



Ambush Predation of Stingless Bees (*Tetragonisca angustula*) by the Solitary-Foraging Ant *Ectatomma tuberculatum*

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Abstract

Social insect colonies are high-value foraging targets for insectivores, prompting the evolution of complex colony defensive adaptations as well as specialized foraging tactics in social insect predators. Predatory ants that forage on other social insects employ a diverse range of behaviors targeted at specific prey species. Here, we describe a solitary foraging strategy of the ant *Ectatomma tuberculatum*, on nest guards of the stingless bee *Tetragonisca angustula*. We observed multiple instances of *E. tuberculatum* ambushing and successfully capturing the hovering and standing guards of *T. angustula* near nest entrances. The unique hovering behavior of the guard caste of this bee species, an adaptation to frequent cleptoparasitism by other stingless bees, may make these guards particularly vulnerable to ground-based, ambush attacks by *E. tuberculatum*. Likewise, the behavior of the foraging ants appears to adaptively exploit the defensive formations and activity patterns of these bees. These observations suggest an adaptive and targeted predatory strategy aimed at gathering external guard bees as prey from these heavily fortified nests.

Keywords Sit-and-wait · bee eating · selva ant · jataí · abejas angelitas

Introduction

Predatory foraging strategies can broadly be placed into two categories based on the energy expended while looking for food: sit-and-wait versus active foraging (Schoener 1971). Social insects further vary in active foraging strategies by either foraging

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solitarily or using mass recruitment to overcome either large or numerous prey (Gotwald Jr 1995; Matsuura and Sakagami 1973; O'Donnell et al. 2005). However, such group-foraging behaviors often preclude these species from successfully preying upon a vigilant and well-defended target. Many social insects that rely on solitary stealth maneuvers have evolved behavioral strategies for overcoming this challenge (Matsuko 1984; Gronenberg 1996; Jackson and Pollard 1996; Murphy and Patek 2012). For example, *Ectatomma ruidum* are facultatively solitary foragers, enabling the use of a prolonged stealth approach to capture food items from heavily defended colonies of other social insects (Lima and Antonialli-Junior 2013; McGlynn et al. 2015; Schatz and Wcislo 1999).

Ectatomma tuberculatum hunt for a wide variety of live insects, with social insects comprising a large portion of returning forager prey items (Wheeler 1986). This apparent preference for feeding on social insects is also common in other species of *Ectatomma* (Lima and Antonialli-Junior 2013; Schatz and Wcislo 1999). Individual behavioral specialization on different foraging strategies has been demonstrated in *Ectatomma ruidum*, where foragers may preferentially perform either “typical foraging” or “thievery” (McGlynn et al. 2015). Ambush predation entails similar behaviors and may represent another valuable foraging strategy employed by a behavioral sub-caste of *Ectatomma* foragers. Though ambush predation at the nest entrances of social insects has been observed for at least one other *Ectatomma* species (Schatz and Wcislo 1999), this behavior is previously unreported at the heavily defended nests of the stingless bee, *Tetragonisca angustula*.

Social insect nests can be a high-quality resource for insectivores, selecting for strong nest defense in many species (Shorter and Rueppell 2012; Tian and Zhou 2014). Specialized nest-entrance guarding in the stingless bee *T. angustula* is also selected for by inter-colonial kleptoparasitism by both conspecific and heterospecific bees (Bowden et al. 1994; Grüter et al. 2011, 2016, 2017; van Zweden et al. 2011; Wittmann 1985; Wittmann et al. 1990). However, the environments in which these nest-guarding behaviors evolved are biodiverse and include ground-based threats as well as airborne. Colonies of *T. angustula* defend themselves from insect invaders at night by physically closing their wax and resin nest-entrance tubes (Roubik 2006). During the day, *T. angustula* colonies deploy a mixture of standing and hovering guard bees to defend the open tube when the colony is actively foraging (Hammel et al. 2016; Kärcher and Ratnieks 2009). Here we present novel observations of *E. tuberculatum* ambushing and capturing winged prey at the heavily-defended nest entrances of the stingless bee *T. angustula*. We further discuss how predation by solitary ambush predators such as *E. tuberculatum* may be an under-evaluated cost of foreign-bee nest guarding by *T. angustula*.

Observations

Ambush Tactics

Ectatomma tuberculatum foragers were observed at two nests of *T. angustula*. The first nest was located in a gap in the trunk of a tree approximately 1 m above the ground near Agua Salud, in Soberania National Park, Panama (09.217°, -79.783°), and was

observed on 17 January 2013. During a 5-min observation period, two to three workers of *E. tuberculatum* stood close to the *T. angustula* nest entrance tube (Fig. 1a). These workers stood upright (front legs extended) with their mandibles open and antennae



Fig. 1 **a** Two *Ectatomma tuberculatum* foragers in waiting posture at the nest entrance of *Tetragonisca angustula* colony in Agua Salud. **b** An *E. tuberculatum* forager gradually approaching standing guards of *T. angustula* from the side of the nest entrance in Gamboa. **c** A single *E. tuberculatum* in waiting posture near the nest entrance of the Gamboa colony. **d** A forager of *E. tuberculatum* returning to the nest while carrying a captured *T. angustula* hovering guard

raised and extended in what will henceforth be referred to as “waiting posture” (Fig. 1 a&c). All workers angled their head away from the tree trunk and one to two workers stood with heads angled toward the standing guards. During the short observation period, beginning at approximately 14:00, ants did not attack or capture bees.

The second colony was located 1.8 m above the ground in a concrete electric meter housing amidst a stand of trees along a fence line in Gamboa, Panama (09.1164°, -79.6991°), and was observed from 12 to 18 January 2018. On all days when this colony was observed, 1–2 workers of *E. tuberculatum* were within 10 cm of the nest entrance tube. Additionally, on several occasions, a third *E. tuberculatum* could be seen transiently walking on a vine approximately 15–20 cm above the nest entrance tube. These actively foraging ants would approach the nest gradually, then stand for minutes to hours within a few centimeters of the *T. angustula* nest entrance tube with open mandibles, antennae extended, and heads angled upwards towards the flying hovering guards or nearby standing guards. If a passing hovering guard neared one of these ants in waiting posture, the ant would lunge forward, rapidly closing its mandibles. Twice on 12 January and twice on 13 January, *E. tuberculatum* were observed slowly approaching and making contact with the wax and resin nest entrance tube in an apparent attempt to retrieve one of the standing guards on the exterior of the tube. Most of these attempts were unsuccessful due to the evasion of *T. angustula* standing guards, as they temporarily retreated into the nest or to the other side of the tube in response (Fig. 1b).

Prey Capture

We observed four successful prey capture events at the Gamboa colony; two of guarding bees, one of a forager, and one scavenging of a dead bee.

At 17:20 on 12 January 2018, two *E. tuberculatum* workers had been intermittently standing near the entrance tube for over 30 mins when a *T. angustula* hovering guard landed near the nest entrance tube and then proceeded to walk towards the two ants. The nearest ant ran towards the guard bee and grasped hold of its thorax. This was quickly followed by the *E. tuberculatum* stinging the guard bee twice, immobilizing it, and then retreating with this captured prey (Fig. 1d).

At 11:30 on 15 January 2018, during a period of heightened flight activity near the entrance of the *T. angustula* nest, the entrance tube was being patrolled by approximately 10 hovering guards. A lone *E. tuberculatum* worker in waiting posture approximately 1.5 cm from the nest tube began lunging and biting at the hovering guard bees. Eventually, one hovering guard strayed too near to the waiting-postured ant and was grasped by the thorax, stung, and carried away.

At 13:40 on 18 January 2018, a *T. angustula* forager was blown to the side of the nest entrance tube by a sudden gust of wind while returning to the colony, causing increased proximity to the wall beside the tube. A nearby *E. tuberculatum* worker in waiting posture lunged forward, grasped the forager out of the air, then proceeded to sting and carry away the immobilized bee.

At 11:08 on 15 January 2018, a lone *E. tuberculatum* forager approached the nest entrance tube, which was devoid of standing guards at the time. The ant antennated the tube at its base, rapidly locating and retrieving a single dead *T. angustula* hanging from the side of the tube. We speculate that this dead bee was incompletely removed from the nest by an undertaker.

Diurnal Foraging Pattern and Success Rate

To quantify ant and bee activity at the Gamboa colony, we recorded the number of *E. tuberculatum* and *T. angustula* present every two hours from 08:00 to 18:00 on 12 January 2018, and from 07:00 to 21:00 on 13 January 2018. *Ectatomma tuberculatum* presence at the nest coincided with mid-day peak diurnal *T. angustula* activity, with foraging ants reliably appearing at the stingless bee nest entrance from 11:00 to 15:00 each day. However, only one or two *E. tuberculatum* were present within 10 cm of the stingless bee nest entrance at any given point in time.

We also recorded four hours of high resolution video of the Gamboa colony nest entrance from 11:00 to 13:00 on 15 January 2018 and from 12:18 to 14:18 on 18 January 2018. *Ectatomma tuberculatum* foragers were within 10 cm of the nest for a total of 1.84 h out of this 4 h of observation. Ants were only observed in waiting posture within 10 cm of the nest. Length of time an individual spent motionless in a single waiting posture position varied from 49 s to 28 mins, with average waiting posture duration of 6.77 mins. 1.69 cumulative hours across ants was spent motionless in waiting posture, resulting in the capture of 3 prey items (1 scavenged dead bee, 2 aerial live captures; the fourth capture was observed but not video recorded). We therefore observed a success rate of approximately 1 live bee capture per every 50.8 min an ant spent in waiting posture.

Following the end of these observations, we paint marked two *E. tuberculatum* foragers seen simultaneously in waiting posture at the Gamboa *T. angustula* nest entrance using oil-based paint pens (Sharpie®). We observed only unmarked ants foraging at similar mid-day frequencies on three subsequent days, indicating either that our markings did not persist, or that foraging at this one stingless bee nest was accomplished by groups of *E. tuberculatum* larger than two.

Lack of Threat Detection by Bees

We never observed a stingless bee attacking *E. tuberculatum*. However, on 15 January 2018 at 11:00, we observed standing guards avoid contact with an approaching *E. tuberculatum* forager at the nest entrance. As the foraging ant contacted the base of the nest entrance tube, 4 standing guards on the side of the tube near the ant either retreated into the nest or moved to the other side of the tube. Application of a freeze-killed *E. tuberculatum* to a naïve colony elicited a behavioral response in only one of two colonies tested. In the case of the responsive colony, two standing guards retreated into the nest following contact of the dead *E. tuberculatum* with the tube. However, a similar proportion of bees retreated into the nest of the reactive colony when the nest tube was contacted with a bit of wire or forceps. This did not suggest olfactory recognition of ant *E. tuberculatum* threat so much as response to vibrational disturbance of the nest tube.

Interpretations and Implications

Defense tactics of *T. angustula* are adapted to identify and neutralize aerial nest-invasion threats, presumably due to nest robbing by conspecifics as well as various

other species (Grüter et al. 2011, 2017). However, by sending in ambush parties in small numbers, and by attacking guard bees rather than attempting nest invasion, *E. tuberculatum* ambush predators appear to go relatively undetected. The behavior represents a potentially important cost to nest guarding for *T. angustula* and is an especially effective strategy for *E. tuberculatum* foraging at stingless bee nests.

The foraging of *E. tuberculatum* at nest entrances of *T. angustula* appears to be generally a low-cost strategy. While standing in waiting posture for long periods of time is not an overtly energetically expensive behavior, time investment of individual *E. tuberculatum* workers is substantial. However, it may be advantageous for a small number of unoccupied foragers to wait at social insect nest entrances for infrequent but high pay-offs as opposed to similarly standing still within the nest. Additionally, although *E. tuberculatum* is reported to be a predominantly nocturnal forager in the region of this study (McCluskey 1987; Wheeler 1986), we observed diurnal predation that coincided with bee flight activity. This pattern suggests that *E. tuberculatum* feeding at *T. angustula* nests is unlikely to be the result of an opportunistic encounter, and instead likely represents a targeted foraging strategy.

This time investment in solitary ambush foraging for social insect prey is not without precedent in the genus *Ectatomma*. For example, *Ectatomma ruidum* foragers that similarly wait at nest entrances of the sweat bee *Lasioglossum umbripenne* have approximately a 35% success rate per hour (Schatz and Wcislo 1999), substantially lower than the hourly success rate estimated here. Even so, sweat bees make up as much as 48% of prey intake for *E. ruidum* colonies in close vicinity of nests (Schatz and Wcislo 1999). Stingless bees may similarly be an important source of nutrition to *E. tuberculatum* colonies when available. Although *E. tuberculatum* have been observed previously in waiting posture at nest entrances of the sweat bee *Megalopta genalis* (Smith et al. 2003), there have been no previous accounts of successful prey capture, likely due to the relatively larger size of *M. genalis*. Together with our reports of *E. tuberculatum* successfully capturing both standing and flying prey at *T. angustula* nests, these observations suggest that ambush predation of tropical bee nests may represent an adaptive and highly successful foraging strategy for *E. tuberculatum* colonies.

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References

- Bowden RM, Garry MF, Breed MD (1994) Discrimination of con- and heterospecific bees by *Trigona* (*Tetragonisca*) *angustula* guards. *J Kansas Entomol Soc*:137–139
- Gotwald WH Jr (1995) *Army ants: the biology of social predation*. Cornell University Press
- Gronenberg W (1996) The trap-jaw mechanism in the dacetine ants *Daceton armigerum* and *Strumigenys* sp. *Br J Exp Biol* 199:2021–2033

- Grüter C, Kärcher M, Ratnieks F (2011) The natural history of nest defence in a stingless bee, *Tetragonisca angustula* (Latreille)(Hymenoptera: Apidae), with two distinct types of entrance guards. *Neotropical Entomology* 40:55–61
- Grüter C, von Zuben LG, Segers FHID, Cunningham JP (2016) Warfare in stingless bees. *Insectes Sociaux* 63(2):223–236
- Grüter C, Segers FHID, Menezes C, Vollet-Neto A, Falcón T, von Zuben L, Bitondi MMG, Nascimento FS, Almeida EAB (2017) Repeated evolution of soldier sub-castes suggests parasitism drives social complexity in stingless bees. *Nat Commun* 8:4
- Hammel B, Vollet-Neto A, Menezes C, Nascimento FS, Engels W, Grüter C (2016) Soldiers in a stingless bee: work rate and task repertoire suggest they are an elite force. *Am Nat* 187:120–129
- Jackson R, Pollard S (1996) Predatory behavior of jumping spiders. *Ann Rev Entomol* 41:287–308
- Kärcher MH, Ratnieks FL (2009) Standing and hovering guards of the stingless bee *Tetragonisca angustula* complement each other in entrance guarding and intruder recognition. *J Apic Res* 48:209–214
- Lima LD, Antonialli-Junior WF (2013) Foraging strategies of the ant *Ectatomma vizottoi* (Hymenoptera, Formicidae). *Revista Brasileira de Entomologia* 57:392–396
- Matsuko K (1984) Studies on the predatory biology of oriental dacetine ants (Hymenoptera: Formicidae) I. Some Japanese species of *Strumigenys*, *Pentastruma*, and *Epitritus*, and a Malaysian *Labidogenys*, with special reference to hunting tactics in short-mandibulate forms. *Insectes Sociaux* 31:429–451
- Matsuura M, Sakagami SF (1973) A bionomic sketch of the Giant hornet, *Vespa mandarinia*, a serious Pest for Japanese apiculture. Series V I Zoology Journal of the Faculty of Science Hokkaido University 19:125–162
- Murphy E, Patek S (2012) Strike mechanics of an ambush predator: the spearing mantis shrimp. *Br J Exp Biol* 215:4374–4384
- McGlynn TP, Graham R, Wilson J, Emerson J, Jandt JM, Jahren AH (2015) Distinct types of foragers in the ant *Ectatomma ruidum*: typical foragers and furtive thieves. *Anim Behav* 109:243–247
- O'Donnell S, Kaspari M, Latke J (2005) Extraordinary predation by the Neotropical Army ant *Cheliomyrmex andicola*: Implications for the evolution of the Army ant syndrome. *Biotropica* 37:706–709
- Roubik DW (2006) Stingless bee nesting biology. *Apidologie* 37:124–143
- Schatz B, Wcislo WT (1999) Ambush predation by the ponerine ant *Ectatomma ruidum* Roger (Formicidae) on a sweat bee *Lasioglossum umbripenne* (Halictidae). *Panama Journal of Insect Behavior* 12:641–663
- Schoener TW (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369–404
- Shorter JR, Rueppell O (2012) A review on self-destructive defense behaviors in social insects. *Insectes Sociaux* 59:1–10
- Smith AR, Wcislo WT, O'Donnell S (2003) Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). *Behav Ecol Sociobiol* 54:14–21
- Tian L, Zhou X (2014) The soldiers in societies: defense, regulation and evolution. *Int J Biol Sci* 10:296–308
- van Zweden JS, Grüter C, Jones SM, Ratnieks FL (2011) Hovering guards of the stingless bee *Tetragonisca angustula* increase colony defensive perimeter as shown by intra- and inter-specific comparisons. *Behav Ecol Sociobiol* 65:1277–1282
- Wheeler DE (1986) *Ectatomma tuberculatum*: foraging biology and association with *Crematogaster* (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 79:300–303
- Wittmann D (1985) Aerial defense of the nest by workers of the stingless bee *Trigona* (*Tetragonisca*) *angustula* (Latreille)(Hymenoptera: Apidae). *Behav Ecol Sociobiol* 16:111–114
- Wittmann D, Radtke R, Zeil J, Lübke G, Francke W (1990) Robber bees (*Lestrimelitta limao*) and their host chemical and visual cues in nest defense by *Trigona* (*Tetragonisca*) *angustula* (Apidae: Meliponinae). *J Chem Ecol* 16:631–641