Army-ant following in Neotropical birds: A review and prospectus

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ABSTRACT

Army-ants (particularly swarm-raiding species *Eciton burchellii* and *Labidus praedator*) are keystone predators in Neotropical forests. Hundreds of associated species from diverse taxa depend on them for survival, the most conspicuous of which are the ant-following birds. These birds forage on cryptic arthropods and vertebrates as they attempt to escape raiding army-ants. Despite capturing the attention of tropical biologists for centuries, research on ant-following birds has been largely limited to natural history observations until more recently. Here, we argue that this complex system provides unique and underappreciated opportunities for testing hypotheses in 5 main areas of interest: (1) competitive interactions among attendant birds, (2) cognitive and behavioral adaptations for locating swarms, (3) evolution of ant-following behavior, (4) biogeography of ant-following behavior, and (5) conservation of ant-following birds. For each research area, we review the current state of knowledge and make suggestions for fruitful research avenues that we believe will help address important questions in the fields of ecology, evolution, and behavior.

Keywords: ant-following birds, army-ants, bivouac-checking, *Eciton burchellii*, *Labidus praedator*, mixed-species flock, Neotropics

LAY SUMMARY

- Army-ant following birds are an iconic element of the ecology of Neotropical forests.
- Studies are increasingly using army-ant following birds to test ecological and evolutionary hypotheses.
- We highlight opportunities to use army-ant following birds as a model system for exploring new conceptual frameworks.

Seguimiento de hormigas guerreras en aves neotropicales: Una revisión y prospecto

RESUMEN

Las hormigas guerreras (particularmente las especies *Eciton burchellii* y *Labidus praedator* que atacan en enjambre) son depredadores clave en los bosques neotropicales. Cientos de especies asociadas de diversos taxones dependen de ellas para su supervivencia, de las cuales las más conspicuas son las aves que siguen hormigas guerreras. Estas aves se alimentan de artrópodos y vertebrados crípticos a medida que tratan de escapar del avance de las hormigas guerreras. A pesar de haber llamado la atención de los biólogos tropicales por siglos, la investigación de las aves que siguen hormigas guerreras ha estado hasta hace poco mayormente limitada a observaciones de historia natural. Aquí, argumentamos que este complejo sistema brinda oportunidades únicas y subestimadas para evaluar hipótesis en cinco áreas principales de interés: 1 interacciones competitivas entre aves acompañantes, 2 adaptaciones cognitivas y conductuales para localizar a los enjambres, 3 evolución del comportamiento de seguimiento de hormigas, 4 biogeografía del comportamiento de seguimiento de hormigas, y 5 conservación de las aves que siguen hormigas. Para cada área de investigación, revisamos el estado actual de conocimiento y hacemos sugerencias para vías de investigación fructíferas que creemos que ayudarán a encarar preguntas importantes en los campos de la ecología, la evolución y el comportamiento.

Palabrasclave: aves que siguen hormigas, bandada de especies mixtas, control de vivac, *Eciton burchellii*, hormigas guerreras, *Labidus praedator*, Neotrópico

INTRODUCTION

Ant-following, the behavior of attending army-ant swarms to forage on flushed arthropods, is an iconic phenomenon of Neotropical rainforests. Army-ant swarms and their attendants present an awesome spectacle that captivated early naturalists (e.g., Bates 1863, Belt 1874) and continue to attract the attention of behavioral ecologists and evolutionary biologists attempting to understand the eco-evolutionary dynamics of this complex system (Willis and Oniki 1978, Willson 2004, Brumfield et al. 2007, Touchton and Smith 2011, O'Donnell et al. 2012). Of the more than 150 army-ant species in Neotropical forests (Kronauer 2009), 2 in particular—*Labidus praedator* and *Eciton burchellii*—forage in large swarms along the forest floor (Willis and Oniki 1978). These predaceous ants stir up cryptic arthropods and small vertebrates from the leaf litter that attempt to escape the swarm (Otis et al. 1986), providing a readily accessible food resource to many other species (Willis and Oniki 1978, Rettenmeyer et al. 2011). Bates first documented interspecific associations between army-ants and attendant species in 1863. Subsequently, more than 550 species across a range of taxa (e.g., birds, butterflies, wasps, flies, mites, beetles, etc. have been observed attending *E. burchellii* swarms alone, 300 of which depend at least in part on army-ants to survive; reviewed in Rettenmeyer et al. 2011). These associations range from direct interactions with army-ants (e.g., birds that follow the ants to find food) to cascading indirect associations such as butterflies that feed on ant-following bird feces (Ray and Andrews 1980) and parasitic Diptera that oviposit eggs in escaping arthropods (Rettenmeyer 1961).

Ant-following birds (hereafter "ant-followers") are arguably the most charismatic ant swarm attendants and comprise the majority of the biomass present at swarms (Rettenmeyer et al. 2011). A rich literature on army-ants and ant-followers exists (though it is predominantly descriptive) that outlines their natural history and highlights the conspicuousness and ubiquity of ant-following behavior throughout Neotropical rainforests. At least 465 species from 41 families—more than 12% Neotropical bird species—have been recorded following army-ants (Stotz et al. 1996), exemplifying swarm-raiding army-ants' role as keystone species (*sensu* Mills et al. 1993) in Neotropical rainforests.

In this paper, we provide a comprehensive review of avian ant-followers and argue that this iconic system presents unique opportunities to address a number of critical research questions. We highlight how early studies paved the way for more recent hypothesis-driven research, which has seen an increasing trend over that last 50 yr, to address
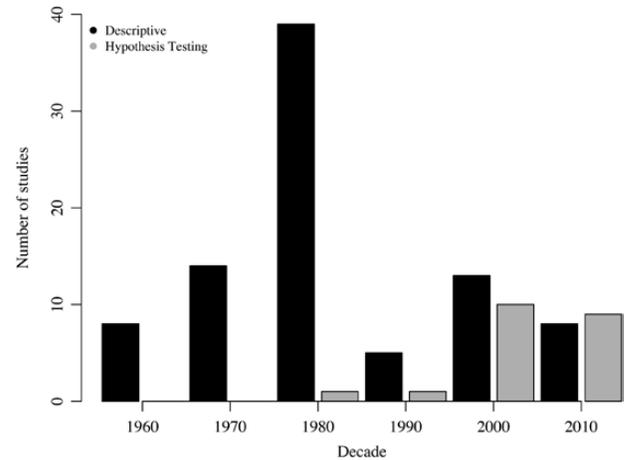
FIGURE 1. Temporal trends in the number of studies on ant-followers since the inception of the field in the 1950s. Black bars represent studies that were purely descriptive (i.e. documenting the number of species at swarms and other natural history observations) whereas gray bars represent the number of studies that have tested hypotheses about the behavior, ecology, or evolution of ant-followers. The figure includes 114 studies of Neotropical ant-followers (Online Supplemental Material Table S1) that were found through the use of either Web of Science or Google Scholar, using all possible combinations of the following search terms: 'army-ant swarm', 'ant swarm', 'ant-follower(s)', 'army-ant-following', 'ant-followers', and 'ant-following bird(s)'. Reviewed studies were assigned to one of two categories: (1) *Hypothesis testing* if an a priori test of a hypothesis was stated in the introduction of a study, regardless of the type of data (manipulative or observational) collected, and (2) *descriptive* if the study described swarm attendants or relied on observations as a means of documenting natural history but did not evaluate a priori hypothesis.

major conceptual issues in ecology, evolution, behavior, and conservation (Figure 1). We then discuss 5 key research areas: (1) competitive dynamics within ant-following bird flocks, (2) behavioral and cognitive adaptations that enable ant-following as a life-history strategy, (3) the evolution of ant-following behavior, (4) biogeographic patterns of ant-following behavior, and (5) conservation issues associated with ant-followers. Each section concludes with what we see as lucrative and important conceptual avenues for future research (see Table 1).

Natural History of Ant-followers

Much of our natural history knowledge of ant-followers is derived from studies on Barro Colorado Island (BCI), Panama, that began with Johnson (1954) and were continued by E. O. Willis in his seminal work on ant-followers from 1960 to 1971 (Willis 1966a, 1967, 1972a, 1972b, 1973). At BCI, the cast of characters is fewer compared to more speciose ant-following flocks characteristic of lowland Amazonia. This relative simplicity facilitated ecologists' understanding of the dynamics between the birds and ants

TABLE 1. Five key research areas and the future opportunities that they present for conceptual advances using ant-followers as a model system.

Research area	Future opportunities
Competitive dynamics	Quantify resource availability and use at swarms and examine the degree of niche overlap and niche partitioning at swarms
	Quantify the costs and benefits of finding and foraging at ant swarms
Cognitive and behavioral adaptations	Test for neurological and behavioral correlates of episodic memory across species varying in dependence on ant swarms
	Evaluate the causes and consequences of social information use at swarms
Evolution	Use functional traits to evaluate the evolution of ant-following behavior
	Explore the evolutionary ontogeny of ant-following behavior in other clades (e.g., Furnariidae)
	Evaluate the relationship between gradients in swarm presence/activity (selective pressure) and specialization on army-ants (functional trait).
Biogeography	Quantify the relationship between army-ant abundance and ant-follower abundance and distribution for species that vary in specialization on ant swarms.
	Apply metabolic theory to evaluate the relationship between biomass of ant swarms and ant-followers.
Conservation	Identify areas that have high probabilities of serving as climate refugia and that are less likely to undergo a significant land-use change
	Understand how variation in army-ant abundance influences ant-follower populations, particularly in the context of fragmentation.
	Evaluate how specialized ant-followers mediate effects of fragmentation and habitat modification for ant-swarm following species aggregations
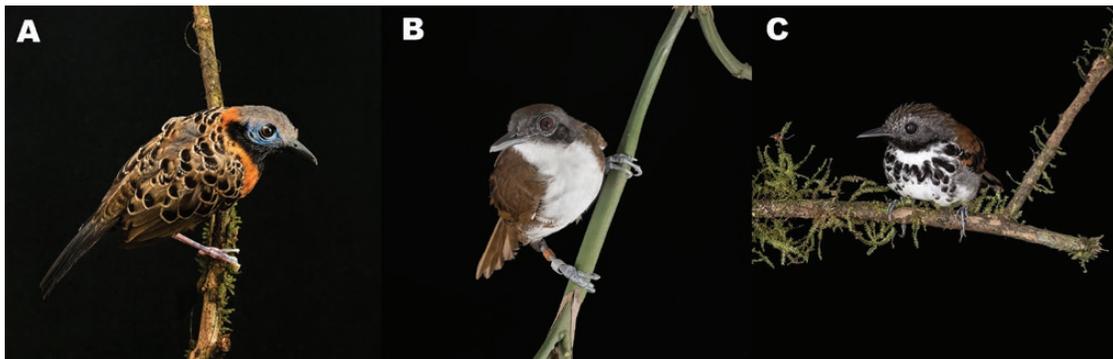
FIGURE 2. The 3 antbird (Thamnophilidae) species that were the focus of Edwin O. Willis' seminal research on army-ants and their avian attendants on Barro Colorado Island, Panama. (**A**) Ocellated Antbird (*Phaenostictus mcleannani*), (**B**) Bicolored Antbird (*Gymnopithys bicolor*), and (C) Spotted Antbird (*Hylophylax naevioides*). Photos courtesy of John Whitelaw © 2016.

in Panama. Moreover, this understanding was augmented by decades of research on the density, movement, and activity patterns of ant swarms, particularly *E. burchellii* (e.g., Schneirla 1933, Schneirla and Piel 1948, Rettenmeyer 1963).

Initial research at Barro Colorado Island focused on the type of territorial system that enabled exploitation of nomadic army-ant raids. Despite the profitability of foraging at ant swarms, the challenge of following a nomadic food source gave rise to questions about the territoriality of ant-following birds. For example, locations of army-ant swarms are patchy and transient in space and time (Swartz 1997, O'Donnell et al. 2012). Swarm activity is reduced during 3 weeks of *E. burchellii*'s 5-week reproductive cycle, during which ant colonies form massive, stationary bivouacs and require fewer resources because larvae have pupated and queens are laden with eggs (Schneirla and Piel 1948, Rettenmeyer 1963, Rettenmeyer et al. 2011). Based on his observations, Johnson (1954) suggested that some ant-followers lacked territories, enabling them to wander alongside the nomadic army-ants. Willis was the first to test this hypothesis. He color-banded individuals of 3 antbird species (family Thamnophilidae)—the Ocellated Antbird (*Phaenostictus mcleannani*), the Bicolored Antbird (*Gymnopithys bicolor*), and the Spotted Antbird (*Hylophylax naevioides*; Figure 2) to assess their space use and territorial dynamics. Based on hundreds of hours of observations of individuals at and away from ant swarms,

Willis was able to identify variation among bird species in their dependence on army-ant swarms for food. He was the first ecologist to suggest that ant-following behavior in birds falls along a continuum ranging from occasional followers that forage opportunistically at ant swarms to obligate ant-followers (e.g., Bicolored and Ocellated Antbirds) that derive the majority of their food from ant swarms (Willis and Oniki 1978).

Subsequently, Willis described how space use and nesting territoriality necessarily varied amongst ant-followers based on their degree of reliance on a patchy, ephemeral resource such as army-ant swarms. In his mapping of locations of color-marked birds, he noted that occasional ant-followers appeared to only join swarms as the raiding ants traversed their all-purpose foraging and nesting territories (Willis and Oniki 1978). In contrast, Willis (1973) found that obligate ant followers occupied large overlapping home-ranges (e.g., Ocellated Antbird: ~175 ha; Bicolored Antbird: ~45 ha) that encompassed multiple ant colonies and allowed them to forage exclusively at swarms. Rather than continuously wandering through the forest alongside the nomadic army-ants, however, the obligate ant-following Ocellated Antbird and Bicolored Antbird adhere to a foraging range, within which they hold and defend nesting territories. Bicolored Antbird nesting areas, for example, are distinct and do not overlap with neighbors' nesting areas, but their foraging regions do so that a given nesting area will be within the foraging range of several pairs (Willis 1967). Coupled with his observations of intraspecific dominance hierarchies at ant swarms, Willis posited that the pair whose nesting territory was closest to the swarm dominated the other pairs present at the swarm (Willis 1967, 1973). He found that dominance was achieved through a complex series of aggressive and submissive displays. Rather than relying on aggressive vocalizations, so common in traditional territorial disputes, Ocellated Antbirds have a series of postures they use to establish and maintain dominance over their neighbors while attending ant swarms in their nesting area and only escalate to chasing other individuals as a last resort. Willis (1973) suspected that Ocellated Antbirds form family clans that nest separately, but forage together and are less aggressive towards relatives. In Bicolored Antbirds, the pair whose nesting area the swarm is traversing aggressively challenges neighboring pairs until even high-ranking neighbors become submissive, establishing the dominance hierarchy for each swarm. Zones between dominance areas appear to be narrow, as sharp reversals of dominance occur between pairs as the ants traverse over the forest floor (Willis 1967). As such, Willis began to call these areas "dominions" and extended the definition of a territory to be an area of dominance, whereby one group or individual dominates others that can become dominant elsewhere

(Willis 1967, 1973, Willis and Oniki 1978). The work by Willis and colleagues, further described below, shed light on the complex dynamics of ant-following behavior and laid the foundation for testing new hypotheses. Below, we highlight how this study system has been used to address questions in 5 different research areas and we provide future directions for each.

RESEARCH AREA 1: COMPETITIVE DYNAMICS OF ANT-FOLLOWING BIRD FLOCKS

Although competition for food is an ever-present aspect of ant-followers foraging at swarms, quantitative approaches to characterize intra- and inter-specific interactions and niche overlap are scarce. We describe how previous studies have laid the groundwork for using the ant-following study system as a model for formal hypothesis testing of important ecological concepts including niche partitioning and patchy resource use.

Intraspecific Competition and Reciprocal Tolerance

While the majority of Willis' findings on territoriality in obligate antbirds were later corroborated by radio-telemetry studies from both Central and South America (e.g., Willson 2004, Chaves-Campos and DeWoody 2008, Chaves-Campos 2011, Touchton and Smith 2011), it was discovered that individuals of Ocellated Antbirds in Costa Rica were not grouped into patrilineal clans as suspected by Willis (1973). Rather, Chaves-Campos and DeWoody (2008) found Ocellated Antbird populations to be structured into roosting and nesting areas occupied by individual mated pairs, similar to the Bicolored Antbird (Willis 1967). The feeding aggregations of Ocellated Antbirds at ant swarms are instead likely the result of reciprocal tolerance of neighbors. By simulating territorial intrusions using acoustic recordings, Chaves-Campos et al. (2009) found that male Ocellated Antbirds only responded aggressively to other males within their own nesting and roosting area, and that responses to adjacent neighbors were less aggressive than to non-neighbors (the "dear enemy" effect; introduced in Fisher 1954, reviewed in Temeles 1994). Additionally, they found that prey intake rates at ant swarms progressively declined with increasing distance from a pair's nesting/roosting area, further supporting the local dominance/reciprocal tolerance paradigm. Presumably, reciprocal tolerance is a behavioral adaptation that reduces intraspecific competition and allows obligate ant-followers to forage exclusively on a patchy resource (Chaves-Campos et al. 2009). Whether or not such local dominance and reciprocal tolerance is the norm among obligate ant-followers remains to be determined. While it requires the type of detailed field studies performed by Chaves-Campos et al. (2009), we encourage

more studies of this kind to examine the different ways in which obligate ant-followers may or may not tolerate each other at ant swarms. Regardless, reciprocal tolerance of neighbors ameliorates intraspecific competition at swarms and may greatly facilitate specialization on a spatially and temporally patchy resource.

Interspecific Competition and Niche Partitioning at Ant Swarms

Ant-followers compete for food resources at swarms: arthropods and small vertebrates that attempt to escape the predaceous army-ants (Otis et al. 1986). The greatest density of escaping arthropods, and likely the richest foraging potential for attending ant-followers, is considered to be near the center of the leading edge of the swarm (Willis and Oniki 1978). Willis and Oniki (1978) suggested that there were general foraging zones of varying profitability distributed in both horizontal and vertical space around swarms, which correspond to the density of escaping prey. Furthermore, they observed that zone occupancy by ant-followers was contingent on a dominance and dependence hierarchy dictated by body size. The largest ant-followers, which are also generally more reliant on army-ants for food, occupy and defend the zones at the front and center of swarms, while the medium- and small-sized birds that are generally less reliant on army-ant swarms for food occupy the progressively less profitable areas along the swarm periphery (Willis 1967, 1972a, 1973; reviewed in Willis and Oniki 1978). In Panama, the large Ocellated Antbird (~50 g) occupies the richest foraging zones, followed by the medium-sized Bicolored Antbird (~30 g), and then the small Spotted Antbird (~18 g; Willis 1972a, Willis and Oniki 1978). This spatial segregation and dominance hierarchy suggest that ant-followers are partitioning food resources at swarms. However, per capita food intake among species foraging in different zones has not been quantified to thoroughly test this hypothesis and merits future study. Ideally, the breeding success and survivorship of species in this hierarchy could potentially reveal the ultimate fitness benefits of following swarms (Jullien and Clobert 2000).

Another aspect of niche partitioning at swarms is division of microhabitats via perch type. For example, woodcreepers (family Furnariidae) perch on large vertical trunks ("climber" guild), antbirds cling to slender vertical saplings ("clinger" guild), large ground birds such as ground-cuckoos (*Neomorphus* spp.) are limited to the edges of swarms ("ground" guild) and other large birds such as motmots (family Momotidae) are limited to large horizontal perches near the ground ("percher" guild), likely limiting the dominance of these individuals (Willis 1966b, 1972b, Willis and Oniki 1978). Similar niche partitioning via dominance hierarchy and microhabitat use has also been noted at ant swarms in the forests of Brazil (Oniki 1972), Mexico (Coates-Estrada and Estrada 1989), and

Peru (Willson 2004). These ant-following flocks demonstrate similar guild structure and hierarchy, although with different species. The patterns of space use and microhabitat use by ant-followers at ant swarms are consistent with niche partitioning—species divide vertical and horizontal microhabitats which reduces competition among co-attending ant-followers, and subsequently enhances the local diversity of swarm followers. More recent work has begun to evaluate the relative contribution of facilitation and competition in influencing patterns of flock attendance at swarms across elevational gradients (O'Donnell 2017). While gregarious species were typically associated with the most speciose flocks, there were cases of competitive exclusion for certain species' pairs suggesting that both facilitation and competition may both be playing a role in influencing species composition in determining flock attendance (O'Donnell 2017).

In South America, however, avian foraging flocks at swarms can contain far more attendant species than the relatively species-depauperate flocks of Central America. While these species appear to partition space-use based upon body mass (Table 2), the ultimate benefits are less clear. At Cocha Cashu in Peru, Willson (2004) found that some species rely on different swarm raiding army-ant species to varying degrees, representing yet another form of niche partitioning among ant-followers. Those

TABLE 2. Obligate ant-following bird species of South America (data from Cocha Cashu, Peru; Willson 2004) and Central America (data from Barro Colorado Island, Panama; Willis 1972a, Willis 1973), including mean body mass (g) and home-range size (ha).

Geographic locality	Species	Mean body mass (g)	Mean home-range size (ha)
South America	Black-spotted Bare-eye *Phlegopsis nigromaculata*	46.0	46
	Sooty Antbird *Hafferia fortis*	46.5	15
	Hairy-crested Antbird *Rhegmatorhina melanosticta*	31.4	48
	White-chinned Woodcreeper *Dendrocinca merula*	47.5	65
	White-throated Antbird *Oneillornis salvini*	25.9	27
Central America	Ocellated Antbird *Phaenostictus mcleannani*	48.6	175
	Bicolored Antbird *Gymnopithys bicolor*	29.4	44
	Spotted Antbird *Hylophylax naevioides*	16.7	3–5

species that primarily forage at *E. burchellii* swarms, for example, display the classical hierarchy according to body size described by Willis and Oniki (1978). Yet, other obligate species, such as Sooty Antbird (*Hafferia fortis*), rely on swarms of *L. praedator* to a greater degree (Willson 2004). The Sooty Antbird vigorously defends ~15 ha territories with only one pair usually present per swarm (Willson 2004). The Sooty Antbird evidently locates a sufficient number of *L. praedator* swarms in addition to *E. burchellii* swarms on their territories to be able to exclusively forage at ant swarms while maintaining an all-purpose territory.

Another interesting yet underexplored area of research relates to the simple costs and benefits of foraging at ant swarms. Do birds get more food or higher quality food from foraging at a swarm? To our knowledge, this has not been examined in ant-followers, although anecdotally, Spotted Antbirds in Panama exhibit high intraspecific variation in foraging rates (J. M. Touchton personal communication). Additionally, there is also the smaller scale question of whether partitioning resources at a swarm results in differential benefits. While there is clear partitioning of space use at ant swarms via dominance and body mass, the relative foraging benefits to this division remain unclear. Does it pay to forage in the "richer" areas at ant swarms and do these areas predictably hold a greater quantity of prey items or perhaps higher quality prey? That more dominant birds repeatedly occupy certain regions at ant swarms certainly is suggestive of the greater foraging value of these locations (e.g., Willis 1973, J. M. Touchton personal communication). Nevertheless, it is not clear whether dominant birds are tracking flushed prey abundance or are repeatedly defending certain areas at swarms that have the highest predictable prey profitability. At *E. burchellii* swarms on Barro Colorado, Panama, for example, Bicolored Antbirds forage near the forest floor; whereas in the forests of the more humid Chocó in Colombia, Bicolored Antbirds often forage above the ground in dense tangles (Willis 1967), due to the ants presumably tracking microhabitats with the highest arthropod abundance. We suggest that future studies aim to sample flushed arthropod abundance in different foraging microhabitats at ant swarms, both for *E. burchellii* and *L. praedator*, and in regions where both more dominant and subordinate individuals are foraging at swarms to help identify to what degree dietary niche overlap and prey availability are driving competitive interactions at ant swarms (*sensu* Wrege et al. 2005). With the advent of meta-barcoding techniques, the ability to evaluate dietary niche overlap has now become a much more feasible endeavor. By obtaining fecal samples from mist-netted birds, the amount of dietary overlap can be quantitatively assessed (Rytkönen et al. 2019). We propose several future directions for research on the competitive dynamics that may underlie species interactions in ant-followers.

Summary and Future Directions

Previous observational work has suggested that traditional ecological interactions such as competition may be the primary species interaction operating at ant-follower aggregations. However, surprisingly little quantitative research on competition at swarms exists in the literature. Cutting-edge molecular approaches (DNA metabarcoding) and analytical techniques (see social networks below) have now made it feasible to assess degree of niche overlap and the strength of competitive interactions amongst different species.

- To what degree does niche overlap and prey availability drive competitive interactions at ant swarms?
- What are the actual benefits (i.e. how much food can be obtained) and costs (i.e. finding swarms and then competing for food) of an ant-following lifestyle?
- Do the ecological benefits of foraging at swarms translate into fitness benefits (i.e. increased reproductive success and/or survival)?

RESEARCH AREA 2: BEHAVIORAL AND COGNITIVE ADAPTATIONS OF ANT-FOLLOWERS

Recent studies have described the remarkable behavioral and cognitive adaptations that ant-followers use to locate nomadic army-ant swarms day after day as the ants move through the forest (Logan et al. 2011, reviewed in O'Donnell et al. 2012). We review 2 primary adaptations that facilitate locating ant swarms by ant-followers—bivouac-checking and social information use. We then propose future studies to expand our understanding of these behaviors.

Locating and Tracking an Ephemeral Resource

Tracking a temporally ephemeral and spatially patchy resource such as army-ant swarms is a challenging prospect. Recent research has focused on the cognitive and behavioral adaptations that ant-followers (particularly obligate species) have evolved to cope with spatiotemporal variation in the availability of ant swarms (Logan et al. 2011, reviewed in O'Donnell et al. 2012). One of the outstanding traits of ant-followers is their ability to locate and track army-ant colonies as they migrate through the forest (Swartz 2001, Chaves-Campos 2003, Willson 2004). In general, swarm-raiding army-ants complete their migration during the night once ant-followers are already roosting (Schneirla 1940). Additionally, army-ant colonies avoid their own recent raid paths and those of other nearby colonies, resulting in further spatial segregation of colonies in a given area (Franks and Fletcher 1983). As a result, ant-followers must rely on additional cues to locate nomadic army-ant colonies rather than simply following the ants or returning to the same area where a swarm was previously encountered. 2 primary behaviors have been documented

that facilitate locating and foraging at ant swarms: 1 bivouac-checking, and 2 social information use.

Bivouac-checking

Bivouacs are massive, temporary nests constructed of the ants themselves, which are formed daily and moved primarily at night (Swartz 2001). Bivouac-checking involves birds actively inspecting army-ant bivouacs of *E. burchellii* to assess swarm activity (*L. praedator* bivouacs are subterranean and generally inaccessible to birds; Swartz 2001). In a review of the behavior, Logan et al. (2011) reported bivouac-checking in 21 bird species from 13 different families. The diversity of species that exhibit bivouac-checking behavior suggests that it may be more common than realized among ant-followers and merits further study. O'Donnell et al. (2012) suggest that this particular activity requires specialized cognitive abilities, and it is potentially a tropical parallel to the activity of food caching by many temperate species (Smith and Reichman 1984). A large body of literature exists on food caching behavior, and bivouac-checking provides a novel opportunity from the tropics to test predictions of existing theory on the cognitive and neural mechanisms underpinning food hoarding type behavior (Smulders et al. 2010). The literature also suggests a direct correlation between caching specialization and hippocampus size (Lucas et al. 2004). Understanding this relationship in the tropics may provide insight into the evolution of ant-following behavior.

It is relatively easy to locate army-ant bivouacs and identify attendant birds. Given that bivouac checking is prevalent among obligate ant-followers, Swartz (2001) proposed that observations of birds at bivouacs would reveal previously unidentified obligate ant-followers. Yet, non-obligate ant followers have also been observed checking bivouacs, such as the facultative Spotted Antbird in Panama or White-shouldered Fire-eye (*Pyriglena leucoptera*; reviewed in Logan et al. 2011). As a defining trait, bivouac-checking may perhaps be limited to facultative and obligate ant-following species but not occasional followers. While it may be fruitful to identify a more comprehensive list of species that check bivouacs to understand the geographic and phylogenetic extent of this behavior, we feel the real advantage may be studying the role of bivouac-checking in the evolutionary progression from occasional to obligate ant-following. Perhaps, the ability to remember and locate bivouacs is a key step in the evolution of becoming an obligate ant-follower.

Social Information Use

Sharing of information seems to be particularly important in the localization of swarms. In addition to reciprocal tolerance at ant swarms, neighboring obligate ant-followers may benefit from collective knowledge regarding the location of army-ant colonies in their neighborhood. While Willis (1973) observed groups of Ocellated Antbirds leaving swarms together, Chaves-Campos (2011) was able to track these birds through the forest using radio-telemetry. Groups leave and travel in a single file and follow a direct path to another ant swarm, indicating that at least one individual in the group has knowledge of the location of the ant colony. Reciprocal reliance on conspecifics for swarm location potentially has an enormous benefit for obligate ant-followers. Willson (2004) estimated that obligate ant-followers would need to keep track of at least 3 colonies of *E. burchellii* to satisfy daily energetic requirements. Collective knowledge of swarm locations between neighbors would reduce the need for individuals to keep track of swarms located far from roosting areas. Information sharing would be a reason to tolerate nonfamilial conspecifics feeding at ant swarms in roosting and nesting areas (Gaston 1978) and could have facilitated the emergence of the specialization of the ant-following life history strategy.

Information transfer at swarms not only includes collective knowledge sharing among conspecifics, but also eavesdropping by heterospecifics. Willis (1967) was the first to propose that eavesdropping birds prospecting for ant swarms may rely on vocalizations of obligate species to locate the swarms. Recent playback experiments in Costa Rica, Ecuador, and Panama have confirmed that vocalizations of obligate species attract a variety of eavesdropping heterospecifics (Chaves-Campos 2003, Batcheller 2017, Martínez et al. 2018). Martínez et al. (2018) used a factorial playback experiment to simulate different types of bird flocks foraging at ant swarms to test how flock composition influenced recruitment of eavesdropping birds. They found that playbacks simulating larger, more speciose flocks with obligate species elicited the strongest responses, suggesting that eavesdropping birds may weigh the costs (competition) and benefits (larger swarms with more prey resources) when deciding whether or not to recruit to a swarm. Furthermore, they found evidence of an information cascade, whereby obligate ant-followers attracted facultative ant-followers, which in turn attracted occasional followers (Martínez et al. 2018). Acoustic eavesdropping may be the primary form of swarm localization for non-obligate species that do not check bivouacs or use collective information sharing to find swarms. Following the loss of the Ocellated Antbird, a keystone information-producing obligate species, recruitment to swarms by eavesdropping birds was considerably dampened, possibly signifying the degradation of this information cascade (Pollock et al. personal communication). The use of social network analysis may provide insight into the different roles that species play in eavesdropping networks and the importance of social information for flock formation at swarms (Wey et al. 2008). It also remains possible that other sensory modalities (e.g.,

olfactory, memory-related) may be involved in finding swarms, and these alternative mechanisms merit further attention.

Summary and Future Directions

Recent studies have provided insight into the different roles that ant-followers play as information producers and receivers at swarms. Evidence of both intraspecific facilitation and interspecific eavesdropping has been documented and demonstrated the importance of social information in localizing swarms. Experimental approaches can now be extended to include social network analysis to evaluate the complex ways in which information is transferred among ant-followers and influences subsequent formation of flocks at swarms. We propose several future directions for research on the behavior and cognition of ant-following behavior in Neotropical birds:

- How does bivouac-checking behavior vary among populations of the same species with varying degrees of ant-following behavior? Across species?
- How is information shared and used between ant-followers? (i.e. collective knowledge regarding army-ant swarm locations) and to what extent is this a logical extension of cooperation or facilitation among species?
- What sensory adaptations (olfactory, visual, auditory, memory-related) allow obligate birds to recognize and find swarms? How do young obligate birds learn these techniques?

RESEARCH AREA 3: EVOLUTION OF ARMY-ANT FOLLOWING

Despite the prevalence of ant-following behavior among Neotropical birds, how or when this behavior evolved was not clear until recently when Brumfield et al. (2007) explored the timing and tempo of evolution of ant-following behavior in typical antbirds (Family Thamnophilidae). Given recent advances in avian molecular biology (e.g., Toews et al. 2016), there is ample opportunity to test conclusions derived from the antbird analysis in other clades. In an innovative phylogenetic analysis of the typical antbirds (Thamnophilidae), Brumfield et al. (2007) employed a robust molecular phylogeny (40 of 46 extant genera) to conduct ancestral state reconstruction and understand the evolution of ant-following behavior. Molecular dating showed that ant-following is an ancient behavior that has persisted in antbirds since at least the late Miocene (~6 mya). They also found that ant-following behavior has tended towards increasing specialization over evolutionary time, with *occasional* following as the ancestral state and *regular/obligate* following evolving as the derived state (Brumfield et al. 2007). *Regular* following

evolved independently 3 times in Thamnophilidae, and in 2 of these clades obligate followers eventually evolved from regular followers. No reversals from the obligate state were detected over evolutionary time (Brumfield et al. 2007), indicating that ant-following is an ancient, phylogenetically conserved behavior. Furthermore, the ecological conditions that permit the evolution of obligate ant-following behavior and the evolutionary changes in functional traits (e.g., body size, see Table 2) associated with obligate ant-following behavior are poorly understood and merit further investigation. Incorporating functional traits such as body size or hippocampus size (i.e. a proxy for memory capacity; Lucas et al. 2004) into ancestral state reconstruction may help resolve the mechanistic basis underlying specialization on ant swarms and group behavior (Brumfield et al. 2007, Martínez et al. 2016).

Using Ecology to Generate Insights into the Evolutionary Progression from Facultative to Obligate Ant-following

Several recent and innovative studies by Touchton and colleagues (Touchton and Smith 2011, Touchton and Wikelski 2015) have also shed light on the evolution of ant-following behavior, particularly the progression from the regular to the obligate state. These authors took advantage of a natural experiment of sorts—the isolation of Barro Colorado Island from the mainland of Panama. In 1914, thousands of acres of lowland forest were flooded to create Lake Gatún and complete the Panama Canal, leaving behind Barro Colorado, an isolated 1,600-ha remnant of foothill forest (Willis 1974). Detailed records of the Barro Colorado avifauna (Willis 1974, Karr 1982, Robinson 1999) have demonstrated that numerous species still present on the mainland have gone extinct on Barro Colorado since its isolation, such as several obligate ant-following species including the dominant Ocellated Antbird. Touchton and colleagues studied the Spotted Antbird on Barro Colorado—a regular ant-follower within their territorial confines on the mainland—to determine how the loss of obligates there has affected the ant-following bird community and behavior.

Touchton and Smith (2011) found that, in the absence of Ocellated Antbirds on Barro Colorado, Spotted Antbirds exhibited demographic compensation and increasingly obligate behavior. Specifically, Spotted Antbird population density increased more than twofold and biomass at swarms increased threefold following the loss of Ocellated Antbirds. Touchton and Wikelski (2015) found further evidence of behavioral shifts from the regular to obligate state occurring in Spotted Antbirds on Barro Colorado. Typically, individuals of Spotted Antbirds maintain small, fixed territories (~4 ha; Willis 1972a, Styrsky 2003) and only forage at swarms when they pass through

their territory (Willis 1967, 1972a). Following the loss of Ocellated Antbirds, however, some individuals of Spotted Antbirds in the population have exhibited territorial breakdown, and now have larger foraging ranges that overlap with several other conspecifics, more similar to traditional obligate ant-following species (Touchton and Wikelski 2015). These "roaming" individuals also spend more time foraging at army-ant swarms than their traditional territorial counterparts both on the Barro Colorado and the nearby mainland (Touchton and Wikelski 2015). Presumably, regular and obligate ant-following behavior evolves when the benefits of foraging regularly or exclusively at swarms (i.e. foraging opportunities) outweigh the costs (i.e. finding the swarms and competing for food resources). Touchton and Wikelski (2015) showed that Spotted Antbirds that exhibited novel "roaming" behavior produced significantly more offspring than ancestral territorial individuals, suggesting that obligate ant-following can provide tangible fitness benefits, although the mechanism of this increased reproductive success remains unclear. Future studies that attempt to quantify the costs and benefits of foraging at vs. away from swarms and the subsequent effects on fitness (see *Interspecific competition and niche partitioning at ant swarms*, above) will shed light on the ecological conditions that permit obligate ant-following behavior to evolve.

Ecological Conditions Favoring the Evolution of Ant-following as a Functional Trait

One unanswered question related to the evolution of ant-following behavior is what ecological conditions favor the evolution of ant-following as a functional trait. The obvious prerequisite for obligate ant-following behavior to evolve is the presence and/or abundance of army-ants. Ultimately, we suggest that understanding the relationship between army-ant abundance, swarm density, and prey abundance and the relative costs and benefits of finding and foraging at swarms will shed light on the evolution of ant-following as a functional trait (Figure 3). Several factors that may influence ant swarm size and density are spatial and seasonal variation in abiotic conditions (e.g., temperature and humidity; Schneirla 1949, Levings 1983, Kumar and O'Donnell 2007, Kumar and O'Donnell 2009) and available habitat area (e.g., Roberts et al. 2000, Meisel 2004). Below, we provide several alternative scenarios that may explain the evolution of obligate ant-following behavior. Under the simplest scenario, the probability of specialization is directly proportional to the abundance or raid intensity of army-ants (Hypothesis I, Figure 3). Alternatively, we might expect the probability of specialization on army-ants to only be likely where abundance or raid intensity of army-ants is extremely high (Hypothesis II, Figure 3). Finally, specialization may occur above an intermediate
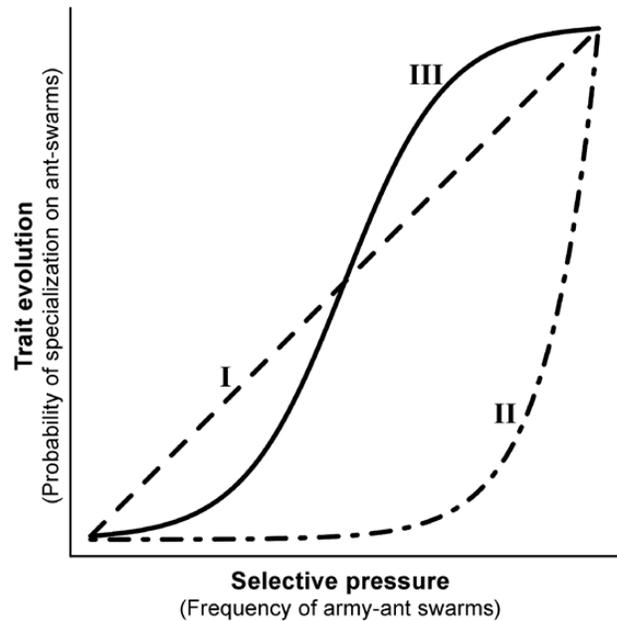
FIGURE 3. Hypothetical evolutionary trajectories relating trait evolution (probability of specialization on ant swarms) to selective pressure (frequency of ant swarm occurrence as a proxy for benefits of specialization) whereby (I) depicts a linear relationship between specialization and ant-following; (II) depicts a relationship where specialization only occurs at a higher frequency of ant swarms; and (III) predicts a threshold response of probability of specialization to high levels of swarming activity.

threshold of army-ant abundance or swarm density (Hypothesis III, Figure 3). Elucidating this pattern may require additional types of ecological data such as swarm density in relation to standing arthropod abundance, and arthropod abundance available for birds as a prey source. Armed with a wealth of data across regions that describe the ant-following bird species and their dependence on ant swarms, ecologists can now assess the collective group of functional traits, from body size and foraging ecology to evolutionary history (Martínez et al. 2016), that may underlie ant-following as a trait.

Summary and Future Directions

Numerous studies across the Neotropics have shed light on variation in ant-following behavior. This variation should encourage future studies that test concepts of evolutionary specialization on ant swarms. We propose several questions for future research on the evolution of ant-following behavior in Neotropical birds:

- Obligate ant-following has also evolved in several other bird families, most notably the woodcreepers (Furnariidae). The recent publication of a highly resolved molecular phylogeny (Derryberry et al. 2011) makes woodcreepers an ideal candidate clade for testing the generality of the conclusions derived from the

antbird analysis (Brumfield et al. 2007). How does the evolutionary ontogeny of ant-following behavior vary across families?

- A broad range of functional traits are widely known in Neotropical birds. These data provide an opportunity to explore potential drivers of variation in the evolution of ant-following behavior. What functional traits play a role in the evolution of ant-following behavior?

- Brumfield et al. (2007) proposed the idea that evolution of ant-following as a novel foraging strategy could accelerate rates of species diversification. This idea has never been tested yet may now be possible given recent advances in molecular and phylogenetic techniques and merits examination. To what extent does the evolution of ant-following influence rates of species diversification?

- Identify gradients of swarm abundance/raiding intensity throughout the biogeographical ranges of ant-followers to evaluate how specialization behavior may be influenced by variation in army-ant abundance (Figure 3). Evaluating the degree of gene flow among populations of ant-followers along such a gradient would generate insight into the degree of phenotypic plasticity vs. genotypic divergence that may explain the rates of divergence of these species across the antbird phylogeny. How do gradients of army-ant abundance influence the degree of specialization on army-ants?

RESEARCH AREA 4: BIOGEOGRAPHY OF ANT-FOLLOWING IN THE NEOTROPICS

Ant-following is a geographically widespread behavior that has been observed in birds throughout the Neotropics (Brumfield et al. 2007). Despite its prevalence, many of the most basic questions relating to the biogeographic and distributional patterns of ant-following behavior are only beginning to be explored. In this section, we review how ant-following behavior varies across environmental gradients and highlight gaps in the current state of knowledge that merit further study.

Biogeographic and Distributional Patterns of Ant-following in the Neotropics

Ant-following in birds has been documented throughout the majority of the continental Neotropics, ranging from central Mexico (Greene et al. 1984, Coates-Estrada and Estrada 1989, Dobbs and Martin 1998) to northern Argentina (Di Giacomo and Di Giacomo 2006, Brumfield et al. 2007; see Appendix Figure 4 and Supplementary Material Table S1). On a geographic scale, the occurrence of ant-following behavior is obviously constrained to locations where swarming army-ant species are present. Presumably, the species richness and/or population densities of ant-followers should be directly related to the

densities or raiding rates of army-ants, yet this idea has never been formally tested. Although little information exists in the literature on population densities of army-ants across the Neotropics, a study spanning 20 Neotropical sites found that raiding rates of army-ants were positively associated with prey abundance and primary productivity (Kaspari and O'Donnell 2003), which is greater in the tropics. Consistent with these results, species richness of ant-followers is inversely related to latitude. Specifically, species richness of obligate ant-followers peaks in western Amazonia, nearest the equator, whereas species richness of regular ant-followers is highest around the southern periphery of the Amazon basin (Brumfield et al. 2007).

Elevation is another important biogeographic correlate of ant-follower abundance and behavior. The abundance of obligate ant-followers declines with increasing elevation (Kumar and O'Donnell 2007, O'Donnell et al. 2011), which may be explained by decreased raiding rates of army-ants at high elevations (Hilty 1974, O'Donnell and Kumar 2006, Pizo and Melo 2010). However, the densities of army-ants actually peak at intermediate (pre-montane) elevations (O'Donnell et al. 2011), and overall attendance of ant-followers at swarms does not seem to vary systematically with elevation. Hilty (1974) suggested that increased attendance of swarms by facultative ant-followers at higher elevations compensated for the loss of obligate ant-followers, and indeed, previous studies have found similar rates of attendance (Pizo and Melo 2010) and total biomass (Wrege et al. 2005, Kumar and O'Donnell 2007) between highland and lowland sites despite fewer obligates being present at high elevations. In fact, the largest bird flock ever recorded at a swarm was in pre-montane forest in Costa Rica (Chaves-Campos 2005). Although obligate ant-follower richness declines with increasing elevation, ant-following behavior is still prevalent among a variety of species at higher elevations.

Summary and Future Directions

We suggest that future directions should include macroecological analyses that incorporate the abundance and density of ant swarms, and the species richness of ant-followers along latitudinal gradients. We also suggest that such analyses should incorporate traits such as body size, hippocampus size, and foraging strategy which may function as drivers of specialization over these larger spatial scales (see Research Area 3 Evolution). Lastly, from an energetic perspective, studies have shown a positive correlation between swarm raid frequency and prey abundance. New studies should attempt to quantify how much prey are available to ant-followers for swarms of varying size in different geographical regions. The energy available to a swarm could be the basis of applying already existing metabolic theory to predicting the biomass of ant-followers

across latitudes and elevations (Brown et al. 2004). We propose several questions for future research on the biogeography of ant-following behavior in Neotropical birds:

- How do population densities of army-ant species influence the distributions and densities of species that vary in their degree of specialization on army-ants?
- Quantifying the standing biomass of ant swarms and ant-followers may allow for the application of metabolic theory. To what extent can metabolic theory explain the relationship between productivity, ant swarm biomass, and ant-follower biomass across latitudinal and elevational gradients?

RESEARCH AREA 5: CONSERVATION OF ANT-FOLLOWERS

Raiding army-ants are keystone species in Neotropical forests (Koh et al. 2004) and the sheer number of bird species that depend on them for food (Rettenmeyer et al. 2011) makes army-ants relevant to the conservation of Neotropical birds. In this section, we focus on two major threats to the conservation of army-ants and the birds that follow them: habitat fragmentation (by detailing recent studies that have documented the impacts of habitat fragmentation on populations of ant-followers) and potential impacts of climate change.

A number of studies have documented the negative demographic impact of fragmentation on populations of ant-followers, both from fragments of South American rainforests (Harper 1989, Stouffer and Bierregaard 1995, Laurance et al. 2002, Stouffer et al. 2006) as well as montane Central American rainforests (Kumar and O'Donnell 2007). Following forest fragmentation, insectivores such as ant-followers decline in abundance disproportionately more quickly than other guilds (Stouffer and Bierregaard 1995) and take longer to re-colonize fragments after forests begin to regenerate (Powell et al. 2013). Army-ant colonies require large areas to roam and scavenge for prey, and, therefore, are thought to be especially susceptible to the microclimatic changes associated with fragmentation (i.e. increased temperature and solar radiation, reduced humidity; Laurance et al. 2002). Furthermore, flocks of ant-followers in fragmented forests have been observed to be smaller, with reduced diversity and lower total biomass relative to those in continuous forests (Kumar and O'Donnell 2007). Similarly, African birds that follow driver ants (*Dorylus* spp.), the Old World equivalent of army-ants, showed large declines in rainforest fragments in Kenya (65–113 ha; Peters and Okalo 2009). Overall, a wealth of studies has documented how understory insectivores in general, and ant-followers in particular, respond negatively to forest fragmentation and degradation

(e.g., Dunn 2004, Maldonado-Coelho and Marini 2004, Bregman et al. 2014). Establishing the mechanistic drivers by which habitat fragmentation causes declines in ant-follower populations is becoming increasingly important. The most obvious explanation is that habitat fragmentation causes declines in army-ant populations, which in turn cascades down to affect ant-follower populations (Laurance et al. 2002). Indeed, declines of army-ant populations following forest fragmentation have been documented in both the Neotropics (Meisel 2004) and Afrotropics (Peters et al. 2008, Peters and Okalo 2009). The mechanistic basis of army-ant declines following fragmentation is unclear, but may be related to a reduction in habitat area (i.e. army-ants have large home-ranges and are highly mobile and may not be able to persist in small fragments, especially where matrix conditions are hostile; Stouffer and Bieregaard 1995), abiotic conditions (microclimatic sensitivity could cause direct mortality or inhibit colony mobility between fragments; Roberts et al. 2000), or altered prey base (i.e. declines of small vertebrates and arthropods following fragmentation). Interestingly, male sex-biased dispersal may allow recolonization or explain the resilience of army-ant populations to island isolation (Berghoff et al. 2008).

Determining the range of colony sizes that produce viable army-ant populations and how different colony sizes persist across land use and fragmentation gradients will be an important first step towards understanding the persistence of obligate army-ant following species (and consequently, ant-followers) at the landscape level. Nevertheless, ant-followers have disappeared from fragments where ant swarms still exist (Touchton and Smith 2011), indicating that ant-follower populations may be subject to other ecological limitations induced by fragmentation (nest predation, social group dynamics, etc.,) and these factors will need to be identified as well. Finally, several studies have affirmed the importance of vocal cues in locating ant swarms (Chaves-Campos 2003, Batcheller 2017, Pollock et al. 2017, Martínez et al. 2018). Disappearance of larger ant-followers from fragments may disrupt information transfer, thereby impeding recruitment of other ant-followers to swarms, negatively affecting their populations (Pollock et al., unpublished data). Social network analysis may prove a useful tool in understanding how social information mediates species interactions along these disturbance gradients (Mokross et al. 2014)

Impacts of Changing Climate on Army-ants and Ant-followers

Just as pressing a conservation concern as land-use changes and forest fragmentation are the implications of a changing climate. Roberts et al. (2000) demonstrated that army-ants avoid hot sunny areas in coffee plantations. The

immediate effects of increasing temperatures have been shown to decrease foraging rates of army-ants (Kumar and O'Donnell 2009). Perhaps more of a threat are predicted changes in precipitation patterns throughout the Amazon basin, which covers the majority of the distribution of ant-followers in the Neotropics. These changes have already had drought-related consequences for Amazonian forests that range from increased tree and liana mortality, to reduced productivity and litterfall (Brando et al. 2008, Phillips et al. 2009). Negative population growth rates were related to prolonged dry seasons for 3 of 4 ant-follower species (Bicolored Antbird, Plain Brown Woodcreeper, and Spotted Antbird) in Panama (Brawn et al. 2017). Willson (2004) suggested that population fluctuations in obligate ant-followers were linked to changes in precipitation. More recently, army-ant-followers were observed to decline over a 10-yr period in a rainforest site in Ecuador coinciding with changes in precipitation related to ENSO conditions (Blake and Loiselle 2015). We agree with the recommendations of these authors that identifying climate-based refugia for both ants and ant-follower populations will be of primary importance in conserving ant-follower populations in the face of future climate change. Climate changes, for example, may also result in elevational range shifts of lowland species which may either lead to the displacement of higher elevation species or increased competition (Colwell et al. 2008) of ant-following species that track range shifts in ant swarms.

Summary and Future Directions

Significant strides have been made in understanding the loss of swarm raiding army-ants and ant-followers from forest areas impacted by land use or that have documented changes in precipitation patterns. Exciting opportunities exist, however, to generate more specific predictions of how changes in the abundance of army-ants can generate both ecological and behavioral cascades to both obligate and non-obligate ant-following species. Studying ecological and behavioral changes along gradients of disturbance may provide the best opportunity to evaluate changes to army-ants and the consequent changes to ant-followers. We propose several future directions for furthering our understanding of the mechanisms of anthropogenic impacts on ant-following Neotropical birds:

- How does the relationship between army-ant abundance and ant-follower abundance predict anthropogenic impacts on ant-follower populations?
- Where will future climate refugia be located, based on the current distribution of army-ants and ant-followers?
- How do specialized army-ant followers influence species interactions across different levels of anthropogenic impact to sustain ant-swarm following aggregations?

FINAL SUMMARY AND CONCLUSION

A growing number of researchers are studying army-ants and the birds that follow them. Encouragingly, in the past few decades, studies on ant-following birds have moved beyond descriptive natural history towards testing hypotheses about the eco-evolutionary dynamics of this complex system (Figure 1). Recent conceptual advances include exploring the cognitive and behavioral adaptations that enable such a unique life-history (Logan et al. 2011, O'Donnell et al. 2012), evaluating the evolutionary origins and phylogenetic distribution of ant-following behavior (Brumfield et al. 2007), and understanding how army-ant and ant-follower abundance and behavior vary across environmental and land-use gradients (Kumar and O'Donnell 2007, Kumar and O'Donnell 2009, O'Donnell et al. 2011). However, as we highlight above, we believe that this biological system has untapped potential in the research areas we have outlined (Table 1), and we suggest several topics for each discipline that are ripe for future study. We specifically recommend more integration and collaboration among biologists studying army-ants and those studying army-ant-followers. Given the importance of army-ants as a keystone species in Neotropical forests, understanding this system has important implications for the conservation of both army-ants and the birds that follow them.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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APPENDIX FIGURE 4. Map of Central and South America marking locations of Neotropical ant-following bird studies. Black dots represent coordinates extracted from 114 studies. Single dots may represent multiple studies or more than one adjacent location. Studies that did not explicitly provide coordinates are not mapped.