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A review of the nest-entrance lurkers of meliponine bees (Hymenoptera: Apidae)

Gerardo Quintos-Andrade[1]

Abstract. Stingless bees (Tribe Meliponini) are a group of considerable biological, economic, and cultural value. Despite their significance, information about their natural enemies remains limited, particularly regarding animals that lurk at the hive entrances and prey on bees entering and exiting the colonies. This study reviews the literature documenting these interactions. A total of 15 publications were compiled, detailing 41 records of 33 different organisms acting as nest-entrance ambushers. In addition, the mantid *Acontista cordillerae* Saussure & Zehntner (Mantodea: Acanthopidae) is reported for the first time ambushing bees at nests of *Scaptotrigona mexicana* (Guérin-Meneville) in a meliponary in central Veracruz, Mexico. The dynamics among the ambush predators and other social bees are discussed, including their defense strategies and nest structures.

Resumen. Las abejas sin aguijón (Tribu Meliponini) son un grupo de interés debido a su valor biológico, económico e histórico. A pesar de dicha relevancia, existe poca información sobre sus enemigos naturales, principalmente aquellos animales que acechan en las piqueras y depredan a las abejas que entran y salen de las colmenas. El presente estudio es una revisión de la literatura que menciona datos sobre esta interacción. En total se recopilaron 15 trabajos, que muestran 41 registros de 33 organismos diferentes que interactúan como acechadores de piqueras. Además, se reporta por primera vez al mantoideo *Acontista cordillerae* Saussure y Zehntner (Mantodea: Acanthopidae), acechando en nidos de *Scaptotrigona mexicana* (Guérin-Meneville) en un meliponario del centro de Veracruz, México. Se discute la dinámica de depredadores en otras abejas sociales, abordando sus estrategias de defensa y estructura de sus nidos.

INTRODUCTION

Meliponines are one of the most charismatic groups of bees in tropical regions. Commonly known as stingless bees or native bees, they are notable for their eusocial lifestyle, relatively easy management, and deep historical significance across diverse social contexts. These characteristics have greatly stimulated research on this group (Zamudio & Hilgert, 2015; Quezada-Euán *et al*., 2018; Grüter, 2020; Mduda *et al*., 2023). Morphologically, meliponines are characterized by females with corbiculae on their hind legs equipped with a penicillium, reduced wing venation, and a vestigial or atrophied sting, features that give rise to their distinctive common name (Ayala, 1999). Throughout history, stingless bees have been closely associated with various Indigenous peoples due to their honey production, resulting in diverse techniques for managing colonies and harvesting honey non-invasively, forming a culture grounded in the sustainable use of these bees (Reyes-González *et al*., 2014; Contreras-Cortés *et al*., 2020; Aldasoro-Maya *et al*., 2023; Delgado *et al*., 2023; Roubik, 2023).

[1] Red de Ecología Funcional, Instituto de Ecología AC, Carretera Antigua a Coatepec 351, El Haya, 91073 Xalapa, Veracruz, México (gerardquintos@gmail.com)

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The literature on stingless bees documents numerous organisms that attack colonies, ranging from predatory mites that enter hives through phoresy to large mammals that destroy nests to consume the larvae or the stored honey (Kajobe & Roubik, 2006; Menezes *et al*., 2009; McLennan, 2014; Dubale & Desha, 2022; Martínez *et al*., 2024). Interest in these predator-prey interactions has recently gained attention with the introduction of the term "Meliponophagy", which refers to spiders whose diet consists largely of stingless bees (Razakamiaramanana *et al*., 2025). This concept was developed from observations of the jumping spiders *Menemerus bivittatus* (Dufour) and *Plexippus petersi* (Karsch) (Araneae: Salticidae) preying on *Liotrigona* Moure and *Hypotrigona* Cockerell in Africa. These spiders generally lurk near the nest entrances, capturing bees as they arrive or depart.

Relatively few records exist of animals that act as nest-entrance lurkers. These animals, mostly arthropods, position themselves near the access tube to capture bees as they enter or exit (Fig. 1). This strategy ensures a higher capture rate for the predator, although it also makes it vulnerable to potential attacks from the hive's guard bees (Gopinatha & Basavarajappa, 2022). Few authors have described this behavior over an extended period (Nogueira-Neto, 1997; Jaapar *et al*., 2018; Gopinatha & Basavarajappa, 2022), leaving a substantial knowledge gap regarding the diversity and ecological significance of these lurking organisms. As a result, no clear concept or framework exists for this behavior. This study aims to open a field of study on nest-entrance lurkers in meliponines by providing a list of known organisms exhibiting this behavior, integrating a new report of this interaction, and discussing potential study areas.

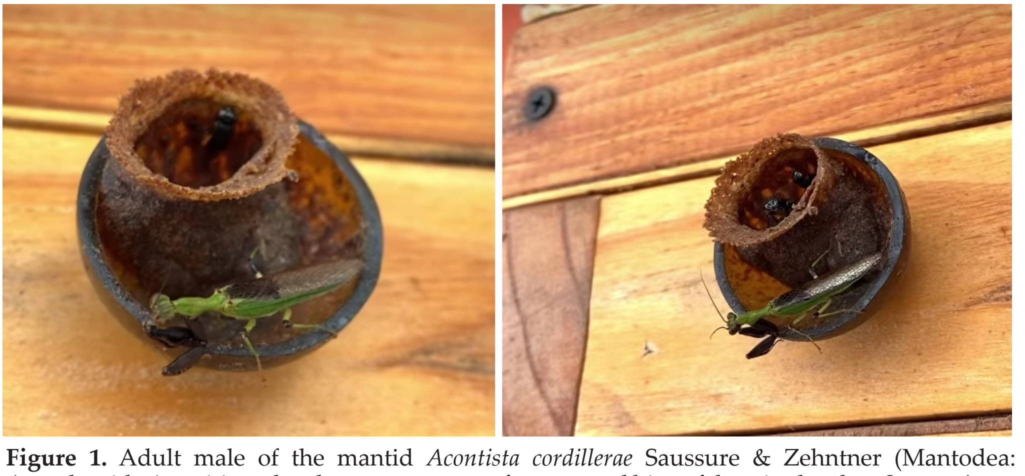

Figure 1. Adult male of the mantid *Acontista cordillerae* Saussure & Zehntner (Mantodea: Acanthopidae) positioned at the nest entrance of a managed hive of the stingless bee *Scaptotrigona mexicana* (Guérin-Meneville). The hive entrance had a plastic bottle mouth, which likely limited the mantis' ability to capture bees. Guard bees are visible inside the hive's entrance tube in both images. Photos by Nahum (Meliponas en la Azotea).

MATERIAL AND METHODS

Report of *Acontista cordillerae* Saussure & Zehntner (Mantodea: Acanthopidae)

The interaction of the mantis *A. cordillerae* as a nest-entrance lurker was documented from an observation made on November 13, 2023, in a meliponary located in the central area of Xalapa, Veracruz (19.5335, -96.9333). The specimen was an adult male found at the entrance of a *Scaptotrigona mexicana* (Guérin-Meneville) nest, whose hive entrance was covered by a bottle mouth, making it difficult for the mantis to capture bees (Fig.

1). The mantis remained near the entrance for approximately two hours, although it was not subsequently recorded whether it succeeded in capturing any bees.

Literature Search for Hive Entrance Lurkers

A literature search was conducted using Google Scholar with the following terms: Predators Meliponini; Predation Meliponini; Prey entrance Meliponini; Hemiptera Meliponini; Asilidae Meliponini; Lizard Meliponini; Mantodea Meliponini; Predation stingless bee; Spider Meliponini; Salticidae Meliponini; Vespidae Meliponini. This search yielded articles and books mentioning organisms lurking at hive entrances. These records were taxonomically classified and compiled along with the preyed meliponine species, and locality.

RESULTS

A total of 15 studies were found, documenting 41 records corresponding to 21 identified species and 12 unidentified species of nest-entrance lurkers (See Table S1, Supplemental Material). These organisms belong to the orders Araneae, Anura, Diptera, Hemiptera, Hymenoptera, Mantodea, and Squamata. Araneae and Hymenoptera include the greatest number of lurkers, with the most frequently reported species being the gray wall jumping spider *M. bivittatus* and the vespid wasp *Polybia ignobilis* (Haliday), each documented in four records.

DISCUSSION

Meliponini is not the only group of social bees, so this phenomenon is not restricted to the predators of this tribe. However, this study focused exclusively on meliponines due to the available number of records. Other bees, such as *Apis* Linneaus, *Bombus* Latreille, or social halictids, show few or no records of this interaction (Ono *et al*., 1987; Wcislo & Schatz, 2003; Wcislo *et al*., 2004). Additionally, meliponine hive entrances are exposed, allowing lurkers to position themselves more strategically. Fewer records may exist for other bees because they can sting predators. In the case of *Bombus*, their nests are subterranean with hidden entrances; known predators include beewolves *Philanthus* Fabricius (Philanthidae) and sphecid wasps (Sphecidae), and there are also reports of conopid flies parasitizing workers, but it is unknown if these attacks occur by strategically lurking at the nest entrance (Dukas, 2005; Hines *et al*., 2007). For *Apis*, the most well-known predators are hornets of the genus *Vespa* Linnaeus, which often wait near nest entrances to attack workers. Some species, such as *Apis cerana* Fabricius, have evolved defensive behaviors, including forming swarms that surround the hornet and suffocate it to death (Ono *et al*. 1987; Koeniger *et al*. 1996; Tan *et al*. 2007).

Meliponines interact dynamically with different lurkers, which may attack at particular times and in specific temporal patterns. For instance, Jaapar *et al*. (2018) found 11 different lurkers in the nests they observed, suggesting that while this strategy can increase capture success, the predators are not specialized and do not rely exclusively on meliponines. *Menemerus bivittatus*, for example, has a broad diet primarily composed of lepidopterans and dipterans, yet multiple reports across countries show a clear affinity for hunting meliponinos (Chaubey *et al*., 2019; Trindade-Santos *et al*., 2023; Razakamiaramanana *et al*., 2025). Similarly, *Polybia ignobilis* has been observed hunting carrion flies and lepidopteran larvae (Gomes *et al*., 2007; Filho *et al*., 2009), but Boff & Alexandre-Somavilla (2024) documented repeated stalking and multiple successful captures at nests of *Tetragonisca angustula* Latreille, suggesting a more consistent lurking strategy in this species. For hemipteran lurkers, although records are few, there is a tendency to find these insects near hive entrances, flowers, or tree resin deposits also visited by meliponines (Wattanachaiyingcharoen & Jongjitvimol, 2007). Among vertebrates, only the listed lizards and amphibians could be considered lurkers (Table S1), as they were observed watching the hive entrance, unlike birds or mammals that attack without lurking or end up opening and destroying the hives (Vyas, 2012; de Melo & Nogueira, 2020; Roubik, 2023).

Meliponines have a significant cultural and social impact on humanity. We know diverse aspects of their behavior, genetics, production, and evolution, and there is a relatively stable consensus on their taxonomy (Hrncir *et al*., 2016; Grüter, 2020; Engel *et al*., 2023). However, interactions such as predation, parasitism, and the nest-entrance lurking behavior reported here remain understudied. Future research could address questions related to the impact of these predators on meliponine populations, predation frequencies, defensive strategies used by bees, and the potential economic consequences of lurkers.

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SUPPLEMENTAL MATERIAL

Table S1. Summary of documented nest-entrance lurkers of Meliponini reported in the literature.

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