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Title

Detection of prey odors underpins dietary specialization in a Neotropical top-predator: How army ants find their ant prey

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Abstract

1. Deciphering the mechanisms that underpin dietary specialization and niche partitioning is crucial to understanding the maintenance of biodiversity. New world army ants live in species-rich assemblages throughout the Neotropics and are voracious predators of other arthropods. They are therefore an important and potentially informative group for addressing how diverse predator assemblages partition available prey resources.
2. New World army ants are largely specialist predators of other ants, with each species specializing on different ant genera. However, the mechanisms of prey choice are unknown. In this study, we addressed whether the army ant *Eciton hamatum:* 1) can detect potential prey odors, 2) can distinguish between odors of prey and non-prey, and 3) can differentiate between different types of odors associated with its prey.
3. Using field experiments, we tested the response of army ants to the following four odor treatments: alarm odors, dead ants, live ants, and nest material. Each treatment had a unique combination of odor sources and included some movement in two of the treatments (alarm and live ants). Odor treatments were tested for both prey and non-prey ants. These data were used to determine the degree to which *E. hamatum* are using specific prey stimuli to detect potential prey and direct their foraging.
4. Army ants responded strongly to odors derived from prey ants, which triggered both increased localized recruitment and slowed advancement of the raid as they targeted the odor source. Odors from non-prey ants were largely ignored. Additionally, the army ants had the strongest

response to the nest material of their preferred prey, with progressively weaker responses across the live ant, dead ant, and alarm odors treatments, respectively.

5. This study reveals that the detection of prey odors, and especially the most persistent odors related to the prey's nest, provides a mechanism for dietary specialization in army ants. If ubiquitous across the Neotropical army ants, then this olfaction-based ecological specialization may facilitate patterns of resource partitioning and coexistence in these diverse predator communities.

Key Words Army Ants, Coexistence, Diet, *Eciton*, Ecology, Neotropics, Olfaction, Specialization

Introduction

Ecological specialization can be a powerful mechanism for reducing the likelihood of competitive exclusion, and thus promoting long-term species coexistence (Hutchinson, 1959; Connell & Orias, 1964; reviewed in Chase & Leibold, 2003; Sapp, 2016). The competitive exclusion principle states that if two species have complete niche overlap then the species with more efficient use of a shared resource will drive the other species to extinction. However, specialization, which can be conceptualized as any reduction in the breadth or relative frequency of resource usage within an n-dimensional niche space (Hutchinson, 1957; Devictor et al., 2010, Irschick et al 2005), can limit overlap, reduce competitive interactions between species, and promote coexistence (Hardin, 1960; Chase & Leibold, 2003). Despite this long-standing insight, how specialization is mechanistically established remains poorly understood for many taxa. This gap is especially pronounced in hyper-diverse tropical communities, wherein most species must contend with the potential for high intraguild competition, and a species-rich and structurally complex environment in which to locate resources (MacArthur, 1972; Sapp, 2016).

Specialization on different resource species has been shown to be especially important in reducing niche overlap and competition across a broad diversity of consumer species (Futuyma & Moreno, 1988; Chase & Leibold, 2003). In particular, ecological specialization on different food resources has long been seen as a primary mechanism promoting coexistence in diverse insect communities, such as insect herbivores (Singer & Stireman, 2005) and pollinators (Michener, 2007; Armbruster, 2017). In such cases, specialization is often underpinned by sensory specialization (Stevens, 2013), including the combination of multiple senses to maximize foraging efficiency (Siemers et al., 2007; Vincent, Shine, & Brown, 2005). Nevertheless, this mechanistic knowledge of specialization is lacking in diverse assemblages of predatory insects (but see Rana, Dixon, & Jarošík, 2002; Xue, Wei, Huang, Li, & Yang, 2018 for species specific examples), which despite their trophic footprint are rarely the focus of studies addressing dietary specialization (but see Kaspari, Powell, Lattke, & O'Donnell, 2011; Hashimoto & Yamane 2014).

New World army ants (monophyletic group of five genera within subfamily Dorylinae: Brady, Fisher, Schultz, &Ward, 2014; Borowiec, 2016) are well-established as ecologically important predators of other ants and live in diverse assemblages of up to 20 species in Neotropical forests (Rettenmeyer, 1963; Schneirla, 1971; Rettenmeyer, Chadab-Crepet, Naumann, & Morales, 1983; Kaspari, Powell, Lattke, & O'Donnell, 2011). Existing data indicates that many army ant species are dietarily specialized on one to a few specific genera of other ants (Rettenmeyer, Chadab-Crepet, Naumann, & Morales, 1983; LaPolla, Mueller, Seid, & Cover, 2002; Powell & Clark 2004; Powell & Franks 2006; Breton, Dejean, Snelling, & Orivel, 2007; Powell, 2011; Hoenle et al., 2019), with a few species adding other non-ant litter invertebrates and social wasps to their diet (Rettenmeyer, 1963; Chadab, 1979; Rettenmeyer et al., 1983; O'Donnell, Kaspari, Lattke, 2005; Kaspari, Powell, Lattke, O'Donnell, 2011). Additionally, all species are obligately nomadic group-predators that roam the forests they inhabit in large collective raids, simultaneously seeking out, attacking, and harvesting their preferred ant prey (Rettenmeyer, 1963; Schneirla, 1933; Schneirla, 1971). Every location within the forest is therefore intensively raided by all resident army ant species through time (Franks & Bossert, 1983; O'Donnell, Lattke, Powell, & Kaspari, 2007; Kaspari, Powell, Lattke, & O'Donnell, 2011), with each species harvesting different ant prey from the same area. Combined, the diet, species-richness, and nomadic predatory behavior of army ants within tropical forests position them as an ideal group for addressing the mechanisms of specialization in diverse predator assemblages. Yet how army ant dietary specialization is mechanistically achieved is not known.

Army ants may use a number of non-mutually exclusive mechanisms to locate their specific prey, but none have been tested to date. First, army ants may be detecting specific odor cues, allowing them to localize their prey as they forage through the forest (Gotwald, 1995). Despite research into the chemical basis of army ant intra-colony communication and chemical signaling used in army ant recruitment (Chadab & Rettenmeyer, 1975; Chadab, 1979), we have only a cursory understanding of how army ants use chemicals to perceive their environment, and especially their prey. Evidence from numerous interactions such as those between *Nomamyrmex esenbeckii* and *Atta* leaf-cutting ants (Powell & Clark, 2004), or *Eciton burchellii* and *Paratrechina longicornis* (Dejean, Corbara, Roux, & Orivel 2013), all suggest that prey species are able to identify army ants by their odors; however, little research has been conducted addressing detection from the predator's perspective. There are many sources of species-specific odor cues that army ants could be detecting, including cuticular hydrocarbons, volatile pheromones used in alarm and recruitment responses, and colony odor on nest material (d'Ettorre & Lenoir, 2010). Prey odors of different kinds may then allow detection of prey across a range of spatial scales. Second, prey movement, and associated visual or vibrational cues, represents another plausible mechanism of prey detection and localization. Army ant vision is known to be exceptionally poor, with eyes absent or reduced to a single facet in most species (Bulova, Purce, Khodak, Sulger, & O'Donnell, 2016). However, visual motion detection may still be possible, and movement may be detected indirectly via vibrations through the substrate (Hill, 2008; Hill, 2009). Nevertheless, it is unclear how visual or vibrational sensory modalities would yield species-specific information to the army ants beyond direct visual identification of the prey. Finally, the simplest scenario is that army ants may not use directed foraging, and instead conduct random walks that lead to direct contact with prey ants at their nests.

Our study provides the first test of the hypothesis that New World army ants use prey-odor cues to detect their preferred ant prey. We do this using *Eciton hamatum* in the moist tropical forest of central Panama. This army ant conducts conspicuous group raids over the forest floor and into the canopy, and has a quantified dietary specialization on *Acromyrmex* leaf-cutting ants in the study site (Fig. 1, Powell & Franks, 2006; Powell, 2011). Combined, this foraging ecology and dietary specialization facilitate highly tractable experimental manipulation and control of different prey-odor cues. More specifically, we address the following critical questions about specialized detection of prey odors: 1) Does *E. hamatum* have the ability to detect prey odors in their natural foraging environment? 2) Can *E. hamatum* differentiate between odors from different ant species? 3) Does *E. hamatum* exhibit differentiated predatory responses to certain types of odor cues produced by its prey? Broadly, this research addresses how a member of a diverse assemblage of cooccurring predators can detect its preferred prey within a hyper-diverse assemblage of potential prey species, shedding light on the mechanisms of resource partitioning within complex communities.

Material & Methods

Study site, study organisms, and colony discovery

Fieldwork was conducted on Barro Colorado Island (BCI), Panama (9°090N, 79°500W) between May and September 2015. BCI is a seasonally dry, 15.6 km^2 island rainforest in central Lake Gatun of the Panama Canal (see Leigh, 1999 and Ziegler & Leigh, 2011 for detailed information). Population size of *Eciton hamatum*, our focal army ant species, has been calculated at 57 colonies on BCI (Powell, 2011). Focal colonies of *E, hamatum* were located by walking trails during daylight hours, until raid columns were encountered (following methods of e.g. Franks, 1980; Franks, 1982; Vidal-Riggs & Chaves-Campos, 2008; O'Donnell, Lattke, Powell, & Kaspari, 2007; Powell, 2011). Species identification used the characters outlined in Watkins (1976). Raid traffic was then tracked in the direction of prey transport, to locate the nest or ‘bivouac’. Colonies were tracked nightly, by following the emigration traffic to the new bivouac site. This ensured the location of the colony was known for data collection the following day (Powell & Franks, 2006; Powell, 2011).

The ant species *Acromyrmex octospinosus* was used as the preferred prey of *E. hamatum*, as determined by relative frequency of prey items and biomass intake by the colony at the same and different sites throughout Central America (Rettenmeyer, Chadab-Crepet, Naumann, & Morales, 1983; Powell & Franks, 2006; Powell, 2011; Hoenle et al., 2019). The non-prey ant used in this study was *Cephalotes atratus*. This species was selected for two reasons. First, it has never been recorded in diet records for any army ant species, which is important for serving as a true non-prey outgroup to our prey species. Second, *Cephalotes* is a closely related genus to several common prey genera within the subfamily Myrmicinae (Ward, Brady, Fisher, & Schultz, 2015), such as *Acromyrmex* and *Pheidole*

(Powell & Franks, 2006; Powell, 2011; Hoenle et al., 2019). Easily accessible colonies of both prey *A. octospinosus* and non-prey *C. atratus* ants were located for use throughout the study.

Odor treatments

Four distinct treatments were prepared from both prey and non-prey ant species and used in odor-detection trials with *E. hamatum* (below). Each treatment had a unique combination of odor sources and mode of detection that the army ants could potentially use. Some movement cues were also present in the two odor treatments containing living ants, because movement could not be entirely eliminated when using live ants in field trials. Nevertheless, each treatment was designed to maximize the focal odor stimuli, while minimizing other odor sources and movement where relevant. The full set of treatments, combined with the behavioral responses of the army ants, allowed us to determine which odor sources army ant found most attractive and which they ignored, as well as what role movement plays in these interactions (Results). The four odor treatments were as follows: 1) Volatile alarm odors from living ants that the army ants could not contact directly ("alarm" treatment hereafter); 2) Dead ants that were freshly killed, to present the cuticular hydrocarbon odors of the ants to the army ant raid without volatile alarm pheromones or movement cues ("dead-ant" treatment hereafter); 3) Living ants that could be contacted directly by the army ants, to provide the combined presence of cuticular hydrocarbons, alarm pheromones, and movement/vibrational cues ("live-ant" treatment hereafter); 4) Nest material that provides a source of gestalt colony odor, including high concentrations of cuticular hydrocarbons (Lenoir, d'Ettorre, Errard, & Hefetz, 2001; d'Ettorre & Lenoir, 2010), to the army ants without the presence of any adult ants ("nest-material" treatment hereafter).

For the alarm treatment, we collected 10 living ants and placed them in wire mesh (square mesh aperture width of 0.125 mm and wire diameter of 0.10 mm) boxes measuring approximately 5 cm x 5 cm x 2.5 cm, to allow the escape of localized alarm pheromones during each trial without direct access to the ants inside. The box was then shaken vigorously for two seconds before each trial, to trigger the release of alarm pheromone. A single agitated ant was enough to elicit a response by army ants in initial trials and the alarm odors from the 10 living ants used in the treatment were easily detectable to the human nose for both prey and non-prey ants. This preparation allowed us to maximize highly volatile alarm odor cues available to the army ants, while minimizing access to low volatility cuticular hydrocarbons and movement cues inherent in using living prey ants in a field setting. Movement cues in this treatment were especially minimal, despite involving live ants, because the test ants had no direct contact with the leaflitter and had no capacity to move the wire box they were held in. For the dead-ant treatment, 10 ants were rapidly euthanized in a -20ºC freezer for 15 minutes and then used in experiments within one hour of removal from the freezer. This preparation provided the cuticular hydrocarbon odors required for the experimental treatment, while ensuring that actively released volatile odors were not present and that the ant had not been dead long enough to be producing "rotting ant" odor cues (Choe & Rust, 2008; Howard & Tschinkel, 1976; Wilson, Durlach, & Roth, 1958). For the live-ant treatment, 10 ants were partially immobilized by a non-lethal procedure cutting just above the joint between the tibia and femur of each leg. This preparation provided the army ants with direct access to the ant's cuticular hydrocarbon and volatile alarm pheromones while the ant also produced movement and vibrational cues without being able to escape. Finally, for the nest-material treatment, fresh nest-material (soil and organic debris) was collected from nest entrances and placed in sealed containers until trials began, with no more than six hours between collection and use. This preparation lacked any adult ants, and lacked any ant-associated volatile odor and movement cues, while providing the army ants a source of gestalt colony odor rich in cuticular hydrocarbons. Observations just prior to collection ensured that the nest entrance was in current use by the ant colony.

Odor detection trials

Prey detection and capture occurs in each raid front of densely packed ants within the overall branching raid system of *E. hamatum* (Rettenmeyer, 1963). Each raid front is usually 10-20 cm wide within an overall branching raid system that covers hundreds of meters (Schneirla, 1934, Schneirla, 1971). Consequently, hundreds of raid fronts are present within a raid system at any given moment, dissolving if they are unsuccessful in finding prey and new ones forming as the overall raid advances through the forest (Rettenmeyer, 1963; Schneirla, 1971). Odor detection within a raid front was therefore the biologically relevant sampling unit for our odor-detection trials, with these trials replicated within and across colonies. In each trial, a randomly selected odor cue from either the prey or non-prey ant species was presented to a raid front at a distance of 20 centimeters, and the responses of the army ants were video recorded for 30 seconds. For the subsequent replication within a colony, newly forming raid fronts were selected at random until all trials were complete. For replication across colonies, a total of seven *E. hamatum* colonies were tested between June and August of 2015. Logistical constraints of tracking and finding colonies resulted in the live-ant treatment replicated across only five colonies. Each trial of an odor treatment and ant type (prey vs. non-prey ant) combination was replicated a minimum of five times per colony, resulting in the following totals for the different trials across colonies: 70 trials for the alarm treatment with prey ants; 82 trials for the dead-ant treatment with prey ants; 55 trials for the live-ant treatment with prey ants; 92 trials for the nest-material treatment with prey ants; 70 trials for the alarm treatment with non-prey ants; 57 trials for the dead-ant treatment with non-prey ants; 52 trials for the live-ant treatment with non-prey ants; 64 trials for the nest-material treatment with non-prey ants. Each trial lasted 30 seconds and was recorded with a 4K (3840 x 2160 resolution) GoPro video camera, to allow subsequent data extraction. The camera was setup in the ultra-wide-angle lens mode and held or mounted at an appropriate distance to capture an overhead view of the interaction between the focal *E. hamatum* raid front and the odor treatment.

Data extraction

The response of the army ants to the odor treatments was captured by extracting three metrics from the video of each trial; 1) army ant recruitment rates measured in ants per second; 2) advancement speed of the raid front measured in centimeters per second; 3) mean running speed of three individual army ants within the raid front, measured in centimeters per second. These metrics were chosen because shifts in ant recruitment and speed are reliable quantitative proxies for army ant attacks against their prey. A raid front has a steady advancing speed with the ants evenly spread over the forest floor as they collectively search for prey (Rettenmeyer, 1963; Schneirla, 1971). Then once prey is detected, individuals are rapidly recruited to the site of the prey within the raid front to create a collective aggregation of ants around the prey (Chadab & Rettenmeyer, 1975), and the speed of both the overall raid front and individuals within it drops as the ants switch into localized search and attack behavior to capture the prey (Rettenmeyer, 1963; Schneirla, 1971). Stronger responses to prey are thus represented by higher recruitment rates and slower raid-front and individual speeds.

To calculate our three metrics of army ant response, a series of still images was captured from each video and analyzed in ImageJ version 1.49 (Schneider, Rasband & Eliceiri, 2012). The interval between images was 0.5 seconds. Frame dimensions of each video were measured using the calibration function of ImageJ. *E. hamatum* recruitment rate to odor treatments was measured by counting the number of ants that interacted with the cue after the first ant discovered the odor source and dividing by the number of seconds remaining in the 30 second trial after this initial contact (see Chadab & Rettenmeyer, 1975 for details of army ant recruitment). Thus, if an individual contacted the odor treatment but no nestmates were subsequently brought to the area by the initial individual, recruitment was zero, as described in Chadab & Rettenmeyer (1975). Advancement speed of the raid was measured by averaging the time spent in the video frame for ten randomly selected army ant individuals in the presence of a given odor treatment. Only ants entering the frame within the last 20 seconds of each trial were used to account for minor variation in times at which the army ant raid fronts entered the frame of the video. Raid advancement speed was not assessed for the alarm treatment, because the physical structure of the mesh box altered the collective movement of the raid and therefore the accurate determination of this metric. Mean individual army ant speed was calculated from instantaneous velocities. The series of captured images was fed into the Manual Tracker plugin of ImageJ, where three randomly selected army ants had their instantaneous velocities measured between two frames for the duration of each 30 second video trial, to allow the calculation of the mean individual running speeds.

Data analyses

We conducted all analyses for this study with R version 3.4.4 for Windows (R Core Team, 2016). For our initial set of analyses comparing army ant recruitment and individual running speeds in response to both prey and non-prey ants, we used ANOVA tests with colony as a factor to first assess whether colony identity had a significant influence on treatment responses ($p>>0.05$ in all cases). Subsequent analyses were then conducted with the colony factor removed. We simplified raw recruitment data into a binomial success/failure outcome because most non-prey recruitment was zero. This binomial data was then analyzed for equality of proportion between successful and failed recruitment across odor treatments and between prey and non-prey, using Chi-square tests. Differences between mean running speeds (± standard deviation) were assessed with two-sample T-tests assuming unequal variances. Given that most non-prey odor trials did not elicit successful recruitment and no non-prey odors trials caused the army ants to slow down relative to prey odor trials (Results below), non-prey odors were dropped from further analyses. This allowed for more powerful parametric tests of the differences in army ant responses among prey-ant odor treatments.

For subsequent analyses of army ant responses among prey-odor treatments, recruitment rate, raid speed, and individual running speed data were transformed appropriately to conform to the assumptions of normality and equality of variance to conduct parametric statistical analyses. We used mixed design analyses of variance (ANOVA) to test for differences in all metrics across prey-odor treatments (fixed effect), while accounting for the potential non-independence of the random colony factor. Post hoc analyses for differences among prey-odor treatments were conducted using the Tukey's Honest Significant Differences test.

Results

Responses to prey ants vs. non-prey ants

E. hamatum recruitment was significantly stronger in response to odors derived from prey ants (*Acromyrmex*) than non-prey ants (*Cephalotes*) across all four treatment types (Alarm, $\chi_1^?$=54.4, *P*<0.001; Dead, $\chi_1^?$ =66.3, *P*<0.001; Live, $\chi_1^?$=31.1, *P*<0.001; Nest, $\chi_1^?$=62.5, *P*<0.001). Mean recruitment rates across all non-prey ant treatments was 0.03 ants/s SD ± 0.05 ants/s (Figure 2, dashed horizontal line), representing a near-zero baseline of recruitment when the advancing front is not responding to prey. Complementing the recruitment result, individual running speed slowed significantly in the presence of all treatments of prey odors, compared to their equivalent non-prey odor treatments (prey vs. non-prey alarm treatments, $t_{412, 420}$ = 19.97, *P*<0.001; live-ant treatments, $t_{273, 300}$ = 18.17, *P*<0.001; dead-ant treatments, $t_{368, 420}$ = 28.38, *P*<0.001; nest-material treatments, $t_{259, 420}$ = 46.23, *P*<0.001). Mean running speed across all non-prey ant treatments was 6.8 cm/s SD ± 1.7 cm/s, representing standard running speed when individuals are not slowing in response to prey detection (Figure 4, dashed horizontal line). Non-prey data was omitted from subsequent analyses for all metrics due to lack of significant army ant response, allowing more powerful statistical tests of the prey data.

Recruitment rates to different prey odor-treatments

Recruitment rates were significantly different across prey treatments (Figure 2, mixed design ANOVA, $F_{3,289} = 91.91$, and $P<0.001$) with no effect of the random colony factor ($\chi^2_1 = 0.01$, and $P=0.94$). Recruitment was strongest in response to the nest-material, followed by live-ant and dead-ant treatments respectively, with the alarm treatment eliciting the weakest recruitment (Figure 2; Post hoc Tukey's HSD, $P<0.001$ for all pairwise comparisons).

Raid speed in response to different prey odor-treatments

Army ant raid advancement speeds were significantly different across the three treatments that allowed the accurate assessment of this metric (Figure 3, mixed design ANOVA, $F_{2,229} = 216.30$, and $P<0.001$) with no effect of the random colony factor ($\chi^2_1 = 0.59$, $P = 0.44$). Army ant raid speeds were slowest for army ants presented with the nest-material treatment, followed by the live-ant treatment, while raid speeds were fastest for the dead-ant treatment (Figure 3, Post hoc Tukey's HSD, $P<0.001$ for all pairwise comparisons).

Individual running speed in response to different prey odor-treatments

Mean individual running speed was significantly different across all prey treatments (Figure 4, mixed design ANOVA, $F_{3,780} = 634.04$, and $P<0.001$), with no effect of the random colony factor ($\chi^2_1 = 0.63$, and $P = 0.43$). Individuals slowed down the most when presented with the nest-material treatment, followed by live-ant and dead-ant treatments, and the alarm treatment respectively (Figure 4, Post hoc Tukey's HSD, $P<0.001$ for all pairwise comparisons).

Discussion

Ecological theory posits that tropical organisms are more narrowly specialized, thus allowing a greater number of species to coexist in a given area (Dobzhansky, 1950; MacArthur, 1969; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). However, the mechanisms of specialization remain poorly understood for the majority of predator assemblages in diverse tropical systems. In this study we examined the role of odor in the detection of potential prey by New World army ants. We found that army ants can distinguish among potential prey odors in a natural context, and differentially respond to several different categories of odors from preferred prey ants. Army ants exhibited the strongest response to nest-material odors, with weaker responses to live-prey odors, dead-prey odors, and prey-alarm odors, respectively. Our results indicate that patterns of dietary specialization in *E. hamatum* can largely be explained by their reliance on olfaction to detect and discriminate among potential prey. This selectivity in olfactory attention may be a major factor contributing to stable species-coexistence within predatory army ant assemblages.

Army ants distinguish between potential prey odor

We observed dramatic army ant recruitment to prey (*Acromyrmex*) odors relative to non-prey (*Cephalotes*) odors across all treatments. This provides compelling support for the hypothesis that army ant dietary specialization is underpinned by their ability to detect and discriminate among ant odors. From one of the few quantitative studies on specialized army ant diets, we know an *Eciton hamatum* raid can reach peak intake rates of 133 *Acromyrmex* prey items/min, with an average total daily intake of nearly 5000 *Acromyrmex* prey items (Powell, 2011). Given the apparently patchy distribution and cryptic nature of the nest cavities used by *Acromyrmex octospinosus* (Fowler, Pereira-da-Silva, Forti, & Saes, 1986), prey odors from nest material and cuticular hydrocarbon profiles appear to represent reliable cues that *E. hamatum* can use to detect and attack its preferred prey. Broadly, our results then provide compelling evidence that army ant foraging is directed at local scales by the detection of and recruitment to persistent and reliable odor cues of their preferred prey.

The army ants used in this study exhibited little interest in non-prey ant odors, as evidenced by their general lack of recruitment and unaltered, faster forager speeds in the presence of all non-prey odor material. Thus, the non-prey odor cues used here were ignored almost entirely by the army ants, and importantly did not cause any kind of repulsion. Consistent with this observation, *E. hamatum* also show no interest in *Atta* leaf-cutting ants, the sister genus to the preferred and actively tracked *Acromyrmex* prey documented here, demonstrating a remarkable ability to differentiated odors of even more closely related taxa (Powell & Clark, 2004; Powell, 2011).

Variation in responses to prey odors as a mechanism of dietary specialization

Our results (Figs. 2-4) indicate that army ants respond more to prey odors that persist in the environment and likely indicate proximity to prey nests, while showing little interest in volatile alarm pheromones of adult ants or movement. While the alarm treatment did contain a small movement cue due to living ants being encased in a wire mesh box, our results show that neither volatile alarm pheromones nor movement from the living ants produced a strong response in the advancing army ants (Figs. 2 & 4). Additionally, the presence of movement cues may partially explain why army ant responses are significantly stronger to the live-ant treatment than the dead-ant treatment; however, the magnitude of this difference is much less than the magnitude of the differences among the other treatments (Figs. 2-4). Logically, it seems most beneficial for army ants to respond the most to the presence of the nest-material odors of prey, as army ants preferentially harvest brood from prey nests (Fig. 1; Rettenmeyer, 1963; LaPolla et al., 2002; Powell & Clark, 2004; Powell, 2011; Hoenle et al., 2019). The relatively high recruitment rates to living and dead ants (Fig. 2) may also be explained by the use of odor cues that indicate proximity to the nest: foragers or refuse piles containing dead adult ants may also reliably signal proximity to a prey nest. Given that nest material contains species-specific cuticular hydrocarbons (CHCs; d'Ettorre & Lenoir, 2010), it is therefore fitting that the army ants have the strongest response to this odor source. The experimental results of this study thus provide compelling evidence that army ants are making use of odor cues that signal proximity to ant nests and brood, and likely the greatest return on foraging investment.

This work demonstrates the importance of olfaction in mechanistically underpinning the dietary specialization of the army ant *E. hamatum* on its preferred ant prey, but it is unclear how widespread this mechanism of prey detection might be across the army ants and other predator ants. The importance of olfaction in food acquisition has been studied in a variety of taxa (reviewed in

Stevens 2013). Yet in social insects, mechanisms of olfactory detection have primarily been assessed in the context of intra-specific communication (reviewed in Van Zweden & d'Ettorre, 2010; Leonhardt, Menzel, Nehring, & Schmitt, 2016). While this is the first demonstration that any army ant uses olfactory cues to detect other ants as prey, previous studies have reported similar olfaction-based prey detection mechanisms in *Megaponera* ants preying on termites (Yusuf, Crewe, & Pirk, 2014; Yusuf, Gordon, Crewe, & Pirk, 2014) and *Crematogaster* ants preying on fig wasps (Schatz, Anstett, Out, & Hossaert-McKey, 2003; Schatz & Hossaert-McKey, 2010). The *Megaponera*-termite interaction offers an especially interesting comparison to the *E. hamatum-Acromyrmex* interaction for two reasons; both represent instances of food-driven combat between large, eusocial insect colonies, and both predator species appear to be most interested in odors associated with the prey nest-material, which are more stimulating than odors from the adult prey themselves (Yusuf, Gordon, Crewe, & Pirk, 2014).

Potential consequences for coexistence:

Mechanisms that allow niche partitioning at fine scales may play an important role in the maintenance of species diversity in the Neotropics (Dobzhansky, 1950; MacArthur, 1969; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009; Sapp, 2016). The ability to detect species-specific prey odors, demonstrated herein with *E. hamatum*, provides a new potential mechanism by which army ants could be partitioning ant prey resources within their diverse ant assemblages. We know that sensory adaptations can increase efficiency in cue reception and transmission, simultaneously resulting in sensory bias on perception in the environment (Endler, 1992; Fuller, Houle, & Travis, 2005; Stevens 2013). This sensory bias can then play a determinative role in species diet by altering sensory access to food (Barclay & Brigham, 1991; Bernays & Wcislo, 1994; Raine & Chittka, 2007), resulting in a mechanism to reduce interspecific competition and facilitating coexistence. Sensory-based variation in prey choice among members of a feeding guild is an understudied mechanism of niche partitioning, requiring detailed field observations and studies of behavior (but see Siemers & Schnitzler, 2004). This information is sorely lacking for most army ants, which are nomadic, largely subterranean and nocturnal, and typically live in assemblages of up to twenty co-occurring species in Neotropical forests (Rettenmeyer, 1963; Schneirla, 1971; Rettenmeyer, Chadab-Crepet, Naumann, &

Morales, 1983; Kaspari, Powell, Lattke, & O'Donnell, 2011). Nevertheless, we hypothesize that the dietary specialization on specific ant genera seen across the New World army ants is underpinned by the same sensory specialization we have shown here for *E. hamatum*, providing a sensory-based mechanism of niche partitioning at the level of the whole assemblage. The critical future test of this hypothesis will then be to contrast dietary and olfactory specialization across cooccurring army ant species. Comparisons among cooccurring *Eciton* species may be particularly tractable for such tests, because they are large-bodied army ants and among the least subterranean in their foraging activities (Rettenmeyer, 1963).

Conclusion

The mechanisms that establish specialization within diverse predator communities are likely critical in maintaining coexistence and promoting biodiversity in tropical systems. Our study demonstrates that olfaction is the primary mechanism by which *Eciton hamatum* is identifying, localizing, and initiating attacks against its preferred ant prey, mechanistically underpinning a strong dietary specialization. If this olfaction of specific prey-derived odors is used across the New World army ants, sensory specialization may be a key mechanism of the observed dietary niche partitioning within the ecologically important assemblages of these top-predators. Our results emphasize the need to account for species-level variation in olfaction preferences, to determine whether each army ant is attracted only to a small subset of potential prey odors within the hyper-diverse and structurally complex foraging environments they occupy.

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Authors' Contributions

JAM and SP conceived the ideas and designed the studies. JAM collected and analyzed the data and led the writing of the manuscript. Both authors contributed critically to drafts and gave final approval for publication.

Data Accessibility

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z34tmpg8q (Manubay & Powell, 2020).

Figures

Figure 1. A prey cache of the army ant *Eciton hamatum* composed primarily of the brood of their preferred prey, *Acromyrmex* leaf-cutting ants. After detecting and overpowering a prey nest, *E. hamatum* harvests the prey's brood and caches it immediately outside the nest entrance, before it is transported back to the army ants' own nest. Note the distinctive spherical larvae (e.g. being carried top left) and the already darkening orange pupae of the *Acromyrmex* brood in the prey cache. (Photograph: Scott Powell)

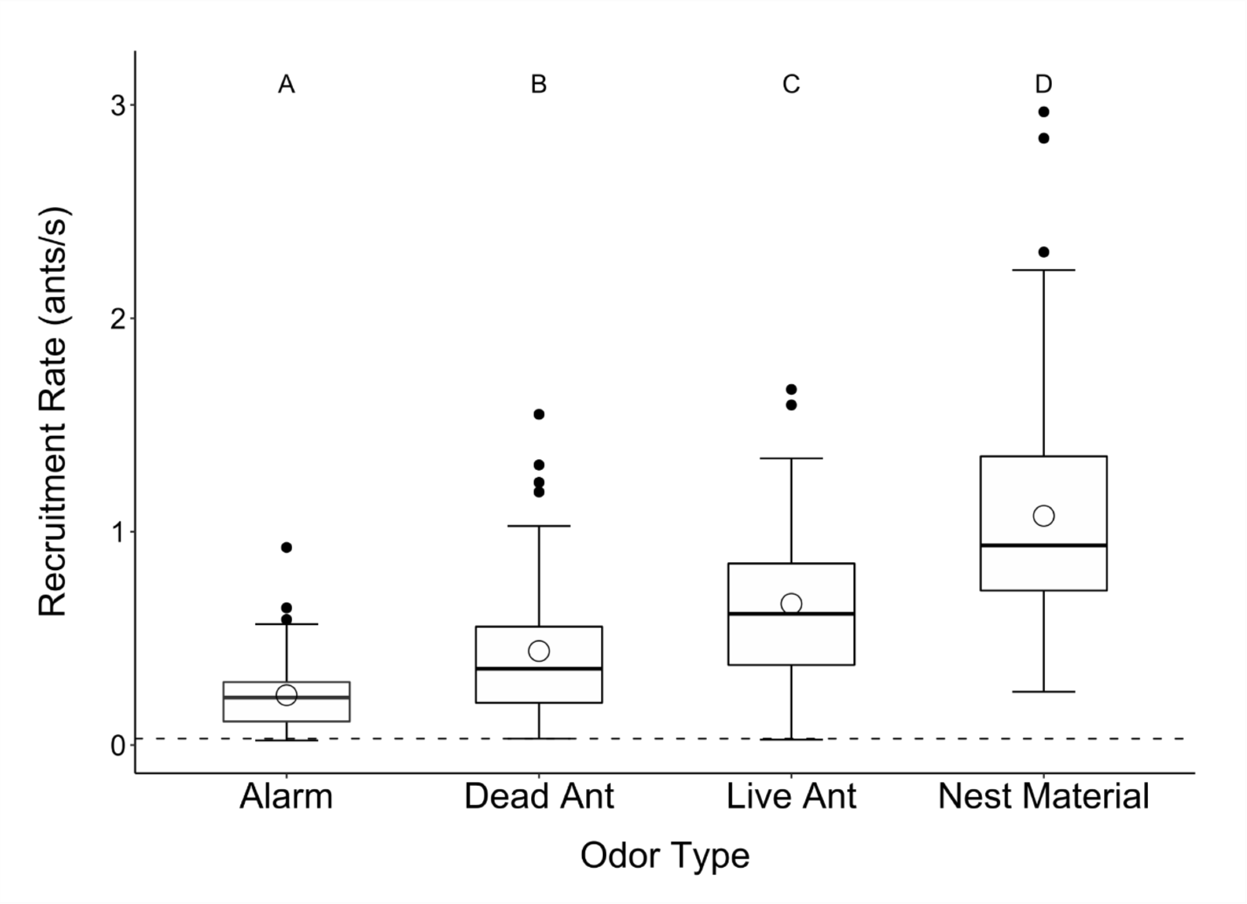

Figure 2. Boxplots of *Eciton hamatum* recruitment rate in ants per second to each odor treatment derived from prey ants (*Acromyrmex octospinosus*). Each box presents combined data from 7 colonies, except for the live ant odor treatment which represents 5 colonies (Alarm trials, N= 70; Dead Ant trials, N= 82; Live Ant trials, N= 55; Nest Material trials, N= 92). In each boxplot, the box encompasses the interquartile range, a line is drawn at the median, an open circle represents the mean, whiskers extend to the upper and lower quartiles (± 1.5 times the interquartile range), and outliers are shown by the filled circles outside the whiskers. The different letters denote significantly different means among odor treatments, following square-root transformation of the data to meet the assumptions of normality and equal variances (post-hoc Tukey's HSD, *P*<0.001 for all comparisons). The dashed horizontal line represents the mean recruitment rate across all

non-prey ant treatments (0.03 ants/s SD ± 0.05 ants/s), emphasizing the lack of recruitment response to non-prey odors.

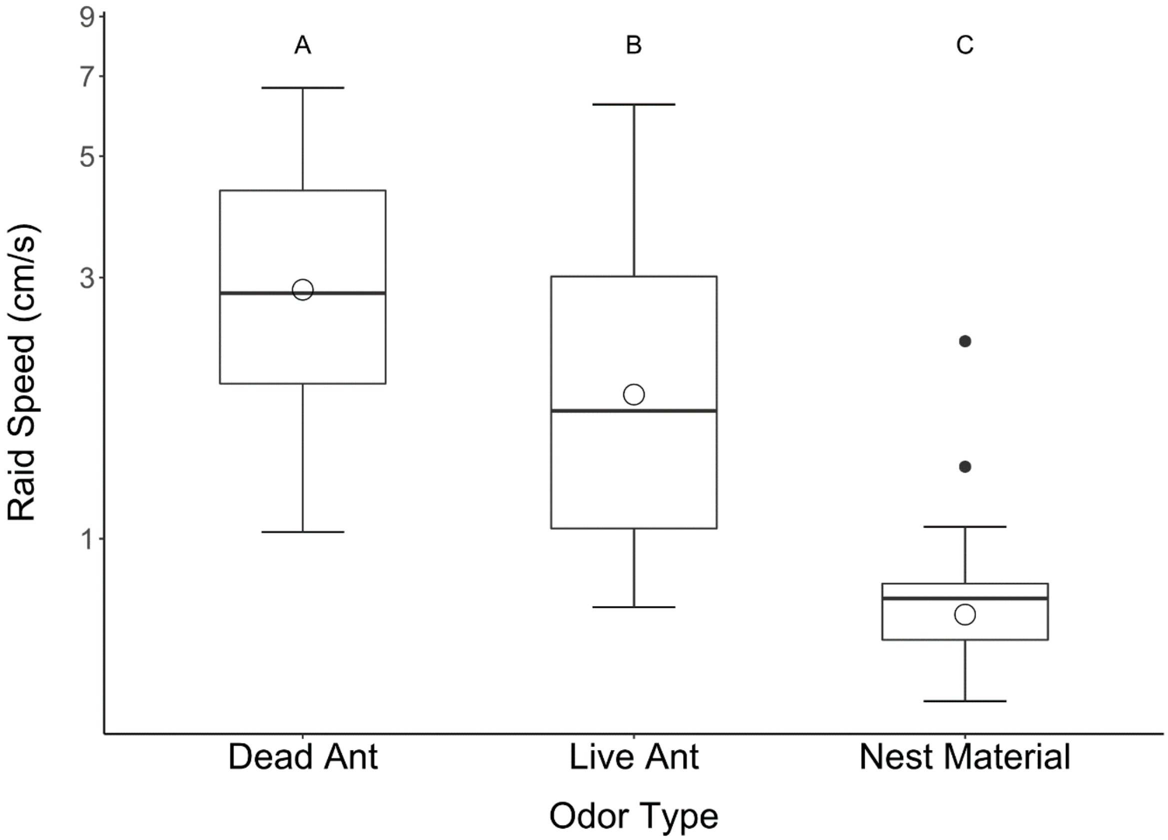

Figure 3. Boxplots of *Eciton hamatum* raid speeds in centimeters per second to each odor type derived from prey ants (*Acromyrmex octospinosus*). Each box presents aggregated data from 7 colonies, except for the live ant odor group which represents 5 colonies (Dead Ant trials, N= 82; Live Ant trials, N= 55; Nest Material trials, N= 92). In each boxplot, the box encompasses the interquartile range, a line is drawn at the median, an open circle represents the mean, whiskers extend to the upper and lower quartiles (± 1.5 times the interquartile range), and outliers are

shown by the filled circles outside the whiskers. The different letters denote significantly different means among odor treatments, following log10 transformation of the data to meet the assumptions of normality and equal variances (post-hoc Tukey's HSD, *P*<0.001).

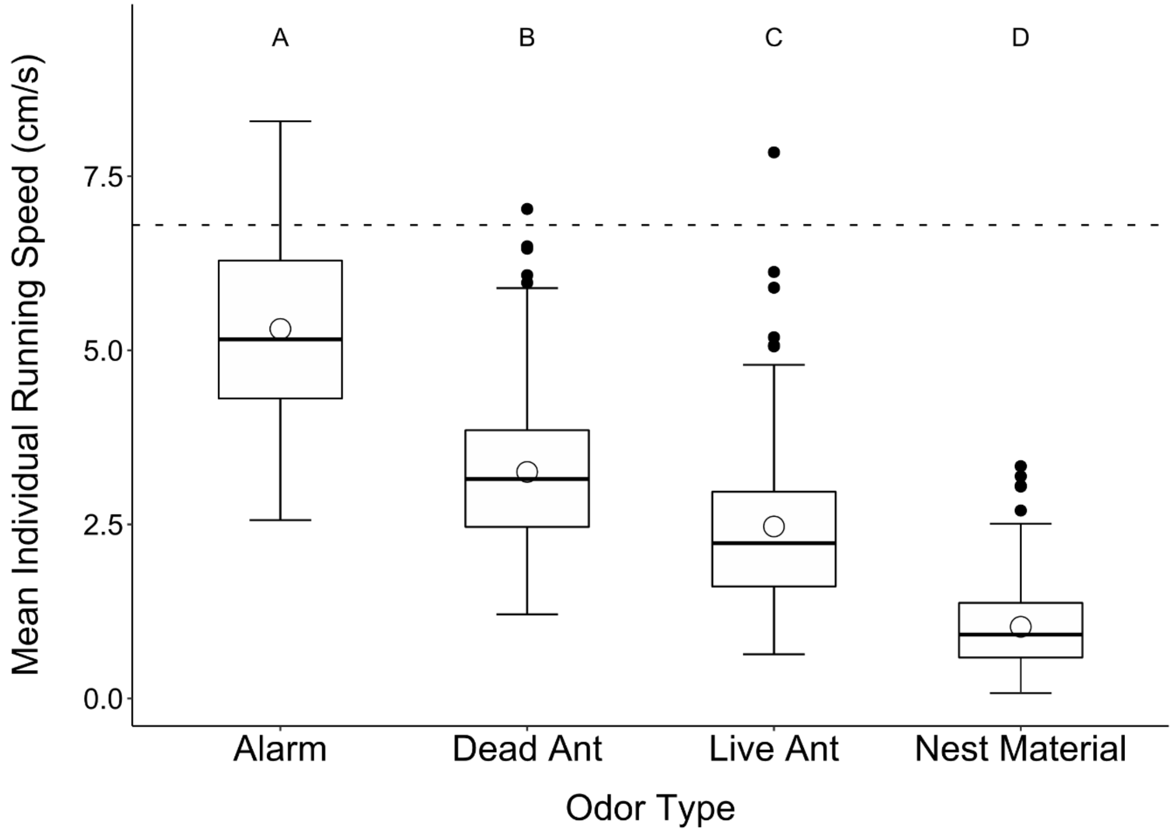

Figure 4. Boxplots of mean individual running speed in centimeters per second to each odor type derived from prey ants (*Acromyrmex octospinosus*). Each box presents aggregate data from 7 colonies save for the Live odor group which represents 5 colonies (Alarm, N= 210 ants; Dead Ant, N= 210 ants; Live Ant, N= 150 ants; and Nest Material, N= 210 ants). In each boxplot, the box encompasses the interquartile range, a line is drawn at the median, an open circle represents the mean, whiskers extend to the upper and lower quartiles (± 1.5 times the interquartile range), and outliers are shown by the filled circles outside the whiskers. The different letters denote

significantly different means among odor treatments, following square-root transformation of the data to meet the assumptions of normality and equal variances (post-hoc Tukey's HSD, $P<0.001$ for all pairwise comparisons). The dashed horizontal line represents the mean individual running speed across all non-prey ant treatments (6.8 cm/s SD ± 1.7 cm/s), emphasizing the higher running speed that is maintained in the presence of non-prey odors.

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