

A Stingless Bee Nesting with a Paper Wasp (Hymenoptera: Apidae, Vespidae)

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ABSTRACT: The tropical stingless bees are known to use diverse nest sites, and some species will nest within the nest of other insects including ants and termites. However, it has not been reported before that a stingless bee, *Trigona cilipes* (Fabricius) (Hymenoptera: Apidae), is able to establish its nest within the nest of the social paper wasp *Epipona tatus* (Cuvier) (Hymenoptera: Vespidae) as reported here. The bell-shaped nest with both wasps and bees was found in secondary forest in Peru, and held under observation for several weeks until collection. Description of nest architecture and some behavioral observations are presented. *Trigona cilipes* is usually found nesting with *Azteca* ants, and the behavioral flexibility that enables them to also colonize wasp nests results in several advantages that may favor wasp associations as discussed in the text.

KEY WORDS: *Trigona cilipes*, *Epipona tatus*, nest biology, Peru, behavioral plasticity

The stingless bees (Hymenoptera: Apidae: Meliponini) are among the least known of all social bees, probably because of their tropical distribution (Michener, 2000). All the stingless bees are eusocial and live in perennial colonies, with up to several thousand workers and a single queen (Sakagami, 1982; Michener, 2000). Some species show intriguing interactions with their biological environment (e.g., Roubik, 1982; Sakagami *et al.*, 1993; Camargo *et al.*, 1992; Camargo and Pedro, 2002). A particularly fascinating aspect of stingless bees' biology is the fact that some species nest only in close association with nests of other social insects (Wille and Michener, 1973; Roubik, 1983). Common South American species of stingless bees like *Scaura latitarsis* (Friese) and *Trigona chanchamayoensis* (Schwarz) always establish their nests inside termite (Isoptera) colonies (Schwarz, 1948; Camargo, 1984), while other species nest in association with ants (Hymenoptera: Formicidae) (e.g., Laroca and Almeida, 1989; Sakagami *et al.*, 1989). Wille and Michener (1973) in their review of stingless bee nesting behavior found that 12% of the species studied can nest with termites, and of these 8% are obligate termite nesters, while another 2% (3 spp.) nest exclusively with ants although more species will nest with ants occasionally (reviewed by Sakagami *et al.*, 1989).

Even closely related species of stingless bees may partition their preference between taxa as different as termites and ants, such as the sibling species *Trigona cilipes* (Fabricius) and *T. mazucatoi* (Almeida). The latter was described mainly based on difference in the color pattern of the wing (Camargo, 1988; Almeida, 1992), but despite their similar morphology, some interesting biological differences have been reported. The nests of both species were described by Kerr *et al.* (1967) as *Trigona c. cilipes* "no. 1" (= *cilipes*) and *T. c. cilipes* "no. 2" (= *mazucatoi*) (Camargo, pers. comm.). They found that *T. cilipes* nested with *Azteca* or *Crematogaster* ants (Hymenoptera: Formicidae) (see also Kempf, 1962; Camargo, 1988), while *T. mazucatoi* nested with termites. Additional differences include in particular the form of the entrance tube, consistent with what I have observed from the present study and additional nests of *T. mazucatoi* examined in Peru. Roubik (1979, cited

as *T. cilipes*), found *T. mazucatoi* to be the most common stingless bee species in French Guiana, where it would nest with nasute termites in tree cavities near the ground. It is less obvious which of the two *Trigona* species have been reported in other studies (e.g., Wille and Michener, 1973), as *T. mazucatoi* was only recently described (Almeida, 1992) and is widespread, found sympatric with *T. cilipes* in Amazonian Brazil, Peru, Bolivia, Colombia, French Guiana, and Guiana (pers. obs.; Almeida, 1992; Nates-Parra, 2001). Both species benefit from their interaction with other social insects. Ant or termite hosts offer protection from predators and provide alternative nest site options in areas where tree cavities, the common nesting site for many stingless bees, may be in short supply.

Social wasps often defend their nests aggressively, and many animals, ranging from katydids to birds, associate with or nest near wasp nests, thereby gaining some degree of protection from predators (Evans and West-Eberhard, 1970; Downhower and Wilson, 1973). Lucas (1889) reported on a colony of the stingless bee *Paratrigona* sp. (cited as *P. lineata* (Lepeletier)) found inside the characteristic wasp nest of *Polybia scutellaris* (White) (Hymenoptera: Vespidae). However, the bees most likely occupied the nest after the wasps abandoned it, as it is common for stingless bees to establish their nests in available cavities. Silva-Matos *et al.* (2000) briefly reported a colony of *T. cilipes* inside the nest of the epipone wasp *Brachygastra* sp. (Vespidae) in Brazil. Otherwise, to my knowledge, this is the first detailed description of any stingless bees nesting inside a social wasp nest. I also discuss the implications for the evolution of nesting associations in the stingless bees and other organisms.

Materials and Methods

All observations on the paper wasp *Epipona tatus* (Cuvier) (Vespidae) nest containing the stingless bee *Trigona cilipes* (Fabricius) (Apidae) were made at the nest site, located close to the River Shilcayo in the town of Tarapoto, department of San Martín, Peru (6°28.819'S, 76°21.315'W, 350 m above sea level). The habitat near the river is secondary rain forest, with many settlements and small-scale agricultural areas. Some primary rain forest remains, mainly on the slopes of the Cerro Escalera (350–900 m a.s.l.) less than 5 km away. It was not possible to locate any other *Epipona* wasp nests in the area despite considerable effort, including interviews with farmers.

The wasp nest was first observed more than two years before the present observation took place, according to the owner of the area. The bee colony was first observed when the author noticed the presence of wax on the outer surface of the wasp nest on February 4, 2003. Aerial netting of swarming insects from the nest confirmed the presence of stingless bees. The nest was attached to a branch 15 m above ground on the *Simira williamsii* (Standl.) Steyererm. (Rubiaceae) tree, locally known as “pucaquiro”. The height of the nest made it difficult to observe any insect activity in detail, and the nest was therefore lowered from its original position during the night of March 1, 2003. The original branch with the nest was attached to the trunk of the same tree, 4 m above ground. However, two days of heavy rain following this episode caused the nest to fall off the branch and most of the insects left the nest before it was collected and kept in the freezer on March 5. All observations were made with binoculars for up to three hours weekly during four weeks until the collection of the nest.

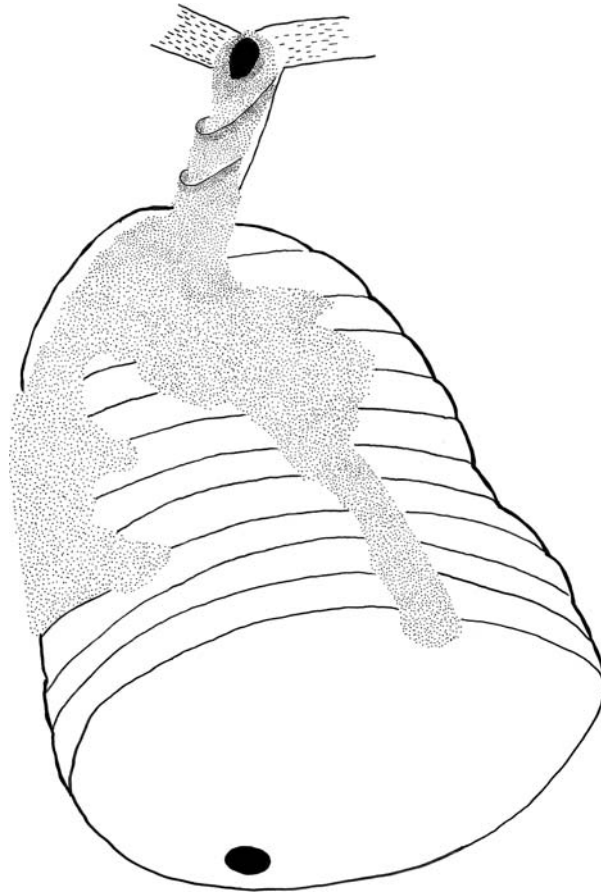


Fig. 1. View from the ground of an *Epipona tatua* wasp nest that has been occupied in part by a colony of the stingless bee *Trigona cilipes*. On the outer surface of the wasp nest, the bees covered a large area with wax, and they moved around and entered the nest undisturbed under cover of this. Note bee entrance attached to branch and wasp entrance at bottom of the bell.

Results

Nest Architecture: Wasps

The bell-shaped wasp nest measured 380 mm in height and approximately 240 mm in diameter at the bottom of the nest (Fig. 1). The nest hung from a 16 mm thick branch encompassing an approx. 120 mm wide but thin layer of the nest envelope. The flexible, but durable, two mm thick nest envelope was made of wood fibers, and was an uneven, light-gray color. The underside of the nest was flat, with a single simple oval nest entrance (approx. 19 by 14 mm), situated 16 mm from the sidewall of the nest (Fig. 1). The entrance led to the inside of the nest with eleven conjoined horizontal combs. Each of the combs was connected through a single 3 mm wide entrance, situated 20 mm from the outer wall of the envelope. Eight of the combs occupied by the wasps had a total of 7610 brood cells, of which 1099 were still sealed and contained wasp brood (Table 1). The lower comb contained no cells and the two combs that had been modified by the bees, as described below, contained a very reduced number of cells.

Table 1. For each comb of the wasp nest the following data are given; the comb number as referred in the text, the external cross diameter of the nest, the number of wasp brood cells, as well as the number of wasp and bee broods present in the brood cells. The sizes given for the bee-brood (italics) in combs six and seven are the maximum measures for each comb, both of which were unevenly formed.

Comb, counted from branch	External diameter of the nest (mm)	Number of wasp brood cells	Number of wasp and bee brood in cells
1	110	244	0
2	130	331	0
3	160	607	0
4	180	939	0
5	190	983	1
6	200	Occupied by bees	Occupied by bees
7	200	Occupied by bees	<i>724 bee brood cells: 87 (55 × 41 mm); 171 (75 × 34 mm); 186 (90 × 70 mm); 185 (92 × 48 mm); 95 (70 × 36 mm)</i>
8	210	1266	248
9	230	1530	493
10	240	1710	357
11	240	0	0
		Sum 7610 wasp cells	Sum 1098 + 1 wasp brood

Nest Architecture: Bees

The bee entrance pointed away from the nest and toward the apical part of the branch (Fig. 1). However, some remains of the bee wax entrance were observed on the inner part of the branch as well. The bees may have had their original entrance there. At the time of the nest dissection, the entrance was made of a dark-brown, firm, but still flexible, inflammable wax, mixed with small amounts of sand grains. The wax was not sticky, with a granular outer and inner surface. Along the branch, particularly in front of the wasp nest attachment, many small and sticky resin droplets were observed. The entrance hole measured 19 mm in width, and projected downward from the supporting branch, thus protecting the inner-side from rain. The nearly cylindrical entrance structure, attached and elevated some 12–15 mm from the branch, extended for 110 mm from the nest to the actual bee entrance (Fig. 1). The nest entrance appears to have been modified on several occasions. Several semi-circular lamellate wax folds on the entrance structure indicate that it probably had been remodeled and extended in length since it was initially constructed. Three obvious folds were visible after 6, 7, and 9 cm on the entrance tube as measured from the nest, along with several other less pronounced folds. It was also found that the previous folds suggested a wider entrance, as confirmed by comparing video recordings from the observation period. Apparently the bees would extend the distance from the wasp nest to the entrance over time and they also reduced the size of their entrance, possibly in response to aggression from the host wasps, rather than other potential enemies. The observation of the basal part of the entrance corresponds with the description by Kerr *et al.* (1967, p. 265), except that the entrance of this nest was much shorter. This may be due to the short length of time since the initial formation of the bees' nest.

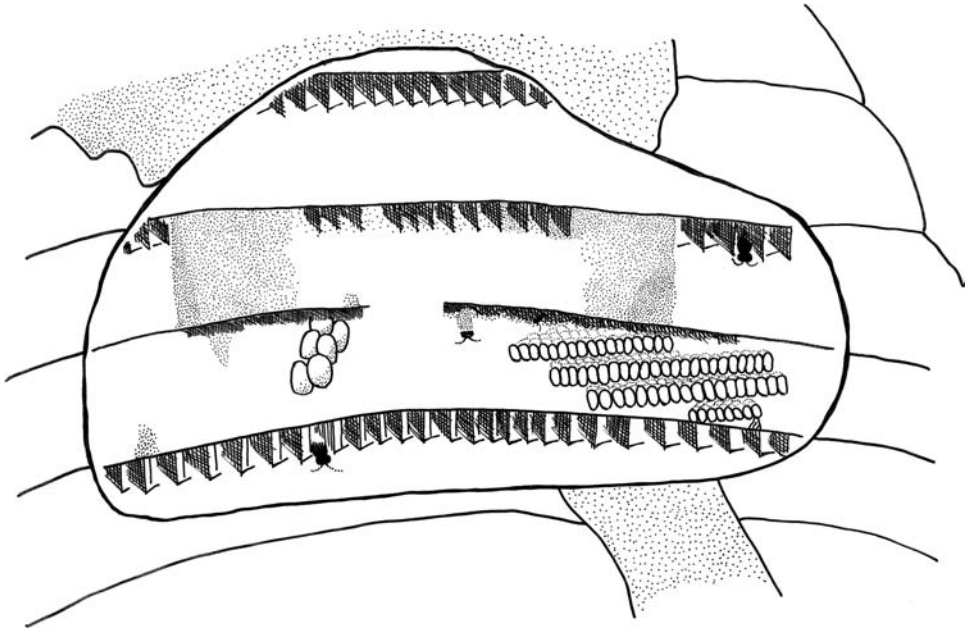


Fig. 2. A window has been opened into the bee and wasp colony. The seventh comb is partly visible with the bee brood cells. See text for details.

The light-brown entrance structure leads from the supporting branch and down over the outer surface of the wasp nest, extending 22 cm on the nest down to the seventh comb (see description below and Fig. 1). Here the bees had penetrated the protecting envelope, with an oval hole measuring 15 by 8 mm. On the inside no internal entrance tube or the like was found. In the first two weeks of observation the entrance structure on the wasp nest was more complex, and expanded over a larger area of the nest, reaching to the bottom and around to the opposite side of the nest. This structure was much larger than the actual entrance, measuring 160 mm at the broadest part, but did not penetrate any part of the nest. As further explained below, bees sometimes spread wax on the nest surface before penetrating the host nest.

To avoid wasps entering from below the seventh comb, the bees had sealed the 3 mm wide entrance to the lower combs with wax. On the wasp's side the wax had been covered again with pulp by the wasps. This well sealed nest made it unnecessary for the bees to construct a supporting and protecting batumen comb, as reported by Kerr *et al.* (1967) for an *Azteca* ant nesting colony of *T. cilipes*.

The bees had modified the design of the original seventh comb constructed by the wasps, by eliminating all wasp brood cells, leaving only a few mm from the base of the majority of the cells and completely covered 95 remaining cells with wax to avoid the emergence of further wasps inside the newly occupied nest (Fig. 2). The inner surface of the seventh comb had been adhered with wax, in particular the outer wall, and to a lesser extent the floor and roof. A few wax deposits were also observed, along with more than 20 dead wasps nearly covered with wax on the floor. Many species of stingless bees pacify exotic insects and avoid their fungal decay in their nest, by covering them with wax if they are too large to be carried away (pers. obs.).

The brood chamber of the bees included five brood combs with 724 bee larvae, and was not protected by any additional involucrum, other than the protecting envelope of the wasp nest. It was not possible to recognize any helix formation of the bee brood combs. Surrounding the brood chamber of the bees and attached to the roof, were five storage pots of honey and several with pollen. However, the precise number was difficult to estimate as the bees had constructed a complex wax structure along with their storage pots. The sixth wasp comb was also occupied by the bees, but not completely as they had only enclosed an area of approximately 114 by 96 mm (Fig. 2, Table 1). Communication to the main seventh wasp comb was through a hole of approx. 55 by 36 mm. The bees likely constructed this hole because the bee brood extended up through the hole, suggesting that the bees made the hole to enlarge their brood chamber. Another smaller hole of approx. 40×21 mm at the sixth wasp comb, had been constructed, and then later again partly covered with bee wax. This appears to have been the location for the original wasp passage hole, enlarged and used by the bees after the occupation. All wasp brood cells were still complete at the sixth floor, though the cells inside the bee enclosure had been closed with wax by the bees. Outside this area the wasps continued to emerge from their cells. The content of all bee combs are summarized in Table 1.

Behavioral Observations

The wasps walked all over the outside of the bell-shaped nest, including toward the bee entrance on the supporting branch. Usually the wasps walked on the nest in circles with vibrating wings, or would make aggressive movements toward the bee entrance. Some wasps touched the bee wax on the nest with their mouthparts, either biting or constructing pulp to cover the bee wax. The different colored wax entrance structure was conspicuous on the entire outer surface of the wasp nest when the nest was first discovered. However, on February 21 the entire entrance structure on the nest had been covered externally with fresh pulp by the wasps and was no longer distinguishable from the remaining nest surface. Upon covering the bee wax with pulp the wasps were observed less frequently on the outside, and no longer stood aggressively near the bee entrance.

During all observation periods, the guard bees remained near their nest entrance, and a number of bees stood along the margins of the entrance vibrating their wings or flying slowly around the entrance. Nocturnal observations revealed that the bees would seal off their entrance with wax, while the wasps remained alert inside the nest and arrived on the outer surface at disturbance. During early observations, a large number of male bees swarmed in front of the colony. They may have been in the process of either swarming away from the colony, or more likely were awaiting the arrival of the queen from the mother nest.

Upon dissecting the nest, only a few adult wasps were found in the lower combs (11–8) occupied by the wasps. In the above two combs occupied by the bees, only the gravid bee queen was still in the nest. In contrast, the fifth and sixth combs above the bees were filled with dead adult wasps. From the sixth comb 26 mature wasps ready to emerge were found. They had removed the cell cap, but were trapped inside the cells, presumably because the large number of dead wasps piled up in the sixth comb made it impossible to emerge. From these combs only one sealed cell with a near mature wasp was found out of a total of 3104 cells (<0.1%). Likely, the bees had sealed off the sixth comb efficiently, making it impossible for the wasp-queen to enter these combs and reuse the brood-cells, thus leaving emerging wasps to die as no other exit holes were found in these combs.

Discussion

Apparently the bees only recently appeared in the nest, as inspection with binoculars four months earlier in October 2002 revealed no entrance structure. The size of the bee brood was small, compared to that described in the literature, suggesting that the colony may have been recently established. Wille and Michener (1973) found between four to ten combs of *Trigona cilipes*, while this nest had only five small combs. In contrast, the size of the *Epipona* nest suggests that it was of a mature size (West-Eberhard, pers. comm.; Wenzel, 1998). The wax structure on the surface of the nest was constructed by the bees initially, evidently to protect them from the nest-defending wasps while establishing the bee colony. Apparently, the wasps did not get stuck on the wax, nor did they attempt to walk over it. A large part of the waxed surface was not in use at the time of the dissection of the nest, and may have been from initial failed attempts to penetrate the nest envelope, or was used by the bees while scouting for an appropriate entrance site into the nest. A somewhat similar case of a *T. cilipes* nest under establishment in an *Azteca* ant nest was studied by J.M.F. Camargo in Brazil (pers. comm.), who found that the bees first built the entrance tube using sticky resins attached to the ant nest, and then gradually opened a gallery into the nest while sealing the opened area with resins. The same colonization procedure has also been reported for termite-nesting *Scaura latitarsis* by Camargo (1984) and ant-nesting *Sundatrigona moorei* (Schwarz) (Apidae) by Sakagami *et al.* (1989).

Once inside, after biting a hole through the nest-envelope, the bees apparently fought with the wasps, as indicated by the dead and wax-covered wasps in the bee part of the nest. Less than 0.1% of the brood cells contained immature wasp brood in the combs (1–5) above the bees, compared to 24.4% below (combs 8–11, Table 1) the bees, suggesting wasps were emerging only in these combs. On the outside of the nest, the wasps were not aggressive toward the bees, either because they accepted the presence of bees or because the wasp population had perhaps declined due to the occupation and fight inside their nest.

For *T. cilipes*, which is usually found nesting with *Azteca* ants, the behavioral flexibility that enables them to also colonize wasp nests results in several advantages that may favor wasp associations. First, the *Epipona* and most other perennial tropical paper wasps provide a protected environment (Evans and West-Eberhard, 1970). However, *Azteca* ants would also provide protection, but may require constant vigilance, unlike the *Epipona* that seems only to defend its nest in the initial phase of the colonization. Second, the bees need much less excavation in the wasp nest than in that of *Azteca* for expanding their brood chamber. In this case comb one to six were readily available without further stressing the wasp hosts, as these combs were no longer used by the wasps due to the presence of bees. Third, this opportunistic nest behavior enables *T. cilipes* to occupy a wider range of nest sites than otherwise possible if *Azteca* colonies may prove to be scarce or too aggressive and expensive to colonize.

Therefore it is tempting to speculate that beside the ant and termite nesting sibling species *T. cilipes* and *T. mazucatoi*, a third—wasp nesting—specialist could arise from this interaction. If such behavioral plasticity as described above is common in the stingless bees, it could also explain some of the diverse nesting behavior found with stingless bees in general (Michener, 1959; Wille and Michener, 1973; Camargo and Roubik, 1991; Camargo and Pedro, 2003), as well as form the base for speciation events of stingless bees. Additional biological observations and detailed collection of comparative nesting biology data of the stingless bees could reveal more about the frequency and importance of behavioral plasticity for the evolution of stingless bees.

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