



Intraspecific Food-Robbing and Neighborhood Competition: Consequences for Anti-Robber Vigilance and Colony Productivity

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ABSTRACT

Most social animals have mechanisms to distinguish group members from outsiders, in part to prevent the exploitation of resources reserved for members of the group. Nevertheless, specialized thieves of the Neotropical ant, *Ectatomma ruidum*, also known as the ‘thieving ant’, regularly enter and steal resources from distinct, neighboring colonies. Here, we examine the mechanisms and consequences of thievery in a population of *E. ruidum*. We show that (1) individuals from nearby colonies were accepted more often than those from farther colonies; (2) rejection rates decreased as individuals interacted more with non-nestmates from the same source colony; and (3) colonies that were experimentally treated to reduce thievery rates had improved productivity. The boost in productivity with thievery reduction was greater in low density populations than in high density populations. We conclude that, as in other species, thievery has negative fitness costs to *E. ruidum*. However, greater acceptance of neighbors than non-neighbors and increased acceptance after habituation to non-nestmates suggest a proximate explanation for the presence of thievery. Moreover, lower fitness costs of thievery at high nesting density, combined with observations of extraordinarily high densities of *E. ruidum* throughout its range, suggest there is little selection pressure among these ants to guard against thieves, thus providing an ultimate explanation why thievery persists among litter-foraging ants.

Abstract in Spanish is available with online material.

Key words: cleptobiosis; *Ectatomma ruidum*; nestmate recognition; thievery.

LIMITED ACCESS TO RESOURCES IMPOSES A FUNDAMENTAL CONSTRAINT ON GROWTH AND REPRODUCTION. Social animals may collectively gather food and share it among group members in a central location. Collective foraging and food sharing confer numerous benefits, including improved efficiency of foraging and reduced caloric expenditure and predation risk (Dornhaus & Powell 2010). However, competitors outside the group may exploit shared resources. For example, hyena clans that hunt large prey items may lose their meal to lions competing for similarly sized resources (Watts & Holekamp 2008). Moreover, as competitors may also be a conspecific social group, robust mechanisms have evolved to recognize and exclude conspecifics from competing social groups (Reeve 1989, Breed *et al.* 2012).

The cost of failing to exclude thieves may change with environmental context (Reeve 1989). When resources are abundant, for example, the relative cost of allowing a thief into the nest may be negligible compared to times when resources are scarce. In some species, nestmates adjust their acceptance thresholds with changes in food availability (*Plagiolepis pygmaea*, Thurin & Aron 2008, *Formica exsecta*, Katzerke *et al.* 2006, *Apis mellifera*, Downs & Ratnieks 2000), thief activity (*Apis mellifera*, Couvillon *et al.* 2008), or proximity to a neighboring nest (*Polistes dominulus*,

Starks *et al.* 1998). This behavior suggests not only that colonies are under strong selection pressure to prevent robbing, but also that there is a cost to maintaining high rejection thresholds, which may include the erroneous rejection of one’s own members due to an overlap of recognition cues (Reeve 1989).

The ant, *Ectatomma ruidum* presents a curious phenomenon, for although acceptance thresholds of conspecifics fluctuate as resource availability changes (Guénard & McGlynn 2013), conspecific acceptance thresholds are generally permissive (Breed *et al.* 1990a, 2012, De Carli *et al.* 1998). This means that *E. ruidum* are very likely to make acceptance errors (*i.e.*, incorrectly accepting a non-nestmate), but are very unlikely to make a rejection error (incorrectly rejecting a nestmate). As a result, the frequency and breadth of thieving among *E. ruidum* colonies is unusually high, and workers do not appear to employ a formal guarding behavior at the nest entrance (Breed *et al.* 1990a). This is different from most other social insects in which guards or tight defenses at the nest entrance are readily observed, and guards aggressively defend the nest from intruders (*e.g.*, Moore *et al.* 1987, Breed *et al.* 1990b, Hölldobler & Wilson 1990, Couvillon *et al.* 2008, Grüter *et al.* 2012). In *E. ruidum* colonies, the nest entrance is constructed such that only one individual may pass through at a time, so perhaps the cost of remaining outside the nest to defend it is too high. Although physical combat is rarely observed, if an immobile or passive non-nestmate is detected

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next to the nest entrance, she may be physically bitten or carried away from the area (Breed *et al.* 1990a, 1992).

Thievery in *E. ruidum* is not the result of polydomy, or individuals transferring food among nests (Breed *et al.* 1999), nor is it exacerbated by an increase in colony density (Breed *et al.* 1999). Thieves specialize in stealing resources from one conspecific colony; they wait inside that colony's nest for food to be delivered by foragers, and then carry that resource back to their home colony. Thieving differs from poaching, another strategy of *E. ruidum*, where individuals loiter outside a conspecific's nest and steal food from a returning forager before the forager can enter the nest with it (also observed in *Messor aciculatus*; Yamaguchi 1995). Thief behavior also differs from that of 'normal' forager behavior in that thieves do not always return directly to their home nest by making a 'bee-line' (characteristic of most foragers after they retrieve a resource), but by walking through dense leaf litter, periodically 'hiding' or walking in a new direction if their movements are interrupted (J. Jandt, Pers. obs.). In addition, the hydrocarbon profile of thieves is chemically distinguishable from that of 'normal' foragers. They have fewer hydrocarbons, and the profiles are distinct from nestmates in their home colony, presumably the result of increased interactions with ants from different colonies (Breed *et al.* 1992, Jeral *et al.* 1997). Therefore, although thieves and foragers both retrieve resources for their colony, the differences between the two groups indicate that thieving is an alternative foraging strategy.

Across social insects, selection pressure tends to favor colonies that have developed mechanisms to keep out intruders. Why, then, does *E. ruidum* have a weakly implemented system to protect colony resources? Does thievery actually incur a cost? Here we examine the mechanisms and consequences of thievery in a population of *E. ruidum*. To understand the mechanisms, we hypothesize that (1) if intruder acceptance is affected by distance between nests, individuals from nearby nests will be accepted more often than those from farther nests; and (2) if intruder acceptance is affected by habituation, then rejection rate will decrease as individuals interact with non-nestmates. Finally, to understand the fitness consequences of thievery, we hypothesize that (3) if thievery is costly to the victim colony, removal of thieves from a population will increase productivity of the victim colony.

METHODS

STUDY SITE.—We collected the data in May–July 2011 at La Selva Biological Station in northeastern Costa Rica (10°26' N, 84°00' W). La Selva is located in a lowland tropical wet forest, receiving *ca* 4 m of rain annually (McDade 1994). We established all plots in areas with a partially closed high canopy that was cleared of understory, within 50 m of the Sendero Surá on the La Selva Trail System, in the arboretum. This particular location has been the site of prior work on the behavior and ecology of *E. ruidum* (Breed *et al.* 1992, 1999, Jeral *et al.* 1997, McGlynn 2010, Guénard & McGlynn 2013). More information about La Selva is available at www.ots.ac.cr.

PLOT TREATMENTS.—We established nine square 100 m² plots in the arboretum, either adjacent to or within 10 m of each other. We located nests within each plot after extensive searches and marked them with a numbered flag. We divided the plots randomly into three treatment groups: (1) all thieves removed from all nests; (2) thieves removed from half the nests; and (3) thieves not removed (control). To control for changes in plot density due to worker removal in treatments 2 & 3, we also removed random individuals (see below).

We demarcated four nests in the central area of each plot as 'experimental nests'. All of these colonies were at least 5 m away from any adjacent plots subjected to a different treatment. We ensured that, in the 'remove half' treatment (2), thieves were removed from two experimental nests, but not from another two. We performed accept/reject experiments and measured colony productivity on all experimental nests across all plots.

IDENTIFICATION AND REMOVAL OF THIEVES.—We placed five consistently attractive supplemental food items (condensed balls of commercially produced white bread, *ca* 2 mm diameter) next to each nest entrance inside the plot. We observed activity at the entrance for a minimum of 5 min after food collection, following a protocol similar to that reported in Breed *et al.* (1990a) and Guénard and McGlynn (2013). Typically, the ants quickly brought the food items inside their nest. (When foraging activity was low and the food was not retrieved promptly, we dropped food items directly inside the nest.) We defined thieves as any individual that left the nest carrying a food item and walked in a straight line away from the nest. When a thief left the nest entrance carrying a food item, we followed it to its home nest, collected it before it could enter, and killed it in ethanol. To control for the phenomenon that food supplementation decreases incidence and intensity of thievery in *Ectatomma* (Guénard & McGlynn 2013), in treatments 2 and 3 (half removed and no thieves removed), we placed five food items at the remaining nest entrances throughout the plot where we did not remove thieves. After we removed thieves in plots with treatments 1 and 2, we removed additional random individuals in treatments 2 and 3 from the plots to ensure the proportion of ants removed from a plot remained constant. As we could not remove all thieves from a nest during one removal bout, we repeated thief removal on a weekly basis for the duration of the experiment (6 wk), and we regularly detected and removed a small number of thieves throughout this process.

ACCEPT/REJECT EXPERIMENT.—We adapted methods for this experiment from the protocol developed by Breed *et al.* (1987). In each trial of the experiment, we captured four ants from each of the four experimental nests within the plot, and four from a randomly selected experimental nest from a different plot (= 20 ants). We captured ants in glass vials, and placed them on ice to slow movement. One at a time, we presented a total of five chilled ants to each of the four experimental nests (one from its own nest [nest-mate], three from within-plot neighboring nests [neighbor non-nestmate], and one from a different plot non-neighbor nest [non-

neighbor non-nestmate]). We observed the chilled ant for 2 min. We scored the chilled ant as ‘accepted’ if ants from the experimental nest ignored it and/or carried it inside the nest. We scored the chilled ant as ‘rejected’ if they bit it or carried it away from the nest. After 2 min, we removed the chilled ant from the area and allowed it to warm up and return to its nest of origin. We randomized the order that the five ants (nestmates, neighbors, and non-neighbors) were introduced in each trial.

We performed five accept/reject trials on all experimental nests, with 2–7 d between trials for each nest. Therefore, we were able to analyze not only the difference in a colony’s willingness to accept foreign ants after thieves were removed from the colony, but also if the colony’s willingness to accept foreign ants (neighbors or non-neighbors) changed over time.

MEASURING COLONY PRODUCTIVITY.—To test if thieves affected colony productivity, we excavated the experimental nests in all plots at the end of the experiment, and collected all workers, reproductives, and brood. We counted individuals and categorized them as queens, males, workers, pupae, larvae, eggs. We calculated colony productivity using the pupae:worker ratio (Kaspari 1996, McGlynn 2006, 2010). The number of pupae represents the success that the workers had on rearing brood under the treatment conditions during the 2 mo of experimentation, and therefore the amount of new biomass added to the colony in a constant period of time within the scope of the experiment. This measurement also allowed us to measure brood production while controlling for differences in colony size. We also determined the relationship between colony size (number of workers in a nest) and nest density (number of nests in a plot).

We did not collect thieves from all colonies designated for thief removal in treatments 2 and 3, as in some trials no thieves emerged within the 5 min after providing food to the nest. Therefore, for colony-level analyses, we categorized colonies, independent of plot, into ‘thieves removed’ and ‘no thieves removed’.

DATA ANALYSES.—We analyzed all data using JMP v. 8.0.1 (SAS Institute, Cary, North Carolina, U.S.A.). We conducted least

squares regression to evaluate the relationship between nest density and colony size. We conducted each analysis with appropriate degrees of freedom and each observation was independent of the other. We conducted an ANCOVA to test for heterogeneity of treatment and control slopes in the relationship between nest density and productivity. When analyzing the accept/reject trials, we compared the relative rates of rejection with respect to the distance between nest pairs (measured in meters), proximity in the plot (same nest, neighboring nest, and non-neighboring nest), and plot treatment category; this analysis was a logistic regression with rejection rate as the response variable.

RESULTS

ANTS REJECTED NON-NESTMATES.—Colonies were less likely to reject nestmates than neighbor non-nestmates or non-neighbor non-nestmates (Fig. 1A; $\chi^2_2 = 39.99$, $P < 0.0001$). Our treatments did affect the rate at which colonies rejected foreign ants: colonies from treatment 1 (plots from which thieves were removed from all nests) rejected ants less often than those from treatment 2 (plots from which thieves were removed from half the nests), or from treatment 3 (plots from which no thieves were removed (Fig. 1B; $\chi^2_2 = 20.61$, $P < 0.0001$)). The actual distance between colonies had no effect on rejection rate (nominal logistic regression: whole model $\chi^2_{69} = 105.7$, $P = 0.003$; distance [treatment,nest] $\chi^2_{35} = 47.38$, $P = 0.08$).

HABITUATION LOWERED REJECTION RATES.—Colonies decreased their rejection rate of non-nestmates (both neighbors and non-neighbors) as trial number increased, regardless of the distance of the ant’s colony presented in the trial (Fig. 2; whole model $\chi^2_{14} = 78.04$, $P < 0.0001$; trial number[plot] $\chi^2_{12} = 38.05$, $P = 0.0002$).

REDUCED FITNESS IN PLOTS WITH LOW NEST DENSITY.—Colonies from treatment 1 (all thieves removed) had higher productivity (measured as pupae:worker ratio) than colonies from treatment 3 (thieving individuals were allowed to remain [Fig. 3A; whole

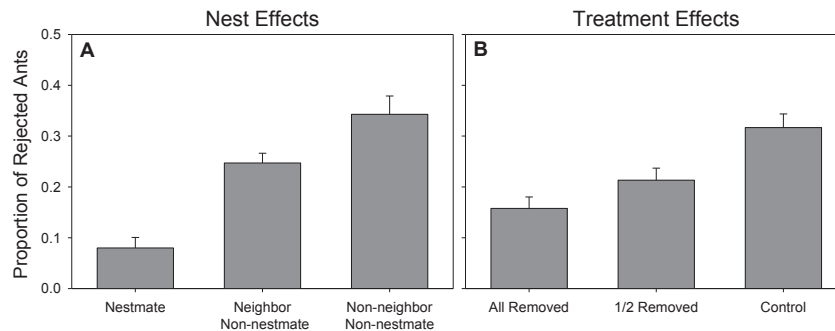


FIGURE 1. Rejection rates of chilled ants presented at the nest. (A) Colonies were more likely to reject neighbor non-nestmates and non-neighbor non-nestmates than they were to reject nestmates. (B) Ants from plots where thieves were removed exhibited lower rejection rates (of nestmates and non-nestmates combined) than did those where thieves were removed from half the colonies or from no colonies. Error bars represent SE.

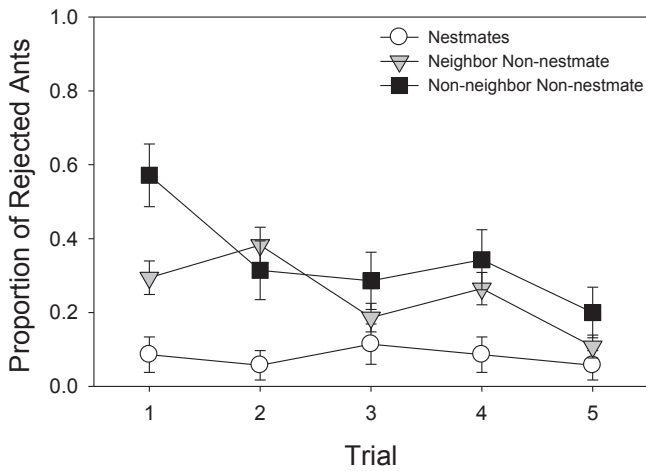


FIGURE 2. Rejection rates decreased with increasing habituation to neighbor and non-neighbor non-nestmates. Accept/reject trials were conducted for each nest on five different days (with 2–7 d between trials). For each trial, nests were presented with one ant from its own nest (nestmate), three from within-plot neighboring nests (neighbor non-nestmate), and one from a nest in a different plot (non-neighbor non-nestmate). Symbols represent average rejection \pm SE.

model $\chi^2_8 = 22.13$, $P = 0.0047$; plot[treatment] $\chi^2_6 = 19.67$, $P = 0.0032$; treatment $\chi^2_2 = 6.06$, $P = 0.048$). Furthermore, among the colonies from treatment 2 (thieves removed from half the nests), those from which thieves were removed had higher productivity than did colonies within the same plot from which thieves were allowed to remain (Fig. 3A).

Because ‘plot’ was a significant factor that predicted productivity, we explored the role of nest density. Among all treatments,

there was a weak negative relationship between nest density and colony size (Fig. 3B; $R^2 = 0.145$; workers = $174.1 - 2.14$ nests/100 m²; $F_{1,32} = 5.421$; $P = 0.026$). In treatment 3 colonies (thieves not removed), colony productivity was independent of density (Fig. 3B; $R^2 = 0.062$; productivity = $1.11 - 0.023$ nests/100 m²). However, for colonies from treatment 1, the removal of thieves resulted in a robust negative relationship between density and productivity ($R^2 = 0.693$; productivity = $0.482 - 0.005$ nests/100 m²). The slopes of these two relationships were significantly different from one another (ANCOVA whole model $F_{3,30} = 8.957$; $P = 0.0002$; $t_{\text{density} \times \text{treatment}} = 2.51$; $P = 0.017$).

We analyzed colonies that were monitored for thieves (all colonies from treatment 1 and approximately half the colonies from treatment 2) to determine if the number of thieves removed from the colony (min = 0, max = 8, AVE \pm SE 2.39 ± 0.55) or the number of colonies that thieves were from (min = 1, max = 6, AVE \pm SE 2.07 ± 0.40) affected productivity. Of the experimental colonies, we did not find thieves in four colonies. There was no evidence that nests in higher density plots had more thieves ($R^2 = 0.13$, $F_{1,17} = 2.32$, $P = 0.65$) or thieves visiting them from more colonies ($R^2 = 0.02$, $F_{1,13} = 0.22$, $P = 0.15$). Further, there was no evidence that the number of thieves removed affected colony productivity (whole model $\chi^2_7 = 16.89$, $P = 0.018$; plot[treatment] $\chi^2_4 = 15.45$, $P = 0.004$; treatment $\chi^2_1 = 9.98$, $P = 0.32$; # thieves removed $\chi^2_1 = 0.33$, $P = 0.57$, treatment \times # thieves removed $\chi^2_1 = 0.56$, $P = 0.45$).

DISCUSSION

We show here that thief removal was particularly effective at increasing the fitness of the victim colony under low nest density (Hypothesis 3). Why then, if thievery negatively affects fitness of a victim colony, does it persist in such high frequency in the

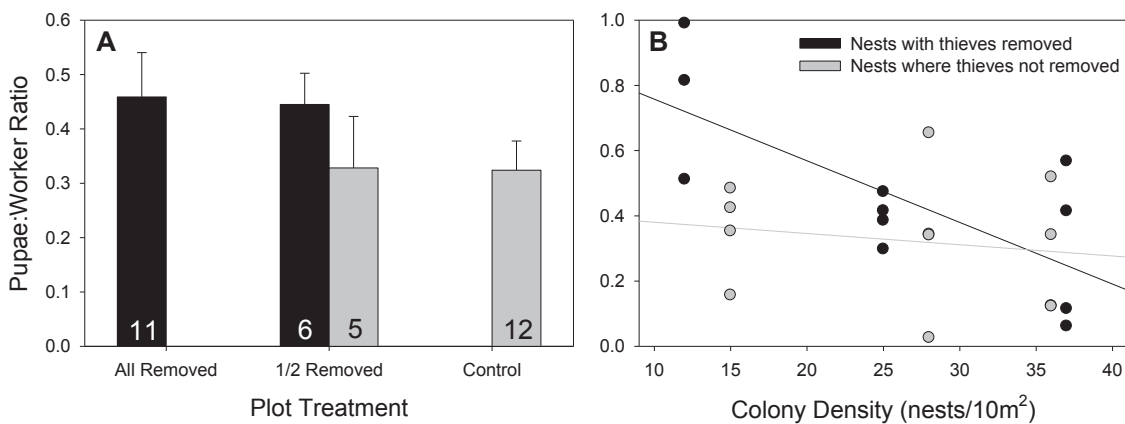


FIGURE 3. The presence of thieves negatively affected colony productivity. (A) Colony productivity across plots exposed to three different treatment types. In plots with all thieves removed or no thieves removed, productivity could only be measured on one or the other treatment type. In plots with half the thieves removed, colonies with all thieves removed and no thieves removed could be compared. Numbers represent the number of nests with thieves removed or no thieves removed in each treatment type. Error bars represent SE. (B) Differences between treatments in productivity changed with nest density (all thieves removed and no thieves removed treatments only). In both plots, black bars or symbols represent those nests where thieves were removed, and gray bars or symbols represent those nests where thieves were not removed.

population? *E. ruidum* naturally nest at extraordinarily high densities (Perfecto & Vandermeer 1993, Schatz & Lachaud 2008, McGlynn 2010), and when we removed thieves from colonies under high nest density, we saw little to no fitness gain (Fig. 3). Moreover, we found no evidence that those colonies nesting in higher density plots were visited by more thieves than those nesting in lower density plots, an additional piece of evidence that high nest density did not incur a disproportionately higher thieving cost. As thievery is widespread throughout the geographic range (Breed *et al.* 1999), the very high nesting densities indicative of *E. ruidum* populations, and reduced benefit to those colonies when thieves are removed, suggest there is little to no selection pressure to maintain a guarding behavioral caste.

Nest density likely also influences neighbor recognition/habituation. In general, neighbors will come across one another more often in high nesting densities than in low nesting densities. Breed and colleagues (1992) showed that *E. ruidum* can acquire recognition cues from non-nestmates if they are in contact with one another, and hypothesized that repeated attempts to gain entry into a foreign nest might be enough for a thief to acquire these cues. We have shown that when individuals regularly come into contact with conspecifics (Hypothesis 1) from nearby neighboring nests (Hypothesis 2), they adopt a more permissive acceptance threshold. This ‘dear-enemy’ phenomenon has been described for a variety of species where aggression levels are lower toward neighboring colonies than toward distant colonies – regardless of genetic similarity (Langen *et al.* 2000, Dimarco *et al.* 2010). Close proximity to non-nestmates with similar chemical profiles (Nunes *et al.* 2008), indirect transfer of hydrocarbons by coming in contact with nest soil (Bos *et al.* 2011), or constant interaction with neighbors (Breed *et al.* 1992, Langen *et al.* 2000, Dimarco *et al.* 2010) may all increase acceptance of neighboring non-nestmates in *Ectatomma*.

Aside from gaining entrance to a conspecific’s nest, thieves behave differently from ‘normal foragers’ on their run back to their home nest. Thieves are quicker to hide if there is a small disturbance in the immediate area (leaf litter), and are more likely to drop their cargo. They also differ from poachers (Yamaguchi 1995). Due to generally high nesting densities, small holes that make it difficult for a guard to inspect incomers, and the behavioral and chemical differences between thieves and foragers, thieves clearly represent a distinct type of forager in *E. ruidum*.

What ecological conditions would allow a colony to permit thieves rather than maintain guards? The acceptance threshold in a colony may be affected by the relative risk of thievery (*i.e.*, low food availability = high risk) and/or prevalence of thievery (Downs & Ratnieks 2000, Couvillon *et al.* 2008). In *E. ruidum*, thievery rates decline when food abundance is high (Guénard & McGlynn 2013). Therefore, the colony may use resources to produce foragers and thieves to exploit food caches within the area. The benefit, at high densities, to maintaining multiple foraging strategies rather than guarding, is evident here as the removal of thieves (simulating highly effective nest guards) had no effect on colony fitness (Figure 3B). It has yet to be determined if acceptance thresholds change with food abundance.

Why do *E. ruidum* nest in high densities? Close proximity to potentially thieving colonies may increase interactions among ants, enabling thieves to accumulate odors from neighbors or guards to habituate to a thief’s scent (Breed *et al.* 1992, Fig. 2). Further, productivity was reduced at high vs. low nesting densities when thieves were removed from nests. There may be little selective pressure for colonies living in high population densities to guard their nest, but what are the mechanisms that maintain colony fitness when closely packed against one another? Perhaps there is an environmental factor that attracts queens to nest in areas with pre-existing conspecific colonies, or perhaps queens do not disperse far from their natal nests. Understanding these colony life history strategies may be the key to understanding this perplexing ecological phenomenon.

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LITERATURE CITED

- BOS, N., L. GRINSTED, AND L. HOLMAN. 2011. Wax on, wax off: Nest soil facilitates indirect transfer of recognition cues between ant nestmates. *PLoS One* 6: e19435.
- BREED, M. D., P. ABEL, T. J. BLEUZE, AND S. E. DENTON. 1990a. Thievery, home ranges, and nestmate recognition in *Ectatomma ruidum*. *Oecologia* 84: 117–121.
- BREED, M. D., C. COOK, AND M. O. KRASNEC. 2012. Cleptobiosis in social insects. *Psyche* 2012: 7.
- BREED, M. D., J. H. FEWELL, A. J. MOORE, AND K. R. WILLIAMS. 1987. Graded recruitment in a ponerine ant. *Behav. Ecol. Sociobiol.* 20: 407–411.
- BREED, M. D., T. P. MCGLYNN, E. M. STOCKER, AND A. N. KLEIN. 1999. Thief workers and variation in nestmate recognition behavior in a ponerine ant, *Ectatomma ruidum*. *Insectes Soc.* 46: 327–331.
- BREED, M. D., G. E. ROBINSON, AND R. E. J. PAGE. 1990b. Division of labor during honey bee colony defense. *Behav. Ecol. Sociobiol.* 27: 395–401.
- BREED, M. D., L. E. SNYDER, T. L. LYNN, AND J. A. MORHART. 1992. Acquired chemical camouflage in a tropical ant. *Anim. Behav.* 44: 519–523.
- COUVILLON, M. J., E. J. H. ROBINSON, B. ATKINSON, L. CHILD, K. R. DENT, AND F. L. W. RATNIEKS. 2008. En garde: rapid shifts in honeybee, *Apis mellifera*, guarding behaviour are triggered by onslaught of conspecific intruders. *Anim. Behav.* 76: 1653–1658.
- DE CARLI, P., J. P. LACHAUD, G. BEUGNON, AND J. A. LÓPEZ MÉNDEZ. 1998. Études en milieu naturel du comportement de cleptobiose chez la fourmi néotropicale *Ectatomma ruidum* (Hymenoptera, Ponerinae). *Insectes Soc.* 11: 29–32.
- DIMARCO, R. D., A. G. FARJI-BRENER, AND A. C. PREMOLI. 2010. Dear enemy phenomenon in the leaf-cutting ant *Acromyrmex lobicornis*: Behavioral and genetic evidence. *Behav. Ecol.* 21: 304–310.
- DORNHAUS, A., AND S. POWELL. 2010. Foraging and defence strategies. *In* L. Lach, C. L. Parr, and K. L. Abbott (Eds.). *Ant ecology*, pp. 210–230. Oxford University Press, Oxford, U.K.
- DOWNES, S. G., AND F. L. W. RATNIEKS. 2000. Adaptive shifts in honey bee (*Apis mellifera* L.) guarding behavior support predictions of the acceptance threshold model. *Behav. Ecol.* 11: 326–333.

- GRÜTER, C., C. MENEZES, V. L. IMPERATRIZ-FONSECA, AND F. L. W. RATNIEKS. 2012. A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee. *Proc. Natl Acad. Sci. U. S. A.* 109: 1182–1186.
- GUÉNARD, B., AND T. P. MCGLYNN. 2013. Intraspecific thievery in the ant *Ectatomma ruidum* is mediated by food availability. *Biotropica* 45: 497–502.
- HÖLDOBLER, B., AND E. O. WILSON. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.
- JERAL, J. M., M. D. BREED, AND B. E. HIBBARD. 1997. Thief ants have reduced quantities of cuticular compounds in a ponerine ant, *Ectatomma ruidum*. *Physiol. Entomol.* 22: 207–211.
- KASPARI, M. 1996. Testing resource-based models of patchiness in four neotropical litter ant assemblages. *Oikos* 76: 443–454.
- KATZERKE, A., P. NEUMANN, C. W. W. PIRK, P. BLISS, AND R. F. A. MORITZ. 2006. Seasonal nestmate recognition in the ant *Formica exsecta*. *Behav. Ecol. Sociobiol.* 61: 143–150.
- LANGEN, T. A., F. D. R. TRIPET, AND P. NONACS. 2000. The red and the black: Habituation and the dear-enemy phenomenon in two desert Pheidole ants. *Behav. Ecol. Sociobiol.* 48: 285–292.
- MCDADE, L. A. 1994. *La Selva: Ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, Illinois.
- MCGLYNN, T. P. 2006. Ants on the move: Resource limitation of a litter-nesting ant community in Costa Rica. *Biotropica* 38: 419–427.
- MCGLYNN, T. P. 2010. Polygyny in thief ants responds to competition and nest limitation but not food resources. *Insectes Soc.* 57: 23–28.
- MOORE, A. J., M. D. BREED, AND M. J. MOOR. 1987. The guard honey bee: Ontogeny and behavioral variability of workers performing a specialized task. *Anim. Behav.* 35: 1159–1167.
- NUNES, T. M., F. S. NASCIMENTO, I. C. TURATTI, N. P. LOPES, AND R. ZUCCHI. 2008. Nestmate recognition in a stingless bee: Does the similarity of chemical cues determine guard acceptance? *Anim. Behav.* 75: 1165–1171.
- PERFECTO, I., AND J. H. VANDERMEER. 1993. Cleptobiosis in the ant *Ectatomma ruidum* in Nicaragua. *Insectes Soc.* 40: 295–299.
- REEVE, H. K. 1989. The evolution of conspecific acceptance thresholds. *Am. Nat.* 133: 407–435.
- SCHATZ, B., AND J. P. LACHAUD. 2008. Effect of high nest density on spatial relationships in two dominant ectatommine ants (Hymenoptera: Formicidae). *Sociobiology* 51: 623–643.
- STARKS, P. T., D. J. FISCHER, R. E. WATSON, G. L. MELIKIAN, AND S. D. NATH. 1998. Context-dependent nestmate discrimination in the paper wasp, *Polistes dominulus*: A critical test of the optimal acceptance threshold model. *Anim. Behav.* 56: 449–458.
- THURIN, N., AND S. ARON. 2008. Seasonal nestmate recognition in the polydomous ant *Plagiolepis pygmaea*. *Anim. Behav.* 75: 1023–1030.
- WATTS, H. E., AND K. E. HOLEKAMP. 2008. Interspecific competition influences reproduction in spotted hyenas. *J. Zool.* 276: 402–410.
- YAMAGUCHI, T. 1995. Intraspecific competition through food robbing in the harvester ant, *Messor aciculatus* (Fr. Smith), and its consequences on colony survival. *Insectes Soc.* 42: 89–101.