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LOCALIZATION OF ARMY-ANT SWARMS BY ANT-FOLLOWING BIRDS ON THE CARIBBEAN SLOPE OF COSTA RICA: FOLLOWING THE VOCALIZATION OF ANTBIRDS TO FIND THE SWARMS

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Resumen. – Localización de enjambres de hormigas guerreras por aves en la vertiente Caribe de Costa Rica: Siguiendo los llamados de los hormigueros para encontrar los enjambres. – En la vertiente Caribe de Costa Rica, los seguidores obligatorios de hormigas guerreras (llamadas también arrieras en algunos países) encuentran los enjambres de estas hormigas antes que otras aves. En particular, los Hormigueros Ocelados (*Phaenostictus mcleannani)* localizaron los vivaques antes que otros seguidores obligatorios. En un experimento sistemático con vocalizaciones grabadas de especies seguidoras de hormigas, los llamados de hormigueros Ocelados y Bicolores (*Gymnopithys leucaspis*) atrajeron otras especies seguidoras de hormigas. Estos datos indican que algunas especies seguidoras de hormigas siguen los cantos de especies seguidoras obligatorias como ayuda para encontrar las hormigas guerreras.

Abstract. – On the Caribbean Slope of Costa Rica, obligate army-ant-following birds find army-ant swarms before other birds. In particular, Ocellated Antbirds (*Phaenostictus mcleannani)* arrived to swarms before other obligate ant-following species. In a systematic experiment with recorded vocalizations, the calls of Ocellated and Bicolored (*Gymnopithys leucaspis*) antbirds attracted other ant-following birds. These data indicate that some ant-following birds track the calls of obligate ant-following species to help finding army ants. *Accepted 20 October 2002.*

Key words: Antbirds, ant-following birds, army ants, *Eciton burchelli*, Costa Rica.

INTRODUCTION

About 50 species of Neotropical birds regularly feed on arthropods that try to escape from army-ant swarms (Willis 1983). Some of these species are considered "professional" or obligate followers (birds dependent on foraging with army ants), but there are many more species in which ant following can be considered an opportunistic behavior (Willis & Oniki 1978, 1992; Swartz 2001).

In the Neotropical region, the most frequently followed species of army ant is *Eciton*

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burchelli (Willis & Oniki 1978). Although a potentially rich food-flushing resource, colonies of this species neither forage regularly nor remain in a constant location. *E. burchelli* swarms only 65–75% of days during the 20-day statary period and moves the bivouac (temporary nests constructed with the ants' living bodies) 100–200 m away almost every night during the 14-day nomadic phase (Schneirla 1971, Swartz 2001). Obligate army-ant-followers inspect the bivouacs in order to follow the ants' trail to the foraging front, and when a bivouac has shifted position they search for it along the path of the previous day's raid (Willis 1967, 1972b, 1973; Swartz 2001). Opportunistic followers less often show such behavior (Swartz 2001).

It has been hypothesized that both obligate and opportunistic ant-followers find swarms by following the calls of some obligate ant-following birds that find swarms before other species (see Willis 1967 for reference, Swartz 1997). However, this hypothesis has not been satisfactorily tested (Willis 1967). Here I present data from the Caribbean Slope of Costa Rica suggesting that both obligate and opportunistic ant-followers use the calls of obligate ant-following antbirds to help locating the swarms.

STUDY AREA AND METHODS

The study was conducted within a 500-ha old-growth forest at La Selva Biological Station in the lowlands of the Caribbean slope of Costa Rica (10°25'N, 84°01'W). La Selva covers approximately 1500 ha and is connected to Braulio Carrillo National Park (45,000 ha). The area receives 3962 mm of rain annually (average), with less precipitation between February and April (Sanford *et al.* 1994). Most ant-following bird species of Costa Rica are present at La Selva (Stiles 1983, Levey & Stiles 1994).

I located and tracked *Eciton burchelli* colonies during February 1999 (12 days) and July 2000 (20 days). As Swartz (2001), I conducted bivouac vigils from inconspicuous positions (5–10 m from the bivouacs) to document bivouac-checking behavior, beginning when sunlight was sufficient for accurate viewing and ending when ants started to swarm (usually between the 05:30 and 07:00 h). I also recorded the order and timing of arrival of ant-following birds to swarms (birds that took arthropods between 0 and 15 m around the swarm front and the line of ants) during at least the first hour of swarming.

To determine if other ant-followers were attracted by the call of some obligate ant-following species, I played back obligate ant-following bird vocalizations (loud songs the birds make when foraging at swarms) at sites without swarms, and used the call of a bird not heard at swarms as control. Obligate ant-following birds selected were the Ocellated Antbird (*Phaenostictus mcleannani*) and the Bicolored Antbird (*Gymnopithys leucaspis*) because Willis (1967, 1973) reported that ant-following birds incidentally come to the playing of recorded songs of these species at Panama. Both species were frequently found checking bivouacs (see below), and making calls while foraging at swarms at La Selva. I selected the calls of the Northern-Barred Woodcreeper (*Dendrocolaptes sanctithomae*) as the bird not heard at swarms because it is one of the most common species foraging at army-ant swarms in La Selva (Stiles & Levey 1994, Levey & Stiles 1994) but is usually silent at swarms in Costa Rica (pers. observ.). Every afternoon for 20 days (July 2000), I systematically selected points every 100 m along existing trails inside the study area, played the vocalization of a species for 5 min at each point (keeping broadcast volume constant), and registered the birds that were attracted to the tape-recorded vocalization. The calls of the three species were alternated every 100 m.

TABLE 1. Frequency of occurrence (%) and mean number of individuals (± one SD) of the 12 species most frequently foraging at *Eciton burchelli* swarms (n = 16), and frequency (%) of checks at inactive bivouacs early in the morning (n = 10) at La Selva Biological Station, Costa Rica. Species listed according to American Ornithologists' Union (1998).

English common names	Scientific names	Frequency of occurrence at swarms	Frequency of bivouac checking	Mean number of birds at swarms
Ocellated Antbird	*Phaenostictus mcleannani*	93.8	90.0	2.58 ± 1.16
Plain-brown Woodcreeper	*Dendrocincla fuliginosa*	50.0	20.0	1.08 ± 1.00
Northern-Barred Woodcreeper	*Dendrocolaptes sanctithomae*	50.0	20.0	0.75 ± 0.62
Bicolored Antbird	*Gymnopithys leucaspis*	37.5	40.0	0.75 ± 0.87
White-breasted Wood-Wren	*Henicorhina leucosticta*	31.3		0.83 ± 1.03
Broad-billed Motmot	*Electron platyrhynchum*	25.0		0.42 ± 0.67
Black-faced Antthrush	*Formicarius analis*	25.0		0.33 ± 0.49
Great Tinamou	*Tinamus major*	18.8		0.25 ± 0.45
Slaty-breasted Tinamou	*Crypturellus boucardi*	18.8		0.25 ± 0.45
Rufous Motmot	*Baryphthengus martii*	18.8		0.25 ± 0.45
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	18.8		0.17 ± 0.39
Spotted Antbird	*Hylophylax naevioides*	12.5	40.0	0.25 ± 0.62

Each bird that flew directly to the tape recorder and perched 1–2 m away was considered as attracted to the vocalization source. The minimum distance between two consecutive attractions was 1000 m; therefore, samples are considered independent. Attractions of conspecifics were not counted for the analysis.

Statistical analysis. I used a two-way ANOVA to detect variation in time of arrival to swarms (dependent variable) for Ocellated Antbirds, other obligate species (lumped into one category), and opportunistic species (lumped into one category). I used each swarm as a block. Variables were tested for normality with a Wilk-Shapiro test. Means are presented with one standard deviation. A possible relationship between frequency of bivouac checking and percentage of attendance at swarms was compared using a Spearman rank correlation test. I also used a homogeneity test to detect possible bias in the proportion of birds attracted to the played calls of each species.

RESULTS

Bird arrival to bivouacs and swarms. I found 13 different army-ant colonies (12 in nomadic, one in statary phase) and 16 different swarms. Twenty species of birds were recorded foraging with army ants (Appendix 1). Only five species showed bivouac checking (Table 1) and were classified as obligate ant-followers; others species were considered opportunistic ant-following birds (Swartz 2001). The Ocellated, Bicolored, and Spotted (*Hylophylax naevioides*) antbirds checked several bivouacs at the same time without aggressive interactions. Plain-brown (*Dendrocincla fuliginosa*) and Northern-Barred woodcreepers were found perched near (1–2 m) some bivouacs while ants were inactive. According to Swartz's (2001), definition they should be considered as checking the bivouac.

With the exception of the Spotted Antbird, species that checked bivouacs were also the species most frequently found at swarms. However, there was no correlation between the percentage of bivouac checking and the

percentage of occurrence at swarms (r_s = 0.11, P = 0.86).

The Ocellated Antbird was the species most frequently found checking bivouacs and foraging at swarms and was also the most abundant species foraging with army ants (Table 1). The Ocellated Antbird also was the only species seen checking inactive bivouacs in new sites during the nomadic phase. This species also started foraging at swarms before other obligate or opportunistic ant-following birds (F_{2-23} = 3.94, P = 0.03). Ocellated Antbirds started foraging when the ants began to swarm (0.0 ± 0.0 min), while other obligate ant-followers began to forage at swarms after several minutes (36.2 ± 39.8 min), and the opportunistic species foraged even later (44.9 ± 30.6 min). Ocellated, Bicolored, and Spotted antbirds called regularly while checking bivouacs and foraging at swarms; Plain-brown and Northern-Barred woodcreepers were mostly silent while checking and foraging.

Playback experiment. During the study, I completed 106 playbacks: 37 for Ocellated and Bicolored antbirds and 32 for the Northern-Barred Woodcreeper. Only the vocalizations of the two antbirds attracted other ant-following bird species (G_2 = 6.59, P = 0.04). The Ocellated Antbird vocalizations attracted other ant-following birds on 5 occasions (1–2 birds each time), the Bicolored Antbird's vocalizations only 3 times. The species attracted by the Ocellated Antbird's vocalizations were the Plain-brown (3 times) and Northern-Barred (twice) woodcreepers, and the species attracted by vocalizations of the Bicolored Antbird were the Ocellated Antbird (twice) and the Plain-brown Woodcreeper (once). The Wedge-billed Woodcreeper (*Glyphorynchus spirurus*), Bright-rumped Attila (*Attila spadiceus*), White-breasted Wood-Wren (*Henicorhina leucosticta*), and Red-throated Ant-Tanager (*Habia fuscicauda*) were observed within a 5-m radius around the tape-recorder after I started playing Ocellated or Bicolored antbirds' calls. Although all these species were recorded foraging at swarms, I could not determine whether they were attracted by the calls or not and did not include them in the analysis.

DISCUSSION

In general, the species that checked inactive bivouacs most often were also the species most frequently found foraging with army ants. However, the Spotted Antbird did not follow this pattern. This species seemed to check bivouacs more frequently than woodcreepers, but it was rarely found at swarms. According to Willis (1972b), Spotted Antbirds usually stay away from the larger Ocellated and Bicolored antbirds and find the swarms an hour or two later than these species. The Ocellated Antbird was present in more than 90% of sampled swarms, and my samples were mainly done during the first hour of swarming. This is probably the reason why I recorded few Spotted Antbirds at swarms.

The Ocellated Antbird is probably the most obligate ant-follower at La Selva. This species checked bivouacs and foraged at swarms more frequently than other species, but this frequency at swarms is not proportional to its abundance at La Selva. Ocellated Antbirds take almost all their food at swarms (Willis 1973) while Northern-Barred Woodcreepers take only about 70% of their preys at swarms (Willis 1972b, 1992). However, Ocellated Antbirds are less abundant at La Selva than Northern-Barred Woodcreepers (Stiles & Levey 1994). Therefore, Ocellated Antbirds should be more dependent on army ants than Northern-Barred Woodcreepers at La Selva. Plain-brown Woodcreepers and Bicolored and Spotted antbirds are as uncommon as Ocellated Antbirds at La Selva (Stiles &

Levey 1994) but checked bivouacs and foraged at swarms less frequently. These species also forage away from swarms more often than do Ocellated Antbirds (Willis 1966, 1967, 1972a, 1973), suggesting that they are less dependent on army ants than Ocellated Antbirds. This high dependence on army ants could explain why the Ocellated Antbird was recorded foraging at swarms before other obligate or opportunistic species.

The vocalizations of the obligate species that first found the swarms could attract other ant-followers to those swarms. Some obligate ant-following birds were clearly attracted by played-back vocalizations of Ocellated and Bicolored antbirds, suggesting that they follow the calls of these species to help locating the swarms. During the statary phase army-ant colonies do not forage every day. Therefore, it would be an advantage for species dependent on army ants to use the calls of other ant-followers to locate swarms. The Ocellated Antbird was the species most frequently found at swarms at La Selva, and this species seems to take all its food from army-ant swarms (Willis 1973). Hence, following the calls of Ocellated Antbirds should help to locate swarms very frequently. Calls of Bicolored Antbirds are very similar to calls of Ocellated Antbirds (Willis 1973), and this species seldom stays away from swarms (Willis 1967). Following the calls of this species in order to locate swarms should be very successful as well.

Some opportunistic or facultative ant-following birds may also use the vocalizations of obligate antbirds to locate swarms. Following the calls of obligate species can also explain how some non-obligated species find swarms, even during the statary phase of the ant colonies. Some opportunistic ant-following birds regularly find army-ant swarms at La Selva, such as the Bright-rumped Attila and the Red-throated Ant-Tanager (Levey & Stiles 1994). Opportunistic species must find a swarm by chance; however, there is only one *E. burchelli* colony every 19 ha at La Selva (J. T. Longino, unpubl. data), and the probability of this occurring seems very low.

The data suggest that, at La Selva, some ant-following birds are attracted to swarms by the vocalizations of foraging antbirds. Interestingly, Ocellated and Bicolored antbirds seem to forage silently at swarms in Panama (Willis 1967, 1973). Additional studies in other areas should be conducted to determine if following the calls of foraging birds in order to locate army-ant swarms is the rule or the exception in ant-following bird assemblages.

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APPENDIX 1. Species found foraging at army-ant swarms at La Selva Biological Station, Costa Rica. Species listed according to American Ornithologists' Union (1998).

Great Tinamou (*Tinamus major*), Slaty-breasted Tinamou (*Crypturellus boucardi*), Rufous Motmot (*Baryphthengus martii*), Broad-billed Motmot (*Electron platyrhynchum*), Plain-brown Woodcreeper (*Dendrocincla fuliginosa*), Northern Barred-Woodcreeper (*Dendrocolaptes sanctithomae*), Wedge-billed Woodcreeper (*Glyphorynchus spirurus*), Bare-crowned Antbird (*Gymnocichla nudiceps*), Spotted Antbird (*Hylophylax naevioides*), Bicolored Antbird (*Gymnopithys leucaspis*), Ocellated Antbird (*Phaenostictus mcleannani*), Black-faced Antthrush (*Formicarius analis*), Bright-rumped Attila (*Attila spadiceus*), Bay Wren (*Thryothorus nigricapillus*), Stripe-breasted Wren (*Thryothorus thoracicus*), White-breasted Wood-Wren (*Henicorhina leucosticta*), Nightingale Wren (*Microcerculus philomela*), Song Wren (*Cyphorhinus phaeocephalus*), Red-throated Ant-Tanager (*Habia fuscicauda*), Orange-billed Sparrow (*Arremon aurantiirostris*).