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RESEARCH ARTICLE

Effects of *Azteca trigona* alarm pheromones on heterospecific ant behavior

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Abstract

Animals communicate with each other using a variety of signal modalities, any of which can provide useful information to non-intended receivers, or eavesdroppers. Eavesdropping on chemical signals is a widespread phenomenon but its role in shaping the behavior of multi-species assemblages is poorly known. Here, we tested the hypothesis that workers of multiple Neotropical ant species change their behaviors when exposed to odors of the common canopy ant, *Azteca trigona*. We exposed workers of 16 canopy ant species (five subfamilies) to *A. trigona* alarm pheromones and compared their behavioral responses to the behavior of ants in control treatments (ambient air). Seven species showed distinct responses to *A. trigona* odors relative to the control. The most common behavioral responses were increased antennation and running. The results of this study suggest that eavesdropping on heterospecific alarm signals allows ants to avoid generalized threats or negative interactions with aggressive *A. trigona* workers. Such eavesdropping presumably is selectively advantageous and may determine local arboreal ant species distributions and interspecific differences in access to resources in the forest canopy.

Keywords Formicidae · Eavesdropping · Canopy ants · Chemical signals · Tropical forest

Introduction

Animals use a variety of signaling modalities (e.g., visual, mechanical, chemical) to communicate vital information to nestmates, conspecifics, and heterospecifics (Endler 1992; Wyatt 2014). Chemical signaling is widespread in nature, in part, because pheromones and other chemical messages often are relatively inexpensive to produce, and can provide important contextual physiological and ecological information over long distances (Bossert and Wilson 1963; Symonds and Elgar 2008; Wyatt 2014). For insects, and especially social insects such as ants (Hymenoptera: Formicidae), chemical signaling is a ubiquitous part of life. Ants use a variety of compounds to organize individual behaviors and maintain colony structure (Hölldobler and Wilson 1990; Roitberg and Isman 1992). Ants also leverage volatile chemical signals as alarm pheromones in part because they are detectable over longer distances than are non-volatile chemicals (Blum 1969; Wyatt 2014; Leonhardt et al. 2016).

Alarm pheromones in some ant species occur as relatively conspicuous plumes of volatile compounds (Blum 1969; Attygalle and Morgan 1984; Keeling et al. 2004). These volatile chemical signals can be problematic because the strength and distribution of the message cannot be controlled once it is emitted (Bossert and Wilson 1963; Wyatt 2014). Such signals become freely available "public" information that is a reliable cue for exploitation by unintended receivers (i.e., eavesdroppers; Peake 2005) including ant-associated eavesdroppers, especially parasitoids and predators (Feener et al. 1996; Mathis et al. 2011; Cárdenas et al. 2012; reviewed by Adams et al. 2020). Indeed, chemical eavesdropping is common in diverse groups of animals and is well-studied in insects (Stowe et al. 1995; Wyatt 2014). However, to our knowledge, no studies have explored the possibility that co-occurring ants eavesdrop on heterospecific ant alarm pheromones.

Interspecific eavesdropping on alarm pheromones is likely to be advantageous for co-occurring competitive or

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antagonistic species. Given that ant workers are valuable to their colonies directly as biomass (Wilson 1968) and indirectly via foraging and defensive behaviors (Carroll and Janzen 1973), selection should favor eavesdropping on any warning signals that consistently prevent worker loss by inducing avoidance behaviors in submissive species. Eavesdropping on heterospecific alarm pheromones could provide such a mechanism because alarm pheromones are reliable indicators of nearby dangers, including negative interspecific interactions among competing ants, the presence of predators and parasitoids, or any generalized threat or disturbance (Blum 1969).

Azteca chartifex/trigona (Dolichoderinae) is a common Neotropical canopy ant species complex that has conspicuous nests (Fig. S1), large polydomous colonies, distinct alarm pheromones, and aggressive workers (Wheeler 1986; Adams 1994; Longino 2007). Hereafter, we refer to this species complex as *A. trigona* for simplicity. In some forests, *A. trigona* influences local ant community structure via territorial behaviors creating a mosaic of species distributions (Adams 1994). Alarm pheromones coordinate *A. trigona* defensive behaviors (Adams 1994), but the effects of *A. trigona* alarm pheromones on other ant species are unknown.

Chemical components of alarm pheromones frequently are conserved within genera or subfamilies (Blum 1969; Wheeler et al. 1975; Norman et al. 2017), thus eavesdropping species are likely to be closely related to the emitting species. Additionally, some behaviorally dominant ants competitively exclude other ant species that are ecologically or morphologically similar (Hölldobler and Wilson 1990; Andersen and Patel 1994; Adams 2016). If ants respond to the alarm pheromones of closely related heterospecific species, and if *A. trigona* similarly influences local species assemblages via competitive exclusion, we expect eavesdropping on *A. trigona* pheromones to be best developed in phylogenetically and behaviorally similar subordinate or codominant species. Our personal observations in the forests of Panama (e.g., Yanoviak and Kaspari 2000, Adams et al. 2017) indicate that most canopy ants avoid direct interactions with *A. trigona* workers while foraging. We also frequently observe strong negative behavioral responses (i.e., fleeing) by some arboreal species when presented with forceps contaminated with *A. trigona* alarm pheromones. These observations suggest that chemical cue recognition and eavesdropping on *A. trigona* are common among canopy ants.

The principal objective of this study was to determine if tropical canopy ants eavesdrop on the alarm pheromones of *A. trigona* ants. We asked if canopy ants change their behaviors when exposed to *A. trigona* alarm pheromones, how their behaviors change, and whether behavioral responses are more common in certain subfamilies. We predicted that differences in behavioral responses would be associated with ant subfamily identity, and species that are more phylogenetically similar to *A. trigona* would exhibit the greatest frequency of responses. We experimentally tested these predictions in Panama with freshly captured worker ants of 16 species.

Methods

This study was conducted on Barro Colorado Island (BCI) in Panama (9.15 °N, 79.85 °W) between July 2016 and October 2018. BCI is a seasonally moist lowland forest with a wet season spanning May to December. All data for this study were collected during wet season months. More details about the site are provided elsewhere (Croat 1978; Leigh et al. 1996).

All worker ants used in experiments were collected by hand or with forceps from tree trunks and branches on BCI. Workers of a given species were collected from multiple colonies, and ants collected from a given colony (usually < 5 workers) were housed together in a vial until the start of an experiment. All ants were used in experiments within 48 h of collection and were provided with water and honey during the holding period. The 16 focal ant species (Table 1) were chosen to maximize phylogenetic diversity and to include species that commonly co-occur in trees with *Azteca trigona* at the study site (Adams et al. 2017).

Alarm pheromone trials

To determine which ant species responded to *A. trigona* alarm pheromones and how they responded, we placed a single ant (hereafter *recipient ant*) in a small glass arena (25.4 × 76.2 × 76.2 mm; Figs. S2, S3) and allowed it to acclimate for 3–5 min before each trial. At the beginning of each trial, *A. trigona* volatile odors (hereafter *alarm pheromones*) were obtained by aggravating ca. 30 workers inside a plastic vial (i.e., by continuously shaking the vial for 5 s) and then drawing air from the vial into a 20 mL polypropylene syringe (Norm-Ject, Henke Sass Wolf GmbH, Germany). Twelve milliliters of air containing *A. trigona* alarm pheromones were then injected into the chamber via the syringe. Control treatments followed the same protocol using a new conspecific recipient ant worker for each trial and a clean syringe filled only with ambient air. All trials were conducted at temperatures ranging 26–30 °C.

We recorded recipient ant behavior for multiple individual workers of 16 different species (Table 1). In each case, ant behavior was recorded 5 s before and 5 s immediately after exposure to *A. trigona* alarm pheromones using the video function of a compact digital camera (Canon-PowerShot ELPH 180, Canon Inc., Japan). We observed the videos

Table 1 Summary of tests conducted on workers of 16 recipient ant species exposed to *Azteca trigona* alarm pheromones and ambient air (*Control*)

Recipient species	Odor source *A. trigona*	 Control
Dolichoderinae		
Azteca trigona	46	31
Dolichoderus bispinosus	44	47
Dolichoderus debilis	31	34
Dolichoderus laminatus	20	14
Ectatomminae		
Ectatomma tuberculatum	29	26
Formicinae		
Camponotus sericeiventris	31	30
Camponotus sp. 1	21	19
Myrmicinae		
Atta colombica	37	37
Cephalotes atratus	35	25
Cephalotes basalis	29	27
Cephalotes umbraculatus	24	16
Crematogaster acuta	13	11
Pseudomyrmecinae		
Pseudomyrmex boopis	19	17
Pseudomyrmex elongatus	13	12
Pseudomyrmex gracilis	21	18
Pseudomyrmex oculatus	31	25

Numbers indicate sample size; each worker ant was used only once

blindly (i.e., odor treatments were unknown to the viewer) and noted the following conspicuous changes in behavior of recipient ants: increased or decreased running speed, increased or decreased frequency of antennal movement, mandible flaring, and gaster flagging/tucking (i.e., positioning the gaster approximately orthogonal to the body axis either dorsally or ventrally; Curtis 1985; Obin and van der Meer 1985; Fig. 1). Changes in behavior were visually estimated. If individuals exhibited two or more of the behavior changes listed above, we recorded a behavioral change in response to the odor source. We similarly quantified the behavioral responses of recipient ants in control treatments.

Analyses

Analyses were performed in the R statistical environment (R Core Team 2019). We used Fisher's Exact tests to determine if the frequency of behavioral responses to *A. trigona* alarm pheromones differed from controls. A separate test was conducted for each species. We used a mixed-effect generalized linear model to compare subfamily responses to *A. trigona* and control odor treatments (*glmer*, package lme4). Responses of *A. trigona* workers to *A. trigona* and control odors were excluded from this analysis. The response term was a binomial variable (behavioral response or no response), subfamily and odor treatment were fixed effects, and species was a random effect. Stepwise model reduction with likelihood ratio tests removed the non-significant interaction between subfamily and odor source. To compare subfamily responses to *A. trigona* alarm pheromones and control odors separately, we used a mixed-effect generalized linear model comparing subfamily responses using only recipient ants exposed to *A. trigona* alarm pheromones and a separate model with only recipient ants exposed to

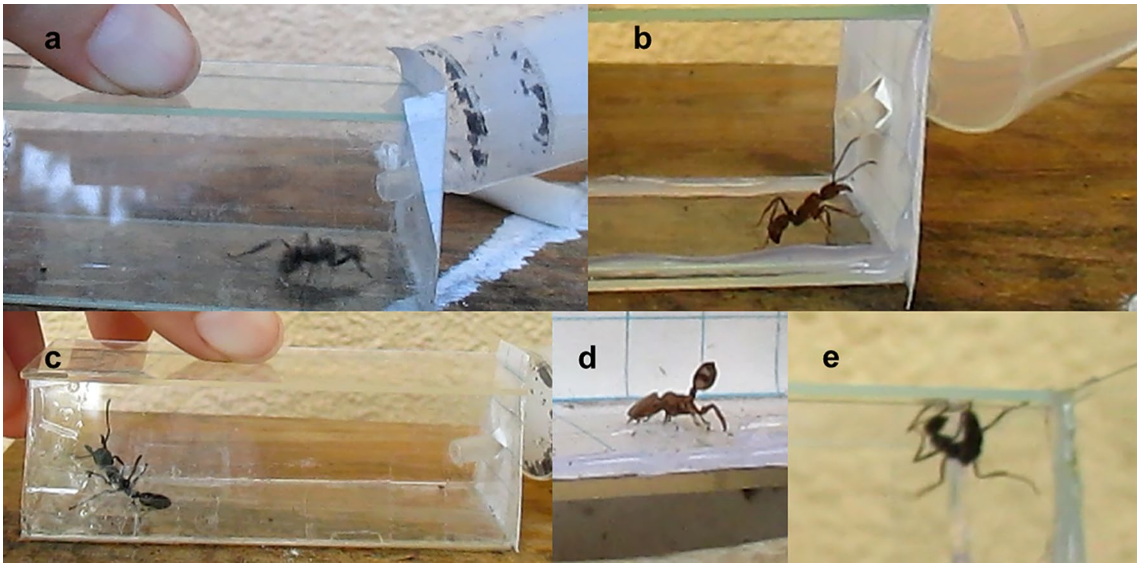

Fig. 1 The stereotypical ant responses to odors observed in this study: running (**a**), antennating (**b**), mandible flaring (**c**), and gaster flagging or tucking (**d**, **e**)

control odors. The response term was again a binomial variable, subfamily was the only fixed effect, and species was a random effect. Subfamily-level differences in behavioral responses were determined with post-hoc Tukey HSD tests.

Results

Seven of the 16 focal ant species responded more frequently to *A. trigona* odors than to ambient air (Fig. 2). Those seven species represented four distinct subfamilies; three were dolichoderines. Ants in all five focal subfamilies showed at least some behavioral response to *A. trigona* pheromones. Specifically, when worker responses were pooled at the subfamily level, response frequencies for *A. trigona* odors were consistently higher than for controls ($\chi^2 = 68.82$, df = 1, $p < 0.001$) and differed among subfamilies ($\chi^2 = 13.61$, df = 4, $p = 0.009$). However, only dolichoderines responded to *A. trigona* pheromones at a higher frequency than myrmicines and pseudomyrmecines (Table S1, Fig. S4). Response frequencies to the ambient air control also differed among subfamilies ($\chi^2 = 15.53$, df = 4, $p = 0.004$), with dolichoderines and formicines responding to control odors at a higher frequency than myrmicines and pseudomyrmecines (Table S1, Fig. S4).

In all, 334 individual ants (out of 833) changed their behaviors when exposed to pheromones or ambient air. Half (53%) of the 444 ants that were exposed to *A. trigona* pheromones showed a behavioral response, whereas only 25% of the 389 ants exposed to control odors responded. Most (75%) of the responding ants exhibited a combination of altered running speed and increased antennating frequency (Table 2, A + R). The least common behavioral change was gaster flagging, although dolichoderines exhibited combined

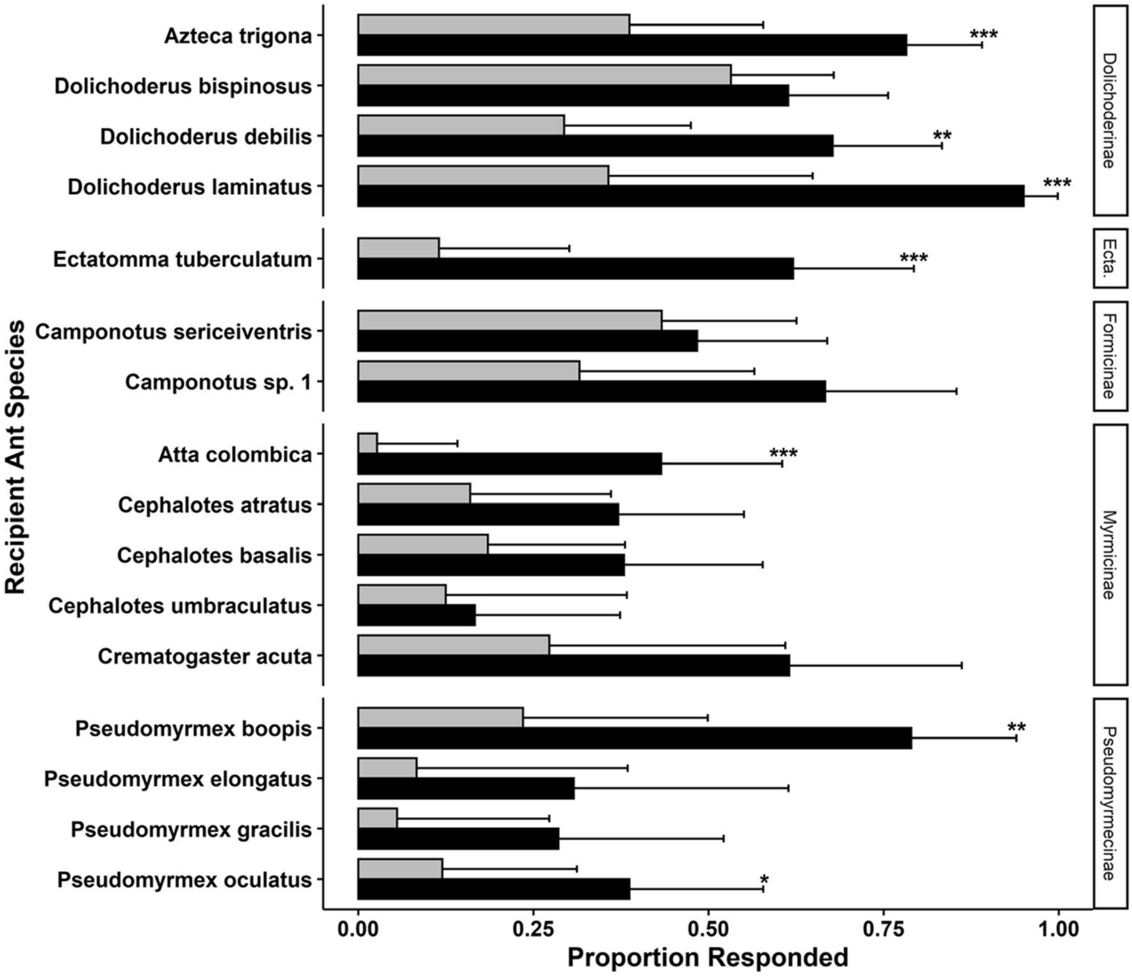

Fig. 2 The proportion (with ± 95% Clopper-Pearson CI) of trials in which workers of 16 recipient ant species exhibited behavioral responses when exposed to the alarm odors of *Azteca trigona* (black bars) and ambient air controls (gray bars). *Ecta.* = Ectatomminae. Significant differences between responses to *A. trigona* alarm pheromones and control ambient air are indicated as *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$

Table 2 The different combinations of qualitative behavioral responses (*Behavior*) observed in this study

Behavior	*A. trigona*	Control	Total
None	40	60	288
A	41	59	155
R	68	42	47
M	20	80	5
G	50	50	4
A+R	72	28	250
A+M	60	40	15
A+G	33	67	9
G+R	40	60	5
M+R	100	0	3
G+M	0	100	1
A+G+R	91	9	33
A+M+R	56	44	16
A+G+M	100	0	1
G+M+R	0	0	0
A+G+M+R	0	100	1

Values under *A. trigona* and *Control* are the percentage of recipient ants that exhibited a given *Behavior*. *Total* = the total number of ants exhibiting a given *Behavior* (each ant was assigned to only one *Behavior*). *R* = changed running speed, *A* = changed antennation frequency, *M* = mandible flaring, *G* = gaster flagging (see Fig. 2). In all, 444 ants were exposed to *Azteca trigona* alarm pheromones and 389 ants were exposed to ambient air control. Each ant was exposed to only one odor source

behaviors that included gaster flagging in 26% of responses (Table S2).

Discussion

Here we show that multiple Neotropical canopy ant species across a broad distribution of subfamilies change their behaviors when exposed to *Azteca trigona* alarm pheromones. Four of the five subfamilies tested included species that were both responsive and non-responsive to *A. trigona* pheromones (except for Ectatomminae, in which only one species was tested), suggesting that eavesdropping is a selective phenomenon among coexisting ant species that is not based on phylogenetic relatedness. Eavesdropping species occur across all domains of life (Stowe et al. 1995; Joint et al. 2007; Frost et al. 2008) and eavesdropping specifically on heterospecific alarm signals in animals is likely to be advantageous in many circumstances (Stowe et al. 1995; Adams et al. 2020). In this study, aggressive responses to *A. trigona* odors were uncommon (77% of responders exhibited what appeared to be flight behaviors—more frequent antennation and faster running speeds—which was similar to the 72% response frequency to control air including these behaviors). This suggests that avoidance of a potentially threatening species is the basis for eavesdropping behaviors among the focal ants. Such an "ecology of fear" occurs among many animal taxa (Pfeiffer 1962; Apfelbach et al. 2005; Goodale and Nieh 2012).

The results of this study do not support the prediction that species responding to *A. trigona* alarm pheromones would be closely related (i.e., dolichoderines). The major components of alarm pheromones that elicit worker responses are often specific within ant subfamilies or genera (Blum 1969; Norman et al. 2017). For example, among ants, cyclopentanoid monoterpenes and sulcatone (6-methyl-5-hepten-2-one) apparently occur only in *Azteca* alarm pheromones (Wheeler et al. 1975; McCann et al. 2013). These compounds elicit sustained alarm responses in *Azteca* workers (Blum 1969; Wheeler et al. 1975; McCann et al. 2013). Ants often respond to pheromones only with a specific compound ratio (Blum 1969; Pokorny et al. 2020), suggesting that species that do not respond more to *A. trigona* odors either do not detect the odors of *A. trigona*, or ignore them. Additional research is needed to isolate the specific compound or compounds within the *A. trigona* alarm pheromone that elicit behavioral responses from heterospecifics.

Given the lack of strong phylogenetic signal, it is likely that the observed ant responses to *A. trigona* alarm pheromones reflect ecological pressures. It is potentially advantageous for foraging workers (regardless of their identity) to recognize the presence of potential heterospecific competitors, or to detect the existence of a nearby disturbance that is provoking an alarm response by one or more species. Indeed, in a related pilot study, we found that a subset of the species used in this study also responded to alarm pheromones from ants other than *A. trigona*, although with different frequencies. Thus, we hypothesize that the species responding to *A. trigona* alarm pheromones are those that are more likely to have negative interactions with *A. trigona* workers (i.e., competing species). For example, *A. trigona* tend to have non-overlapping foraging territories with the responding species *Atta colombica* and *Ectatomma tuberculatum* (Jutsum et al. 1981; Armbrecht et al. 2001). We also cannot exclude the possibility that co-occurring species eavesdrop on other *A. trigona* cues, such as trail pheromones or chemical footprints, similar to the trail parasites *Cephalotes maculatus* and *Camponotus beebei* (Wilson 1965; Adams 1990; Wüst and Menzel 2017). Ultimately, additional field-based studies and natural history observations are needed to clarify links between pheromone eavesdropping and foraging decisions among potentially competing ants (Adams et al. 2020).

The results of this study are consistent with observations of eavesdropping in a variety of non-ant systems (Pfeiffer 1962; Goodale and Nieh 2012). However, the specific compounds that elicit responses, and the ecological consequences of responding to *A. trigona* alarm pheromones (e.g., potential loss of access to food resources) remain unknown.

Understanding such patterns will clarify the role of chemical eavesdropping on species interactions, foraging behavior, and community structure in arboreal ants.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00040-021-00836-2.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection, and analyses were performed by RLW. All authors contributed to the writing, and read and approved the final version.

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Availability of data and material Raw data for this project are available on FigShare with the following https://doi.org/10.25422/azu.data.13963886.

Code availability Not applicable.

Declarations

Conflict of interest None.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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