 2001, 2005; Rozen 2003; Rocha-Filho et al. 2008). Adults of the cicindelid beetle *T. brasiliensis* (Coleoptera: Cicindelidae) were found inside three nests. The presence of specimens of this species and family associated with *Epicharis* nests is here recorded for the first time. However, in the months of March and April, very close to the site of the aggregation of *E. dejeanii* were observed some nests containing cicindelid larvae. Therefore, it is possible that the *T. brasiliensis* adults found in nests were only looking for oviposition cavities, although they are voracious predators of invertebrates (Pearson and Vogler 2001). Interactions involving cleptoparasitism or predatism are not known for this genus of beetle and Centridini bees.

New data on the nesting habits of *E. dejeanii* are presented here, among them the nest architecture, the deepest nests so far found in Centridini, as well as information on the morphology of

immatures. Other information corroborates characteristics such as a well-defined seasonality, short time of activity of adults, and long period of development of the immatures, diapause in the pre-pupa stage in subtropical or temperate regions, as well as univoltinism, reinforcing to attributes present in the genus *Epicharis*.

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AUTHOR'S CONTRIBUTIONS

Both the authors participated in the interpretation of the data; E.Dec wrote the paper and F. Vivallo participated in the revisions of it. All authors read and approved the final manuscript.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest The authors declare that they have no conflict of interest.

Biologie de nidification et stades immatures de l'abeille collectrice d'huile *Epicharis dejeanii* (Apidae: Centridini)

abeille solitaire / développement larvaire / architecture de nidification / Baía da Babitonga

Nestbiologie und präimaginale Entwicklungsstadien der Öl-sammelnden Biene *Epicharis dejeanii* (Apidae: Centridini)

Solitärbiene / Larvenentwicklung/ Nestarchitektur/ Baía da Babitonga

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