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Abstract: Nest architecture of *Megachile yaeyamaensis* was studied in Iriomote Island (24°40′N). The nests were found in the deserted burrows of a lizard, *Eumeces stimpsoni,* suggesting that *M. yaeyamaensis* is a basically non-burrowing bee. One to 16 brood cells per nest (mean±SD : 6.0±4.3, N=34) were involved in completed nests. The types and numbers of leaf pieces used for making one brood cell and for closing the entrance are also described. As natural enemies, a fly, *Cylindrothecum angustifrons* and several other species of associates were found in the nests.

Key words: nesting site, nest architecture, voltinism, leaf-cutting bees, *Megachile,* natural enemies.

Introduction

As red-haired, leaf-cutting bees of the group of *Megachile bicolor,* 5 species are known to occur in East Asia (Yasumatsu & Hirashima, 1964). *Megachile yaeyamaensis* Yasumatsu *et* Hirashima is one of species of the *bicolor* group, however, nesting biology of these 5 species is little known. In a previous paper, we described the nesting site and nest architecture of *M. yaeyamaensis,* and regarded this species as a burrowing bee (Maeta *et al.,* 2004). Nesting of *M. yaeyamensis* was observed at 3 banks near and in the campus of the Tropical Biosphere Research Center, Iriomote Station, Ryukyu University (TBRC) on Iriomote Island (24°40′N) between September 17 and October 27, 2004. Through excavation of 57 nests, we added new findings on the nesting habits of *M. yaeyamaensis,* as described below.

Materials and Methods

The nests found in 3 banks were excavated, when bees' nesting had ceased. Nest architecture was studied by making sketches of the nests and surrounding cavities at excavation. These nests were kept in an air-conditioned room (ca. mean temp. : 27 °C). Dissection of brood cells was made from October 1 to October 27, 2004, so as to examine structure of brood cells and contents of cells.

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The numbers of leaf pieces, which composed of each brood cell, were counted. Cocoon size was also measured by vernier caliper.

Results and Discussion

1. Nesting sites

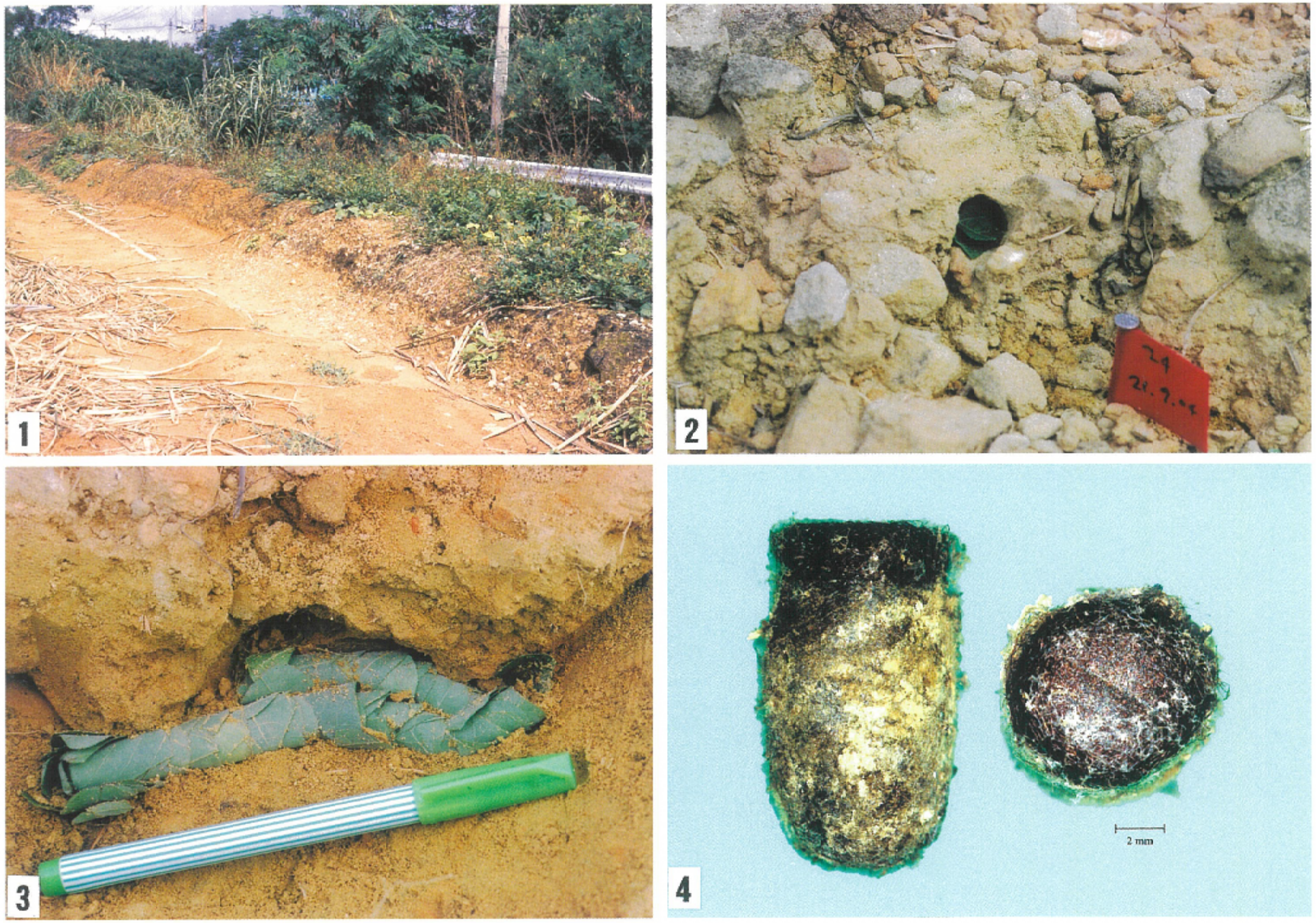
Fifty-seven nests were studied. The first nesting site (site A) was found in soil on the slope of a bank in the campus of TBRC on September 17, 2004. The slope of the bank is 50 m long and 1.7—2.0 m wide, facing toward the south. The slope gently declines about 40° and is next to a road. Four nests was found on the slope. The second and third nesting sites (sites B and C), were found on September 20, 2004. The site B was situated over one kilometer away from the site A. The height of bank, forming a ridge 80 cm wide at the top surface, was 50 cm above the ground. The length of the ridge extended to 120 m long at north-east direction along a sugar cane field (Fig. 1). A total 42 nests were found in the bank. The third nesting site (site C) was located about 150 m away from site B, which was separated by a deep slope and natural vegetation that was situated as in site B, and the bank was of similar height and structure as site B. It was over 50 m long, beside a pineapple field. There were 11 nests in this site. All nests at sites B and C were found in nearly vertical surfaces of the bare banks, facing south-west. No shade on the nesting sites by plants was seen at sites B and C, but site A became partially shady in the afternoon. The nesting activity of bees was also confirmed at site B in the same period of 2003.

The 3 nesting sites were compactly hardened, with clayish sandy soil, and the slopes of the banks were almost naked. All nests were found exclusively in the deserted cavities of a lizard, *Eumeces stimpsoni* Thompson. Formerly, *M. yaeyamaensis* was regarded as a non-burrowing bee (Maeta, *et al.*, 2004). However, the present findings revealed that this species is a non-burrowing bee. Iwata (1941) mentioned that *M. xanthothrix* Yasuamtsu *et* Hirashima, which is in the same bicolor group, prefers various pre-existing holes in the ground, such as deserted nests of a sphecid wasp, *Sphex diabolicus flammitrichus* Strand and burrows excavated by wild mice.

Nesting of *M. yaeyamaensis* continued only for about 40 days at the banks in 2004, although this species is multivoltine. The adult flying period extends about 9 months from late April to late December (Maeta, unpubl.). Presumably, they might be obliged to migrate to another place to search for the next available fresh pre-existing cavities. One female bee may use several lizards' cavities so as to lay all her eggs.

2. Nest architecture

Among 57 nests, 47 were excavated at 3 banks, and the architecture of 16 representative nests are examined. Out of 16 nests, 9 were composed of a single layer of brood cells (56.1%, Fig. 5, A—D), but 7 nests was formed by double layers, reflecting a large-sized cavity (43.8%, Fig. 5, E—F). The nests with entrance plugs were regarded as completed ones (34 nests, Figs. 2 and 5), and those nests without entrance plugs were tentatively treated as incomplete ones (25 nests). The number of brood cells per nest per completed nest were 1—16 (mean$\pm$SD : 6.0$\pm$4.3, N=34). Each brood cell, forming a series, partially attached to the wall of a lizard's cavity, so as to maintain their position within an irregular shaped-cavity. In *Megachile pseudoanthidiodes* Moure, which nested in wooden boxes, a series of brood cells was suspended in the air, only the first brood cell



Figs. 1–4 Nesting sites, a mass of brood cells in the lizard's cavity, and cocoons of *Megachile yaeyamaensis* found in the slopes of banks. 1—Nesting site (site B). 2—Entrance of nest closed by leaf pieces (Nest no. 24). 3—Two series of brood cells are found in a cavity of a lizard (Nest no. 4). 4—Lateral (right) and frontal (left) view of cocoon. Fecal pellets on the surface of cocoon were partially removed.

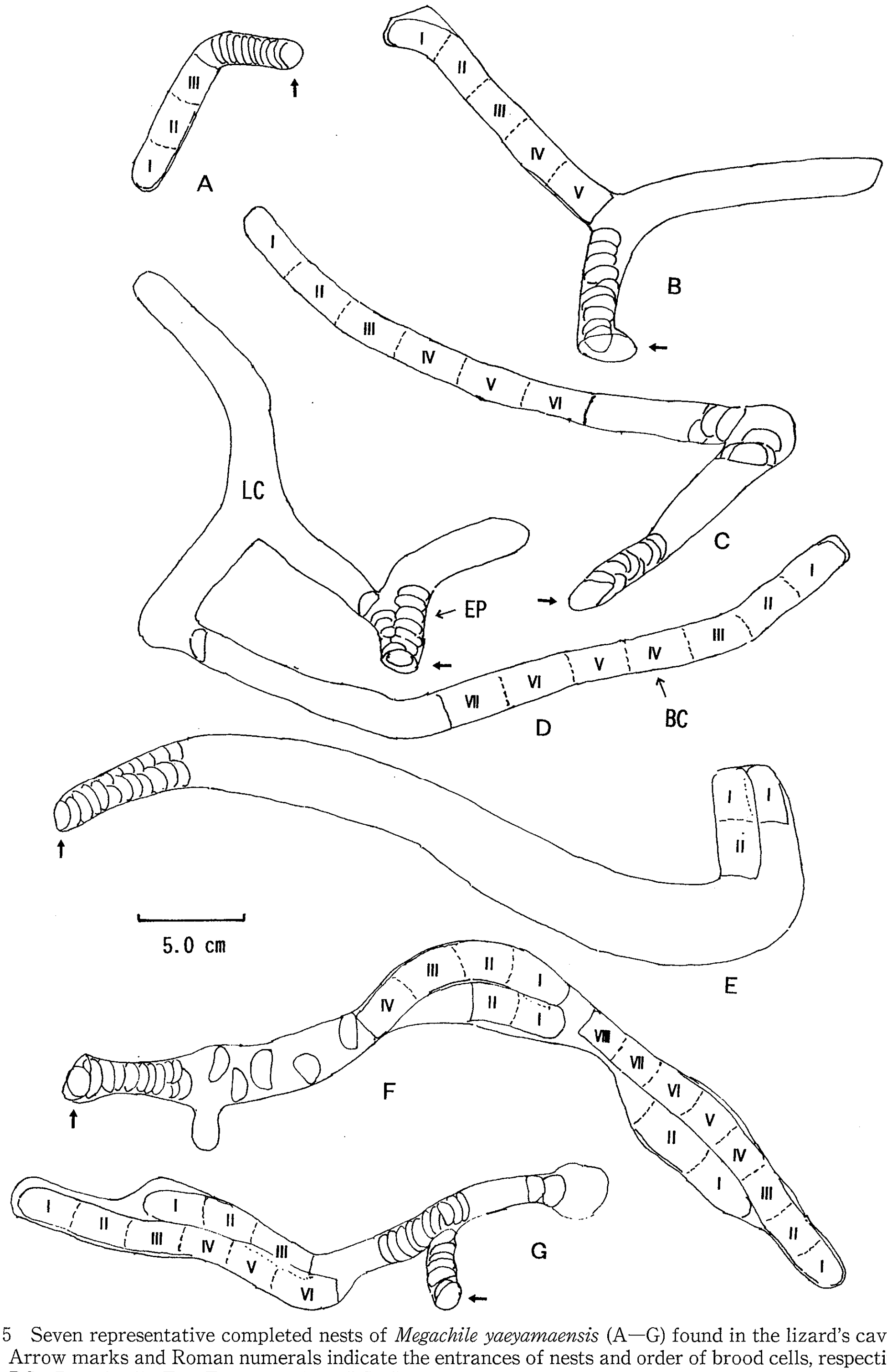


Fig. 5 Seven representative completed nests of *Megachile yaeyamaensis* (A—G) found in the lizard's cavities. Arrow marks and Roman numerals indicate the entrances of nests and order of brood cells, respectively. BC—Brood cells. Ep—Entrance plugs. LC—Lizard cavity in soil. Detailed explanations of these nests are in the text.

was attached to the wall or floor of the wooden box. It may be sustainable in the air, as each brood cell is made by intermixing mud between leaf pieces (Zillkens & Steiner, 2004).

The situation of the brood cells was variable in *M. yaeyamaensis,* depending on the shape of the deserted cavities of *E. stimpsoni.* The structure of 7 representative completed nests is described below.

Nest no. 22 (Site B, Fig. 5, A) : Three brood cells were made in a shallow burrow (12.6 cm). The entrance was round (1.3×1.3 cm), and the entrance plug was formed with 9 leaf pieces in the vestibular space between the entrance and the last brood cell (5.3 cm).

Nest no. 1 (Site A, Fig. 5, B) : In the left burrow (15.5 cm), which was ramified at 6.0 cm from the entrance, 5 brood cells were found. The entrance plug was formed with 10 leaf pieces in the vestibular space (6.2 cm). The entrance was oval (3.0×1.2 cm).

Nest no. 54 (Site B, Fig. 5, C) : Six brood cells were made in a burrow (17.9 cm), which was sharply bent to the left. The vestibular space (24.2 cm) was not completely filled with a total of 16 leaf pieces. The entrance was irregular (2.5×1.3 cm).

Nest no. 34 (Site B, Fig. 5, D) : The structure of the nest cavity was very complicated. Seven brood cells were found in one of burrows (23.6 cm). The vestibular space (7.7 cm) near part of the entrance was closed with 14 leaf pieces. The entrance was oval (1.7×1.0 cm).

Nest no. 37 (Site B, Fig. 5, E) : Three double layered brood cells were found at the inner part of a large cavity (42.0 cm). The vestibular space (6.2 cm) was filled with 19 leaf pieces near the entrance (6.2 cm). The entrance was nearly oval (1.5×0.8 cm).

Nest no. 58 (Site C, Fig. 5, F) : In this nest 16 brood cells were found in a single burrow (42. 5 cm). Apparently, 4 series of brood cells were recognized, which were formed in double layers at the inner and middle. The vestibular space (15.0 cm) was filled with 18 leaf pieces, but roughly filled in. The entrance was irregular (2.4×1.2 cm).

Nest no. 24 (Site B, Fig. 5. G) : Nine brood cells were formed in double layers at the inner part of the burrow (20.0 cm), which sharply curved toward left from the entrance. The vestibular space was filled with 18 leaf pieces, but 2 leaf pieces were found at right side of the burrow. The entrance was nearly round (1.4×1.1 cm).

3. Leaf pieces

Three different types of leaf pieces, *i.e.,* large oval-shaped (A—1, C—1), small oval-shaped (A—2, C—2), and semiround-shaped (A—3, B—2, and C—1) were used in nests of *M. yaeyamaensis* (Maeta *et al.,* 2004). These leaf pieces were used for both filler and firm leaves (Michener, 1956). In *M. yaeyamaensis,* pieces in the latter tightly adhered. To fill an extra space around the brood cells, only A—1 were used. A—2 and A—3 were used to form the cell cup, but A—3 at the inner part of the cell cup. Only B—2 were used to close the cell cups. These B—2 were tightly attached each other. The entrances of nests were closed with 3 types of leaf pieces (C—1, C—2 and C—3), depending on the caliber of the gallery. However, each leaf piece was vertically placed, with a certain interspace between them, not as in cell caps. Fresh leaf pieces of *Pueraria montana* Merrill (Leguminosae) were often used for nest materials.

The number of leaf pieces used for making one brood cell and for closing the vestibular space was as follows (mean±SD, Table 1) : For making one cell cup and filling its surrounding space,

Table 1 Number of leaf pieces used for construction of brood cells and nest entance plugs in *Megachile yaeyamaensis.*

Category of leaf pieces[1]	Place used	Type of leaf pieces[2]	Range and mean numbers/cell or nest[3] (*N*)	Size of leaf pecies (mm)[3]
Filler leaf	Cell cup	Large oval-shaped (A—1)	8—22 12.2±3.2 (104)	27.1±2.2× 17.6±1.4 (30)
Firm leaf	Cell cup	Small oval-shaped (A—2)	3—8 4.0±1.0 (104)	19.3±0.9× 13.5±0.8 (30)
		Semiround-shaped (A—3)	2—7 3.7±1.2 (104)	12.1±0.6× 10.7±0.5 (30)
Filler+ firm leaf	Cell cap	Semiround-shaped (B—2)	1—9 4.1±2.0 (104)	12.0±0.5× 10.7±0.7 (30)
Filler leaf	Nest entrance plug	Large oval-shaped (C—1)	0—21 1.7±4.5 (34)	24.9±1.3× 16.0±0.7 (20)
		Small oval-shaped (C—2)	0—45 4.0±8.5 (34)	19.2±1.6× 14.2±0.5 (27)
		Semiround-shaped (C—3)	1—61 14.6±11.7 (34)	14.2±1.3× 11.6±0.9 (26)

[1] Follows Michener (1953). [2] The size and shape are same between A—1 and C—1, A—2 and C—2, and among B—2, A—3, and C—3, but the places used are different. [3] Given as mean±SD. [4] Indicated by long and short axes. Thirty leaf pieces of each type, randomly selected, were measured.

19.9±4.0 (A—1, A—2, and A—3) were used. For closing the cell, 4.1±2.0 (B—2) were used. The vestibular space was closed by 20.3±14.8 (C—1, C—2, C—3), but C—3 were predominant. The margins of leaf pieces were partially attached to the wall of the cavity. There were no differences in both shape and size (Table 1) between A—1 and C—1, between A—2 and C—2, and among A—3, B—2, and C—3 ($p<0.05$, t—test). Therefore, *Megachile yaeyamaensis* can cut 3 different types of leaf pieces, used for nests.

Eickwort *et al.* (1981) suggested that nesting in pre-existing cavities is a derived trait that has repeatedly evolved in *Megachile* and other genera. They also hypothesized that ancestors to the Megachilinae dug soil nests with unlined cells, and that the Megachilinae evolved the behavior of using foreign materials as an alternative to using glandular secretions to waterproof cells in the soil. In those species, belonging to the subgenus *Megachile,* which nest in the soil, mostly B—2 are used, to close cells. In hole-using species belonging to the subgenera *Megachile* and *Eutricharaea,* mainly or always use B—1 (Kitamura *et al.,* 2000, 2001). Maeta & Miyanaga (1997) estimate that technique to cut completely round leaf piece (B—1) gained through selection of nesting sites. The habit to cut B—1 seems to be evolved, especially in some species which use tubes with round diamaters. This hypothesis is applicable to *M. yaeyamaensis,* which uses pre-existing burrows and solely closes brood cup with semiround leaf pieces (B—2) for closing cells.

4. Cocoons

The shape of cocoons made by larvae of *M. yaeyamaensis* in their brood cells islike a straw rice-bag, but the anterior part is flat, due to depression of the plug, which closes the brood cells, as in other species of leaf-cutting bees (Fig. 4). The cocoon is separable into 3 layers of silky threads, intervening with pollen and larval feces between layers, which thicken the cocoon wall. Color of cocoons is deep brown. The outermost layer is the thickest and relatively roughly spun, while the innermost layer is thinner and compact. The thickness at the middle part of the 3

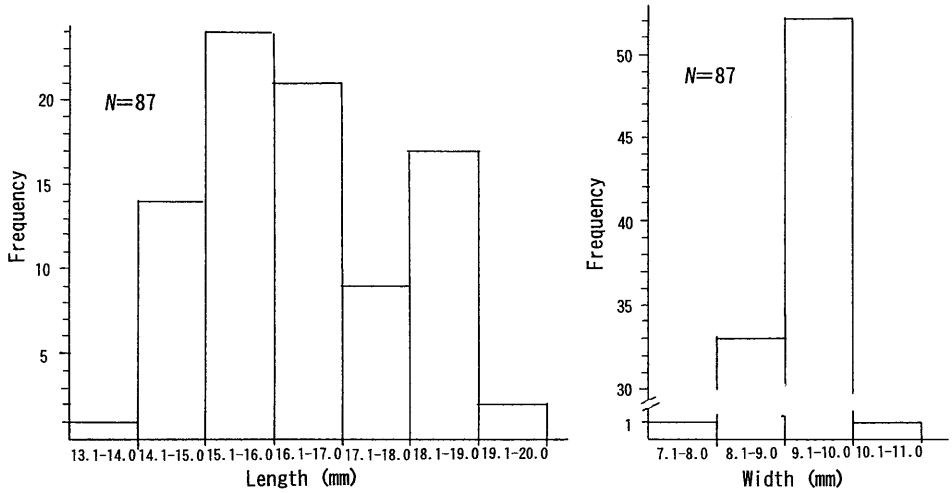


Fig. 6 Distributional frequency of the sizes of cocoons in *Megachile yaeyamaensis.*

layered cocoons, including neither interspace nor debris, is 0.125—0.150 mm, remarkably thicker than those of other species, which nest pre-existing holes above the ground (Maeta, 1999 ; Maeta & Minagi, 1999).

The size of 87 cocoons (represented by length and diameter at the widest part) was measured. There were 2 distict peaks in length of cocoons, presumably reflecting a difference between sexes of bees (Fig. 6). The size range of cocoons, including the both sexes, are 1.35—2.00 mm in length and 0.8—1.10 mm in width.

5. Natural enemies

Megachile yaeyamaensis here is newly recorded as a host of a fly, *Cylindrothecum angustifrons* (Townsend) (Anthomyiidae). Fifty-nine percent of total brood cells (152/260) were infested by this fly. The maggots feed on host provision and form puparia within the host cells. One to 21 larvae were found in each brood cell. Adults emerged from puparia between October 5 to October 27, 2004. Ten other species of megachilid bees are known from Japan and Taiwan as hosts of *C. angustifrons* (Kitamura *et al.,* 2001).

All of prepupae in cocoons of *M. yaeyamaensis* (87) were infested by *Melittobia sosui* Dahms in the laboratory. However, no infestation by this chalcid wasp was known from species which nest under ground (Maeta, 1985). Other associates include 2 unknown species of coleopteran larvae, one belonging to the Elateridae (12 individuals) and the other to an unknown family (one individual). Each larva of 2 coleoptran species was found from a single host brood cell in 8 nests. Both species consumed provisions in the host cells. A flog (species unknown) was also found in a few nests where they destroyed the nests by defecation. A slug, *Laevicaulis* sp. destroyed a nest by ingesting provision stored in the brood cells.The infestation rates of the latter 2 species were not studied.

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