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First report of hovering guard bees of the Paleotropical stingless bee *Tetrigona apicalis* (Hymenoptera: Apidae: Meliponini)

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Abstract – For eusocial bees, colony defense is paramount. An uncommon strategy is the deployment of hovering guard bees, which has been previously described for only a few species of Neotropical meliponines. This report describes the use of flying guards for the Paleotropical stingless bee species *Tetrigona apicalis* (Smith) which is the first known species in the region to incorporate this defense strategy. The first appearance of hovering guards occurs ca. 0800, and the number of guards increases until an assemblage of ca. several to 25 guards is formed within an hour of the first appearance of a flying guard. The cloud of hovering guards remains throughout the day until dusk and has a continuous presence unless interrupted by rain. The group hovers in front of the entrance tube out to a distance of 10 to 35 cm with the guards facing the entrance tube. The length of time an individual hovering guard bee spends in flight averaged 17 min 52 s ± 18 min 2 s. The longest hovering flight was 1 h 48 min 46 s. This compares to a reported guard flight time of ca. 58 min for the Neotropical meliponine *Tetragonisca angustula*, the only other stingless bee species where flying guard flight times have been investigated.

flying guard bees / *Tetrigona apicalis* / length of hovering flight

1. INTRODUCTION

Meliponini (stingless bees) are the largest taxon of social bees with known 556 described species (Rasmussen and Gonzalez 2013). For social bees, colony defense is paramount, and stingless bees have evolved numerous strategies to protect nests from predators and parasites. Various stingless bee nest defenses are reviewed by Roubik (2006). An infrequent defense mechanism is the incorporation of aerial guard bees, and only a few stingless

bee species are known to utilize this strategy. Two Neotropical species, *Tetragonisca angustula* Latreille and *Tetragona clavipes* F., are known to employ flying guards (Roubik 2006; Wittmann 1985; Zeil and Wittmann 1989). The Paleotropical stingless bee *Tetragonula carbonaria* Smith is known to utilize defensive swarms during usurpation and robbing events that are reported to last for days or even weeks (Gloag et al. 2008), but this is separate from employing a continuous group of hovering guards.

Of the ca. 90 described stingless bee species in SE Asia (Rasmussen 2008), none has been reported to employ a permanent flying guard bee cadre. The result of an intensive literature review fails to find any previous mention of the use of flying guards by *T. apicalis*; therefore, this is the first

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declaration of the phenomenon for this species. *Tetrigona apicalis* was first described by Smith (1857) as *Trigona apicalis* from material originally provided by A.R. Wallace from Borneo. The species is widely distributed throughout its SE Asian and Indo-Malayan/Australasian range (Rasmussen 2008). *T. apicalis* is a medium-sized bee with bicolorous wings and a body length of 5.5–6 mm. *T. apicalis* nests normally occupy tree cavities but they are known to advantageously utilize anthropogenic cavities, i.e., wall voids (Burgett, personal observation). *T. apicalis* nest entrance tubes are stereotypically elongate and in the form of a flattened trumpet bell. In mature colonies, entrance tubes are ca. 15 to 25 cm in length and comprised almost entirely of hardened plant resins. The Neotropical species *Tetragonisca angustula* is known to use both flying guards and stationary guards immediately inside and outside of the nest entrance tube. These separate groups of both stationary guards just interior to the nest entrance and the hovering guards are felt to complement each other (Karcher and Ratnieks 2009; Grüter et al. 2011) in intruder defense and recognition of conspecific nest mates. Guards of *T. angustula* have been shown to be morphologically distinct from forager bees and are designated as a specialized major caste (Grüter et al. 2012).

The length of hovering flight time for guard bees has been inadequately addressed. Wittmann (1985) discussing *Tetragonisca angustula* states that labelled guards were observed hovering for more than 70 min. Grüter et al. (2011) also reporting on *T. angustula* state an average hovering time of 56.7 ± 1.51 min. Additionally, they comment that individual flying guards interrupt their flight with a 3.3-min hive return before recommencing flight. Our work reports on hovering flight times of *T. apicalis* guards as observed in Northern Thailand.

2. MATERIALS AND METHODS

One of the *T. apicalis* colonies used for observations was recovered from a discarded armoire that had been thrown from a 2nd story dormitory balcony on the Chiang Mai University campus (Chiang Mai province, Northern

Thailand) in mid-January of 2018. We rehoused the colony into a wooden domicile with an internal volume of 26.46 L and kept it in situ on the dormitory balcony for 7 days allowing the bees to readjust to the new nest cavity. The colony was then relocated in the evening to a meliponary adjacent to the Chiang Mai University Postharvest Technology Research Center ca. 2 km from its original location. At this location were an additional 10 stingless bee colonies composed of *Tetragonula laeviceps* (Smith), *Tetragonula fuscobalteata* (Cameron), and *Lepidotrigona flavibasis* (Cockerell). The *T. apicalis* colony was placed on a stand at a height of 25 cm above ground level. A single 5-mm diameter hole, 10 cm from the base of the domicile, provided the only ingress/egress for the bees. The morning following relocation, the colony recommenced foraging flights and flying guards appeared 24 h later. As this colony had undergone the trauma of dislocation and rehousing, the number of flying guard bees was initially quite small (1–3 individual bees) and the construction of an entrance tube took several months. For our observation in January of 2019, an entrance tube ca. 6 cm in length had been formed. This turned out to be quite advantageous as tracking individual guard flights was made easier because of the reduced number of flying guards. No attempt was made to tag the individual guards.

To assess flying guard flight times, we initiated a video record using a GoPro 1080P sports camera set ca. 40 cm from the nest entrance with a visual field of ca. 75×75 cm parallel to the side of the colony. White cardboard panels were set 1 m opposite the camera view to facilitate viewing guard bee flight. Flight video records of the hovering guards were undertaken in February and March of 2018 and January of 2019. Daily videos commenced at 0800 h and ceased at 1700 h during 13 non-contiguous days of observation. As a quality check, every 10th flight time was recalculated by a second observer.

Two additional *T. apicalis* colonies nesting in situ in tree cavities (*Ficus religiosa* L.) were used for observations concerning guard hovering behavior.

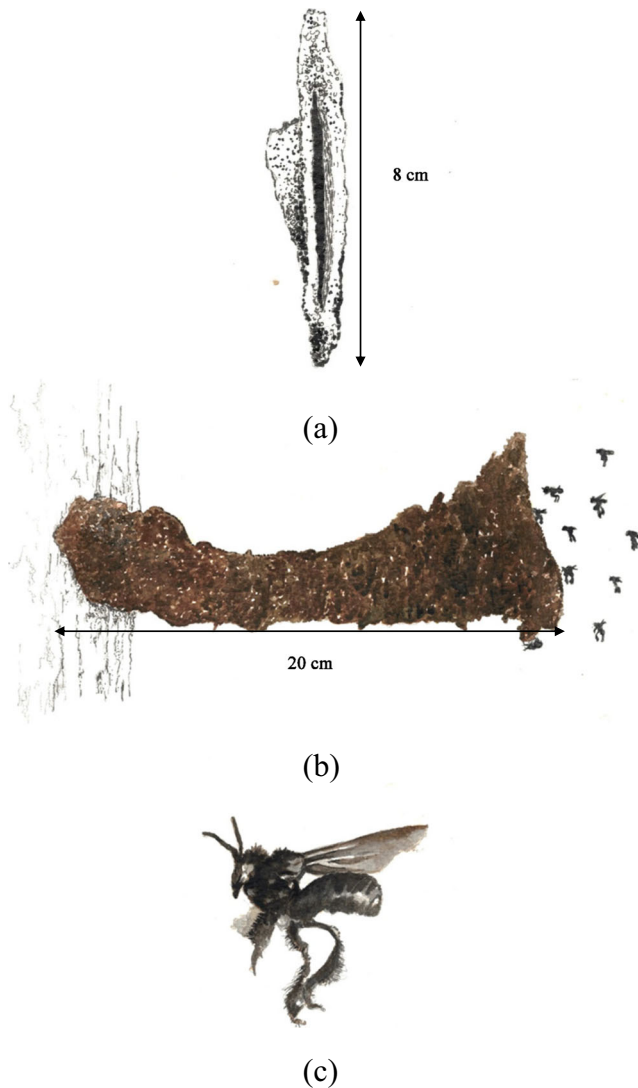


Figure 1 Bio-illustration of a stereotypic *Tetrigona apicalis* nest entrance. **a** Nest entrance front view. **b** Nest entrance side view with hovering guard bees. **c** Flight posture of a hovering guard.

3. RESULTS

During diurnal flight periods, a cadre of several to 25 flying guard bees hovers 10–35 cm in front of and to the sides of the entrance tube opening, oriented with their heads facing the nest entrance. This cloud of hovering guards is slow moving and can shift both laterally and vertically. Individual hovering guards will move short distances in response to the exit and return of forager

bees. Figure 1 illustrates a stereotypic colony entrance.

Figure 2 displays the observed flights classed by 10-min intervals. Eighty percent of observed flights were between 1 and 30 min in length. Seven of the 203 observed flights (3.4%) were greater than 1 h with the longest flight at 1 h 48 min 46 s. The average length of flight was 17 min 52 s \pm 18 min 2 s (SD). Hovering flights of ≤ 1 m were not included in

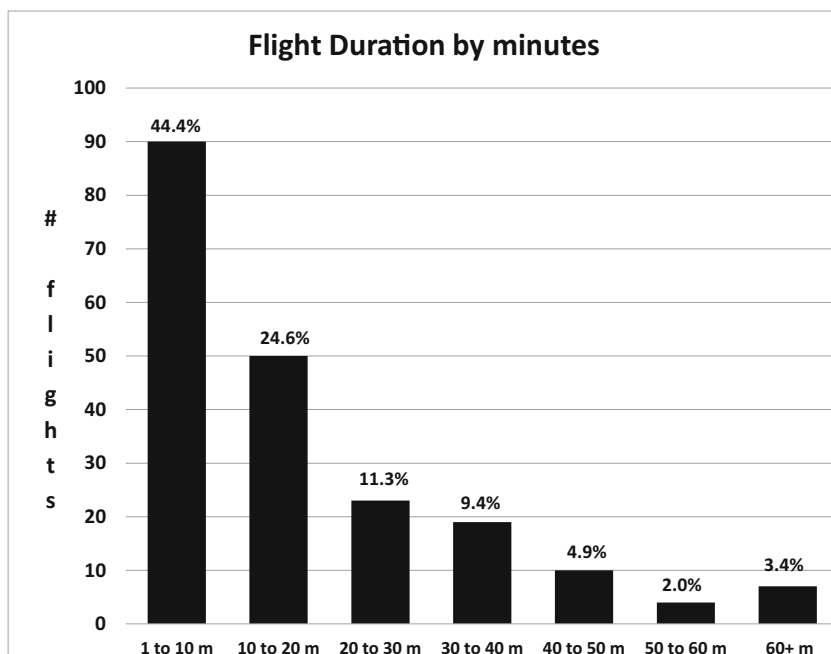


Figure 2 Hovering *Tetrigona apicalis* aerial guard flights classed by 10-min periods. Percent of total flights ($n = 203$).

determining the average flight time as these could have been new forager orientation flights. Figure 3 displays all observed flights in a scatter plot from the shortest to the longest in seconds.

4. DISCUSSION

The use of flying guards must certainly be energetically expensive for a stingless bee colony and is only known to occur in a small

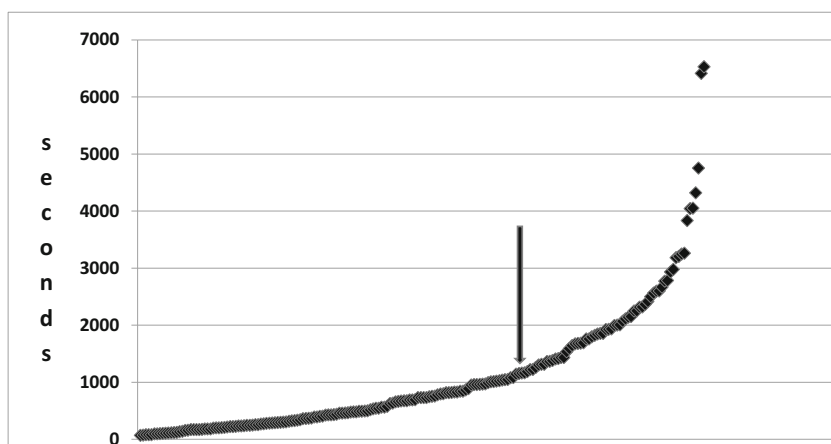


Figure 3 All hovering flights from the shortest to the longest in seconds ($n = 203$). Arrow denotes average flight time (1072 s).

number of the ca. 560 described meliponine species. The question arises as to efficacy of this defense strategy. The best studied species of the meliponines utilizing flying guards is *Tetragonisca angustula*. Van Zweden et al. (2011) in a review of the multiple defense mechanisms of *T. angustula* hypothesized that predation by conspecifics and allospecifics, especially the obligate robber stingless bee *Lestrimelitta limao* (Smith), has brought about, as they state, "... one of the most sophisticated guarding systems known amongst social bees." The 56.7-min average hovering time of *T. angustula* flying guards reported by Grüter et al. (2011) is three times the length of *T. apicalis* hovering guard flights (17 min 52 s) that we report here. Our flight time observations come from a single colony that had undergone the stress of being rehived and relocated, which in all likelihood reduced the adult bee population. That said, the colony demonstrated foraging activity and the appearance of a small group of flying guards within 24 h of relocation which we believe is an accurate reflection of normal colony behavior.

In our 104 h video record of *T. apicalis*, we never observed a defensive response by a hovering guard bee even though numerous instances were seen where allospecifics, most often *Tetragonula laeviceps*, flew within centimeters of the nest entrance in the presence of hovering guards. We did not see however any instance where an allospecific attempted to enter the colony itself, which may account the lack of a defensive response on the part of *T. apicalis* aerial guards. We were unable to identify stationary guard bees just interior to the nest entrance in observations of two additional *T. apicalis* colonies suggesting that this species would appear to rely on hovering guards as the main nest entrance defense strategy.

Grüter et al. (2012) have shown that the stationary and flying guards of *T. angustula* differ in weight and morphology from foragers and designate the guards as a distinct physical caste. Previous to the work of Grüter et al., one could assume that guarding is part of a temporal polyethism continuum. Whether such is the case with *T. apicalis* is unknown but very worthy of further investigation.

No specialist predators of *T. apicalis* are reported from the limited literature on this species. It remains unclear as to why this singular SE Asia meliponine has evolved a flying guard bee defense, and we anticipate further studies to clarify the role of *T. apicalis* aerial guards

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AUTHORS' CONTRIBUTION

MB and BC conceived the research. PS and JY performed the bulk of the observations and video review of flight times and interpretation of data. MB and BC wrote the first draft and all authors contributed in manuscript revisions. All authors read and approved the final manuscript.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest The authors declare that they have no conflict of interest.

Premier signalement d'abeilles gardienne pour *Tetrigona apicalis* (Hymenoptera : Apidae : Meliponini).

abeilles volantes de garde / *Tetrigona apicalis* / durée du vol stationnaire.

Ein erster Bericht von Wächterbienen der stachellosen Biene *Tetrigona apicalis* (Hymenoptera: Apidae: Meliponini).

Fliegende Wächterbiene / *Tetrigona apicalis* / Länge des Wächterfluges.

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