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Unusual nesting habits, floral associations, and natural enemies of the Neotropical leaf-cutter bee *Megachile exaltata* Smith (Hymenoptera: Megachilidae)


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& Victor H. Gonzalez²

Abstract. Leaf-cutter bees (genus *Megachile* Latreille) represent a diverse group whose biology remains poorly documented, especially in the tropics. Here, we describe the nesting behavior, cell morphology, floral associations, and natural enemies of *Megachile* (*Austromegachile*) *exaltata* Smith, based on nests found in Western Costa Rica. Brood cells were built entirely from leaf pieces of *Euphorbia* (*Chamaesyce*) (Euphorbiaceae), and many were built in the open, rather than within pre-existing cavities. These exposed cells were placed among a wide range of man-made objects, such as umbrellas, plastic panels, black plastic bags, and even clothing. Bees also nested in pre-existing cavities, such as crevices, bamboo canes, and abandoned nests of black mud dauber wasps (Sphecidae: *Sceliphron* spp.). Palynological analyses of brood provisions showed that pollen consisted exclusively of *Muntingia calabura* L. (Muntingiaceae), a widely distributed Neotropical shrub or tree, indicating monofloral foraging. Brood cells were parasitized by the cuckoo bee *Coelioxys otomita* Cresson, parasitic wasps (Chalcididae: *Brachymeria* sp.), and phorid flies [Phoridae: *Megaselia scalaris* (Loew)]. These findings expand our understanding of the nesting plasticity and ecological interactions of Neotropical leaf cutter bees.

INTRODUCTION

Leaf-cutter bees (genus *Megachile*) are a diverse monophyletic group of solitary species that are best known for their ability to cut and manipulate petal or leaf pieces to build their nest cells (Michener, 2007). Such leaf-cutting behavior is unique among bees, and it is often associated with the presence of sharp edges among teeth (interdental laminae) in the female mandibles. However, these structures are reduced or secondarily lost in some species, resulting in a more limited use of leaf pieces and incorporation of other nesting materials such as mud or resin (Gonzalez *et al.*, 2019). Leaf-cutter bees nest in pre-existing cavities, either above or below the ground, or in self-excavated burrows within dead wood, pithy stems, or loose soil (Michener, 2007; Müller *et al.*, 2024). Although many species visit a wide range of plants for both pollen and nectar, others appear to show strong preference for particular plant families and have evolved specialized morphological adaptations to facilitate collection. For example, females of *Megachile* (*Megachile*) *pilicrus* Morawitz, which are oligolectic on

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Asteraceae of the tribe Cardueae, have a dense brush of apically wavy, stiff bristles on the ventral side of the hind trochanter and femur for combing pollen from aster inflorescences (Müller & Bansac, 2004). However, detailed biological information exists for only a few very common species and remains scarce or entirely absent for many others.

Leaf-cutter bees are cosmopolitan in distribution, inhabiting a wide range of ecosystems and elevations, from deserts to tropical rain forests, and from sea level to high-altitude habitats in the Andes (Michener, 2007). Leaf-cutter bees are both ecologically and economically important. Several species are effective pollinators, including *Megachile* (*Eutricharaea*) *rotundata* (Fabricius), the most intensively managed and produced solitary bee in the world, used for alfalfa seed production (Pitts-Singer & Cane, 2011). However, the biology of many species, particularly those from tropical regions, remains poorly documented. This knowledge gap limits not only our understanding of their ecological roles and interactions but also our ability to promote their conservation and sustainable use.

The purpose of this study is to document the nesting behavior, floral associations, and natural enemies of the Neotropical leaf-cutter bee *Megachile exaltata* Smith. Nests of these species were discovered in Western Costa Rica and were brought to our attention by local residents who observed numerous individuals flying inside their homes. *Megachile exaltata* is widely distributed in the Neotropical region and was formerly placed in its own subgenus, *Holcomegachile* Moure, based on distinctive external morphological features. It is currently assigned to the subgenus *Austromegachile* Mitchell, which consists of approximately 30 species ranging from Mexico to Argentina (Michener, 2007; Moure *et al.*, 2007; Gonzalez *et al.*, 2019).

MATERIAL AND METHODS

We conducted field observations at the end of the dry season, between April 21 and May 18, 2017, in the town of Guadalupe de Esparza (N10°00'02", W84°34'15", 391 m), Puntarenas Province, Costa Rica. Fieldwork was carried out by I.A.M. and E.H.G. Brood cells were collected on May 2 and 4 and kept in Petri dishes in the laboratory at ambient temperature until adult emergence. Bees and associated organisms were euthanized, pinned, and labeled for identification. We measured the maximum length and width of nest cells using a digital caliper (CaliPro®, 0–150 mm). To describe brood cell morphology, leaf pieces were separated and counted after emergence. The botanical origin of the leaves was made by Alejandra Barrantes Vásquez (Environmental Science Program, Universidad Nacional, Costa Rica) based on morphological features and knowledge of the local flora.

To identify the pollen hosts of *M. exaltata*, we analyzed pollen contents from 14 brood cells. Each sample was transferred to a separate vial containing 10 ml of distilled water and centrifuged at 4,500 rpm for 5 minutes. After removing the supernatant, the procedure was repeated, and 1 cm³ of safranin was added to stain the pollen grains. For each sample, two slides were prepared using Kaiser's glycerin and examined under a compound microscope at 40× and 100× magnification. Pollen grains were counted and identified along a transect of 500 grains per slide. Palynological analyses were conducted by L.S.

V.H.G. identified the bee specimens by comparing them with reference material in the Snow Entomological Collection (SEMC), University of Kansas, Lawrence, USA. Brian Brown (Natural History Museum of Los Angeles County, California, USA) identified the phorid fly. Voucher specimens of bees and associated organisms are deposited in the insect collections of the Centro de Investigaciones Apícolas Tropicales (CINAT), Universidad Nacional, Heredia, Costa Rica, and SEMC.

RESULTS

Nests of *M. exaltata* were discovered by residents, who reported the species to be abundant in and around their homes, particularly in semi-open spaces such as sheds or indoors (Video S1). Many brood cells were built in the open, rather than within pre-existing cavities. These exposed cells were placed among a wide range of man-made objects, such as umbrellas, plastic panels, black plastic bags, mesh shade tarps, backpacks, and even piles of clothing. Bees also nested in pre-existing cavities, such as crevices, bamboo canes, and abandoned nests of black mud dauber wasps (Sphecidae: *Sceliphron* sp.) (Figs. 1–4). The leaf pieces that ended up on the ground were later collected by leaf-cutter ants (Formicidae: *Atta* spp.).

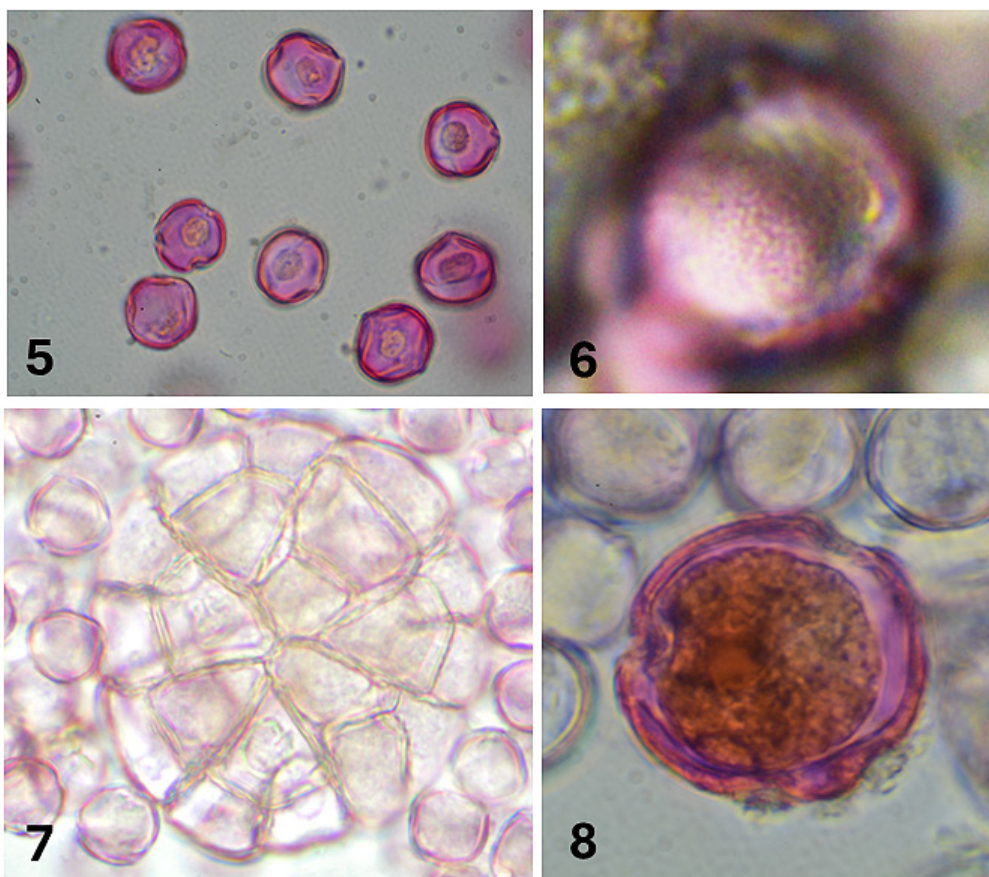


Figures 1–4. Nests of *Megachile* (*Austromegachile*) *exaltata* Smith constructed with leaf pieces of *Euphorbia* (*Chamaesyce*) (Euphorbiaceae) in Costa Rica. **1.** Brood cells among clothing. **2.** Brood cells inside abandoned nests of black mud dauber wasps (Sphecidae: *Sceliphron* spp.). **3.** Detail of brood cells. **4.** Brood cells showing larvae of the phorid fly larvae *Megaselia scalaris* (Loew).

Bees used leaves of at least two species of *Euphorbia* (*Chamaesyce*) (Euphorbiaceae) and an unidentified plant species in the family Myrtaceae or Rutaceae. They used suboval (one side with relatively straight margin) leaf disks to make their brood cells, bending them to form the cell distal end and sides. Cell length ranged from 7.73 to 11.24 mm (9.53 ± 0.134 , $n = 42$) and cell diameter from 4.41 to 5.83 mm (5.04 ± 0.048 , $n = 42$). The number of leaf pieces used to build each cell varied from 9 to 16 (12.69 ± 0.644 , $n = 13$), while the number used for cell cap ranged from 2 to 10 (3.57 ± 0.541 , $n = 14$). These two variables were not significantly correlated (Spearman's correlation $r = -0.321$, $p = 0.285$).

All slides we analyzed contained pollen of strawberry-tree *Muntingia calabura* L. (Muntingiaceae) (Figs. 5, 6), a widely distributed shrub or tree in the Neotropical region (POWO, 2025), including our study site in Costa Rica. The pollen grains of this species are small, prolate-spheroidal, with a semitectate exine, and a homobroccate reticulate sexine. They are tricolporate, usually display equatorial constriction, and measure approximately $13\text{--}15 \times 11.5\text{--}13.5\ \mu\text{m}$ (see Roubik & Moreno, 1991). Only individual grains of *Inga* sp. (Fabaceae) and *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae) were found on two slides (Figs. 7, 8); these were considered incidental contamination from the nest material or pollen load rather than intentionally collected by the leaf-cutter bees.

According to the residents, bees began their nesting activity around April 1, 2017. By early May, nesting activity had already declined, and by May 17 no active bees were observed. Nest cell samples collected between May 2 and 10 revealed the presence of larvae and pupae of the phorid fly larvae *Megaselia scalaris* (Loew). On May 18, we observed the first newly emerged adults of *M. scalaris*, the parasitic wasp *Brachymeria*



Figures 5–8. Pollen from brood cells of *Megachile* (*Austromegachile*) *exaltata* Smith in Costa Rica. 5, 6. Pollen grains of *Muntingia calabura* (Muntingiaceae). 7, 8. Large pollen grains of *Inga* sp. (Fabaceae) and *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae), respectively, surrounded by smaller, abundant *Muntingia* pollen. Pollen grains of these two species were found in only two samples and likely represent incidental contamination from nest material or pollen loads, rather than intentional collection by leaf-cutter bees.

sp. (Hymenoptera: Chalcididae), and the cuckoo bee *Coelioxys otomita* Cresson. In the laboratory, males of *M. exaltata* began emerging on May 30, suggesting that the species may be bi- or multivoltine.

DISCUSSION

We report, for the first time, the nesting biology and key ecological traits of *M. exaltata*, a Neotropical leaf-cutter bee that, despite its wide distribution across the Americas, remains poorly known. The most remarkable finding is its nesting plasticity. Like other leaf-cutter bees, it nests in pre-existing cavities, yet it can also construct fully exposed nests without the need for confined or concealed spaces. Whether this behavior reflects population pressure or a shortage of suitable nesting sites remains unclear.

Although uncommon, the construction of fully or partially exposed nests by leaf-cutter bees has been reported a few times. For example, Packer (1987) described two single-cell nests of *Megachile* (*Litomegachile*) *pseudobrevis* Mitchell built among grasses on the ground, both parasitized by meloid beetles. Similarly, Sheffield (2017) reported several nests of the alfalfa leaf-cutter bee *Megachile* (*Eutricharaea*) *rotundata* (Fabricius) inside the radiator of an antique farm tractor, where half of each brood cell was left exposed. These observations illustrate the flexibility of leaf-cutter bees in both nesting choice and substrate use. This flexibility also includes nesting materials, as some species have been observed incorporating or even substituting synthetic materials, such as plastics, when leaves were unavailable (MacIvor & Moore, 2013; Allasino *et al.*, 2019; Wilson *et al.*, 2024).

Given that nests with exposed cells are generally more susceptible to parasitism than those built within cavities, it is not surprising that the nests of *M. exaltata* were attacked by cuckoo bees, parasitic wasps, and phorid flies. Compared to concealed nests, exposed or partially exposed nests are more vulnerable to attack, particularly when females are away foraging and the brood is unguarded. Although we did not quantify parasitism rates, the nests we examined showed clear evidence of high parasitism. All recorded parasitoids in this study are known to target bees or other insects. For instance, the phorid fly *Megaselia scalaris* is a generalist species capable of causing myiasis in a wide range of both vertebrate and invertebrate hosts, including honey bees (*Apis mellifera*) (Ricchiuti *et al.*, 2016; Rossi *et al.*, 2024). To our knowledge, the only other published record of natural enemies of *M. exaltata* is that of Parker & Stange (1965), who reported the mantisfly *Plega yucatanae* Parker & Stange (Mantispidae) parasitizing up 71% of brood cells in nests found in crevices in the ceiling of a cenote cave in Yucatán, Mexico.

The way leaf-cutter bees use leaf pieces to build brood cells varies among taxa and may provide useful biological traits for phylogenetic reconstruction. For example, some species of the subgenera *Litomegachile*, *Megachiloides*, *Megachile* s. str., and *Xanthosarus* use small, circular discs to form the distal end of the brood cell (Williams *et al.*, 1986; Krombein & Norden, 1995). In contrast, in some species of *Eutricharaea*, *Melanosarus*, *Pseudocentron*, and *Zonomegachile*, the distal end of the cell is formed by folding or bending the same leaf pieces that form the cell walls (Medler, 1965; Kim, 1992; Gonzalez *et al.*, 2018). This latter construction method also characterizes the nests of *M. exaltata* and is consistent with observations of other South American species of *Austromegachile*, such as *M. habilis* Mitchell (Laroca *et al.*, 1987) and *M. sejuncta* Cockerell (Marinho *et al.*, 2018).

Our palynological analysis revealed that *M. exaltata* provisions its brood exclusively with pollen from *Muntingia calabura* L. (Muntingiaceae) at our study site in Costa Rica, indicating a high degree of at least local floral specialization. Such oligolectic foraging behavior is consistent with previous studies showing that many leaf-cutter bees specialize on a limited range of floral resources that meet their nutritional needs

(e.g., Buschini *et al.*, 2009). Likewise, *M. calabura* has been identified as a non-native pollen source for *Anthidiellum smithii* (Ritsema) in Singapore (Soh *et al.*, 2016). In Costa Rica, this plant flowers nearly year-round (Frankie *et al.*, 2013), providing a reliable pollen source that likely facilitates the extended or flexible nesting activity of *M. exaltata*. However, we analyzed a relatively small number of brood provisions, which may not be representative of the studied population. Given that this bee species is widely distributed across the Americas and is possibly bi- or multivoltine, future studies are likely to document additional host plants depending on their local availability. Nonetheless, our findings reveal that *M. exaltata* is a bee species that is both behaviorally flexible and ecologically specialized, capable of exploiting diverse nesting sites while maintaining strong local floral fidelity.

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SUPPLEMENTAL MATERIAL

Video S1. Video clip showing the exposed nests of *Megachile* (*Austromegachile*) *exaltata* Smith built on a plastic bag and among clothing inside a house in Costa Rica.

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