Intraspecific Thievery in the Ant *Ectatomma ruidum* is Mediated by Food Availability

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ABSTRACT

Animals modify their foraging strategies in response to environmental changes that affect foraging performance. In some species, cleptobiosis represents an alternative strategy for resource access. The environmental factors that favor the incidence or prevalence of cleptobiosis, however, are poorly described. The cleptobiotic Neotropical ant *Ectatomma ruidum* is characterized by a high frequency of thievery behavior, a specific type of intraspecific cleptobiosis, in which specialized thief workers insinuate themselves into nests of neighboring colonies and intercept food items brought into these nests. Here, we evaluate how colonies adjust thievery behavior in response to food availability. We supplemented food availability and measured how the incidence and intensity of thievery responded to resource availability. We found that the incidence and intensity of thievery decline in response to supplemental food, suggesting that thievery behavior is a response to resource limitation at the population scale. This finding indicates that the phenomenon of intraspecific thievery, although a rare strategy in among colonies of social animals, is a viable alternative foraging tactic in the context of competition and food limitation.

Abstract in Spanish is available in the online version of this article.

Key words: cleptobiosis; *Ectatomma ruidum*; food supplementation; foraging behavior; Formicidae; thievery.

FOOD RESOURCE AVAILABILITY CAN BE UNPREDICTABLE IN SPACE AND TIME, WHETHER FOR HUNTER-GATHERER HUMANS, dung beetles, or ants. This unpredictability has led to the evolution of strategies to maximize the benefit of foraging and to minimize the cost associated with foraging. Costs include time and energy spent during foraging (Fewell 1988, McGlynn *et al.* 2003), risk of predation (Nonacs 1990), exposure to environmental hazards (Cerdá *et al.* 1998), and interference competition (Traniello 1989). Because of these costs, natural selection acts heavily on strategies to maximize food discovery and retrieval, and in some cases, the evolution of alternative foraging tactics involving less foraging effort and risk may be favored (*e.g.*, Mathot & Giraldeau 2008).

In social insects, foragers collect food items within a home range and bring them to the nest. This leads to 'central-place foraging', where the 'central place' is the nest where successful foragers converge with food resources. While central place foraging may ameliorate the unpredictability of food resources (McGlynn *et al.* 2003), it also may incur costs. Specifically, sedentary nests are potentially susceptible to parasitic species that, rather than forage for food, exploit the aggregation of resources within nest sites (Buschinger 1986). Cleptobiosis is a particular form of social parasitism, in which thieves intercept the food collected by workers at areas around the nest or on trails used by foragers (Hölldobler 1986, Richard *et al.* 2004, LaPierre *et al.* 2007, Breed *et al.* 2012) and, in doing so, reduce their own foraging costs

(Curio 1976, Passera & Aron 2005). In ants, this behavior has been described several times at an inter-specific level (Hölldobler 1986, Perfecto & Vandermeer 1993, Espadaler *et al.* 1995, Grasso *et al.* 2004, Richard *et al.* 2004). In at least two cases, however, intraspecific cleptobiosis has been observed, in *Messor aciculatus* (Fr. Smith) in Japan (Yamaguchi 1995) and in the Neotropical *Ectatomma ruidum* (Roger) (Breed *et al.* 1990, 1992, 1999). A key difference between cleptobiosis between species and that within species, is that intraspecific cleptobiosis can be symmetrical, which is to say that any given colony can be the villain and the victim.

Ectatomma ruidum (Formicidae, Ectatomminae) is widespread throughout the Neotropics, from Mexico to Brazil (Fernández & Sendoya 2004). Colonies of this species are monodomous (single-nested) and monogynous, containing 50–300 workers (Lachaud *et al.* 1984, Breed *et al.* 1990, 1992, 1999, Schatz & Lachaud 2008, Lenoir *et al.* 2011). Nests have a single entrance, about 3–4 mm wide dug in the ground (Lachaud *et al.* 1984, Breed *et al.* 1990). This species exhibits a unique form of intraspecific cleptobiosis, which has been called thievery behavior, in which a worker of one nest will enter a neighboring nest of the same species, wait within the foreign nest, intercept food brought by a forager, and then leave the foreign nest with the food and bring it to its own nest (Breed *et al.* 1990, 1992, 1999). While resident *E. ruidum* workers tend to repel foreign workers outside of their nests and territories without injuries (Breed *et al.* 1990, 1992), thieves are able to infiltrate colonies through chemical camouflage and no specific aggressiveness is directed toward them (Breed

et al. 1992, Jeral *et al.* 1997). Thievery behavior is common within populations of *E. ruidum* and has been noted at several locations within the species' range (De Carli *et al.* 1998, Breed *et al.* 1999).

To date, studies of thievery have focused on a precise description of the behavior (Breed *et al.* 1990, 1992, 1999, Jeral *et al.* 1997) and the ecological consequences on foraging and nest distribution for the different protagonists (Yamaguchi 1995). Little is known about the factors that influence the frequency or even simply occurrence of intraspecific cleptobiosis in ants. In 1990, Breed and collaborators hypothesized that thievery within populations of *E. ruidum* might be a facultative response to high colony densities or to food competition. Later on, it was shown that the rate of thievery was independent of nest density (Breed *et al.* 1999), but the possibility that thievery rates are related to food supplies remains untested. Here, we hypothesize that food supplementation will modify the intensity of thievery observed in a population of *E. ruidum*. In this study, we modified food availability with daily additions of food and measured the foraging responses of *E. ruidum*. We expect that, as a result of this manipulation, colonies receiving supplemental food will experience a reduction in the rate of thievery, as well as lower rates of thievery relative to surrounding nests that do not receive supplemental food.

METHODS

SITE LOCATION AND DESIGN.—Work was conducted in the arboretum of La Selva Biological Station, Heredia Province, Costa Rica in June 2008. Six sites were selected. Each site had an area of 452 m^2, comprised of a circle with a 12 m radius. Each plot was separated from one another by at least 50 m, from edge to edge, far greater than the maximal foraging distance of any *E. ruidum* worker. For each site, a focal nest of *E. ruidum* was located at the center of a 5 m radius circle in the middle of the site and corresponded to the treated area receiving food supplementation. Each inner circle was delimited with flagging and each plot was exhaustively searched (for a minimum of twenty person-hours) until all colonies of *E. ruidum* were found, following a protocol involving direct searching for nests, feeding foragers, and baiting, as conducted in previous work (McGlynn *et al.* 2010). Nests outside the inner circle, when discovered, were also marked (up to 12 m from the center) (Fig. 1). During the food supplementation, any additional nests that were detected were marked.

PRE-TREATMENT ASSAY.—Forty-eight hours after we completed the establishment of sites with marked nests, six to seven study nests per site were randomly selected to measure the rate of thievery. Three to four nests were located within the inner circle areas, and two to three were located outside the inner circle. In total, twenty nests within treatment areas were measured for thievery (including the focal nests), and nineteen were measured outside treatment areas.

For each nest, ten food items (4-mm long cylinders of condensed white bread) were presented at the nest entrance. Over a
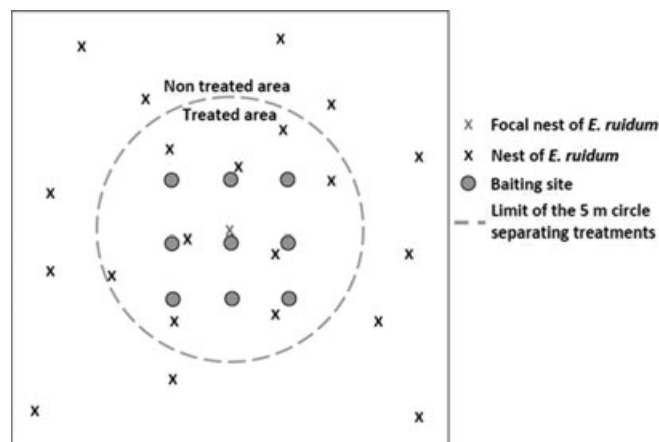

FIGURE 1. Design of the treated area for one selected site.

10-min duration, the number of items collected outside of the focal nest was recorded. Three different events were observed and recorded: (1) Collecting event—the food item was collected by a resident worker and brought within the focal nest; (2) Collecting and thievery events—the food item was collected and brought by a resident worker within the focal nest, but then intercepted within the focal nest by a thief which left the focal nest and transport the food item into a different nest; and (3) Exploiting event—the food item was collected by a worker from a foreign nest (later qualified as 'exploiters') which transport it to its nest. The number of thieves departing the nest with the supplemental food was recorded and followed (by a second observer) to the destination nest. For each thievery event, distances between origin nests and destination nests were measured. For each study nest, we calculated the proportion of food collected (number of food items collected/number of food items offered) and the proportion of thievery observed (number of food items stolen within the nest by a thief/number of food items collected).

FOOD SUPPLEMENTATION PROCEDURE.—Over seven consecutive days, about 3 mg of food was deposited daily adjacent to the entrance of each nest present within the treated area (within the 5 m radius circle). The supplemental food was alternated, either a mix of tuna and honey, or peanut butter, both of which are known to be rich in proteins, lipids, and carbohydrates. Furthermore, to adjust for the possibility that we might have not detected some nests within our treatment area, we added extra food that could be exploited by all the nests present in the area. Within the treated area, we added nine stations where food was deposited daily. The stations were separated by 1.5 m from each other within a square grid configuration (see Fig. 1). After a week of food provisioning, 24 hr elapsed without any food provisioning before the commencement of the post-treatment assay.

POST-TREATMENT ASSAY.—Using the same methods as in the pre-treatment assay, we measured thievery rate for areas inside and outside our treatment area on the same study nests. Four study

nests (three inside and one outside the supplementation area) that were used for pre-treatment measurements were not active or had relocated to new positions, so these nests were excluded; to accommodate this reduction in sample size, eight arbitrarily selected nests that had not been measured during the pretreatment assay were incorporated in the post-treatment measurement (three inside and five outside).

THIEVERY OCCURRENCE.—Thievery was considered to occur if at least one event of thievery was observed for the observed nest during the 10 min period of our observation. We used a chi-square test to compare the occurrence of thievery inside and outside of the treated areas before and after the application of treatments.

FOOD ITEMS COLLECTED BY FOREIGN WORKERS (EXPLOITERS).—We monitored the number of food items that were collected by exploiters while the food was standing outside of the focal nest entrance. Exploiters are individuals foraging on the territory of others, in this case at the vicinity of other nest entrances.

STATISTICAL ANALYSIS.—We evaluated the effect of food addition on the different foraging behaviors observed in *E. ruidum*. All our analyses used non-parametric Wilcoxon tests to compare the effects of the treatments. Non-parametric tests were used on account of ordinal and non-normally distributed data. We compared the proportion of food collected before and after the food addition for the areas located inside and outside the treated areas. We then compared the rate of thievery observed before the treatment between the treated areas and the non-treated areas. Similarly, we compared the effect of food addition on thievery rate after the food addition. Then we compared the rate of thievery observed before and after the food addition within the two different treatments with matched-pairs Wilcoxon signed-rank tests. Similar analyses were conducted on the proportion of total food and the proportion of food collected by exploiters. For these analyses, we used a subset of seventeen nests within the treated areas and of 18 nests within the non-treated areas for which we had data prior and after food supplementation. The larger dataset (20 nests inside the treated areas and 23 nests within the non-treated areas) included supplemental nests that did not have data for both periods.

RESULTS

NEST DENSITIES.—Within our six treatment areas, the mean nest density was 0.22 nest/m^2 (range: 0.10–0.37 nest/m^2), which corresponds to a mean 17.3 nests per treated area (range: 8–29 nests per 5 m radius area).

MEAN DISTANCE TRAVELED BY THIEF ANTS.—Forty-three thievery events were observed in their entirety, to measure the distance traveled by thieves. The distance traveled by thieves between the origin and destination nests ranged from 40 to 480 cm (mean $\pm$ SD = 148 $\pm$ 111 cm).

PERCENTAGE OF FOOD ITEMS COLLECTED.—Food supplementation did not modify the proportion of food items collected before and after within (mean $\pm$ sd: Interior zone: X $_{before}$ = 82.9 $\pm$ 2.6; X $_{after}$ = 71.3 $\pm$ 5.4; N = 17; Z = −18.5; P = 0.40, Wilcoxon matched-pairs signed-ranks test) or outside (mean $\pm$ SD: Exterior zone: X $_{before}$ = 89.2 $\pm$ 4.2; X $_{after}$ = 82.3 $\pm$ 4.8; N = 18; Z = −9.5; P = 0.54, Wilcoxon matched-pairs signed-ranks test) the treated areas.

OCCURRENCE OF THIEVERY.—Thievery was observed from 67 percent of the 39 nests surveyed prior to the application of food supplementation. No difference between the nests inside and outside the treated areas was observed (N = 39, χ^2 = 0.22, P = 0.63). After food supplementation, the overall occurrence of thievery observed was lower, with only 42 percent of occurrence observed. The twenty nests within the treated areas had a lower thievery frequency (25%) than the 23 nests outside the treated areas (57%) (N = 43, χ^2 = 4.37, P = 0.037).

INTENSITY OF THIEVERY.—Prior to food supplementation, no difference in the percentage of food robbed was observed (N = 39; Z = −0.07; P = 0.94) between the nests located inside or outside the treated areas (mean $\pm$ SD inside = 19.4 $\pm$ 4.5; outside = 15.3 $\pm$ 4.9). After food supplementation, the percentage of food robbed was significantly lower (N = 43; Z = −1.95; P = 0.05) for the nests located inside than outside the treated areas (mean $\pm$ SD inside = 7.2 $\pm$ 4.1; outside = 17.8 $\pm$ 5.2) (Fig. 2). When comparing the proportion of food robbed before and after food supplementation, we observed a significant decrease for the nests located within the treated areas (N = 17; Z = −27; P = 0.01, Wilcoxon matched-pairs signed-ranks test), but no change in the nests located outside of the treated areas (N = 18; Z = −4.5; P = 0.36, Wilcoxon matched-pairs signed-ranks test).
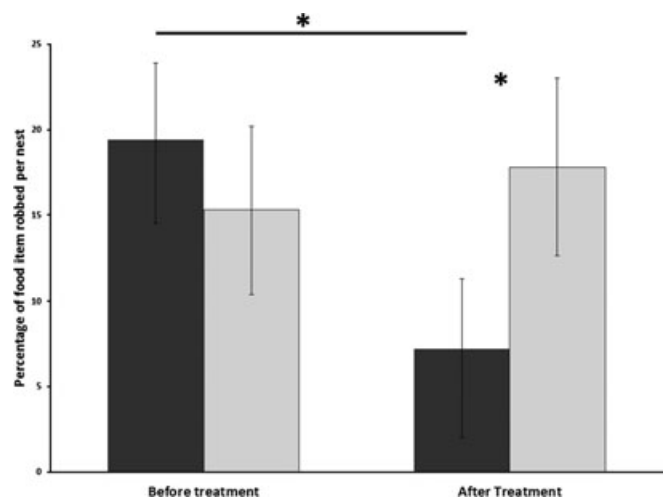

FIGURE 2. Percentage of food items stolen per nest before and after the treatment. In black are presented the nests located within the food-supplemented area and in light gray, the nests located outside the treated area. Significant differences between pairs are represented by a star.

FOOD ITEMS COLLECTED BY FOREIGN WORKERS (EXPLOITERS).—Prior to food supplementation, the fraction of food items collected by exploiters was greater inside the treated areas ($N = 39$, $Z = 2.10$, $P = 0.04$); as these areas were assigned independent of treatment, this P-value below alpha presumably is an instance of Type I error. After food supplementation, this difference was not observed, with a similar effect size, and the fraction of stolen items was not significantly different ($N = 43$, $Z = 1.65$; $P = 0.10$; Fig. 3). When comparing the percentage of exploiters for a similar area before and after food supplementation, we observed no difference between inside ($N = 17$, $Z = 18.5$; $P = 0.40$, Wilcoxon matched-pairs signed-ranks test) and outside the treated areas ($N = 18$, $Z = 9.5$; $P = 0.54$, Wilcoxon matched-pairs signed-ranks test).

DISCUSSION

MANY ANT SPECIES HAVE THE CAPACITY TO EXPRESS FLEXIBILITY IN THEIR FORAGING STRATEGIES, ACROSS SPACE AND TIME, as a function of local conditions. Foraging decisions are context-dependent in relation to the properties of food and environmental conditions outside of the nest (Carroll & Janzen 1973, Traniello 1989). For instance, ant colonies can adjust their foraging strategies to optimize food intake on the basis of food quality or quantity (Bernstein 1975, Breed et al. 1987), competition (Vepsäläinen & Savolainen 1990, Andersen & Patel 1994, Cerdá et al. 1998) or predation pressure (Feener 1988, LeBrun 2005). The importance of those factors has been highlighted over the past decades, but their importance on the expression of social parasitism–such as cleptobiosis–is still uncertain. In this study, we experimentally demonstrated that the rate of cleptobiosis observed in populations of E. ruidum is directly related to food limitation.
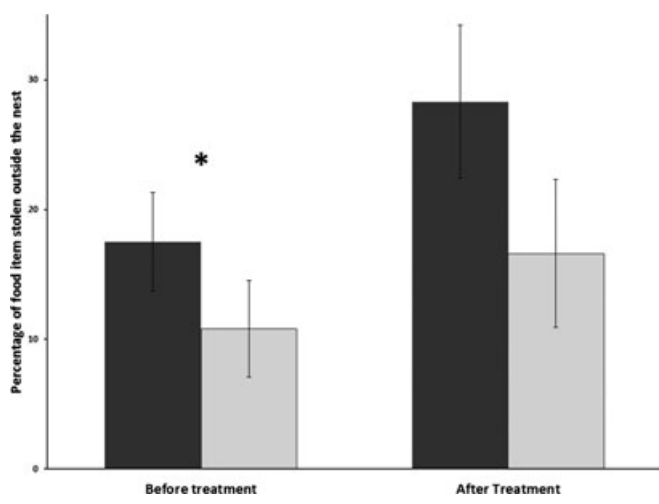

FIGURE 3. Mean number per nest of items stolen by exploiters outside the nest entrance before and after the treatment. In black are presented the nests located within the food-supplemented area and in light gray, the nests located outside the treated area. Significant differences between pairs are represented by a star.

Thievery was frequent among the nests of E. ruidum that we surveyed. Prior to our treatment, under natural conditions, at least two-thirds of the nests were experiencing some impact of thievery from workers of surrounding nests. These results are similar to those of Breed and collaborators who found that 7 of 10 nests suffered from thievery (1990). After only a week of food addition, and while no difference in foraging activity (number of food items collected per nest) was observed, the frequency of thievery decreased to be observed in only a quarter of the nests surveyed. Non food-supplemented nests maintained a similar rate of thievery to that observed prior to the experiment. Similar to frequency, thievery intensity responded negatively to food addition (Fig. 2). Fifteen to twenty percent of the food items collected by foragers were stolen in areas without food supplementation, but thievery rate was reduced by half in areas with food supplementation.

The nest density of E. ruidum found in our study of 0.22 nest/m^2 is similar, although in the lower tail of other studies reporting nest density for E. ruidum (Table 1). Despite this relatively low density of nests, thievery behavior was common in the population surveyed, further indicating that, as suggested by Breed et al. (1999), thievery is not limited to populations with high nest density.

In Mexico, E. ruidum had a strong predatory effect on the insect community in a coffee plantation, with a daily estimate per hectare of 150,000 insects collected (Lachaud et al. 1990). If rate of thievery is constant and estimated to be 15 to 20 percent of the prey brought to the nest as our results indicate, this could represent 22,000 to 30,000 prey items that could be stolen each day in similar conditions. As indicated by previous studies and our results, however, thievery rate is not uniform among colonies of E. ruidum (Breed et al. 1990) or as observed for the other known intraspecific cleptobiotic species M. aciculatus (Yamaguchi 1995), and this asymmetry could lead to strong difference in colony growth performance between colonies within a population. Two different evolutionary strategies could emerge within the population. First, colonies may invest in foraging and defensive strategies to protect the food collected from thieves; and second, colonies may invest more in thievery and less in foraging. In this context, thievery and foraging behaviors in E. ruidum relate to the producer-scrounger game developed for other organisms such as birds. In bird population, some individuals find food resources (producer tactic), while other individuals exploit their discoveries (scrounger tactic) (Barnard & Sibly 1981, Giraldeau & Beauchamp 1999). The expression of one of these strategies can be individual-dependent (Morand-Ferron et al. 2011, David & Giraldeau 2012) or context-dependant (Coolen 2002, Barta et al. 2004). As a counterpoint to work on birds, thievery in E. ruidum represents a great social insect model to study evolutionary aspects of foraging and of alternative strategies, and the factors that determine the use of thievery by specific colonies. In this regard, our results tend to show that the use of thievery as an alternative strategy is reduced by an increase of food within the population.

The mean distance covered by a thief to its destination nest was about 1.5 m with a maximum distance observed of 4.8 m. This corresponds to the foraging distance observed in other

TABLE 1. *Estimation of the nest density in Ectatomma ruidum according to several studies.*

References	Nest density (nest/m^2)	Location	Habitat description
Schatz & Wcislo 1999,	0.05	East Panama	Open habitat
Santamaría *et al.* 2009,	0.06	Southwestern Colombia	Shaded pasture
Breed *et al.* 1990,	0.14	La Selva, Costa Rica	Open habitat
Santamaría *et al.* 2009,	0.19	Southwestern Colombia	Sunny pasture
Jeral *et al.* 1997,	0.2	La Selva, Costa Rica	-
This study	**0.22**	**La Selva, Costa Rica**	**Arboretum (old growth)**
Lachaud 1990,	0.27	Chiapas, Mexico	Coffee and cacao plantation
Breed *et al.* 1999,	0.31	BCI, Panama	Mature secondary forest
Levings & Franks 1982,	0.33	BCI, Panama	Tropical deciduous forest
Schatz & Lachaud 2008,	0.61	Chiapas, Mexico	Cacao plantation
Pratt 1989,	1.06	BCI, Panama	Scrubby young forest
Schatz & Lachaud 2008,	1.12	Chiapas, Mexico	Coffee plantation
McGlynn *et al.* 2010	1.96	La Selva, Costa Rica	Same as present study

study of about 3 m although occasional distance up to 30 m has been noted (Lachaud *et al.* 1984). Several authors have noticed that the high nests density should favor the overlapping of foraging territory (Lachaud *et al.* 1984, Breed *et al.* 1999, Schatz & Lachaud 2008), with the exception of the results of Breed and collaborators (1990) who found that only few workers foraged outside of their territories. Here, we confirm those observations with the demonstration of a consequent percentage of food items (10–30%) collected by exploiters directly at the vicinity of other nest entrances. Our results indicate that the addition of food did not modify the intensity of exploiters and so we did not see a switch from thievery (collection of food inside the nest) to exploiting (collection at the vicinity of other nest entrance). Future studies focusing on worker polyethism, perhaps through the use of marking techniques and in laboratory colonies, should emphasize the flexibility of workers to exploit food within their environment either as thieves or exploiters.

In conclusion, colonies of *E. ruidum* use a complex foraging strategy mixing social parasitism and exploitative competition, which is responsive to the availability of food in the environment. The rarity of intraspecific thievery, compared with heterospecific food robbing, remains a conundrum. We propose that the evolution of intraspecific thievery may not be favored when encounters between thief and victim result in injury or death. In most social insects, interactions between workers from separate colonies at the nest site typically result in major aggression, although this is not the case in most *Ectatomma* species (Breed *et al.* 1990, 1992, Zinck *et al.* 2008), nor in *M. aciculatus* where intraspecific cleptobiosis is common (Yamaguchi 1995). The new question posed by our findings is to understand how thievery represents an evolutionarily stable strategy, and whether this phenomenon functions as a form of parasitism or a form of mutualism.

ACKNOWLEDGMENTS

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