



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



Terrence P. McGlynn^{a,*}, Russell Graham^a, Jane Wilson^b, Jeremy Emerson^a, Jennifer M. Jandt^c, A. Hope Jahren^d

^a Department of Biology, California State University Dominguez Hills, Carson, CA, U.S.A.

^b Columbine Middle School, Montrose, CO, U.S.A.

^c Department of Zoology, University of Otago, Dunedin, New Zealand

^d Department of Geology and Geophysics, University of Hawaii at Manoa, Honolulu, HI, U.S.A.

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A principal benefit of social living is the communal defence of resources. However, in the 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 behavioural assays to determine whether robbers (or 'thieves'), carrying pilloined food, manifest behaviours that minimize the probability of detection relative to nonthieving individuals. We found several lines of evidence that individuals carrying stolen food behave distinctly from normal nonthieving 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 travelling 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 nonthieves, we conclude that both groups were accessing the same food sources, using different behaviours to repartition a common resource. We conclude that, although thieves are morphologically indistinguishable from nonthieving foragers, their food retrieval behaviours 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 *E. ruidum*.

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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 defence 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*, behaviourally 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. Nevertheless, in *E. ruidum*, intraspecific thievery among adjacent

* Correspondence: T. P. McGlynn, Department of Biology, California State University Dominguez Hills, Carson, CA 90747, U.S.A.

E-mail address: terry.mcglynn@gmail.com (T. P. McGlynn).

colonies is readily observed (Guénard & McGlynn, 2013). *Ectatomma ruidum* thieves specialize in stealing food from another 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 colony from which they are removing food, presumably obfuscating nestmate recognition cues, and thieves are not known to switch to a nonthieving 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 behaviour 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* suggests very poor abilities in protecting resources, but this species is nevertheless 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 neighbouring nests are distinct from 'normal' (nonthief) foragers that collect resources from the surrounding leaf litter.

Here we tested whether intraspecific thieves are behaviourally and physiologically distinct from nonthieves, 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, and they drop food and switch course, making them more difficult to follow (Jandt et al., 2015). If thieves that remove food from other colonies function as a distinct type of forager, then thieves should engage in a particular set of behaviours after retrieving stolen materials to avoid being 'caught in the act' of thieving. Alternatively, if thieves are not behaviourally distinct from other foragers (i.e. they are only different from nonthieves with respect to the location of food collection), then individuals that retrieve food from a victim nest should show the same behaviours as other foragers. We also investigated whether thieves and nonthieves are compositionally different from one another, using stable isotope composition to evaluate differences in the food source of tissue. All together, we explored whether or not thieves can be considered a separate group, or caste, from normal foragers.

METHODS

We studied *E. ruidum*, an omnivorous ground-nesting ant species, with workers measuring about 7 mm in length. Colonies contain up to a few hundred workers, and the diets of colonies typically consist 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 10 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 nonthieves 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 about 4 m, with the majority occurring during May–December. Work was conducted on colonies nesting within the arboretum of the research station. This area has an open understory and a shallow leaf litter layer that has also facilitated previous experiments on *E. ruidum* (Guénard & McGlynn, 2013; Jandt et al., 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). We arbitrarily selected 24 colonies and delineated home ranges by following the movements of foragers, after the methodology of Breed et al. (1999) and McGlynn, Shotell, and Kelly (2003). We conducted field assays to quantify the behaviour of individuals while carrying a food item (8 mm³ piece of ham). Each food item was readily handled by foragers in a way that did not disrupt movement and was equivalent to a high-quality, although 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 behaviour back to the home nest.

Rates of Travel and Encounters with Conspecifics

We determined the rate of travel 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 nonthieves, food was presented about 50 cm 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 nonthieves were standardized to the rate of cm/s; in three observations, the distance was less than 50 cm before the thief reached its home nest. In the 13 colonies with mapped home ranges, we divided the data 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, the number of pauses and the duration of pauses that ensued post-encounter while the focal individual (thief or nonthief) 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 2 s.

Response to Perturbation

We conducted a bioassay to compare the response of thieves and nonthieves to external perturbation. The tool we used for perturbation was a freeze-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 metres from any of our sites (and therefore, unlikely to have been a member of the home or the victim colony used in the assay). As in the assays for rate of travel, for nonthieves, we presented food to arbitrarily selected wandering individuals in the leaf litter within the home range, and for thieves, we observed individuals as food was carried out from the victim nest. We identified an active focal individual (thief or nonthief) and followed her for at least 20 cm. We waved the conspecific target in front of the focal ant four times for 1 s, at a distance of about 3 mm from her antennae. We observed the behaviour of the focal ant and scored two nonexclusive responses:

pause (lack of forward movement for a minimum of 2 s), and change in direction (change in direction of movement $>90^\circ$). After the focal individual recommenced 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 nonthieves 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 nonthieves. Individuals were oven-dried for 24 h at 50°C , legs were removed, and about 1 mg of leg material was weighed on an analytical balance and enclosed in a tin capsule (Costech Analytical Technologies, Valencia, CA, U.S.A.). Samples were analysed 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 Vienna Pee Dee Belemnite (VPDB) and air, respectively (Post et al., 2007). When we compared the carbon and nitrogen isotopic composition, as well as the C:N mass ratio, of 50 individuals sampled within our study.

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

Statistical Analyses

We compared the frequency of pauses and encounters using ordinal logistic regression, and we evaluated movement rates of thieves inside and outside the home ranges 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 transformed prior to

analysis to normalize distributions. Statistical analyses were conducted using JMP 11.0 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

Rates of Travel and Encounters with Conspecifics

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

Response to Perturbation

Thieves responded differently to the perturbation assay than nonthieves (Fig. 2). Relative to nonthieves, thieves reversed direction more frequently (32% versus 77%; GLM: $\chi^2_1 = 14.5$, $P < 0.0001$) and paused more frequently (59% versus 89%; $\chi^2_1 = 8.26$, $P = 0.004$). Among individuals that paused, the mean \pm SE duration of the pause was longer in thieves (14.5 ± 1.6 s) than in nonthieves (6.25 ± 1.3 s) ($\chi^2_1 = 12.5$, $P = 0.0004$). After individuals were picked up with forceps at the end of a trial, thieves dropped their food item 67% of the time, while nonthieves dropped the food item 36% of the time ($\chi^2_1 = 5.36$, $P = 0.021$).

Isotope Analysis

We observed no difference in isotopic 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 nonthieves ($\delta^{13}\text{C} = -26.5 \pm 0.5\text{‰}$; $\delta^{15}\text{N} = 8.3 \pm 0.5\text{‰}$; 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, and 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, Mambelli, Plamboeck, Templer, & Tu, 2002), after taking into account the widely accepted values of isotopic enrichment during tissue

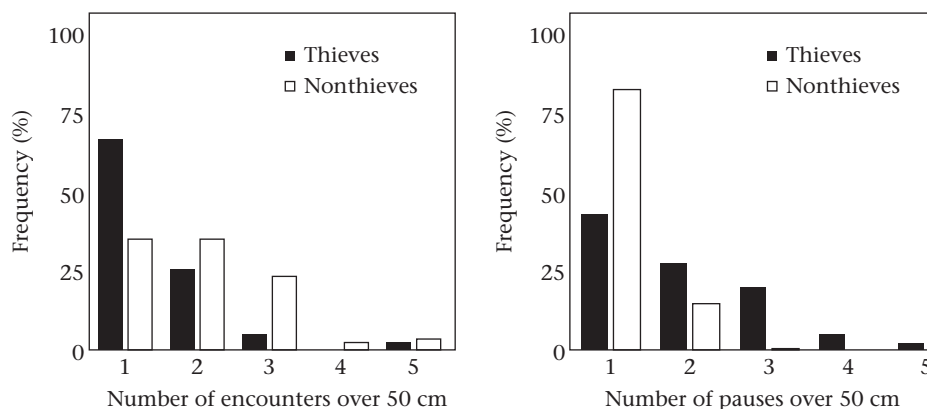


Figure 1. Mean frequency of the number of individuals encountered and the number of pauses made by *E. ruidum* thieves and nonthieves after experimental provisioning of a food item and 50 cm of travel (see Results for statistical analyses).

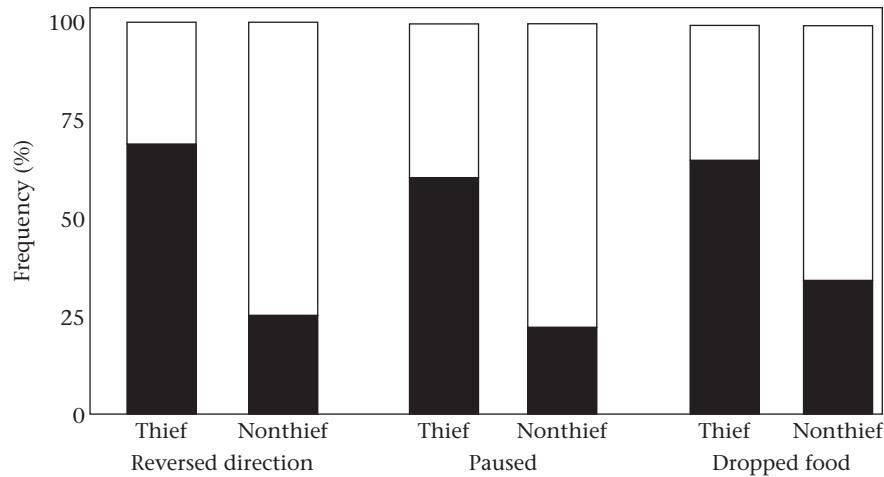


Figure 2. Percentages of *E. ruidum* thieves and nonthieves that reversed direction, paused or dropped food after encountering a conspecific target (a freeze-killed ant mounted on a probe). Black bars indicate the frequency of behaviours (see Results for statistical analyses).

synthesis after dietary assimilation (i.e. Feldhaar, Gebauer, & Blüthgen, 2010; McCutchan, Lewis, Kendall, & McGrath, 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 (Natehoffer & Fry, 1988). Ponsard and 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, and 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 behaviourally distinct from one another but rely upon a common pool of food resources. The disparate behaviours 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 that is outside their own 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 to 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 labour. The identification of a distinct foraging strategy, but for the same type of food, is uncommon. *Polybia occidentalis* wasp foragers specialize on either pulp or prey/nectar (O'Donnell & Jeanne, 1990) and honeybee (*A. mellifera*) foragers specialize on either pollen or nectar (Page, Rueppell, & Amdam, 2012), but these examples describe individuals that have different foraging preferences. The predilection for specialized foraging behaviours 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 nonreproductive individuals. However, unlike soldiers and workers, thieves are not morphologically different from foragers. Aside from behaviours 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 lack of differentiation extends to diet, as the carbon and nitrogen compositions of thieves and non-thieves do not differ. The etiology of thievery in *E. ruidum* remains enigmatic, and it is not known whether it is a learned behaviour. 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 fed a different food source during development or consume a different food source than other members of the colony. Their distinct behavioural 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, although this cost is reduced in denser populations (Jandt et al., 2015). The cost of detection is very low for thieves: they are physically removed from the victim colony environment unharmed, but they soon return to steal from the same colony again. The lack of lethal aggression against detected thieves must influence the cost–benefit trade-offs 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 *Ectatomma tuberculatum* (Zinck, Hora, Châline, & Jaisson, 2008). *Ectatomma ruidum* is known for nesting in open environments and in high density (Schatz & Lachaud, 2008), which may influence the success of food robbing and facilitate the rapid egress of thieves (Paulson, 1985). Most species of ants, especially those in the tropics, are not subjected to intense colony-level behavioural experimentation, and it may be that thievery is not a rare phenomenon, but one that is widely undocumented.

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