Tropical Zoology 21: 227-242, 2008

Nesting behavior and natural enemies of *Epicharis* (*Epicharis*) *bicolor* Smith 1854 (Hymenoptera Apidae)

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Received 17 July 2007, accepted 17 April 2008

Nesting behavior and natural enemies of *Epicharis (Epicharis) bicolor* Smith 1854 were studied in a Cerrado area near Uberlândia, in Minas Gerais State, Brazil. The nesting site included an area of 224 m^2, with densely aggregated nests (24 to 40 entrances/m^2) on flat sandy soil and sand banks with herbaceous and shrub vegetation. Isolated cells, measuring 1.47-2.82 cm length and 0.96-1.88 cm width were built horizontally, vertically or inclined and at a depth of 10 to 25 cm. Females and males of *E. bicolor*, cleptoparasite bees *Mesoplia* (*Mesoplia*) *rufipes* (Perty 1833) and beetles *Tetraonyx (Tetraonyx) sexguttata* Olivier 1795 emerged from 26 of 43 cells maintained in the laboratory. Although the last two species were the only enemies to emerge from laboratory-maintained cells, other possible natural enemies of *E. bicolor* were captured in the nesting site. *Banisteriopsis malifolia* (Nees & Mart.) B. Gates and *Byrsonima intermedia* A. Juss. were the most common oil and pollen sources used by females of *E. bicolor* around the study site. Recently-emerged females were surrounded by a group of males that patrolled the nesting site but copula occurred with only one of them. Nest structure and natural enemies of *E. bicolor* were very similar to the records for *Epicharis (Epicharis) nigrita* Friese 1990.

KEY WORDS: Cerrado, cleptoparasites, Malpighiaceae, nesting behavior, solitary bees.

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INTRODUCTION

Epicharis Klug 1807 (Hymenoptera Apidae) is a genus found in some Neotropical ecosystems, especially in the Brazilian savanna (Cerrado) (GAGLIANONE 2003). They are considered solitary bee species that dig their nests in the soil (GAGLIANONE 2005), although some species can form large agreggations (ROUBIK & MICHENER 1980, HILLER & WITTMANN 1994, INOUYE 2000).

Epicharis (Epicharis) bicolor Smith 1854 occurs throughout the Brazilian Cerrado and Caatinga biomes (NEVES & VIANA 2001, SILVEIRA et al. 2002). Data for this species include the interactions with Malpighiaceae flowers (GAGLIANONE 2003) and its importance for the pollination of native (FRANKIE et al. 1976, VINSON et al. 1997) and cultivated plants (MARTINS et al. 1999, CASTRO 2002). Nesting behavior and reproduction of the species have not been reported as yet. In the Cerrado areas, *E. bicolor* occurs in sympatry with other species of the genus such as *Epicharis (Epicharis) nigrita* (Friese 1900), considered the closest species phylogenetically (M.C. GAGLIANONE pers. comm.). *E. nigrita* nests on sandy soils and builds isolated cells, which are supplied with pollen from *Byrsonima* Rich. ex Kunth (Polygalales Malpighiaceae) (GAGLIANONE 2005). The present work aimed to describe nesting behavior, natural enemies and potential floral resources of *E. bicolor* in order to understand the ecological interactions among these sympatric congeneric species.

MATERIAL AND METHODS

Study area

The study was carried out from September 2003 to December 2004 in the Ecological Reserve of Clube Caça & Pesca Itororó in Uberlândia, Minas Gerais State, Brazil (18°55'S 48°17'W). The reserve covers 127 ha with predominant Cerrado sensu stricto sections interspersed with a gallery forest (APPOLINÁRIO & SCHIAVINI 2002). The local climate well-defined has dry and humid seasons, with ca 1,550 mm annual rainfall and 22 °C average temperature; frost events are common in winter (NIMER & BRANDÃO 1989).

Nesting area

The nesting area of *E. bicolor* was found on November 29, 2003 on the side of the road which stretches along the reserve. The place was predominantly covered with shrubby-herbaceous vegetation and had been excavated for soil removal before the study. The area was measured and delimited with metal poles. Soil samples were collected for analysis at the Soil Laboratory, Universidade Federal de Uberlândia (UFU). The field observations were carried out once a week from December 2003 to April 2004, from 7:30 to 11:30 a.m., and once a month from May 2004 to December 2004. Samples of species in the nesting area were collected for identification and deposited in the Entomological Collection at the Universidade Federal de Uberlândia (UFU) and DZUP Collection — Universidade Federal do Paraná (UFPR).

Female nesting activities

Square plots of approximately 1 m^2 were delimited to record activities of females of *E. bicolor* and their natural enemies. Within the plots, observations were carried out for nests where females had already started supplying food and those at the beginning of construction on December 3, 11 and 12 2003, from 7:30 a.m. to 4:30 p.m. (total of 27 observation hours).

Female activities on flowers

To identify sources used as food for adults or larvae, flowering plants on a 2 km-long path near the nesting area were inspected to verify the presence of *E. bicolor* bees collecting resources in order. The observations occurred monthly from 7:30 to 11:30 a.m. from September 2003 to December 2004. The flowers visited by *E. bicolor* were identified in loco whenever possible or collected for identification. Exsiccates were deposited in the "Herbarium Uberlandensis" (HUFU), Universidade Federal de Uberlândia.

Cell content and adult emergence

Two plots (ca 1 m^2) were delimited on two distinct spots in the nesting area and excavated down to 40 cm. One of them was excavated on December 12, 2003 and the other on January 10, 2004. A total of 79 cells (19 in the first excavation and 60 in the second) were sampled. Twenty cells (10 from each plot) were opened soon after collection; their content was preserved in alcohol 70% for further analysis. The remaining cells (9 from the first excavation and 50 from the second) were kept in small, black plastic flasks under environmental conditions to check emergence in the laboratory. In-soil depth and measurements of cells (length and maximum width) were reported for 28 cells sampled out of excavations. Emergence and mating behavior were observed in the nesting site from 7:30 to 11:30 a.m. on February 14, 18 and 20, 2004 (total amount of 12 hr of direct observations).

RESULTS

Nesting area and nest architecture

The nesting site covered an approximate area of 224 m^2 on sandy soil (yellow latosol). Herbaceous plants such as Poaceae species predominated in

the area. Shrubs and trees such as *Ageratum fastigiatum* (Gardner) R.M. King & H. Rob. (Asterales Asteraceae), *Andira humilis* Mart. ex Benth. (Rosales Fabaceae), *Hyptis lippioides* Pohl ex Benth. (Lamiales Lamiaceae), *Byrsonima intermedia* A. Juss., *Banisteriopsis malifolia* (Nees & Mart.) B. Gates (Polygalales Malpighiaceae), *Hancornia speciosa* Gomez (Gentianales Apocynaceae), and *Dalbergia miscolobium* Benth. (Rosales Fabaceae) also occurred.

Nests were aggregated (Fig. 1A) with density rates of 24-60 entrances/m^2 (mean of 40 ± 15.59 entrances/m^2). Nests presented mostly a single cell (n = 17) , but a linear two-cell arrangement was also observed (n = 2) (Fig. 1B). Cells were 10-25 cm deep (19.61 ± 4.84 cm; n = 19). At the end of each tunnel, cells were transversely, horizontally or vertically positioned in relation to the soil surface. Cells were 1.47 to 2.82 cm long (2.11 ± 0.32 cm; n = 28) and 0.96 to 1.88 cm wide (1.46 ± 0.21 cm; n = 28). The cell walls were

Fig. 1. — A, detail of a square plot to determine nest density of *Epicharis bicolor*; B, isolated and linear two-cell arrangement; C, *E. bicolor* female during tunnel excavation; D, open cell with an egg of *E. bicolor* and recently hatched larva of Ericrocidini. (20 ×).

constructed from agglutinated sand and had a rough exterior covered with sand grains. Inside the cell was lined with a hard shiny layer.

Nesting activities

Females were observed in activity at the nesting site from November to December 2003. Nesting activities were not recorded after this period, even during the same period in 2004.

Before nest building, females selected excavation sites by searching and inspecting the area and other nests already built. During tunnel excavation, females removed sand from the tunnel and placed it around the nest entrance (Fig. 1C), forming the tumulus. Females excavated in circles with fore and mid legs, separating and pressing down soil mounts. Fifteen to 60 min (n = 6) after excavation started, females flew for the first time and were always away for 22 to 60 min (n = 6) probably to collect oil. Scopae content analyses showed that females collected oil and pollen during subsequent flights. After supplying the nest, females closed it with earth. All studied nests were closed the day after construction started.

Female activities on flowers

Banisteriopsis malifolia and *Byrsonima intermedia* were the only oil and pollen sources available in the area to *E. bicolor* females; many nectar sources were used by males and females (Table 1). Although activities in the nesting site were observed from November to December, females of *E. bicolor* were seen in activity on flowers throughout the year, except from June to August (Fig. 2).

Cell content and adult emergence

Ten cells obtained during the first excavation and opened soon after collection contained only eggs and no emergence was observed. In one of them, there was an egg of *E. bicolor* and a recently emerged larva of Ericrocidini (Hymenoptera Apidae) (Fig. 1D). The remaining cells of the first excavation (n = 9) were opened again 90 days after excavation and only larvae, which apparently died soon after the eggs hatched, were found inside them.

Six larvae of the last instar, a pupa of *E. bicolor* and three larvae of *Tetraonyx (Tetraonyx) sexguttata* Olivier 1795 (Coleoptera Meloidae) in later stages were found in the other ten cells of the second excavation which were opened soon after collection in the laboratory.

There was no immature development and only earth was found inside seven of 50 cells obtained in the second excavation and kept in the laboratory. There was emergence in 60.5% of the 43 remaining cells (Fig. 3). *E. bicolor* (n = 16) and *Mesoplia (Mesoplia) rufipes* (Perty 1833) (Hymenoptera Apidae) (n = 5) emerged from January to May 2004, whereas *T. sexguttata* (n

Table 1.

Plant species and floral resources collected by *Epicharis bicolor* and cleptoparasite species found within the nesting site from September 2003 to December 2004 at the Ecological Reserve of Clube Caça & Pesca Itororó in Uberlândia, Minas Gerais State, Brazil.

Species	Visited plants	Floral resource(s)
Epicharis bicolor (female)	*Arrabidaea brachypoda* (DC.) Bur. & K. Schum. (Bignoniaceae)	Nectar
	Banisteriopsis malifolia (Nees & Mart.) B. Gates (Malpighiaceae)	Oil + Pollen
	Byrsonima intermedia A. Juss. (Malpighiaceae)	Oil + Pollen
	Declieuxia fruticosa (Wild. ex Roem. & Schult.) (Rubiaceae)	Nectar
	Erythroxylum suberosum A. St.-Hil. (Erythroxylaceae)	Nectar
	Ipomoea virgata Meisn. (Convolvulaceae)	Nectar
	Palicourea rigida H.B.K. (Rubiaceae)	Nectar
Epicharis bicolor (male)	*Arrabidaea brachypoda* (DC.) Bur. & K. Schum. (Bignoniaceae)	Nectar
	Centrosema pascuorum Benth. (Fabaceae)	Nectar
	Declieuxia fruticosa (Wild. ex Roem. & Schult.) (Rubiaceae)	Nectar
	Memora axillaris K. Schum (Bignoniaceae)	Nectar
	Memora peregrina (Miers) Sandwith (Bignoniaceae)	Nectar
Mesoplia rufipes and *Mesonychium asteria*	*Andira humilis* Mart. ex Benth (Fabaceae)	Nectar
	Couepia grandiflora (Mart. & Zucc.) Benth (Chrysobalanaceae)	Nectar
	Declieuxia fruticosa (Wild. ex Roem. & Schult.) (Rubiaceae)	Nectar
Rhathymus unicolor	*Declieuxia fruticosa* (Wild. ex Roem. & Schult.) (Rubiaceae)	Nectar
	Palicourea rigida H.B.K. (Rubiaceae)	Nectar
Rhathymus bicolor	*Declieuxia fruticosa* (Wild. ex Roem. & Schult.) (Rubiaceae)	Nectar

= 5) emerged in October 2004; five individuals of *E. bicolor* and four individuals of *T. sexguttata* were found dead inside cells (Table 2). Two cells contained unidentified larvae contaminated by fungi and in six cells we found unidentified cocoon remains.

Male and female emergence events of *E. bicolor* were observed within the nesting area from February 13 to April 04, 2004, corresponding to the emergence period in the laboratory.

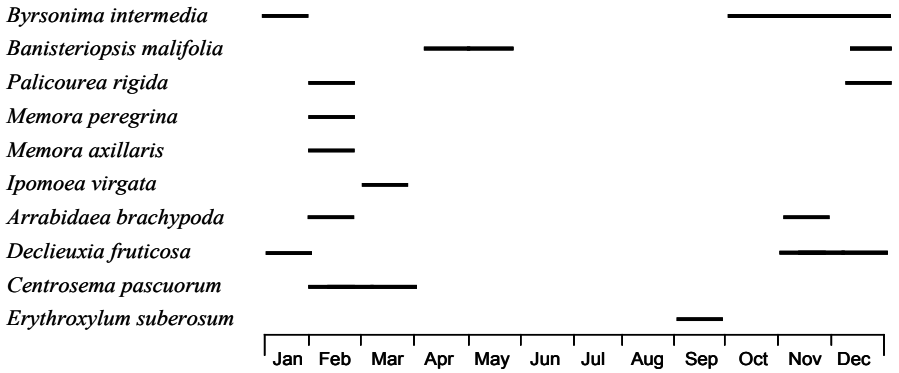

Fig. 2. — Phenology of *Epicharis bicolor* according to flower-visiting behavior throughout the year.

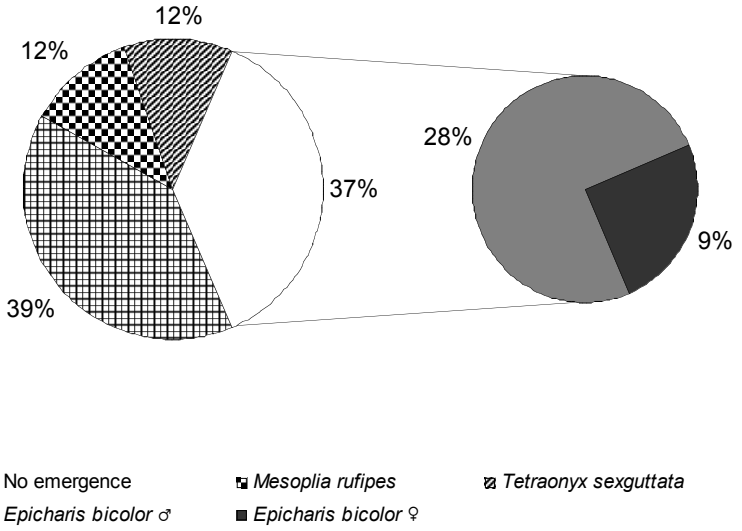

Fig. 3. — Percentage emergence of *Epicharis bicolor, Mesoplia rufipes* and *Tetraonyx sexguttata* from cells kept in the laboratory.

Mating behavior

Recently-emerged females of *E. bicolor* were surrounded by 7 to 18 males as they left nests (n = 11) and formed groups (Fig. 4A) which persisted for ca 3 min (n = 5). Mating occurred only with one male (Fig. 4B). The mean mating time was 2 min 9 sec (n = 5). Some males approached recently-mated females but immediately retreated without trying to mate. Females of *E. bicolor* were neither observed in activity within the nesting site nor

Table 2.

Emergence date and sex of *Epicharis bicolor*, *Mesoplia rufipes* and *Tetraonyx sexguttata* individuals that emerged from cells kept in the laboratory.

Cell	Species	Sex	Emergence date
1	*E. bicolor*	Female	January 23 2004
2	*M. rufipes*	Female	January 29 2004
3	*M. rufipes*	Male	January 29 2004
4	*M. rufipes*	Female	February 2 2004
5	*M. rufipes*	Female	February 2 2004
6	*E. bicolor*	Male	February 6 2004
7	*E. bicolor*	Male	February 7 2004
8	*M. rufipes*	Male	February 7 2004
9	*E. bicolor*	Male	February 8 2004
10	*E.bicolor*	Male	February 8 2004
11	*E. bicolor*	Male	February 8 2004
12	*E. bicolor*	Female	February 8 2004
13	*E. bicolor*	Male	February 9 2004
14	*E. bicolor*	Male	February 10 2004
15	*E. bicolor*	Female	February 10 2004
16	*E. bicolor*	Male	February 11 2004
17	*E. bicolor*	Male	February 11 2004
18	*E. bicolor*	Male	February 14 2004
19	*E. bicolor*	Male	May 18 2004
20	*E. bicolor*	Female	February 14 2004
21	*E. bicolor*	Male	May 2 2004
22	*T. sexguttata*	?	October 29 2004
23	*T. sexguttata*	?	October 13 2004
24	*T. sexguttata*	?	October 13 2004
25	*T. sexguttata*	?	October 13 2004
26	*T. sexguttata*	?	October 15 2004
27	*E. bicolor*	—	No emergence
28	*E. bicolor*	—	No emergence
29	*E. bicolor*	—	No emergence
30	*E. bicolor*	—	No emergence
31	*E. bicolor*	—	No emergence
32	*T. sexguttata*	—	No emergence
33	*T. sexguttata*	—	No emergence
34	*T. sexguttata*	—	No emergence
35	*T. sexguttata*	—	No emergence

Fig. 4. — A, group of males fighting for a female of *Epicharis bicolor*; B, mating; C, *Mesoplia rufipes* female going out of an *E. bicolor* nest; D, *Hoplomutilla myops* female entering an *E. bicolor* nest.

remained at the place during the subsequent weeks that followed the mating period. Such females apparently spread to other places.

Natural enemies

Twenty-one species reported as natural enemies of bees and wasps in general were captured in the nesting area (Table 3). A cleptoparasitic behavioral pattern was verified for only two species, *M. rufipes* and *T. sexguttata* that emerged from cells of *E. bicolor* kept in the laboratory. *M. rufipes* was observed entering opened nests (n = 8) (Fig. 4C) while host females were out, and also opening nests that had already been closed (n = 2). One female of *Mesonychium asteria* (Smith 1854) (Hymenoptera Apidae) was observed fly-

Table 3.

Natural enemies collected in the nesting site of *Epicharis bicolor* from September 2003 to October 2004 at the Ecological Reserve of Clube Caça & Pesca Itororó in Uberlândia, Minas Gerais State, Brazil.

Orders	Families	Tribes	Species
Coleoptera	Meloidae	Tetraonycini	*Tetraonyx (Tetraonyx) sexguttata* Olivier 1795 [1]
Diptera	Conopidae	Physocephalini	*Physocephala bipunctata* (Macquart 1843) [2]
Hymenoptera	Apidae	Ericrocidini	*Mesonychium asteria* (Smith 1854) [2]
			Mesoplia (Mesoplia) rufipes (Perty 1833) [1]
		Rhathymini	*Rhathymus bicolor* Lepeletier & Serville 1828 [2]
			Rhathymus unicolor (Smith 1854) [2]
	Mutillidae	Mutillini	*Timulla pictoria* Mickel 1938 [2]
		Pseudomethocini	*Darditilla araxa* (Cresson 1902) [2]
			Hoplocrates miles (Burmeister 1854) [2]
			Hoplomutilla anthracina (Gerstaecker 1874) [2]
			Hoplomutilla myops (Burmeister 1854) [2]
			Horcomutilla fronticornis (Burmeister 1854) [2]
			Mickelia cressoni Suárez 1966 [2]
			Pertyella sp. nov.[2]
			Pseudomethoca gounellei (André 1895) [2]
		Sphaeropthalmini	*Leucospilomutilla staurogastra* Suárez 1973 [2]
			Suareztilla centrolineata (André 1906) [2]
			Traumatomutilla juvenilis (Gerstaecker 1874) [2]
			Traumatomutilla moesta (Gerstaecker 1874) [2]
			Traumatomutilla spectabilis (Gerstaecker 1874) [2]
			Traumatomutilla trochantera (Gerstaecker 1874) [2]

[1] Direct evidence of cleptoparasitism or parasitism; [2] indirect evidence of cleptoparasitism or parasitism.

ing over nest entrances of *E. bicolor*, but no invasion was reported. Females of *Rhathymus unicolor* (Smith 1854) (Hymenoptera Apidae) invaded opened nests of *E. bicolor* (n = 4). Aggressive behavior was reported for females of *E. bicolor* against females of *R. unicolor*, which were expelled from nests by the hosts. A recently-emerged female of *Rhathymus bicolor* Lepeletier & Serville 1828 was collected near one of the studied nests. Similarly to *M. asteria*, females of such species reappeared in the nest area in October 2004.

Ericrocidini and Rhathymini (Hymenoptera Apidae) were seen collecting nectar on some of the plant species found around the nest area, some them also used as floral resources by *E. bicolor* (Table 1).

Fifteen species of Mutillidae (Hymenoptera) were captured in the nesting area, although evidence of parasitism was only observed for one of them. One female of *Hoplomutilla myops* (Burmeister 1854) (Hymenoptera Mutillidae) was observed invading opened nests of *E. bicolor* (n = 2) (Fig. 4D) while the host female was out for approximately 1.5 min. During another event, a closed nest of *E. bicolor* was excavated by a female of *H. myops*, which remained inside for about 3 min.

T. sexguttata emerged from cells of *E. bicolor* (n = 5), and some individuals were observed mating in the study area in October 2004. Individuals of *Physocephala bipunctata* (Macquart 1843) (Diptera Conopidae) emerged within the nesting site of *E. bicolor* in October 2004. Such flies walked on soil and, if a branch or leaf was found ahead, they climbed to the top and only started flying after the wings were completely extended.

DISCUSSION AND CONCLUSIONS

All the characteristics described for *E. bicolor* showed great resemblance to *E. nigrita* (Gaglianone 2005) regarding nest architecture, unbranched tunnel, isolated cells and aggregations on sandy soils. However, the cell orientation in different directions and higher cell densities rates found for *E. bicolor* do not conform to the patterns found for *E. nigrita*, which always builds diagonal cells in the soil (Gaglianone 2005). Other species which nest in dense aggregations, such as *Epicharis (Parepicharis) metatarsalis* Friese 1899 (Inouye 2000) and *Epicharis (Anepicharis) dejeanii* Lepeletier 1841 (Hiller & Wittmann 1994), present lower cell densities than those found for *E. bicolor*. Differently from *E. nigrita*, our results for *E. bicolor* suggest the existence of more than one generation a year, corroborating data regarding flower visits obtained in other Cerrado areas (Gaglianone 2003).

In relation to nectar sources, *E. bicolor* was generalist and visited species belonging to at least five families of plants. On the other hand, it collected oil only from Malpighiaceae, the only source of flower oil to *Epicharis* bees (Gaglianone 2002). Univoltine species of *Epicharis* seem to restrict pollen collection to a few plant species, though-truly oligolectic patterns have been suggested for *E. nigrita* on flowers of *Byrsonima* (Gaglianone 2005). Flowers of this genus have also been considered important pollen sources to other species of *Epicharis* (Roubik & Michener 1980, Raw 1992). In the present study, *E. bicolor* was observed only on two species of Malpighiaceae which were the only pollen sources during the nesting period. However, nesting pollen analyses would be necessary to confirm the importance of these plants as larval food.

Since nesting activities were observed only between November and December and emerged females did not nest in the study area after mating, it is likely that they dispersed to other nesting sites distant from the study area. Information on resource sources has suggested that there might be a long period of collecting activity for *E. bicolor*, similar to the one observed by Gaglianone (2003). Data regarding nesting activities and observations on

foraging activities seem to suggest the occurrence of at least two generations a year, unlike *E. nigrita* and most species of *Epicharis* studied so far (see Roubik & Michener 1980, Raw 1992, Hiller & Wittmann 1994), which are univoltine with pre-pupal diapause.

The patrol of nesting sites by males of *E. bicolor* was also reported for *Epicharis (Anepicharis) melanoxantha* (Moure 1945), *Epicharis (Triepicharis) analis* Lepeletier 1841 (Raw 1992), *E. dejeanii* (Hiller & Wittmann 1994) and *E. nigrita* (Gaglianone 2005). This seems to be a characteristic behavior of protandrous, soil-nesting solitary bees (Alcock et al. 1978, Eickwort & Ginsberg 1980, O'toole & Raw 1991). The number of *E. bicolor* males patrolling the area and their behavior indicate that females did not leave the nesting site without mating, and that they mated with only one male. Likewise, the "lack of interest" of males toward copulated females supports the hypothesis of protandry. According to Raw (1992), mating with only one male is common to many solitary bees. Thus, the ability of males to detect females that have already mated would be an advantage as they need to compete for virgin females.

The maintenance conditions of the cells in the aboratory were satisfactory since more than 60.5% of cells from the second excavation showed emergence. However, the method has to be associated with later developmental stages of the immature individuals. All cells of the first excavation failed to develop in the laboratory. Earlier collected cells contained only eggs and seemed to be more sensitive to manipulation and laboratory conditions.

Earth-filled cells were reported for some species, such as *Centris* (*Ptilotopus*) *scopipes* Friese 1899 (Hymenoptera Apidae) (Gaglianone 2001), which builds tunnels with more than one cell, closing one of them with earth only. This behavior might be interpreted as protection against parasitic attacks. In *E. bicolor*, protection against cleptoparasitic attack might also be provided by the construction of a single cell at each tunnel end with different orientation. Also the placement of nests in large aggregations may be viewed as complementary protection. Although females were not marked, it is probable that each female built more than one nest, placed among nests of other females. Thus, each offspring of a female would be less vulnerable to the attack of such natural enemies. Many natural enemies were obtained at the nesting site, although only *M. rufipes* and *T. sexguttata* emerged from breeding cells in the laboratory.

Species of Ericrocidini occur exclusively throughout the Americas and apparently only parasitize nests of Centridini (Snelling & Brooks 1985). Species of this tribe, *M. rufipes* and *M. asteria*, were also reported by Gaglianone (2005) within nesting areas of *E. nigrita*.

Bees of the genus *Rhathymus* Lepeletier & Serville 1828 (Hymenoptera Apidae) have been reported invading nests of *E. bicolor* and attacking *Epicharis (Hoplepicharis) fasciata* Lepeletier & Serville 1828 (Vesey-Fitzgerald 1939), *E. flava* (Camargo et al. 1975), *E. analis*, *E. melanoxantha* (Raw 1992), *E. dejeanii* (Hiller & Wittmann 1994) and *E. nigrita* (Gaglianone 2005). *Rhathymus* seems to parasitize species of *Epicharis* only (Michener 2000), whereas *Mesoplia* Lepeletier 1841 and *Mesonychium* Lepeletier & Serville 1825, which flew over nests along with females of *E. bicolor*, parasitized

nests of *Epicharis* and some species of *Centris* Fabricius 1804 (Hymenoptera Apidae) (Snelling & Brooks 1985). Higher specificity rates of *Rhathymus* toward its hosts might explain a more aggressive behavior shown by females of *E. bicolor* in relation to *R. unicolor* than to *M. rufipes*. Species that strongly reject parasites may be more specific hosts (see Davies & Brooke 1989, Rothstein 1990). In this case, each part might have evolved by responding to the selective pressure of the other side. Whereas hosts would probably have developed better skills to detect and repel parasite species, the latter would in turn have developed strategies to neutralize such behavior. Aggressive behavior patterns shown by *Epicharis* in relation to *Rhathymus* may be minimized if the cleptoparasitized species is not easily detected by the host female. Hiller et al. (1992) have biochemically demonstrated that recently emerged females of *Rhathymus* sp., which had been covered with floral oils of Malpighiaceae, were less attacked by females of *E. dejeanii* than those that had not been spread. Chemical mimicry has been reported by Tengö & Bergström (1977) to species of *Nomada* Scopoli 1770 (Hymenoptera Apidae) that parasitize nests of *Andrena* Fabricius 1775 (Hymenoptera Andrenidae). By mimicking their host's odor, cleptoparasites would have adapted to successfully invade their nests.

Mutillidae are ectoparasitoids of several groups of Hymenoptera. Females of *Hoplomutilla* Ashmead 1899 have been reported as parasitoids in nests of Euglossini (Hymenoptera Apidae), especially *Eulaema* Lepeletier 1841 and *Eufriesea* Cockerell 1909 (Lenko 1964, Roubik 1990, Cameron & Ramírez 2001). Besides Hymenoptera, Mutillidae may also parasitize immature stages of some species of Diptera, Coleoptera and Lepidoptera (Cambra & Quintero 1992). Although generalist parasitoids, Mutillidae may select hosts by their size (Brothers 1972, Pitts & Parker 2005). Manley & Deyrup (1989) reported some species as probable hosts for *Dasymutilla pyrrhus* (Fox 1899) (Hymenoptera Mutillidae) based on the parasitoid's size. Thus, the relatively large species found within the study area, such as *H. myops*, *Leucospilomutilla staurogastra* Suárez 1973, *Mickelia cressoni* Suárez 1966, *Traumatomutilla spectabilis* (Gerstaecker 1874) and *Hoplocrates miles* (Burmeister 1854) (Hymenoptera Mutillidae) might be associated with *E. bicolor*, which is similar in size to those species. *Timulla pictoria* Mickel 1938 (Hymenoptera Mutillidae) may also be a natural enemy of *E. bicolor*, as its males are often much bigger than females, which would consequently need differently sized hosts to produce males or females (Cambra & Quintero 1992, 1993). Mutillidae individuals within nest areas of *E. nigrita* were also reported by Gaglianone (2005), although these parasitoids did not emerge from breeding cells.

Reports on species of *Tetraonyx* Latreille 1833 (Coleoptera Meloidae) showed evidence that they parasitize soil-nesting bees, such as *Epicharis* and *Centris* (Selander 1983). Meloids are probably the most diverse and widespread group of Coleoptera that parasitize bee nests, especially the subfamily Nemognathinae (Selander 1987). *T. sexguttata* was also reported in nests of *E. dejeanii* (Hiller & Wittmann 1994) and *E. nigrita* (Gaglianone 2005). Little is known about its biology, although our results agree with former observations (M.C. Gaglianone pers. comm.) that this species is univoltine.

Species of Conopidae (Diptera) are said to be parasitoids of aculeate Hymenoptera, parasitizing them with in-flight attacks (KENNETH et al. 1987). Bees of the genera *Apis* Linnaeus 1758 (Hymenoptera Apidae), *Bombus* Latreille 1802 (Hymenoptera Apidae), *Eulaema* and *Megachile* Latreille 1802 (Hymenoptera Megachilidae) (MIHAJLOVIC et al. 1989, ROUBIK 1989, SCHMID-HEMPEL & STAUFFER 1998, OTTERSTATTER et al. 2002, RASMUSSEN & CAMERON 2004) have been reported as hosts for *Physocephala* Schiner 1861 (Diptera Conopidae). According to SCHMID-HEMPEL (2001), host bees dig into soil and die consumed by parasitoid larvae after being parasitized by Conopidae. Conopidae flies parasitizing Centridini bees were confirmed by the emergence in the laboratory of an individual of *Physocephala inhabilis* (Walker 1849) from a *Centris (Hemisiella) vittata* Lepeletier 1841 female (S.C. AUGUSTO pers. comm.). Thus, the parasitism of *E. bicolor* by such flies cannot be ignore since many individuals emerged within the nesting area.

ACKNOWLEDGEMENTS

The authors are grateful to CNPq for providing a scholarship to the first author, Dr Sílvia R.M. Pedro (FFCLRP/USP), Dr Gabriel A.R. Melo (UFPR) for identifying cleptoparasitic bees, Dr Roberto A. Cambra (Universidad de Panamá) for identifying Mutillidae, Dr Cleide Costa (MZ/USP) for identifying Meloidae, Dr Leonardo Silvestre (MNRJ) for identifying Conopidae, Dr Gilberto Fernandes (UFU) for identifying soil samples, Dr Paulo Eugênio Alves Macedo de Oliveira (UFU) for very useful suggestions and the anonymous reviewers for improvements to the manuscript.

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