Distinct types of foragers in the ant *Ectatomma ruidum*: typical foragers and furtive thieves

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Abstract

A principal benefit of social living is the communal defense of resources. However, in ant *Ectatomma ruidum*, specialized thieves often circumvent detection by conspecific non-nestmates, and those detected are peacefully expelled. Colonies can gather food through typical foraging (opportunistically tracking prey or nutrients in the home range) or by robbing (entering a conspecific nest, waiting for, and then removing a newly arrived food item carried in by a forager). Here, we conducted behavioral assays to determine if robbers (or “thieves”), carrying purloined food, manifest behaviors that minimize the probability of detection relative to non-thieving individuals. We found several lines of evidence that individuals carrying stolen food behave distinctly from normal non-thieving foragers. When returning to their home nest with a stolen food item, thieves had fewer encounters with conspecifics, were more likely to pause during movement, and were more likely to release food when grasped. Thieves walked faster while traveling in the victim’s home range, compared to their own home range. When experimentally perturbed, thieves were more likely to reverse their direction of movement, while normal foragers continued moving in the same direction. Because the carbon and nitrogen stable isotope composition, as well as the C:N ratio, was the same for both thieves and non-thieves, we conclude that both groups were accessing the same food sources, using different behaviors to repartition a common resource. We conclude that, although thieves are morphologically indistinguishable from non-thieving foragers, their food retrieval behaviors are distinct in a manner that reduces the probability of detection and aggressive interactions with other conspecifics. We propose that thieves are a distinct caste of forager in *Ectatomma ruidum*.

Introduction

Food often limits fitness, and animals in want of food may rob it from other individuals (Breed, Cook, & Krasnec, 2012; Brockmann & Barnard, 1979). A critical function of social groups is the collective defense of shared food resources. Food robbing is commonly known to occur when an individual of one species robs from another species, but intraspecific food robbing is observed in a variety of lineages as well (Steele & Hockey, 1995).

The selective pressure for food robbing is typically matched with the evolution of strategies to detect, deter and punish individuals that attempt to rob food (Breed et al., 2012). For example, in the honeybee *Apis mellifera*, behaviorally specialized guard workers monitor the nest entrance to screen individuals entering the colony and will engage in potentially mortal combat if individuals from other colonies are detected at the nest entrance (Mann & Breed, 1997; Moore, Breed, & Moor, 1987). Conspecific food robbing events occurs between honeybee colonies, but as food scarcity and thieving attempts increase, successful rejections of non-nestmates also increase (Couvillon et al., 2008; Downs & Ratnieks, 2000).

In ants, mechanisms that prevent food robbing are so effective that intraspecific thievery has only been documented in two species: *Messor aciculatus* (Yamaguchi, 1995) and *Ectatomma ruidum* (Breed, Snyder, Lynn, & Morhart, 1992; Perfecto & Vandermeer, 1993). Intraspecific food robbing remains undetected in other ant species, despite extensive observation of many other species. Nonetheless, in *E. ruidum*, intraspecific thievery among adjacent colonies is readily observed (Guénard & McGlynn, 2013). *E. ruidum* thieves specialize in stealing food from one

other colony (i.e., the 'victim nest'); the cuticular hydrocarbon profile of thieves is intermediate between the colony to which they are bringing food and the single colony from which they are removing food, presumably obfuscating nestmate recognition cues, and thieves are not known to switch to a non-thieving foraging habit (Breed et al., 1992; Jeral, Breed, & Hibbard, 1997). Thievery is thought to be evolutionarily stable only at low frequencies (Brockmann & Barnard, 1979; Ruxton & Broom, 1999), but thieving is a common activity in *E. ruidum* colonies, at least in Costa Rica and Panama (Breed, McGlynn, Stocker, & Klein, 1999). Like other social insects, colonies of *E. ruidum* are less vigilant against interlopers when food is relatively abundant in the environment (Guénard & McGlynn, 2013).

Thievery in *E. ruidum* is uniquely overt and widespread, and is undetected in other ant species. Intraspecific kleptoparasitic behavior in *E. ruidum* persists despite the fact that colonies are more vigilant against thieves when more thieving occurs (Jandt, Hunt, & McGlynn, 2015). It is broadly accepted that the ecological success of social insect colonies emerges from the collective ability to acquire resources and defend them from competitors. Thievery within *E. ruidum* suggest very poor abilities in protecting resources, but nonetheless this species is among the most widespread and locally abundant ants in the Neotropics (Schatz & Lachaud, 2008). To address this apparent contradiction, we wish to understand how foragers that act as thieves and collect resources from the insides of neighboring nests are distinct from 'normal' (non-thief) foragers that collect resources from the surrounding leaf-litter.

Here we test whether intraspecific thieves are behaviorally and physiologically distinct from non-thieves, in addition to their obvious specialization in acquiring purloined food items. Anecdotal evidence from prior investigations suggested that thieves are sneaky: they are fast,

they hide, they drop food, and switch course – making them more difficult to follow (Jandt, Hunt & McGlynn 2015). If thieves that remove food from other colonies function as a distinct type of forager, then we expect thieves will engage in a particular set of behaviors after retrieving stolen materials to avoid being “caught in the act” of thieving. Alternatively, if thieves are not behaviorally distinct from other foragers (i.e., they are only different from non-thieves with respect to the location of food collection), then individuals that retrieve food from a victim nest should exhibit the same behaviors as other foragers. We also investigated if thieves and non-thieves were compositionally different from one another, using stable isotope composition to evaluate differences in the food source of tissue. All together, we explore whether or not thieves can be considered a separate group, or caste, from normal foragers.

Methods

We studied *Ectatomma ruidum*, an omnivorous ground-nesting ant species, with workers sized ca. 7 mm in length. Colonies contain up to a few hundred workers, and the diets of colonies typically consists of arthropods and nectar. The pattern of thievery in this species was described by Breed et al. (1992), Jeral et al. (1997) and Perfecto and Vandermeer (1993). Each colony receives food from a relatively small number of thieves (less than ten individuals), each of which specializes on removing food items from a particular colony nesting in the vicinity of their home colony. The relative concentrations of hydrocarbon compounds on the exoskeletons of *E. ruidum* serve as nestmate recognition pheromones, and the hydrocarbons found on the thieves are intermediate between the colonies from which they are delivering food and those from which they are removing food (Jeral et al., 1997). Thieves may be distinguished from non-thieves by

being observed in the act of removing food from the nest of one colony and carrying it towards the nest of a different colony. As *E. ruidum* is a monodomous species, the field identification of thieves from their behaviour is straightforward.

Fieldwork was conducted during June-August 2014 at La Selva Biological Station, located in a lowland tropical wet forest in the Caribbean slope of Costa Rica. La Selva receives a mean annual rainfall of ca. 4m, with the majority occurring during May-Dec. Work was conducted on colonies nesting within the arboretum of the research station. This area has an open understory and a shallow litter layer that has also facilitated previous experiments on *E. ruidum* (Guénard & McGlynn, 2013; Jandt, Hunt & McGlynn 2015; McGlynn, Dunn, Wayman, & Romero, 2010).

We established four sites, in which all colonies of *E. ruidum* were detected through exhaustive searching and baiting (n = 58 colonies). Twenty-four colonies were arbitrarily selected, and home ranges were delineated by following the movements of foragers, after the methodology of Breed, McGlynn, Stocker, & Klein (1999) and McGlynn, Shotell, & Kelly (2003). Field assays were conducted to quantify the behavior of individuals while carrying a food item as follows: the food item used throughout the experiments, a 8 mm³ piece of ham, was readily handled by foragers in a way that did not disrupt movement. This piece of ham is equivalent to a high quality, though modestly sized, item of prey that might be collected by foragers. To establish home ranges, we provided food items to ants using forceps, which immediately elicited food-carrying behavior back to the home nest.

Rates of Travel and Encounters with Conspecifics

The rate of travel was determined by measuring the time and distance for an individual to carry a food item from the site of presentation to the entrance of a nest. For non-thieves, food was presented ca. 50cm from the nest entrance. For trials involving thieves, individuals were observed as food was carried out from the victim nest for a distance of 50 cm towards their home nest. All replicates of 47 thieves and 84 non-thieves were standardized to the rate of cm/s; in three observations, the distance was less than 50cm before the thief reached their home nest. In the 13 colonies with mapped home ranges, data were divided into rates of travel outside and inside the home range. In these colonies, workers were followed the entire route to their home nest.

We recorded the number of encounters with conspecifics, and the number of pauses and duration of pauses that ensued post-encounter while the focal individual (thief or non-thief) travelled back to its home nest. An **encounter** was recorded if an antenna of the focal individual touched another conspecific ant, or if an antenna of the conspecific ant touched the focal individual. A **pause** was recorded if the ant stopped forward movement for more than two seconds.

Response to Perturbation

A bioassay was conducted to compare the response of thieves and non-thieves to external perturbation. The tool we used for perturbation was a freezer-killed *E. ruidum* worker mounted on the tip of a 25 cm piece of wire (i.e., “conspecific target”). The individual used for this target was collected hundreds of meters from any of our sites (and therefore, unlikely to have been a member of the home or victim colony used in the assay). As in the ‘Rate of Travel’ assays, for

non-thieves, food was presented to arbitrarily selected wandering individuals in the leaf-litter within the home-range, and for thieves, individuals were observed as food was carried out from the victim nest. An active focal individual (thief or non-thief) was identified and followed for at least 20 cm. The conspecific target was waved four strokes in front of the focal ant over one second, at a distance of ca. 3mm from her antennae. The behavior of the focal ant was observed and two non-exclusive responses were scored: **pause** (lack of forward movement for a minimum of two seconds), and **change in direction** (change in direction of movement > 90°). After the focal individual re-commenced carrying the food item back to the nest for a minimum of 15 cm, we picked the ant up by its legs with forceps and recorded whether the ant dropped the food item as a result. This protocol was immediately repeated for a pairwise comparison, with thieves and non-thieves from the same colony.

Isotope Analysis

Individuals from the external perturbation bioassay were collected for stable isotope analysis to infer differences in diet, by using the relative proportion of ^{13}C and ^{15}N comprising the tissue of thieves and non-thieves. Individuals were oven dried for 24 h at 50° C, legs were removed, and ca. 1 mg of leg material was weighed on an analytical balance and enclosed in a tin capsule (Costech Analytical Technologies, Valencia, USA). Samples were analyzed for carbon and nitrogen stable isotope and total mass composition using a Eurovector Elemental Analyzer configured with a Delta V Stable Isotope Ratio Mass Spectrometer; carbon and nitrogen stable isotope values are reported in standard delta-notation relative to the standards VPDB and air, respectively (Post et

al., 2007). When we compared the C and N isotopic composition, as well as the C:N mass ratio, of 50 individuals sampled within our study.

Assessment of the C and N stable isotope composition of arthropod tissues is an established method used to perform diet analysis, to reconstruct food webs and to examine feeding behavior (Hood-Nowotny & Knols, 2007) that has a long and useful history of application within ant ecology (e.g., Fisher, Sternberg & Price, 1990; Blüthgen, Gebauer & Fiedler, 2003; Tillberg 2004). There are developmental distinctions in isotopic composition of ants that have not yet been accounted by differences diet, as adult worker ants have exhibited higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than brood (Tillberg et al., 2006). Ottonetti et al. (2008) found that $\delta^{15}\text{N}$ value was significantly correlated with multiple indices of ecological performance.

Statistical Analyses

For statistical analyses, the frequency of pauses and encounters were compared using ordinal logistic regression. Movement rates of thieves inside and outside the home ranges were evaluated using matched pairs tests. All other analyses were conducted using a Generalized Linear Model, using a binomial response for response variables with two categories. Rates of travel were log converted for analysis to normalize distributions. Statistical analyses were conducted using JMP 11.0 (SAS Institute, Cary, NC, USA).

Results

Rates of Travel and Encounters with Conspecifics

As thieves were removing experimentally-introduced food from a colony, their movements were different from the movements demonstrated by non-thieves that were traversing the same distance carrying an equivalent experimental food item (Figure 1). Over a distance of 50cm, the thieves paused more frequently than non-thieves (Figure 1; GLM $\chi^2_1 = 24.2$, $N=124$, $p<0.0001$), and the thieves encountered fewer individuals than non-thieves (GLM $\chi^2_1 = 12.5$, $p=0.0004$). Even though thieves paused more frequently, the mean rate of movement of thieves in the home range of the nest from which food was removed was 1.77 ± 0.20 SE cm/s, compared to a mean rate of 1.36 ± 0.17 cm/s after crossing the border into their home range (matched pairs test, $t_{12}=2.37$, $N=13$, $p=0.035$).

Response to Perturbation

Thief ants responded differently to the perturbation assay than non-thief ants (Figure 2). Thieves subjected to the perturbation assay reversed direction more frequently (77%) than non-thieves (32%; GLM $\chi^2_1 = 14.5$, $p<0.0001$). The frequency of pausing was higher in thieves (89%) than non-thieves (59%; GLM $\chi^2_1 = 8.26$, $p=0.004$). Among individuals that paused, the mean duration of the pause was longer in thieves ($14.5 \text{ s} \pm 1.6$) than non-thieves ($6.25 \text{ s} \pm 1.3$; GLM $\chi^2_1 = 12.5$, $p=0.0004$). After individuals were picked up with forceps at the end of a trial, thieves dropped their food item 67% of the time, while non-thieves dropped the food item 36% of the time (GLM $\chi^2_1 = 5.36$, $p=0.021$).

Isotope Analysis

We observed no difference within each of these measures between thieves ($\delta^{13}\text{C} = -26.6 \pm 0.6 \text{ ‰}$ SD; $\delta^{15}\text{N} = 8.1 \pm 0.6 \text{ ‰}$; C:N = 3.65 ± 0.06 ; n=23) and non-thieves ($\delta^{13}\text{C} = -26.5 \pm 0.5 \text{ ‰}$; $\delta^{15}\text{N} = 8.3 \pm 0.5 \text{ ‰}$; C:N = 3.60 ± 0.03 ; n = 27). The $\delta^{13}\text{C}$ values that we observed were similar to those seen in large-scale studies across arthropod families (e.g., Halaj, Peck & Niwa [2005] sampled 22 species within 22 arthropod families and found $\delta^{13}\text{C}$ values ranging from -27 to -21 ‰), and indicative of a reliance upon C3 plant tissue, across various stages of decomposition (Dawson et al., 2002), after taking into account the widely accepted values of isotopic enrichment during tissue synthesis after dietary assimilation (i.e., Feldhaar, Gebauer & Blüthgen, 2010; McCutchan et al., 2003).

The $\delta^{15}\text{N}$ values that we observed are consistent with other terrestrial ants foraging for arthropod prey, consistent with soil organic matter as a food source (Natlhoffer & Fry, 1988). Ponsard & Arditi (2000) found that the $\delta^{15}\text{N}$ value of soil macro-invertebrates commonly reflects the local $\delta^{15}\text{N}$ value of leaf litter, and the values that we found were similar to those reported for *Tetramorium* sp. studied by Penick, Savage & Dunn (2015).

Discussion

Every colony of *E. ruidum* simultaneously maintains individuals that collect the same type of food item, but with two distinct foraging strategies. Workers of these foraging types are behaviorally and distinct from one another, but rely upon a common pool of food resources. The disparate behaviors that make up these two strategies effectively serve to repartition the original pool of resources gained during primary foraging. The first foraging strategy is “normal,” with workers that collect food from within their territories. These individuals find food within the

home range, walk in a straight line back to the nest, encounter other ants along the way, interact with them, and carry on in a nonchalant fashion. The second foraging strategy is thievery, in which workers collect food from inside a colony outside the home colony's home range. These individuals walk more slowly, pause more frequently, and avoid encountering conspecifics en route. These individuals are also more prone to reverse direction when perturbed and drop their pilfered food items when grabbed.

The presence of distinct foraging strategies in *E. ruidum* is notable because individual differences in social insects are more often recognized with respect to reproductive potential or division of labor. The identification of a distinct foraging strategy – but for the same type of foraging substrate – is uncommon. *Polybia occidentalis* wasp foragers specialize on pulp vs prey/nectar foraging (O'Donnell & Jeanne, 1990) and honeybee (*Apis mellifera*) foragers specialize on pollen vs nectar foraging (Page, Rueppell, & Amdam, 2012), but these examples describe individuals that have different preferences for what they will forage on. The predilection for specialized foraging behaviors also occurs in *E. ruidum*, as foragers may be subdivided into individuals that attack prey by stinging and those that transport food that has already been killed (Schatz, Lachaud, & Beugnon, 1996).

Like soldiers and workers in other species of ants, thieves and foragers are non-reproductive individuals. However, unlike soldiers and workers, thieves are not morphologically different from foragers. Aside from behaviors that may be characterized as “sneaky” – such as ducking under nearby leaves, trying to outrun an approaching pair of forceps, or dropping their food – thieves and foragers are indistinguishable. The Carbon and Nitrogen composition of the thieves does not differ from non-thieves, which may reflect differences in larval provisioning or

feeding behaviors as an adult. The etiology of thievery in *E. ruidum* remains enigmatic, and it is not known if this is a learned behavior. The lack of overt dietary differences provides an additional piece of evidence for investigation into the development of thieves. It does not appear that thieves are consuming, or being fed during development, a different food source than that is provided to the rest of the colony. Their distinct behavioral repertoire merely repartitions resources primarily gained through initial foraging.

The apparent rarity of conspecific thievery in ants leads us to ask whether any properties of *E. ruidum* may have facilitated the evolution of thievery. Colonies can incur a reduction in productivity when thieves are present in the population, though this cost is reduced in denser populations (Jandt, Hunt & McGlynn. 2015). The cost of detection is very low for the thief, which is physically removed from the environment temporarily, but remains unharmed and will soon return to steal from the same colony in the future. The lack of lethal aggression against detected thieves must influence the cost/benefit tradeoffs of thieving and vigilance against thieves. The genetic structuring of populations may have caused low levels of intercolonial aggression, as is known in the congener *E. tuberculatum* (Zinck et al., 2008). *E. ruidum* is known for nesting in open environments and in high density (Schatz & Lachaud, 2008), and the physical structure of the environment may influence the success of food robbing, and open environments may facilitate the rapid egress of thieves (Paulson, 1985). Most species of ants, especially those in the tropics, are not subjected to intense colony-level behavioral experimentation, and it may be the case that thievery is not a rare phenomenon, but one that is widely undocumented. With the lack of data, we do not have an opinion on this matter. Until that time comes, the present work on

furtive thievery in *E. ruidum* is a foundation for understanding the maintenance of intraspecific thievery in ants.

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Figure 1. After experimental provision of a food item and 50 cm of travel, thieves were less likely to encounter other individuals and more likely to pause while traveling. Statistical analyses are in results.

Figure 2. After encountering a conspecific target (a freeze-killed ant mounted on a probe), thieves were more likely to reverse direction, pause, and drop food than non-thief ants. Black bars indicate the frequency of behaviors. Statistical analyses are in the results.

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