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ANTBIRDS PARASITIZE FORAGING ARMY ANTS

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Abstract. In the tropical forests of Central and South America, army ants of the *Ecitonini* tribe, and the numerous animals that follow them through the understory, share a complex relationship that has far-reaching effects on population dynamics and community structure. Although considerable study has been made of various participants in this relationship, no research has explicitly examined the nature of the interaction between the ants and the most important group of followers, the ant-following birds. Here we show, through use of exclusion experiments, that ant-following birds are parasites on *Eciton burchellii*, significantly reducing the ants' success rate in capturing prey. This has important implications for our interpretation of ant behaviors during swarm-raiding, competitive interactions among the ant-following birds, and possibly also the relative abundance of those social hymenopterans that are typically preyed upon by army ants.

Key words: *antbirds; ant-following bird guild; army ants; Eciton burchellii; Ecitonini; Formicariidae; interspecific competition; leaf-litter arthropod community; parasitism; social hymenopterans.*

INTRODUCTION

One of the most impressive phenomena encountered in the American tropics is the massive swarm-raiding of army ants attended by a community of birds, insects, some lizards, and even mammals (Schneirla 1971, Gotwald 1995). Although the bird community in particular has attracted considerable study, whether its relationship to the swarming ants is commensal, mutualistic, or parasitic has not been explored.

Army ants play a key role in the dynamics of tropical forests because they regulate the populations of many other social hymenopterans (Franks 1982a, b, Gotwald 1995); locally impact the leaf-litter arthropod community both by direct predation and by facilitating parasitism by a range of insects that attend swarms (Franks 1982b, Otis et al. 1986); and support the community of specialist birds that obtain most of their food by capturing arthropods and small vertebrates attempting to escape from ant swarms (Willis and Oniki 1978).

Ant-following birds and parasitoids regularly attend only the few army ants in the *Ecitoninae* tribe that develop swarm raids when foraging (other species have less conspicuous foraging behavior and either lack attendants or attract them only sporadically). Colonies of the predominant swarm raider, *Eciton burchellii* (formerly *E. burchelli*; see Bolton 1995), can reach sizes of 1.5×10^6 ants and may scour $>1000 \text{ m}^2$ of forest floor per day (Schneirla 1971, Franks 1982a, Gotwald 1995). Conditions that affect the foraging success of this species could thus not only influence the growth and reproductive rates of its own colonies, but also impact social and leaf-litter arthropod populations.

Early studies such as that of Willis and Oniki (1978) suggest that the presence of attending birds might have been instrumental in the evolution of swarm-raiding in the *Ecitonini*, and that the relationship could be mutualistic, the ants benefiting from prey being flushed back by the birds into the oncoming raid. More recent accounts of antbird ecology fail to explicitly mention the type of relationship.

In this study, we report the results of experiments designed to quantify the relationship between ant-following birds and the army ant *E. burchellii*, and we explore the consequences of this relationship for army ant demography, foraging behavior, and arthropod diversity in Neotropical forest systems.

METHODS

In 2001 and 2002, we conducted experiments on the Smithsonian Tropical Research Institute 100-ha "Lim-

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bo" plot (Brawn et al. 1995), located in the Soberanía National Forest, Republic of Panama (9° N, 79° W). The forest is a combination of mature old-growth forest and advanced second-growth forest. In each year, we conducted experimental trials on two different colonies of *Eciton burchellii*. The ant-following bird community was resident and, consequently, many of the same individual birds attended each experiment within a year and probably also between years. The birds habituated to our presence within a few days and were undisturbed by any slow, careful movement during trials.

The experiment consisted of paired, 10-min trials, during which we quantified the capture success of the army ant swarm in the presence, and then in the absence, of attendant birds. We could usually exclude birds from the experimental area simply by standing immediately adjacent to the area and gesticulating with our arms. The occasional persistent bird was discouraged with a shot of water from a squirt gun, or by throwing a fragment of bark into the leaf litter nearby when the bird began to approach too closely. We could not randomize the order of the control and exclusion parts of each paired trial because some antbird species tended to remain away from the swarm for a considerable length of time after being excluded.

We initiated trials when we expected the ant swarm to traverse relatively homogeneous habitat, and when the attending ant-followers were active and generally numerous (>3 birds). The location of the swarm front was marked with flagging tape at the beginning of the experiment, again after 10 min when the exclusion trial began, and at the end of the experiment. During each trial the number and species of attending birds were noted (2002), and landmarks were identified that would be used to define lateral boundaries of the control and experimental areas. This created a pair of adjacent plots (ranging in area from 6 to 21 m², mean = 11 m²): a control plot in which birds had fed and an exclusion plot in which they had not.

E. burchellii aggregate on prey items just after capture when prey are larger than can be handled by a single worker. These groups of ants then subdue and dismember the prey (Rettenmeyer 1963, Schneirla 1971, Gotwald 1995). As prey size increases, the number of workers involved in subduing and processing increases, and "aggregations" on prey larger than ~0.8 cm persist sufficiently long to be counted as a measure of foraging success. In 2001, we presented crickets, or parts of crickets, to foraging *E. burchellii* and monitored the persistence of the aggregations for the purpose of estimating the size ranges of prey likely to be counted, beginning 20 min after the ants passed through an area. Based on 42 presentations in three size classes (<0.8 cm, 1–1.5 cm, 1.5–2 cm), prey items >1 cm long attracted aggregations that persisted >20 min. Our actual counts might have included somewhat smaller prey items because the processing of live prey would also include the time it takes the ants to immobilize

each item. Insects on the order of 1–1.5 cm long also represent the average size of prey captured by antbirds (Willis 1967, Britton et al. 1996, Partridge et al. 1996).

At the end of each 20-min pair of trials, we immediately began to mark the location of aggregations of ants in the control plot. We looked for, and marked, aggregations for a period of exactly 10 min, initially covering the entire control plot relatively quickly, then carefully re-examining the plot area several times in succession. The marking of aggregations proceeded in an identical manner in the exclusion plot. Thus, each plot was searched beginning exactly 20 min after the front first entered the plot, and was searched for an identical period of time. Care was taken not to disturb the braided lines of ants moving to the front and carrying prey back from the front. We counted the total number of marked aggregations in each plot, and calculated plot area from measurements of each plot's geometry. To evaluate the impact of foraging birds on prey capture by army ants, we estimated prey biomass using the correlation between insect body length and dry mass (Rogers et al. 1976, Stork and Blackburn 1993).

RESULTS

During the 18 experimental trials, the number of ant-following birds in attendance averaged 6.1 ± 2.2 birds (mean \pm 1 SD), and always included several *Gymnospithys leucaspis* (Bicolored Antbirds) and one or more *Dendrocincla fuliginosa* (Plain-brown Woodcreepers), usually *Phaenostictus mcleannani* (Ocellated Antbirds) and *Hylophylax naevioides* (Spotted Antbirds), and occasionally *Neomorphus geoffroyi* (Rufous-vented Ground-Cuckoos) and other species such as *Dendrocolaptes sanctithomae* and *Xiphorhynchus lachrymosus* (woodcreepers). The higher number of aggregations per unit area in exclusion vs. control plots reveals that ant-following birds are parasites of the army ants (Fig. 1). The vast majority of insects captured by the ant-following birds would be unavailable were it not for the army ants forcing insects out of the leaf litter. Although birds rarely actually take prey from the mandibles of an army ant (Schneirla 1971, Willis and Oniki 1978), a large proportion of the prey they eat would otherwise be captured by the ants.

The number of attending birds in the flock induces a proportional cost on the foraging success of the army ants (Fig. 2). Data for this analysis were from trials in 2002, when flock size and composition were carefully noted. We excluded woodcreepers from the calculation of flock size or biomass because this guild forages primarily on tree trunks well above the ground and probably has little effect on ant foraging success. Only one of eight trials in 2002 (and none in 2001) included active foraging by the very large Rufous-vented Ground-Cuckoo, and this one case appears to be an outlier in Fig. 2a (open symbol). Although very little is known about specifics of the diet of this species, its

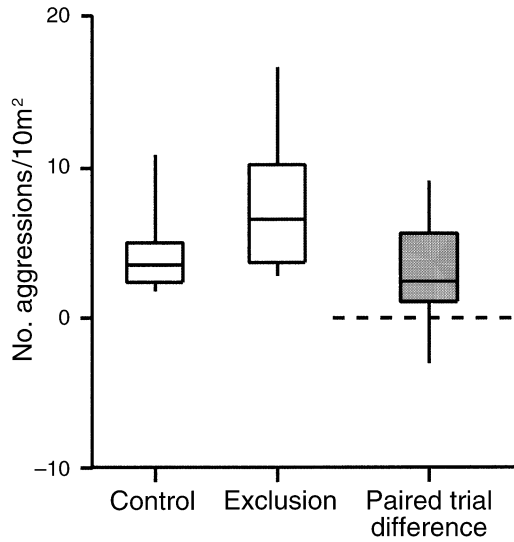


FIG. 1. The effect of ant-following birds on the foraging success of the army ant *Eciton burchellii*. Shown are the standardized numbers of ant aggregations observed in each area of 18 paired trials (open boxes) and the difference between paired exclusion and control areas (shaded box). Boxes indicate the interquartile range with median, and vertical lines indicate the range. Differences are significantly greater than zero ($t = 3.8$, $df = 17$, $P = 0.0014$), indicating that ants achieve higher success in the absence of birds.

large size and terrestrial habit suggest that it probably takes relatively large, slow-moving prey items, consistent with anecdotal observation (P. H. Wrege). Thus it is not surprising that this species has a disproportional effect on the foraging success of the army ants. If this one outlier is omitted, a regression of relative cost as the number of attendant birds increases (Fig. 2a) shows that each pair of antbirds joining the flock costs the ants about one large prey item (≥ 1 cm) per 10 m² of forest raided ($r^2 = 0.79$, $\beta = 0.58$, $P = 0.005$, $n = 7$). Fig. 2b shows the same relationship but uses total flock biomass as the independent variable instead of flock size, and includes all eight trials ($r^2 = 0.85$, $P < 0.001$, $n = 8$).

We estimated the overall energetic cost to a colony of *Eciton burchellii* of having ant-following birds attending the foraging swarm, using published estimates of army ant foraging success. An average nomadic colony in central Panama consumes ~22 g of leaf-litter arthropods each day, plus 24 g of social insect brood, in raids that cover 700 m² of forest floor (Franks 1982a). Because ant-followers attend raids throughout the day, we estimate that every day they steal an average of >200 large prey items from the ants. Most prey captured by antbirds, and counted by us in aggregations, were at least 1–1.5 cm long (Willis 1967, Britton et al. 1996, Partridge et al. 1996; see *Methods*), for a total dry mass of ~6.8 g (Rogers et al. 1976, Stork and Blackburn 1993). This represents at least 30% of the ants' daily leaf-litter arthropod intake, or

15% of the entire daily food requirement of a migrating colony.

DISCUSSION

Our data show that, far from providing a mutualistic or even a commensal relationship, birds attending the raiding swarms of army ants are in fact parasites, inflicting a cost proportional to the number of birds in the flock. At larger flock sizes, and probably also at smaller swarms, this linear relationship is expected to asymptote because of aggressive exclusion by dominant avian participants. The regular, or "professional," ant-followers maintain intra- and interspecific dominance hierarchies that regulate foraging position relative to the best locations near the swarm front (Willis and Oniki 1978). Time and energy in aggressive interactions presumably begin to reduce foraging success as flock sizes increase, with smaller antbird species and "non-professionals" paying the highest cost. Flock

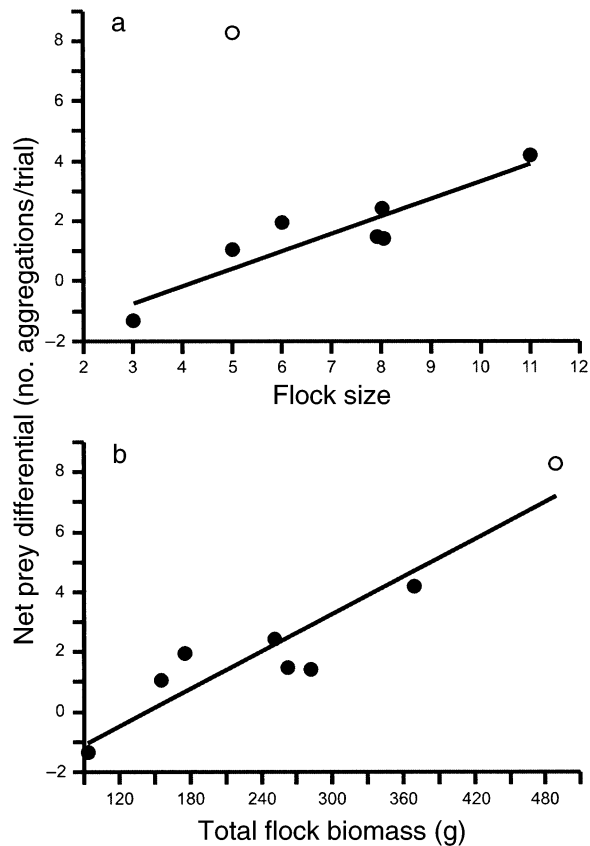


FIG. 2. Costs to *Eciton burchellii* increase with number and species composition of attending ant-followers. (a) The disproportionate effect of participation by the very large, cursorial *Neomorphus geoffroyi* (Rufous-vented Ground-Cuckoo) clearly marks the one trial (open symbol) as an outlier when simply counting flock size (fitted regression excluding open symbol: $df = 6$, $R^2 = 0.79$, $\beta = 0.58$, $t = 4.9$, $P = 0.005$). (b) The same data as presented in panel (A), converted to total flock biomass (fitted regression on all data: $df = 7$, $R^2 = 0.85$, $t = 6.4$, $P < 0.001$).

size might remain close to, or below, the level of asymptote, because the most subordinate individuals leave to forage at alternate swarms (if available) where intake rates may be higher (Willis 1967, 1972, 1973), and “non-professionals” may decide to forage away from army ant swarms altogether (Willis 1972).

The exact nature of associations between animal species, whether commensal, mutual, or parasitic, is sometimes difficult to determine. Several recent studies of presumed mutualisms have found these relationships to be complex, and whether they should be described as mutual or parasitic sometimes depends on the specific local context, which may change over time or in different habitats (e.g., oxpeckers [Weeks 2000], cleaner fish [Bshary and Sch  ffer 2002, Freckleton and C  t   2003]). From the perspective of ant-followers, the ant-bird-army ant system fits the “by-product benefits” model of cooperation (sensu Sachs et al. 2004), in which the unidirectional benefit to attendant ant-followers is an automatic consequence of self-interested foraging behavior by army ants. It seems likely that this relationship is always a parasitic one from the perspective of the ants, and the cost sustained through loss of potential prey is likely to represent an important selective pressure on ant foraging tactics.

Extensive field study (Willis and Oniki 1978, Franks 1982a) and modeling (Franks 1985, Britton et al. 1996, Partridge et al. 1996) suggest that the economy of these ant populations is marginal and that sufficient growth for colony reproduction (fission) is, in part, limited by foraging efficiency. Their massive raids are severely time constrained (Britton et al. 1999, Boswell et al. 2001), and colonies exhibit many adaptations to maximize their foraging efficiency, including collective transport of large prey by teams of ants (Franks et al. 2001) and the formation of traffic lanes on their main foraging columns to maximize the flow of ants to and from the nest (Couzin and Franks 2003). Leaf-litter arthropods represent nearly half of the total prey consumption by *E. burchellii* (Franks 1982a). With an estimated average reduction in potential foraging success of ~30% when ant-following birds are present, the evolution of following behavior may be responsible for reducing a secure foraging strategy to one on the margins of profitability.

The ecologically significant costs imposed by the community of ant-following birds may be responsible for a number of behaviors expressed by *E. burchellii* that appear to have an anti-kleptoparasite function. Some of these behaviors also may have evolved, in part, as a response to exploitation by other kleptoparasites such as some lizards, marine toads (*Buffo marinus*), and other insects, but all of these are relatively uncommon attendants compared to the birds. When large prey items are captured and aggregations of workers develop to subdue and process them, majors (the large “soldier” caste) are highly visible facing outward around the periphery and over the top of the massed

workers (C. W. Rettenmeyer, *personal communication*; P. H. Wrege, M. Wikelski, J. T. Mandel, T. Rassweiler, and I. D. Couzin, *personal observations*). Large prey items are frequently dragged out of sight under the leaf litter, where they are then processed (*personal observations*), and food caches often develop along the foraging trail (C. W. Rettenmeyer 1963 and *personal communication*), usually well hidden and attended (possibly “guarded”) by majors (*personal observations*). In addition, majors are conspicuous on the trail used to transport booty to the bivouac, although majors serve no known function in prey capture, processing, or transport. During this study we observed a few instances of direct prey stealing by ant-following birds, but in general this does not appear to be a strategy pursued by most species in the guild (Schneirla 1971, Willis and Oniki 1978). Nonetheless, these ant behaviors are consistent with an evolutionary history of kleptoparasitism.

Parasitism by ant-following birds may have other important consequences for army ant biology. Colonies under pressure of parasitism would require a longer time to reach the threshold size for fission (the means by which army ant colonies reproduce), so that the queen would be more likely to die before reproduction. This may have profound consequences for expected extinction rates. In order to properly parameterize models of army ant population dynamics, it may be important to quantify habitat quality by recording not only the abundance of potential prey items, but also the expected reduction in foraging efficiency due to the local community of ant-following birds.

Finally, the significant impact that ant-followers have on army ant foraging success may play a role in maintaining the relative abundance and diversity of arthropods in lowland Neotropical forests. Slightly more than half of the diet of *E. burchellii* consists of the brood of other social hymenopterans, particularly ants (Rettenmeyer 1963, Franks 1982a), and predation by army ants has a major effect on the diversity, relative abundance, and average surviving colony size of leaf-litter ant species (Franks 1982b, Franks and Bossert 1983). In the absence of ant-followers, army ants might satisfy more of the colony’s food requirement with leaf-litter arthropods, reducing predation pressure on social insect prey, and perhaps affecting the population dynamics of these species.

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