FORAGING AT ARMY ANT SWARMS BY FIFTY BIRD SPECIES IN THE HIGHLANDS OF COSTA RICA

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Forrajeo en ejambres de hormigas soldado por cincuenta especies de aves en las tierras altas de Costa Rica.

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Much has been written concerning the use of raiding swarms of army ants by Neotropical birds in lowland forests. Bird-ant foraging associations are much less common at higher (subtropical) elevations, and no highland species have been identified as professional or regular ant-followers. All known professional army ant followers in the Neotropics occur below 1000 meters elevation (Ridgely & Tudor 1994). Even attendance at army ant swarms by montane birds has seldom been reported, and previous authors have described observations made at a single, or at most six, highland army ant swarms (Hilty 1974, Gochfeld & Tudor 1978 and Dobbs & Martin 1998). In this note, I report observations of 50 species of birds attending 17 separate raiding army ant swarms in subtropical forests of the Cordillera de Tilaran at Monteverde, Costa Rica.

During January, November and December 1996, and from January through May 1997, I made opportunistic observations of birds at army ant swarms in the vicinity of Monteverde. Elevations were estimated using topographical maps. Army ant swarms were

encountered at sites ranging in elevation from 1100 to 1620 meters, on both the east and west slopes of the Cordillera de Tilaran. Thirteen swarms were found inside forest and four were found in edge (disturbed) habitats.

When birds were located feeding at an army ant swarm, I recorded the species and number of individuals present. All swarms were watched for at least one hour to ensure that all species and individuals using the swarm were detected. Species were considered to be "ant following" if they remained with the swarm for the total period of observation and were observed capturing, or attempting to capture, prey flushed by the advancing ants.

I recorded a total of 244 individuals at 17 separate army ant swarms. The total number of individuals detected at any one swarm ranged from 5 to 24 (average = 15.59, SD = 4.887). The number of species attending a single swarm ranged from 3 to14 (average = 8.76, SD = 3.134). Of the 50 species at these swarms, 20 have apparently not previously been reported following ants (Table 1). Only one species, *Myrmeciza immaculata* (present at

TABLE 1. Species recorded at highland army ant swarms.

Species	Number of swarms (n = 17) where present	Average number of individuals	SD**
Geotrygon chiriquensis*	1	1	0
Eupherusa eximia*	1	1	0
Momotus momota	6	2.3	.7
Premnoplex brunnescens	7	1.42	.4
Margarornis rubiginosus*	2	1.5	.5
Syndactyla subalaris	1	1	0
Thripadectes rufobrunneus*	1	1	0
Dendrocincla homochroa	1	1	0
Sittasomus grisecapillus	1	1	0
Xiphorhynchus erythropygius	2	1	0
Dysthamnus mentalis	2	1.5	.5
Myrmotherula shisticolor	1	2	0
Myrmeciza immaculata	5	2	.6
Formicarius rufipectus*	1	2	0
Mionectes olivaceus*	1	1	0
Platyrinchus mystaceus	2	1	0
Empidonax flavescens*	3	1	0
Chiroxiphia linearis*	1	1	0
Cyanocorax morio	3	1.6	.4
Cyanolyca cucullata*	3	1.6	.9
Thryothorus modestus	2	2	0
T. rufalbus	3	2	0
Troglodytes aedon	1	1	0
T. ochraceous*	1	1	0
Henicorhina leucophrys	9	1.8	.3
Myadestes melanops	2	1	0
Catharus aurantiirostris	3	1.3	.4
C. fuscater	10	3.1	1.3
C. frantzii*	4	1	0
C. ustulatus	2	1	0
Hylocichla mustellina	3	1	0
Turdus assimilis	2	2	0
T. obsoletus	1	1	1
T. grayi	2	1	0
Vermivora chrysoptera*	1	1	0
Mniotilta varia	1	1	0
Seirus aurocapillus	1	1	0
Oporornis formosus	2	1	0
Wilsonia pusilla	2	1	0
Myioborus miniatus*	3	1.3	.4
M. torquatus*	4	2.25	.4
Basileuterus culcivorus	5 -	1.8	.4
B. tristriatus*	7	2.4	1.1

TABLE 1. Continuation.

Species	Number of swarms (n = 17) where present	Average number of individuals	SD**
Chlorospingus opthalmicus*	4	3.5	.86
Tangara dowii*	1	1	0
Lysurus crassirostris	1	1	0
Pselliophorus tibialis*	2	2	0
Atlapetes albinucha*	3	2	0
Buarremon brunneinuchus	5	1.2	.4
Melozone leucotis*	3	2	0

^{*}Species not previously reported attending ant-swarms.

five swarms), has been considered to be a regular ant-follower (Willis 1985b).

Willis & Oniki (1978) pointed out that "irregular" or "casual" ant followers, dominate species lists in peripheral forests. My observations support this conclusion in that 39 of the 50 species I recorded were present at three or fewer of the 17 swarms surveyed, including five species generally considered to be frugivores; Geotrygon chiriquensis, Mionectes olivaceous, Chiroxiphia linearis, Myadestes melanops and Tangara dowii (Slud 1964). At one swarm I observed a largely nectivorous species, Eupherusa eximia, making short sallies, presumably for small insects. To the best of my knowledge, this is the first observation of a hummingbird foraging in association with an army ant-swarm.

The ovenbirds Margarornis rubiginosus and Thripadectes rufobrunneus were present at two and one army ant swarms respectively. To the best of my knowledge, this is the first report of this behavior in either genus. Margarornis rubiginosus is a frequent member of mixed flocks (Slud 1964). Although I was able to confirm that the individuals I watched were feeding in direct association with army ant swarms, it is possible that these birds were initially attracted by the presence of other mixed-flocking species, a behavior that Willis

(1983c) has termed "indirect" ant following.

I recorded two individuals of *Formicarius* rufipectus at one swarm. This appears to be the first record of this species foraging in association with army ants. Willis (1985a) noted that three of the five other *Formicarius* species are sometimes seen feeding at army ant swarms, and commented that "antthrushes could easily follow ants regularly... it is not clear why anttrushes are not good followers".

Willis (1983a) considered ant following in the Tyrannidae insignificant, but noted that flycatchers sometimes follow ants well in the highlands. Flycatchers (Tyrannidae) were not well represented at the swarms I encountered. *Empidonax flavescens* was present at three swarms. Willis (1983a) reported three other *Empidonax* species attending army ant swarms. *Mionectes olivacens* was present at one swarm. Willis noted occasional ant following in *Mionectes macconnelli* (Willis (1983a).

A single male *Chiroxiphia linearis* was present at one swarm. Willis (1984a) noted two other *Chiroxiphia* species attending army ant swarms, but remarked that for Pipridae in general, leking activity, frugivory and other factors must "...interfere with (ant) following".

Hardy (1974) and Haemig (1989) have both discussed the use of ant swarms by

^{**}SD = Standard deviation.

Neotropical jays. Willis (1983b) describes observations of four species of *Cyanocorax* jays attending army ant-swarms. Both *Cyanocorax morio* and *Cyanolyca cucullatta* were present (three observations each) at the swarms I watched. This seems to be the first record of ant-following for the genus *Cyanolyca*. As Hardy remarked, jays are known for their "omnivorous and enterprising behavior." Opportunistic use of ant swarms by jays is not surprising, but it has rarely been noted.

In general, few New World wrens (Troglodytidae) are regularly recorded at army ant swarms (Willis 1983d). A single individual of *Troglodytes ochraceous* was present at one of the swarms I watched. This seems to be the first record of ant following in this mostly arboreal (Slud 1964) species. The understory wren *Henicorhina leucophrys* is known to follow army ant swarms occaisionally (Gochfeld & Tudor 1978, Willis 1983d). *Henichorhina leucophrys* was present at 9 (59%) of the swarms I watched, including all swarms above 1400 meters elevation.

Willis (1966, 1978, 1984b) described the Turdidae as "fairly regular" attendants at army ant swarms, but noted that "New World thrushes are mostly birds of montane or semi-open habitats, in which ants are uncommon because of unfavorable climates" and that "...several factors are unfavorable for ground birds near ants". My observations suggest that at least some Catharus thushes will follow army ants when they are present. Catharus fuscater was the most commonly encountered species at the swarms I observed, being present at 10 (59%) of the swarms. Among the species I observed, C. fuscater also had the largest number of individuals (2-10) at the swarms where I recorded it. Taken together with C. frantzii and C. ustulatus (generally replacing frantzii at lower elevations), resident Catharus thrushes were present at 14 (82%) of the seventeen swarms I encountered, including all swarms occurring above 1400 meters. Catharus fuscater was generally the most active and aggressive species at the swarms where it occurred. Groups of two to 10 C. fuscater often occupied the area around the central leading edge of an advancing swarm, presumably the most productive zone for fleeing invertebrate prey. Individuals of this species alternated between pursuing prey on the ground near the lead edge of the swarm, and making rapid, low flights to displace conspecifics. Intraspecific interactions in this species were generally accompanied by bouts of calling and wing-shivering.

Willis (1986) remarked that *Basileuterus* warblers should be able to follow ants and he detailed observastions of six lowland *Basileuterus* species at army ant swarms. *Basileuterus* tristriatus, a highland species not mentioned by Willis, was present at seven of the swarms I watched. This species is a common member of mixed flocks and this may be another example of "indirect following" (Willis 1983c). Similarly, *Myioborus* warblers are also frequent members of mixed species flocks. These warblers seem not to have been previously recorded following army ant swarms. *Myioborus miniatus* and *M. torquatus* were present at three and four swarms respectively.

Melozone leucotis, Pselliophorus tibialis, and Lysurus crassirostris, were present at three, two, and one swarm respectively. All three species are generally insectivorous and characteristically feed low in dense montane undergrowth (Slud1964), and thus seem fairly well suited to exploit army ant swarms. My observations represent the first report of which I am aware of army ant following in these montane genera.

The migrant warbler *Vermivora chrysoptera* is seasonally fairly common at Monteverde, but was present at only one of the army ant swarms I watched. This species has not previously been recorded following army ants.

Willis (1966) has discussed at length the use of army ant swarms, particularly those of

Labidus praedator, by Nearctic-Neotropical migrants. Seven (14%) of the 50 species I recorded were Nearctic-Neotropical migrants including two thrushes (Turdinae), and five warblers (Parulinae). These were represented by a total of 12 individuals, accounting for only 5% of all individuals recorded at all the swarms I observed. Migrants were generally present only at lower elevation swarms in edge habitats. Migrants accounted for 26% of individuals at those swarms were they occurred. Migrants were present at all four swarms in edge habitats, but at only at two of the swarms found in forest interiors.

The 50 species which I recorded attending army ant swarms includes canopy species, species with flock-adapted feeding behaviors, as well as species which are not principally insectivorous. The use of army ant swarms by highland birds is thought to represent a facultative, opportunistic use of a scarce resource (Dobbs & Martin 1998). The absence of competition from "professional" ant followers at army ant swarms in highland habitats likely allows the opportunistic use of army ant swarms by species which lack the behavioral specializations of lowland ant followers.

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