

Specializations of birds that attend army ant raids:
an ecological approach to cognitive and behavioral studies

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ABSTRACT

Tropical birds forage at army ant raids on several continents. Obligate foraging at army ant raids evolved several times in the Neotropical true antbird family (Thamnophilidae), and recent evidence suggests a diversity of bird species from other families specialize to varying degrees on army ant exploitation. Army ant raids offer access to high prey densities, but the ant colonies are mobile and widely spaced. Successful army ant exploitation requires solving a complex foraging problem because army ant raids are unpredictable in space and time. Birds can counteract the challenges posed by the ants by using strategies that raise their chances of detecting army ant raids, and birds can use additional strategies to track army the ant colonies they have located. Some features of army ant biology, such as their conspicuous swarms and columns, above-ground activity, and regular cycles of behavior, provide opportunities for birds to increase their effectiveness at exploiting raids. Changes in sensory, cognitive and behavioral systems may all contribute to specialized army ant exploitation in a bird population. The combination of specializations that are employed may vary independently among bird species and populations. The degree of army ant exploitation by birds varies geographically with latitude and elevation, and with historical patterns such as centers of distribution of obligate thamnophilid antbirds. We predict the set of specializations a given bird population exhibits will depend on local ecology, as well as phylogenetic history. Comparative approaches that focus on these patterns may indicate ecological and evolutionary factors that have shaped the costs and benefits of this foraging strategy. The development of army ant exploitation in individual birds is poorly understood, and individual expression of these specializations may depend on a combination of genetic adaptation with cognitive plasticity, possibly including social and experiential learning. Future

studies that measure developmental changes and quantify individual differences in army ant exploitation are needed to establish the mechanisms underlying this behavior.

1. Introduction

1.1 Birds attending army ant raids

Bird attendance at army ant raids to obtain food is one of the most striking biotic interactions in Neotropical and African tropical forests (Willis & Oniki 1978, 1992; Peters et al. 2008; Peters & Okalo 2009). Two species of Neotropical army ants, *Eciton burchellii* and *Labidus praedator*, and African *Dorylus* driver ants in the subgenus *Anomma*, forage by sending massive raid parties of workers to sweep through the leaf litter (Kronauer 2009; Moffett 2010). Birds attend the swarm fronts of army ant raids to feed on invertebrates and other small-bodied animals that flee the advancing ant workers. Raid-attending birds are cleptoparasites, reducing army ant prey capture by consuming larger food items (Wrege et al. 2005). Some species of birds, the obligate raid-attendants, are so reliant on the ants they are considered symbionts (Rettenmeyer et al. 2011). Obligate raid-attendants are mainly species of true antbirds (Thamnophilidae) and woodcreepers (Dendrocolaptidae) (Zimmer & Isler 2003; Brumfield et al. 2007). However, army ant exploitation is ecologically important to a wider array of birds than the obligate raid-attending species. We use the term raid-attending to refer to birds that obtain food from army ant swarm fronts. A diverse array of birds from other taxa attends raids in Neotropical and African forests (Willis & Oniki 1978; Peters et al. 2008). Previously it was often assumed these birds were unspecialized opportunists, attending only those raids that passed through their habitat or territories (Willis 1986a; Brumfield et al. 2007). Recent evidence suggests this assumption is incorrect. Some birds that use non-army ant food resources can track army ant colony

movements, and even birds that do not track ant colonies may have other specializations for army ant exploitation, such as enhanced ability to detect ant raids (O'Donnell et al. 2010).

Army ant raids offer a high-quality food source, but present unique spatial and temporal challenges to birds. The study of bird exploitation of army ants provides an excellent system for exploring the evolution and development of specialized foraging behavior and cognition. We suggest ant-bird interactions parallel other spatio-temporal cognitive challenges such as food caching and host-nest selection by brood parasites (Grodzinski & Clayton 2010; Feeney et al. 2012; Lea et al. 2012). In each of these ecological settings birds must keep track of location and timing of previous experiences, and compare several options to make adaptive foraging choices. Furthermore, social dynamics are relevant in each system: social affiliates or information parasites can influence the fitness costs and benefits of a bird's foraging decisions, such as potential pilferers observing where a food-cacher has hidden its food (Clayton et al. 2001, Clayton et al. 2003, Watanabe & Clayton 2007).

Bird sensation and cognition are challenged in unusual and interesting ways by army ants (Logan et al. 2011). We review the benefits and challenges to birds presented by army ants, and we outline known and plausible bird specializations that promote exploitation of army ant raids (Table 1). Specializations may include behavioral, sensory, and cognitive elements. Our thesis is that any given bird species or population (and possibly even individuals within populations) may exhibit a subset of these specializations. Specializations may occur in various combinations within and among bird populations. Army ant-attending birds occur across a wide range of latitudes and elevations. The diversity of species and ecological contexts of avian army ant exploitation will allow comparative studies that identify factors affecting the expression of this

unique foraging behavior. We propose local ecology can be used to predict which specializations will be favored and expressed in a given geographic area.

1.2 Bird species/population differences in army ant raid attendance

Across the ranges of swarm-raiding army ants there is dramatic geographic variation in the species composition of raid-attending bird flocks. Ecological factors such as latitude and elevation (e.g., different Holdridge life zones) influence the array of bird species that attend raids at a given site (Zimmer & Isler 2003; Brumfield et al. 2007; O'Donnell et al. 2010). With enough observation effort, long lists of bird species that attend army ant raids accumulate at sites where swarm-raiding army ants occur (Oniki 1972; Coates Estrada & Estrada 1989; Roberts et al. 2000; Vallely 2001; Peters et al. 2008; Faria & Rodriguez 2009). For example, in a Costa Rican montane forest, over 75 species of birds have been observed feeding at army ant raids (Vallely 2001; Kumar & O'Donnell 2007; O'Donnell et al. 2010). Raid attendants are predominantly insectivores, but members of other feeding guilds also collect insects at army ant raids including nectarivores, granivores, raptors, and frugivores (Willis 1986b; Roberts et al. 2000; Vallely 2001; Kumar & O'Donnell 2007). Bird species vary widely in their frequencies of raid attendance within sites. When variation in a species' relative abundance is accounted for, high rates of raid attendance can indicate specialization for foraging at army ant raids by some birds (Peters et al. 2008; O'Donnell et al. 2010). Species rates of performance of some of the specialized army ant exploitation behaviors outlined below correlate positively with their relative frequency of raid attendance (Swartz 1997, O'Donnell et al. 2010). However, raid attendance frequency itself, even if corrected for variation in abundance, does not necessarily reflect the importance of army ant exploitation to a bird species. Army ants can provide an important food

source even to occasional raid attending birds because of the relatively high density of prey available at army ant raid fronts.

Studies initiated by Willis and colleagues (Willis & Oniki 1978) suggest bird species vary in their reliance on army ant raids as a food source (Swartz 1997; Peters et al. 2008). Swartz (1997; also see Zimmer & Isler 2003 and Brumfield et al. 2007) reviewed terms for classifying bird species by their degree of reliance on army ants. Terms include obligate, regular, professional, and high-fidelity for birds that attend raids at higher rates while birds that attend at lower rates are referred to as opportunistic, facultative, or occasional raid attendants. Molecular phylogenies suggest the degree of ant specialization increases within lineages of the true antbirds (Thamnophilidae): obligate raid attendance is derived from regular raid attendance and is evolutionarily conserved once it arises (Brumfield et al. 2007). Phylogenetic history can therefore play a role in army ant exploitation, and high degrees of specialization may constrain the ability of some species to access other food resources. Obligate thamnophilid antbirds are so strongly dependent on army ants that some species may be incapable of foraging away from army ant raids (Willson 2004). After army ants are lost from recently isolated forest fragments, obligate thamnophilid antbirds disappear within several days, indicating a high degree of specialization on this one resource (Bierregaard & Lovejoy 1989, Harper 1989).

However, ecological and behavioral specializations are relative, not absolute. Categorizing a bird species' degree of reliance on army ants can be difficult. There is a range of army ant reliance both within and among bird species, and non-obligate raid attending birds can exhibit specializations for exploiting army ants. Variation in cognition and behavior can exist within specialization categories, including the obligate raid attending bird category. For example, some species categorized as obligate antbirds forage away from ant raids at least occasionally

(Willis 1973, Chaves-Campos 2003, Willson 2004), and some occasionally follow mammals (including humans) and other “beaters of prey” (Skutch 1996, DiGiacomo & DiGiacomo 2006, S. O’D. pers. obs.). Some authors have proposed diet criteria for distinguishing obligate or professional raid attending bird species, such as requiring at least 50% of food to be obtained at raid fronts (Oniki 1972; Oniki & Willis 1972). While operational, such criteria are arbitrary: it isn’t clear why 50% (or any other percent) should be chosen as a cutoff. The percent of diet criterion is difficult to assess in the field and has not been applied in practice (Swartz 2001). Descriptive species categories overlook the range of adaptations that favor army ant exploitation. Species categories can mask behavioral variation within and among populations, and may encourage researchers to disregard the behavior of less dependent bird species-- opportunistic, facultative, or occasional raid attendants. Recent research shows these species can exhibit specializations for interacting with army ants (O’Donnell et al. 2010), and we expect more examples will be documented in future studies.

Army ant exploitation can affect the fitness of non-obligate raid attending birds. Fitness effects of army ant exploitation potentially accrue for any bird that attends army ant raids. As an alternative to species categorization (i.e., identifying bird species as obligate, regular, or facultative raid attendants), we propose a research approach that focuses on quantifying particular cognitive and behavioral specializations for army ant exploitation (Table 1). This approach emphasizes the array of specializations that could promote army ant exploitation and provides insight into how and why particular species/populations exploit army ants. To understand avian adaptations for exploiting army ant raids, it is useful to consider army ant behavior and the unique challenges and opportunities it presents to birds.

2. Opportunities and challenges presented by army ant behavior

2.1 General features of army ant behavior

Army ants exhibit an unusual suite of behaviors called the army ant syndrome (Brady 2003). One of the defining features of the syndrome is mass or swarm foraging. As the ants sweep through the forest they drive leaf-litter dwelling animals before them. Exposed, and possibly distracted, prey items are readily caught by birds at the raid front. Even for birds capable of feeding elsewhere, foraging at army ant raids can represent a food intake bonanza. The mass of insects caught in leaf litter sticky traps increased 6-7 fold at *E. burchellii* raids over control samples (Harper 1989), and Meisel (2001) estimated Northern Barred Woodcreeper (*Dendrocolaptes sanctithomae*) prey capture rates at army ant raids were approximately three times higher than when the birds foraged away from raids in the same forests. Similar increases in prey capture at raids are reported for other species (Willis 1972, Zimmer & Isler 2003). The value of foraging at army ant raids is so great it can alter birds' patterns of habitat use. For example, forest birds are more likely to enter human-altered habitats when following ant swarms (Roberts et al. 2000). The evolution of an increased ability to exploit army ant raids can drive increases in ecological success. In undisturbed Brazilian Amazonian forests, obligate antbirds accounted for 27.8% of understory bird individuals but comprised only 7.5% of species (Stouffer & Bierregaard 1995).

Despite these benefits, Neotropical swarm-raiding army ants and African driver ants present challenges to birds. Army ant colonies are mobile: they do not construct or excavate nests; instead, they shelter the queen and brood inside a living nest of linked workers -- the bivouac. Foraging workers depart the bivouac en masse, collect food, and return. Bivouacs move among temporary nest sites when the colony emigrates, often traversing linear distances of 100 m or more in a single move (Kronauer 2009).

2.2 Biology of *Eciton burchellii*

The almost completely above-ground activities of *E. burchellii*, combined with their large diurnal swarm raids, are unique among army ants (Schneirla 1971, Gotwald 1995). *Eciton* swarm raid fronts are connected to bivouac sites by continuous above-ground columns of workers. Bivouacs are usually placed above ground, and the mass of ants forming the bivouac is often at least partly visible (Schneirla et al. 1954; Soare et al. 2011). *Eciton burchellii*'s above-ground diurnal activity increases their conspicuousness and accessibility to birds.

Eciton burchellii colonies have cyclical synchronous brood development that is tightly linked to changes in colony foraging behavior and movement. During the roughly two week nomadic phase when the colonies produce larvae, raids often start shortly after sunrise and typically last seven hours (Swartz 1997). Nomadic phase raids often travel over 100 m linear distance from the bivouac site (Schneirla 1971; Franks 1982a,b). Bivouac emigrations occur almost daily and are often nocturnal (O'Donnell et al., 2009). Emigrations follow the path of the day's foraging raid and the new bivouac site is placed along the raid route, typically 70-80 m from the old site (Swartz 1997). Nomadic colony raids are temporally regular (daily), but colony movements increase their spatial unpredictability. At the end of the nomadic phase the larvae pupate and the colony enters the approximately three week statory phase. Statory colonies remain at the same bivouac site, but raid in different directions on most days, generating a radial pattern of raid paths. The ants choose a random compass bearing each day, leading to uncertainty about raid location. Birds can reduce this uncertainty if they know the bivouac site starting point (Swartz 1997). The queen lays eggs during this phase, and because pupae and eggs do not feed, colony foraging effort is reduced. Statory phase foraging raids often start later in the day, last as little as four hours, and statory colonies frequently skip days of raiding altogether (Swartz 1997).

This decreases the temporal reliability of raiding. Stately colonies discard thousands of silken pupal cases from newly-emerged workers outside the bivouac site for a few days prior to starting the nomadic phase (Rettenmeyer 1963). It is not known whether birds respond to this visual cue of ant colony developmental stage.

Eciton burchellii's visible swarm raids and columns, and their frequent use of visible bivouac sites, favor exploitation by birds. The regularity of colony activity cycles may also favor avian exploitation, allowing the opportunity for birds to track and anticipate the ants' behavioral changes across their five-week cycle.

2.3 Biology of *Labidus* species and *Dorylus* driver ants

In tropical Africa, massive surface swarm raids of *Dorylus* (subgenus *Anomma*) are attended by birds (Peters et al. 2008; Peters & Okalo 2009). These army ants have behavior similar to Neotropical *Labidus* species and likely present similar challenges to raid-exploiting birds (Gotwald 1995). In contrast to *Eciton*, *Labidus* and *Dorylus* bivouacs form underground and are therefore inaccessible to birds. However, these widespread and often-abundant army ants can conduct dense swarm raids across the forest floor and raids are attended by birds (Willson 2004; Peters et al. 2008). Raids often travel on the surface but then disappear into tunnels in the soil, thus *Labidus* and *Dorylus* surface raids are not always connected to the bivouac site by above-ground columns of ants (Rettenmeyer 1963; Moffett 2011; S.O'D. pers. obs.). Colonies are not as predictably cyclical in their emigration patterns as *E. burchellii* and the above-ground parts of their raids are also unpredictable in space and time (Rettenmeyer 1963; Dowsett-Lemair 1983; Willson 2004, Peters et al. 2008). Despite the difficulties birds face in locating and tracking *L. praedator* raids, *Labidus* raids are important resources to a diversity of raid attending birds,

including obligate antbirds (Willis 1966a; Willson 2004; Kumar & O'Donnell 2007). While *Labidus praedator* raids are more abundant than *E. burchellii* raids at some locations (Willson 2004; O'Donnell et al. 2007, 2011), their subterranean behavior, and the irregular raids and emigrations of *Labidus* and *Dorylus*, may limit or preclude some avian adaptations that are useful for exploiting *Eciton burchellii* raids as discussed below.

3. Behavioral, sensory and cognitive specializations for exploiting army ants

3.1 Locating and recognizing foraging army ants

The first problem birds face is finding an active army ant swarm. The probability that a bird will randomly encounter a raid front in the forest is low because army ant swarms are widely and randomly dispersed. Estimates of *E. burchellii* daily raid densities range from 0.036 to 0.110 swarms/ha (Franks 1982b, Swartz 1997, Willson 2004, Vidal-Riggs & Chaves-Campos 2008). Swarm raid fronts are relatively small -- they typically range from approximately 2 m wide up to 15 m wide and a few m deep, though 25 m wide raid fronts have been reported (Rettenmeyer 1963; Willson 2004). Raid fronts are also mobile -- *Eciton burchellii* raids progress away from the bivouac site at about 15 m/h on a roughly linear path (Swartz 1997). *Labidus praedator* raids can also be mobile, but they progress in a complex swirling motion (Rettenmeyer 1963). Sometimes *Labidus* raids remain in one area for several hours, after which the ants disappear underground (S. O'D. & C.L., pers. obs.).

Birds that do not know the location of an army ant bivouac may search for raids as they move through the forest. Searching birds could benefit from enhanced sensory or cognitive abilities allowing for the detection of army ants in swarms and raid columns from greater distances. Vision is likely to be the major mode of detection, but other modalities such as smell

could be used. Neotropical army ants have a distinctive musky odor and some human observers can locate bivouacs by smell (Rettenmeyer 1963; S. O'D. pers. obs.). Evidence is accumulating that birds use olfaction in diverse behavioral contexts (Bonadonna & Nevitt 2004, Nevitt & Bonadonna 2005, Mardon et al. 2010). Birds may also hear and attend to sounds made by the ants and/or fleeing prey. Human observers can hear approaching raids, which produce a rustling sound, from several meters distance. Birds that forage closer to the ground may be more likely to encounter raiding army ants, or the prey that flee the raids (Cody 2000). Army ant raid attendance may select for decreased foraging height.

3.2 Avian social interactions: responding to other birds

Raid attending birds often vocalize in the vicinity of army ants, allowing other birds to use these vocalizations to locate army ant raids. Raid attending birds are attracted to playbacks of obligate antbird calls (Willis 1972, Chaves-Campos 2003, Chaves 2008.) Chaves-Campos (2003) reported some obligate thamnophilid antbirds called or sang while foraging at raid fronts and while inspecting bivouacs; other species were generally silent in these contexts. Several species of ant following birds sing just before leaving army ant swarms to travel to other swarms, and some sing or call the loudest when leaving or traveling between raids (Willis 1972; Swartz 1997; Chaves 2008). In montane forests, several species of birds sing in the morning from the vicinity of army ant bivouacs (O'Donnell et al. 2010). Other authors have noted bird vocalizations given at army ant swarms or at bivouacs that are rarely or never produced in other contexts (Willis 1967; Hardy 1974; S. O'D., pers. obs.). If such vocalizations are signals to mates or kin, they could inadvertently recruit incidental signal interceptors, either conspecifics or other species,

which could impose fitness costs to the senders. Alternatively, such recruitment may reduce predation risk via predator dilution or promote increased vigilance at raids.

Raid attending bird flocks may be visually attractive to other birds traveling through the forest. Birds may also travel together. Naïve birds may maintain visual and/or auditory contact with birds that have memorized the location of army ant raids or bivouacs. Ocellated Antbirds follow conspecifics departing raids and groups travel through the forest single-file (Chaves 2008). Similar trains comprising three species of *Thamnophilidae* were seen travelling to and from *E. burchellii* raids in Costa Rica (S. O'D. pers. obs.).

3.3. Bird behavior at raid fronts

3.3.1 Tameness

In birds, as in humans, cognitive attention focusing on one stimulus leads to decreased ability to respond to other stimuli (Dukas & Kamil 2000, Dukas 2004, Smith & Blumstein 2008, Dehaene et al. 2010). Observers of birds at army ant swarm fronts frequently note the birds are exceptionally tame or unresponsive to close human approach, even for species that are otherwise notably intolerant of human presence such as jays (Sutton 1951; Hardy 1974; Dowsett-Lemair 1983; Haemig 1989). On one occasion an Azure-hooded Jay (*Cyanolyca cucullata*) foraged at an *E. burchellii* raid within 1 m of an observer's feet for several minutes (S. O'D. pers. obs.).

Tameness may indicate increased attention to the ants and/or to fleeing prey. Increased attention may increase prey capture rates (Sullivan 1984, Poysa 1987). If tameness at raids decreases birds' vigilance, it could increase predation risk. This would suggest a high fitness payoff to army ant raid attendance.

3.3.2 Elevated aggression

Interference competition via aggressive interactions is thought to be fundamentally important in structuring bird guilds at army ant raids in Neotropical lowland forests (Willis & Oniki 1978). Foraging position at army ant raid fronts may be of critical importance to prey capture success: central positions near the front of the advancing swarm and positions near the ground are favored by dominant birds (Willis & Oniki 1978). Interference competition among birds may reduce the value of raid attendance to the point of exclusion of inferior competitors. Raid front width was the best predictor of the number and diversity of attending birds in Neotropical rainforest, with wider raids permitting more birds. Increased spacing among birds at raids allows birds to avoid aggression from competitors (Swartz 1997). Within a guild of obligate ant following birds, stomach content analysis showed that species dominance rank predicted the amount of food consumed, while body size and bill shape did not predict the types of food the birds consumed (Chesser 1995). These findings suggest inter-specific competition among birds at raid fronts could strongly affect the fitness benefits of foraging with army ants. Sensory and behavioral capacities for rapid prey detection and identification are likely to be strongly favored in the face of intense competition among birds at swarm raids (Bond & Kamil 2006, Stevens 2007, Hauber & Zuk 2010).

The conspicuous colored skin patches around the eyes of some thamnophilid antbirds and woodcreepers may function in aggressive displays at swarm raids (Zimmer & Isler 2003). The White-necked Rockfowl (*Picathartes gymnocephalus*) regularly attends African *Dorylus* raids; this species is aggressive toward other raid attendants and has a brightly colored bald head

(Willis 1983). Other regular African raid-attending birds (e.g., Turdidae) can be highly aggressive at raids but do not have bare skin on their heads (Willis 1985b).

The possibility of kin-related nepotism at raids is poorly studied. Nepotism was not supported in Ocellated Antbirds, where genetic relatedness did not predict co-foraging of birds (besides mated pairs) at *E. burchellii* swarms (Chaves 2008).

3.3.3 Prey Capture Abilities

Neotropical army ants bite and sting, and *Eciton burchellii* stings can be fatally toxic to birds (Swartz 1997). Driver ants cannot sting but bite fiercely and pose a risk to attending birds (Willis 1985a; 1986b). Birds must exercise caution to avoid the ants at raid fronts, both on the ground and in low vegetation which the ants often climb. Some Neotropical birds increase foraging heights and movement rates at *Eciton* raids relative to *Labidus* raids, possibly because *Eciton* workers are more aggressive and pose greater sting risk (Willis 1983). The ability to move rapidly with agility and to capture prey while avoiding ant stings may be requisite for successful *Eciton* and *Dorylus* raid attendance. The ability to perch near the advancing army ant swarm front, particularly by clinging to vertical branches and stems, is thought to be a determinant of bird foraging success at *Eciton* raids (Willis & Oniki 1978, 1992; Willis 1981). Thamnophilid antbirds, particularly species that attend army ant raids, are noted for their exceptionally strong legs and feet (Zimmer & Isler 2003). Some thamnophilid antbird species have modifications of their toes and soles that promote gripping. Such anatomical and physiological adaptations have not been explored in other bird taxa that attend army ant raids.

4. Following or tracking army ants

After army ant raids or bivouacs are located, birds can benefit by maintaining the ability to exploit the same colony across days. Birds may track nomadic colonies as they emigrate across the landscape. The location of statary colonies can be learned and memorized.

4.1 Bivouac Checking

Some species of raid-attending birds visit *E. burchellii* nest sites, often approaching within a few meters and peering at the bivouac. Bivouac checking birds are thought to assess ant activity, and possibly also memorize the location of the colony (Swartz 2001). Birds check bivouacs in the morning before raiding starts, and in the evening as the ants are returning from the day's raid. The benefit of this behavior is likely to be purely informational because birds do not feed while bivouac checking. At lowland Neotropical sites, nearly all bivouac checking is performed by obligate raid attending birds (Swartz 2001; Chaves-Campos 2003; Willson 2004). Radio-tagged Ocellated Antbirds checked one to five (typically two) *Eciton burchellii* colonies daily, with up to five days elapsing between visits to a single colony (Chaves 2008). In montane forests where thamnophilid antbirds do not occur, a diverse array of birds check bivouacs (eleven species from eight families; O'Donnell et al. 2010; S. O'D. pers. obs.). Some African birds that attend driver ant raids (genus *Althene*) may check bivouacs as well (Willis 1986b). Bivouac checking likely involves a number of cognitive abilities including memory, discrimination among multiple resources, and delayed rewards for behavior. Bivouac checking shares a number of features with other complex foraging tasks, and may provide a novel example of episodic-like memory (the

ability to remember the what, where and when of past events) and the ability to plan ahead in animals in the field (Logan et al. 2011).

4.2 Loss of Territoriality

One of the key behavioral features of obligate ant following birds is their lack of territoriality when feeding (Willis 1967, 1973; Brumfield et al. 2007). Mated pairs of some army ant following birds maintain exclusive territories for roosting or nesting, but not feeding (Willson 2004; Chaves 2008). Some birds follow raids through the forest and range widely when tracking army ant colonies, venturing beyond their roosting/nesting territory and crossing others. Ocellated Antbirds travel linear distances of over 500 m on average from their roosting sites to the army ant colonies at which they feed, often crossing several conspecific roosting territories (Chaves 2008). Observations of marked (color banded) birds show other ant following species can visit at least three raids per day, separated by up to 1 km (Willson 2004).

Brumfield et al. (2007) mapped army ant raid attendance behavior onto a molecular phylogeny of *Thamnophilidae*. Their analysis suggested that the loss of feeding territories and the ability to follow ant swarms through the forest (“regular” following) evolved four times in the family *Thamnophilidae*. Regular following evolved to obligate army ant following twice in *thamnophilids* with no reversals to the regular follower trait (see also Moyle et al. 2009).

4.3 Life history and social learning

Adult obligate ant following *thamnophilid* birds attend raids with their fledglings, which may provide opportunities for observational learning and behavioral transmission of army ant specialization. Observational learning from conspecifics has been found in a variety of bird taxa

and in a variety of circumstances. Food preferences or food processing abilities can be transmitted via observational learning in Icteridae (Blackbirds), Corvidae (Crows) and Trochilidae (Hummingbirds) (Mason & Reidinger 1981; Altshuler & Nunn 2001; Dally, Clayton & Emery 2008). Ant following birds are long-lived and have extended periods of parental care (Willson 2004). Long life spans may provide greater opportunities for social interactions to affect young birds' competence at exploiting army ant raids (Brown et al. 1995; Swartz 1997). There may be a sensitive period during which exposure to army ant raids triggers exploitative behavior in juvenile birds, as seen in the development of tool use in Woodpecker Finches (*Camarhynchus pallidus*) (Tebbich et al. 2001). Observational learning, perhaps during a sensitive period, is a plausible but untested mechanism for the social transmission of army ant exploitation.

5. Implications and remaining questions

Two major lines of investigation can contribute to a better understanding of the diversity of avian army ant exploitation. At the species/population level, geographic variation in rates of raid attendance may be associated with expression of specializations for army ant exploitation. At the individual level, important questions remain about how army ant exploitation behavior develops. Answering these questions will build an understanding of the mechanisms that underlie this interaction.

5.1 Geographic variation

We predict the specializations birds exhibit for army ant raid attendance will vary with the local profitability of army ant raids. Several factors may interact to determine the profitability of

foraging with army ants for a given bird species at a given location. Aggressive behavior at raid fronts and other specializations for army ant tracking are thought to lead to effective interference and exploitation competition abilities of obligate raid attending thamnophilid antbirds.

Interactions among raid attending birds are likely to be critically important: aggression from obligate thamnophilid ant following birds may preclude or limit army ant exploitation for other birds at many sites. Phylogeographic analyses by Brumfield et al. (2007) suggested that the ranges of obligate ant following birds partly exclude other raid-attending ant following birds. Conversely, the absence of dominant obligate ant following birds at some sites may increase the relative profitability of raid attendance for other bird species, promoting local convergence on ant following bird behavior (O'Donnell et al. 2010). We predict the degree of army ant specialization by other birds will vary depending on whether they co-occur with obligate thamnophilid antbirds. Obligate thamnophilid density and diversity generally decrease with latitude and elevation.

Features of army ant behavior and ecology, such as the density of colonies and swarm frequency and intensity, are of central importance in determining the costs and benefits of exploiting army ants (O'Donnell et al. 2007, 2011). Recent quantitative data on *E. burchellii* and *L. praedator* raid rates suggest army ant raids are most dense in middle-elevation forests, above the local elevational limits of obligate thamnophilid antbirds (O'Donnell et al. 2011). The profitability of ant raids may not depend strictly on raid density, and could be reduced at higher elevations if raids are smaller or move too slowly, and local variation in leaf litter prey stocks may also affect the profitability of raid attendance for birds (Willis 1985b). Some raid-attending bird species vary seasonally in how often they forage away from army ants (Willis 1972, 1985b; Dowsett-Lemair 1983), suggesting seasonal effects on the profitability of army ant exploitation.

Seasonal changes in rates of attending ant swarms may depend in part on the need for adult birds to collect prey for their nestlings. Raid attendance rates increase can increase when adult birds are accompanied by young (Willis 1983).

In some bird species, populations differ in their degree of reliance on army ants, as indicated by the observed relative frequency of foraging with, versus away from, ant swarms. Population differences in the frequency of army ant attendance are known in Gray-headed Tanagers (*Eucometis penicillata*; Willis 1985b) and Plain-brown Woodcreepers (*Dendrocincla fuliginosa*; Willis 1966b; Willson 2004). Such population differences provide rich opportunities for comparative analyses of ecological factors that affect army ant exploitation. We predict additional intraspecific examples will be found for geographic variation in the frequency of army ant raid attendance, and of other specializations for army ant exploitation.

5.2 Development of army ant exploitation

A fundamental unresolved issue is how army-ant specializations develop at the individual level. Specializations for army ant exploitation may have evolved genetically by allelic replacement. Adaptive changes in behavior and cognition may be driven by selection for better army ant exploitation in diverse avian taxa. Comparative studies of the ordering of transitions of traits on avian phylogenies can help distinguish novel specializations from traits present in a lineage that predispose birds to forage with army ants (Wenzel & Carpenter 1994).

Army ant exploitation could also arise via learning, without changes in allele frequencies. Associative learning, either by classical or operant conditioning, seems likely to play a role in the development of other birds' responses to obligate antbird vocalizations. This and other putative cases of learned specializations could be studied in young, naïve birds, or may be indicated by

individual differences in adult behavior if only some birds learn the association of obligate antbirds with raid fronts. If social factors such as observational learning or sensitive period exposure to army ants are important to the development of army ant raid attendance, there is potential for individual differences among birds within populations. Individual variation in army ant exploiting behavior within populations has rarely been assessed. Measuring individual differences will require observations and/or tracking of marked individuals, and sampling foraging and search time budgets, including time spent away from ant swarms.

6. Conclusions

A diverse array of cognitive and behavioral abilities can promote the exploitation of army ant swarm raids as a food source by birds. The set of specialized abilities expressed varies among and within species. This variability precludes straightforward categorization of bird species degree of reliance on army ants. As an alternative to categorizing bird species according to their dietary reliance on army ants, we suggest research on bird-army ant interactions should focus on identifying which behavioral and cognitive specialization(s) birds exhibit and in which ecological settings.

Most of the studies we reviewed present data from the Neotropics. To some extent this is because no other army ant species shares the advantages to bird attendants, such as above-ground bivouacs and relatively regular foraging and emigration schedules, of the widespread Neotropical species *Eciton burchellii*. However, birds do attend driver ant raids in African forests. Some African birds show evidence of spending much of their foraging time at army ant swarms (Willis & Oniki 1978, 1992; Peters et al. 2008; Peters & Okalo 2009). The ideas about bird specializations we present here should apply globally, wherever birds interact with army ants.

Future work should emphasize both taxonomic and geographic variation in the expression of army ant exploiting traits. This approach will encourage more inclusive comparative studies, and will pave the way for research on developmental, neural and genetic effects on avian exploitation of army ants.

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Table 1. Known and predicted avian adaptations for exploiting army ant swarm raids as a food source. Literature references for adaptations supported by field studies are listed in parentheses.

<u>Challenge posed by army ants</u>	<u>Bird solutions</u>
Defensive behavior/toxic stings	Strong legs and feet/Able to cling to vertical branches; rapid movement and agility (14, 17, 19)
Widely spaced raids	Detect ants from greater distances: See, smell or hear ants or fleeing prey Detect other birds at raids (1, 2, 12) Follow other birds to raids (2)
Irregular raid schedules	Bivouac checking; track multiple colonies (2, 6, 9, 16, 18)
Limited space at raid fronts	Increased aggression at raids (10, 11, 15, 18) Increased tameness/attention focusing (3, 4, 5, 7)
Mobile ant colonies: long raids and emigration routes	Loss of feeding territoriality (2, 11, 13, 18)
Emigrations usually nocturnal	Search along previous day's raid route (8)
<u>Opportunities presented by army ant biology</u>	<u>Bird responses</u>
Regular colony development cycles	Recognize ant colonies' developmental stages
Above ground bivouacs and emigrations (mainly <i>Eciton</i>)	Bivouac checking (2, 6, 9, 16, 18)
Visually and sonically conspicuous masses of ant workers and fleeing prey	Visual and auditory acuity; sensory tuning to army ant cues
Columns of ants connect raid front to bivouac	Detect and follow ant columns (8)
Strong, distinctive army ant odor	Enhanced olfactory sense/specific receptors for army ant odors

Supporting references

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